Mémoire d'Habilitation à Diriger des Recherches

École doctorale GAIA (N°584)

Écologie Fonctionnelle et Sciences Agronomiques

Distribution, dynamique et rôles fonctionnels des macrophytes benthiques dans les écosystèmes côtiers et littoraux anthropisés

Vincent Ouisse

Ifremer, Laboratoire Environnement Ressources, Languedoc-Roussillon

UMR MARBEC – Marine Biodiversity, Exploitation and Conservation

Novembre 2023

"Je déclare avoir respecté, dans la conception et la rédaction de ce mémoire d'HDR, les valeurs et principes d'intégrité scientifique destinés à garantir le caractère honnête et scientifiquement rigoureux de tout travail de recherche, visés à l'article L.211-2 du Code de la recherche et énoncés par la Charte nationale de déontologie des métiers de la recherche et la Charte d'intégrité scientifique de l'Université de Montpellier. Je m'engage à les promouvoir dans le cadre de mes activités futures d'encadrement de recherche."

REMERCIEMENTS

TABLE DES MATIÈRES

RÉSUMÉ

Par définition, les espèces ingénieures modulent la disponibilité des ressources pour d'autres espèces en modifiant les conditions biotiques ou abiotiques de leur environnement. Leur disparition, sous l'effet d'une modification des conditions environnementales, pourrait induire des changements dans la structure et le fonctionnement d'un écosystème. Ce concept est d'importance majeure aussi bien en biologie de la conservation qu'en écologie de la restauration. Parmi ces espèces ingénieures, les macrophytes benthiques couvrent environ 4 millions km^2 en zone côtière et sont naturellement soumis à d'importantes fluctuations environnementales naturelles et anthropiques. C'est dans ce contexte que s'inscrivent mes travaux de recherche sur la dynamique et le rôle fonctionnel des espèces ingénieures benthiques dans des systèmes côtiers ou littoraux anthropisés. Au travers de résultats issus de projets que j'ai coordonnés, mon mémoire d'Habilitation à Diriger des Recherches illustre dans un premier temps mon activité de recherche sur la période 2012-2023 dont la majorité a été menée dans les lagunes méditerranéennes. Dans un premier axe, j'aborde le rôle central de l'observation en mettant en avant l'importance des réseaux dans plusieurs de mes projets et mon rôle dans le déploiement de nouveaux observatoires dans le cadre du changement climatique. Souvent acquises aujourd'hui dans un cadre réglementaire, les données hydrologiques et biologiques collectées et bancarisées de manière pérenne m'ont permis, dans le cadre d'un deuxième axe de recherche, (1) d'étudier les facteurs qui contrôlent la répartition des macrophytes et (2) de décrire la dynamique à long terme des communautés benthiques (macrophyte et macrofaune) en lien avec les dynamiques temporelles de l'environnement. Dans le troisième axe de recherche, je présente les principaux résultats obtenus autour des notions de résistance, seuils de basculement et successions écologiques des espèces ingénieures face aux pressions anthropiques. Dans un quatrième axe, je développe enfin plusieurs exemples autour de la caractérisation et la quantification du rôle du compartiment benthique dans le maintien de la biodiversité et la régulation des cycles de la matière. Dans une deuxième partie du mémoire, je présente mes perspectives de recherche qui visent à (1) développer des outils réactifs permettant d'anticiper les changements structurels et fonctionnels des habitats/communautés benthiques et (2) dissocier les effets du changement climatique des effets des pressions anthropiques locales. Ce mémoire illustre enfin mon implication dans la gestion de projets et la formation par la recherche via l'encadrement de stagiaires, doctorants et post-doctorants. Tous ces travaux sont à replacer dans un contexte d'appui à la gestion des écosystèmes côtiers afin de mettre en avant comment la recherche peut contribuer aux politiques publiques et à la prise de décisions.

CURRICULUM VITAE

Vincent OUISSE
Cadre de recherche
Écologie benthique en milieu côtier et littoral
Plongeur professionnel CIIB
38 ans

vincent.ouisse@ifremer.fr
04 99 57 32 83

Ifremer - *Laboratoire Environnement Ressources LR*
UMR MARBEC - *MARine Biodiversity, Exploitation and Conservation*

Avenue Jean Monnet – CS 30171
34203 Sète cedex

THÉMATIQUES DE RECHERCHE

- Rôle des espèces ingénieures dans la structuration et fonctionnement des écosystèmes côtiers et littoraux
- Réponses des espèces ingénieures face aux perturbations anthropiques

DOMAINES DE COMPÉTENCES

Domaine d'expertise : Écologie côtière et littorale, Compartiment benthique, Approche fonctionnelle (biodiversité, cycle de la matière)

Administration : Coordination et gestion de projets, Encadrement et animation

Valorisation des travaux : Communication et publication dans des revues scientifique et technique, Rapport, Présentation orale, Poster

Expérience de terrain : Organisation de campagne de terrain, Acquisition de données, prélèvements d'échantillons en plongée

Compétences techniques : Expérimentation, Analyses laboratoire (biométrie), Identification des macrophytes, Gestion des données, Création et valorisation de bases de données

Informatique : Bureautique, Programmation (Matlab, R), Bases de données

PARCOURS PROFESSIONNEL

2013-Présent	Cadre de recherche, Ifremer (Sète)
2012-2013	Post-doctorat, Ifremer (Sète)
2011	ATER, Université de La Rochelle (La Rochelle)
2010-2011	ATER, Université de Lille1 (Station biologique de Wimereux)
2007-2010	Doctorat, Université Pierre et Marie Curie (Station biologique de Roscoff)

FORMATION

2010	Doctorat en Océanographie Biologique, Université Pierre et Marie Curie
2007	Master en Océanographie, Université Pierre et Marie Curie

VALORISATION DES TRAVAUX DE RECHERCHE

✓ 23 publications scientifiques
✓ 29 rapports scientifiques
✓ 11 jeux de données scientifiques
✓ 30 présentations orales et 7 posters présentés dans des congrès internationaux

1. MON POSITIONNEMENT DANS LA RECHERCHE

Depuis l'obtention de mon doctorat en 2010 à l'université Pierre et Marie Curie (Paris VI), j'ai tout d'abord enseigné à l'université de Lille1 (Novembre 2010 – Août 2011) puis à l'université de La Rochelle (Septembre 2011 – Décembre 2011) en tant qu'Attaché Temporaire d'Enseignement et de Recherche (ATER). Je suis principalement intervenu en Licence et Master dans des unités d'enseignement d'écologie, de biostatistiques et de d'océanographie physique. En termes de recherche, mon implication n'a pu être que limitée au vue des charges d'enseignement que j'ai assurées en 14 mois. En janvier 2012, j'ai intégré l'Ifremer et le Laboratoire Environnement Ressources du Languedoc-Roussillon (LERLR) à Sète dans le cadre d'un post-doctorat qui portait sur l'évaluation du rôle du sédiment et des herbiers à phanérogames dans la restauration des écosystèmes lagunaires. Ce nouveau projet de recherche s'intégrait dans un besoin de connaissances sur le rôle central du compartiment benthique dans la restauration des lagunes méditerranéennes vis-à-vis de l'eutrophisation. En juillet 2013, j'ai été recruté au LERLR de l'Ifremer à Sète en tant que "Chercheur en écologie lagunaire" en charge plus particulièrement du développement d'activités de recherche innovantes en écologie fonctionnelle ciblées sur les milieux lagunaires et les scénarios possibles de restauration de ces milieux soumis aux perturbations anthropiques. Le LERLR a intégré en janvier 2015 la nouvelle UMR MARBEC (Biodiversité Marine, Exploitation et Conservation) qui compte aujourd'hui 173 agents permanents (Novembre 2023). Entre janvier 2015 et décembre 2020, j'ai assuré le rôle de co-représentant du thème "Systèmes Littoraux à Usages Multiples". Au delà de la sphère académique, je suis membre du comité scientifique de la réserve naturelle de Biguglia (Corse) et expert dans le cadre de la création d'une liste rouge des écosystèmes pour l'IUCN. C'est dans ce contexte que les parties suivantes décrivent mon activité de recherche passée et future.

2. CADRE CONCEPTUEL, CONTEXTE ET QUESTIONS DE RECHERCHE ABORDÉES

L'écologie[1], au sens scientifique, peut être définie comme « l'étude des relations des organismes avec leur environnement ». Cette discipline scientifique se structure autour de deux axes : (1) l'étude de la dynamique et du fonctionnement des populations et des peuplements qui inclut des travaux de recherche sur la dynamique des espèces et leurs interactions et (2) l'étude d'objets de recherche qui ne sont plus exclusivement biologiques en s'intéressant aux cycles de la matière et aux flux d'énergie qui les structurent. L'écologie fait ainsi appel à de nombreux champs disciplinaires allant de la génétique à la biogéographie et des niveaux d'organisation du vivant allant du gène à l'écosystème ou la biosphère. Chacun de ces niveaux a ses propres caractéristiques (structure), et la manière dont s'effectuent les échanges de matière et d'énergie (fonction) y est propre et nécessite des outils adaptés.

Parmi les nombreuses questions abordées en écologie, l'une d'entre elle s'attache à comprendre comment l'apparition ou la disparition d'espèces affecte la structure et le fonctionnement d'un écosystème. Cette question fait entre autre référence à la notion d' *espèce structurante* ou *espèce clé* qui peut être définie comme une espèce qui a des impacts significatifs sur

---

[1] Le terme « écologie » vient du grec *oikos* qui signifie maison et « logos » qui signifie la *science*.

la structure des communautés et des écosystèmes et de leurs fonctions. Tout d'abord décrit d'un point de vue trophique ou les prédateurs peuvent exercer un rôle clé en limitant la prolifération de certaines proies et en favorisant ainsi la coexistence d'autres espèces moins compétitives sur la ressource, la notion d'*espèce clé* a été étendue à des espèces qui modifient la structure du milieu. On parle alors d'*espèces modificatrices du milieu* ou d'*espèces ingénieures de l'écosystème*. Elles sont définies comme des espèces qui *"directement ou indirectement, modulent la disponibilité des ressources pour d'autres espèces en modifiant les conditions biotiques ou abiotiques de leur environnement"* [2]. Ces espèces ingénieures modifient, maintiennent ou créent ainsi des habitats. Par définition, la disparition de ces espèces structurantes, sous l'effet d'une modification des conditions environnementales ou suite à l'arrivée d'une espèce plus compétitive pour la ressource, pourrait induire des changements dans la structure et le fonctionnement d'un écosystème. Ce concept est d'importance majeure aussi bien en biologie de la conservation (discipline qui étudie et vise à protéger la biodiversité) qu'en écologie de la restauration (discipline qui étudie les processus écologiques mis en jeu pendant la restauration écologique et s'intéresse notamment à suivre l'évolution des milieux suite à des actions de restauration écologiques[3]). En écologie où il apparaît aujourd'hui impossible d'étudier tout, partout, ce concept simplificateur du monde réel complexe sous-entend que certains travaux de recherche pourraient être orientés sur un petit nombre d'espèces dites structurantes.

Parmi les espèces ingénieures, les macrophytes benthiques couvrent environ 4 millions km^2 en zone côtière aussi bien sur substrat rocheux (macro-algues) que sur substrat meuble (principalement phanérogames et mangrove). La croissance et la répartition des ces macrophytes dans les écosystèmes côtiers sont principalement influencées par des facteurs biotiques (p. ex. broutage, concurrence) et abiotiques tels que la disponibilité des nutriments et de la lumière[4-5-6], la configuration des courants[7], la température[89] et la salinité [10-11]. Parmi les rôles fonctionnels connus, ils représentent un compartiment biologique majeur du point de vue de leur production primaire avec une production globale nette évaluée à 2 Pg C/an[12]. À la base de certains réseaux trophiques, les macrophytes soutiennent directement ou indirectement (*via* la matière détritique) la production secondaire aussi bien localement[13-14] qu'à plus large échelle au niveau d'écosystèmes adjacents[15]. Les macro-algues contribueraient également à la formation d'habitats structurellement complexes

---

[2] Jones C. G. , Lawton J. H., Shachak M. (1994) Organisms as Ecosystem Engineers. Oikos 69:373–386

[3] SER (2004) L'ABCDaire sur l'écologie de la restauration de la SER internationale. The SER International Primer on Ecological Restoration. www.ser.org & Tucson: Society for Ecological Restoration International.

[4] Dennison W. C. (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. Aquatic Botany. 27: 15–26.

[5] Duarte C. M. (1991) Seagrass depth limits. Aquatic Botany. 40:363–377. doi: 10.1016/0304-3770(91)90081-F

[6] Duarte C. M. (1995) Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia. 41: 87–112.

[7] Fonseca M. S., Kenworthy W. J. (1987) Effects of current on photosynthesis and distribution of seagrasses. Aquatic Botany. 27: 59–78.

[8] Larkum A., Orth R. J., Duarte C. M. (2006) Seagrasses: Biology, Ecology and Conservation. Springer, The Netherland.

[9] Hurd C. L., Harrison P. J., Bischof K., Lobban C. S. (2014) Seaweed ecology and physiology. Cambridge University Press, 2014. Cambridge, New York.

[10] Lehmann A. (1998) GIS modeling of submerged macrophyte distribution using Generalized Additive Models. Plant Ecology139 :113–124.

[11] Steinhardt T., Selig U. (2011) Influence of salinity and sediment resuspension on macrophyte germination in coastal lakes. Journal of Limnology 70: 11–20.

[12] Duarte C. M. (2017) Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. Biogeosciences. 14, 301–310

décrits dans certains milieux comme des zones de nurserie pour les poissons[16-17] où les juvéniles peuvent trouver d'une part des abris pour se protéger des prédateurs[18] et d'autre part de nombreuses proies potentielles qui favorise leur croissance[19]. Dans les substrats meubles enfin, le développement de phanérogames marines pourvu d'un système racinaire jouerait sur le cycle de la matière[20-21].

Les macrophytes et plus généralement l'ensemble des organismes présents dans les écosystèmes côtiers sont soumis naturellement à d'importantes fluctuations environnementales aussi bien spatiales que saisonnières. Depuis le début de l'anthropocène, de nombreuses pressions anthropiques auxquelles les macrophytes sont particulièrement sensibles viennent s'y ajouter, comme par exemple des apports excessifs de nutriments[22-23-24] qui provoquent des phénomènes d'eutrophisation voire d'anoxie critique à travers le monde (Figure 1). Les changements de dominance des macrophytes le long d'un gradient d'eutrophisation sont particulièrement bien décrits et font l'objet d'un modèle schématique[25] qui a par exemple servi de cadre à l'utilisation des

---

13 Ouisse V., Riera P., Migné A., Leroux C., Davoult D., 2012. Food web analysis in intertidal Zostera marina and Zostera noltii communities in winter and summer. Marine Biology, 165-175.

14 Schaal G., Riera P., Leroux C. (2010) Trophic ecology in a Northern Brittany (Batz Island, France) kelp (Laminaria digitata) forest, as investigated through stable isotopes and chemical assays. Journal of Sea Research. 63, 24–35. https://doi.org/10.1016/j.seares.2009.09.002

15 Schaal G., Riera P., Leroux C. (2008) Trophic coupling between two adjacent benthic food webs within a man-made intertidal area: a stable isotopes evidence. Estuarine, Coastal and Shelf Science. 77, 523–534.

16 Beck M. W., Heck K. L., Able K. W., Childers D. L., Eggleston D. B., Gillanders B. M., Halpern B., Hays C. G., Hoshino K., Minello T. J., Orth R. J., Sheridan P. F., Weinstein M. P. (2001) The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site- specific variability in nursery quality will improve conservation and management of these areas. BioScience. 51: 633–641.

17 Blandon A., Zu Ermgassen P. S. E. (2014) Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. Estuarine, Coastal and Shelf Science. 141. Elsevier: 1–8.

18 Cheminée A., Sala E., Pastor J., Bodilis P., Thiriet P., Mangialajo L., Cottalorda J.M., Francour P. (2013) Nursery value of Cystoseira forests for Mediterranean rocky reef fishes. Journal of Experimental Marine Biology and Ecology. 442: 70–79. https://doi.org/10.1016/j.jembe.2013.02.003.

19 Thiriet P. (2014) Comparison of fish assemblage structure and underlying ecological processes, between Cystoseira forests and less structurally complex habitats in North-Western Mediterranean rocky subtidal rocky reefs. Thesis. Université Nice Sophia Antipolis.

20 Deborde J., Abril G., Mouret A., Jézéquel D., Thouzeau G., Clavier J., Bachelet G., Anschutz P. (2008) Effects of seasonal dynamics in a Zostera noltii meadow on phosphorus and iron cycles in a tidal mudflat (Arcachon Bay,France). Marine Ecology Progress Series. 355:59-71.

21 Eyre B. D., Maher D., Oakes J. M., Erler D. V., Glasby T. M. (2011) Differences in benthic metabolism, nutrient fluxes, and denitrification in Caulerpa taxifolia communities compared to uninvaded bare sediment and seagrass (Zostera capricorni) habitats. Limnology and Oceanography. 56:1737-1750

22 Cloern J. E. (2001) Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series. 210: 223–253.

23 de Jonge V. N., Elliott M., Orive E. (2002) Causes, historical development, effects and future challenges of a common environmental problem: eutrophication. Hydrobiologia. 475–476: 1–19.

24 McGlathery K. J., Sundbck K., Anderson I. C. (2007). Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. Marine Ecology Progress Series. 348: 1–18.

25 Schramm W. (1999) Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. Journal of applied Phycology. 11: 69–78.

macrophytes en tant qu'indicateurs de la qualité de l'eau dans certains écosystèmes côtiers[26-27-28]. Au delà de cette pression aujourd'hui relativement bien quantifiée, d'autres pressions comme la contamination chimique[29] ou le changement climatique[30] viennent s'ajouter avec des effets sur les macrophytes qui pourraient être cumulatifs, synergiques ou même opposés[31-32]. Dans ce contexte où les perturbations sont nombreuses, la dynamique des espèces ingénieures de l'écosystème en réponse aux fluctuations des conditions environnementales suppose des modifications en cascade au niveau des fonctions écologiques qu'ils assurent tant d'un point de vue biologique (biodiversité associée) que du cycle de la matière et des flux d'énergie dans ces systèmes.

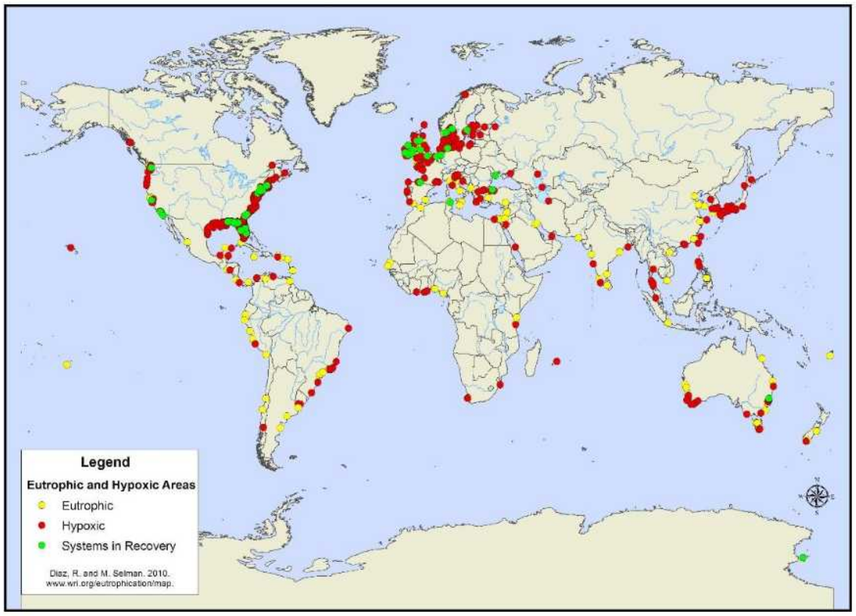


Figure 1: Carte mondiale représentant les zones côtières eutrophisées (en jaune) et ayant connue des cas d'anoxie et d'hypoxie (en rouge). Les zones en voie de restauration sont figurées en vert[33].

---

[26] Orfanidis S., Dencheva K., Nakou K., Tsioli S., Papathanasiou V., Rosati I. (2014) Benthic macrophyte metrics as bioindicators of water quality: towards overcoming typological boundaries and methodological tradition in Mediterranean and Black Seas. Hydrobiologia. 740: 61–78.

[27] Sargian P., Andral B., Derolez V. (2013) Réseaux de surveillance DCE-Campagne 2012-District "Rhône et côtiers méditerranéens". Ifremer.

[28] Sfriso A., Facca C., Ghetti P. F. (2009) Validation of the Macrophyte Quality Index (MaQI) set up to assess the ecological status of Italian marine transitional environments. Hydrobiologia. 617: 117–141.

[29] Munaron D., Tapie N., Budzinski H., Andral B., Gonzalez J-L. (2012) Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: results from a pilot survey using passive samplers. Estuarine, Coastal and Shelf Science. 114:82–92

[30] IPCC (2014) Climate Change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working group II to the fifth assessment report of the Intergovernemental Panel on Climate Change. Cambridge university Press, Cambridge, United Kingdom and New York, NY, USA

[31] Crain C. M., Kroeker K., Halpern B. S. (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecological Letters. 11:1304–15. doi: 10.1111/j.1461-0248.2008.01253.x

[32] Halpern B. S., Walbridge S., Selkoe K. A., Kappel C. V., Micheli F., D'Agrosa C., Bruno J. F., Casey K. S., Ebert C., Fox H. E., Fujita R., Heinemann D., Lenihan H. S., Madin E. M. P., Perry M. T., Selig E. R., Spalding M., Steneck R, Watson R. (2008) A global map of human impact on marine ecosystems. Science. 319:948–52. doi: 10.1126/science.1149345

[33] Diaz R., Selman M. (2010) http://www.wri.org/resource/world-hypoxic-and- eutrophic-coastal-areas.

C'est dans ce contexte que s'inscrivent mes travaux de recherche **sur la dynamique et le rôle fonctionnel des espèces ingénieures dans des systèmes côtiers ou littoraux anthropisés**. Centrés sur les macrophytes benthiques, les projets développés ici visent à comprendre :

(1) Quels sont les facteurs qui contrôlent la distribution spatiale de ces macrophytes ?

(2) Comment ces espèces ingénieures structurent les habitats benthiques ?

(3) Quels sont les rôles des macrophytes dans la structuration des communautés benthiques et bentho-démersales associées ?

(4) Comment ces macrophytes contribuent à la régulation des cycles de la matière en milieu côtier ?

(5) Comment répondent les macrophytes benthiques aux modifications environnementales d'origine anthropique ?

Pour répondre à ces questions, je m'appuie principalement sur l'analyse de données historiques et l'acquisition de données dans les milieux lagunaires méditerranéens.

3. PRINCIPAUX RÉSULTATS DE MES TRAVAUX DE RECHERCHE

Mes travaux s'inscrivent dans une recherche appliquée, en prise indirecte avec les politiques publiques, dans laquelle les objectifs et les résultats ont des implications directes en terme de compréhension des processus mis en jeu, de définition d'indicateurs et d'évaluation de l'état vis-à-vis de pressions anthropiques. Même si nombre de mes projets sont en amont d'actions de gestion, ils alimentent des réflexions menées sur le rôle central des habitats benthiques dans l'interprétation des indicateurs biotiques (Figure 2), la notion d'espèce de référence et l'estimation du temps d'atteinte du « bon état » dans le cadre de la Directive Cadre sur l'Eau (DCE). Ils s'intègrent également dans la définition de la notion d'état de conservation utilisée dans le cadre de la Directive Habitat Faune-Flore (DHFF). Ainsi, la majorité des projets décrits est menée en collaboration avec l'Agence de l'Eau Rhône Méditerranée Corse (AERMC) et l'Office Française de la Biodiversité (OFB) dans un contexte où l'étude des processus biologiques impliqués dans la structuration et le fonctionnement des habitats benthiques se fait en lien avec les pressions anthropiques. De manière générale, toutes les connaissances acquises au cours de ces projets de recherche viennent ainsi nourrir l'expertise autour du rôle des espèces et des habitats benthiques dans le fonctionnement des écosystèmes littoraux et côtiers.

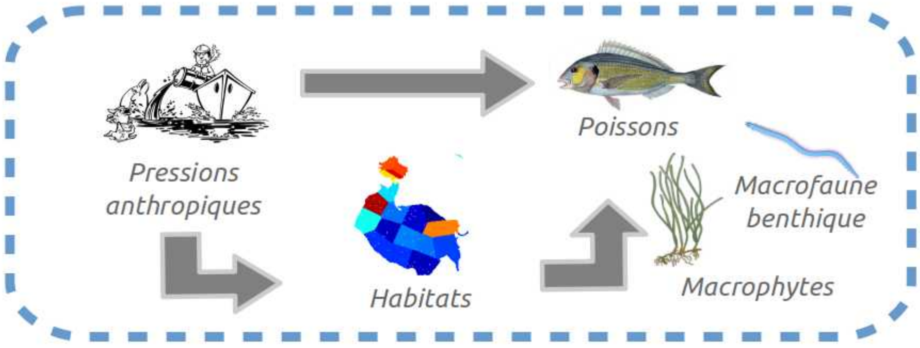


Figure 2: Représentation schématique des relations entre les pressions anthropiques, les habitats et les indicateurs biotiques utilisés dans le cadre de la Directive Cadre sur l'Eau (DCE)

Les principaux résultats de mes travaux sont présentés dans la suite de ce document. La liste exhaustive des projets est donnée dans la partie 5 de ce document. Les résultats sont issus de travaux collaboratifs que j'ai pour la plupart coordonnés. Bien que la première personne du singulier soit utilisée principalement, ces résultats sont pour nombre d'entre eux issus de travaux de Master, de Doctorat et de post-doctorat que j'ai co-encadrés. Les résultats sont présentés sous forme de quatre axes principaux de recherche :

[Axe 1] L'**observation** : source de données pour répondre aux questions de recherche,

[Axe 2] De la **distribution** d'espèces clés aux habitats benthiques,

[Axe 3] **Résistance, seuils de basculement et successions écologique** des espèces clés face aux pressions anthropiques, et

[Axe 4] **Rôles fonctionnels** du compartiment benthique.

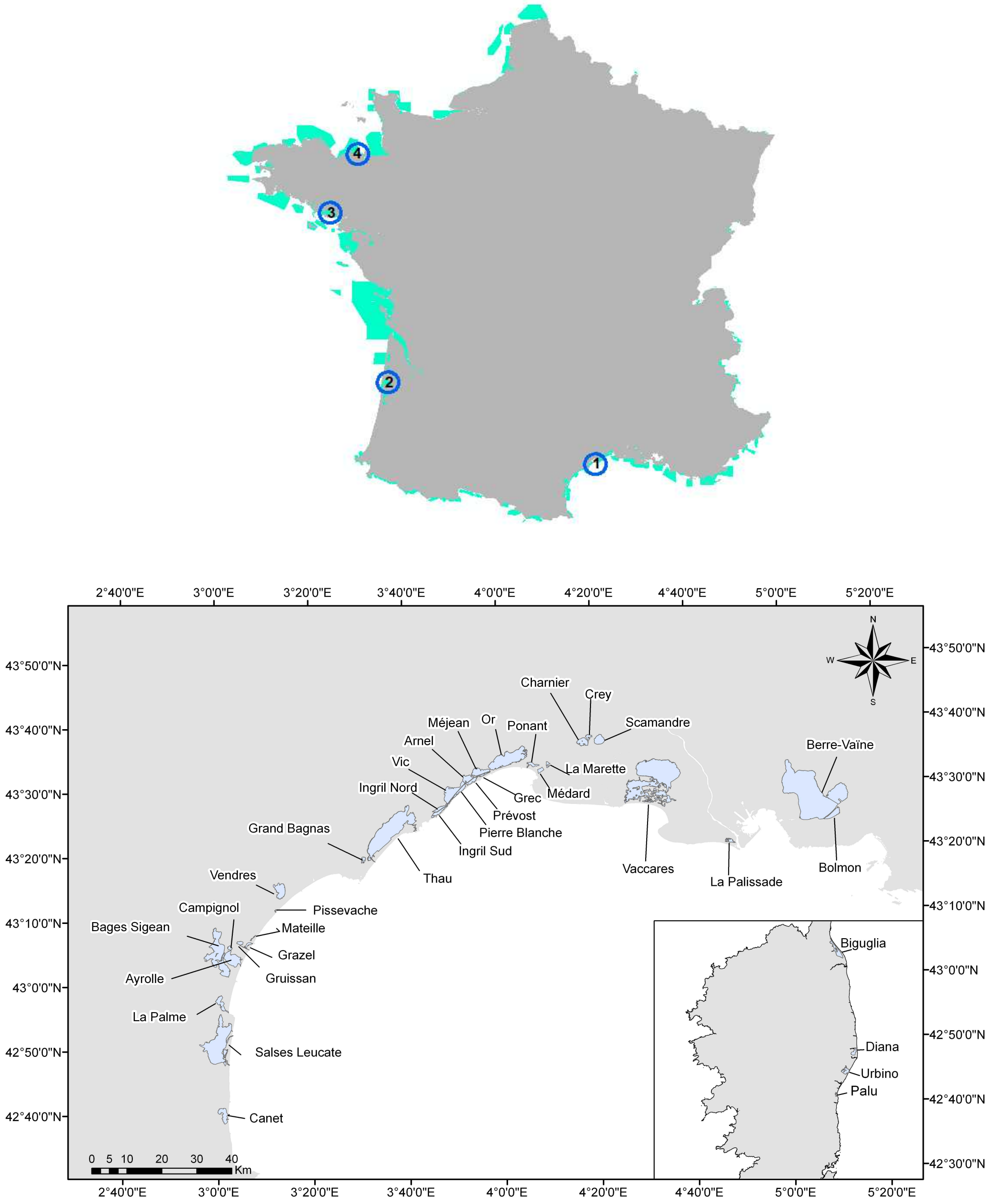


Figure 3: Principaux sites d'étude (en haut) à l'échelle du littoral français (1=lagunes méditerranéennes, 2=bassin d'Arcachon, 3=Golfe du Morbihan, 4=Baie de Saint-Malo) et (en bas) des lagunes méditerranéennes.

3.1. Principaux sites d'étude

Mon activité de recherche s'appuie en partie sur l'acquisition de données pour décrire et comprendre les processus impliqués dans la dynamique des espèces structurantes et de leurs rôles fonctionnels dans des systèmes côtiers ou littoraux soumis aux pressions anthropiques. Je mène des actions sur des sites côtiers répartis aussi bien sur les façades Manche, Atlantique que Méditerranée même si la plus grande partie de mes recherches est menée dans les écosystèmes lagunaires méditerranéens (Figure 3).

En Europe, les lagunes côtières occupent environ 5 % des côtes et sont particulièrement nombreuses le long des côtes méditerranéennes (Figure 3 bas)[34-35]. De manière générale, elles constituent une interface privilégiée entre les bassins versants qui les alimentent en eau douce, les zones humides périphériques et le milieu marin. Les échanges entre la lagune et la mer peuvent être permanents ou temporaires selon les lagunes. Ainsi, l'efficacité des échanges avec la mer est variable et principalement liée aux marées, en particulier pour les zones soumises aux régimes microtidal (amplitude entre 0.5 m et 2 m), mésotidal (amplitude entre 2 et 4 m) et macrotidal (> 4 m). En Méditerranée, la dynamique des masses d'eau lagunaire est en revanche restreinte et principalement liée aux vents et aux pressions atmosphériques, particulièrement dans les lagunes nanotidales (amplitude des marées inférieure à 0.5 m)[36]. Dans ces conditions, l'efficacité des échanges entre la lagune et la mer est souvent limitée et fait de ces milieux des masses d'eau relativement confinées[37]. Les apports en eau douce provenant du bassin versant et le caractère temporaire ou permanent des échanges avec le milieu marin, confèrent aux eaux lagunaires une salinité variable allant des eaux oligohalines (salinité comprise entre 0,5 et 5) à des eaux hyperhalines (salinité > 40)[38]. Les conditions environnementales peuvent également être variables au sein même d'une lagune selon les processus physiques ou biologiques considérés[39]. Temporellement enfin, ces milieux sont fluctuants (salinité, température, lumière, nutriments disponibles…). Ces contraintes physiques et chimiques naturelles représentent ainsi une source potentielle de stress pour les communautés biologiques associées[40].

---

[34] Barnes, R. S. K. (1980) Coastal Lagoons : the natural history of a neglected habitat. Cambridge University Press, Cambridge.

[35] Cromwell J. E. (1971). Barrier coast distribution: a world-wide survey. Second National Coastal Shallow Water research Conference. Baton Rouge, LA: 50.

[36] Tagliapietra D., Ghirardini A. V. (2006) Notes on coastal lagoon typology in the light of the EU Water Framework Directive: Italy as a case study. Aquatic Conservation: Marine and Freshwater Ecosystems. 16: 457–467.

[37] Guelorget O., Perthuisot J. P. (1992) Paralic ecosystems. Biological organization and functionning. Vie Milieu. 42: 215–251.

[38] Venice System (1958) The Venice System for the Classification of Marine Waters According to Salinity. Limnology and Oceanography. 3: 346–347.

[39] Fiandrino A., Ouisse V., Dumas F., Lagarde F., Pete R., Malet N., Le Noc S., de Wit R. (2017) Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. Marine Pollution Bulletin. 119: 132–144.

[40] Guelorget O., Perthuisot J. P. (1984) Indicateurs biologiques et diagnose écologique dans le domaine paralique. Bulletin d'écologie. 15: 67–76.

3.2. L’observation : source de données pour répondre aux questions de recherche

Complémentaire à l’expérimentation, l’acquisition de données dans le cadre d’observatoires ou de suivis des milieux représente une source de données essentielle pour la compréhension de la distribution et de la dynamique des écosystèmes benthiques et des processus écologiques sous-jacents. Cette approche permet de disposer d’une large quantité de données acquises, à large échelle, avec un protocole standardisé. Bien qu’elles soient souvent collectées dans un cadre réglementaire visant par exemple à caractériser l’état des masses d’eau et répondre aux directives européennes, elles peuvent également être utilisées pour répondre à des questions de recherche. Dans le cadre de mes travaux, j’ai ainsi utilisé et valorisé des données acquises depuis 1999 dans le cadre du Réseau de Suivi Lagunaire (RSL) puis de la Directive Cadre sur l’Eau (DCE) dans les lagunes méditerranéennes françaises. Ces données hydrologiques et biologiques, toutes bancarisées de manière pérenne, offrent en effet une opportunité unique pour décrire la dynamique à long terme des communautés benthiques (macrophyte et macrofaune en particulier) en lien avec les dynamiques temporelles de l’environnement comme cela a pu être fait dans les projets MALAG (Effet de l’eutrophisation sur la macrofaune benthique des lagunes méditerranéennes, 2019-2022) et MARES (Rôle des macrophytes dans la restauration des milieux lagunaires, 2014-2018). Ces mêmes données sont également à l’origine de la première cartographie des habitats lagunaires méditerranéens proposée dans le cadre du projet CHAMILA (Cartographie des HAbitats en MIlieux LAgunaires, 2018-2023). Les principaux résultats de ces projets sont résumés dans les parties suivantes.

La résolution temporelle des réseaux d’observation et de suivi actuellement opérationnels ne permet néanmoins pas de répondre parfaitement aux questions liées aux effets du changement climatique dans les lagunes méditerranéennes. Pourtant, le changement climatique joue un rôle considérable dans la modification des conditions environnementales qui contrôlent la répartition et la survie des écosystèmes[41]. La zone littorale est déjà naturellement soumise à de fortes fluctuations locales et saisonnières, ainsi qu’à des pressions grandissantes d’origine anthropique[42-43]. C’est en particulier le cas des lagunes méditerranéennes qui sont soumises à de nombreuses pressions liées à leurs usages (exploitations ostréicoles, pêche, tourisme) et au développement d’activités humaines sur leurs bassins versants[44-45]. A ce jour, les principaux changements attendus au sein de ces lagunes seraient une augmentation de la température moyenne et du niveau moyen

---

[41] Duarte C. M. (2014) Global change and the future ocean : a grand challenge for marine sciences. Frontiers in Marine Science 1:. doi: 10.3389/fmars.2014.00063

[42] Halpern B. S., Walbridge S., Selkoe K. A., Kappel C. V., Micheli F., D'Agrosa C., Bruno J. F., Casey K. S., Ebert C., Fox H. E., Fujita R., Heinemann D., Lenihan H. S., Madin E. M. P., Perry M. T., Selig E. R., Spalding M., Steneck R, Watson R. (2008) A global map of human impact on marine ecosystems. Science. 319:948–52. doi: 10.1126/science.1149345

[43] Lloret J., Marín A., Marín-Guirao L. (2008) Is coastal lagoon eutrophication likely to be aggravated by global climate change? Estuarine, Coastal and Shelf Science. 78:403–412. doi: 10.1016/j.ecss.2008.01.003

[44] de Wit R., 2011. Chapiter 2. Biodiversity of coastal lagoon ecosystems and their vulnerability to global change Ecosystems Biodiversity : 29–40.

[45] Munaron D., Tapie N., Budzinski H., Andral B., Gonzalez J-L. (2012) Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: results from a pilot survey using passive samplers. Estuarine, Coastal and Shelf Science. 114:82–92

de la mer ainsi qu'une augmentation de la fréquence et de l'intensité des Évènements Climatiques Extrêmes (ECEs) tels que les vagues de chaleur, les périodes de sécheresse et de crues. Contrairement au milieu côtier "marin" méditerranéen au sein duquel le réseau CALOR (Suivi de la température en Méditerranée, AERMC, Andromède Océanologie) a été déployé depuis 2013 sur 157 stations (chiffre de 2017), aucun observatoire pérenne n'est aujourd'hui déployé pour qualifier et quantifier ces changements sur l'ensemble des lagunes françaises méditerranéennes malgré les nombreux réseaux d'observations et de suivis existants. Pourtant, ces milieux peuvent être extrêmement fluctuants dans le temps et l'espace[46] et seul un suivi haute fréquence pourrait permettre de capter ces ECEs dans ces milieux. C'est dans ce contexte que j'ai initié un observatoire du changement climatique au sein des lagunes méditerranéennes. Il comprend aujourd'hui 28 stations réparties sur 21 lagunes poly-halines françaises (Figure 4). Résolument centré aujourd'hui sur la température, la salinité et les herbiers de phanérogames, cet observatoire permettra d'interpréter les changements structurels et fonctionnels observés dans les lagunes méditerranéennes françaises en lien avec les évolutions du climat. À l'échelle de la façade méditerranéenne française, il permettra plus spécifiquement de caractériser (fréquence et intensité) à court terme les ECEs (vagues de chaleur ou vagues de froid qui peuvent durer de quelques jours à quelques mois), de caractériser la variabilité spatiale de la dynamique de la température au sein des lagunes méditerranéennes françaises et de disposer à long terme de données permettant de quantifier la dynamique de la température et de la salinité dans les masses d'eau lagunaires méditerranéennes.

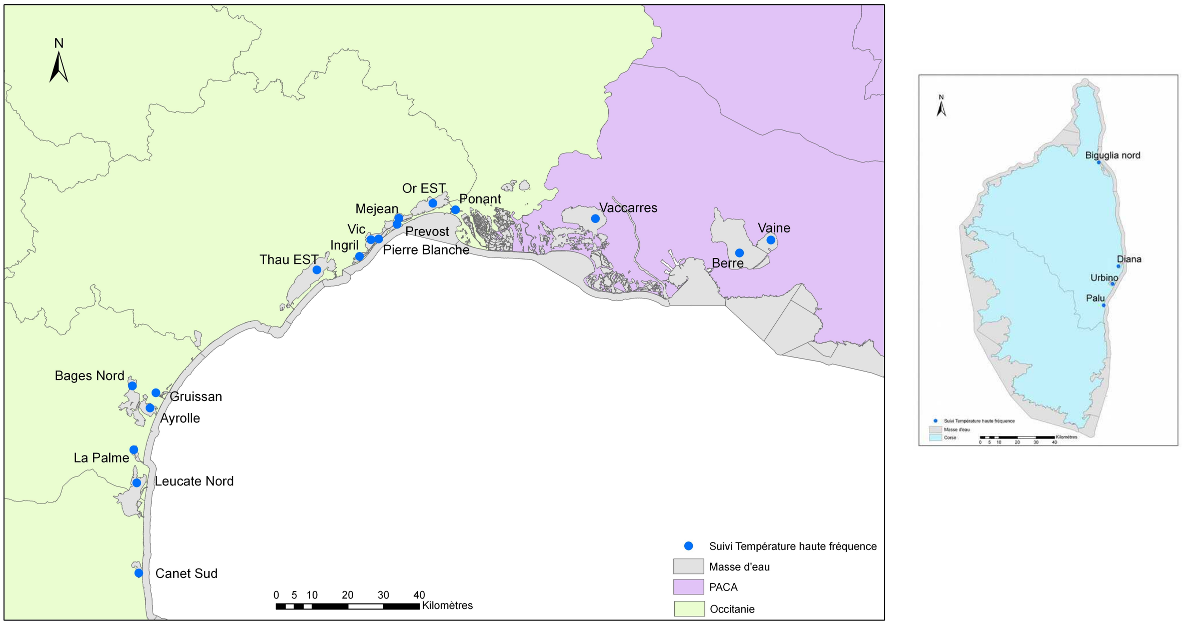


Figure 4: Localisation des stations de l'observatoire sur la façade méditerranéenne française.

---

[46] Menu, M., Vaz S., Bajjouk T., Derolez V., Fiandrino A., Giraud A., Grillas P., Ouisse V. (2019). Rapport final du projet CHAMILA (Cartographie des habitats en milieu lagunaire méditerranéen). IFREMER.

Au delà du périmètre des lagunes méditerranéennes, comprendre et anticiper les changements de la biodiversité marine côtière en réponse aux effets de changements globaux apparaît comme un sujet majeur de la recherche actuelle et future. Pour pouvoir répondre à ces questions, la communauté scientifique s'attache aujourd'hui à constituer de longues séries temporelles acquises dans un contexte pluridisciplinaire permettant : (i) de mettre en évidence sans ambiguïté les changements de diversité (ii) de les relier avec des changements de paramètres environnementaux d'origine naturelle et/ou anthropique et (iii) d'évaluer leurs conséquences fonctionnelles. C'est dans ce contexte qu'a été créé un nouveau Service National d'Observation (SNO) consacré à l'observation du macrozoobenthos (SNO BENTHOBS) et associant de manière coordonnée les moyens et les compétences du CNRS, de l'Ifremer, du MNHN ainsi que des universités. Impliqué dans cet observatoire depuis 2021, je suis à l'origine de deux nouvelles stations de suivi, l'une dans l'étang de Thau, l'autre au large de Sète. Échantillonnées deux fois par an, ces nouvelles stations viennent s'intègrer dans un réseau de 20 stations réparties en Manche (8 stations), Atlantique (8 stations) et Méditerranée (4 stations). Ces séries de données, acquises en parallèle d'autres observatoires ou réseau de suivi (SNO PHYTOBS[47] et COAST-HF[48], SOMLIT[49], DCE…), ouvriront la perspective exceptionnelle de conduire, sur le long terme, une analyse intégrée de la dynamique spatio-temporelle d'un ensemble de communautés benthiques. Cette étape est déterminante pour permettre la prédiction du devenir à long terme de ces éléments majeurs des écosystèmes côtiers en réponse au changement global.

3.3. De la distribution d'espèces clés aux habitats benthiques

Parmi les espèces clés dans ces lagunes, les phanérogames marines sont actuellement utilisées comme indicateur écologique des perturbations humaines, en particulier dans le contexte de la directive Cadre sur l'Eau (DCE). Pourtant, leur présence ou leur absence résulte également des conditions environnementales naturelles telles que la lumière, la salinité ou bien la nature du sédiment par exemple. Pour explorer ces relations, la modélisation prédictive s'est peu à peu développée pour caractériser la distribution d'espèces animales ou d'espèces végétales terrestres[50] ou aquatiques[51], en fonction des paramètres environnementaux. Basée sur un jeu de données de paramètres environnementaux spatial associé à des données de présence, de présence / absence ou abondance d'une espèce, cette méthode permet ainsi de produire une carte de distribution des probabilités d'occurrence de l'espèce[52-53-54]. Dans le cadre du projet MARES1 (Rôle des Macrophytes dans la REStauration des milieux lagunaires : distribution spatiale de *Zostera noltei*, 2014), nous

---

[47] Réseau d'observation du Phytoplancton

[48] Coastal OceAn observing SysTem – High Frequency

[49] Service d'observation en Milieu Littoral

[50] Guisan A., Theurillat J-P., Kienast F. (1998) Predicting the potential distribution of plant species in an alpine environment. Journal of Vegetal Science. 9, 65–74.

[51] Lehmann A. (1998) GIS modeling of submerged macrophyte distribution using Generalized Additive Models. Plant Ecology139 :113–124.

[52] Dormann C. F., Schymanski S. J., Cabral J., Chuine I., Graham C., Hartig F., Kearney M., Morin X., Römermann C., Schröder B., Singer A. (2012) Correlation and process in species distribution models: bridging a dichotomy. Journal of Biogeography. 39, 2119-2131.

[53] Elith J., Leathwick J. R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics. 40, 677-697.

[54] Kearney M. (2006) Habitat, environment and niche: what are we modelling? Oikos 115, 186-191.

avons tout d'abord proposer un modèle conceptuel des interactions entre les facteurs environnementaux, les processus mis en jeu et la présence de *Zostera noltei* dans les lagunes méditerranéennes (Figure 5). Nous avons ensuite pu tester le lien entre 29 variables environnementales issues principalement des réseaux d'observation et l'absence ou la présence de *Zostera noltei* sur 547 stations benthiques dans 16 lagunes du Languedoc-Roussillon de 2001 à 2013. Les prédictions du meilleur modèle, sélectionné comme celui ayant la meilleure qualité de prédiction, étaient conformes aux observations dans 88% des cas et les quelques erreurs de prédiction étaient attribuées aux conditions environnementales locales non résolues à fine échelle spatiale pour certaines variables. Ce modèle de distribution prédictive incluait à la fois des variables naturelles et anthropiques mettant en évidence que la distribution de *Zostera noltei* serait principalement contrainte dans les lagunes méditerranéennes par le cisaillement du fond (effet positif) résultant des actions du vent, la lumière disponible au fond et les concentrations en nutriments et en chlorophylle *a* dans l'eau (effet négatif). Hormis la lumière, ces résultats semblent en partie contre-intuitifs et peu documentés dans la littérature où l'augmentation des courants et la diminution de la concentration en nutriments ne sont jamais décrits en laboratoire directement comme des paramètres clés pour expliquer la distribution de cette espèce et plus largement des phanérogames marines. L'hypothèse la plus probable pour expliquer ces résultats serait un effet indirect de ces facteurs *via* les autres espèces de macrophytes qui couvrent les fonds des lagunes méditerranéennes qui elles, ne pourraient supporter une contrainte de cisaillement élevée (absence de système d'ancrage dans le sédiment) et une faible teneur en nutriments dans l'eau (assimilation impossible des nutriments dans les sédiments riches en azote et en phosphore).

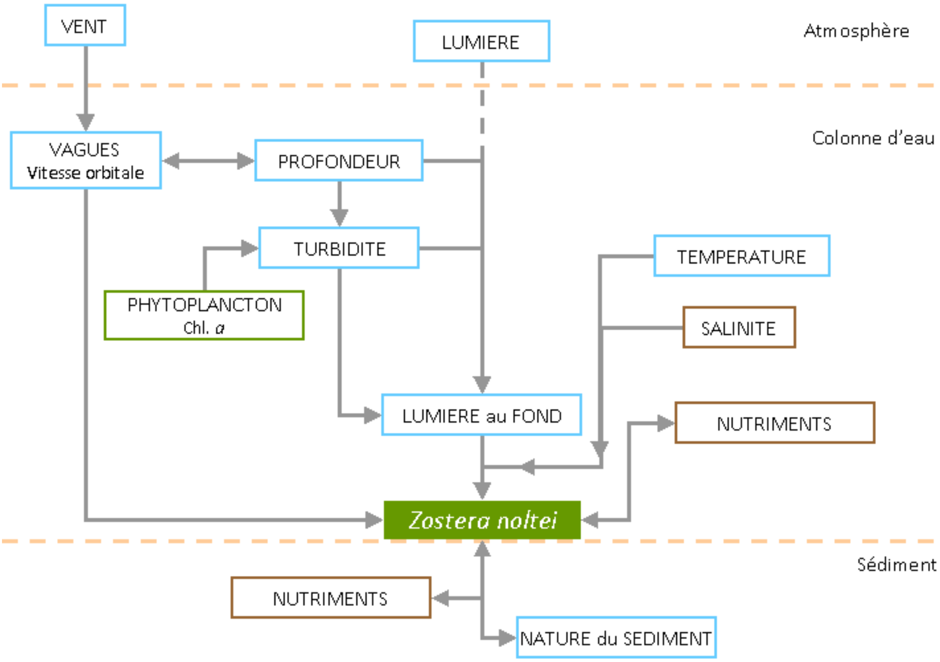


Figure 5: Schéma conceptuel des interactions entre les facteurs environnementaux et Zostera noltei (vert :paramètres biologiques, bleu : paramètres physiques, marron :paramètres chimiques).

Complémentaire à l'approche précédente centrée sur une seule espèce, nous nous sommes dans un deuxième temps intéressés à la distribution spatiale des macrophytes au sens large dans les lagunes méditerranéennes françaises dans le cadre du projet MARES2 (Rôle des macrophytes dans la restauration des milieux lagunaires : successions écologiques, 2014-2018). Les résultats présentés sont issus d'un travail de thèse (I. Le Fur) que j'ai co-encadré. Le premier axe de ce projet visait à déterminer et hiérarchiser les principaux facteurs expliquant la distribution des macrophytes dans 34 lagunes méditerranéennes françaises, caractérisées par des salinités, des profondeurs et des niveaux trophiques contrastés. Pour cela, nous avons analysé les données d'observation acquises au cours des suivis opérés dans le cade du RSL (Réseau de Suivi Lagunaire), de la DCE et par les gestionnaires de lagunes (GIPREB, Réserve Nationale de Camargue). Une analyse statistique multivariée (analyse canonique des correspondances) basée sur les données à long terme (1998 - 2015) de la colonne d'eau et des macrophytes, a permis de mettre en évidence que la salinité, la profondeur et le niveau trophique étaient les facteurs environnementaux structurants la répartition des macrophytes dans les sédiments meubles des 34 lagunes étudiées. Nous avons également émis l'hypothèse que la profondeur était un facteur indirect expliquant la présence de macro-algues exotiques dans les lagunes profondes. En effet, la présence d'activités conchylicoles dans les lagunes les plus profondes expliquent la présence d'espèces exotiques provenant en grande partie de l'importation des huîtres[55-56]. Par ailleurs, nos résultats ont également permis de confirmer le modèle théorique proposé par Schramm[57] (1999) dans les lagunes euhalines et polyhalines avec une présence d'herbiers et de macro-algues pérennes dans des conditions oligotrophes et la présence d'algues opportunistes et de phytoplancton dans les conditions eutrophes et hyper-eutrophes (Figure 6). Dans les lagunes oligohalines et mésohalines, nous avons en revanche proposé que la succession des macrophytes le long du gradient d'eutrophisation était probablement un intermédiaire entre la succession décrite par Sand-Jensen and Borum (1991)[58] pour les petits lacs des milieux tempérés et celle décrite par Schramm (1999)[59] pour les milieux côtiers à plus fortes salinités. En effet, certaines espèces de macrophytes observées dans les lagunes oligohalines et mésohalines, comme l'angiosperme *Stuckenia pectinata*, seraient adaptées à des milieux naturellement plus turbides et à des niveaux d'eutrophisation plus élevés que les herbiers marins tels que *Zostera spp.*

---

[55] Verlaque M. (2000) Actualisation de la flore des macrophytes des étangs de Thau (Hérault) et de Salses-Leucate (Aude-Pyrénées-Orientales). In: PNEC "Lagunes Méditerranéennes", Thème 1, le compartiment "Macrophytes". GIS Posidonie - IFREMER Report, Marseille. : 64p + annexes.

[56] Verlaque M. (2001) Checklist of the macroalgae of Thau Lagoon (Hérault, France), a hot spot of marine species introduction in Europe. Oceanologica Acta. 24: 29–49.

[57] Schramm W. (1999) Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. Journal of applied Phycology. 11: 69–78.

[58] Sand-Jensen K., Borum J. (1991) Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. Aquatic Botany. 41: 137–175.

[59] Schramm W. (1999) Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. Journal of applied Phycology. 11: 69–78.

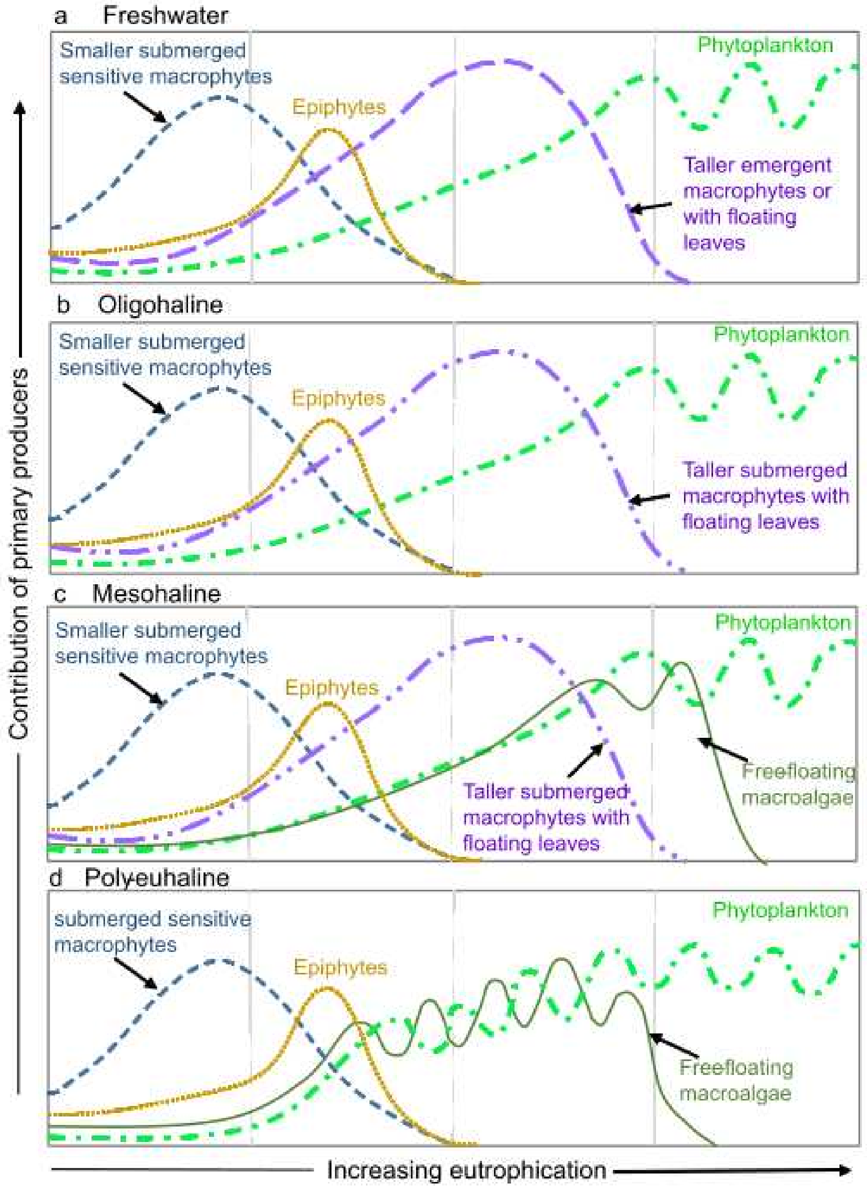


Figure 6: Représentation conceptuelle de la succession des producteurs primaires le long d'un gradient d'eutrophisation croissant dans (a) des lacs tempérés peu profonds. d'eutrophisation dans (a) des lacs tempérés peu profonds [modifié d'après Sand-Jensen (1980)[60], Sand-Jensen and Borum (1991)[61]], (b) lagunes oligohalins et (c) lagunes mésohalins [cette étude],(d) lagunes polyhalins et euhalins d) lagunes polyhalins et euhalins [modifié d'après Schramm and Nienhuis (1996)[62]]. Issue de Le Fur et al. (2018)[63]

---

[60] Sand-Jensen K. (1980) Balancen mellem autotrofe komponenter i tempererede søer med forskellig næringsbelastning. Vatten 36: 104–115.

[61] Sand-Jensen K., Borum J. (1991) Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. Aquatic Botany. 41: 137–175.

[62] Schramm W., Nienhuis P. (1996) Marine Benthic Vegetation: Recent Changes and the Effects of Eutrophication. Springer Science & Business Media.

[63] Le Fur I., de Wit R., Plus M., Oheix J., Simier M., Ouisse V. (2018) Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth. Hydrobiologia. 808(1), 175-200. https://doi.org/10.1007/s10750-017-3421-y

Après avoir exploré le lien entre les conditions environnementales et la distribution des macrophytes, j’ai souhaité aborder la question de la structuration des habitats dans les lagunes méditerranéennes. Entité structurelle et fonctionnelle dans un secteur géographique reconnaissable, la notion d’habitat est définie à la fois par ses caractéristiques abiotiques et ses assemblages biologiques associés. Chaque lagune est reconnue comme un habitat unique caractérisé par des conditions environnementales qui lui sont propres et qui varient entre lagune selon leur connexion à la mer, la quantité d’eau douce provenant du bassin versant ou bien selon leur morphologie (profondeur par exemple) et leur localisation (exposition au vent par exemple). Les connaissances aujourd’hui disponibles ont abouti récemment à la création d’une typologie simple (au sens classification) permettant de subdiviser les lagunes méditerranéennes selon leur salinité moyenne (lagunes oligo-mésohalines vs. Poly-euhalines). Cette classification a conduit par exemple, de manière pratique, au développement d’indicateurs spécifiques pour l’évaluation de l’état biologique dans le cadre de la Directive Cadre sur l’Eau (2000/60/CE). Bien qu’adaptée à la DCE, la description de chaque lagune comme une entité homogène ne reflète pas la variabilité spatiale et temporelle des conditions environnementales rencontrées dans ces milieux. De part leur situation, ces milieux peuvent par exemple être caractérisés par de forts gradients de salinité[64] ou bien des communautés végétales très variées[65]. Chaque lagune doit donc être décrite non pas comme un habitat mais comme une entité, elle-même constituée d’une multitude d’espaces homogènes appelés habitats où chacun d’eux serait défini par des composantes abiotiques et biotiques. Cette définition des lagunes méditerranéennes en tant que "super habitat" revêt un sens particulier lorsque l’on y ajoute une dimension fonctionnelle (partie 3.5). En effet, chacun des habitats qui constitue cette mosaïque d’habitats assurerait des fonctions propres pouvant être complémentaires pour de nombreuses espèces[66]. Ainsi, la richesse fonctionnelle d'une lagune serait par exemple la résultante de la multitude de niches créées par la complexité des habitats rencontrés (salinité, profondeur, structure 3D de la végétation…). A cette échelle, la notion d'habitat en lagune est pourtant peu utilisée car aucune représentation cartographique n’existe à cette échelle. Dans ce contexte, j’ai coordonné le premier projet de cartographie des habitats lagunaires méditerranéens (CHAMILA, Cartographie des HAbitats en MIlieux LAgunaires, 2018-2023). Basée sur la typologie EUNIS (European Nature Information System), nous avons tout d’abord décrit une nouvelle typologie adaptée au contexte lagunaire méditerranéen intégrant 7 critères structurants (Persistance de la masse d’eau, Température-Salinité, Substrat, Zone biologique, Hydrodynamisme, Niveau trophique et Biologie). Celle-ci permet ainsi aujourd’hui de définir les habitats d'une façon cohérente, de sorte que "des données semblables soient constamment associées à des types d'habitats précis, afin que l'on puisse comparer ces données d'une région géographique ou d'une époque à une autre" (Guide MESH, 2008). La cartographie actualisée des habitats lagunaires, basée sur les données acquises *via* les réseaux d’observation, est aujourd’hui disponibles sur 36 masses

---

[64] Fiandrino A., Ouisse V., Dumas F., Lagarde F., Pete R., Malet N., Le Noc S., de Wit R. (2017) Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. Marine Pollution Bulletin. 119: 132–144.

[65] Le Fur I., de Wit R., Plus M., Oheix J., Simier M., Ouisse V. (2018) Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth. Hydrobiologia. 808(1), 175-200. https://doi.org/10.1007/s10750-017-3421-y

[66] Iotti M., Darnaude A. M., Bouriat A., Ouisse V. (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries and Coasts. Estuaries And Coasts. 46(1), 198-226.

d’eau lagunaires françaises (Figure 7) sous forme d’un atlas cartographique[67] et de couches géoréférencées[68].

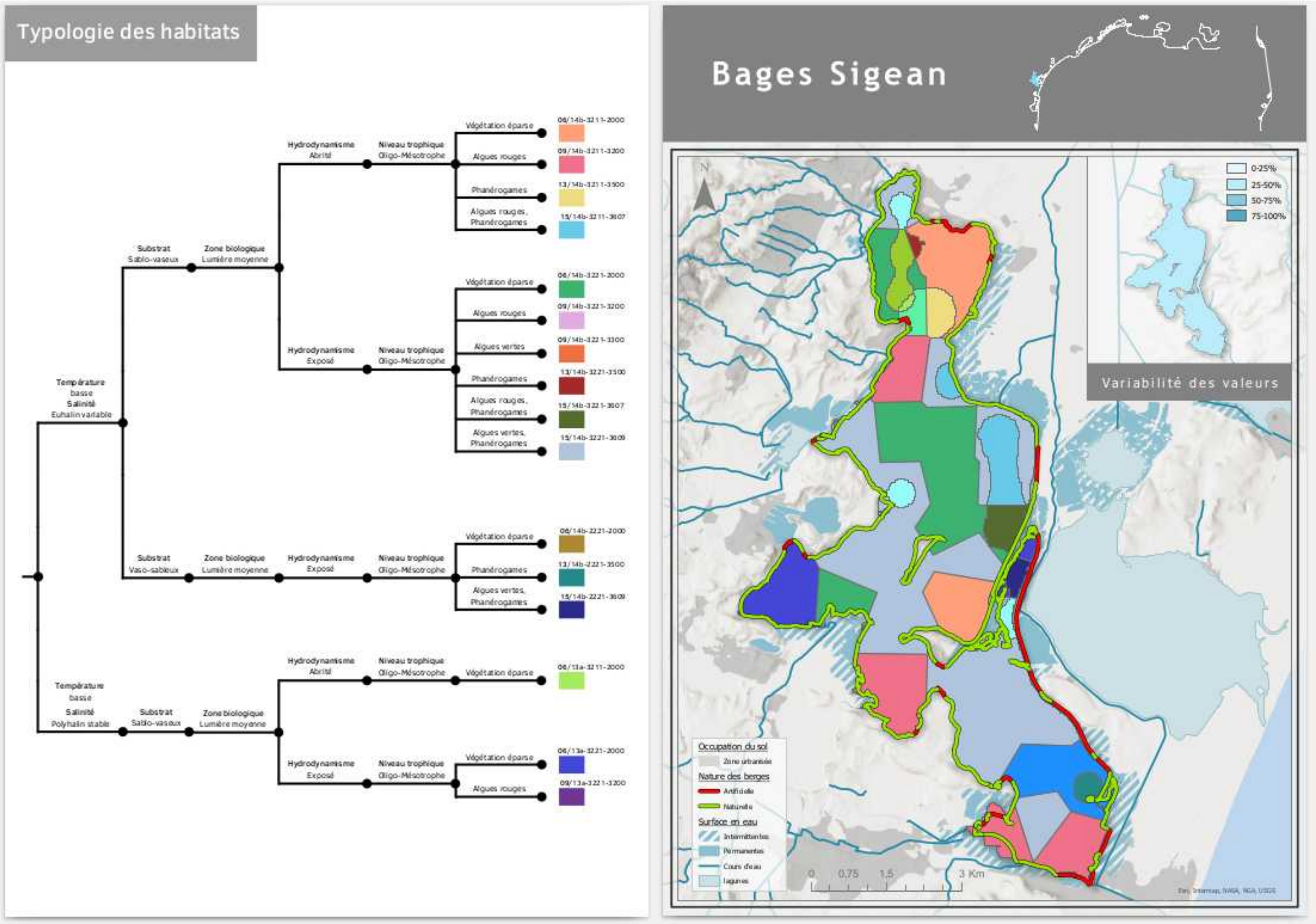


Figure 7: Exemple de cartographie d’habitats aujourd’hui disponible pour la lagune de Bages-Sigean[69]

Cette cartographie fine des habitats dispose également d’une carte d’incertitudes associées permettant son interprétation. 169 habitats sont aujourd’hui décrits sur la période 2016-2022 à l’échelle des lagunes méditerranéennes côtières françaises. L’analyse des résultats soulignent l’unicité des habitats lagunaires à l’échelle de la façade où 148 d’entre eux ne sont présents que dans une seule lagune. La majorité de ces habitats est couverte par des macrophytes, les habitats dépourvus de macrophyte représentent ainsi uniquement 13 % en nombre d’habitats et 3 % en terme de surface. Au delà du premier résultat cartographique, ce projet a permis de croiser de nombreuses données stationnelles ou spatialisées issues de programmes d’observation différents

---

[67] Ouisse V., Miramont A., Bajjouk T., Cimiterra N., Derolez V., Fontes H., Giraud A., Vaz S. (2023). Atlas Cartographique des habitats en milieu lagunaire méditerranéen. Projet CHAMILA - Partie 3. Ifremer, 80p

[68] Miramont A., Menu M., Vaz S., Ouisse V. (2023) Carte des Habitats de niveau 6 des lagunes méditerranéennes françaises listées au titre des masses d’eau de transition de la Directive Cadre sur Eau. IFREMER. https://doi.org/10.12770/3a8c573f-4cb3-418b-a342-df4aaefb4822

[69] Ouisse V., Miramont A., Bajjouk T., Cimiterra N., Derolez V., Fontes H., Giraud A., Vaz S. (2023). Atlas Cartographique des habitats en milieu lagunaire méditerranéen. Projet CHAMILA - Partie 3. Ifremer, 80p

(DCE, REPHY[70], FILMED[71], Image satellite Landsat 8 et 9). Cette nouvelle représentation spatialisée des connaissances constitue ainsi un outil important de gestion et de planification spatiale aussi bien aux échelles locales que régionales. Ces résultats doivent maintenant alimenter la réflexion sur la gestion de ces entités uniques vis-à-vis des enjeux de conservation. Ces travaux renforcent la notion de complexité des écosystèmes lagunaires dont la richesse fonctionnelle résulte en partie de la mosaïque des habitats qu'ils abritent. La compréhension des liens fonctionnels entre ces habitats et les fonctions (biodiversité, cycle du carbone…) qu'ils assurent représente un axe de travail important actuel (Partie 3.5) et futur dont ces travaux constituent une base concrète.

3.4. Résistance, seuils de basculement et successions écologiques des espèces clés face aux pressions

Les milieux côtiers et littoraux sont soumis à de nombreuses pressions anthropiques qui affectent la distribution des organismes soit directement à travers la modification des conditions environnementales soit indirectement *via* la disparition d'espèces clés indispensables à leur développement et leur survie (ces liens seront illustrés dans la partie 3.5). Si les changements environnementaux sont souvent graduels au cours du temps (variation de température, apports de nutriments par exemple), la réponse des organismes et en particulier des espèces est souvent non linéaire. Des études sur divers écosystèmes (lacs, récifs coralliens, océans, forêts, milieux arides) ont en effet montré que sous l'effet de pressions croissantes, ces écosystèmes pouvaient atteindre des seuils critiques à partir desquels ils subissent des transformations brusques passant d'un état à un autre[72]. Les mécanismes de changement d'états sont complexes et se produisent lorsque le système atteint un point de basculement (ou un point de bifurcation). Lorsqu'un système est dans un équilibre défini comme un état stable de référence[73-74], il peut s'adapter à des conditions externes variant progressivement. Au cours du temps, l'augmentation continue des perturbations externes réduit la résilience du système[75] et, par conséquent, même une petite perturbation au-dessus du seuil critique peut faire basculer le système vers un état stable alternatif[76-77-78] ce qui peut impliquer l'effondrement du système. Dans ce contexte, les notions de résilience (capacité d'un système à revenir à son état initial après une perturbation), de résistance (capacité d'un système à rester dans son état initial sous contrainte d'une perturbation) et de succession écologique face aux pressions anthropiques ou naturelles en écologie fonctionnelle sont souvent uniquement abordées de

---

[70] REseau d'observation et de surveillance du PHYtoplancton et des phycotoxines

[71] Forum Interrégional des Lagunes MEDiterrannéenne

[72] Scheffer M., Carpenter S., Foley J. A., Folke C., Walker B. (2001) Catastrophic shifts in ecosystems. Nature. 413: 591–596.

[73] Scheffer M., Carpenter S., Foley J. A., Folke C., Walker B. (2001) Catastrophic shifts in ecosystems. Nature. 413: 591–596.

[74] Scheffer M., Bascompte J., Brock W. A., Brovkin V., Carpenter S. R., Dakos V., Held H., van Nes E. H., Rietkerk M. Sugihara G. (2009) Early-warning signals for critical transitions. Nature. 461:53–9. doi: 10.1038/nature08227

[75] van Nes E. H., Scheffer M. (2007) Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. American Naturalist. 169:738–47. doi: 10.1086/516845

[76] Chisholm R. A., Filotas E. (2009) Critical slowing down as an indicator of transitions in two-species models. Journal of Theoretical Biology. 257:142–9. doi: 10.1016/j.jtbi.2008.11.008

[77] Scheffer M., Carpenter S., Foley J. A., Folke C., Walker B. (2001) Catastrophic shifts in ecosystems. Nature. 413: 591–596.

[78] Scheffer M., Bascompte J., Brock W. A., Brovkin V., Carpenter S. R., Dakos V., Held H., van Nes E. H., Rietkerk M. Sugihara G. (2009) Early-warning signals for critical transitions. Nature. 461:53–9. doi: 10.1038/nature08227

manière théorique, faute de données disponibles. Dans le cadre de mes travaux de recherche, j'ai commencé à explorer ces notions en me basant sur l'observation de milieux perturbés, l'analyse de données historiques, la modélisation et l'écologie expérimentale.

Basé sur une approche couplée observation-modélisation dans la baie des prieurés à Dinard, le projet IMOZ (Impact des zones de MOuillage sur les herbiers de zostères, 2015) a permis de mettre en évidence un effet diffus et variable des mouillages sur la structure d'un herbier de *Zostera marina* (Figure 8). Au delà de la zone proche du mouillage où la plante a complètement disparu, la hauteur de la canopée est tout d'abord inférieure à celle du site de référence, probablement en raison des perturbations physiques régulières causées par les chaînes d'amarrage. Inversement, la densité des pousses y est plus élevée que dans le site de référence. Cette réponse adaptative semble contrebalancer la diminution de la hauteur de la canopée à ces distances. Les fluctuations de la structure du couvert de zostères (nombre de pousses, longueur des feuilles) à une petite échelle spatiale étaient clairement en accord avec l'intensité de raclage simulée par le modèle MARS3D (Figure 8).

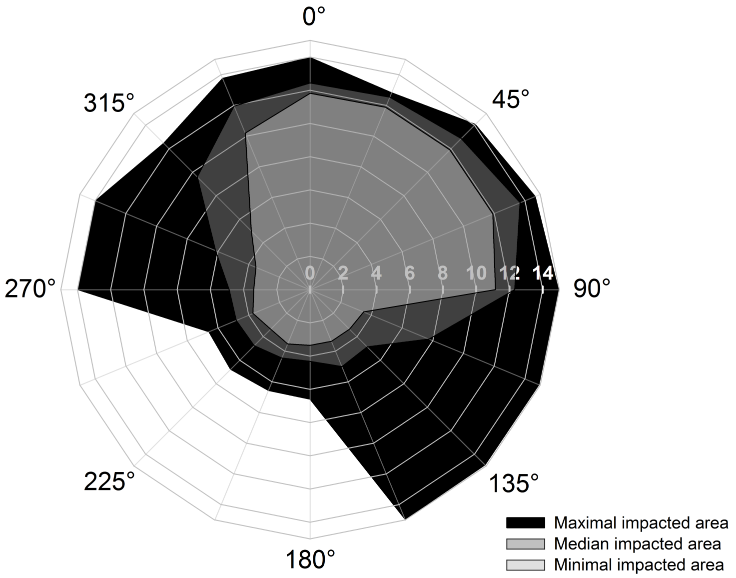


Figure 8: Modélisation des risques de dégradation du fond par le mouillage. Issue de Ouisse et al. (2020)[79]

Les courants de marée couplés à la variabilité de l'amplitude de la marée impliquent à petite échelle un effet hétérogène du mouillage permanent sur le compartiment benthique, qui ne peut être détecté par des études aériennes. Ces résultats viennent confirmés que ces plantes marines peuvent modifier leurs traits morphologiques et physiologiques à un certain niveau de stress comme cela a déjà été démontré par d'autres auteurs[80-81-82]. Ces modifications importantes

---

[79] Ouisse Vincent, Marchand-Jouravleff Irina, Fiandrino Annie, Feunteun Eric, Ysnel Frederic (2020). Swinging boat moorings: Spatial heterogeneous damage to eelgrass beds in a tidal ecosystem . Estuarine Coastal And Shelf Science , 235, 106581 (9p.) . Publisher's official version : https://doi.org/10.1016/j.ecss.2020.106581, Open Access version : https://archimer.ifremer.fr/doc/00599/71151/

[80] Cabaço S., Machás R., Santos R. (2009) Individual and population plasticity of the seagrass Zostera noltii along a vertical intertidal gradient. Estuarine Coastal and Shelf Science. 82:301–308. doi: 10.1016/j.ecss.2009.01.020

pourraient avoir un impact plus fonctionnel, comme la perte de biodiversité et la séquestration du carbone.

A travers le projet post-doctoral HEALSEA (Innovative indicators of resilience to protect the health status of seagrass meadows: from ecological theory to conservation, 2018-2020) porté par L. Soissons, j'ai abordé la question des seuils et des signaux précurseurs de basculement des systèmes. De telles transitions dans les écosystèmes ont été observées et décrites dans des modèles mathématiques, et seulement quelques exemples de changement d'état ou de ralentissement critique ont été identifiés dans les écosystèmes benthiques marins[83-84-85]. Basés sur la théorie écologique et la recherche expérimentale sur les indicateurs de résilience, le projet HEALSEA avait pour objectif de tester l'effet d'une perturbation (ajout local d'azote et de phosphore) sur un système modèle (ici l'herbier de *Zostera noltei*) afin de définir un seuil de changement d'état. Les résultats issus de ce projet montrent généralement que les augmentations de nutriments (perturbation) ont conduit à un déclin des caractéristiques des herbiers marins. Ce déclin a été plus fort et plus brutal après une perturbation supplémentaire, conduisant à un effondrement complet et à l'absence de rétablissement. Cela confirme que les changements brusques suggérés par la théorie écologique peuvent s'appliquer aux prairies sous-marines et que des seuils (ici 50 mmol $N.j^{-1}$) et des indicateurs (basés sur des mesures biométriques) peuvent être identifiés. Le passage d'une communauté d'herbiers à une communauté dominée par les algues peut être facilement identifié et anticipé en examinant les estimations de la couverture végétale (Figure 9). A terme, ces résultats viendront contribuer à la préservation des herbiers marins en fournissant des outils innovants, afin d'anticiper les changements potentiels dans la résilience des herbiers marins avant qu'ils n'atteignent un état dégradé.

---

[81] Peralta G. , Brun F. G., Hernández I., Vergara J. J., Pérez-Lloréns J. L. (2005) Morphometric variations as acclimation mechanisms in beds. Estuarine, Coastal and Shelf Science. 64:347–356. doi: 10.1016/j.ecss.2005.02.027

[82] Soissons L. M. , van Katwijk M. M., Peralta G., Brun F. G., Cardoso P. G., Grilo T. F., Ondiviela B., Recio M., Valle M., Garmendia J. M., Ganthy F., Auby I., Rigouin L., Godet L., Fournier J. (2018) Seasonal and latitudinal variation in seagrass mechanical traits across Europe: The influence of local nutrient status and morphometric plasticity. Limnology and Oceanography. 63:37–46. doi: 10.1002/lno.10611

[83] Connell S. D., Fernandes M., Burnell O. W., Doubleday Z. A., Griffin K. J., Irving A. D., Leung J. Y. S., Owen S., Russell B. D., Falkenberg L. J. (2017) Testing for thresholds of ecosystem collapse in seagrass meadows? Conservation Biology. 1–12. doi: 10.1111/cobi.12951

[84] Rindi L., Bello M. D., Dai L., Gore J, Benedetti-Cecchi L. (2017) Direct observation of increasing recovery length before collapse of a marine benthic ecosystem. Nature Ecology and Evolution. 1:0153. doi: 10.1038/s41559-017-0153

[85] van Belzen J., van de Koppel J., Kirwan M. L., van der Wal D., Herman P. M. J., Dakos V., Kéfi S., Scheffer M., Guntenspergen G. R., Bouma T. J. (2017) Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. Nature Communication. 8:15811. doi: 10.1038/ncomms15811

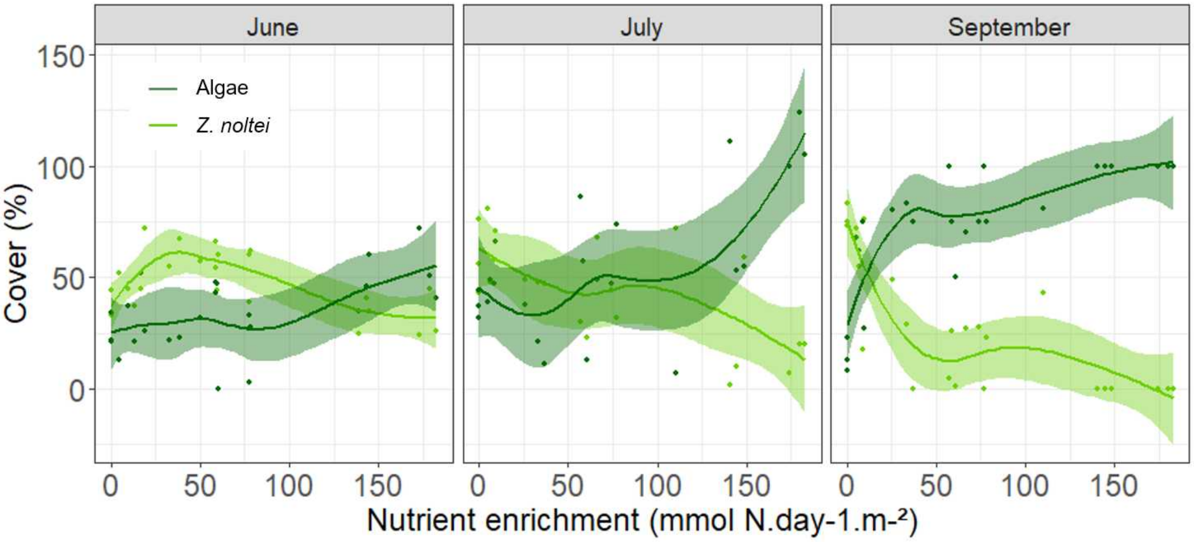


Figure 9: Changements dans la couverture végétale (Zostera noltei en vert clair, algues en vert foncé) le long du gradient d'enrichissement en nutriments pour les parcelles non coupées en juin, juillet et septembre. Les lignes représentent le modèle de réponse non linéaire le long du gradient, basé sur un lissage loess avec SE. Issue de Soissons et al. (en préparation)[86]

Troisième aspect de cet axe de recherche sur la réponse des espèces benthiques aux perturbations, la question de la dynamique à long terme des espèces clés face aux perturbations a été étudiée dans les lagunes méditerranéennes. De par leur faible profondeur, leur confinement et leur faible degré d'échanges avec la mer, les milieux lagunaires ont une tendance naturelle à accumuler les nutriments les rendant plus vulnérables à l'eutrophisation[87-88-89]. Ainsi, les lagunes méditerranéennes n'ont pas été épargnées par ce phénomène d'eutrophisation[90-91-92]. L'eutrophisation a conduit à une dégradation de la qualité de l'eau de ces milieux[93], une modification de la structure[94], du fonctionnement[95]. Face aux risques liés à la dégradation de la qualité de ces milieux et de l'impact de ces dégradations sur les services et biens rendus par ces écosystèmes, les

---

[86] Soissons L. M. , Dakos V., Ouisse V., Le Fur M., Morla J., Benedetti-Cecchi L., Rossi F. (en préparation) Experimental evidence of loss of resilience and non-linear response to multiple disturbances in seagrasses

[87] Barnes, R. S. K. (1980) Coastal Lagoons : the natural history of a neglected habitat. Cambridge University Press, Cambridge.

[88] Kjerfve B. (1994) Chapter 1 Coastal Lagoons In Kjerfve, B. (ed), Elsevier Oceanography Series. Elsevier: 1–8.

[89] Glibert P. M., Hinkle D. C., Sturgis B., Jesien R. V. (2014) Eutrophication of a Maryland/Virginia Coastal Lagoon: a Tipping Point, Ecosystem Changes, and Potential Causes. Estuaries and Coasts. 37: 128–146.

[90] Facca C., Sfriso A., Ghetti P. F. (2004) Phytoplankton community composition and distribution in a eutrophic coastal area (Venice lagoon, Italy). Acta Adriatica : international journal of Marine Sciences. 45: 163–180.

[91] Orfanidis S., Panayotidis P., Ugland K. (2011) Ecological Evaluation Index continuous formula (EEI-c) application: a step forward for functional groups, the formula and reference condition values. Mediterranean Marine Science .12(1). 10.12681/mms.60

[92] Souchu P., Bec B., Smith V. H., Laugier T., Fiandrino A., Benau L., Orsoni V., Collos Y., Vaquer A. (2010) Patterns in nutrient limitation and chlorophyll a along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Canadian Journal of Fisheries and Aquatic Sciences. 67: 743–753.

[93] Ifremer, 2014. Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2013. Ifremer: 219p.

[94] Bec B., Collos Y. , Souchu P., Vaquer A., Lautier J., Fiandrino A., Benau L., Orsoni V., Laugier T. (2011) Distribution of picophytoplankton and nanophytoplankton along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Aquatic Microbial Ecology. 63: 29–45.

politiques publiques ont donc mis en œuvre des actions de gestion visant à réduire les apports en nutriments et restaurer ces écosystèmes. Aujourd'hui, certaines lagunes sont en phase de restauration[96-97] et s'engagent vers une trajectoire d'oligotrophisation. Dans ce contexte, j'ai coordonné deux projets basés sur l'analyse rétrospective de données acquises dans le cadre du Réseau de Suivi Lagunaire (RSL) puis de la Directive Cadre sur l'Eau (DCE). Un des volets du projet MALAG (Effet de l'eutrophisation sur la macrofaune benthique des lagunes méditerranéennes, 2019-2022) avait pour objectif d'étudier la dynamique temporelle de la macrofaune benthique en lien avec les conditions environnementales. Les résultats n'ont malheureusement pas permis d'illustrer un lien clair entre l'évolution des conditions environnementales et la strucure des communautés benthiques en lagune. Bien que nos résultats montrent que le M-AMBI (indicateur écologique) semble être un indicateur sensible à l'eutrophisation à travers les composantes de richesse spécifique et de diversité (Shannon) de l'indice, la dynamique de la macrofaune benthique ne répondrait pas uniquement aux fluctuations des pressions anthropiques mais également aux conditions environnementales locales comme l'hydromorphologie et la structure des habitats benthiques. Couramment utilisés comme indicateur dans le cadre de la DCE, ces résultats obtenus sur la macrofaune benthique interrogent sur l'utilisation de ces données pour caractériser l'évolution de l'état écologique des masses d'eau.

Le deuxième axe du projet MARES2 (Rôle des macrophytes dans la restauration des milieux lagunaires : successions écologiques, 2014-2018) a quant à lui permis de décrire les successions écologiques des macrophytes (remplacement des espèces) au cours de la restauration vis-à-vis de l'eutrophisation[98]. La diminution des charges en azote et phosphore dans l'eau conduit à un remplacement des espèces, passant d'espèces avec de fortes affinités pour les nutriments (conditions eutrophes) à cycle de vie court, à des espèces adaptées aux conditions oligotrophes à cycle de vie long comme les herbiers (Figure 10). Trois bassins d'attractions ont été définis. un premier bassin dominé par le phytoplancton dans les milieux les plus eutrophisés, un deuxième dominé par des macro-algues opportunistes et enfin un troisième dominé par des macrophytes pérennes dans des milieux non dégradés. Au cours de la dynamique de restauration des lagunes vis-à-vis de l'eutrophisation, un basculement du premier bassin d'attraction (phytoplancton) vers le deuxième bassin d'attraction (macro-algues opportunistes) a été observé. En effet, dans les systèmes les plus eutrophisés, la réduction des apports externes a induit une diminution des nutriments disponibles dans la colonne d'eau et a conduit ainsi à un basculement rapide d'un système dominé par le phytoplancton à l'apparition de macro-algues opportunistes et en particulier de l'espèce *Ulva rigida*. Ce basculement (régime shift en anglais) résulterait à la fois d'un

---

95 Carlier A., Riera P., Amouroux J-M., Bodiou J-Y., Desmalades M., Grémare A. (2008) Food web structure of two Mediterranean lagoons under varying degree of eutrophication. Journal of Sea Research. 60: 264–275.

96 Derolez V., Bec B., Munaron D., Fiandrino A., Pete R., Simier M., Souchu P., Laugier T., Aliaume C., Malet N. (2019) Recovery trajectories following the reduction of urban nutrient inputs along the eutrophication gradient in French Mediterranean lagoons. Ocean & Coastal Management 171: 1–10. https://doi.org/10.1016/j.ocecoaman.2019.01.012.

97 Leruste A., Malet N., Munaron D., Derolez V., Hatey E., Collos Y., de Wit R., Bec B. (2016) First steps of ecological restoration in Mediterranean lagoons: Shifts in phytoplankton communities. Estuarine, Coastal and Shelf Science. 180: 190–203.

98 Le Fur I., de Wit R., Plus M., Oheix J., Derolez V., Simier M., Malet N., Ouisse V. (2019) Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. Marine Ecology Progress Series. 608, 13-32. Publisher's official version : https://doi.org/10.3354/meps12814, Open Access version : https://archimer.ifremer.fr/doc/00474/58555/

changement de source d'azote et de phosphore (externe puis issue de la reminéralisation dans le sédiment) et d'une augmentation de la lumière disponible au fond (diminution de l'ombrage par le phytoplancton et de la remise en suspension du sédiment en particulier). Au sein de ce même bassin d'attraction dominé par les macrophytes opportunistes, la dynamique d'oligotrophisation s'est traduite par un remplacement progressif des algues vertes du genre *Ulva* par des algues rouges du genre *Gracilaria* et des algues vertes filamenteuses du genre *Chaetomorpha*. Ce changement serait induit par une limitation progressive par l'azote, favorisant des espèces moins nitrophiles. Enfin, dans les cas de restauration les plus avancés un basculement des macro-algues opportunistes vers un système dominé par les macrophytes pérennes serait largement dépendant de facteurs physiques limitants en particulier l'arrivée de nouvelles propagules ou graines. Ce basculement n'a pour le moment pas pu être observé dans les lagunes méditerranéennes françaises.

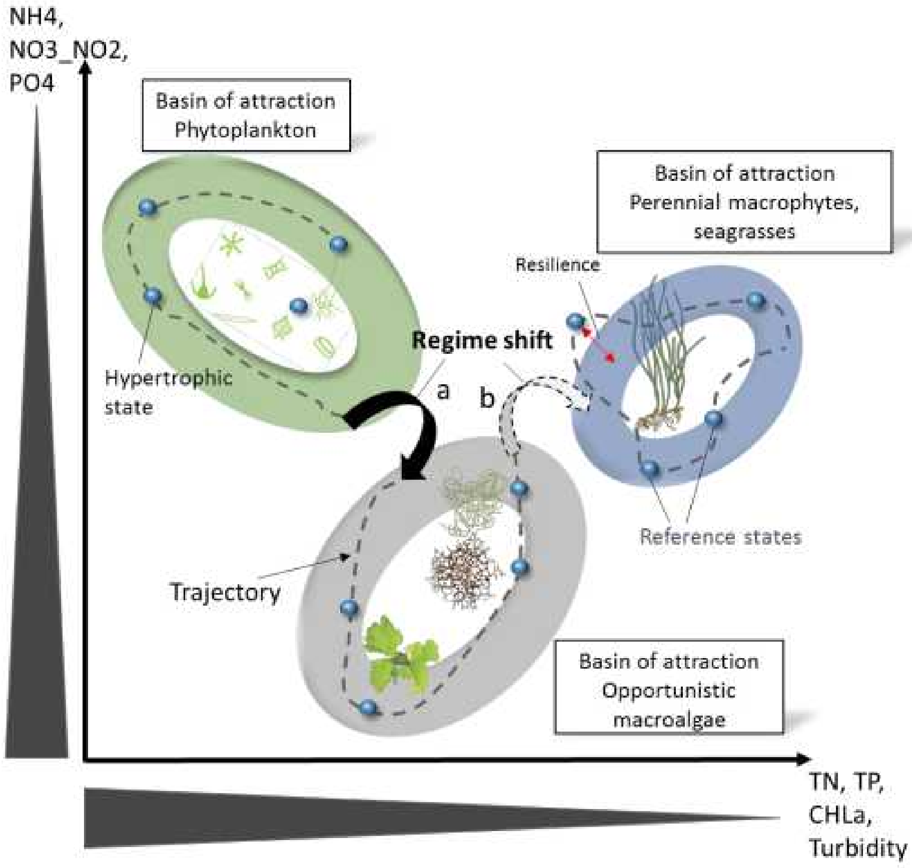


Figure 10: Représentation conceptuelle des successions des macrophytes au cours de la restauration. Issue de Le Fur et al. (2019)[99]

---

[99] Le Fur I., de Wit R., Plus M., Oheix J., Derolez V., Simier M., Malet N., Ouisse V. (2019) Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. Marine Ecology Progress Series. 608, 13-32. Publisher's official version : https://doi.org/10.3354/meps12814, Open Access version : https://archimer.ifremer.fr/doc/00474/58555/

3.5. Rôles fonctionnels du compartiment benthique

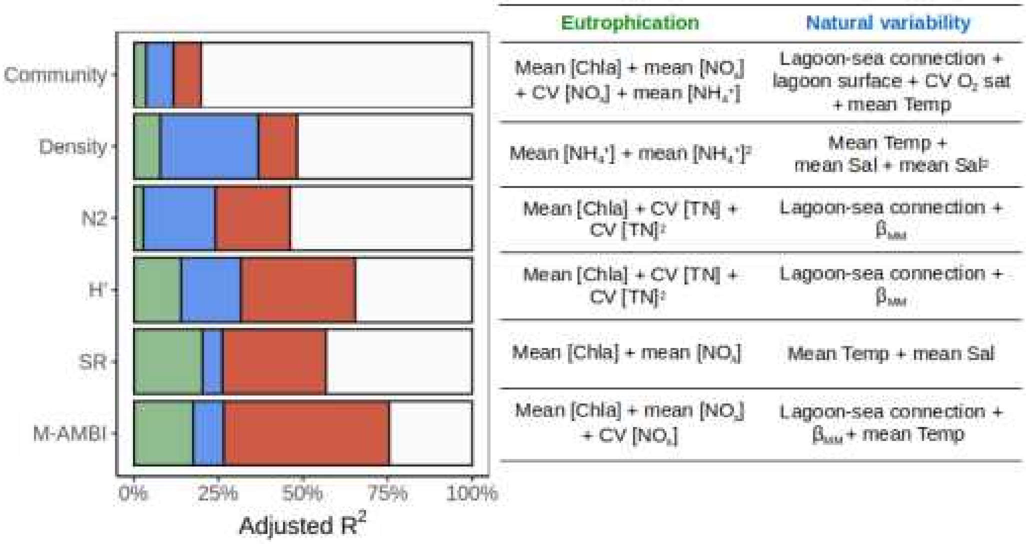
Les fonctions écologiques sont définies comme les processus biologiques assurés par l'ensemble des espèces qui composent une communauté ou forment un habitat. Parmi ces fonctions, une partie de mes actions de recherche est aujourd'hui centrée sur la caractérisation et la quantification du rôle du compartiment benthique dans le maintien de la biodiversité et la régulation des cycles de la matière.

Rôle des espèces ingénieures dans la structuration de la biodiversité

La cartographie des habitats lagunaires (voir partie 3.3) est notamment à la base des projets MALAG (Effet de l'eutrophisation sur la macrofaune benthique des lagunes méditerranéennes, 2019-2022), NURSE (Rôle des lagunes littorales dans le cycle biologique des poissons méditerranéens : comprendre pour mieux préserver, 2018-2022) et INPOLAG (Développement d'un INdicateur POissons en LAGune, 2019-2023). Ces trois projets que j'ai coordonné s'attachent à comprendre les liens fonctionnels entre l'habitat et la biodiversité dans les milieux lagunaires méditerranéens. Le projet MALAG était quant à lui focalisé sur la distribution de la macrofaune dans les lagunes méditerranéennes. Support initial d'une thèse, ce projet a finalement fait l'objet d'un post-doctorat. À travers l'utilisation d'approches taxonomiques et fonctionnelles à plusieurs échelles de temps et d'espace, les résultats de ce projet mettent en évidence la complexité du lien entre l'environnement ou l'habitat et la distribution de la macrofaune benthique au sein des lagunes méditerranéennes. Une première approche à l'échelle de la façade (29 lagunes) a permis de mettre en évidence que la structuration spatiale de la macrofaune benthique serait déterminée principalement par (i) l'hydromorphologie des lagunes (niveau de connexion avec la mer, surface et profondeur) et la variabilité en termes de salinité et de température, et (ii) la diversité de l'habitat benthique à l'échelle de la lagune (Figure 11)[100]. L'eutrophisation et les facteurs de stress associés comme la faible teneur en oxygène dissous agiraient sur les communautés existantes en réduisant la richesse et la diversité taxonomique. A cette échelle, l'eutrophisation semble agir sur le macrobenthos lagunaire par des mécanismes relativement directs (toxicité des composés azotés inorganiques) et indirects (simplification des habitats benthiques et modifications biogéochimiques des sédiments). L'acquisition de données à l'échelle intra-lagunaire et intra-annuelle dans le cadre de ce projet a également permis d'illustrer la variabilité de la structure des communautés benthiques au sein même des lagunes méditerranéennes. La structuration de l'habitat et en particulier la couverture en macrophyte est ici décrite comme un facteur clé expliquant la distribution de la macrofaune benthique aussi bien dans le temps et dans l'espace. L'absence de prise en compte de cette variabilité dans les stratégies d'acquisition de données dans le cadre de la DCE explique vraisemblablement une partie des difficultés rencontrées dans l'interprétation des données.

---

[100] Jones A. G., Schaal G., Boyé A., Creemers M., Derolez V., Desroy N., Fiandrino A., Mouton T. L., Simier M., Smith N., Ouisse V. (en révision). Disentangling the effects of eutrophication and natural variability on macrobenthic communities across French coastal lagoons. PCI Ecology.



Eutrophication	Natural variability
Mean [Chla] + mean $[NO_x]$ + CV $[NO_x]$ + mean $[NH_4^+]$	Lagoon-sea connection + lagoon surface + CV O_2 sat + mean Temp
Mean $[NH_4^+]$ + mean $[NH_4^+]^2$	Mean Temp + mean Sal + mean Sal²
Mean [Chla] + CV [TN] + CV [TN]²	Lagoon-sea connection + β_{MM}
Mean [Chla] + CV [TN] + CV [TN]²	Lagoon-sea connection + β_{MM}
Mean [Chla] + mean $[NO_x]$	Mean Temp + mean Sal
Mean [Chla] + mean $[NO_x]$ + CV $[NO_x]$	Lagoon-sea connection + β_{MM} + mean Temp

Figure 11: À gauche, variance (R2 ajusté) des données sur les communautés de macrofaune (Community), densité totale de macrofaune (Density), inverse de la dominance de Simpson (N2), diversité de Shannon (H'), richesse spécifique (SR) et AMBI multivarié (M-AMBI) attribués uniquement à l'eutrophisation (vert), uniquement à la variabilité naturelle (bleu) et attribués conjointement aux deux effets (rouge). La variance résiduelle est représentée en blanc. A droite, les variables d'eutrophisation et les variables liées à la variabilité naturelle prises en compte dans la répartition de la variance de la macrofaune et des indices taxonomiques macrobenthiques. Issue de Jones et al. (2023)[101].

Afin d'avoir une vision plus large du rôle fonctionnel des habitats benthiques, j'ai exploré le lien entre la distribution des poissons bentho-démersaux et les habitats dans les milieux lagunaires méditerranéens. Le projet NURSE a constitué un cadre scientifique et financier pour deux thèses réalisées au sein de l'UMR MARBEC, l'une portant sur le volet juvénile de poissons que j'ai co-encadrée et l'autre sur le volet adulte. Ce projet basé sur l'observation *in situ* dans une lagune atelier (la lagune du Prévost au sud de Montpellier) visait à qualifier et quantifier les interactions entre les habitats et les poissons au sein des lagunes méditerranéennes. Sur le volet adulte, les lagunes méditerranéennes semblent être des écosystèmes clés en fournissant un habitat d'alimentation répondant à leurs besoins en terme de croissance. Les trois espèces de poissons étudiées, la daurade royale (*Sparus aurata*), le loup (*Dicentrarchus labrax*) et le mulet (*Mugil sp.* et/ou *Liza sp.*) exploitent la lagune de manière très fidèle dans le temps mais contrastée durant la phase chaude, probablement du fait de ressources alimentaires non chevauchantes entre elles[102]. Elles montrent également toutes un effet saisonnier important dans sa fréquentation, essentiellement durant la phase hivernale en lien avec les basses températures et la phase de reproduction. Concernant les juvéniles, la structuration du peuplement de poissons varie dans l'année mais reste marquée spatialement au sein de la lagune. Nos résultats soulignent la pertinence de se placer à

---

[101] Jones A. G., Schaal G., Boyé A., Creemers M., Derolez V., Desroy N., Fiandrino A., Mouton T. L., Simier M., Smith N., Ouisse V. (en révision). Disentangling the effects of eutrophication and natural variability on macrobenthic communities across French coastal lagoons. PCI Ecology.

[102] Mignucci A., Bourjea J., Forget F., Allal H., Dutto G., Gasset E. McKenzie D. (2021) Cardiac and behavioural responses to hypoxia and warming in free-swimming gilthead seabream Sparus aurata. Journal of Experimental Biology. 224 : 242397.

l'échelle de l'habitat pour préciser la fonction de nurserie des lagunes. Ils montrent que la qualité de l'environnement lagunaire varie temporellement et spatialement à l'échelle de l'habitat, aussi bien pour les juvéniles des espèces migratrices que pour les espèces résidentes (Figure 12). La distribution des poissons au stade juvénile serait en effet dictée par les caractéristiques des habitats et en particulier des macrophytes qui peuvent à la fois constituer des zones de protection (structure 3D) et abriter des proies[103]. Ceci se traduit par une modification de l'abondance, de la répartition spatiale et de la composition du peuplement juvénile de la lagune.

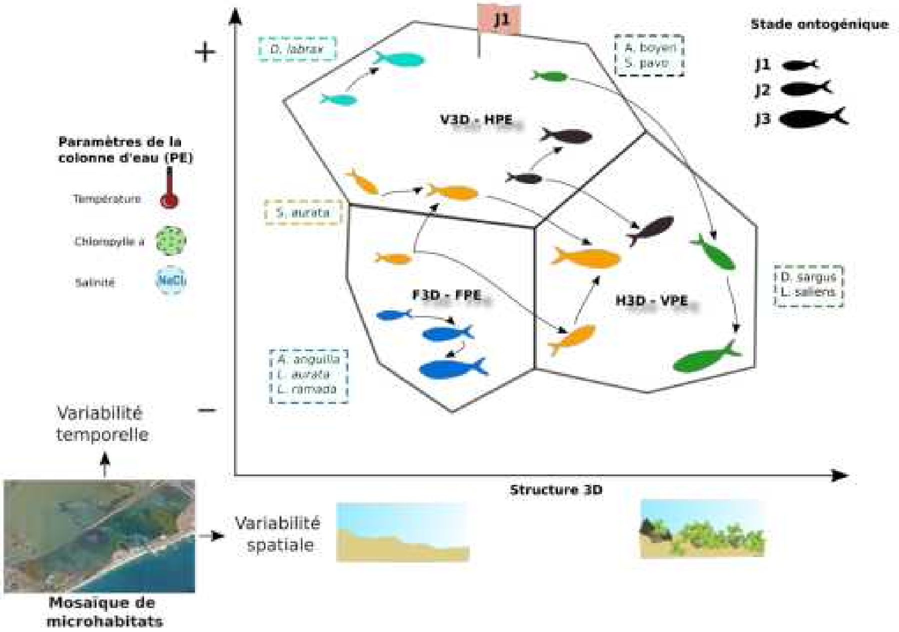


Figure 12: Micro-habitats composant la lagune du Prévost et micro-habitats préférentiels des juvéniles de poissons selon leur espèce et leur stade ontogénique. F3D-FPE= Faible structure tridimensionnelle -Faibles valeurs des paramètres de l'eau, V3D-HPE= Structure tridimensionnelle variable - Hautes valeurs des paramètres de l'eau, H3D-VPE = Haute structure tridimensionnelle - Valeurs des paramètres de l'eau variables. Issue de Ouisse et al. (2022)[104].

Ces résultats font écho aux discussions récentes autour de la définition des zones de nurserie et des mesures de gestion de l'environnement qui en découlent. En effet, jusqu'à récemment, les habitats de nurserie des poissons correspondent par définition aux habitats qui permettent de contribuer à maintenir et renouveler la population adulte. Ils sont soit définis comme ceux contribuant le plus, par unité de surface (notion de densité forte), à cette population adulte[105],

---

[103] Iotti M., Darnaude A. M., Bouriat A., Ouisse V. (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries and Coasts. Estuaries And Coasts. 46(1), 198-226.

[104] Ouisse V., Bourjea J., Iotti M., Mignucci A., Darnaude A. (2022) Rôle des lagunes littorales dans le cycle biologique des poissons méditerranéens: comprendre pour mieux préserver . Projet NURSE – Rapport final. R.ODE/UL/LERLR 22-20. https://doi.org/10.13155/93668

[105] Beck M. W., Heck K. L., Able K. W., Childers D. L., Eggleston D. B., Gillanders B. M., Halpern B., Hays C. G., Hoshino K., Minello T. J., Orth R. J., Sheridan P. F., Weinstein M. P. (2001) The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site- specific variability in nursery quality will improve

soit comme ceux présentant des densités faibles de juvéniles mais couvrant une grande surface[106]. Des travaux plus récents[107] proposent une toute autre approche, qui considère les nurseries comme une mosaïque d'habitats différents mais aux fonctions complémentaires pour les juvéniles de poissons. Cette approche cherche également à intégrer les processus dynamiques qui interviennent dans le lien habitat-poissons. Ainsi, s'il est effectivement possible d'identifier des "hot-spots" de juvéniles définis comme des zones où les plus fortes abondances sont observées et pour lesquels les juvéniles présentent une certaine fidélité, ils doivent être identifiés pour chaque stade de la vie juvénile, afin de prendre en compte l'évolution des besoins des poissons au cours de leur développement[108]. Dans cette logique, chaque habitat ayant permis la survie et la bonne condition des juvéniles à un stade donné contribue au maintien global de la population.

Cette question du lien entre habitats et poissons a été élargie à d'autres lagunes dans le cadre du projet INPOLAG. Ce projet s'inscrit plus généralement dans le contexte réglementaire de la Directive Cadre sur l'Eau (DCE) et visait quant-à lui à développer un indicateur "poissons DCE-compatible" adapté au contexte français. En d'autres termes, il s'agissait de comprendre comment le compartiment poissons répondait au pressions anthropiques dans les lagunes méditerranéennes françaises. Comme cela a été souligné dans le projet NURSE ou dans plusieurs discussions récentes issues de projets de recherche[109-110-111-112-113], il semble indispensable pour répondre à cette question d'intégrer la compréhension des liens fonctionnels entre le compartiment "poisson" et les habitats fréquentés afin de mieux comprendre leurs réponses face aux perturbations. En effet, l'altération naturelle ou anthropique des habitats en lagune pourrait largement affecter la distribution des organismes dans ces milieux (Figure 2). Basé sur un échantillonnage à deux saisons (printemps et automne) de 122 stations réparties sur un panel de 8 lagunes, ce travail a permis de décrire les peuplements de poissons, principalement les juvéniles ou les espèces peu mobiles, en parallèle des conditions environnementales. Les données collectées mettent en évidence les variabilités spatiales (entre habitats, Figure 13) et saisonnières (printemps vs. automne) de la densité et de la composition des peuplements. L'analyse spatio-temporelle des communautés bentho-démersales a

---

conservation and management of these areas. BioScience. 51: 633–641.

[106] Dahlgren C. P., Kellison G. T., Adams A. J., Gillanders B. M., Kendall M. S., Layman C. A., Ley J. A., Nagelkerken I., Serafy J. E. (2006) Marine nurseries and effective juvenile habitats: concepts and applications. Marine Ecology Progress Series. 312: 291–295.

[107] Nagelkerken I., Sheaves M., Baker R., Connolly R.M. (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish and Fisheries. 16: 362–371. https://doi.org/10.1111/faf.12057.

[108] Nagelkerken I., Sheaves M., Baker R., Connolly R.M. (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish and Fisheries. 16: 362–371. https://doi.org/10.1111/faf.12057.

[109] Franco A., Franzoi P., Malavasi S., Riccato F., Torricelli P., Mainardi D. (2006) Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science. 66: 67–83.

[110] Franco A., Torricelli P., Franzoi P. (2009) A habitat- specific fish-based approach to assess the ecological status of Mediterranean coastal lagoons. Marine Pollution Bulletin. 58: 1704- 1717

[111] Iotti M., Darnaude A. M., Bouriat A., Ouisse V. (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries and Coasts. Estuaries And Coasts. 46(1), 198-226.

[112] Perry H. J., Goodridge Gaines L. A., Borland H. P., Henderson C. J., Olds A. D., Mosman J. D., Gilby B. L. (2023) Identifying optimal values of coastal habitat condition for management and restoration. Estuarine, Coastal and Shelf Science 282, 108250. https:// doi.org/10.1016/j.ecss.2023.108250

[113] Zucchetta M., Scapin L., Cavraro F., Pranovi F., Franco A., Franzoi P. (2016) Can the Effects of Anthropogenic Pressures and Environmental Variability on Nekton Fauna Be Detected in Fishery Data? Insights from the Monitoring of the Artisanal Fishery Within the Venice Lagoon. Estuaries and Coasts. 39 (4) :1164-1182

ainsi permis de mettre en évidence un effet de la lagune sur la structure de ces communautés (18% de la variabilité) avec un effet temporel certe limité (2% de la variabilité) mais relativement marqué par des captures au printemps avec l'arrivée d'espèces marines migrantes telles que *Sparus aurata*, *Liza ramada* et *Solea solea*. L'occurrence et la diversité des poissons dans les habitats lagunaires seraient donc fortement influencée par la saisonnalité du recrutement, la dynamique des populations et les schémas de migration comme cela a pu être démontré dans des études antérieures[114-115-116-117].

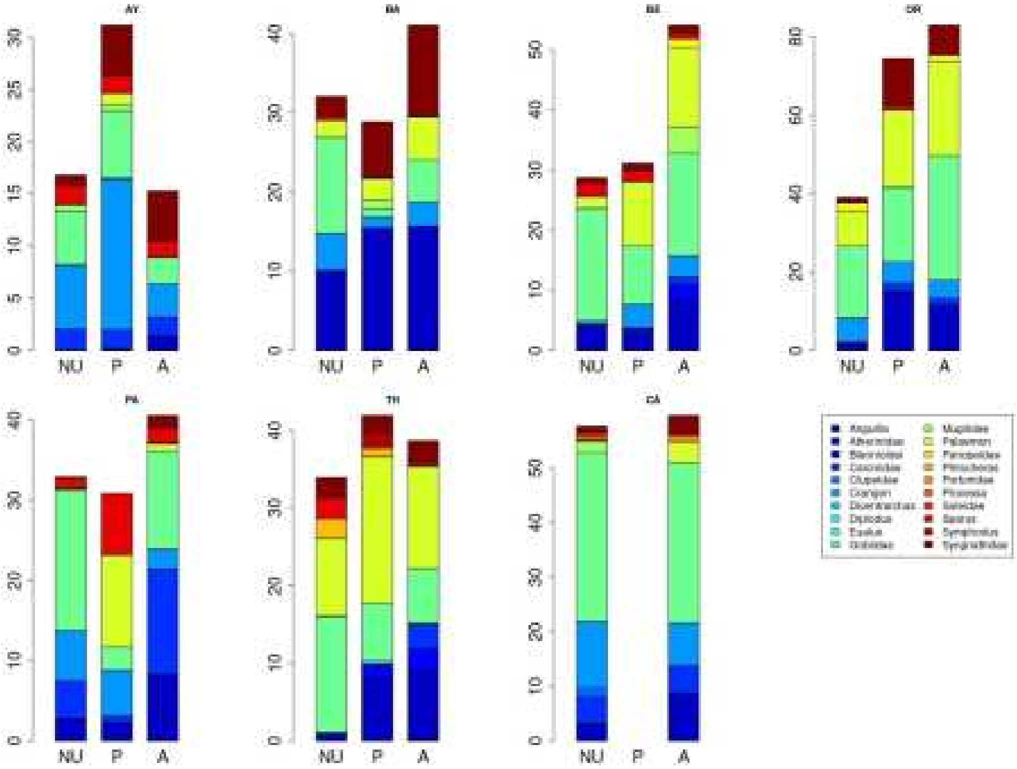


Figure 13: Distribution en abondance (effectifs) des taxons au sein de chaque lagune (AY pour Ayrolle, BA pour Bages-Sigean, BE pour Berre, OR pour Or, PA pour Palavasien, TH pour Thau et CA pour Canet), par couverture végétale dominante (N pour sédiment nu, P pour Phanérogames et A pour Macro-algues). Issu de Ouisse et al. (2023)[118]

---

[114] Franco A., Franzoi P., Malavasi S., Riccato F., Torricelli P., Mainardi D. (2006) Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science. 66: 67–83.

[115] Gordo L., Cabral H. (2001) The fish assemblage structure of a hydrologically altered coastal lagoon: The Óbidos lagoon (Portugal). Hydrobiologia. 459: 125–133. https://doi.org/10.1023/A:1012510608231

[116] Iotti M., Darnaude A. M., Bouriat A., Ouisse V. (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries and Coasts. Estuaries And Coasts. 46(1), 198-226.

[117] Mainardi D., Fiorin R., Franco A., Franzoi P., Granzotto A., Malavasi S., Pranovi F., Riccato F., Zucchetta M., Torricelli P. (2004). Seasonal distribution of fish fauna in the Venice Lagoon shallow waters: preliminary results. In: Campostrini, P. (Ed.), Scientific Research and Safeguarding of Venice, Corila Research: Program 2002 Results. Multigraf, Venezia, pp. 437–447.

[118] Ouisse V., Aliaume C., Amilhat E., Badts V., Bourdeix J-H., Cheret I., Cimiterra N., Darnaude A., Derolez V., Faliex E., Jadaud A., Laugier T., Metral L., Millot J., Motte M., Nicolas D., Orozco L., Schull Q., Simier M., Simon G., Vaz S., Villeneuve R., Violette H., Certain G. (2023) Développement d'un indicateur poissons en lagune adapté au contexte

Rôle des espèces ingénieures dans la régulation des flux de matière

La quantification du rôle des communautés benthiques dans la régulation des flux de matière a fait l'objet de quatre projets successifs. Tous se placent dans un contexte de restauration des milieux lagunaires méditerranéens vis-à-vis de l'eutrophisation (voir partie 3.4) où le compartiment benthique et en particulier les macrophytes pouvaient jouer un rôle majeur dans la régulation du relargage sédimentaire d'azote et de phosphore. Les projets RESTOLAG (Restauration des écosystèmes lagunaires : évaluation du rôle du sédiment et des herbiers à phanérogames, 2012-2013) puis DEPART (DEvenir du Phosphore et de l'Azote dans un contexte de ResTauration des milieux lagunaires méditerranéens, 2013-2014) avaient pour objectif d'évaluer la cinétique de transfert de l'azote et du phosphore entre le sédiment et la colonne d'eau en s'attachant spécifiquement à l'influence de la présence d'herbier de zostères. Les résultats obtenus en laboratoire (incubation de carottes sédimentaires dans des conditions contrôlées) ont confirmé le rôle central des herbiers dans la régulation des flux d'azote et de phosphore. Ces plantes marines ainsi que l'ensemble des organismes associés limitent le relargage d'azote et de phosphore du compartiment benthique vers la colonne d'eau. En présence d'herbier, le compartiment benthique apparaît même comme un puit d'azote et de phosphore au printemps. Bien que ces plantes favorisent la sédimentation et l'accumulation de matière organique dans les sédiments, elles favorisent d'une part la reminéralisation de cette matière *via* les communautés bactériennes associées et utilisent directement d'autre part cette source d'azote et de phosphore limitant ainsi le relargage sédimentaire dans la colonne d'eau. Les stocks sédimentaires d'azote et de phosphore ainsi que la température variable au cours de la saison apparaissent également comme des sources de variabilité des flux benthiques. Quelques auteurs décrivent que le rôle des phanérogames marines dans la régulation de matière peut également varier avec l'âge de l'herbier[119]. Cette dimension est rarement prise en compte dans les projets. J'ai eu la possibilité d'aborder cette question dans le cadre du projet MARHA (2018-2025) dont j'ai coordonné le WP "Fonctionnalité des herbiers". Sur 4 sites (Dinard, Golfe du Morbihan, Arcachon et Sète) répartis le long de la façade maritime française (Figure 3), nous avons quantifié les flux de matière (azote, phosphore et carbone) dans des herbiers de *Zostera marina* et *Zostera noltei* au niveau (1) du cœur d'herbier, (2) de la périphérie et (3) en dehors de l'herbier. Les résultats sont en cours de valorisation dans le cadre du Post-Doctorat de É. Lacoste (2022-2024).

Pour aller plus loin, j'ai étendu cette compréhension du rôle dans la régulation des flux benthiques à d'autres communautés benthiques structurantes. Dans le cadre du projet MARES2, nous avons étudié six communautés benthiques caractéristiques des différents stades du processus d'oligotrophisation (voir partie 3.4): trois communautés appartenant au bassin des macro-algues opportunistes (*Ulva rigida*, *Gracilaria sp.* et *Chaetomorpha aerea*) et trois communautés appartenant au bassin des espèces pérennes (*Zostera marina*, *Zostera noltei* et *Halopytis incurva*). Les flux benthiques d'oxygène, de carbone, d'azote et de phosphore des différentes communautés ont été estimés à partir d'incubations *in situ* (enceintes benthiques). Dans un premier temps, nos résultats ont permis de mettre en évidence des flux benthiques plus importants pour les espèces éphémères, quels que soient la saison et l'élément suivi (Figure 14). En effet, le métabolisme et les demandes en

---

français. Rapport final - Projet INPOLAG. 71p + Annexes

[119] Barrón C., Duarte C., Frankignoulle M., Borges A. (2006) Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (Posidonia oceanica) meadow. Estuaries and Coasts. 29(3): 417–426

azote et en phosphore de ces espèces sont souvent plus importants que les espèces pérennes. Chacune des communautés étudiées, de part son métabolisme, contribue ainsi à l'utilisation de l'azote et du phosphore relargué dans des proportions variées. Il semble ainsi possible de dégager le rôle essentiel joué par les macrophytes dans la régulation des flux de matières issues du compartiment benthique. Les mesures réalisées à l'échelle des communautés benthiques soulignent l'utilisation, quelle que soit la communauté, de l'azote et du phosphore issus de la reminéralisation bactérienne dans les sédiments. Cela se ferait soit à proximité du sédiment pour les macro-algues, soit directement dans le sédiment en association avec la communauté bactérienne dans le cas des phanérogames marines. De manière fonctionnelle, les macrophytes limiteraient ainsi le relargage sédimentaire et donc la disponibilité de nutriment pour le phytoplancton, contribuant activement au processus de restauration des lagunes méditerranéennes vis-à-vis de l'eutrophisation.

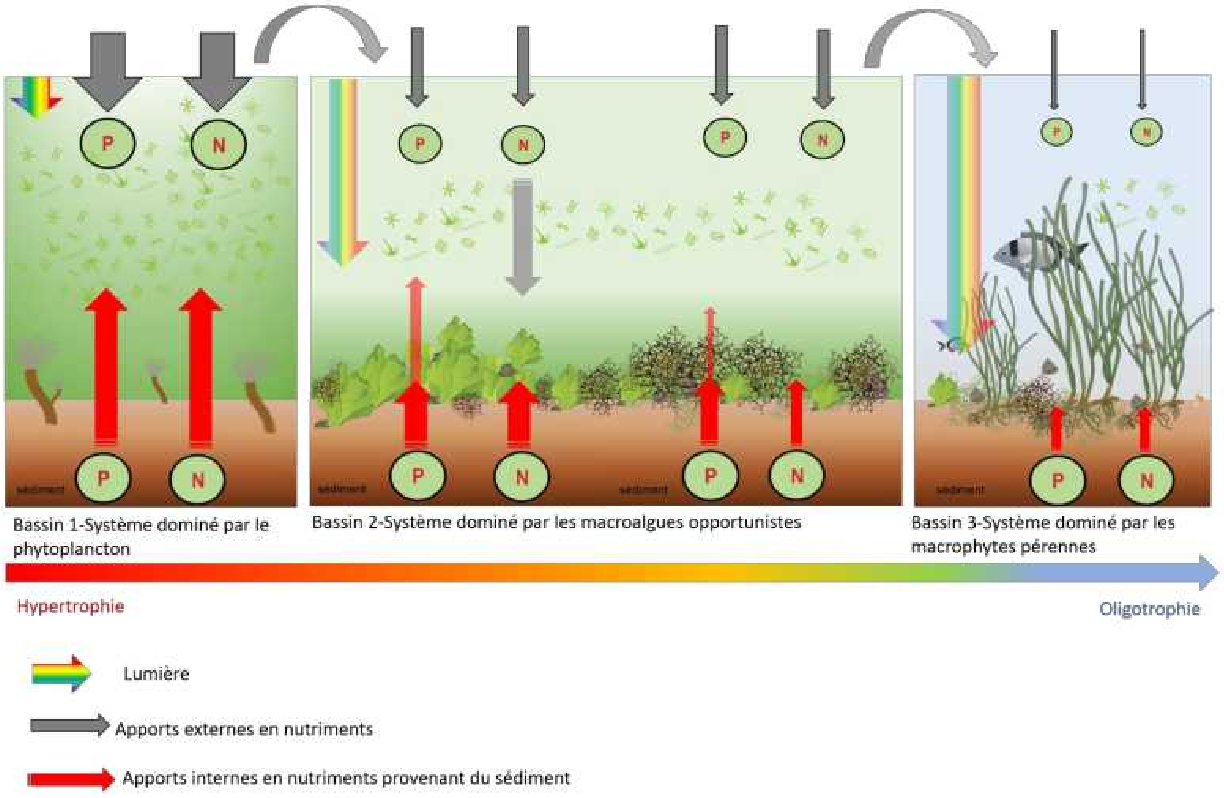


Figure 14: Représentation de l'impact de la réduction des apports en nutriments sur le changement au sein des producteurs primaires et du rôle des communautés sur les flux d'azote et de phosphore. Issue de Le Fur (2018)[120].

La quantification des processus benthiques est donc complexe. Elle est basée principalement sur des mesures *in situ* (projet MARHA et MARES2 par exemple) ou *ex situ* (projets RESTOLAG et DEPART par exemple) acquises dans le cadre de campagnes ponctuelles dans le temps et dans l'espace. Ces résultats sont aujourd'hui à la base de toutes interprétations et raisonnement scientifique. Pourtant, les processus benthiques impliqués dépendent d'une part des espèces présentes (macrophyte, macrofaune, bactéries associées) et d'autre part des conditions

---

[120] Le Fur Ines (2018). Rôle des macrophytes dans la restauration des milieux lagunaires : successions écologiques. Université de Montpellier. 210p

environnementales naturelles et anthropiques (lumière, température, disponibilité en oxygène…), deux composantes extrêmement variables en milieu côtier à petite et grande échelle. Parmi les méthodes couramment utilisées, les enceintes benthiques ont l'avantage de perturber *a minima* le milieu permettant ainsi de quantifier des flux benthiques dans des conditions naturelles de température, de lumière, de pression et de concentrations en nutriments (azote et phosphore en particulier). En travaillant à l'échelle de l'habitat (intégration des organismes dans leur environnement), elles permettent également d'intégrer les interactions entre les organismes comme la facilitation de l'assimilation due à la présence de deux organismes différents par exemple[121]. L'emprise spatiale des mesures est cependant relativement limitée (rarement supérieure à 0,7 m²) mais cet inconvénient peut être compensé par le déploiement de plusieurs enceintes. En revanche, cette méthode ne permet pas d'étudier les variations temporelles à petite échelle (intra-journalière y compris la nuit et inter-journalière selon les conditions climatiques) des flux benthiques. En effet, cette méthode *in situ*, par manque d'automatisation, nécessite l'intervention de plongeurs en milieu subtidal pour la mise en place, la récupération du matériel mais surtout pour effectuer des prélèvements réguliers (toutes les 1 à 2 heures environ) d'échantillons à l'intérieur de l'enceinte afin d'estimer les flux de carbone, d'oxygène et de nutriments à différents moments de la journée d'une part et d'autre part afin de renouveler l'eau entre deux incubations pour rester relativement proche des conditions environnementales (oxygène, pH, concentration en nutriment). Ces contraintes techniques ont ainsi largement limité le nombre de données disponibles, en particulier la nuit ou dans des conditions climatiques contrastées (vent, pluie, courant...). Dans ce contexte, j'ai coordonné à partir de 2016 le projet CHAMAUT (CHAMbres benthiques AUTomatiques, 2016-2018) qui avait pour objectif de développer des enceintes automatiques pilotant des instruments déjà existants ou en cours de développement comme les analyseurs CHEMINI (CHemical MIniaturised aNalIzers) ou les préleveurs automatiques. Couplé à un système de renouvellement d'eau, l'ensemble de ce matériel haute-fréquence pourrait ainsi permettre de répéter des mesures dans le temps (incubations successives) et ainsi d'appréhender la variation temporelle à petite échelle (jour/nuit, conditions climatiques contrastées) des flux benthiques *via* l'utilisation de système autonome.

De manière pratique, cette nouvelle station de fond, autonome pendant 48h, pilote aujourd'hui un ensemble d'outils (Figure 15) permettant de répliquer dans le temps, des mesures de flux de matière entre le compartiment benthique et la colonne d'eau, dans des conditions jusqu'à là non accessibles (nuit, période de tempête…). Issu d'une collaboration interdisciplinaire, ce nouvel outil va permettre dans un futur proche de lever un verrou scientifique majeur. Il a déjà été déployé dans le cadre d'un suivi mensuel sur un herbier de *Zostera noltei* dans la lagune de Thau. Entre janvier 2021 et février 2022, les données mettent en évidence les fluctuations des flux de carbone et d'oxygène sur 48h (Figure 16 pour exemple) qu'il faudra intégrer dans la quantification du rôle fonctionnel des habitats benthiques.

---

[121] Risgaard-Petersen N., Ottosen L. D. M. (2000) Nitrogen cycling in two temperate Zostera marina beds: seasonal variation. Marine Ecology Progress Series. 198:93-107

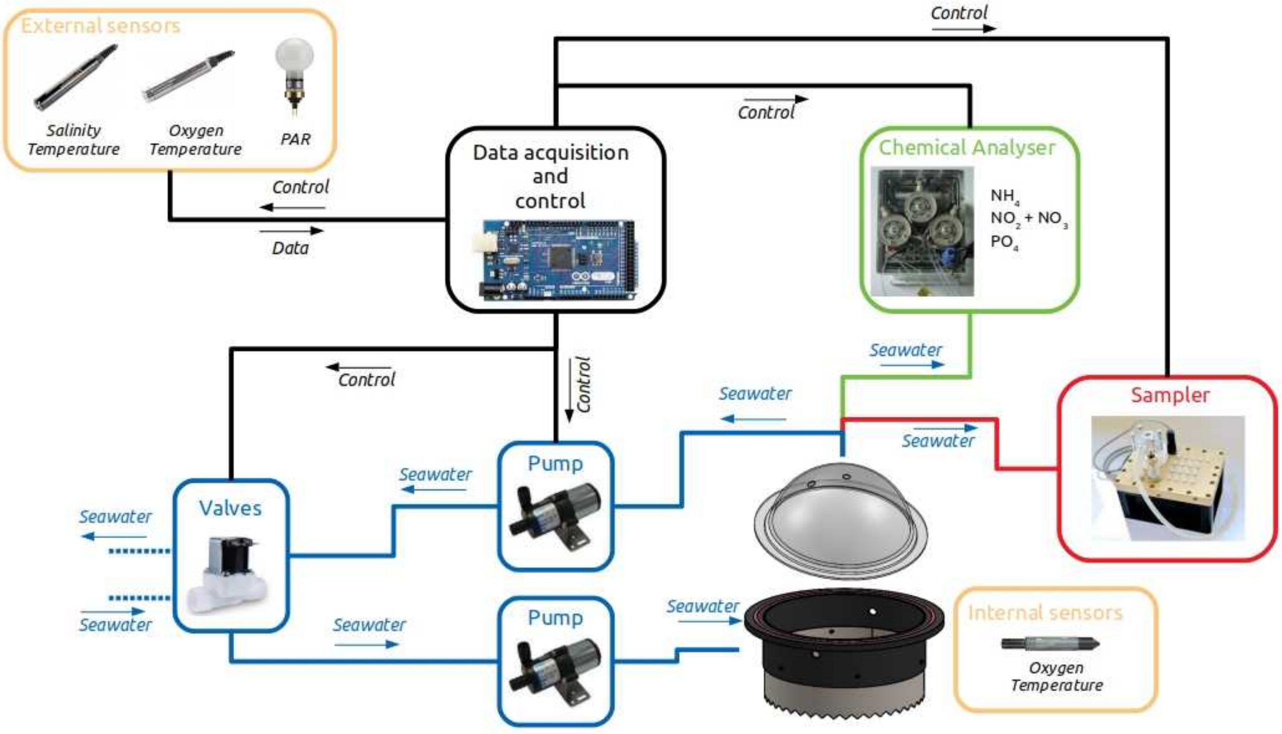


Figure 15: Description schématique de la chambre benthique autonome in situ. La synchronisation et le stockage des données sont effectués par le microcontrôleur. Pendant la période d'incubation, l'eau de mer (en bleu) est continuellement homogénéisée dans la chambre fermée par deux pompes de circulation. Les électrovannes sont ouvertes pour renouveler l'eau dans le système pendant la période de rinçage (lignes bleues en pointillés). En fonction des paramètres à mesurer, la chambre autonome in situ peut être couplée à un échantillonneur d'eau autonome in situ (en rouge) et à un analyseur chimique in situ (en vert), tandis que des capteurs internes et externes effectuent des mesures en continu à l'intérieur et à l'extérieur de la chambre (en jaune). Les flèches indiquent la direction de la communication des informations (en noir) ou la direction du flux d'eau de mer (en bleu). Issue de Ouisse et al. (en préparation)[122].

---

[122] Ouisse V., Cotty C., Bellamy E., Beriet P., Cimiterra N., Coail J-Y., Davy R., Fortune M., Foucault E., Hocdé R., Le Floc'h E., Le Piver D., Messiaen G., Munaron D., Parin D., Richard M., Rigaud S., Régis J., Rousseaux P., Stieglitz T.C. (en préparation) High-frequency multi-day monitoring of biogeochemical fluxes in coastal ecosystems with a new autonomous benthic chamber.

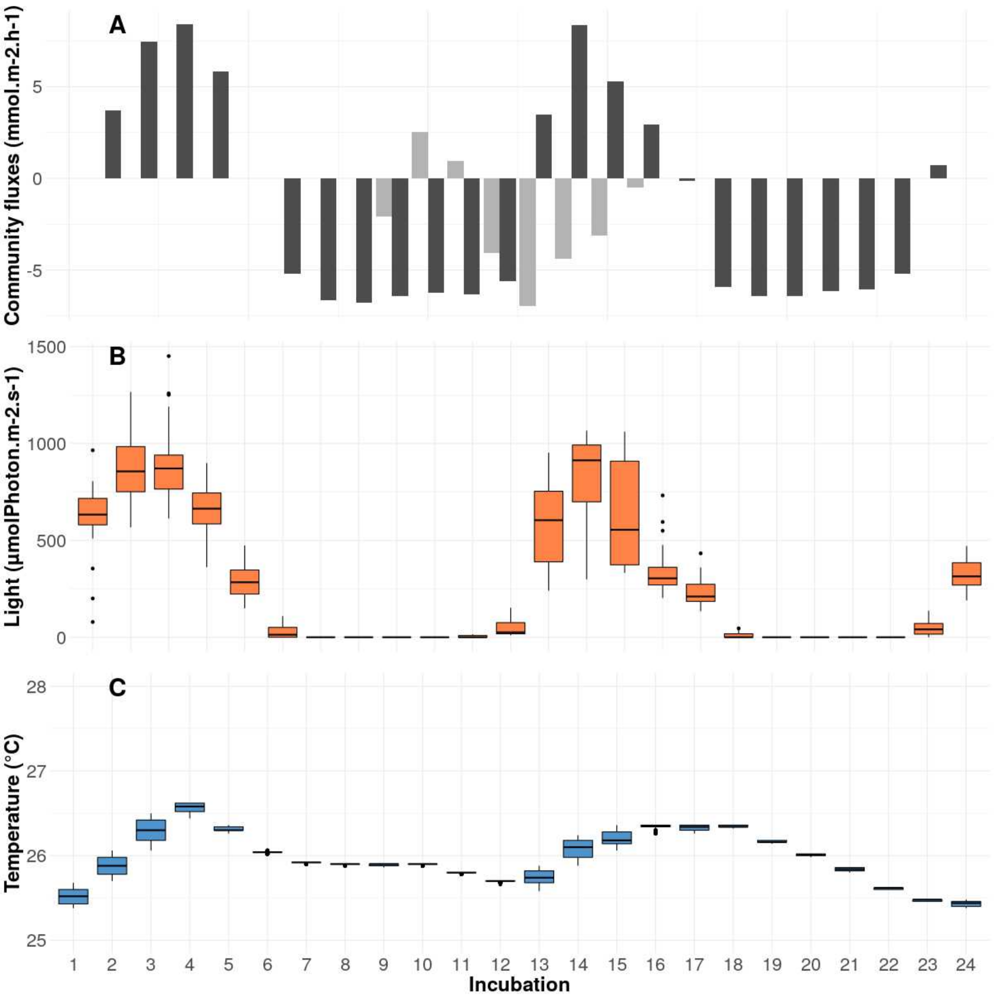


Figure 16: (A) Flux d'oxygène (gris foncé) et de carbone (gris clair) en mmol.m-2.h-1, (B) PAR en en µmolPhoton.m-2.s-1) et (C) température en °C à l'intérieur de la chambre benthique en juillet 2021. Issue de Ouisse et al. (en préparation)[123].

---

[123] Ouisse V., Cotty C., Bellamy E., Beriet P., Cimiterra N., Coail J-Y., Davy R., Fortune M., Foucault E., Hocdé R., Le Floc'h E., Le Piver D., Messiaen G., Munaron D., Parin D., Richard M., Rigaud S., Régis J., Rousseaux P., Stieglitz T.C. (en préparation) High-frequency multi-day monitoring of biogeochemical fluxes in coastal ecosystems with a new autonomous benthic chamber.

4. PERSPECTIVES DE RECHERCHE

Le bilan présenté dans la partie 3 résume ma dynamique de recherche passée autour de la compréhension de la dynamique et du rôle fonctionnel des espèces ingénieures dans des systèmes côtiers ou littoraux anthropisés. Au delà des résultats, ces projets ont mis en évidence des perspectives de recherche dans cette thématique sur lesquelles je souhaiterai aujourd'hui m'impliquer. Mes projets de recherche futurs s'inscrivent donc en partie dans la continuité des actions menées mais viendront également s'ancrer davantage dans le contexte du changement climatique pour lequel le groupe intergouvernemental d'experts sur l'évolution du climat (GIEC) a prédit une augmentation significative de la température de l'océan, jusqu'à 2-4°C d'ici à 2100, ainsi que des changements majeurs dans le rayonnement UV-B, les précipitations, les tempêtes et la salinité[124]. A l'échelle mondiale, cela se traduit par un réchauffement de la masse d'eau, une acidification des océans et l'élévation du niveau des mers. Cependant, certains de ces changements se manifestent également de façon soudaine et relativement courte lors d'évènements climatiques extrêmes (ECEs[125]) comme par exemple les vagues de chaleur ou vagues de froid qui peuvent durer de quelques jours à quelques mois, des épisodes d'anoxie (généralement liés aux vagues de chaleur), des périodes de sécheresse et de fortes crues ou encore des tempêtes qui s'amplifient[126-127]. La zone littorale est quant-à elle déjà naturellement soumise à de fortes fluctuations locales et saisonnières, ainsi qu'à des pressions grandissantes d'origine anthropique[128-129]. C'est en particulier le cas des lagunes méditerranéennes qui sont soumises à de nombreuses pressions liées à leurs usages (exploitations ostréicoles, pêche, tourisme) et au développement d'activités humaines sur leurs bassins versants[130-131]. Quelques études indiquent déjà que les milieux lagunaires sont particulièrement sensibles aux pressions, notamment lorsque d'autres facteurs de stress et perturbations causés par les ECEs interagissent[132-133]. Cependant, l'état des connaissances actuelles ne permet pas de prédire quel sera l'impact du changement climatique

---

[124] IPCC (2014) Climate Change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working group II to the fifth assessment report of the Intergovernemental Panel on Climate Change. Cambridge university Press, Cambridge, United Kingdom and New York, NY, USA

[125] Easterling D. R., Meehl G. A., Parmesan C., Changnon S. A., Karl T. R., Mearns L. O. (2000) Climate extremes: observations, modeling, and impacts. Science. 289:2068–2074. doi: 10.1126/science.289.5487.2068

[126] Hobday A. J., Oliver E. C. J., Sen Gupta A., Benthuysen J. A., Burrows M. T., Donat M. G., Holbrook N. J., Moore P. J., Thomsen M. S., Wernberg T., Smale D. A. (2018) Categorizing and naming marine heatwaves. Oceanography 31:162-173. doi: https://doi.org/10.5670/oceanog.2018.205

[127] Jentsch A., Beierkuhnlein C. (2008) Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. Comptes Rendus Geoscience. 340:621–628. doi: 10.1016/j.crte.2008.07.002

[128] Halpern B. S., Walbridge S., Selkoe K. A., Kappel C. V., Micheli F., D'Agrosa C., Bruno J. F., Casey K. S., Ebert C., Fox H. E., Fujita R., Heinemann D., Lenihan H. S., Madin E. M. P., Perry M. T., Selig E. R., Spalding M., Steneck R, Watson R. (2008) A global map of human impact on marine ecosystems. Science. 319:948–52. doi: 10.1126/science.1149345

[129] Lloret J., Marín A., Marín-Guirao L. (2008) Is coastal lagoon eutrophication likely to be aggravated by global climate change? Estuarine, Coastal and Shelf Science. 78:403–412. doi: 10.1016/j.ecss.2008.01.003

[130] de Wit R., 2011. Chapiter 2. Biodiversity of coastal lagoon ecosystems and their vulnerability to global change Ecosystems Biodiversity : 29–40.

[131] Munaron D., Tapie N., Budzinski H., Andral B., Gonzalez J-L. (2012) Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: results from a pilot survey using passive samplers. Estuarine, Coastal and Shelf Science. 114:82–92

[132] de Wit R., 2011. Chapiter 2. Biodiversity of coastal lagoon ecosystems and their vulnerability to global change Ecosystems Biodiversity : 29–40.

et comment cela pourrait modifier la structure et le fonctionnement des communautés biologiques associées aux habitats benthiques, d'une part, et leur rôle écologique et socio-économique, d'autre part.

Dans ce contexte, mes travaux de recherche actuels et futurs visent particulièrement à (1) développer des outils réactifs permettant d'anticiper les changements structurels et fonctionnels des habitats/communautés benthiques et à (2) dissocier les effets du changement climatique des effets des pressions anthropiques locales/régionales. Fort de l'expérience acquise au travers de mes prises de responsabilités passées, ils sont ou seront évidemment construits autour de projet de formation et d'encadrement (thèse, post-doctorat) en collaboration avec d'autres scientifiques dont les compétences complémentaires apportent une plus-value à chacun des projets. Les idées et projets présentés ci-dessous ont tout juste commencé ou sont en cours de construction.

4.1. Détecter des signaux précurseurs de basculement pour anticiper les changements

Cet axe de travail sera tout d'abord basé sur le renforcement des observatoires existants, en particulier, les observatoires C2ZO (température et salinité) et BENTHOBS (macrofaune benthique) ont débuté respectivement en 2022 et 2021. Tous deux ont pour objectif de constituer des séries temporelles à long terme permettant de mieux interpréter les changements structurels et fonctionnels observés dans les environnements côtiers et littoraux. L'analyse des données de température dans les milieux lagunaires méditerranéens (C2ZO) permettra de caractériser la dynamique à long terme de la température d'une part et de caractériser les Évènements Climatiques Extrêmes (ECEs) aussi bien en termes d'intensité et de fréquence d'autre part. Ces données, ainsi que celles collectées dans les autres observatoires existants portant sur les conditions environnementales (DCE par exemple), formeront ainsi une base solide pour interpréter les changements de communautés aussi bien benthique (BENTHOBS) que planctonique (PHYTOBS) dans les milieux lagunaires. Au delà de l'aspect scientifique sur lequel l'acquisition de données et la bancarisation sont les principales actions à mener, mon activité à court terme vise donc à consolider ces deux observatoires tant en termes financier avec la recherche de financements réguliers, qu'en termes humain avec une demande de recrutement technique.

En terme de gestion des milieux lagunaires, l'évaluation actuelle de l'état des masses d'eau dans le cadre de la Directive Cadre sur l'Eau (DCE) est basée sur des observations de terrain (reconnaissance morphologique, diversité et abondance des espèces) selon une stratégie spatiale et temporelle définie pour 4 compartiments : le phytoplancton, les poissons, la macrofaune et les macrophytes. Ces inventaires sont réalisés régulièrement afin de décrire les peuplements et de calculer des indicateurs utilisés dans le cadre de plans de gestion pour évaluer l'état des masses d'eau comme dans le cadre de la DCE. L'interprétation de ces indicateurs comparables à l'échelle européenne a permis de mettre en place des politiques de gestion des masses d'eau et de leurs

---

133 Lloret J., Marín A., Marín-Guirao L. (2008) Is coastal lagoon eutrophication likely to be aggravated by global climate change? Estuarine, Coastal and Shelf Science. 78:403–412. doi: 10.1016/j.ecss.2008.01.003

bassins versants conduisant dans de nombreux cas à des dynamiques de restauration des lagunes[134-135-136]. Ces outils sont standardisés et reproductibles mais, dans un contexte d'augmentation de la fréquence et de l'intensité des ECEs et plus généralement de changement climatique, il apparaît indispensable d'être en mesure (1) de détecter les espèces rares et/ou nouvelles adaptées à ces nouvelles conditions environnementales de manière précoce et (2) d'évaluer l'état physiologique des organismes qui pourrait être un indicateur de santé des lagunes avant leur déclin. Dans ce contexte, je souhaite développer des outils complémentaires, basés sur des marqueurs précoces, qui permettraient d'anticiper les basculements de ces écosystèmes. Je contribuerai ainsi à une meilleure compréhension de la dynamique future de ces écosystèmes et à la mise en place éventuelle de mesures de gestion préventives.

Apport de l'ADNe pour anticiper les changements de communautés benthiques

Parmi les approches aujourd'hui disponibles, les méthodes utilisant l'ADN environnemental (ADNe) comme le metabarcoding, constituent des approches intégratives permettant de décrire la biodiversité au sein de différents compartiments (e.g. phytoplancton, bactéries, poissons) à partir d'un même échantillon environnemental. Cette méthode représente un atout majeur pour la détection fine d'espèces au sein d'un même groupe et l'identification de nouvelles espèces dans le milieu. L'utilisation du metabarcoding est plutôt bien développée pour les micro-organismes et les métazoaires[137-138]. Dans les lagunes méditerranéennes, des protocoles adaptés existent ou sont en cours de développement pour le phytoplancton (e.g. projet ROME de l'IFREMER) et les poissons (projet en cours porté par le Laboratoire d'Ecologie Alpine – Univ. Grenoble). En revanche, il n'existe à notre connaissance pas de consensus sur ces approches pour les macrophytes marins alors que ce compartiment biologique pourrait être directement impacté par des vagues de chaleurs et plus largement par les effets du changement climatique en lagune. Outre ce lien direct, il est aujourd'hui également admis que la composition du microbiome (e.g. bactéries, champignons, protistes) associé aux macrophytes est dynamique et liée à l'état de santé de l'hôte. En s'appuyant sur ces hypothèses et en collaboration avec A. Gobet (CR Ifremer, Sète), nous construisons actuellement un projet de recherche (MACDNA, Anticiper les changements de communautés de macrophytes: apport de l'ADN environnemental comme outil complémentaire, 2024-2027) incluant le co-encadrement d'un doctorat pour [Obj. 1] évaluer la performance d'outils moléculaires pour identifier les macrophytes, [Obj. 2] caractériser le microbiome associé à l'état physiologique des macrophytes et [Obj. 3] optimiser la stratégie d'échantillonnage *in situ* et les outils de capture de l'ADNe pour les

---

134 Derolez V., Bec B., Munaron D., Fiandrino A., Pete R., Simier M., Souchu P., Laugier T., Aliaume C., Malet N. (2019) Recovery trajectories following the reduction of urban nutrient inputs along the eutrophication gradient in French Mediterranean lagoons. Ocean & Coastal Management 171: 1–10. https://doi.org/10.1016/j.ocecoaman.2019.01.012.

135 Le Fur I., de Wit R., Plus M., Oheix J., Derolez V., Simier M., Malet N., Ouisse V. (2019) Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. Marine Ecology Progress Series. 608, 13-32. Publisher's official version : https://doi.org/10.3354/meps12814, Open Access version : https://archimer.ifremer.fr/doc/00474/58555/

136 Leruste A., Malet N., Munaron D., Derolez V., Hatey E., Collos Y., de Wit R., Bec B. (2016) First steps of ecological restoration in Mediterranean lagoons: Shifts in phytoplankton communities. Estuarine, Coastal and Shelf Science. 180: 190–203.

137 Taberlet P., Bonin A., Zinger L., Coissac E. (2018) Environmental DNA: For biodiversity research and monitoring. Oxford University Press.

138 Zinger L., Gobet A., Pommier T. (2012) Two decades of describing the unseen majority of aquatic microbial diversity. Molecular Ecology. 21(8), 1878–1896. https://doi.org/10.1111/j.1365-294X.2011.05362.x

macrophytes dans les lagunes méditerranéennes. Outre la mise à disposition d'un nouvel outil réactif et complémentaire, il viendra compléter les outils basés sur l'ADNe déjà développés ou en cours de développement sur les poissons ou le phytoplancton dans les lagunes méditerranéennes. A terme, cette démarche d'utilisation de l'ADNe pour l'évaluation biologique des écosystèmes aquatiques dans un contexte de gestion des milieux viendra enfin en complément des travaux menés en eau douce[139].

L'expérimentation pour déterminer les seuils de basculement

Parmi les habitats identifiés en milieu lagunaire (voir partie 3.3), ceux formés par les herbiers de phanérogames (ou angiospermes) marines jouent un rôle écologique particulièrement important par leur fonctionnement. Les herbiers marins de manière générale contribuent largement à la séquestration du carbone[140-141], au cycle des nutriments[142] et interagissent avec d'autres écosystèmes clés tels que les mangroves ou les récifs coralliens dans les systèmes tropicaux[143-144], ou d'autres espèces de macrophytes dans les systèmes tempérés[145-146]. De plus, ils sont couramment utilisés comme bio-indicateurs du bon état écologique des masses d'eau et font l'objet de nombreux suivis dans le cadre de la Directive Cadre sur l'Eau (DCE) depuis sa mise en place en Europe en 2000 (WFD, 2000/60/EC). Il a été établi que, dans certains cas, ces plantes marines peuvent modifier leurs traits morphologiques et physiologiques à un certain niveau de stress[147-148-149]. En tant qu'ingénieurs de l'écosystème, ils peuvent également agir directement sur l'effet d'un stress et l'atténuer pour

---

[139] Pawlowski J., Apothéloz-Perret-Gentil L., Mächler E., Altermatt F. (2020). Utilisations de l'ADN environnemental pour la surveillance et l'évaluation biologiques des écosystèmes aquatiques. Directives. Office fédéral de l'environnement, Berne. Connaissance de l'environnement n°2010 : 80p.

[140] Fourqurean J. W., Duarte C. M., Kennedy H., Marbà N., Holmer M., Mateo M. A., Apostolaki E. T., Kendrick G. A., Krause-Jensen D., McGlathery K. J., Serrano O. (2012) Seagrass ecosystems as a globally significant carbon stock. Natural Geoscience. 5:505–509. doi: 10.1038/ngeo1477

[141] Macreadie P. I., Baird M. E., Trevathan-Tackett S. M., Larkum A. W. D., Ralph P. J. (2014) Quantifying and modelling the carbon sequestration capacity of seagrass meadows - A critical assessment. Marine Pollution Bulletin. 83:430–439. doi: 10.1016/j.marpolbul.2013.07.038

[142] Hemminga M., Harrison P. G., Van Lent F. (1991) The balance of nutrient losses and gains in seagrass meadows. Marine Ecology Progress Series. 71:85–96. doi: 10.3354/meps071085

[143] Gillis L. G., Bouma T. J., Cathalot C., Ziegler A. D., Herman P. M. (2015) Particulate Matter in Mangrove Forests and Seagrass Beds as a Nitrogen Source in Tropical Coastal Ecosystems. 47:286–291. doi: 10.1111/btp.12220

[144] Lai S., Gillis L. G., Mueller C., Bouma T. J., Guest J., Last K. S., Ziegler A. D. Todd P. (2013) First experimental evidence of corals feeding on seagrass matter. Coral Reefs. 32:1061–1064. doi: 10.1007/s00338-013-1062-9

[145] Hyndes G. A., Nagelkerken I., Mcleod R. J., Connolly R. M., Lavery P. S., Vanderklift M. A. (2014) Mechanisms and ecological role of carbon transfer within coasta- Mémoire d'Habilitation à Diriger des Recherches -l seascapes. Biological Reviews. 89:232–254. doi: 10.1111/brv.12055

[146] Le Fur I., de Wit R., Plus M., Oheix J., Derolez V., Simier M., Malet N., Ouisse V. (2019) Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. Marine Ecology Progress Series. 608, 13-32. Publisher's official version : https://doi.org/10.3354/meps12814, Open Access version : https://archimer.ifremer.fr/doc/00474/58555/

[147] Cabaço S., Machás R., Santos R. (2009) Individual and population plasticity of the seagrass Zostera noltii along a vertical intertidal gradient. Estuarine Coastal and Shelf Science. 82:301–308. doi: 10.1016/j.ecss.2009.01.020

[148] Peralta G. , Brun F. G., Hernández I., Vergara J. J., Pérez-Lloréns J. L. (2005) Morphometric variations as acclimation mechanisms in beds. Estuarine, Coastal and Shelf Science. 64:347–356. doi: 10.1016/j.ecss.2005.02.027

[149] Soissons L. M. , van Katwijk M. M., Peralta G., Brun F. G., Cardoso P. G., Grilo T. F., Ondiviela B., Recio M., Valle M., Garmendia J. M., Ganthy F., Auby I., Rigouin L., Godet L., Fournier J. (2018) Seasonal and latitudinal variation in seagrass mechanical traits across Europe: The influence of local nutrient status and morphometric plasticity. Limnology and Oceanography. 63:37–46. doi: 10.1002/lno.10611

augmenter leur résilience[150]. Toutefois, quand ce stress augmente et que leur capacité d'acclimatation diminue, les herbiers peuvent présenter un changement abrupt dans leur état au-delà d'une valeur seuil qui peut les faire passer à un état dit dégradé[151]. Il a été en effet démontré qu'en raison de leur diversité et de leur complexité, de nombreux écosystèmes benthiques de la zone littorale, y compris ceux formés par les plantes marines, peuvent suivre la théorie des états stables. Cette théorie décrit un risque d'effondrement rapide et abrupt avec un passage d'un état stable de référence vers un état stable alternatif dit dégradé[152-153-154] (Figure 17). Les mécanismes impliqués sont complexes et se manifestent lorsque le système atteint un point de basculement (ou un point de bifurcation). L'augmentation continue des perturbations externes réduit en effet la résilience du système jusqu'à ce point de basculement[155] (Figure 17) où, même une faible perturbation au-dessus du seuil critique (en terme d'intensité) peut faire basculer le système vers un état stable alternatif[156-157-158]. D'après cette théorie, nous pouvons supposer que l'effet des évènements climatiques extrêmes (ECEs) sur des organismes vivant en milieu stressé pourrait avoir des conséquences importantes non seulement sur l'état écologique du système, mais aussi sur sa résilience à long terme. Ce changement pourrait devenir critique notamment dans les zones d'interface de la zone littorale telles que les lagunes, déjà affectées par l'accroissement de leurs usages et des pressions anthropiques[159]. En termes d'évaluation de l'état de santé, cela pourrait également signifier un changement potentiel de l'état de référence du système et de son rôle écologique.

---

[150] Soissons LM, van Katwijk MM, Li B, Han Q., Ysebaert T., Herman P. M. J., Bouma T. J. (2019) Ecosystem engineering creates a new path to resilience in plants with contrasting growth strategies. Oecologia. 191:1015–1024. doi: 10.1007/s00442-019-04544-4

[151] Connell S. D., Fernandes M., Burnell O. W., Doubleday Z. A., Griffin K. J., Irving A. D., Leung J. Y. S., Owen S., Russell B. D., Falkenberg L. J. (2017) Testing for thresholds of ecosystem collapse in seagrass meadows? Conservation Biology. 1–12. doi: 10.1111/cobi.12951

[152] Scheffer M., Carpenter S., Foley J. A., Folke C., Walker B. (2001) Catastrophic shifts in ecosystems. Nature. 413: 591–596.

[153] Scheffer M., Carpenter S. R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution. 18:648–656. doi: 10.1016/j.tree.2003.09.002

[154] van Nes E. H., Scheffer M. (2007) Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. American Naturalist. 169:738–47. doi: 10.1086/516845

[155] van Nes E. H., Scheffer M. (2007) Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. American Naturalist. 169:738–47. doi: 10.1086/516845

[156] Chisholm R. A., Filotas E. (2009) Critical slowing down as an indicator of transitions in two-species models. Journal of Theoretical Biology. 257:142–9. doi: 10.1016/j.jtbi.2008.11.008

[157] Scheffer M., Carpenter S., Foley J. A., Folke C., Walker B. (2001) Catastrophic shifts in ecosystems. Nature. 413: 591–596.

[158] Scheffer M., Bascompte J., Brock W. A., Brovkin V., Carpenter S. R., Dakos V., Held H., van Nes E. H., Rietkerk M. Sugihara G. (2009) Early-warning signals for critical transitions. Nature. 461:53–9. doi: 10.1038/nature08227

[159] Lloret J., Marín A., Marín-Guirao L. (2008) Is coastal lagoon eutrophication likely to be aggravated by global climate change? Estuarine, Coastal and Shelf Science. 78:403–412. doi: 10.1016/j.ecss.2008.01.003

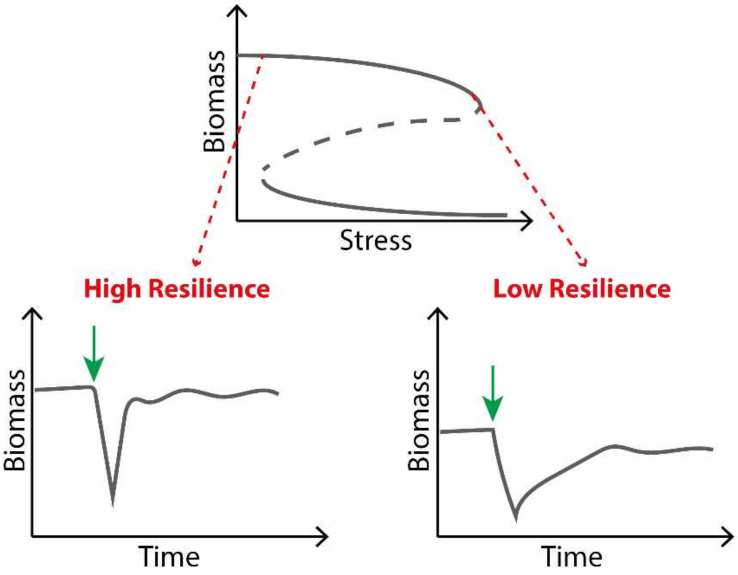


Figure 17: Représentation des deux états stables (lignes pleines sur le graphique du haut) d'un système représenté par sa biomasse le long d'un gradient de stress. À haute résilience, si une petite perturbation se produit (flèche verte), le système récupérera rapidement sa biomasse d'origine. À faible résilience, et près d'un point de bifurcation, si une petite perturbation se produit, il faudra plus de temps au système pour récupérer pour peut-être ne pas revenir à sa biomasse d'origine, c'est le phénomène de ralentissement critique (CSD). Au point de bifurcation, le système passera à un deuxième état stable. La ligne pointillée sur la figure du haut représente l'état instable entre deux états stables (lignes pleines). Figure adaptée d'après van Nes and Scheffer (2007)[160].

La deuxième phase du projet C2ZO (Effet des épisodes extrêmes en milieu méditerranéen stressé, 2022-2025) s'inscrit dans la quantification de la réponse d'espèces structurantes (phanérogames marines) face aux vagues de chaleur. Les processus impliqués dans les ECEs et en particulier lors de vagues de chaleur seront étudiés *via* une approche expérimentale. Parmi les hypothèses testées, les perturbations liées aux vagues de chaleur induiraient des changements morphologiques (plasticité phénotypique) et physiologiques des plantes (capacité photosynthétique, marqueurs de stress) qui dépendraient :

- de l'espèce de phanérogame marine (quatre espèces sont répertoriées dans les lagunes méditerranéennes mais leur capacité à supporter une augmentation de la température varierait largement)[161],
- des caractéristiques intrinsèques des vagues de chaleur (intensité, longueur, période de l'année), et
- de l'état initial de stress des phanérogames marines lié à un précédent stress (répétition de vagues de chaleur) ou à un niveau de stress existant naturellement dans le milieu (autres perturbations comme les contaminants chimiques).

---

[160] van Nes E. H., Scheffer M. (2007) Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. American Naturalist. 169:738–47. doi: 10.1086/516845

[161] Durreau A., Soissons L., Ouisse V. (2021) Effet des épisodes extrêmes en milieu méditerranéen stressé. Phase 1 : étude bibliographique et mise en place d'outils tests in situ. 65P + Annexes

Sur la base des projections du GIEC et des données acquises dans le cadre des différents observatoires décrits précédemment, nous explorons actuellement, à travers un doctorat que je co-encadre, la réponse de trois espèces de phanérogames marines (*Zostera noltei*, *Ruppia cirrhosa* et *Cymodocea nodosa*) à une vague de chaleur (trois intensités de température, +2°C, +4°C et +6°C par rapport au contrôle) au printemps et en été. Les premiers résultats sur la réponse morphologique sont en cours de traitement et font l'objet d'une nouvelle collaboration scientifique avec la station de Naples. L'utilisation de marqueurs complémentaires de stress comme les composés volatiles pourrait venir s'ajouter à ces analyses dans le futur. De nouvelles expérimentations sont prévues en 2024 pour évaluer l'impact de vagues de chaleur cumulées.

Cette approche expérimentale au laboratoire permet de contrôler une grande partie des facteurs physico-chimiques qui jouent sur la croissance de ces plantes marines (température, salinité, lumière, hydrodynamique). En revanche, il est relativement difficile d'appliquer ces approches au laboratoire en intégrant l'ensemble des organismes associés, en particulier dans le sédiment. Pourtant, leur prise en compte dans une expérimentation pourrait moduler la réponse des herbiers en tamponnant l'effet des vagues de chaleur (jeu d'interactions biotiques en particulier). L'expérimentation *in situ*, encore trop peu développée, représente à mon avis une approche indispensable pour étudier les effets du changement climatique sur les herbiers des lagunes méditerranéennes. Cela passe par le développement d'outil innovant. Fort de collaboration créées par le passée et mon expérience dans le développement d'enceintes benthiques autonomes projet CHAMAUT (CHAMbres benthiques AUTomatiques), je souhaite développer un système expérimental *in situ* permettant de contrôler la température et l'oxygène. De manière fonctionnelle, cette chambre expérimentale permettrait de contrôler la température (température « expérimentale ») à l'intérieur du mésocosme en fonction de la température extérieure (température « normale ») pendant une vingtaine de jours (Figure 18). Cette expérimentation serait menée dans un herbier peu profond potentiellement soumis aux vagues de chaleur futures.

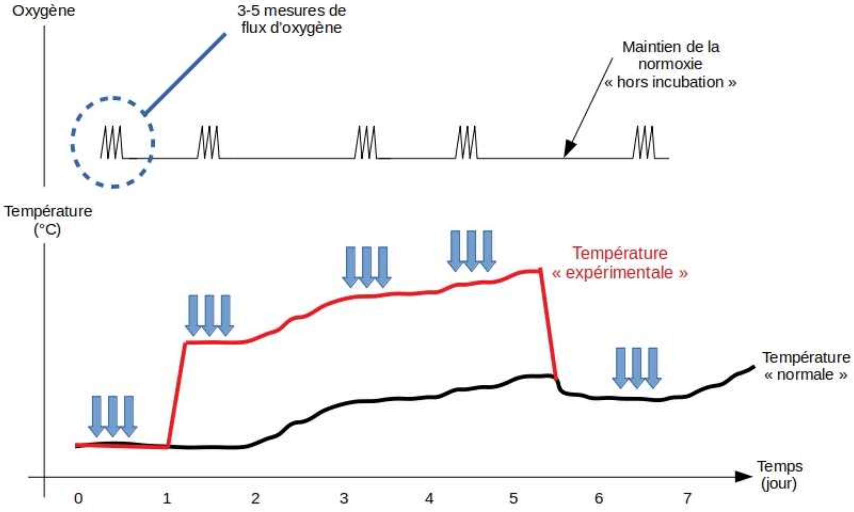


Figure 18: Représentation schématique du fonctionnement d'un système expérimental permettant de tester l'effet d'une élévation de température sur le fonctionnement d'une communauté benthique. Pour permettre de rester dans des conditions proches de celles rencontrées à l'extérieur du système, la concentration en oxygène se également régulée hormis pendant les périodes d'incubations indiquées par les flèches bleues.

Parmi les perspectives de recherche sur cette thématique, la question de l'effet des pressions cumulées pourrait également être abordée à moyen terme dans le cadre d'un futur projet Post-Doctoral (É. Lacoste, co-encadrement D. Munaron). Les milieux côtiers et littoraux et en particulier les lagunes méditerranéennes sont en effet largement exposés aux contaminations chimiques issues des bassins versants[162]. Si ces contaminants - notamment des pesticides - sont souvent retrouvés à des doses individuelles en dessous de leur norme de qualité environnementale, on ignore d'une part les effets cocktails (mélange de polluants) qui pourraient entraîner une sous-estimation du risque pour l'environnement[163] et d'autre part leur effets sur des organismes déjà stressés sous l'effet des évènements climatiques extrêmes.

L'analyse de l'ensemble de ces résultats et la sélection des variables d'intérêts (compromis entre la qualité de la réponse et de la facilité de la mesurée) permettra de définir des seuils et des signes précurseurs de basculement indispensables à la mise en place des politiques de gestion adaptées et réactives. En termes de gestion des milieux lagunaires, l'acquisition de connaissances fondamentales sur ces espèces dites de référence (terme lié à l'application de la DCE) conduira à la fois à une réflexion sur la définition de l'état de référence futur mais également au choix des indicateurs d'état utilisés aujourd'hui dans le cadre des différentes directives (DCE, DHFF). Enfin, ces résultats pourront être mis en perspectives des travaux menés sur le rôle des macrophytes dans la restauration des milieux lagunaires (projet MARES2, 2014-2018) durant lesquels le rôle fonctionnel des herbiers était décrit comme central dans la régulation des flux de matière à l'interface entre le compartiment benthique et la colonne d'eau en milieu lagunaire.

Implications des changements structurels des habitats benthiques sur leurs rôles fonctionnels en milieu côtier et littoral

La modification de la structure des habitats benthiques en réponse aux changements des conditions environnementales va avoir un impact sur la biodiversité associée et les flux de matière à l'intérieur du système. Derrière le terme « structure », j'entends ici à la fois la notion de structure physique de l'habitat dans l'espace et également la notion d'espèce structurante de l'habitat. Dans le premier cas, la structure 3D des habitats benthiques semble en effet être l'une des caractéristiques qui permet d'expliquer une partie des rôles fonctionnels assurés par ces habitats pour de nombreuses espèces (voir Partie 3.5). En effet, la rugosité de l'habitat, le nombre d'anfractuosités et leur taille sont autant de caractéristiques qui peuvent permettre de créer des espaces utilisés par des organismes pour se protéger face aux prédateurs. Cependant, leur description est complexe et représente aujourd'hui encore un verrou technique où seuls des indicateurs simples sont disponibles actuellement (taille, aspect…). La morphologie des macrophytes ou plus largement des habitats benthiques doit ainsi être mieux définie dans de futurs travaux comme cela est fait dans des milieux côtiers rocheux[164]. L'existence de méthodes aujourd'hui

---

[162] Munaron D., Tapie N., Budzinski H., Andral B., Gonzalez J-L. (2012) Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: results from a pilot survey using passive samplers. Estuarine, Coastal and Shelf Science. 114:82–92

[163] Munaron D., Mérigot B., Derolez V., Tapie N., Budzinski H., Fiandrino A. (2023). Evaluating pesticide mixture risks in French Mediterranean coastal lagoons waters . Science Of The Total Environment , 867, 161303 (15p.) . https://doi.org/10.1016/j.scitotenv.2022.161303

[164] Thiriet P., Cheminée A., Mangialajo L., Francour P. (2014) How 3D complexity of macrophyte-formed habitats affect the processes structuring fish assemblages within coastal temperate seascapes? In Underwater Seascapes, 185–199. Springer.

développées pour la caractérisation des habitats de substrats durs comme la photogrammétrie ouvrent des perspectives pour qualifier et quantifier le rôle structurel d'espèces clés voire d'habitats entiers. Cette méthode est déjà utilisée en milieu tropical ou bien sur des organismes rigides non mobiles (coraux en particulier)[165]. Elle est basée sur la photographie d'un objet puis sa reconstruction numérique à l'aide d'algorithmes. Cet objet numérisé pourrait permettre ensuite de calculer des métriques décrivant de manière plus complète la structure 3D des habitats benthiques en milieu côtier peu profond. Le développement de cette méthode dans les herbiers ou plus largement dans les habitats de substrat meuble couverts de macrophytes constitue un des axes de travail pour le futur. Au vue de la surface que recouvrent les macrophytes à l'échelle des lagunes méditerranéennes, cela pourrait permettre à termes de préciser leurs contributions à la valeur fonctionnelle globale de l'écosystème. Dans le deuxième cas, les changements d'espèces structurantes aura une conséquence certaine sur la régulation des flux de matière au sein du système (voir partie 3.5). Je projette donc de poursuivre la quantification de ces changements, à l'aide en particulier de méthodes innovantes développées dans le cadre de mes projets (voir Partie 3.5), afin de pouvoir à terme contribuer à la consolidation de modèles écosystémiques.

4.2. Dissocier les effets du changement climatique des effets des pressions anthropiques

Une des difficultés majeures rencontrées dans la compréhension des réponses des espèces structurantes ou des habitats reste la dissociation des effets liés aux pressions locales/régionales ou liés aux changements globaux. Les milieux lagunaires et plus largement les milieux côtiers et littoraux métropolitains sont en effet soumis à de nombreuses pressions d'origine anthropique pour lesquelles il est difficile de dissocier les effets, même sur la base de chroniques temporelles longues (projet MALAG, MARES2 par exemple). Dans ce deuxième axe principal de travail, je souhaiterai aborder ce sujet à travers l'étude de la réponse structurelle et fonctionnelle de phanérogames marines. Pour cela, je projette de comparer deux systèmes contrastés :

- les herbiers de Mayotte (Figure 19), largement soumis aux pressions anthropiques locales et régionales. Ces herbiers sont pour la plupart d'entre eux en déclin. Plus généralement, le contexte socio-économique et géopolitique de Mayotte est à l'origine d'une augmentation récente et particulièrement rapide de la population humaine et des pressions associées. L'érosion des sols est l'une des principales pressions agissant sur les dynamiques des écosystèmes récifaux et associés. Par ailleurs, les volumes d'eaux polluées atteignant le lagon ont fortement augmenté ces dernières années avec l'accroissement de la consommation d'eau et la multiplication des rejets d'eaux usées. L'assainissement diffus est un problème majeur avec seulement 10 % de la population raccordés à un réseau d'assainissement.

- les herbiers des îles éparses et en particulier sur les îles des Glorieuses et de Geyser (Figure 19) où cinq espèces de phanérogames marines sont recensées selon une distribution hétérogène (*Halophila ovalis-minor*, *Halodule uninervis*, *Cymodocea rotundata*, *Thalassia hemprichii*, *Thalassodendron ciliatum*). En dehors des activités illégales et non encadrées ciblant les espèces

---

[165] Burns J., Delparte D., Gates R., Takabayashi M. (2015) Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. PeerJ 3:e1077. https://doi.org/10.7717/peerj.1077

benthiques présentes dans les herbiers, ces derniers sont uniquement soumis aux changements climatiques globaux et dans une moindre mesure à la pollution plastique et aux hydrocarbures. Éloignés des pressions anthropiques majeures, les herbiers des îles Éparses représentent ainsi une situation exceptionnelle de référence à l'échelle régionale pour comprendre les effets des pressions anthropiques.

Dans ce nouveau cadre géographique, de nouvelles actions de recherche viseront à quantifier les rôles fonctionnels actuels des herbiers sur ces deux zones. Pour cela, je mobiliserai mes compétences et mes capacités à fédérer autour des questions de biodiversité (macrofaune et juvéniles de poissons) et piégeage du carbone à travers à la fois le maintien des collaborations existantes et le développement de nouvelles collaborations, en particulier avec le CUFR de Mayotte. A terme, ces résultats permettront de comprendre la dynamique récente du déclin des herbiers monospécifiques à *Thalassodendron* à l'échelle de Mayotte. Une partie de ces actions pourrait s'inscrire rapidement dans le cadre du projet BRIDGES, actuellement en cours de construction.

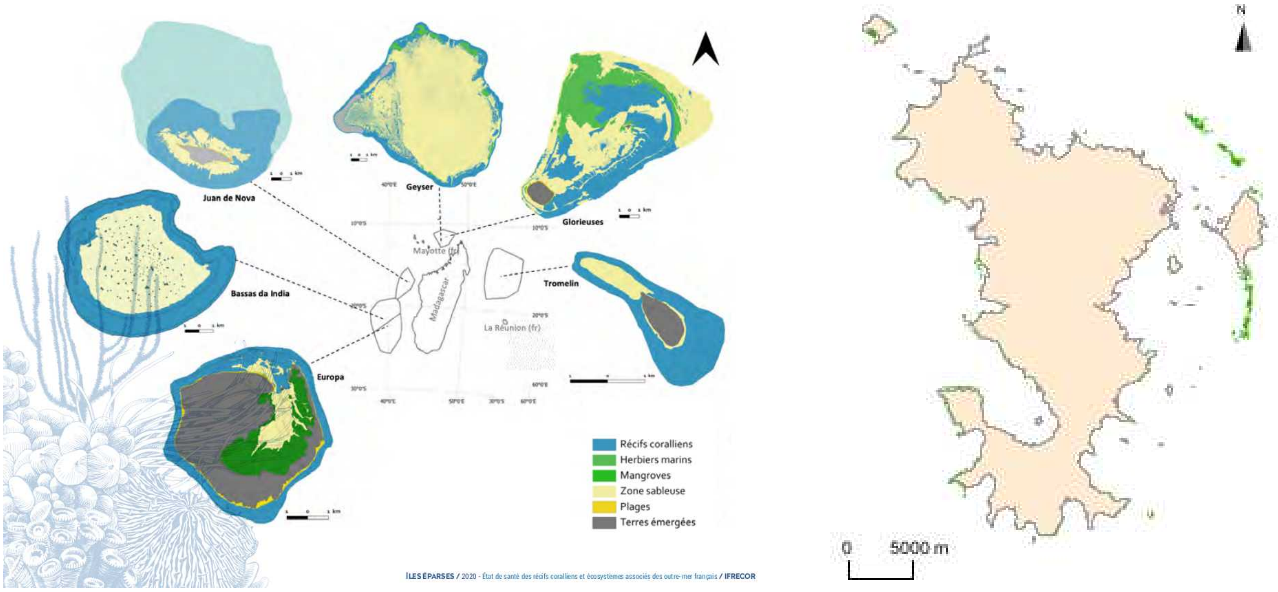


Figure 19: Distribution des herbiers (en vert) sur (à gauche) les îles éparses et (à droite) Mayotte (IFRECOR)

5. GESTION DE PROJETS : DE LA RECHERCHE DE FINANCEMENTS À L'ANIMATION SCIENTIFIQUE

Les projets de recherche et d'expertise sont au centre mon activité depuis mon recrutement en 2013. Tous viennent s'insérer dans des axes de recherche centrés sur la compréhension du rôle des espèces et des habitats clés dans le fonctionnement des systèmes côtiers et littoraux. Ces projets m'ont permis d'aborder de manière complémentaire les différents aspects de cette problématique pour une compréhension plus globale des processus impliqués. Cette approche a nécessité l'appropriation de nombreux concepts et méthodes faisant appel à des compétences spécifiques issues de nombreux champs disciplinaires tels que la chimie, la physique et la biologie. Principalement porteur de projets, j'ai ainsi coordonné depuis 2012 des actions de recherche impliquant des scientifiques issus de différents laboratoires nationaux et internationaux (Figure 20). Ces projets ainsi que mon implication sont résumés dans le Tableau 1.

Figure 20: Représentation schématique des principales collaborations scientifiques et relations avec les agences de l'état et les structures de gestion dans le cadre des projets de recherches.

Tableau 1: Liste des projets de recherche, financement, budget, objectif, période et contribution personnelle. Axe de recherche : 1 = Observation, 2 = Distribution d’espèces clés et des habitats benthiques, 3 = Résistance, seuils de basculement et successions écologique et 4 = Rôles fonctionnels

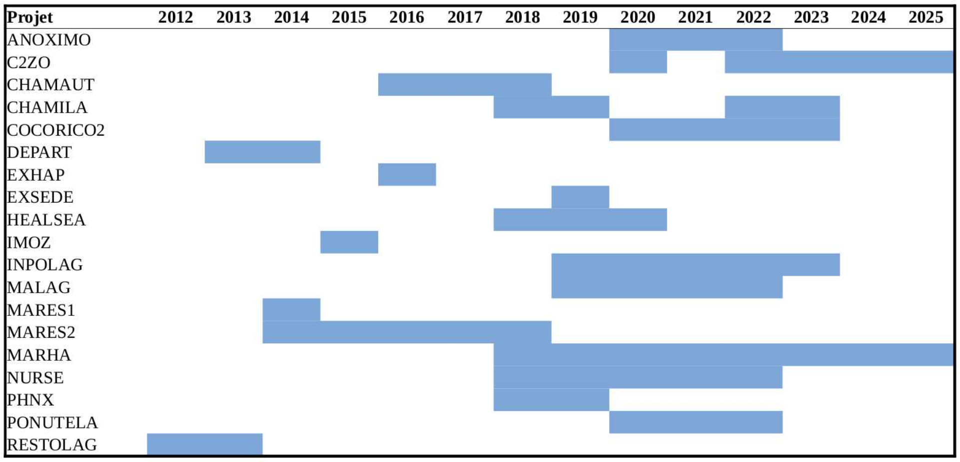
Description des projets de recherche			**Axe de recherche**
ANOXIMO	*Nom*	Effet de l'anoxie et des mortalités d'huîtres sur les flux biogéochimiques et les communautés	3
	Année	2020-2022	
	Financement	EC2CO, Ifremer (DS)	
	Budget	-	
	Objectif	Analyser les effets de l'anoxie et des mortalités d'huîtres sur le fonctionnement de la lagune de Thau dans un contexte de crise liée au changement global. Ce sujet est original/novateur pour son approche en mésocosmes et sa multidisciplinarité. Il fédère des chercheurs régionaux/internationaux. Les résultats valorisés internationalement, aideront à la gestion de crise par les parties prenantes.	
	Responsabilité	Collaborateur	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), CHROME (Univ. Nîmes), Ifremer (IHPE), MEDIMEER (CNRS, Univ. Montpellier), MIO (Univ. Aix-Marseille, Univ. Toulon, CNRS, IRD)	
C2ZO	*Nom*	Effets des épisodes extrêmes en milieu méditerranéen stressé	1, 3, 4
	Année	2020-2025	
	Financement	Agence de l'Eau Rhône Méditerranée Corse	
	Budget	583 000 €	
	Objectif	Comprendre les effets du changement climatique et des ECEs sur les milieux lagunaires méditerranéens en général avec un focus sur les phanérogames marines inféodées à ces milieux.	
	Responsabilité	Porteur/Coordinateur du projet – Encadrement Doctorat (C. Bourdier)	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), DECOD (INRAE, Ifremre, Institut Agro Rennes-Angers)	
CHAMAUT	*Nom*	Chambres benthiques automatiques en milieu côtier: vers des mesures hautes-fréquences	4
	Année	2016-2018	
	Financement	CNRS (défi instrumentation aux limites), Ifremer (DS)	
	Budget	107 000 €	
	Objectif	Développer trois systèmes automatiques et autonomes (sur 24 à 72h et jusqu'à 10 mètres de profondeur) permettant de reproduire dans l'espace et dans le temps des mesures aujourd'hui trop ponctuelles ou quasi inexistantes (mesures de nuit ou lors d'événements climatiques extrêmes par exemple) en milieu côtier peu profond.	
	Responsabilité	Porteur/Coordinateur du projet	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), CEREGE (CNRS, IRD, Univ. Aix-Marseille, Collège de France), MEDIMEER (CNRS, Univ. Montpellier), Ifremer (SI2M, LDCM)	
CHAMILA	*Nom*	Cartographie des habitats en milieux lagunaires	2
	Année	2018-2023	
	Financement	Agence de l'Eau Rhône Méditerranée Corse	
	Budget	400 000 €	
	Objectif	Établir une cartographie des habitats au sein des lagunes méditerranéennes françaises qui tiendra compte de leurs variabilités temporelle et spatiale.	
	Responsabilité	Porteur/Coordinateur du projet	
	Collaboration	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), La Tour du Valat	
COCORICO2	*Nom*	La conchyliculture dans un monde riche en CO2	1
	Année	2020-2023	
	Financement	FEAMP	
	Budget	-	
	Objectif	Observer, analyser, anticiper et remédier les effets des changements environnementaux (acidification et réchauffement de l'eau) sur la conchyliculture afin d'évaluer la vulnérabilité des écosystèmes, des espèces en élevage et des entreprises vis-à-vis du changement environnemental et plus particuliérement du risque « acidification ».	
	Responsabilité	Collaborateur	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), Ifremer (PFOM, UL) + LOV (CNRS, Univ. Sorbonne)	
DEPART	*Nom*	Devenir du phosphore et de l'azote : restauration des milieux lagunaires eutrophisés	4
	Année	2013-2014	
	Financement	EC2CO, Agence de l' Eau Rhône Méditerranée Corse	
	Budget	155 000 €	
	Objectif	Caractériser et quantifier les principaux flux de matière qui participent à la diminution des stocks internes d'azote et de phosphore des lagunes méditerranéennes et améliorer la paramétrisation des modéles mathématiques de bilan afin de définir des scénarios-types de dynamique de restauration des lagunes méditerranéennes.	
	Responsabilité	Porteur/Coordinateur du projet	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE)	
EXHAP	*Nom*	Expertise Habitats-Poissons au sein des lagunes méditerranéennes françaises	2,4
	Année	2016	
	Financement	Agence de l'Eau Rhône Méditerranée Corse	
	Budget	38 000 €	
	Objectif	Produire une expertise collective portant sur l'analyse critique des connaissances disponibles sur les compartiments benthiques et poissons et sur le développement d'un « outil intégrateur » en axant la réflexion sur les fonctions de l'écosystème.	
	Responsabilité	Porteur/Coordinateur du projet	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), LaTour du Valat, CEFREM (CNRS, Univ. Perpignan)	
EXSEDE	*Nom*	Expertise sur le sédiment des lagunes méditerranéennes françaises	1
	Année	2019	
	Financement	Agence de l'Eau Rhône Méditerranée Corse	
	Budget	22 000 €	
	Objectif	Apporter une expertise scientifique sur les stocks sédimentaires en milieu lagunaire afin d'aider la prise de décision (risques de non atteinte des objectifs dans le cadre de la DCE en particulier).	
	Responsabilité	Porteur/Coordinateur du projet	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE)	
HEALSEA	*Nom*	Résistance et résilience des herbiers à Zostère face aux perturbations anthropiques : de la théorie à l'expérimentation	3
	Année	2018-2020	
	Financement	Programme Européen Marie-Curie	
	Budget	-	
	Objectif	Contribuer à la préservation de la santé des herbiers marins et prévenir de leur perte en apportant une compréhension globale de leur réponse aux conditions changeantes, et des outils pour évaluer leur résilience, sur la base d'un modèle d'évaluation de la résilience. outils pour évaluer leur résilience, basés sur une nouvelle approche inspirée d'études mathématiques.	
	Responsabilité	Collaborateur – Encadrement Post-Doctorat (L. Soissons)	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), Univ. Pisa	

Description des projets de recherche			Axe de recherche
IMOZ	*Nom*	Impact des mouillages sur les herbiers de zostéres	3
	Année	2015	
	Financement	-	
	Budget	-	
	Objectif	Quantifier l'impact des mouillages) petite échelle sur la morphologie de la plante	
	Responsabilité	Porteur/Coordinateur du projet	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), BOREA (MNNHN, CNRS, Univ. Caen, Univ. Sorbonne, IRD, Univ. Antilles)	
INPOLAG	*Nom*	Développement d'un indicateur Poissons en lagune adapté au contexte français	4
	Année	2019-2023	
	Financement	Office Française pour la biodiversité	
	Budget	477 000 €	
	Objectif	Développer un indicateur « poisson » DCE-compatible, adapté au contexte français	
	Responsabilité	Porteur/Coordinateur du projet	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), CEFREM (CNRS, Univ. Perpignan), La Tour du Valat	
MALAG	*Nom*	Effet de l'eutrophisation sur la bio-diversité de la macrofaune benthique des lagunes méditerranéennes	4
	Année	2019-2022	
	Financement	Office Française pour la biodiversité	
	Budget	230 000 €	
	Objectif	Rechercher des échelles pertinentes, spatiale (intra et inter-lagune) et temporelle (mensuelle et inter-annuelle), auxquelles les effets des fluctuations environnementales naturelles (ici confinement, nature du substrat et qualité des sources de nourriture disponibles) et anthropiques (ici l'eutrophisation) s'appliquent et identifier les niveaux d'intégration, taxonomiques ou fonctionnels (via une approche de traits biologiques) auxquels ces effets s'expriment	
	Responsabilité	Porteur/Coordinateur du projet – Encadrement Doctorat (T. Mouton) et Post-Doctorat (A. jones)	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), Ifremer LEBCO, LEMAR (IRD, Ifremer, CNRS, Univ. Brest Occidentale)	
MARES1	*Nom*	Rôle des Macrophytes dans la REStauration des milieux lagunaires : distribution spatiale de *Zostera noltei*	2
	Année	2014	
	Financement	Agence de l'Eau Rhône Méditerranée Corse	
	Budget	43 000 €	
	Objectif	Identifier les facteurs qui gouvernent la distribution spatiale d'une espéce ingénieure (Zostera noltei) en milieu lagunaire	
	Responsabilité	Porteur/Coordinateur du projet	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), Ifremer LEBCO	
MARES2	*Nom*	Rôle des MAcrophyes dans la REStauration des milieux lagunaires : Successions écologiques	2, 3, 4
	Année	2014-2018	
	Financement	Agence de l'Eau Rhône Méditerranée Corse	
	Budget	178 800 €	
	Objectif	Caractériser la dynamique et le rôle fonctionnel des macrophytes dans la restauration vis-à-vis de l'eutrophisation des milieux lagunaires	
	Responsabilité	Porteur/Coordinateur du projet – Encadrement Doctorat (I. Le Fur)	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), Ifremer (PELAGOS)	
MARHA	*Nom*	Approche intégrée pour la caractérisation de l'état de conservation des herbiers de zostéres : Échelle biogéographique	4
	Année	2018-2025	
	Financement	LIFE+	
	Budget	150 000 € (budget estimé)	
	Objectif	Comprendre la dynamique de l'habitat emblématique « herbiers de zostéres », sa variabilité et ses réponses aux pressions locales et/ou globales, afin de caractériser l'état de santé des herbiers, de définir leur capacité de résilience, d'identifier des mesures de conservation efficace et d'améliorer les prédictions.	
	Responsabilité	Porteur/Coordinateur du WP3 « Fonctionnalité des herbiers de Zostera » - Encadrement Post-Doctorat (E. Lacoste)	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), Ifremer LEBCO, Ifremer LERBN, Ifremer LERAR	
NURSE	*Nom*	Rôle des lagunes littorales dans le cycle biologique des poissons méditerranéens : comprendre pour mieux préserver	4
	Année	2018-2022	
	Financement	Office Française pour la biodiversité	
	Budget	230 000 €	
	Objectif	Hiérarchiser les facteurs naturels et anthropiques influençant la répartition spatiale et temporelle des principales espéces de poissons à leur stade juvénile et adulte et définir une stratégie spatiale et temporelle de travail pour la qualification de ces milieux vis-à-vis des pressions, adaptée aux milieux confinés tels que les lagunes méditerranéennes.	
	Responsabilité	Porteur/Coordinateur du projet – Encadrement Doctorat (M. Iotti)	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE)	
PHNX	*Nom*	Systéme spectrophotométrique innovant de pHT	1
	Année	2018-2019	
	Financement	Ifremer (DS)	
	Budget	-	
	Objectif	Adaptater un spectrophotométre miniaturisé in situ, le Chemini, pour en faire un appareil de mesure de référence de pH Total en milieu marin.	
	Responsabilité	Collaborateur	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), Ifremer (LDCM, SI2M, LERPC, PFOM)	
PONUTELA	*Nom*	Impact des hypoxies sur le devenir des polluants et nutriments des sédiments dans les écosystémes lagunaires méditerranéens	3
	Année	2020-2022	
	Financement	EC2CO	
	Budget	-	
	Objectif	Caractériser l'impact des variations des concentrations en oxygène dans la colonne d'eau sur le devenir des polluants à l'interface eau-sédiment dans l'une des lagunes du complexe lagunaire Palavasien: l'étang du Prevost.	
	Responsabilité	Collaborateur	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE), CHROME (Univ. Nîmes)	
RESTOLAG	*Nom*	Restauration des écosystémes lagunaires : évaluation du rôle du sédiment et des herbiers à phanérogames	4
	Année	2012-2013	
	Financement	Agence de l'Eau Rhône Méditerranée Corse, Région Languedoc-Roussillon	
	Budget	273 000 €	
	Objectif	Évaluer les stocks d'azote et de phosphore dans les sédiments des lagunes méditerranéennes françaises, évaluer la cinétique de transfert de l'azote et du phosphore entre le sédiment et la colonne d'eau et définir des scénarios "type" afin d'estimer le temps nécessaire pour réduire les charges internes à des niveaux de référence.	
	Responsabilité	Post-Doctorat	
	Laboratoire impliqué	MARBEC (IRD, Ifremer, CNRS, Univ. Montpellier, INRAE)	

Au-delà de mon implication scientifique et technique (acquisition de données, plongée…), ma position de coordinateur et porteur fait appel à mes compétences en gestion de projet que j'ai pu acquérir au cours de ces années. J'ai ainsi démontré des capacités à fédérer une équipe projet autour de thématiques, à rechercher des financements, à créer des relations de confiance avec les partenaires techniques et financiers et à animer les différents projets. Mes collaborations sont aujourd'hui multiples en interne et en externe, tant d'un point de vue disciplinaire que géographique.

Tout en continuant à m'impliquer dans l'acquisition de connaissances dans le cadre de ces projets, mon activité de recherche a ainsi rapidement évolué vers la recherche de financements dont l'Agence de l'Eau Rhône Méditerranée Corse (AERMC) et l'Office Française pour la Biodiversité (OFB) constituent deux des sources principales. Ceci résulte d'une part du travail de contextualisation des problématiques abordées dans un contexte de directives européennes (Directive Cadre sur l'eau, Directive Habitats Faune Flore) et d'autre part d'un ancrage important des problématiques abordées dans un contexte régional et national en lien avec la gestion des écosystèmes littoraux et côtiers. L'implication financière de ces deux "partenaires" dans mes projets depuis maintenant plus de 10 ans traduit la relation de confiance que j'ai pu construire au cours du temps.

La coordination et l'animation scientifique au sein des projets sont aujourd'hui au cœur de mon activité de recherche. Les problématiques abordées au sein des différents projets font souvent appel à des compétences complémentaires qu'il faut être en mesure de comprendre sans pour autant être spécialiste. Parmi les projets dont j'ai assurés la coordination, les projets liés au développement technologique (projets CHAMAUT et C2ZO) ont impliqué des partenaires issus du monde de l'ingénierie pour lesquels les langages et les objectifs sont souvent différents. Cela a représenté un réel défis dans la coordination et l'animation scientifique du projet. Plusieurs projets ont également nécessité le recrutement de nombreux scientifiques en contrat pour mener à bien des actions d'acquisition (projet MARHA, CHAMILA, INPOLAG) ou de traitement de données (CHAMILA). Tous ces projets, au-delà des résultats simplement scientifiques, m'ont permis d'acquérir de l'expérience dans le domaine de l'animation de la recherche et une connaissance approfondie du fonctionnement et de la gestion des projets.



Projet	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024	2025
ANOXIMO									▨	▨	▨			
C2ZO									▨		▨	▨	▨	▨
CHAMAUT					▨	▨	▨							
CHAMILA							▨	▨			▨	▨		
COCORICO2									▨	▨	▨	▨		
DEPART		▨	▨											
EXHAP					▨									
EXSEDE								▨						
HEALSEA							▨	▨	▨					
IMOZ				▨										
INPOLAG								▨	▨	▨	▨	▨		
MALAG								▨	▨	▨	▨			
MARES1			▨											
MARES2			▨	▨	▨	▨	▨							
MARHA							▨	▨	▨	▨	▨	▨	▨	▨
NURSE							▨	▨	▨	▨	▨			
PHNX							▨	▨						
PONUTELA									▨	▨	▨			
RESTOLAG	▨	▨												

Figure 21: Chronogramme des projets développés dans le cadre de mes travaux de recherche entre 2012 et 2025.

Entre 2013 et 2022, mon implication dans plusieurs projets n'a cessé d'augmenter pour atteindre 8 projets en parallèle entre 2019 et 2022 dont au moins 5 en tant que coordinateur (Figure 21). Cette période a été riche en acquisition de données. Une partie de ces projets s'appuyait sur des ressources humaines temporaires et le travail de valorisation est encore en cours. Ce fonctionnement, courant dans la recherche scientifique, m'a ainsi permis de développer mes compétences dans la gestion du temps, de la recherche de financement à l'animation continue tout au long du projet. Ce modèle n'est en revanche pas tenable en raison des difficultés de recrutement à long terme ou sur projet à l'Ifremer. Depuis maintenant 2 ans, mon implication dans chacun des projets que je coordonne reste très important mais le nombre de ces projets est plus restreint afin de dégager plus de temps à la valorisation. C'est dans ce cadre que s'inscrivent mes futurs projets détaillés dans la partie 4.

6. TRANSMISSION DES CONNAISSANCES

6.1. Formation par la recherche

Par définition, la recherche en écologie est un processus collectif qui implique souvent des scientifiques expérimentés ainsi que de jeunes scientifiques en devenir. Au delà des collaborations établies avec des chercheurs et techniciens reconnus dans leur domaine, j'ai attaché une importance particulière à la formation et à l'encadrement d'étudiants et de jeunes scientifiques en les intégrant directement aux projets de recherche que j'ai coordonnés.

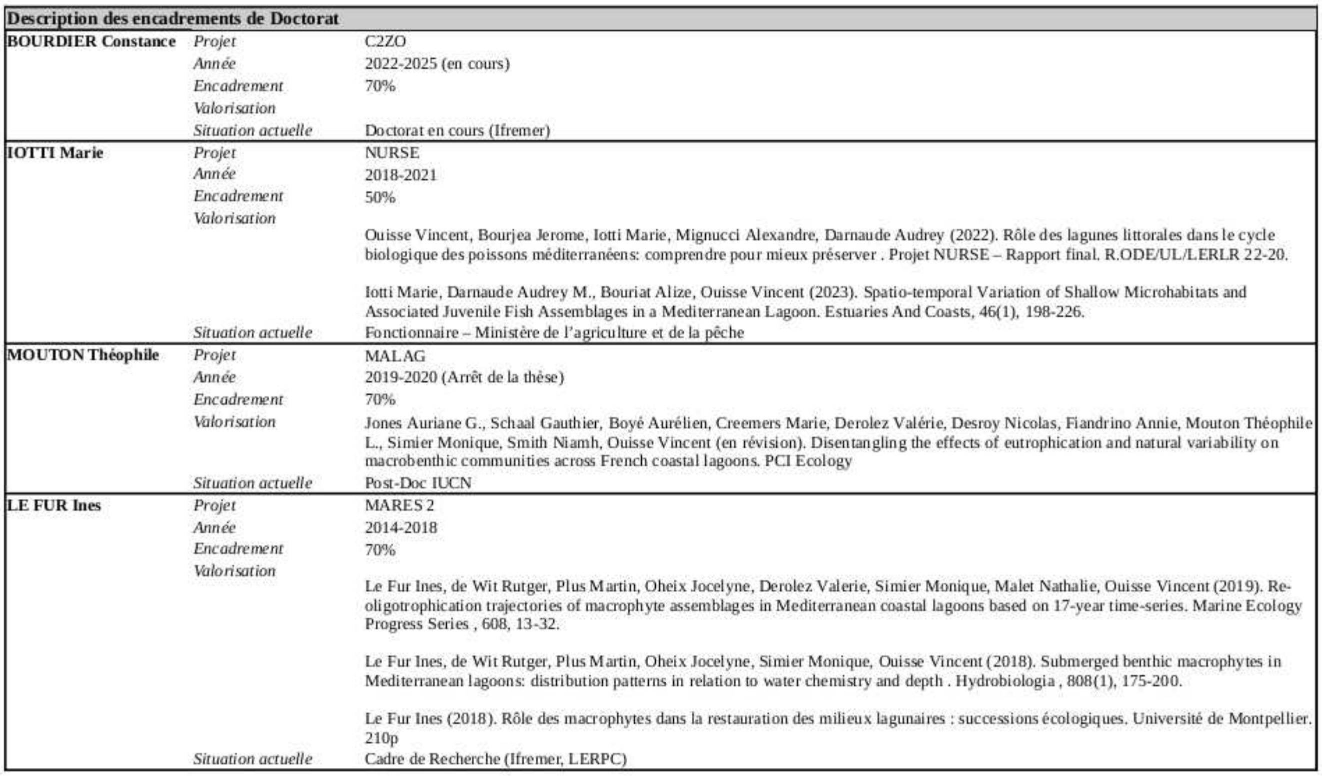
A travers des co-encadrements dans la plupart des cas, j'ai ainsi pu former des étudiants de niveau Master 1 (9) et Master 2 (10, Tableau 2). Souvent synonyme de premier stage long, j'axe la formation des étudiants en Master 1 sur la compréhension et l'application rigoureuse de la démarche scientifique. Plus que des résultats, cette période d'accueil au laboratoire permet ainsi au stagiaire d'acquérir les bases du travail scientifique et, dans la plupart des cas de confirmer ou non leur projet professionnel. En Master 2, l'approche est complémentaire. Elle reste néanmoins pour moi un exercice de style dans lequel il faut à la fois réussir à rendre accessible en peu de temps les connaissances existantes sur le sujet, les intégrer dans un contexte de recherche et d'expertise et ainsi rendre pertinent l'utilisation d'outils adaptés tant en termes de traitement de données que de rédaction pour répondre aux questions posées. Outre ce cadre qu'il faut adapter à chaque personne et chaque sujet, mon implication dans l'encadrement a évoluer pour prendre parfois le rôle d'encadrant principal lorsque la problématique est centrée sur mes compétences ou bien le rôle de co-encadrant lorsque les compétences requises étaient plutôt apportées par les autres scientifiques impliqués.

Tableau 2: Liste des encadrements en Master2.

Description des encadrements de Master 2		
BOURDIER Constance	*Projet*	C2ZO
	Encadrement	70%
	Valorisation	Bourdier Constance (2022) Effets d'une vague de chaleur printanière sur deux espèces de phanérogames marines présentes en lagune Méditerranéenne, *Zostera noltei* et *Cymodocea nodosa* : Approche expérimentale. Mémoire Master2, Univ. La Rochelle
	Situation actuelle	Doctorat en cours (Ifremer)
SMITH Niamh	*Projet*	MALAG
	Encadrement	50%
	Valorisation	Smith Niamh (2020) Impact de l'eutrophisation sur la biodiversité de la macrofaune benthique lagunaire méditerranéenne. Mémoire Master2, Sorbonne Université Jones Auriane G., Schaal Gauthier, Boyé Aurélien, Creemers Marie, Derolez Valérie, Desroy Nicolas, Fiandrino Annie, Mouton Théophile L., Simier Monique, Smith Niamh, Ouisse Vincent (en révision). Disentangling the effects of eutrophication and natural variability on macrobenthic communities across French coastal lagoons. PCI Ecology
	Situation actuelle	VSC Mayotte, Recherche de Doctorat
ROYER Aurélien	*Projet*	MARHA
	Encadrement	60%
	Valorisation	Royer Aurélien (2020) Evaluation de l'état de conservation des herbiers de zostères le long d'un gradient latitudinal français par une approche fonctionnelle. Rapport Master 2, Univ. Bretagne Occidentale
	Situation actuelle	CDD Univ. Bretagne Ouest
DURREAU Alice	*Projet*	C2ZO
	Encadrement	50%
	Valorisation	Durreau Alice (2020) Comprendre l'impact des épisodes extrêmes sur le fonctionnement et le changement d'état des écosystèmes lagunaires méditerranéens. Mémoire Ingénieur, AgroSup Dijon
	Situation actuelle	-
IOTTI Marie	*Projet*	NURSE
	Encadrement	50%
	Valorisation	Iotti Marie (2018) Caractérisation des habitats et du peuplement de poissons associés dans les milieux lagunaires méditerranéens. Mémoire Ingénieur, AgroSup Dijon Iotti Marie, Darnaude Audrey M., Bouriat Alize, Ouisse Vincent (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries And Coasts, 46(1), 198-226.
	Situation actuelle	Fonctionnaire – Ministère de l'agriculture et de la pêche
DUJON Nicolas	*Projet*	CHAMAUT
	Encadrement	30%
	Valorisation	Dujon Nicolas (2018) Station de fonds côtiers : Vers une communication à distance, Mémoire Ingénieur, ESIREM Dijon
	Situation actuelle	CDI Aéronautique
VASCOTTO Ivano	*Projet*	MARES 2
	Encadrement	40%
	Valorisation	Vascotto Ivano (2016) Functional redundancy of seagrasses in French Mediterranean lagoons: carbon, oxygen and nutrient cycles. Mémoire Master 2, Univ. Trieste
	Situation actuelle	Doctorat en cours (Slovénie)
PATACCINI Marianela	*Projet*	-
	Encadrement	50%
	Valorisation	Pataccini Marianela (2015) Co-évolution des habitats benthiques et des usages sur une lagune méditerranéenne : la lagune de Thau de 1950 à nos jours. Mémoire Master 2, Univ. Paris Diderot
	Situation actuelle	Chargée d'ingénieurie de formation pédagogique, AgroParisTech
PERRON Carole	*Projet*	MARES 1
	Encadrement	80%
	Valorisation	Perron Carole (2014) Distribution potentielle des herbiers à Zostera noltii en milieu lagunaire méditerranéen. Mémoire Master 2, Univ Sorbonne
	Situation actuelle	Chargée de mission, Parc naturel marin des estuaires picards et de la mer d'Opale
BENARD Samuel	*Projet*	RESTOLAG
	Encadrement	100%
	Valorisation	Benard Samuel (2013) Rôle des herbiers de zostères dans la restauration de lagunes méditerranéennes eutrophisées. Mémoire Master 2, Univ. La Rochelle
	Situation actuelle	-

Depuis 2014, j'ai été impliqué dans l'encadrement de 4 doctorants (Tableau 3). Il s'agit pour moi d'une période de formation clé qui permet aux étudiants de devenir des jeunes scientifiques spécialistes dans leurs domaines d'expertise. J'ai ainsi pu aborder mon travail de recherche sous un angle de supervision, de formation et de suivi du travail de recherche. Intégrés dans les projets MARES2, MALAG, NURSE et C2ZO, j'ai obtenu des financements couvrant à la fois les salaires et le fonctionnement associé (AERMC, OFB et Ministère de l'Agriculture et de la pêche). Co-encadrant, mon implication a toujours été supérieure ou égale à 50 %. A ce jour, seule une des trois thèses finalisée a été soutenue. La doctorante occupe aujourd'hui un poste d'ingénieur à l'Ifremer. Bien que ce bilan ne soit pas parfait, il s'explique d'une part par le type de financement de l'une des doctorantes (Financement Complémentaire Pour la Recherche, FCPR). Ce financement a pour objectif de permettre à un jeune diplômé fonctionnaire de poursuivre pendant trois ans sa formation dans un laboratoire de recherche. Cette doctorante a ainsi intégré, dès la fin de ses trois année de formation, son poste au Ministère de la Pêche. L'arrêt d'une seconde thèse après 9 mois a été en revanche une difficulté que j'ai due gérer au mieux. Cette expérience m'a permis de développer mes capacités en gestion des conflits, des risques, et en sortie de crise.

Tableau 3: Liste des encadrements en Doctorat.

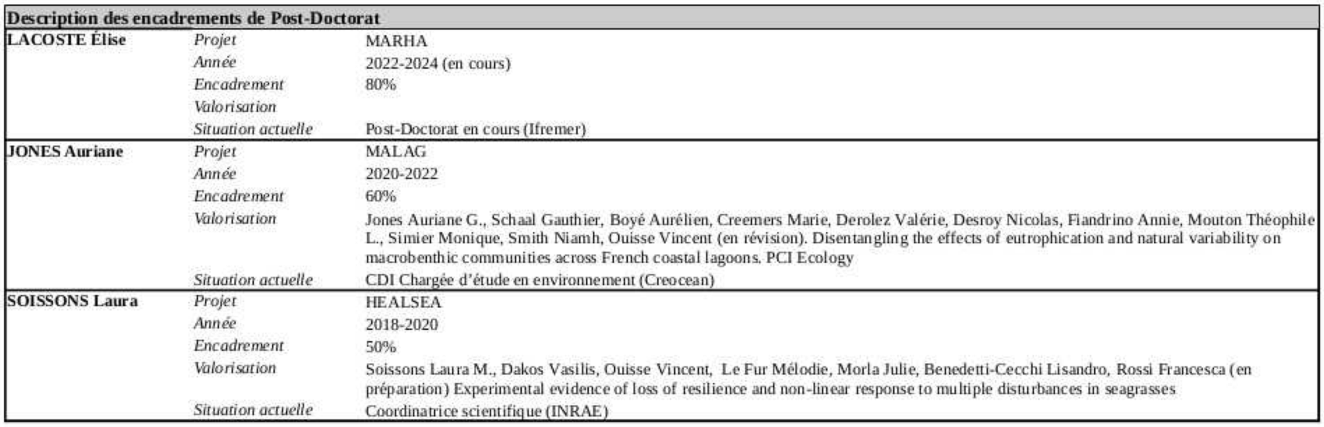


Description des encadrements de Doctorat		
BOURDIER Constance	*Projet*	C2ZO
	Année	2022-2025 (en cours)
	Encadrement	70%
	Valorisation	
	Situation actuelle	Doctorat en cours (Ifremer)
IOTTI Marie	*Projet*	NURSE
	Année	2018-2021
	Encadrement	50%
	Valorisation	Ouisse Vincent, Bourjea Jerome, Iotti Marie, Mignucci Alexandre, Darnaude Audrey (2022). Rôle des lagunes littorales dans le cycle biologique des poissons méditerranéens: comprendre pour mieux préserver . Projet NURSE – Rapport final. R.ODE/UL/LERLR 22-20. Iotti Marie, Darnaude Audrey M., Bouriat Alize, Ouisse Vincent (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries And Coasts, 46(1), 198-226.
	Situation actuelle	Fonctionnaire – Ministère de l'agriculture et de la pêche
MOUTON Théophile	*Projet*	MALAG
	Année	2019-2020 (Arrêt de la thèse)
	Encadrement	70%
	Valorisation	Jones Auriane G., Schaal Gauthier, Boyé Aurélien, Creemers Marie, Derolez Valérie, Desroy Nicolas, Fiandrino Annie, Mouton Théophile L., Simier Monique, Smith Niamh, Ouisse Vincent (en révision). Disentangling the effects of eutrophication and natural variability on macrobenthic communities across French coastal lagoons. PCI Ecology
	Situation actuelle	Post-Doc IUCN
LE FUR Ines	*Projet*	MARES 2
	Année	2014-2018
	Encadrement	70%
	Valorisation	Le Fur Ines, de Wit Rutger, Plus Martin, Oheix Jocelyne, Derolez Valerie, Simier Monique, Malet Nathalie, Ouisse Vincent (2019). Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. Marine Ecology Progress Series , 608, 13-32. Le Fur Ines, de Wit Rutger, Plus Martin, Oheix Jocelyne, Simier Monique, Ouisse Vincent (2018). Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth . Hydrobiologia , 808(1), 175-200. Le Fur Ines (2018). Rôle des macrophytes dans la restauration des milieux lagunaires : successions écologiques. Université de Montpellier. 210p
	Situation actuelle	Cadre de Recherche (Ifremer, LERPC)

Plus récemment, j'ai également été largement impliqué dans 3 projets post-doctoraux (Tableau 4). Dans ce cadre, mon rôle a été centré sur l'accompagnement de ces scientifiques, toutes déjà expertes dans leur domaine scientifique, dans l'acquisition de nouvelles compétences complémentaires (mesures des flux biogéochimiques ou connaissances du contexte lagunaire par exemple). Ces collaborations se sont inscrites dans le cadre de deux projets dont j'ai été le coordinateur et dans le cadre d'une bourse européenne d'excellence Marie-Curie.

De manière générale, ces travaux menés dans le cadre de cette formation ont fait l'objet de présentations lors de congrès internationaux et d'articles scientifiques publiés ou en cours de publication (Tableau 4).

Tableau 4: Liste des encadrements en Post-Doctorat.



Description des encadrements de Post-Doctorat		
LACOSTE Élise	*Projet*	MARHA
	Année	2022-2024 (en cours)
	Encadrement	80%
	Valorisation	
	Situation actuelle	Post-Doctorat en cours (Ifremer)
JONES Auriane	*Projet*	MALAG
	Année	2020-2022
	Encadrement	60%
	Valorisation	Jones Auriane G., Schaal Gauthier, Boyé Aurélien, Creemers Marie, Derolez Valérie, Desroy Nicolas, Fiandrino Annie, Mouton Théophile L., Simier Monique, Smith Niamh, Ouisse Vincent (en révision). Disentangling the effects of eutrophication and natural variability on macrobenthic communities across French coastal lagoons. PCI Ecology
	Situation actuelle	CDI Chargée d'étude en environnement (Creocean)
SOISSONS Laura	*Projet*	HEALSEA
	Année	2018-2020
	Encadrement	50%
	Valorisation	Soissons Laura M., Dakos Vasilis, Ouisse Vincent, Le Fur Mélodie, Morla Julie, Benedetti-Cecchi Lisandro, Rossi Francesca (en préparation) Experimental evidence of loss of resilience and non-linear response to multiple disturbances in seagrasses
	Situation actuelle	Coordinatrice scientifique (INRAE)

6.2. Suivi de la formation continue par la recherche

Participation à des comités de thèse

- Coquin Salomé (en cours). Les métabolites spécialisés des Magnoliophytes marines benthiques. Université Aix-Marseille
- Brosse Rémi (2023). Étude de l'écologie du gastéropode *Terebralia palustris* (Linnaeus, 1767), élément témoignant des interactions contribuant à la bonne santé du système socio-écologique des mangroves de Mayotte. Université de Bretagne Occidentale
- Houngnandan Fabrice (2020). Rôle des pressions anthropiques et de l'environnement sur l'état des herbiers de posidonies en méditerranée française. Université de Montpellier

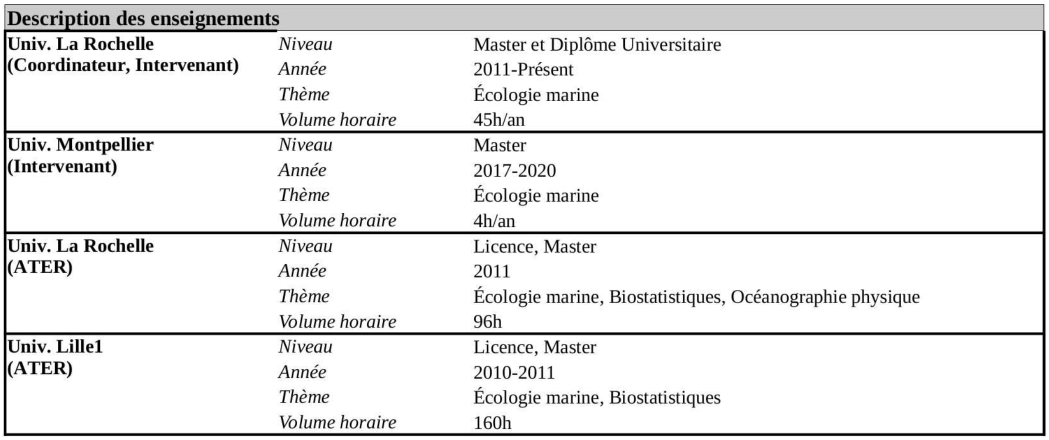
Participation à un jury HDR

- Rossi Francesca (2017). Stabilité écologique face aux perturbations et conservation des prairies sous-marines et des écosystèmes associés. Université de Nice

6.3. Partage des connaissances par l'enseignement

De par mon parcours universitaire, j'ai toujours été très impliqué dans l'enseignement à l'université. Tout d'abord à l'Université de Lille 1 puis de l'Université de La Rochelle, j'ai ainsi assuré des enseignements en biostatistiques et en écologie marine en tant qu'Attaché Temporaire d'Enseignement et de Recherche aussi bien au niveau Licence que Master (Tableau 5). Suite à mon recrutement à l'Ifremer en 2013, j'ai souhaité continuer à m'impliquer dans la formation à l'université. Depuis maintenant plus de 10 ans, j'interviens principalement auprès d'un public averti (niveau Master) ou en formation continue (Diplôme Universitaire) dans le cadre d'enseignements en écologie marine. Je co-coordonne en particulier un Diplôme Universitaire de l'Université de La Rochelle intitulé « Biosurveillance des Écosystèmes Méditerranéens Marins en Plongée Autonome : Méthodes et Outils de Suivis » (https://formations.univ-larochelle.fr/du-bioem). Cette formation à la fois pratique et théorique, basée sur l'intervention complémentaire de scientifiques issus de plusieurs instituts français, a pour objectif de former des plongeurs professionnels spécialisés dans la mise au point de protocoles de suivis des principales biocénoses subtidales méditerranéennes côtières et dans l'éducation à l'environnement marin. J'interviens enfin dans l'évaluation des rapports de fin d'étude (Master, Ingénieur) à l'université de Montpellier et à AgroSup Dijon.

Tableau 5: Liste des principales formations dispensées



Description des enseignements		
Univ. La Rochelle (Coordinateur, Intervenant)	*Niveau*	Master et Diplôme Universitaire
	Année	2011-Présent
	Thème	Écologie marine
	Volume horaire	45h/an
Univ. Montpellier (Intervenant)	*Niveau*	Master
	Année	2017-2020
	Thème	Écologie marine
	Volume horaire	4h/an
Univ. La Rochelle (ATER)	*Niveau*	Licence, Master
	Année	2011
	Thème	Écologie marine, Biostatistiques, Océanographie physique
	Volume horaire	96h
Univ. Lille1 (ATER)	*Niveau*	Licence, Master
	Année	2010-2011
	Thème	Écologie marine, Biostatistiques
	Volume horaire	160h

7. VALORISATION DES TRAVAUX

Depuis 2010, mon activité scientifique s'est traduite par :

- ✓ 23 publications scientifiques
- ✓ 30 présentations orales et 7 posters présentés dans des congrès internationaux,
- ✓ 29 rapports scientifiques
- ✓ 11 jeux de données scientifiques

[Étudiant, doctorant et post-doctorant encadrés]

7.1. Articles scientifiques

23 **Jones Auriane G.**, Schaal Gauthier, **Boyé Aurélien**, Creemers Marie, Derolez Valérie, Desroy Nicolas, Fiandrino Annie, **Mouton Théophile L.**, Simier Monique, **Smith Niamh**, **Ouisse Vincent** (en révision). Disentangling the effects of eutrophication and natural variability on macrobenthic communities across French coastal lagoons. PCI Ecology **[IF= -]**

22 **Iotti Marie**, Darnaude Audrey M., Bouriat Alize, **Ouisse Vincent** (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries And Coasts, 46(1), 198-226. https://doi.org/10.1007/s12237-022-01102-9 **[IF=2.8]**

21 Lacoste Elise, Bec Beatrice, Le Gall Patrik, Boufahja Fehmi, Raimbault Patrick, Messiaen Gregory, **Ouisse Vincent**, Roque D'Orbcastel Emmanuelle, Munaron Dominique, Fiandrino Annie, Lagarde Franck, Mas Sébastien, Callier Myriam, Gaertner-Mazouni Nabila, Richard Marion (2022). Benthic-pelagic coupling under juvenile oyster influence in a French Mediterranean coastal lagoon (Thau Lagoon). Estuarine Coastal And Shelf Science, 267, 107779 (10p.). https://doi.org/10.1016/j.ecss.2022.107779 **[IF=2.9]**

20 Derolez Valerie, Malet Nathalie, Fiandrino Annie, Lagarde Franck, Richard Marion, **Ouisse Vincent**, Bec Beatrice, Aliaume Catherine (2020). Fifty years of ecological changes: Regime shifts and drivers in a coastal Mediterranean lagoon during oligotrophication. Science Of The Total Environment, 732, 139292 (17p.). https://doi.org/10.1016/j.scitotenv.2020.139292 **[IF=10.2]**

19 Lacoste Elise, Boufahja Fehmi, Pelaprat Corinne, Le Gall Patrik, Berteaux Tom, Messiaen Gregory, Mortreux Serge, Oheix Jocelyne, **Ouisse Vincent**, Roque D'Orbcastel Emmanuelle, Gaertner-Mazouni Nabila, Richard Marion (2020). First simultaneous assessment of macro- and meiobenthic community response to juvenile shellfish culture in a Mediterranean coastal lagoon (Thau, France). Ecological Indicators, 115, 106462 (9p.). https://doi.org/10.1016/j.ecolind.2020.106462 **[IF=5.8]**

18 de Wit Rutger, Leruste Amandine, **Le Fur Ines**, Maki Sy Mariam, Bec Beatrice, **Ouisse Vincent**, Derolez Valerie, Rey-Valette Hélène (2020). A Multidisciplinary Approach for Restoration Ecology of Shallow Coastal Lagoons, a Case Study in South France. Frontiers In Ecology And Evolution, 8(108), 20p. https://doi.org/10.3389/fevo.2020.00108 **[IF=3.7]**

17 **Ouisse Vincent**, **Marchand-Jouravleff Irina**, Fiandrino Annie, Feunteun Eric, Ysnel Frederic (2020). Swinging boat moorings: Spatial heterogeneous damage to eelgrass beds in a tidal ecosystem. Estuarine Coastal And Shelf Science, 235, 106581 (9p.) . https://doi.org/10.1016/j.ecss.2020.106581 **[IF=2.9]**

16 Kermagoret Charlene, Claudet Joachim, Derolez Valerie, Nugues Maggy M., **Ouisse Vincent**, Quillien Nolwenn, Baulaz Yoann, Le Mao Patrick, Scemama Pierre, Vaschalde Diane, Bailly Denis, Mongruel Remi (2019). How does eutrophication impact bundles of ecosystem services in multiple coastal habitats using state-and-transition models. Ocean & Coastal Management, 174, 144-153. https://doi.org/10.1016/j.ocecoaman.2019.03.028 **[IF=3.9]**

15 Richard Marion, Bec Beatrice, Vanhuysse Charles, Mas Sébastien, Parin David, Chantalat Camila, Le Gall Patrik, Fiandrino Annie, Lagarde Franck, Mortreux Serge, **Ouisse Vincent**, Rolland Jean-Luc, Degut Anaïs, Hatey Elise, Fortune Martine, Roque D'Orbcastel Emmanuelle, Messiaen Gregory, Munaron Dominique, Callier Myriam, Oheix Jocelyne, Derolez Valerie, Mostajir Behzad (2019). Changes in planktonic microbial components in interaction with juvenile oysters during a mortality episode in the Thau lagoon (France). Aquaculture, 503, 231-241. https://doi.org/10.1016/j.aquaculture.2018.12.082 **[IF=4.4]**

14 **Le Fur Ines**, de Wit Rutger, Plus Martin, Oheix Jocelyne, Derolez Valerie, Simier Monique, Malet Nathalie, **Ouisse Vincent** (2019). Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series . Marine Ecology Progress Series , 608, 13-32.https://doi.org/10.3354/meps12814 **[IF=2.6]**

13 **Le Fur Ines**, de Wit Rutger, Plus Martin, Oheix Jocelyne, Simier Monique, **Ouisse Vincent** (2018). Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth. Hydrobiologia, 808(1), 175-200 . https://doi.org/10.1007/s10750-017-3421-y **[IF=2.4]**

12 Richard Marion, Bourreau Juliette, Montagnani Caroline, **Ouisse Vincent**, Le Gall Patrik, Fortune Martine, Munaron Dominique, Messiaen Gregory, Callier Myriam, Roque D'Orbcastel Emmanuelle (2017). Influence of OSHV-1 oyster mortality episode on dissolved inorganic fluxes: An ex situ experiment at the individual scale. Aquaculture, 475, 40-51. https://doi.org/10.1016/j.aquaculture.2017.03.026 **[IF=4.4]**

11 Fiandrino Annie, **Ouisse Vincent**, Dumas Franck, Lagarde Franck, Pete Romain, Malet Nathalie, Le Noc Sandrine, de Wit Rutger (2017). Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. Marine Pollution Bulletin, 119(1), 132-144. https://doi.org/10.1016/j.marpolbul.2017.03.006 **[IF=6.7]**

10 de Wit Rutger, Rey-Valette Helene, Balavoine Juliette, **Ouisse Vincent**, Lifran Robert (2017). Restoration ecology of coastal lagoons: new methods for the prediction of ecological trajectories and economic valuation. Aquatic Conservation-marine And Freshwater Ecosystems, 27(1), 137-157. https://doi.org/10.1002/aqc.2601 **[IF=2.6]**

9 Migne Aline, Davoult Dominique, Spilmont Nicolas, **Ouisse Vincent**, Boucher Guy (2016). Spatial and temporal variability of CO_2 fluxes at the sediment-air interface in a tidal flat of a temperate lagoon (arcachon bay, France). Journal Of Sea Research, 109, 13-19. https://doi.org/10.1016/j.seares.2016.01.003 **[IF=1.9]**

8 Ouisse Vincent, Migne Aline, Davoult Dominique (2014). Comparative study of methodologies to measure *in situ* the intertidal benthic community metabolism during immersion. Estuarine Coastal And Shelf Science, 136, 19-25 . https://doi.org/10.1016/j.ecss.2013.10.032 **[IF=2.9]**

7 Coz Richard, **Ouisse Vincent**, Artero Celine, Carpentier A., Crave Alain, Feunteun Eric, Olivier J. -M., Perrin Benjamin, Ysnel F. (2012). Development of a new standardised method for sustainable monitoring of the vulnerable pink sea fan *Eunicella verrucosa*. Marine Biology , 159(6), 1375-1388 . https://doi.org/10.1007/s00227-012-1908-7 **[IF=2.5]**

6 Ouisse Vincent, Riera Pascal, Migne Aline, Leroux Cedric, Davoult Dominique (2012). Food web analysis in intertidal *Zostera marina* and *Zostera noltii* communities in winter and summer. Marine Biology, 159(1), 165-175 . https://doi.org/10.1007/s00227-011-1796-2 **[IF=2.5]**

5 Migne Aline, **Ouisse Vincent**, Hubas Cedric, Davoult Dominique (2011). Freshwater seepages and ephemeral macroalgae proliferation in an intertidal bay: II. Effect on benthic biomass and metabolism. Estuarine Coastal And Shelf Science, 92(1), 161-168 . https://doi.org/10.1016/j.ecss.2010.12.023 **[IF=2.9]**

4 Ouisse Vincent, Riera Pascal, Migne Aline, Leroux Cedric, Davoult Dominique (2011). Freshwater seepages and ephemeral macroalgae proliferation in an intertidal bay: I Effect on benthic community structure and food web. Estuarine Coastal And Shelf Science, 91(2), 272-281 . https://doi.org/10.1016/j.ecss.2010.10.034 **[IF=2.9]**

3 Ouisse Vincent, Migne Aline, Davoult Dominique (2011). Community-level carbon flux variability over a tidal cycle in *Zostera marina* and *Z. noltii* beds. Marine Ecology Progress Series, 437, 79-87 . https://doi.org/10.3354/meps09274 **[IF=2.6]**

2 Carpentier Alexandre, Artero Celine, **Ouisse Vincent**, Perrin Bertrand, Ysnel Frederic (2011). Monitoring the subtidal macroalgae percentage cover in an assessment of the human impact on diving sites in Brittany (France): direct estimation versus photography. Cahiers De Biologie Marine, 52(3), 247-252. **[IF= -]**

1 Ouisse Vincent, Migne Aline, Davoult Dominique (2010). Seasonal variations of community production, respiration and biomass of different primary producers in an intertidal *Zostera noltii* bed (Western English Channel, France). Hydrobiologia, 649(1), 3-11 . https://doi.org/10.1007/s10750-010-0254-3 **[IF=2.4]**

7.2. Présentations orales dans des congrès internationaux

30 Régis J, Richard M, Leray J, Bec B, **Ouisse V**, Munaron D, Grenz C, Deflandre B, Bancon-Montigny C, Freydier R, Delpoux S, Verdoux P, Techer I & Rigaud S. ASLO Aquatic Sciences Meeting. Juin 2023, Majorque, Espagne. "Impact of oxygen depletion on the biogeochemistry of benthic habitats in Mediterranean lagoons with contrasted eutrophication status"

29 Dupuy C, Agogué H, Amann B, Azémar F, Becu N, Bergeon L, Bertin X, Bocher P, Bout E, Brenon I, Carpentier A, Ceaux S, Chaumillon E, Choquet C, Colin B, Deborde J, Dubillot E, Emery C, Ferrari S, Gaucherel C, Geairon P, Gilbert S, Jeannin M, Jourde J, Kalenitchenko D, Lachaussée N, Lacoue-Labarthe T, Lanneluc I, Lavaud L, Lavaud S, Lefrancois C, Le Fouest V, Le Fur I, Long N, Mahieux PY, Mayen J, Marais C, Metzger E, Moncelon R, **Ouisse V**, Péreau JC, Pétillon J, Philippine O, Pineau P, Pignon-Mussaud C, Polsenaere P, Sabot R, Refait P, Reveillac E, Robin FX, Rouquette H, Sable S, Sauriau PG, Tackx M, Turcry P, Vagner M, Vincent J & Volto N. ECSA 59 symposium : Using the best scientific knowledge for the sustainable management of estuaries and coastal seas. September 2022, Kursaal, Spain. "Towards carbon neutrality by 2040 in La Rochelle metropolitan area (France): quantifying the role of wetlands and littoral zone in the capture and sequestration of blue carbon".

28 **Jones AG**, Schaal G, Derolez V, Simier M, **Boyé A**, **Smith N**, Desroy N, Fiandrino A, **Mouton T**, Creemers M, & **Ouisse V**. Webinaire. Novembre 2021. "Disentangling the effects of eutrophication and natural variability on macrobenthic communities in French coastal lagoons"

27 Derolez V, Mongruel R, Malet N, Bec B, Rey-Valette H, Fiandrino A, Lagarde F, Richard M, Kermagoret C, **Ouisse V**, Benidri S, Lautredou-Audouy N & Aliaume C. 18th Japanese-French Oceanography Symposium. Octobre 2020. Ebisu, Tokyo."Trajectory of Thau lagoon socio-ecosystem: 50 years of regime shifts and changes in bundle of ecosystem services during oligotrophication".

26 Menu M, Vaz S, Bajjouk T, Derolez V, Fiandrino A, Giraud A, Grillas P & **Ouisse V**. IX Eurolag Conference. Janvier 2020. Venise, Italie. "Mapping heterogeneity: an adapted habitat classification system for Coastal Mediterranean lagoons"

25 **Iotti M**, **Ouisse V**, Bouriat A & Darnaude A. IX Eurolag Conference. Janvier 2020. Venise, Italie. "Preferential micro-habitats of marine juvenile fish and drivers of their spatio-temporal distribution in the Prévost lagoon (NW Mediterranean)"

24 **Soissons L**, **Ouisse V**, Dakos V, Le Fur M, Morla J, Benedetti-Cecchi L & Rossi F. IX Eurolag Conference. Janvier 2020. Venise, Italie. "Before it is too" late: identifying seagrass response patterns and anticipating their loss in stressed environments"

23 Richard M, Le Gall P, Mortreux S, **Ouisse V**, Lagarde F, Fiandrino A, Fortune M, Munaron D, Messiaen G, Oheix J, Derolez V, Bellamy E, Foucault E, Devique G, Roque D'Orbcastel E, Bec B, Mostajir B, Hatey E, McKenzie D, Callier M, Montagnani C, Rolland JL, Mas S, Parin D, Keck, Dedet, Singevin, Bourreau J, Vanhuysse C, Chantalat C, Degut A, Neveu, Bourguoin, Fournier, Navarro, Zecchinon, Trabouriech, Galavielle, Avila, Chastel &, Anthony. AQUA 2018 - World Aquaculture Society Meetings. Août 2018, Montpellier, France. "Consequences of oyster mortality episodes on benthic-pelagic coupling in Thau lagoon (France)".

22 Richard M, Bec B, Vanhuysse C, Mas S, Parin D, Chantala C, Le Gall P, Fiandrino A, Lagarde F, Mortreux S, **Ouisse V**, Rolland JL, Degut A, Hatey E, Fortune M, Roque D'Orbcastel E, Messiaen G, Munaron D, Callier M, Oheix J, Derolez V, Mostajir B. AQUA 2018 - World Aquaculture Society Meetings. Août 2018, Montpellier, France. "Changes on planktonic microbial components in interaction with oyster juveniles during a mortality episode in the Thau Lagoon (FRANCE)".

21 **Ouisse V**, Bellamy E, Cotty C, Davy R, Delauney L, Dussud L, Fortune M, Laës-Huon A, Le Floc'h E, Le Fur I, Le Piver D, Mas S, Messiaen G, Munaron D, Parin D, Richard M, Rodellas V, Rousseaux P & Stieglitz T. European Conference on Scienti#c Diving. Mars 2017. Funchal, Portugal. "Automatic benthic chambers in coastal environment: towards high frequency measurements".

20 Ysnel F, **Ouisse V**, **Marchand-Jouravlef I**, Fiandrino A & Feunteun E. European Conference on Scientific Diving. Mars 2017. Funchal, Portugal. "Structural responses of eelgrass beds (*Zostera marina*) to the scraping mooring chain movements intensity in permanent anchorage areas: a new request for eco-mooring".

19 Richard M, Bourreau J, Montagnani C, **Ouisse V**, Le Gall P, Fortune M, Messiaen G, Munaron D, Callier M, McKenzie D, Mortreux S, Lagarde F, Parin D, Mas S, Mostajir B, Bec B, Rolland JL, Chiantella C, Fiandrino A, Derolez V, Oheix J, Roque D'Orbcastel E. AE2016 - Aquaculture Europe 16 "Food for thought". Septembre 2016, Edinburgh, Scotland. "Dissolved fluxes: an *ex-situ* experiment at individual scale".

18 Vanhuysse C, Richard M, Bec B, Mostajir B, Hatey E, Mas S, Chiantella C, Parin D, Lagarde F, Le Gall P, Mortreux S, Messiaen G, **Ouisse V**, Fiandrino A, Chantalat C, Degut A, Callier M, McKenzie D, Derolez V, Oheix J, Roque D'Orbcastel E. AE2016 - Aquaculture Europe 16 "Food for thought". Septembre 2016, Edinburgh, Scotland. "Influence of infection and mortality of oyster spats on planktonic communities: an in situ experiment in the Thau lagoon (France)"

17 **Le Fur I**, **Ouisse V**, Plus M & de Wit R. Mediterranean Conservation Sciences Conferences. Mars 2016. Tour du Valat, Arles. "The spatial distribution of macrophytes in the French Mediterranean lagoons".

16 **Le Fur I**, **Ouisse V**, Simier M, Malet N, Oheix J, Derolez V, Plus M & de Wit R. V Eurolag Conference. Mars 2016. Murcia, Espagne. "Ecological successions of macrophytes during the restoration process of French Mediterranean coastal lagoons".

15 **Ouisse V**, **Perron C**, Fiandrino A, Oheix J, Giraud A & Rochette S. V Eurolag Conference. Mars 2016. Murcia, Espagne. "Potential distribution of *Zostera noltei* in Mediterranean French lagoons".

14 Derolez V, Fiandrino A, **Ouisse V**, **Pataccini-Alvarez M**, Cesmat L, de Wit R & Malet N. V Eurolag Conference. Mars 2016. Murcia, Espagne. "Historical restoration trends of the Thau lagoon in response to changes in anthropogenic nutrient inputs".

13 Massey JL, Pasqualini V, Baldi Y, Bec B, Derolez V, Fiandrino A, Garrido M, Orsoni V, Rébillout P, **Ouisse V**, de Wit R, Durieux E, Malet N. 7th Eurolag. March 2016. Murcia, Spain "From seascape to habitat functioning: An ecosystem based approach to assess the status of Mediterranean micro-estuaries".

12 Malet N, Massey JL, Garrido M, Pasqualini V, Bald Y, Orsoni V, Rebillout P, Bec B & **Ouisse V**. ECSA 55, Septembre 2015. Londres, Grande-Bretagne. "Resource sudsidles across a micro-temporary estuary to oligotrophic Mediterranean coastal bay (Santu bay, Agriates, Corsica Island)".

11 Richard M, Bourreau J, Montagnani C, **Ouisse V**, Le Gall P, Fortune M, Munaron D, Callier M, Messiaen G, Mortreux S, Lagarde F, Rolland JL, Chiantella C, Fiandrino A, Derolez V, Oheix J, Roque D'Orbcastel E. Aquaculture 2015 - Cutting Edge Science in Aquaculture. Août 2015. Montpellier, France. "Influence of mortality events of oyster spats on biogeochemical fluxes: first experiment results at individual scale".

10 Schaal G, **Boye A**, Derolez V, Simier M & **Ouisse V**. ABEC, Août 2015. Liverpool, Grande-Bretagne. "Disentangling the effects of eutrophication and natural variability on benthic community structure in French Mediterranean lagoons".

9 **Ouisse V**, **Perron C**, Fiandrino A, Giraud A & Rochette S. 4th Mediterranean Seagrass Workshop. May 2015. Oristano, Italie. "Potential distribution of *Zostera noltei* in Mediterranean French lagoons"

8 Balavoine J, Diop H, Rey-Valette H, Lifran R, **Ouisse V** & de Wit R. Resilience, Juillet 2014. Montpellier, France. "Ecological restoration and its socioeconomic valuation for back-shifting ecosystem states in coastal lagoons towards a desired state featuring Magnoliophyta vegetation".

7 **Ouisse V**, Fiandrino A, de Wit R, Munaron D, Le Noc S, Fortune M, Oheix J, Jouanneaud C, **Baleux M**, Durozier M, Garcia N, Lagadec V, Raimbault P, Buscail R, Aubert D, Giraud A, Barral M, Malet N. VI Eurolag & VII Lagunet Conference. Decembre 2013, Lecce, Italy. "Benthic compartment in eutrophied Mediterranean lagoons : nutrient sink or sources?".

6 Derolez V, Fiandrino A, Baehr A, Munaron D, **Ouisse V**, Malet N, Kloareg M, Cadoret M, Bissery C, Hebert M, Barral M & Moragues L. VI Eurolag & VII Lagunet Conference. Decembre 2013. Lecce, Italie. "12 years of eutrophication monitoring on French lagoons (Languedoc-Roussillon, France): relevance of an assessment tool to highlight restoration paths".

5 Leruste A, **Ouisse V**, Zilius M, Bec B, Fiandrino A, Malet N, Le Noc S, Pilkaityte R, Razinkovas-Baziukas A & de Wit R. BSSC, Aout 2013, Littuanie. "Impact of nutrient reduction on phytoplankton and benthic metabolism in coastal lagoons; a first comparison between Mediterranean and Baltic lagoons".

4 **Ouisse V** , Fiandrino A, de Wit R, Munaron D, Fortune M, Oheix J, Jouhanneaud C, **Baleux M**, **Durozier M**, Garcia N, Raimbault P, Buscail R, Aubert D & Malet N. CIESM. Octobre 2013. Marseille, France. "Benthic compartment in eutrophied mediterranean lagoons: nutrient sink or sources?".

3 Fiandrino A, de Wit R, Dumas F, Lagarde F, Malet N, Le Noc S & **Ouisse V**. CIESM. Octobre 2013. Marseille, France. "Mixing volume: a hydrodynamic indicator for ecological studies".

2 **Ouisse V**, Migné A & Davoult D. 39 th Benthic Ecology Meeting. Mars 2010. Wilmington, NC, USA. "Seagrass community metabolism in intertidal areas: in situ measurements on *Zostera marina* and *Zostera noltii* over a tidal cycle".

1 Thouzeau G, Abril G, Migné A, Davoult D, Clavier J, Amice E, Boucher G, Bujan S, Deborde J, Guérin F, Marc R, Masson A, **Ouisse V**, Robineau C & Spilmont N. XI International Symposium on Oceanography of the Bay of Biscay. Avril 2008. San Sebastian, Spain. "Spatial and temporal variability of CO_2 fluxes at the sediment-water, sediment-air and air-sea interfaces in the Arcachon Lagoon (France)".

7.3. Posters dans des congrès internationaux

7 **Bourdier C**, De Ronne E, Soissons L, de Wit R & **Ouisse V**. X Eurolag Conference, Juin 2023, Gdansk, Pologne. "Effects of the intensity of a spring heat wave on *Cymodocea nodosa* : An experimental approach".

6 Le Ray J, Bec B, Fiandrino A, Olla L, Lagarde F, Cimiterra N, **Ouisse V**, Rigaud S, Régis J & Richard M. Aquaculture America, Fevrier 2023, New Orleans, Louisiane. "Which benthic community prevents the development of anoxia under lagoonal oyster farming sites?".

5 Dupuy C, Agogué H, Amann B, Azémar F, Becu N, Bergeon L, Bertin X, Bocher P, Bout E, Brenon I, Carpentier A, Ceaux S, Chaumillon E, Choquet C, Colin B, Deborde J, Dubillot E, Emery C, Ferrari S, Gaucherel C, Geairon P, Gilbert S, Jeannin M, Jourde J, Kalenitchenko D, Lachaussée N, Lacoue-Labarthe T, Lanneluc I, Lavaud L, Lavaud S, Lefrancois C, Le Fouest V, Le Fur I, Long N, Mahieux PY, Mayen J, Marais C, Metzger E, Moncelon R, **Ouisse V**, Péreau JC, Pétillon J, Philippine O, Pineau P, Pignon-Mussaud C, Polsenaere P, Sabot R, Refait P, Reveillac E, Robin FX, Rouquette H, Sable S, Sauriau PG, Tackx M, Turcry P, Vagner M, Vincent J & Volto N. ECSA 59 symposium : Using the best scientific knowledge for the sustainable management of estuaries and coastal seas. Septembre 2022, Kursaal, San Sebastian, Spain. "Towards carbon neutrality by 2040 in La Rochelle metropolitan area (France): quantifying the role of wetlands and littoral zone in the capture and sequestration of blue carbon".

4 Ysnel F, Danet V, **Ouisse V**, Perrin B & Feunteun E. European Conference on Scientific Diving. Mars 2017. Funchal, Portugal. "Pratical use of subtidal epibiota indicator groups to access good ecological statute of Western French Marina".

3 Richard M, Montagnani C, **Ouisse V**, Bourreau J, Le Gall P, Fortune M, Munaron D, Messiaen G, McKenzie D, Mortreux S, Lagarde F, Parin D, Mas S, Mostajir B, Bec B, Rolland JL, Chantalat C, Chiantella C, Fiandrino A, Derolez V, Oheix J, Callier M & Roque d'Orbcastel E. Aquaculture. Septembre 2015. Montpellier, France. "Influence of mortality events of oyster spats on biogeochemical fluxes: first experiment results at individual scale".

2 **Ouisse V**, Fiandrino A, Malet N, Munaron D, Fortune M, Oheix J, Baleux M, Lagarde F, Le Noc S, de Wit R. 5 th annual Sino-FrEnch program for Environment and sustainable Development. Octobre 2012. Montpellier, France."Phosphorus and nitrogen future in eutrophised mediterranean lagoons".

1 **Ouisse V**, Migné A & Davoult D. Advancing the Science of Limnology and Oceanography (ASLO) meeting. Février 2009. Nice, France. "Seasonal variation of metabolism in *Zostera noltii* community".

7.4. Rapports scientifiques

29 Ouisse Vincent, Miramont Arthur, Bajjouk Touria, Cimiterra Nicolas, Derolez Valérie, Fontes Hugo, Giraud Anais, Vaz Sandrine (2023). Description méthodologique et analyse de la distribution des habitats en milieu lagunaire méditerrannéen. Projet CHAMILA – Partie 1. Ifremer, 64p + Annexe

28 Ouisse Vincent, Miramont Arthur, Bajjouk Touria, Cimiterra Nicolas, Derolez Valérie, Fontes Hugo, Giraud Anais, Vaz Sandrine (2023). Fiches descriptives des habitats en milieu lagunaire méditerranéen. Projet CHAMILA - Partie 2. Ifremer, 42p

27 Ouisse Vincent, Miramont Arthur, Bajjouk Touria, Cimiterra Nicolas, Derolez Valérie, Fontes Hugo, Giraud Anais, Vaz Sandrine (2023). Atlas Cartographique des habitats en milieu lagunaire méditerranéen. Projet CHAMILA - Partie 3. Ifremer, 80p

26 Ouisse Vincent, Aliaume Catherine, Amilhat Elsa, Badts Vincent, Bourdeix Jean-Hervé, Cheret Isabelle, Cimiterra Nicolas, Darnaude Audrey, Derolez Valérie, Faliex Elisabeth, Jadaud Angélique, Laugier Thierry, Metral Louisa, Millot Jade, Motte Marie, Nicolas Delphine, Orozco Lucie, Schull Quentin, Simier Monique, Simon Gaël, Vaz Sandrine, Villeneuve Rémi, Violette Hervé, Certain Grégoire (2023) Développement d'un indicateur poissons en lagune adapté au contexte français. Rapport final - Projet INPOLAG. 71p + Annexes

25 Ouisse Vincent, Aliaume Catherine, Derolez Valérie, Motte Marie, Vaz Sandrine, Certain Grégoire. (2023) Méthode d'évaluation du compartiment poissons des masses d'eau lagunaires. 11p

24 Ouisse Vincent, **Jones Auriane**, Creemers Marie, Derolez Valerie, Desroy Nicolas, Fiandrino Annie, Simier Monique, Schaal Gauthier (2022). Effet de l'eutrophisation sur la macrofaune benthique des lagunes méditerranéennes . Projet MALAG – Rapport final. R.ODE/UL/LERLR 22-21 . https://doi.org/10.13155/93667

23 Cimiterra Nicolas, Derolez Valerie, **Ouisse Vincent** (2022). Diagnostic du compartiment macrophyte dans 17 masses d'eau de transition lagunaires sur la période du plan de gestion 2016-2021 . ODE/UL/LER/LR. https://doi.org/10.13155/93222

22 Ouisse Vincent, Bourjea Jerome, **Iotti Marie**, Mignucci Alexandre, Darnaude Audrey (2022). Rôle des lagunes littorales dans le cycle biologique des poissons méditerranéens: comprendre pour mieux préserver . Projet NURSE – Rapport final. R.ODE/UL/LERLR 22-20. https://doi.org/10.13155/93668

21 Munaron Dominique, Gianaroli Camille, Cimiterra Nicolas, Derolez Valerie, **Ouisse Vincent**, Giraud Anaïs (2022). OBSLAG - Pesticides. Bilan 2020-2021 du suivi des lagunes méditerranéennes. Rapport de la Convention AERMC-Ifremer 2020, n° ODE/UL/LER-LR/22.12, aout2022. 90p. https://archimer.ifremer.fr/doc/00795/90672/

20 Cimiterra Nicolas, Messiaen Gregory, **Ouisse Vincent** (2022). Stratégie pour la mise en place d'un Observatoire de la température et des herbiers dans les lagunes méditerranéennes françaises. Projet C2ZO. Rapport intermédiaire (Livrable 1). R.ODE/UL/LERLR 22-04 . https://archimer.ifremer.fr/doc/00761/87264/

19 **Durreau Alice**, Soissons Laura, **Ouisse Vincent** (2021). Effet des épisodes extrêmes en milieu méditerranéen stressé. Phase 1 : étude bibliographique . R.ODE/UL/LERLR 21-22 . https://doi.org/10.13155/80623

18 La Rivière Marie, Michez Noémie, Delavenne Juliette, Andres Salomé, Fréjefond Charlène, Janson Anne-Laure, Abadie Arnaud., Amouroux Jean-Michel, Bellan Gérard, Bellan-Santini Denise, Chevaldonné Pierre, Cimiterra Nicolas, Derolez Valerie, Fernez Thierry, Fourt Maïa, Frisoni Guy-François, Grillas Patrick, Harmelin Jean-Georges., Jordana Esther, Klesczewski Mario, Labrune Céline, Mouronval Jean-Baptiste, **Ouisse Vincent**, Palomba Laura, Pasqualini Vanina, Pelaprat Corinne, Pérez Thierry, Pergent Gérard., Pergent-Martini Christine, Sartoretto Stephane, Thibaut Thierry, Vacelet Jean, Verlaque Marc. (2021). Fiches descriptives des biocénoses benthiques de Méditerranée. UMS PatriNat (OFB-CNRS-MNHN), Paris : 660 pp. https://archimer.ifremer.fr/doc/00796/90751/

17 Motte Marie, **Ouisse Vincent**, Certain Gregoire (2020). Projet INPOLAG (Indicateur Poisson en Lagunes). Résultats de la première campagne d'Automne 2019 . R.ODE/UL/LER/LR/20.08. Rapport intermédiaire . https://archimer.ifremer.fr/doc/00630/74196/

16 **Ouisse Vincent**, Fiandrino Annie, Giraud Anais (2020). EXpertise sur les stocks SEDimentaires en milieu lagunairE. Projet EXSEDE . R.ODE/UL/LER/LR 20.13 . https://doi.org/10.13155/75435

15 Menu Marion, Vaz Sandrine, Bajjouk Touria, Derolez Valerie, Fiandrino Annie, Giraud Anais, Grillas Patrick, **Ouisse Vincent** (2019). Rapport final du projet CHAMILA (Cartographie des habitats en milieu lagunaire méditerranéen) . R.ODE/UL/LER/LR/19.34 . https://doi.org/10.13155/70545

14 Aliaume Catherine, Darnaude Audrey, Certain Gregoire, Derolez Valerie, **Ouisse Vincent** (2019). Synthèse bibliographique sur les bio-indicateurs « poissons » des eaux de transition dans le contexte DCE . Projet INPOLAG – Livrable 1. R.ODE/UL/LERLR 19-38 . https://doi.org/10.13155/93666

13 Derolez Valerie, Bec Béatrice, Munaron Dominique, Foucault Elodie, Fiandrino Annie, **Ouisse Vincent**, Messiaen Gregory, Hatey Elise, Connes Coralie, Soudant Dominique, Brun Melanie, Fortune Martine, Mortreux Serge, Serais Ophelie, Crottier Anais, Malet Nathalie (2019). OBSLAG 2018 - volet eutrophisation. Lagunes méditerranéennes (période 2013-2018). Etat DCE de la colonne d'eau et du phytoplancton, tendance et variabilité des indicateurs . RST/LER/LR/19.12 . https://archimer.ifremer.fr/doc/00507/61862/

12 Grouhel Anne, Chiffoleau Jean-Francois, Crochet Sylvette, **Ouisse Vincent**, Galgani Francois, Munaron Dominique (2018). Contamination chimique des sédiments des lagunes méditerranéennes françaises - Bilan de la Campagne ROCCHSED 2017 . RST-RBE-BE-2018-01 . https://doi.org/10.13155/57885

11 Gimard Antonin, Derolez Valerie, Oheix Jocelyne, **Ouisse Vincent**, Dijoux Laury (2018). Cahier des charges. Gestion des données DCE/OBSLAG acquises sur les lagunes méditerranéennes. Volet Macrophytes .

10 Fiandrino Annie, **Ouisse Vincent**, Bellamy Elise, Pete Romain (2017). Note sur le suivi d'une crue de la Berre. Lagune de Bages-Sigean . Rapport final de la convention n°16/3212408. R.INT.ODE/UL/LER-LR 17.15 .

9 Derolez Valerie, Gimard Antonin, Munaron Dominique, **Ouisse Vincent**, Messiaen Gregory, Fortune Martine, Poirrier Samuel, Mortreux Serge, Guillou Jean-Louis, Brun Melanie, Provost Charlotte, Hatey Elise, Bec Béatrice, Malet Nathalie, Fiandrino Annie (2017). OBSLAG 2016 - volet eutrophisation. Etat DCE des lagunes méditerranéennes (eau et phytoplancton, période 2011-2016). Développement d'indicateurs de tendance et de variabilité . RST-LER/LR 17.10 . https://archimer.ifremer.fr/doc/00386/49744/

8 Oheix Jocelyne, **Ouisse Vincent**, Munaron Dominique, **Le Fur Ines**, Derolez Valerie (2015). Etude de Ruppia cirrhosa dans la lagune de Canet-St-Nazaire. RST.ODE/UL/LER/LR/15-29. https://archimer.ifremer.fr/doc/00280/39091/

7 Derolez Valerie, Oheix Jocelyne, **Ouisse Vincent**, Munaron Dominique, Fiandrino Annie, Messiaen Gregory, Hubert Clarisse, Lamoureux Alice, Malet Nathalie, Fortune Martine, Berard Lucas, Mortreux Serge, Guillou Jean-Louis (2015). Suivi estival des lagunes méditerranéennes françaises - Bilan des résultats 2014 . RST/LER/LR/15.17 . https://archimer.ifremer.fr/doc/00273/38461/

6 **Ouisse Vincent**, Fiandrino Annie, Rochette Sebastien (2014). Rôle des Macrophytes dans la REStauration des milieux lagunaires : distribution spatiale de Zostera noltei (MARES1) . ODE/UL/LERLR 14-21 .

5 **Ouisse Vincent**, Fiandrino Annie, de Wit Rutger, Giraud Anaïs, Malet Nathalie (2014). DEvenir du Phosphore et de l'Azote dans un contexte de ResTauration des milieux lagunaires méditerranéens - DEPART - . R.INT.ODE/UL/LER-LR 2014-14-22 .

4 Ifremer (2014). Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2013 . RST/LER/LR/14.07 . https://archimer.ifremer.fr/doc/00210/32154/

3 Derolez Valerie, **Ouisse Vincent**, Fiandrino Annie, Munaron Dominique, Bissery Claire, Kloareg Maela (2013). Analyse statistique des données du RSL - Etude des trajectoires écologiques des lagunes entre 2001 et 2012 . RST-LER/LR 13-06 . https://archimer.ifremer.fr/doc/00173/28423/

2 **Ouisse Vincent**, Fiandrino Annie, de Wit Rutger, Malet Nathalie (2013). Restauration des écosystèmes lagunaires : évaluation du rôle du sédiment et des herbiers à phanérogames . RST/LERLR 13-09 . https://archimer.ifremer.fr/doc/00166/27774/

1 Fiandrino Annie, Derolez Valerie, **Ouisse Vincent**, Munaron Dominique, Kloareg Maela (2013). Analyse statistique des données du RSL. Etude des trajectoires écologiques des lagunes entre 2001 et 2011. Rapport d'étape . RST-LER/LR 13-05 .

7.5. Mise à disposition de jeux de données

11 Miramont Arthur, Menu Marion, Vaz Sandrine, **Ouisse Vincent** (2023). Carte de Température-Salinité des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau : critère 1 de la typologie d'habitats lagunaires du projet CHAMILA. IFREMER. https://doi.org/10.12770/aa238b1d-f9f0-4b82-b894-4713621c2714

10 Miramont Arthur, Menu Marion, Vaz Sandrine, **Ouisse Vincent** (2023). Carte du Substrat des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau : critère 2 de la typologie d'habitats lagunaires du projet CHAMILA. IFREMER. https://doi.org/10.12770/b887bc5c-0114-4f13-8624-4c47c095abbe

9 Miramont Arthur, Menu Marion, Vaz Sandrine, **Ouisse Vincent** (2023). Carte de la Zone Biologique des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau : critère 3 de la typologie d'habitats lagunaires du projet CHAMILA. IFREMER. https://doi.org/10.12770/c7e55cea-688b-48b2-b74b-85e3f61e7d4a

8 Miramont Arthur, Menu Marion, Vaz Sandrine, **Ouisse Vincent** (2023). Carte de l'Hydrodynamisme des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau : critère 4 de la typologie d'habitats lagunaires du projet CHAMILA. IFREMER. https://doi.org/10.12770/c39ba8d4-32c6-459d-bc23-3d2b9a5de989

7 Miramont Arthur, Menu Marion, Vaz Sandrine, **Ouisse Vincent** (2023). Carte du Niveau Trophique des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau : critère 5 de la typologie d'habitats lagunaires du projet CHAMILA. IFREMER. https://doi.org/10.12770/0fbf6e0e-697f-45db-a455-da73df48a2b2

6 Miramont Arthur, Menu Marion, Vaz Sandrine, **Ouisse Vincent** (2023). Carte de la Biologie des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau : critère 6 de la typologie d'habitats lagunaires du projet CHAMILA. IFREMER. https://doi.org/10.12770/a3f8dda9-c857-449f-91a1-830b95b52c75

5 Miramont Arthur, Menu Marion, Vaz Sandrine, **Ouisse Vincent** (2023). Carte des Habitats de niveau 6 des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau. IFREMER. https://doi.org/10.12770/3a8c573f-4cb3-418b-a342-df4aaefb4822

4 Miramont Arthur, Vaz Sandrine, **Ouisse Vincent** (2023). Carte des incertitudes liées à la définition des habitats de niveau 6 des lagunes méditerranéennes françaises listées au titre des masses d'eau de transition de la Directive Cadre sur Eau. IFREMER. https://doi.org/10.12770/5f928677-129f-451a-8de2-c3cb7c7b4449

3 Petton Sébastien, Pernet Fabrice, Le Roy Valerian, Huber Matthias, Martin Sophie, Mace Eric, Bozec Yann, Loisel Stéphane, Rimmelin-Maury Peggy, Grossteffan Emilie, Repecaud Michel, Quéméner Loïc, Retho Michael, Manach Soazig, Papin Mathias, Pineau Philippe, Lacoue-Labarthe Thomas, Deborde Jonathan, Costes Louis, Polsenaere Pierre, Rigouin Loic, Benhamou Jeremy, Gouriou Laure, Lequeux Joséphine, Labourdette Nathalie, Savoye Nicolas, Messiaen Gregory, Foucault Elodie, Lagarde Franck, Richard Marion, **Ouisse Vincent**, Voron Florian, Mas Sébastien, Giannecchini Léa, Vidussi Francesca, Mostajir Behzad, Leredde Yann, Kempf Valentin, Alliouane Samir, Gattuso Jean-Pierre, Gazeau Frédéric (2023). French coastal carbonate dataset from the CocoriCO2 project . SEANOE . https://doi.org/10.17882/96982

2 Motte Marie, Certain Gregoire, Vaz Sandrine, Amilhat Elsa, Bellamy Elise, Bourdeix Jean-Herve, Cheret Isabelle, Cimiterra Nicolas, Contournet Pascal, Darnaude Audrey, Derolez Valerie, Faliex Elisabeth, Gianaroli Camille, Iotti Marie, Jadaud Angelique, Orozco Lucie, Metral Luisa, Nicolas Delphine, Simon Gael, Schull Quentin, Villeneuve Remi, Violette Herve, **Ouisse Vincent** (2023). Fish catches from French Mediterranean lagoons INPOLAG surveys (2019-2021). SEANOE . https://doi.org/10.17882/91950

1 Kermagoret Charlene, Claudet Joachim, Derolez Valerie, Nugues Maggy M., **Ouisse Vincent**, Quillien Nolwenn, Bailly Denis (2019). Dataset on marine ecosystem services supplied by coral reefs, sandy beaches and coastal lagoons in different eutrophication states . Data In Brief , 25, 104078 (10p.) . Publisher's official version : https://doi.org/10.1016/j.dib.2019.104078 , Open Access version : https://archimer.ifremer.fr/doc/00500/61145/

ANNEXES : PRINCIPALES PUBLICATIONS SCIENTIFIQUES

Iotti Marie, Darnaude Audrey M., Bouriat Alize, **Ouisse Vincent** (2023). Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon. Estuaries And Coasts, 46(1), 198-226. https://doi.org/10.1007/s12237-022-01102-9 **[IF=2.8]**

Derolez Valerie, Malet Nathalie, Fiandrino Annie, Lagarde Franck, Richard Marion, **Ouisse Vincent**, Bec Beatrice, Aliaume Catherine (2020). Fifty years of ecological changes: Regime shifts and drivers in a coastal Mediterranean lagoon during oligotrophication. Science Of The Total Environment, 732, 139292 (17p.). https://doi.org/10.1016/j.scitotenv.2020.139292 **[IF=10.2]**

de Wit Rutger, Leruste Amandine, **Le Fur Ines**, Maki Sy Mariam, Bec Beatrice, **Ouisse Vincent**, Derolez Valerie, Rey-Valette Hélène (2020). A Multidisciplinary Approach for Restoration Ecology of Shallow Coastal Lagoons, a Case Study in South France. Frontiers In Ecology And Evolution, 8(108), 20p. https://doi.org/10.3389/fevo.2020.00108 **[IF=3.7]**

Le Fur Ines, de Wit Rutger, Plus Martin, Oheix Jocelyne, Derolez Valerie, Simier Monique, Malet Nathalie, **Ouisse Vincent** (2019). Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. Marine Ecology Progress Series, 608, 13-32.https://doi.org/10.3354/meps12814 **[IF=2.6]**

Le Fur Ines, de Wit Rutger, Plus Martin, Oheix Jocelyne, Simier Monique, **Ouisse Vincent** (2018). Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth. Hydrobiologia, 808(1), 175-200 . https://doi.org/10.1007/s10750-017-3421-y **[IF=2.4]**

de Wit Rutger, Rey-Valette Helene, Balavoine Juliette, **Ouisse Vincent**, Lifran Robert (2017). Restoration ecology of coastal lagoons: new methods for the prediction of ecological trajectories and economic valuation. Aquatic Conservation-marine And Freshwater Ecosystems, 27(1), 137-157. https://doi.org/10.1002/aqc.2601 **[IF=2.6]**

Ouisse Vincent, Migne Aline, Davoult Dominique (2011). Community-level carbon flux variability over a tidal cycle in *Zostera marina* and *Z. noltii* beds . Marine Ecology Progress Series , 437, 79-87 . https://doi.org/10.3354/meps09274 **[IF=2.6]**

Estuaries and Coasts
https://doi.org/10.1007/s12237-022-01102-9

Spatio-temporal Variation of Shallow Microhabitats and Associated Juvenile Fish Assemblages in a Mediterranean Lagoon

Marie Iotti[1,2] · Audrey M. Darnaude[3] · Alizé Bouriat[4] · Vincent Ouisse[2]

Received: 17 June 2021 / Revised: 31 March 2022 / Accepted: 6 June 2022

Abstract

Coastal lagoons are known to host numerous resident and migrant fish species. Spatio-temporal variation in abiotic and biotic conditions in these ecosystems results, however, in a mosaic of microhabitats that could differently affect juvenile growth and survival. To deepen our understanding of juvenile fish habitat requirements and their spatio-temporal use of lagoons, microhabitat characteristics and fish assemblages were monitored jointly in a small temperate lagoon (the Prévost lagoon), from March to October 2019. A total of 2206 juvenile fishes belonging to 22 species were collected. Resident lagoon species, especially *Atherina boyeri*, dominated the assemblage (74%), while, among migrant species, *Sparus aurata* (8%) and *Liza aurata* (5%) were the most represented. Changes in overall juvenile abundance were mainly temporal, following the seasonal shifts in water temperature, salinity, and chlorophyll *a* concentration (44.9% of the co-inertia). However, our results revealed that distinct types of microhabitats exist in small lagoons and that juvenile fish distribution among them is non-random. Indeed, fish species richness mainly differed among sampling sites in relation to their distance from the inlet and the complexity of the three-dimensional habitat structure (36.5% of the co-inertia). Juveniles preferentially selected microhabitats with medium to high structural complexity, which were essentially created by macroalgae. However, microhabitat preferences were both species and ontogenetic stage dependent, with more contrasting microhabitat requirements in young juveniles. These results underline the need for conservation measures to consider each lagoon as a dynamic mosaic of microhabitats with radically different importance for the juveniles of the various fish species that colonize them.

Keywords Juvenile fish · Ontogenetic stage · Microhabitat preference · Environmental factors · Nursery · Coastal lagoon

Introduction

Located at the land-sea interface, coastal lagoons are recognized as highly productive habitats (Kennish and Paerl 2010), supporting multiple ecosystem services, including fish production (Levin et al. 2001; Elliott and Hemingway 2002). They often host numerous resident fish and are colonized by the juveniles of varied migrant species (e.g., Ribeiro et al. 2012; Bruno et al. 2013; Rodríguez-Climent et al. 2013; Verdiell-Cubedo et al. 2013). Indeed, the high productivity and macrophyte cover of most coastal lagoons provide optimum food and shelter for juvenile fish (Levin et al. 2001), and their lower salinities can reduce osmoregulation costs to the benefit of growth (Potter et al. 1986). Therefore, many coastal lagoons match the definition of fish nursery habitats (Beck et al. 2001), including species of high commercial value (Franco et al. 2006b; Dufour et al. 2009; Grati et al. 2013; Isnard et al. 2015). This makes them key environments for the conservation of coastal fish populations. However, environmental conditions in these transitional ecosystems are highly disparate. For example, lagoon waters vary from oligohaline to hypersaline depending on the weather (rainfall, evaporation) and the intensity of local freshwater inputs or marine water intrusions (Barnes 1980; Alongi 1998; Tagliapietra et al. 2009). Water temperature is also highly variable in lagoons (Tagliapietra et al. 2009;

Communicated by Henrique Cabral

✉ Marie Iotti
marie.iotti@ifremer.fr

[1] ENGREF AgroParisTech, Paris, France

[2] MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France

[3] MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Montpellier, France

[4] Univ Brest, Ifremer, CNRS, Unité Biologie et Ecologie des Ecosystèmes marins Profonds (BEEP), Plouzané, France

Ifremer 2014) and often reaches extreme values that threaten local fauna and flora at some times of the year (Kennish et al. 2014). Given this variability, sustainable management of the fish populations that depend on lagoon ecosystems requires deepening our understanding of the relationship between lagoon environmental conditions and juvenile fish habitat requirements.

This is particularly true for the north-western Mediterranean lagoons, as most measures aimed at identifying, protecting, and managing key coastal ecosystems in the European Union consider them as a single homogeneous type of habitat (European Commission DG Environment 2013) while they differ highly, not only in terms of marine and terrigenous inputs (Fiandrino et al. 2017) but also in terms of substrate types, depths, macrophyte covers, and anthropogenic pressures (Pérez-Ruzafa and Marcos 2012; Sfriso et al. 2017). This leads to marked inter-lagoon differences in contamination levels, productivity, and eutrophication status (Pérez-Ruzafa et al. 2007a; Souchu et al. 2010; Munaron et al. 2012; Derolez et al. 2019). In addition, the environmental parameters (e.g., temperature, salinity, oxygen) in each lagoon tend to vary considerably throughout the year, with anoxic events and extremely high temperatures frequently observed in summer, and particularly low temperatures in winter (Christia and Papastergiadou 2007; Como and Magni 2009).

Ichthyofauna diversity and abundance differ among lagoons and throughout the year (Koutrakis et al. 2005; Manzo et al. 2016; Franco et al. 2019; Selfati et al. 2019). These variations are not only due to inter-specific differences in spawning periods (Tsikliras et al. 2010; Manzo et al. 2011), but also depend on the suitability of local environmental conditions for the needs and tolerances of the juveniles of each species (Pérez-Ruzafa et al. 2004, Rountree and Able 2007). To fully understand the relationship between environmental characteristics and juvenile fish densities in coastal lagoons, this suitability, and its temporal changes have to be studied. However, to go beyond the knowledge gathered so far (e.g.,Yáñez-Arancibia et al. 1994; Marshall and Elliott 1998; Cuadros et al. 2017), this has to be done at a much finer spatial scale than that of the whole lagoon. Indeed, most lagoon ecosystems consist of a dynamic mosaic of interconnected yet different micro-habitats (Nagelkerken et al. 2015). This is particularly true in Mediterranean lagoons where marked physico-chemical gradients and the alternation of patches of seagrass bed or macroalgae on varied types of substrates form a highly heterogeneous “seascape” (Le Fur et al. 2018; Menu et al. 2019). This fine-scale variability in environmental conditions modulates the composition and productivity of local prey communities and also affects juvenile fish physiology, behavior, and physical condition (Peterson et al. 2000, Pichavant 2001, Como et al. 2014), with potential consequences on their survival and growth rates (Bouchereau et al. 2000; Vasconcelos et al. 2010; Isnard et al. 2015). For example, the three-dimensional structure resulting from the presence of certain types of substrate (e.g., rocks) or macrophytes can, not only provide shelter from predation for juvenile fish (Thiriet 2014; Whitfield 2017), but also attract specific benthic invertebrates that they exploit as prey (Mistri et al. 2000; Woodland et al. 2019). As a result, the response of juvenile fish to habitat quality is species-dependent (Colombano et al. 2020) but also evolves with changes in the nutritional and protective needs of juveniles during growth (Dahlgren and Eggleston 2000; Félix-Hackradt et al. 2014). This implies both interspecific differences and intraspecific changes in the preferred microhabitats of juvenile fish (Vigliola and Harmelin-Vivien 2001).

To investigate these differences and deepen our understanding of the relationship between lagoon environmental conditions and the habitat requirements of juvenile fish, the present study simultaneously monitored fine spatio-temporal changes in environmental characteristics and the composition of juvenile fish assemblage within a small but typical Mediterranean lagoon. By characterizing the main drivers of juvenile fish abundance in this heterogeneous ecosystem and identifying the preferred lagoon microhabitats of juveniles for several fish species at different ontogenetic stages, we hoped to gather valuable information for species conservation and lagoon management, both at local and regional scales.

Material and Methods

Study Area

For this study, we chose the Prévost lagoon (43°30′N, 3°54′E), a small (2.4 km^2 area) and shallow (1.5 m deep) expanse of water of 2.7 Mm^3 permanently connected to the sea by a 30-m large, 393-m long, and 1.7-m deep straight canal located on its southern shore (Fig. 1). The mean daily volume of marine water entering the lagoon is about 0.6 Mm^3 (Fiandrino et al. 2012). The average daily net balance of water is, however, negative (-0.15 Mm^3) due to continuous inputs of brackish water from the Rhône-to-Sète canal, through three channels located on the northern and eastern sides of the lagoon. Local water salinities and temperatures vary from 25 to 39 and from 8 to 24 °C, respectively, with minima generally observed in the winter and maxima in the summer for both factors (Ifremer 2014). Although relatively small, the Prévost lagoon displays heterogeneous environmental conditions: in its western part, water salinity is highly variable and substrate composition ranges from sand to mud, whereas in its eastern part, the salinity is quite stable and muddy bottoms dominate (Menu et al. 2019). Even if

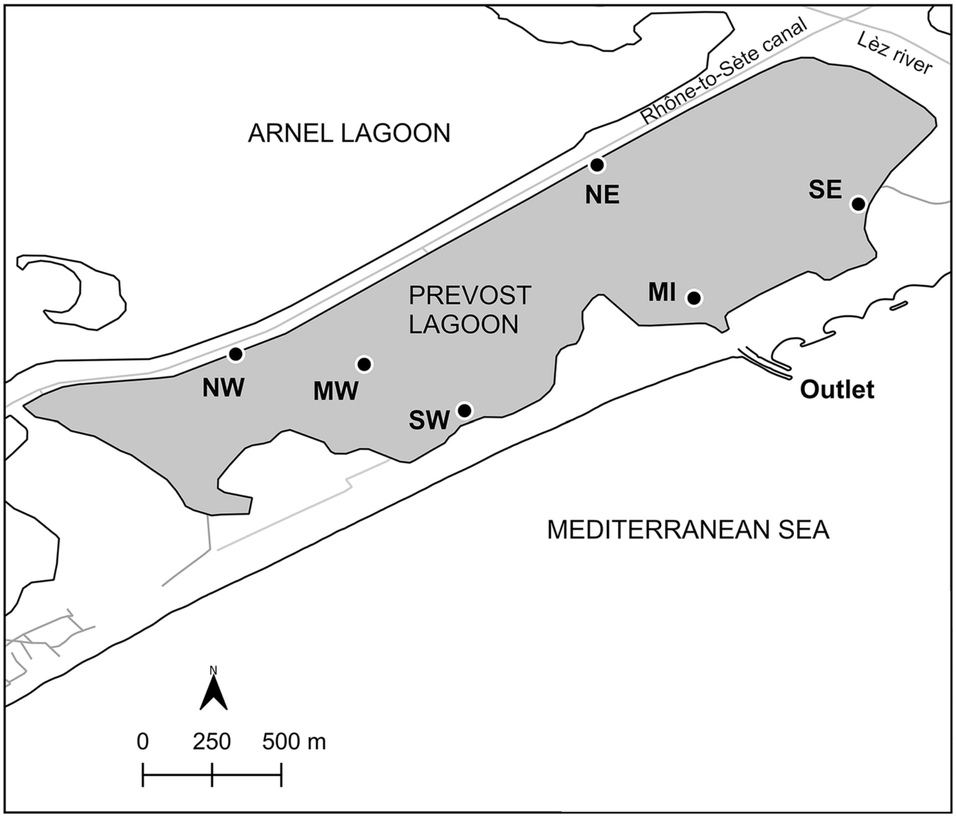


Fig. 1 Location of the six sites (NW, North-West; SW, South-West; MW, Middle-West; MI, Middle Inlet; NE, North-East; SE, South-East) surveyed in the Prévost lagoon (NW Mediterranean, France)

water quality in the lagoon has improved over the last decade (Leruste et al. 2016; Derolez et al. 2019), anoxic events are still frequently observed, especially during the warmer summer months (Bachelet et al. 2000). Eutrophication in the lagoon results in a general dominance of opportunistic green macroalgae on the bottom (Bachelet et al. 2000; Le Fur et al. 2018), but red and brown macroalgae and seagrass meadows are also present in certain areas (Cimiterra et al. 2020).

To date, 61 fish species, all commonly found in French Mediterranean lagoons at the adult and/or juvenile stages, have been reported in the lagoon (Kara and Quignard 2018d). Among them, three residents (*Atherina boyeri*, *Pomatoschistus microps*, *Pomatoschistus minutus*) and two migratory species (*Anguilla anguilla* and *Engraulis encrasicolus*) represent about 90% of both the local juvenile and adult abundances (Bouchoucha et al. 2012). Although no specific studies have been conducted on fish juvenile assemblages, the other fish species reported are mainly migratory ones (Kara and Quignard 2018d) which essentially occupy the lagoon from early spring to late autumn each year (Quignard et al. 1984).

2.2 Sampling

To cover the main period for juvenile fish recruitment and lagoon use in the area (Quignard et al. 1984; Aliaume et al. 1993; García-Rubies and Macpherson 1995), sampling was carried out from March to October 2019. This allowed us to capture the early juvenile stages of most local fish species, including those that recruit in the second half of the winter (Kara and Quignard 2018a, b, c). Sampling was carried out at least once, if possible twice, per 2-month periods (period 1 = March–April, period 2 = May–June, period 3 = July–August, period 4 = September–October), at six sites distributed either along the shoreline (NW, SW, SE, and NE) or in the central part (MW and MI) of the lagoon (Fig. 1). These sampling sites were positioned to reflect not only the west–east salinity gradient of the lagoon, but also local differences in the nature of the substrate (in relation to shoreline use) and the distribution of macrophytes (Menu et al. 2019).

Microhabitat Characterization

For each sampling site, potential accessibility for marine migrants was defined as the shorter distance from the sea inlet when following the edges of the lagoon (DIST). It was assessed prior to sampling, using the Quantum GIS 3.2 software (QGIS.org 2021). On each sampling date, water temperature (TEMP in °C) and salinity (SALI) were measured using a digital multiparameter meter (Multi 3430 WTW) coupled with a standard IDS conductivity cell probe

(TetraCon® 925, WTW), and 2 L of water were collected in a plastic bottle and stored immediately in a cool box to assess local chlorophyll *a* concentrations (CHLA). Water depth (DEPT in cm) and seafloor type cover (i.e., rocks -ROCK-, bare sediment -SEDI-, pebbles -PEBB-, and/or bivalve shells -SHEL- in %) were estimated within nine quadrats (of 0.2 m^2 each) distributed at 3, 6, and 9 m from the shore along three parallel linear transects. These later were positioned perpendicular to the shoreline, approximately 50 m apart, in order to limit disturbance during monitoring and to account for the spatial variability of the habitat at each site. All the macrophytes species present were also sampled after evaluating their respective spatial coverage (MCOV, %) and the overall canopy height (HEIG in cm) in each quadrat. Macrophytes were kept frozen for later identification in the laboratory.

Fish Sampling

To avoid scaring them away during microhabitat description and reduce sampling bias, juvenile fish were always collected before habitat description, between 10 and 12 am. Sampling at each site was done along the three parallel transects described above. To limit sampling bias linked to differences in gear selectivity and provide a more comprehensive image of the juvenile fish assemblage, notably in sites with non-uniform substrates (macrophytes, rocks), three sampling gears were combined (Bryan and Scarnecchia 1992; Franco et al. 2012). For each transect, an 8-m-long beach seine (mesh size: 4 mm), covering an area of 28 m^2 per haul and targeting benthic and demersal juveniles, was first deployed once, perpendicularly to the shore. Then a 1.5-m diameter cast net (mesh size: 3 mm) targeting demersal and pelagic species was cast three times, at 3, 6, and 9 m from the shore. Finally, a dip net (opening: 0.07 m^2, mesh size: 1 mm) was used to catch the smallest fish from the boat and the bank (five attempts at different depths per transect, targeting visible juveniles when present).

Laboratory Analyses

For each site and sampling date, water chlorophyll *a* concentration (in µg L^{-1}) was determined using 1 L of water prefiltered through a 0.47 µm glass microfiber filter GF/F (Whatman®). For this, chlorophyll *a* was extracted in 90% acetone, gently mixed, stored at 6 °C for a minimum of 6 h in the dark, and centrifuged before analysis by spectrophotometry (Aminot and Kérouel 2004).

Macrophytes were identified down to the species level when possible, and the number of taxa corresponded to the macrophyte richness (MRICH). Their respective weights (MBIOM) were measured after drying them in an oven at 60 °C for at least 48 h and until a constant weight was reached.

Juvenile fish were identified down to the species level and measured to the nearest 0.1 mm. Mugilids were identified using the caeca dissection method of Farrugio (1975) and the melanophore patterns method (Minos et al. 2002) for individuals with total lengths between 20 and 30 mm. Species of the *Pomatoschistus* genus were distinguished according to scale arrangement (Kovačić 2020). For resident species, individual fish were considered as juveniles only when their total length was below that reported for sexual maturity in the area (see Annex 1 in the Appendix section).

Data Analyses

All data analyses were performed in R (in particular the packages Ade4, car, factoextra4, labdsv, Stats, and vegan), using 5% as the threshold for statistical significance. Transects were considered replicates for each sampling site. The number of replicates for each site per sampling period thus ranged from three, when only one sampling could be carried out in the corresponding 2 months (this was the case for MI during period 1, MW for all periods, and all sites during period 4), to six, when two samplings were successfully completed per period. To reduce the list of variables used for characterizing microhabitat diversity, a Pearson correlation test was applied to the 13 variables initially investigated (sediment cover, rock cover, pebble cover, shell cover, macrophyte cover, macrophyte richness, macrophyte canopy height, macrophyte biomass, depth, distance from the outlet, temperature, salinity, chlorophyll *a* concentration) and redundant ones (macrophyte canopy height, depth, pebble cover, shell cover) were removed from all analysis when Pearson correlation coefficient was superior to 0.7.

Univariate (ANOVAs) and two-way (ANOVA III type for unbalanced designs) analyses of variance, followed by Tukey's post hoc tests, were used to test for temporal and spatio-temporal differences in environmental variables. To approach the normal distribution for this, cover variables were transformed using a $\mathrm{sqrt}(x) - \mathrm{sqrt}(1 - x)$ transformation, except for macrophyte coverage, for which a $\log(x + 1)$ transformation was applied. To explore environmental variability and describe spatial and temporal environmental gradients in the lagoon, a principal component analysis (PCA) was performed on the mean values per site and per period of the variables describing the microhabitats. This multivariate method allows for the identification of the variables that contribute the most to dataset variability and their synthesis into new orthogonal variables called principal components (Abdi and Williams 2010). Due to the lack of salinity data for the stations MI and MW during period 1, their position in the PCA was estimated using the mean value of the other four other stations during this period. A post-PCA ascendant hierarchical classification based on Ward's clustering method (Ward 1963) was also performed to assess the number of distinct microhabitat types encountered by juvenile fish in the lagoon during the study period, i.e., the number of groups of sampling events (period-site pair) with similar environmental conditions. This was achieved using the "silhouette" method (Charrad et al. 2014). To be retained as a distinct microhabitat type, each group had to gather at least three sampling events. ANOVAs and Tukey's post hoc tests were used to compare environmental characteristics between microhabitat types.

Differences in juvenile fish assemblages were investigated using three parameters: species richness, global fish abundance, and relative species abundances. For this, species richness was estimated from the total number of species captured with the three fishing gears. However, because the abundance of fish in the dip net catches varied greatly depending on fishing conditions and the local presence or absence of juvenile schools at the time of sampling, global and relative abundances were derived only from beach seine and cast net captures only. Fish abundances were originally expressed as catch per unit effort (CPUE) by transect and sampling date, with each value corresponding to the total number of fish caught by the beach seine haul and the three net casts applied on each transect. However, species' relative abundances for each site and period were calculated by grouping data from all transects. The variability in fish assemblage composition among sampling periods and sites was first tested by performing a multivariate analysis (PERMANOVA) on species abundances and considering both factors (period and site) as fixed. Then, two-way analyses of variance (ANOVA III type for unbalanced designs) were used to assess spatio-temporal variations in both the species richness and the global abundance of the juvenile fish assemblage in the lagoon. Again, both factors (period and Site) were considered fixed for this and variables were log 10 $(x+1)$-transformed to approach the normality, if necessary. The effect of the sampling site was further investigated for each period separately, using univariate ANOVAs followed by Tukey's post hoc tests.

Species responses to environmental variation were investigated with a co-inertia analysis comparing mean juvenile abundances per site and period with concomitant mean values of all environmental variables. This multivariate method, commonly used to study species-environment relationships, compares faunistic and environmental data by analyzing the co-structure between them. This approach allows the identification of plans which optimize co-variance between species abundances and environmental variables. The more faunistic and environmental data have similar structures, the more the output of the co-inertia analysis (RV coefficient of similarity) is close to 1. This analysis is recommended when a large number of variables are used in comparison to the number of samples (Dolédec and Chessel 1994), as is the case in the present work. To limit bias in our results, rare fish species (i.e., those with less than five individuals collected over the whole study period) were not included in this analysis. Fish data collected at MI and MW stations during period 1 were excluded from this analysis due to the lack of salinity data.

Species' habitat preferences were investigated based on the list of distinct microhabitat types defined from the hierarchical clustering. For this, we used the Indicator Value (Indval) index (Dufrêne and Legendre 1997), which considers both the selectivity and the fidelity of a species to a type of microhabitat:

$\mathrm{Indval}_{ij} = A_{ij} \times B_{ij} \times 100$; where:

A_{ij} = average abundance of species i across microhabitats of type j / average abundance of species i across all types of microhabitats (relative abundance across types of microhabitats).

B_{ij} = number of microhabitats of type j where species i is present / number of microhabitats of type j (relative frequency across microhabitats of type j).

To account for interspecific differences in the time of lagoon use, the global Indval index for each species was calculated only for the microhabitat types available during the periods when its juveniles were captured in the lagoon. Fish data collected at MI and MW stations during period 1 were also excluded from this analysis as in the previous analysis on the species responses to environmental variation. When possible, this index was also used to assess ontogenetic changes in lagoon microhabitat preferences. For this, the juveniles of each species were split into up to three size classes (J1 to J3, hereafter referred to as "ontogenetic stages"), based on the available knowledge of the changes in habitat requirements (temperature and salinity ranges, preferred substrate and position in the water column) and diet type (e.g., benthivore, planktivore, detritivore, omnivore, piscivore) reported for its juveniles in the literature. Following the protocol from previous studies (e.g., Cattin et al. 2003; Van Hadler et al. 2007; Podani and Csányi 2010), rare species (i.e., with less than five individuals collected) were not included in this analysis and only ontogenetic stages with a minimum of three individuals were retained for the calculation of the Indval index per juvenile stage.

Results

In total, 2206 fish juveniles, with sizes ranging from 8.0 to 88.0 mm TL (except for *Anguilla anguilla* whose sizes ranged from 52.2 to 200.0 mm), were collected over our 8-month survey in the Prévost lagoon (Table 1). They belonged to at least 22 different species in Mediterranean coastal lagoons, classified as resident, migratory, or occasional. Among them, 41 juveniles from the genus *Liza* spp.

Table 1 List of all the fish species for which juveniles were captured in the Prevost lagoon during this survey and their main ecological guild: migrant species (M), marine straggler species (MS), and resident species (R) (Whitfield 1999; Mariani 2001; Koutrakis et al. 2005)

Species	Eco	Abundance								Frequencies		Total length (mm)	
		Period 1		Period 2		Period 3		Period 4		Seine	Cast net	Min	Max
		Nb	CPUE ± SD	Nb	CPUE ± SD	Nb	CPUE ± SD	Nb	CPUE ± SD				
Anguilla anguilla	M	8 (7)	0.2 ± 0.8	2 (2)	0.1 ± 0.2	1 (1)	0.0 ± 0.2	0 (0)	0.0 ± 0.0	0.05	0.02	52.2	200.0
Atherina boyeri	R	154 (154)	5.1 ± 7.7	133 (75)	2.3 ± 5.1	371 (360)	12.0 ± 24.8	846 (842)	46.8 ± 72.8	0.20	0.15	11.9	45.0
Belone belone	MS	0 (0)	NA ± NA	1 (0)	NA ± NA	0 (0)	NA ± NA	0 (0)	NA ± NA	NA	NA	57.7	57.7
Chelidonichthys lucerna	MS	0 (0)	0.0 ± 0.0	*2 (2)*	0.1 ± 0.3	0 (0)	0.0 ± 0.0	0 (0)	0.0 ± 0.0	0.01	0.00	52.8	61.3
Chelon labrosus	M	0 (0)	0.0 ± 0.0	*6 (1)*	0.0 ± 0.2	*18 (18)*	0.6 ± 2.6	0 (0)	0.0 ± 0.0	0.02	0.00	28.4	56.9
Dicentrarchus labrax	M	*1 (1)*	0.0 ± 0.2	*12 (12)*	0.4 ± 0.7	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	0.05	0.02	20.1	40.7
Diplodus puntazzo	M	0 (0)	0.0 ± 0.0	0 (0)	0.0 ± 0.0	0 (0)	0.0 ± 0.0	*1 (1)*	0.1 ± 0.2	0.01	0.01	19.8	198
Diplodus sargus	M	*4 (4)*	0.1 ± 0.6	*1 (1)*	0.0 ± 0.2	*6 (6)*	0.2 ± 0.9	*0 (0)*	0.0 ± 0.0	0.04	0.02	19.1	37.6
Engraulis russoi	MS	0 (0)	0.0 ± 0.0	0 (0)	0.0 ± 0.0	*8 (8)*	0.3 ± 1.5	*4 (4)*	0.2 ± 0.9	0.01	0.01	41.7	5.06
Gobius niger	R	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	*2 (2)*	0.1 ± 0.4	*0 (0)*	0.0 ± 0.0	0.01	0.00	22.0	29.6
Liza aurata	M	*84 (0)*	2.8 ± 10.4	*14 (14)*	0.4 ± 1.3	*1 (1)*	0.0 ± 0.2	*0 (0)*	0.0 ± 0.0	0.05	0.04	18.1	70.2
Liza ramada	M	*27 (27)*	0.9 ± 4.7	*25 (25)*	0.8 ± 3.0	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	0.04	0.00	27.5	54.5
Liza saliens	M	*2 (2)*	0.1 ± 0.3	*0 (0)*	0.0 ± 0.0	*89 (56)*	1.9 ± 9.1	*2 (2)*	0.1 ± 0.5	0.02	0.04	14.5	88.0
Liza spp.	M	*0 (0)*	NA ± NA	*1 (0)*	NA ± NA	*40 (0)*	NA ± NA	*0 (0)*	NA ± NA	NA	NA	8.0	19.4
Mugil cephalus	M	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	*74 (74)*	4.1 ± 17.4	0.01	0.01	23.4	29.0
Pomatoschistus marmoratus	R	*0 (0)*	0.0 ± 0.0	*2 (2)*	0.1 ± 0.3	*4 (4)*	0.1 ± 0.3	*29 (29)*	1.6 ± 3.9	0.02	0.06	18.9	27.7
Pomatoschistus microps	R	*0 (0)*	0.0 ± 0.0	*6 (5)*	0.2 ± 0.4	*28 (28)*	0.9 ± 2.8	*1 (1)*	0.1 ± 0.2	0.07	0.03	18.9	26.9
Salaria pavo	R	*3 (0)*	0.1 ± 0.3	*1 (1)*	0.0 ± 0.2	*8 (8)*	0.3 ± 0.6	*1 (1)*	0.1 ± 0.2	0.06	0.02	21.6	41.8
Sardina pilchardus	MS	*1 (1)*	0.0 ± 0.2	*0 (0)*	0.0 ± 0.0	*6 (6)*	0.2 ± 1.1	*0 (0)*	0.0 ± 0.0	0.02	0.00	52.1	77.9
Sarpa salpa	M	*1 (1)*	0.0 ± 0.2	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	0.01	0.00	29.4	29.4
Solea solea	M	*2 (2)*	0.1 ± 0.3	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	0.01	0.01	21.8	28.4
Sparus aurata	M	*159 (157)*	5.2 ± 6.8	*8 (8)*	0.2 ± 0.8	*0 (0)*	0.0 ± 0.0	*0 (0)*	0.0 ± 0.0	0.08	0.05	18.4	64.8
Syngnathus abaster	R	*0 (0)*	0.0 ± 0.0	*4 (2)*	0.1 ± 0.3	*0 (0)*	0.0 ± 0.0	*2 (2)*	0.1 ± 0.5	0.01	0.01	19.5	49.3

For each species, the total number of individuals caught with (*or without*) the use of the dip net, the mean abundance (CPUE ± standard deviations), the frequency of occurrence in the captures with the beach seine, and the cast net and the range in individual total lengths (mm) are presented for each sampling period (1, March–April; 2, May–June; 3, July–August; 4, September–October). In each case, *NA* indicates when juveniles were only captured with the dip net, which did not allow reliable assessment of mean abundances and frequency of occurrence were impossible to identify down to the species level due to their small size. As they were only captured with the dip net, they were not included in abundance estimates. This was also the case for the only juvenile from *Belone belone* captured and for some of the juveniles of varied species captured with all sampling gears (e.g., *Liza aurata*, *Liza saliens*, *Chelon labrosus*, *Sparus aurata*).

Juvenile abundance in the catches with the beach seine and cast net differed highly according to the species. The juveniles from occasional marine stragglers (*Chelidonichthys lucerna*, *Engraulis russoi*, *Sardina pilchardus*) represented only 1.0% of the total catch. The large majority of the juveniles caught in the lagoon, therefore, belonged to lagoon resident ($N = 6$) or marine migratory ($N = 13$) species, which represented 74.2% and 24.8% of the total abundance, respectively. Surprisingly, six species alone accounted for more than 90% of the total catch. The lagoon resident species *Atherina boyeri* in particular represented 69.9% of the total juvenile fish abundance, followed by five marine migratory species of commercial importance: the sparid *S. aurata* (8.1%) and the mugilids *L. aurata* (4.8%), *Mugil cephalus* (3.6%), *L. saliens* (3.0%), and *Liza ramada* (2.5%).

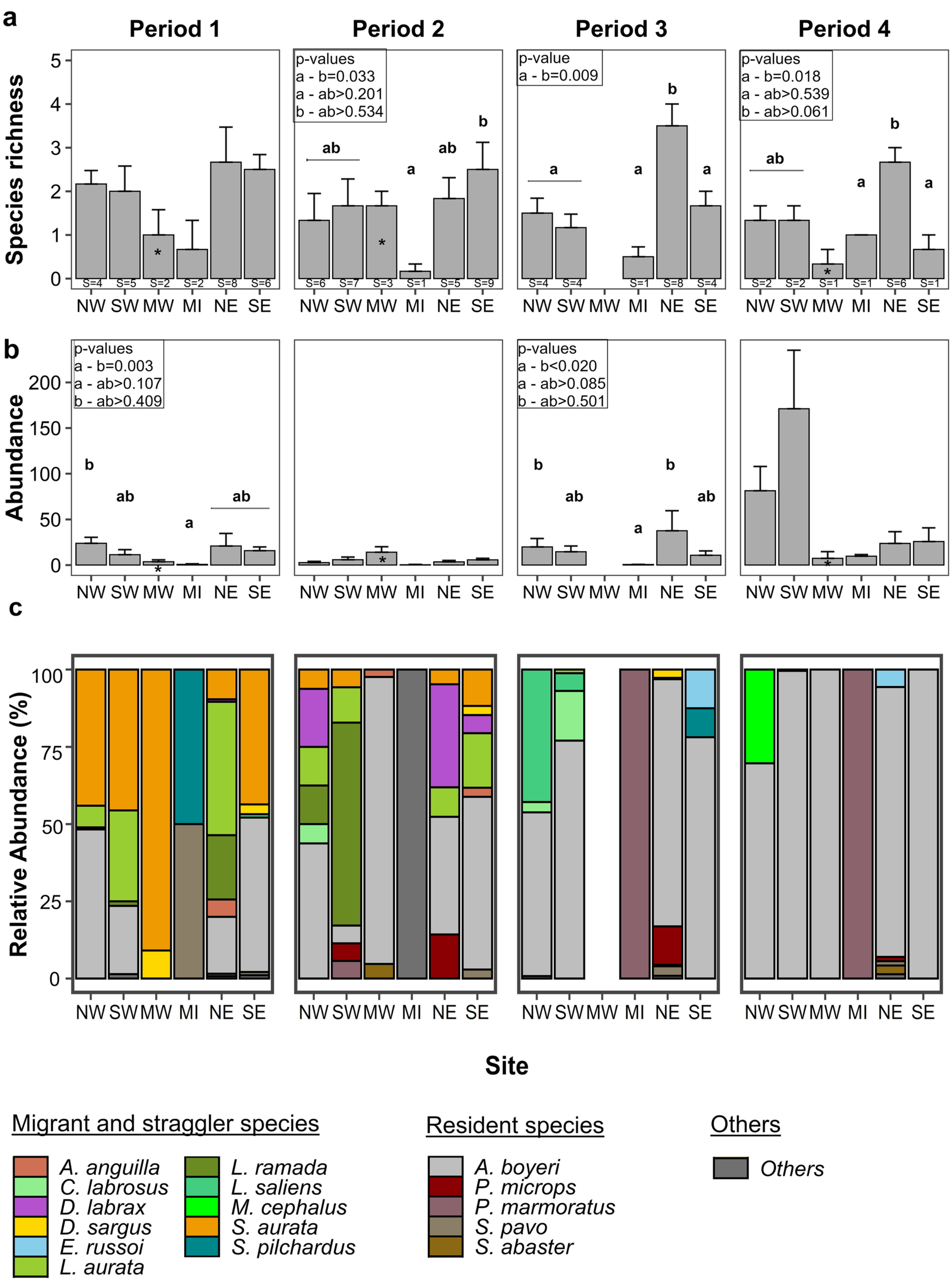
Variation in the Composition of the Juvenile Fish Assemblage

The composition of the juvenile fish assemblage in the lagoon varied highly with both the site (PERMANOVA, $p = 0.010$) and the sampling period (PERMANOVA, $p = 0.010$), with a significant interaction between the two factors (PERMANOVA, $p = 0.010$). This was largely due to significant spatial variation in species richness (ANOVA, $p < 0.001$, Fig. 2a), but also to marked temporal changes (ANOVA, $p < 0.001$) in the abundance of juvenile fish (Fig. 2b). Overall, juvenile fish abundance in the lagoon was minimum (4.6 ± 1.0 ind. transect^{-1}) in period 2 (Tukey's test, $p < 0.010$), and maximum (53.1 ± 17.4 ind. transect^{-1}) in period 4 (Tukey's test, $p < 0.001$). The values for periods 1 and 3 are similar and intermediate (Fig. 2b). Nonetheless, juveniles from migrant species were mostly captured during the first two sampling periods, accounting for 64.3% of the total catch in period 1, and 42.1% in period 2 (Table 1; Fig. 2c). Their proportion in the fish assemblage decreased in periods 3 (18.1%) and 4 (8.5%) when juvenile fish in the lagoon essentially belonged to resident species. As a result, the global composition of the juvenile fish assemblage differed markedly between sampling periods.

The spatial distribution of juvenile fish within the lagoon also differed from one period to the other (Fig. 2). In period 1, the total juvenile fish abundance was maximum (23.8 ± 6.5 ind. transect^{-1}) at NW, where four species were caught, and minimum (0.7 ± 0.7 ind. transect^{-1}) at MI, where only juveniles of the resident species *Salaria pavo* and the marine straggler *S. pilchardus* were captured (Fig. 2b, c). Juvenile abundance was also low (3.7 ± 2.0 ind. transect^{-1}) at MW, where only migratory sparids were collected, with *S. aurata* representing 91% of the catches, and *D. sargus* 9%. Species richness was higher at the four other sites (Fig. 2a), but species composition varied markedly among them. For example, although NW and SE displayed comparable proportions of juvenile *A. boyeri* (48 and 50%, respectively), *S. aurata* (44% at both sites), and *L. saliens* (1% at both sites), *L. aurata* juveniles were only captured at NW, while those of *D. sargus*, *S. pavo*, and of the migratory sparid *Sarpa salpa* were only found at SE (Fig. 2c). At SW, *S. aurata* juveniles were the most abundant (46%), with a similar proportion as in the NW and SE, but *A. boyeri* only represented 22% of global abundance, against 30% for *L. aurata* and *L. ramada*. Lastly, NE was the only site where the juvenile fish assemblage was dominated (64%) by mugilids (*L. aurata* and *L. ramada*) and where juveniles of *A. anguilla* and *Dicentrarchus labrax* were captured. It was also, with SW, one of the only two sites where juveniles of *S. solea* were captured.

In period 2, when the average global juvenile fish abundance in the lagoon was minimal, juvenile abundances were again the lowest (0.3 ± 0.3 ind. transect^{-1}) at MI (Fig. 2b), where only juveniles of the marine straggler *C. lucerna* were captured (Fig. 2c). Juvenile catches were the highest (14.0 ± 6.1 ind. transect^{-1}) at MW (Fig. 2b), where *A. boyeri* specimens dominated (93%) but juvenile *Syngnathus abaster* and *A. anguilla* were also captured (Fig. 2c). *Atherina boyeri* was also the most abundant species (38 to 56%) at SE, NE, and NW, but the juvenile fish assemblages at these three sites had different compositions. Indeed, the next most represented species (> 10%) at these sites were *D. labrax*, *L. aurata*, and *L. ramada* for NW, *L. aurata* and *S. aurata* for SE, and *D. labrax* and *Pomatoschistus microps* for NE. Finally, the SW site exhibited a singular fish assemblage, dominated by juveniles of *L. ramada* (66%). This site was also the only one where the three species most commonly observed in the lagoon (*A. boyeri*, *S. aurata*, and *L. aurata)* represented less than 25% of the global juvenile abundance and where juveniles of the resident gobiids *Pomatoschistus marmoratus* and *P. microps* were present simultaneously.

In period 3, overall juvenile fish abundance was minimal (0.5 ± 0.2 ind. transect^{-1}) at MI, where only specimens of *P. marmoratus* were captured (Fig. 2b and c). The NE and NW displayed significantly higher global juvenile abundances (37.5 ± 22.0 and 19.8 ± 9.3 ind. transect^{-1}, respectively), while the other sites exhibited intermediate values (Fig. 2b). At NE, *A. boyeri* dominated (80%) the juvenile assemblage (Fig. 2c), with the other resident species (*P. microps*, *P.*


a
Period 1
Period 2
Period 3
Period 4
Species richness
0
1
2
3
4
5
p-values
a - b=0.033
a - ab>0.201
b - ab>0.534
p-value
a - b=0.009
p-values
a - b=0.018
a - ab>0.539
b - ab>0.061
ab
a
ab
b
a
a
b
a
ab
a
b
a
*
*
*
S=4 S=5 S=2 S=2 S=8 S=6
S=6 S=7 S=3 S=1 S=5 S=9
S=4 S=4 S=1 S=8 S=4
S=2 S=2 S=1 S=1 S=6 S=1
NW SW MW MI NE SE
b
Abundance
0
50
100
150
200
p-values
a - b=0.003
a - ab>0.107
b - ab>0.409
p-values
a - b<0.020
a - ab>0.085
b - ab>0.501
b
ab
a
ab
b
ab
a
b
ab
*
*
*
c
Relative Abundance (%)
0
25
50
75
100
Site
Migrant and straggler species
A. anguilla
C. labrosus
D. labrax
D. sargus
E. russoi
L. aurata
L. ramada
L. saliens
M. cephalus
S. aurata
S. pilchardus
Resident species
A. boyeri
P. microps
P. marmoratus
S. pavo
S. abaster
Others
Others

◂**Fig. 2** **a** Mean species richness, **b** mean total abundance (ind. transect-1), and **c** taxonomic composition of the juvenile fish assemblages caught with the beach seine and the cast net at each site (for sites codes and locations, see Fig. 1) during the four sampling periods (1, March–April; 2, May–June; 3, July–August; 4, September–October). Note that the MW station could not be sampled in period 3. It was therefore not included in the statistical tests, as signalized by the "*" symbol. In **(a)** and **(b)**, error bars correspond to standard errors. Letters and *p* values indicate results of post hoc multiple comparisons (*t*-test performed after ANOVA and applied to species richness and fish abundance for each period) with *p* values inferior to 0.05 corresponding to significant differences. The absence of letters indicates when the variations found were not significant. In **(c)**, "Others" gathers seven species rarely observed in the lagoon, at least at the juvenile stage: *Diplodus puntazzo*, *Gobius niger*, *Sardina pilchardus*, *Sarpa salpa*, *Solea solea*, *Chelidonichthys lucerna*

marmoratus, and *S. pavo*) and the migratory sparid *D. sargus* accounting 17% and 3% of the total abundance, respectively. NW and SW shared the same species, but in different proportions: *A. boyeri* represented only 53% of the local juvenile catches at NW, against 77% at SW, and, while the rest of the catches mainly consisted of mugilids at both sites, *L. saliens* dominated at NW, and *C. labrosus* at SW. Lastly, besides *A. boyeri* juveniles (77%), the fish assemblage at SE essentially included juveniles of the two marine stragglers *E. russoi* (13%) and *S. pilchardus* (9%).

Finally, in period 4, when the average global juvenile fish abundance in the lagoon was maximal, local juvenile catches varied from 7.3 ± 7.3 ind. transect^{-1} at MW to 171.0 ± 64.1 ind. transect^{-1} at SW, but no significant spatial difference could be demonstrated (ANOVA, $p = 0.075$) due to the high inter-transect variability at most sites (Fig. 2b). Except for MI, *A. boyeri* largely dominated fish assemblages, accounting for 100% of total abundance at SW, MW, and SE, and 70% in the NW. This latter site was the only one where *M. cephalus* juveniles were captured in abundance (30%, Fig. 2c). Species richness at this period was thus low, particularly at MI where only juveniles of the resident gobiid *P. marmoratus* were captured (Fig. 2a and c). The only exception was NE (Fig. 2c), where the fish assemblage was dominated by *A. boyeri* (87%) but also included juveniles of other resident species (*P. microps*, *S. pavo*, *S. abaster*) and rare migratory species (*Diplodus puntazzo*, *E. russoi*).

Intra-lagoon Variation in Environmental Characteristics

During this 8-month study, the environmental conditions encountered in the Prevost lagoon were highly variable with, for example, local values ranging from 12.1 to 28.3 °C for water temperature, from 25.5 to 42.9 for water salinity, from 30 to 100%, and 0 to 48% for sediment and rock covers, respectively; from 0.5 to 5.5 µg L^{-1} for water chlorophyll *a* concentration; and from 2 to 100% for macrophyte cover. Despite this variability, the hierarchical clustering approach distinguished only three broad types of microhabitats in the lagoon (Fig. 3a; Table 2), whose respective extent and location varied over time due to the combined effects of spatial and seasonal variability of local environmental variables. Local differences in environmental conditions were primarily driven by inter-site variation in habitat characteristics, especially in three-dimensional (3D) habitat complexity (Table 2), which was essentially caused by spatial differences in local substrate type (e.g., % of sediment or rock cover, ANOVAs, $p < 0.001$) or in the percentage of macrophyte cover (ANOVA, $p < 0.001$). This is illustrated by the PCA on the environmental variables (Fig. 3b), where the first dimension (explaining 34.8% of the total variance) opposes sites with low 3D complexity (MI, SW, NE, and MW on the left), where sediment was the main substrate type (> 84% of average cover) and average macrophyte cover was low to medium (from 7 to 55%) in MI and NE, respectively, to sites with high 3D complexity (NW and SE on the right), characterized by the highest average rock (9–33%) and macrophyte (57–66%) covers (Table 3). However, annual seasonality also contributed significantly to the environmental variations in the lagoon. First, although macrophyte cover varied mainly by sampling site (ANOVA, $p < 0.001$), this parameter also showed some level of temporal variation at some locations (ANOVA, $p < 0.001$; Fig. 4). Macrophyte cover at SE was significantly the highest in periods 1 and 2 (with means of 80.3 ± 6.9 and 100.0 ± 0.0%, respectively), before decreasing in period 3 (to a minimal value of 23.3 ± 7.1%) and increasing again in period 4 (52.6 ± 1.7%). Although not significant due to high intra-site variability, temporal trends in macrophyte coverage were also observed for NW, MW, NE, and SW, with mean values ranging from 9 to 49% depending on the site (Fig. 4). When reflected in temporal fluctuations in macrophyte biomass (particularly marked at SE, MW, and SW, Table 3), these changes affected habitat characteristics by modulating habitat 3D structure. However, annual seasonality in the Prevost lagoon mostly contributed to environmental variation through temporal changes for the three water parameters investigated (Fig. 3). These changes were only statistically significant for temperature and chlorophyll *a* concentration (ANOVAs, $p < 0.023$), but salinities in the lagoon globally followed the same seasonal cycle as local temperatures, increasing from periods 1 to 3 and decreasing in period 4 (Fig. 5a and b). Temperature variations were most pronounced, ranging from 2.1 (at SW, in period 1) to 28.3 °C (at NW, in period 3), while local salinities varied

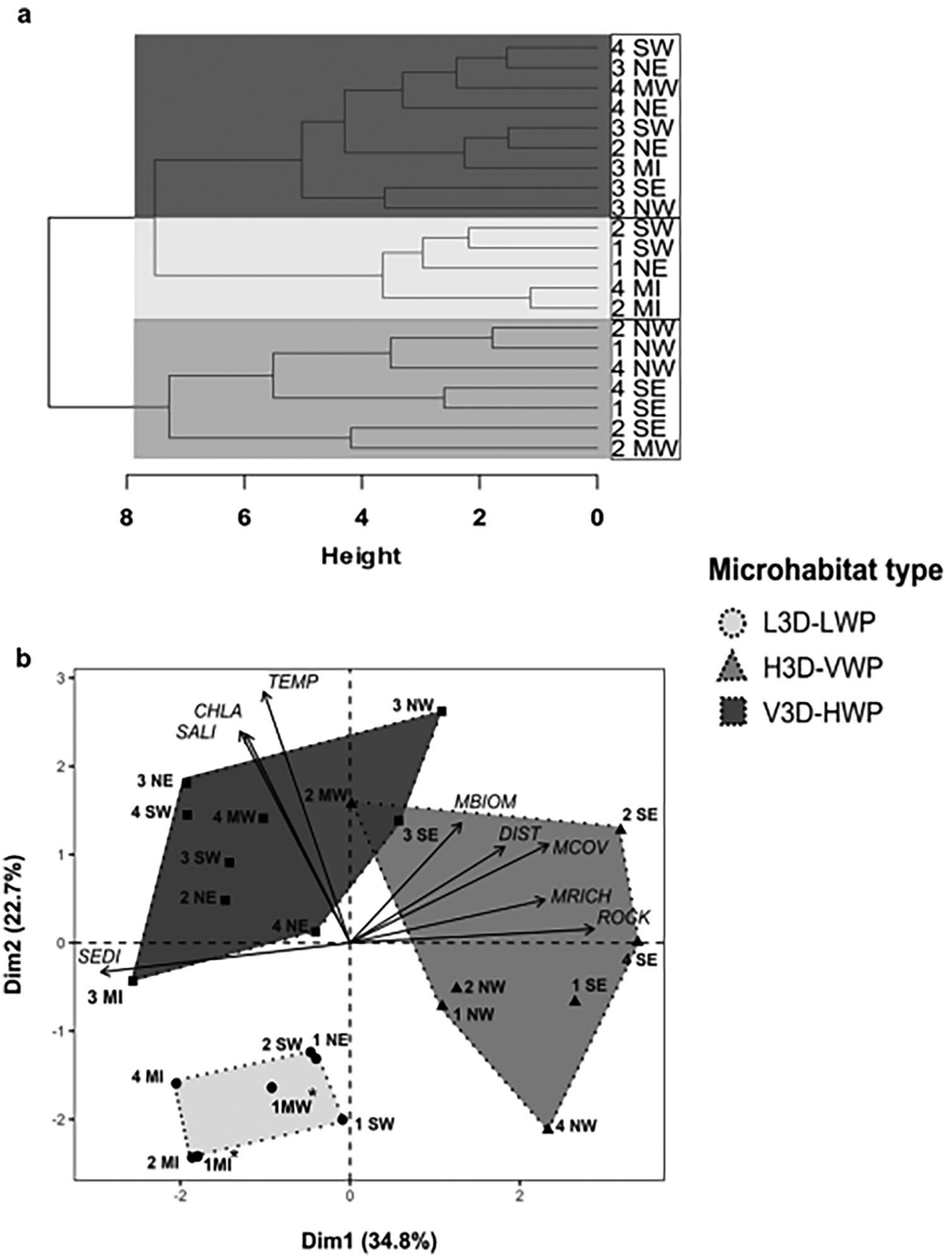


Fig. 3 **a** Hierarchical clustering of sampling events produced by Ward's method depending on their environmental conditions and **b** biplot of the principal component analysis (PCA) investigating environmental variation in the Prévost lagoon. Codes for samples (in bold) include both the sampling period (1, March–April; 2, May–June; 3, July–August; 4, September–October) and the site name (see Fig. 1 for abbreviations and site locations). Grey shades on both figures illustrate the three distinct groups of microhabitats retained: L3D-LWP for "low 3-dimensional complexity and low water parameters," H3D-VWP for "high 3-dimensional complexity and variable water parameters," and V3D-HWP for "variable 3-dimensional complexity and high water parameters". On (**b**), SALI, CHLA, TEMP, MBIOM, DIST, MCOV, MRICH, ROCK, and SEDI correspond to salinity, chlorophyll *a* concentration, water temperature, macrophyte biomass, distance to the inlet channel, macrophyte cover, rock coverage, and sediment coverage, respectively. Asterisk indicates the few sampling events for which the salinity data were missing. To allow positioning them on the PCA, these events were attributed to the mean overall salinity in the lagoon during this period. For period 3, the station MW was not sampled, so it does not appear on the graph. Salinity data were missing for the two sampling events marked by an asterisk, their position on the biplot was estimated using the mean value of the other four stations at this period

Table 2 Global mean (± standard deviation), maximal and minimal values observed for all environmental variables in the three microhabitat types identified by hierarchical clustering analysis (see Fig. 3 for variables and microhabitat codes)

Environmental variables	Code	Microhabitat type						*p* value
		● L3D-LWP		▲ H3D-VWP		■ V3D-HWP		
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	
Sediment cover (%)	SEDI	92.1 ± 11.4	75.3–100.0	56.6 ± 22.6	29.7–100.0	85.3 ± 22.6	34.3–100.0	0.014*
Rock cover (%)	ROCK	0.5 ± 1.0	0.0–2.3	21.2 ± 18.2	0.0–48.0	3.9 ± 7.7	0.0–23.2	0.009**
Macrophyte cover (%)	MCOV	28.5 ± 31.8	1.9–82.2	60.8 ± 22.2	38.8–100.0	36.1 ± 23.3	10.1–88.5	0.039*
Distance from sea outlet (km)	DIST	0.8 ± 0.5	0.2–1.2	1.9 ± 0.5	1.2–2.5	1.3 ± 0.7	0.2–2.5	0.015*
Temperature (°C)	TEMP	17.4 ± 2.3	14.1–19.7	18.9 ± 4.3	13.8–26.1	23.9 ± 3.0	17.0–28.0	0.005**
Salinity	SALI	34.7 ± 2.3	31.1–37.4	34.9 ± 4.2	25.5–37.4	39.2 ± 2.1	36.2–42.9	0.015*
Chlorophyll *a* (mg Chla m^{-2})	CHLA	1.1 ± 0.7	0.5–2.2	1.4 ± 0.4	0.8–2.1	3.7 ± 0.9	2.6–5.5	< 0.001***
Macrophyte biomass (g/quadrat)	MBIOM	2.2 ± 3.0	0.0–6.3	14.7 ± 19.1	0.8–47.5	4.4 ± 3.6	0.1–10.0	0.111 (ns)
Macrophyte richness	MRICH	3.0 ± 0.7	2.2–4.0	4.6 ± 1.3	3.0–7.0	3.7 ± 1.3	2.0–5.9	0.083 (ns)

Asterisks indicate significant effect of microhabitat type on environmental variables (ANOVA test) with different levels of significance: ns, not significant; *$p < 0.05$; **$p < 0.01$; *** $p < 0.001$

mainly between 31.1 (at SW, in period 1) and 42.9 (at NE, in period 3) only, except in period 4 when a minimum value of 25.5 was observed at NW. Chlorophyll *a* concentrations also showed a clear temporal trend (ANOVA, $p = 0.023$; Fig. 5c), with values at most sites starting relatively low (between 0.5 and 1.5 µg L^{-1}) in periods 1 and 2, then increasing significantly to values generally between 2.7 and 4.0 µg L^{-1} in period 3, and decreasing to values globally between 1.5 and 3.3 µg L^{-1} in period 4. The second dimension of the PCA (explaining 22.7% of the total variance) illustrates these temporal trends. Indeed, it contrasts the sampling events, mainly in periods 1 and 2, when the values for temperature, salinity, and chlorophyll *a* concentration were the lowest (Fig. 3b), with the sampling events in periods 3 and 4 with high values for all three water parameters (Fig. 3b).

As a result of these complex spatio-temporal variations in environmental conditions, some sites in the lagoon (e.g., NE, SW, MW) were assigned to a different microhabitat type during certain sampling periods (Fig. 3), and microhabitat type assignment remained stable over most of the survey period for SE, MI, NW, and NE only. The primary type of microhabitat available over the survey period (40% of sampling events, spread over the six study sites) was one with variable 3-dimensional complexity and high water parameters (V3D-HWP). It gathered all the sampling events from period 3, but also some from periods 2 and 4 (at MW and NE), characterized by the highest (Tukey's test, $p \leq 0.04$) water temperatures, salinities, and Chl *a* concentrations (Fig. 3; Table 2). Rock and macrophyte covers in this microhabitat type were variable but significantly lower (Table 2, Tukey's test, $p \leq 0.03$) than in the next most abundant (30% of sampling events, in all periods but only at three different sites) microhabitat type (characterized by a “high 3-dimensional complexity

Table 3 Global mean values (± standard deviations) at every sampling site (for site codes, see Fig. 1) for the nine variables retained to describe environmental variation in the Prévost lagoon, as well as their respective contributions to axis 1 and axis 2 of the PCA (see Fig. 3 for code)

Environmental variables	Code	Site						Contribution (%)	
		NW	SW	MW	MI	NE	SE	Axis 1	Axis 2
Sediment cover (%)	SEDI	60.7 ± 16.0	84.9 ± 22.4	100 ± 0.0	100 ± 0.0	98.4 ± 3.2	40.0 ± 20.1	23.4	0.5
Rock cover (%)	ROCK	8.5 ± 12.5	0.3 ± 1.5	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 5.5	33.0 ± 28.0	22.4	0.1
Macrophyte cover (%)	MCOV	57.3 ± 30.6	25.5 ± 17.9	40.7 ± 26.5	6.8 ± 10.4	55.2 ± 35.9	65.7 ± 33.6	14.8	5.2
Macrophyte richness	MRICH	4.6 ± 0.9	3.4 ± 1.0	3.3 ± 1.0	2.4 ± 0.7	3.5 ± 1.5	4.6 ± 1.6	14.3	1.0
Distance from sea outlet (km)	DIST	2.4 ± 0.0	1.3 ± 0.0	2.2 ± 0.0	0.2 ± 0.0	1.2 ± 0.0	1.3 ± 0.0	9.0	4.9
Macrophyte biomass (g/quadrat)	MBIOM	4.4 ± 3.9	5.9 ± 8.6	13.3 ± 23.8	0.7 ± 2.2	2.1 ± 3.5	18.8 ± 29.4	4.7	7.6
Salinity	SALI	34.8 ± 4.4	36.5 ± 3.4	39.2 ± 2.5	36.3 ± 1.9	38.2 ± 4.6	37.2 ± 1.6	4.6	23.8
Chlorophyll *a* (mg Chla m^{-2})	CHLA	2.3 ± 1.5	2.4 ± 1.9	2.2 ± 1.0	1.3 ± 1.0	3.2 ± 1.8	1.9 ± 1.8	4.1	23.3
Temperature (°C)	TEMP	19.7 ± 6.1	19.8 ± 6.2	21.4 ± 6.1	19.3 ± 4.3	21.1 ± 4.5	20.6 ± 4.1	2.8	33.6

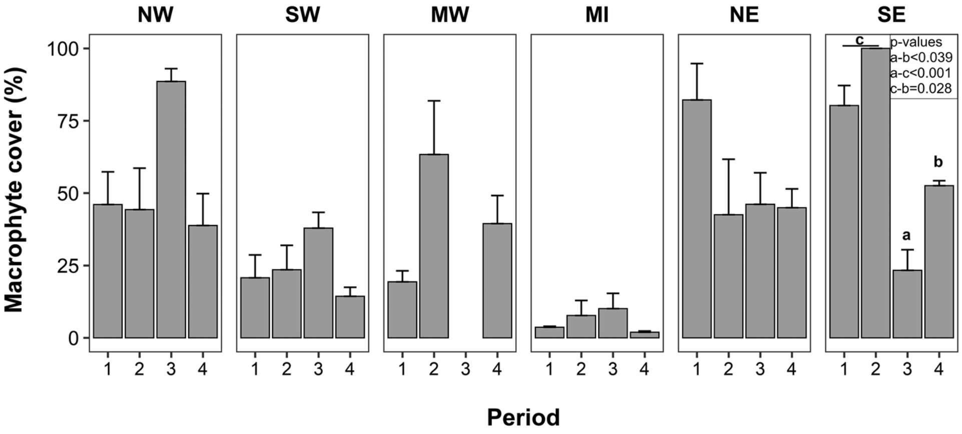


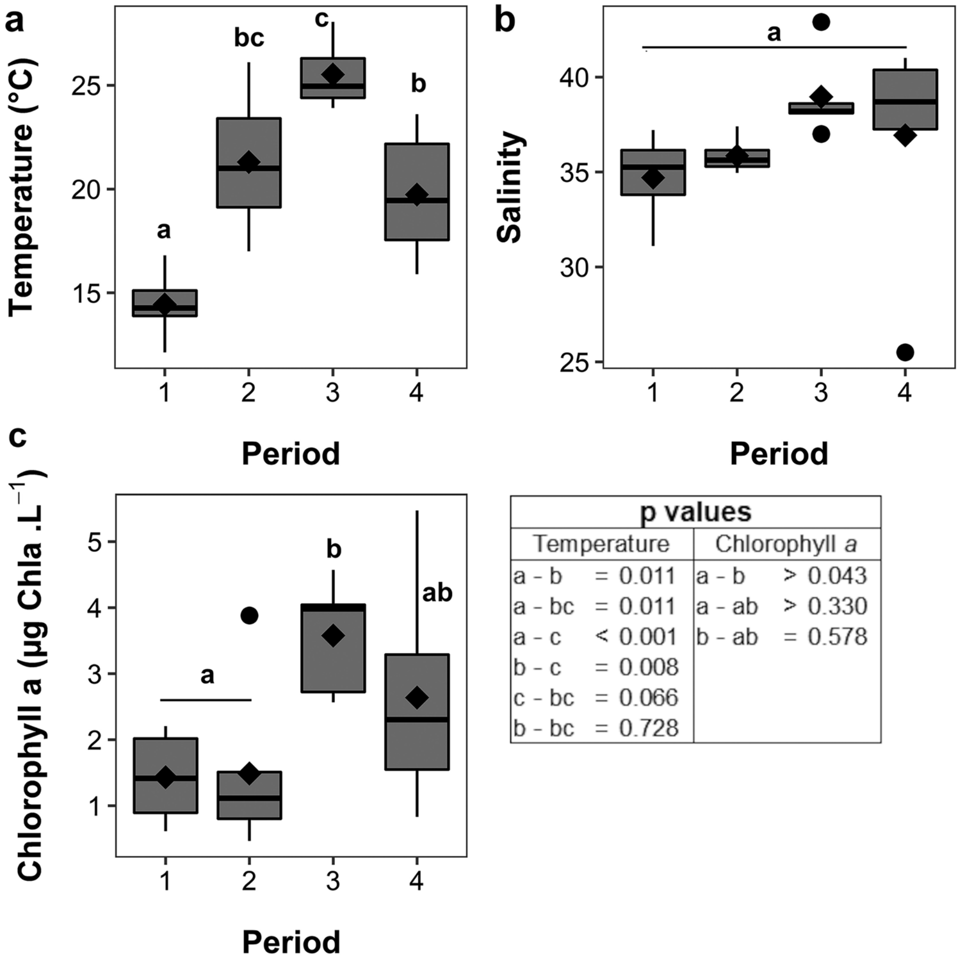
Fig. 4 Mean macrophyte cover at each sampling site (for site location refer to Fig. 1) over the four periods sampled (1, March–April; 2, May–June; 3, July–August; 4, September–October). Error bars correspond to standard errors. Note that the MW station could not be sampled in period 3, and it was therefore not included in the statistical tests. Letters and *p* values indicate results of post hoc multiple comparisons (*t*-test performed after ANOVA and applied to macrophyte cover at each site) with *p* values inferior to 0.05 corresponding to significant differences. The absence of letters indicates when the variations found were not significant

and variable water parameters" (H3D-VWP)). This latter grouped together all the sampling events where the highest values of 3-dimensional complexity were observed, i.e., most of those at NW and SE, plus those at MW during period 2, when the macrophyte cover at this site was the highest (Table 2; Fig. 3). Its values for water parameters were comparable (Tukey's test, $p > 0.640$) to those observed in the last microhabitat type identified (for "low 3-dimensional complexity and low water parameters" (L3D-LWP)), but their variability was much higher (Table 2). The L3D-LWP microhabitat type also represented 30% of the sampling events, but only at four different sites and in three sampling periods. Indeed, it regrouped sampling events characterized by the lowest temperature, salinity, and chlorophyll *a* values (observed during periods 1 and 2, but also at MI in period 4), essentially at sites with very low 3D structure (Fig. 3; Table 2). This was particularly clear for MI, where the average macrophyte cover and biomass were the lowest of all sites, and for SW in periods 1 and 2, when the macrophyte cover was less than 25% (Table 3; Fig. 4). This was also the case for NE in period 1: although the local macrophyte cover was 82% in this period, the corresponding macrophyte biomass was low (6.3 g quadrat^{-1}) as it was only due to the presence of flat green macroalgae (*Ulva* spp.) spread in a thin layer over the bottom.

Juvenile Fish Preferential Microhabitats

Our results revealed that juvenile fish distribution in the lagoon was non-random and largely resulted from variations in lagoon microhabitat preferences depending on the species. Due to the low abundance of juveniles in the captures at several sites and on many dates and to high inter-transect variability in the catches, variations in Indval indexes between microhabitat types could only be assessed for 16 species (Table 4). The corresponding results revealed that, among them, three species (*E. russoi*, *M. cephalus*, and *S. pichardus*) occurred in only one microhabitat type, seven species (*C. labrosus*, *D. sargus*, *L. ramada*, *L. saliens*, *P. marmoratus, P. microps*, and *S. abaster*) excluded one microhabitat, and six species (*A. anguilla*, *A. boyeri*, *D. labrax*, *L. aurata*, *S. pavo*, and *S. aurata*) frequented all three types of microhabitats. The maximum Indval values observed for each species suggested that V3D-HWP microhabitats were the most widely preferred in the Prevost lagoon. Indeed, they were preferentially used by *C. labrosus*, *D. labrax*, *E. russoi*, *L. saliens*, *P. microps*, *S. pavo*, and *S. pilchardus*, but also by *A. boyeri*, although the juveniles of this abundant resident species were also strongly associated with H3D-VWP microhabitats (Table 4). In comparison, only four of the 16 species (*A. anguilla*, *L. aurata*, *L. ramada*, and *P. marmoratus*) preferentially selected L3D-LWP microhabitats and two (*M. cephalus* and *S. aurata*) of those of the H3D-VWP type. Habitat preference for the juveniles of *D. sargus* and *S. abaster* was less clear, even though both species seemed to prefer V3D-HWP microhabitats to the H3D-LWP ones (Table 4).

The co-inertia analysis ($RV = 0.3$) allowed us to further specify the environmental parameters at the origin of microhabitat preference for each species (Fig. 6). Indeed, its first three dimensions explained 81.4% of the common variability between lagoon environmental parameters and



p values	
Temperature	Chlorophyll *a*
a - b = 0.011	a - b > 0.043
a - bc = 0.011	a - ab > 0.330
a - c < 0.001	b - ab = 0.578
b - c = 0.008	
c - bc = 0.066	
b - bc = 0.728	

Fig. 5 Evolution of **a** water temperature, **b** salinity, and **c** chlorophyll *a* concentration over the four periods sampled (1, March–April; 2, May–June; 3, July–August; 4, September–October). In each box plot, the dark full line represents the median and the dark square represents the average value for all stations. Box delineations correspond to the 25th and 75th percentiles, and vertical bars to the 5th and 95th percentiles. When present, outliers are indicated by dark circles

species abundances. Dimension 1 (44.9% of the total inertia) reflected an increasing gradient for all water parameters (temperature, salinity, and chlorophyll *a* concentrations), whereas dimension 2 (20.6% of the total inertia) opposed microhabitats close to the sea outlet and was characterized by high sediment cover and low macrophyte richness to microhabitats far from the sea outlet and combining high rock cover and high macrophyte richness (Fig. 6a). Dimension 3 (15.9% of the total inertia) reflected a joint gradient of increasing macrophyte cover (and biomass) and increasing distance from the sea outlet (Fig. 6b). Confronting the positions of environmental variables and juvenile fish abundances on the co-inertia graphs showed that most of the species preferentially observed in the V3D-HWP microhabitat type mainly responded to high values for water parameters, although differently (Fig. 6a). The juveniles of *A. boyeri* were found to mainly respond to high chlorophyll *a* concentrations (correlation coefficient = 0.52) and those of *S. pavo* to high salinities (0.44). *D. labrax* and *L. saliens* juveniles were mainly associated with higher temperatures (0.28 and 0.52, respectively), although they also positively responded to high macrophyte cover (0.25 and 0.28, respectively, Fig. 6b). For *P. microps*, higher juvenile abundances were associated with joint increases in water salinity (0.40) and chlorophyll *a* concentration (0.38, Fig. 6a), while for *E. russoi*, they positively responded to joint increases in chlorophyll *a* concentration (0.27) and macrophyte richness (0.27, Fig. 6a and b). Only *S. pilchardus* exhibited a higher sensitivity to substrate type than to water parameters, avoiding microhabitats with important sediment covers (− 0.40, Fig. 6b). The distribution of the two species associated with H3D-VWP microhabitats, *S. aurata* and *M. cephalus*, was drawn by high habitat 3D complexity but mainly also by the distance to the sea outlet (0.21 and 0.33, respectively), and by low water parameters, comparable to those observed in L3D-LWP microhabitats (Fig. 6). The position for *M. cephalus* illustrated the affinity of its juveniles with microhabitats (like SE and MW) with important rock (0.15) and low sediment (− 0.19) covers, while that of *S. aurata* mainly reflected its affinity with high macrophyte covers (0.21) and diversity

Table 4 Values for the Indval index illustrating the affinity of different fish species for the three microhabitat types identified by hierarchical clustering (see Fig. 3 for code)

	Indval index		
	L3D-LWP	**H3D-VWP**	**V3D-HWP**
A. anguilla	17.4	3.2	0.4
A. boyeri	1.1	30.9	45.3
C. labrosus	0.0	1.1	10.0
D. labrax	0.3	3.2	84.8
D. sargus	0.0	5.9	6.2
E. russoi	0.0	0.0	8.3
L. aurata	20.7	3.1	0.2
L. ramada	32.3	0.2	0.0
L. saliens	0.0	1.0	15.6
M. cephalus	0.0	16.7	0.0
P. marmoratus	43.5	0.0	0.3
P. microps	1.7	0.0	18.8
S. pavo	0.8	1.7	12.9
S. pilchardus	0.0	0.0	6.7
S. aurata	19.3	34.1	1.0
S. abaster	0.0	3.0	4.6

Note that data for the MW site in period 3 and the MI and MW sites in period 1 were excluded from this analysis because they were missing or incomplete

(0.19). *M. cephalus* responded negatively to high salinities (− 0.70) and *S. aurata* to high temperatures (− 0.61, Fig. 6a). Finally, juvenile distribution in the four species preferentially associated with L3D-LWP microhabitats was drawn by different environmental parameters. For both *L. aurata* and *L. ramada*, juveniles were found to be mainly sensitive to water parameters, but they mainly responded negatively to increasing temperature (− 0.37) or salinity (− 0.33), respectively (Fig. 6b). Conversely, the juveniles of *P. marmoratus* were preferentially attracted to microhabitats close to the sea outlet with a low macrophyte cover (− 0.36). Finally, the juveniles of *A. anguilla* seemed to globally prefer habitats with a significant macrophyte cover (0.46) but from only a few macroalgal species (of low 3D structure), as illustrated by their negative response to macrophyte richness (− 0.28).

Due to low sample sizes (see above), shifts in juvenile microhabitat preferences with growth could only be assessed for nine species. The corresponding results revealed different strategies for lagoon habitat use among them. Hence, only in two species (*L. aurata* and *L. ramada*) did the preferred microhabitat (L3D-LWP) remain unchanged across all the juvenile stages sampled (Indval = 6.7 to 18.3, Fig. 7). In all the remaining species, at least two different microhabitat types were successively preferred at the juvenile stage, but substantial differences in habitat preference were observed between species. The juveniles of *D. sargus* and *L. saliens* were found to both prefer V3D-HWP microhabitats at the J1 stage, and H3D-VWP microhabitats at later juvenile stages (Fig. 7). In *D. labrax*, although J2 and J3 juveniles were found in both H3D-VWP and V3D-HWP microhabitats, J3 juveniles exhibited a significant preference for the V3D-HWP microhabitat type (Indval = 55.6, Permutational test, $p = 0.004$, Fig. 7). In *A. boyeri* and *S. pavo*, the juveniles were largely restricted to V3D-HWP microhabitats at the J1 stage, but they then widened their environmental niche, using both V3D-HWP (Indval = 36.9 and Indval = 7.6, respectively) and H3D-VWP (Indval = 27.8 and Indval = 2.2, respectively) microhabitats at the J2 stage (Fig. 7). In *S. aurata*, all the juveniles preferred H3D-VWP microhabitats (Indval = 8.0–7.8), but their secondary preferential type of microhabitat shifted from L3D-LWP, at the J1 (Indval = 10.5) and J2 (Indval = 11.9) stages, to V3D-HWP, at the J3 stage (Indval = 5.1, Fig. 7). Finally, at least the J1 and J2 juveniles of *A. anguilla* clearly mainly used L3D-LWP microhabitats (Indval = 5.8 to 16.7), but only where significant macroalgal cover was observed. Overall, the J1 juveniles of most species seemed to prefer V3D-HWP (4 species) or L3D-LWP (4 species) microhabitats. H3D-VWP microhabitats were rather preferred by J2 (3 species) or J3 (2 species) juveniles, but sometimes alongside at least one other habitat (4 species).

Discussion

This fine-scale study of the microhabitats and juvenile fish assemblages of the Prévost lagoon allowed clarification of the value of lagoon habitats as nursery sites for Mediterranean fish. While previous works had highlighted differences in environmental quality between lagoons for juvenile fish growth and survival (e.g., Vasconcelos et al. 2007; Chaoui et al. 2012; Isnard et al.2015), very few attempts had been made so far to explain these differences and relate them to differences in lagoon habitat characteristics (Franco et al. 2006a, 2010; Escalas et al. 2015). In this respect, our results demonstrate that juvenile fish are not randomly distributed in coastal lagoons and that their preferential microhabitats differ according to both the species and the ontogenetic stage. This supports the hypothesis that the value of Mediterranean lagoons as nursery habitats for fish is defined at the microhabitat scale, with important consequences for both coastal fish conservation and lagoon management.

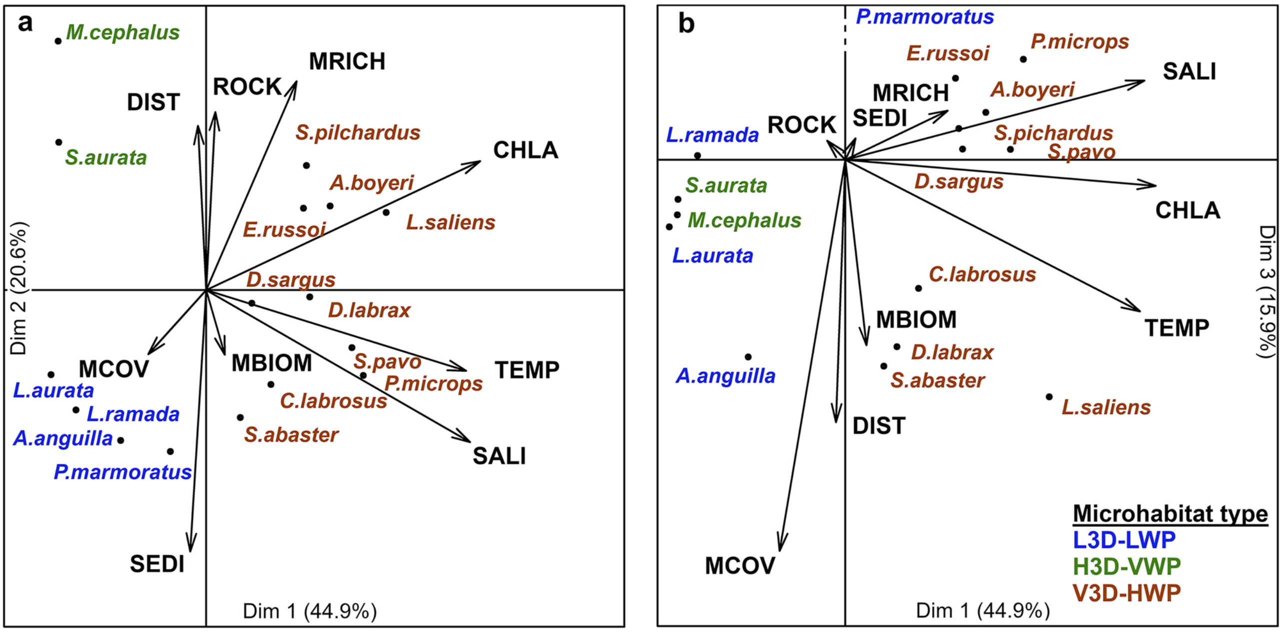
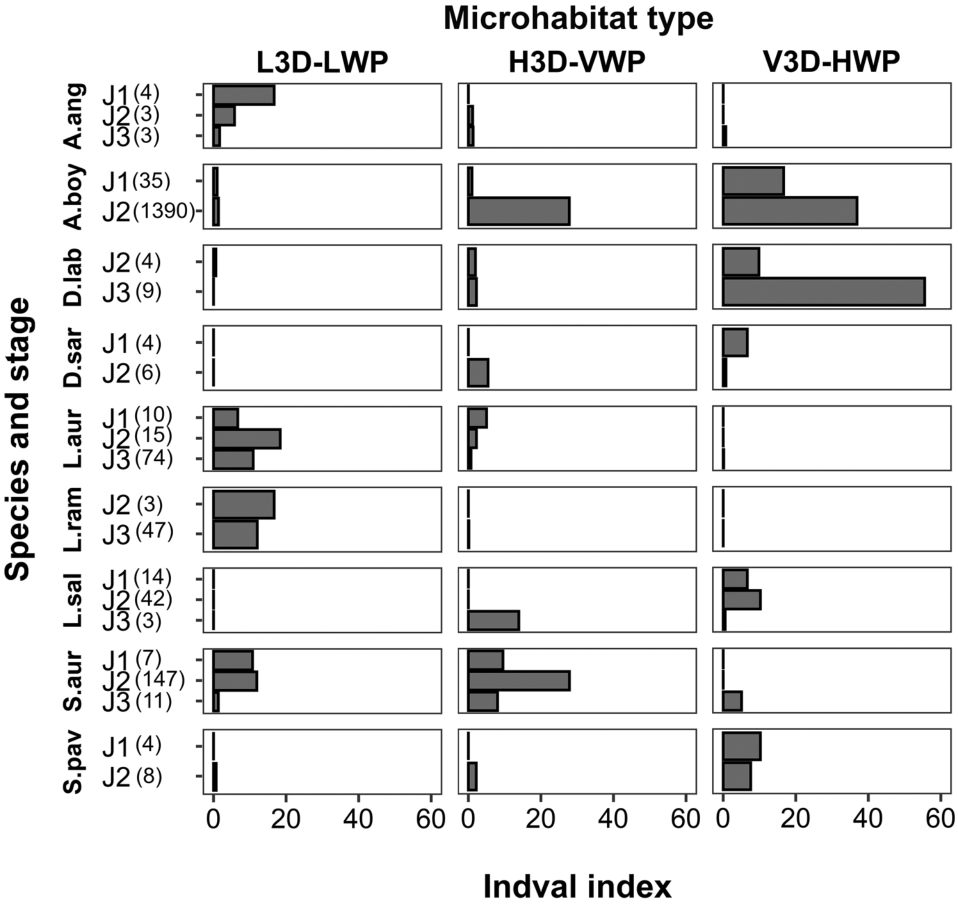


Fig. 6 Results from the co-inertia analysis confronting environmental variables (in bold) and juvenile fish abundances (in italic) for all periods grouped, projected along the first three dimensions: **a** plan formed by dimensions 1 and 2 and **b** plan formed by dimensions 2 and 3. Codes for environmental variables are indicated in Table 2. Colors refer to fish species' preferential type of microhabitat from IndVal analysis (see Table 4). In (**b**), note that a gap was added on the axis for dimension 3 in order to allow fitting of the projection for *P. marmoratus* on the graph. Note that data for the MW site in period 3 and the MI and MW sites in period 1 were excluded from the analysis because they were missing or incomplete

Image of the Juvenile Fish Assemblage

The 22 fish species in our captures mainly belonged to nine families (*Atherinidae*, *Moronidae*, *Anguillidae*, *Sparidae*, *Mugilidae*, *Gobiidae Blennidae*, *Soleidae*, and *Syngnathidae*) commonly reported in Mediterranean lagoons (e.g., Pérez-Ruzafa et al. 2004; Verdiell-Cubedo 2009; Embarek and Amara 2017). This diversity was consistent with the recent results from 2-year monitoring of the lagoon's fish assemblage using fyke nets (Bouchoucha et al. 2012) but represented only a small fraction of the total number of species (61) reported in the lagoon over the past 10 years (Kara and Quignard 2018d). This is not particularly surprising as our survey only targeted juvenile stages and several species only entered the lagoon as adults. Because our survey only lasted from March to October in 2019, we also probably missed several rare species and some migratory ones that only visit the lagoon during winter. Lastly, most of our catches were made in the shallower parts of the lagoon and with a small beach seine, which is most effective for sampling small, slow-swimming bentho-demersal fish (Franco et al. 2012). While small juvenile fish are known to concentrate along the shallow banks of coastal lagoons (Verdiell-Cubedo 2009), large fish tend to prefer deeper areas (Stoll et al. 2008). This partly explains the high numerical dominance of *A. boyeri* juveniles in our samples and the low representation of benthic species and large specimens in the catch. However, the selectivity of the beach seine may also be an important factor in this regard. Indeed, although this sampling gear provided the most comprehensive estimate of fish diversity at most sites, the use of cast and dip nets allowed us to obtain a more complete picture of the juvenile fish community at some sites. This confirmed the relevance of these two later fishing gears for sampling fish in the presence of rocks or thick macroalgal mats that reduce the efficiency of the beach seine (Říha et al. 2008). In particular, the dip net proved to be the most effective in catching the smallest juveniles of most migratory demersal species (e.g., *Sparidae* and *Mugilidae*), which usually live in small schools and flee or hide quickly at the slightest alarm. Unfortunately, the catches with this fishing gear were not standardized enough to be included in our quantitative analysis of fish preferential microhabitats. However, our results call for the combination of several fishing gears with different selectivity and operating modes when sampling lagoon juvenile assemblages, not only to provide a more realistic picture of the species present, but also to better evaluate the respective importance of lagoon

Fig. 7 Values for the Indval index illustrate the affinity of the successive juvenile stages (J1, J2, and J3) of different fish species for the three microhabitat types identified by hierarchical clustering (see codes in Fig. 2). For each species and ontogenetic stage, the number of individuals captured is indicated in parentheses. Abbreviations refer to species' names: A.ang, *Anguilla anguilla*; A.boy, *Atherina boyeri*; D.lab, *Dicentrarchus labrax*; D.sar, *Diplodus sargus*; L.aur, *Liza aurata*; L.ram, *Liza ramada*; L.sal, *Liza saliens*; S.aur, *Sparus aurata*; S.pav, *Salaria pavo*. Note that data for the MW site in period 3 and the MI and MW sites in period 1 were excluded from this analysis because they were missing or incomplete



microhabitats of contrasting structural complexity for the local juvenile ichthyofauna.

The choice of the spatio-temporal scale is central when studying variations in the characteristics of fish assemblages and trying to unveil fish habitat preferences in Mediterranean lagoons. Indeed, as shown, for example, in the Mar Menor (Spain), hydrological conditions, habitat productivity and structure, and fish assemblages in these shallow ecosystems can all exhibit high variability at different spatial and temporal scales (Pérez-Ruzafa et al. 2007b). Lagoon fish assemblage, in particular, can vary at small spatial scales, depending on substrate type, so sampling at the micro-habitat level is essential to properly describe the relationship between fishes and lagoon habitats, especially at the juvenile stage (Maci and Basset 2009). Lagoon fish assemblages also vary on a variety of temporal scales, with seasonal, monthly, but also fortnightly changes (Pérez-Ruzafa et al. 2007b). With this regard, our sampling strategy allowed us to capture most, but not all, of the temporal variability in fish distribution over the period surveyed. Indeed, in most sites, sampling was conducted on a monthly scale, but only during the day. As the catchability and distribution of fish can fluctuate in the course of a day according to species' circadian rhythms and feeding periods (Thiel et al. 1995; Rountree and Able 2007), the spatial image of the juvenile assemblage provided here may not be fully accurate, especially for nocturnal species. This also likely biased the assessment of the value of microhabitats, at least for some species. For example, while the juveniles of *A. anguilla* are usually associated with substrates with high complexity (Table 5), we mainly captured them at sites where sediment (mud) dominated, although covered by dense mats of *Ulva* spp. Since *A. anguilla* is mainly nocturnal and generally displays cryptic behavior during the day (Neveu 1981; Baras et al. 1998), this habitat preference might reflect the need for its juveniles to hide in macroalgae mats to limit predation during their daily resting hours. Night sampling might have revealed a different pattern of habitat use for this species, but also for other nocturnal feeders such as *S. solea* and *A. boyeri* (Lagardère et al. 1998; Pulcini et al. 2008). A more comprehensive sampling at the nycthemeral scale would therefore allow us to considerably deepen our understanding of the value of the

Table 5 Reported recruitment periods from Kara and Quignard (2018a, b, c), microhabitat preferences, and trophic ecology for the juveniles of the main fish species captured in the Prévost lagoon

Species	**Recruitment periods**	**Stage**	**TL (mm)**	**Microhabitat preferences**			**Feeding functional group**	**References**	
				Substrate	Temperature range	Salinity range	Diet	Microhabitat preference	Feeding functional group
A. boyeri	Apr–Jul	J1	< 30	P: middle S: soft (sand-mud) MC: variable*	0–30 °C*	5–56*	Planktivore (zooplankton, phytoplankton)	Franco et al. (2012) and Kiener and Spillmann (1969)	Arias and Drake (1990), Fouda (1995), and Franco et al. (2008)
		J2	30–45				Benthivore-Planktivore (hyperbenthos, zooplankton)		
A. anguilla	Dec–Mar	J1	< 60	P: bottom S: hard (pebbles) MC: high	1–35 °C	0–35	No feeding-planktivore (zooplankton)	Crean et al. (2005), Laffaille et al. (2003), Sadler (1979), Steendam et al. (2020), Westerberg et al. (1993)	Bureau du Colombier et al. (2008) and Lecomte-Finiger and Bruslé (1984)
		J2	60–150				Benthivore		
		J3	> 150	S: hard (gravel) MC: high			Benthivore-Piscivore (meiobenthos, macrobenthos, fish)		
D. labrax	May–Jul	J1	< 25	P: middle S: soft (mud) MC: high	5–33 °C	3–33	Benthivore-Planktivore (hyperbenthos, zooplankton)	Dendrinos and Thorpe (1985), Madeira et al. (2013), and Malavasi et al. (2004)	Arias and Drake (1990), Ferrari and Chieregato (1981), Franco et al. (2008)
		J2	25–30	NA			Benthivore-Piscivore-Planktivore (hyperbenthos, zooplankton, fish)		
		J3	> 30	P: middle S: soft (sand-mud) MC: high			Benthivore-Piscivore (hyperbenthos, fish)		
D. sargus	May–Jun	J1	< 20	P: bottom and middle S: hard (pebbles) MC: high	Tmax = 34 °C*	5–40*	Benthivore (microbenthos, macrobenthos)	Kemp (2009), Madeira et al. (2013), Ventura et al. (2014), Verdiell-Cubedo et al. (2007), Vigliola and Harmelin-Vivien (2001), and Whitfield et al. (2006)	Christensen (1978) and Franco et al. (2008)
		J2	20–45	S: hard (rock) MC: high			Omnivores (macrobenthos, macroalgae)		
		J3	> 45	S: mixed (pebbles, rock, and sand) MC: high			Omnivores (macrobenthos, macroalgae)		
E. russoi	Aug–Oct	J1 (larvae)	< 40	P: middle and surface (no preferred substrate)	10–25 °C	5–41*	Planktivore (zooplankton)	Aldanondo et al. (2011), La Mesa et al. (2009), Lee and Juge (1965), Petitgas et al. (2013), and Whitehead (1988)	Bacha and Amara (2009), Borme et al. (2009), and Costalago et al. (2014)
		J2	40–65		5–25 °C				
		J3	> 65		5–25 °C		Planktivore (zooplankton, occasional macrobenthos)		

Table 5 (continued)

Species	Recruitment periods	Stage	TL (mm)	Microhabitat preferences			Feeding functional group	References	
				Substrate	Temperature range	Salinity range	Diet	Microhabitat preference	Feeding functional group
Mugilidae spp.	*L.aurata*: Oct–Feb *L. ramada*: Nov–Apr *C. labrosus*: Mar–Aug *L. saliens*: Jul–Nov *M. cephalus*: Oct–Feb	J1	< 20	P: middle S: soft (sand-mud) MC: variable	4 (5)–(37) 38 °C	0.5 (4) (16)–40	Planktivore (zooplankton)	Chervinski (1977), Lasserre and Gallis (1975), Madeira et al. (2012), and Shahriari Moghadam et al. (2013)	Albertini-Berhaut (1974), Ferrari and Chieregato (1981), Franco et al. (2008), and Koussoroplis (2010)
		J2	20–30				Benthivore-Planktivore (macrobenthos, zooplankton, phytoplankton)		
		J3	> 30				Omnivore-Detritivore (macrobenthos, zooplankton, phytoplankton, benthic microalgae, sand, and silt)		
S. aurata	Feb–Mar	J1	< 20	P: middle S: soft (sand-mud) MC: variable*	14–35 °C	5–45	Benthivore (meiobenthos)	Bodinier et al. (2010), Elliott and Dewailly (1995), Kyprianou et al. (2010), Madeira (2016), Malavasi et al. (2004), and Verdiell-Cubedo et al. (2007)	Ferrari and Chieregato (1981), Franco et al. (2008), and Rosecchi (1987)
		J2	20–30				Benthivore (meiobenthos, macrobenthos)		
		J3	> 30				Benthivore (macrobenthos, occasional macrophytes)		
S. pavo	Aug–Sept	J1	< 30	P: middle	3–32 °C*	0–36*	Planctivore (zooplankton)	Franco et al. (2006b), Labelle and Nursall (1985), Plaut (1998), and Verdiell-Cubedo et al. (2008)	Compaire et al. (2016) and Velasco et al. (2010)
		J2	30- 44	P: bottom S: mixed (pebbles, rock, and sand)* MC: variable*			Benthivore (macrobenthos, occasional macroalgae)*		

For each species, two to three juvenile stages (J1, J2, and J3) can be distinguished based on fish total length (TL in mm). In the subcolumn "Substrate," the three items refer to the position of fish in the water column (P), the type of preferred substrate (S), and the preference in macrophyte cover (MC). When no information could be found in the literature, asterisks were added to indicate that the information given refers to that for the species in general different types of lagoon microhabitats, notably by assessing whether fish juveniles preferentially use them when foraging or for protection (Nagelkerken et al. 2015).

Variations in the Global Juvenile Fish Assemblage

In spite of the sampling biases mentioned above, we are confident that our study provides relevant information on fine-scale spatio-temporal variations in juvenile fish assemblages and on juvenile microhabitat preferences for most fish species in the Prévost lagoon, at sizes below 10 cm. It is in this size range that the information is most valuable because the smallest size classes are the most critical for survival in fish and the most likely to be sensitive to microhabitat features, as small specimens have low swimming abilities and therefore require protection from predators (Dahlgren and Eggleston 2000; Nagelkerken et al. 2015).

From the temporal point of view, juvenile fish assemblages in Mediterranean lagoons are commonly characterized by strong variability due to the seasonality of lagoon use by juvenile fish (Aliaume et al. 1993; Malavasi et al. 2004; Maci and Basset 2010). This seasonality is thought to be mainly driven by species-specific responses and adaptability to environmental factors, notably water temperature and phytoplanktonic production (Marshall and Elliott 1998; Pérez-Ruzafa et al. 2004), or salinity (Drake and Arias 1991; Marshall and Elliott 1998). However, cycles of migration and reproduction of migrant and resident fish species, which reflect their evolutionary adaptations to exploit environmental conditions favoring the growth and survival of their early life stages (Marshall and Elliott 1998), can sometimes prevail on seasonal patterns in local environmental parameters (Potter et al. 1986). This is apparently the case in the Prévost lagoon. Thus, the abundant juvenile catches observed despite the drops in both water temperatures and chlorophyll *a* concentration in period 4, were due to the massive recruitment of most local resident species, in particular *A. boyeri*, *S. pavo* (Table 5), *P. marmoratus*, *P. microps*, and *S. abaster* (Franzoi et al. 1993; Malavasi et al. 2005; Leitão et al. 2006) in the late summer-early autumn. Conversely, migratory species like *S. aurata*, *L. ramada*, *L. aurata*, and *D. labrax*, which all recruit from early spring to early summer in the Mediterranean (Koutrakis et al. 1994; Mariani 2006; Martinho et al. 2008), dominated in the comparatively small catches of periods 1 and 2.

Besides these biological considerations, disentangling the respective roles of water temperature, primary production, and salinity in the spatio-temporal evolution of the juvenile fish assemblage in the Prévost lagoon is complicated. Temperature is known to have a major influence on fish physiology and life cycle (Beitinger and Fitzpatrick 1979), so juvenile fish assemblage composition primarily depends on species' optimal thermal ranges. Here though, average temperatures in the lagoon only varied from 12.1 to 28.3 °C, remaining within the tolerance range of most of the species captured (Table 5). Therefore, even if water temperature probably affects the global list of species found in the lagoon, it was not the primary direct driver for the observed temporal changes in juvenile fish abundance. Nonetheless, in estuarine and lagoon systems, the primary productivity cycle coincides with that of temperature, usually peaking in the summer (Murrel and Lores 2004; Bertolini et al. 2021), and fish abundances, notably at the larval and juvenile stages, usually follow this annual cycle (Pérez-Ruzafa et al. 2004; Kristiansen et al. 2011). Our study tends to confirm this coupling since the global juvenile fish abundance in the Prevost lagoon was higher during periods 3 and 4 when primary productivity was at its highest. However, this trend was primarily due to temporal fluctuations in the abundance of juvenile *A. boyeri*, which largely dominated the local catches. Because this pelagic species is primarily planktivorous (Table 5), it is not surprising that the evolution of its abundance follows that of lagoon planktonic productivity. However, it is possible that the dominance of *A. boyeri* in the catches partly masked the contrasted response of other, less abundant, species to temporal variations in temperature, at least in certain parts of the lagoon. Notably, the fact that *S. aurata* is sensitive to high temperatures (Heather et al. 2018) probably explains their lower abundance in period 2 at the only site where temperatures > 25 °C were recorded (MW).

Disentangling the respective roles of temperature and salinity is also complicated because the two factors globally co-varied over much of the period studied. In estuarine environments with strong haline gradients, salinity is the main driver for species' distribution, depending on their respective tolerance ranges (Gordo and Cabral 2001; Maci and Basset 2010; Rodríguez-Climent et al. 2013). However, in the Prévost lagoon, the salinity range during our survey (25.5–42.9) was within the tolerance limits for most species (Table 5), and spatial salinity gradients were globally weak irrespective of the sampling period. Therefore, temporal changes in salinity probably only influenced the composition of the juvenile fish assemblage in certain parts of the lagoon, where extreme values were recorded. Notably, the fact that *M. cephalus* juveniles are attracted to lower salinities (Cardona 2006) probably explains their exclusive presence in period 4 at the NW site, where the minimum salinity in our survey (25.5) was measured. Differences in the spatial distribution of the two resident *Gobiidae* species captured within the Prévost lagoon in period

3 can also partly be attributed to salinity: at this time of the year, *P. microps*, which has higher osmoregulatory abilities than *P. marmoratus* (Rigal et al. 2008), was observed at the NE site (where the salinity was above 40), whereas *P. marmoratus* was exclusively observed at MI (where the salinity was close to that of the sea).

The limited spatial differences in water parameters in the lagoon during each sampling period allowed us to investigate the effect of microhabitat structural heterogeneity on juvenile fish abundance and diversity. Small-bodied aquatic organisms, such as macroinvertebrates and fish juveniles, are known to respond strongly to habitat complexity and heterogeneity, which provide physical structure for protection and offer a diversity of feeding grounds (e.g., Kingsford and Choat 1985; Verdiell-Cubedo 2009; Mercader et al. 2017; Ferrari et al. 2018). In the Prévost lagoon, the most complex and structured microhabitats (H3D-VWP and V3D-HWP types), characterized by heterogeneous substrates and/or the presence of macrophytes, were those with the highest juvenile fish diversity and abundance. In contrast, low values for these two parameters were observed in soft-bottom microhabitats, notably where the macrophyte canopy was reduced (i.e., in the L3D-LWP microhabitat type). Because the presence of rocks is scarce in the Prévost lagoon (they are only observed in the SE and NW), macrophyte cover can be considered the main local source of habitat structural complexity (Menu et al. 2019). In this regard, macroalgae were observed in most of the sites sampled, while seagrasses were only present within a small area surrounding the SW site. Seagrass meadows are known to provide refuge and host a diversity of prey for juvenile fish, so their contribution to lagoon nursery function is largely recognized (Thiriet 2014). This is less common for macroalgae beds (McDevitt-Irwin et al. 2016), which are considered unstable microhabitats because of their seasonal cycle (Holmquist 1997; Bachelet et al. 2000). In the present work, the impact of this seasonality on microhabitat structure was observed at various sites, notably at SE, where macrophyte cover varied markedly according to the period. Despite this variability, the attractiveness of macroalgae beds for juvenile fish was particularly clear. Indeed, maximum values for global fish abundance and species richness during the three first sampling periods were consistently observed at the NE, SE, and/or NW sites, where macrophyte cover and biomass were maximum. This confirmed previous suggestions that vegetated microhabitats globally attract higher numbers of fish juveniles than bare soft substrates (Verdiell-Cubedo 2009), and that macroalgae beds are good substitutes for seagrass meadows as nursery habitats for fish (Sogard and Able 1991). Even within seagrass beds, the presence of macroalgae can increase local fish diversity and abundance, as they also enhance protection from predators (Adams et al. 2004; Woodland et al. 2019) and attract many invertebrates (Diehl and Kornijów 1998; Nohrén and Odelgård 2010), thus reducing food competition between the juvenile fish that feed on epibenthic fauna.

Differences in Juvenile Microhabitat Preferences

This study confirmed that small-scale habitat use within Mediterranean lagoons largely differs between species depending on their respective morphology and ethology (Kara and Quignard 2018d). For example, the fact that *S. abaster* juveniles are almost exclusively found in the presence of dense macroalgae beds (mainly in *Chaetomorpha* sp. mats) is probably linked to their body shape, which allows them to easily camouflage within the macrophyte canopy (Malavasi et al. 2007; Selfati et al. 2019). Likewise, the fact that *P. marmoratus* juveniles showed a marked affinity for the MI and SW sampling sites, with high sediment but low macrophyte cover (L3D-HWP microhabitat type), is probably due to the fact that Gobiids are morphologically adapted to bare soft substrates, on which they can easily hide and camouflage (Anne-Marie et al. 1980). The same applies to the few juveniles of *S. solea* that we captured in this study (Post et al. 2017). However, species' microhabitat preferences in the Prévost lagoon apparently also depended on their diet and feeding behavior. For example, the juveniles of *L. aurata* and *L. ramada* preferentially selected microhabitats with a bare soft substrate and low macrophyte cover (L3D-LWP microhabitat type), confirming previous similar observations in the Mar Menor and Venice lagoons (Franco et al. 2006a; Verdiell-Cubedo 2009). This is likely due to their diet, as the two species are partially detritivores and feed on the fine organic fraction of the sediment (Table 5). Similarly, the strong association of *D. labrax* juveniles with high macrophyte covers in our study (notably at the SE and NE sites) could be related to their diet (Table 5), as this species is known to mainly feed on the hyperbenthos (Ferrari and Chieregato 1981; Arias and Drake 1990; Franco et al. 2008), which usually thrive on macroalgae mats (Bachelet et al. 2000). So far, *D. labrax* juveniles have been reported in various types of microhabitats though, ranging from unvegetated mudflats to heterogeneous substrates with high macroalgae covers (Gordo and Cabral 2001; Malavasi et al. 2004; Verdiell-Cubedo 2009; Ribeiro et al. 2012). Such diversity might reflect local differences in biotic settings among locations, as juvenile distribution in fish often aims at avoiding interspecific competition for food (Rooper et al. 2006; Nunn et al. 2012). This latter strategy is also commonly observed in *Gobiidae* species with similar diets (Wilkins and Myers

1992; Leitão et al. 2006). In the Prévost lagoon, this could also partly explain, together with the interspecific differences in salinity tolerance mentioned above, why *P. microps* juveniles were essentially found in V3D-HWP microhabitats (NE), and not where the sediment cover was the highest, and *P. marmoratus* juveniles were mainly found (i.e., in L3D-HWP microhabitats).

Studies investigating ontogenetic changes in microhabitat preference during juvenile life are rare for Mediterranean lagoon fish and mostly limited to *Diplodus* species, for which juvenile ontogenetic stages are well described (Vigliola and Harmelin-Vivien 2001; Ventura et al. 2014). The present work thus provides new insights in this regard. It highlighted ontogenetic changes in microhabitat preferences for most of the fish species investigated. In some species, microhabitat changes were particularly subtle. For example, despite slightly extending their niche to V3D-HWP microhabitats with growth, the juveniles of *A. boyeri* exhibited a wide distribution across the lagoon (at all sites but MI) at all periods irrespective of the juvenile stage. They only noticeably avoided L3D-LWP microhabitats, probably because the low planktonic productivity associated with low chlorophyll *a* concentrations is detrimental to their zooplanktivorous diet (Table 5). Similarly, although *S. pavo* juveniles widened their environmental niche during growth, this shift in habitat preference was restricted to sites (NE and SE) characterized by the notable presence of rocks and macrophyte beds, reflecting the documented attraction to complex structures in *Blennidae*, which typically seek shelter in cavities (Orlando-Bonaca and Lipej 2007). In most species though, microhabitat changes with growth were more pronounced. Among all the species investigated, ontogenetic changes in microhabitat preferences were the most marked in *D. sargus* and *L. saliens*, which were both found to prefer V3D-HWP microhabitats at the J1 stage, and H3D-VWP microhabitats at later juvenile stages. In *Diplodus* species, these habitat shifts have been attributed to a progressive loss of the larval shoaling behavior and a morphological adaptation to the benthic habitat, with a strong preference for hard substrates (Vigliola and Harmelin-Vivien 2001; Ventura et al. 2014). For the other species, the shift in microhabitat preference with growth was less marked. In *D. labrax*, it only consisted of an increasing affinity for the V3D-HWP microhabitat type, probably due to the gradual change of the species' diet, relying increasingly on benthic invertebrates and small fish (Table 5), which thrive in macroalgal beds (Bachelet et al. 2000). In *S. aurata*, the ontogenetic shift in microhabitat use was even more gradual, with juveniles widely distributed in the lagoon at most periods and using at least two different types of microhabitats regardless of the ontogenetic stage. As in the Venice lagoon, this progressive change in the species' habitat could reflect its gradual colonization of the lagoon ecosystem inwards from the sea inlets (Redolfi Bristol 2019). However, the avoidance of the MI site by the juveniles of the species and their preference for H3D-VWP microhabitats at the J2 stage suggest that they are also increasingly seeking substantial algal cover, probably because macroalgae beds attract macroinvertebrates (Bachelet et al. 2000), which are increasingly dominant in their diet (Table 5). This corroborates previous observations in the Mar Menor, where the abundance of *Sparidae* juveniles (including *S. aurata*) is significantly lower on sand beaches than in vegetated habitats (Verdiell-Cubedo et al. 2007) and probably reflects the progressive shift from meiobenthic to macrobenthic prey in *S. aurata* diet (Table 5), as macroinvertebrates are more abundant in macroalgae beds (Bachelet et al. 2000).

Implication for Conservation and Management

The most recent definitions for fish nursery sites express the need to consider them not as unique optimized habitats but as mosaics of microhabitats with different but complementary functions for juvenile fish (Nagelkerken et al. 2015; Litvin et al. 2018). The overall value of lagoon habitats for a species' recruitment, therefore, needs to incorporate the quality of each of the successive microhabitats used during the growth of its juveniles. This implies considering the spatial diversity of microhabitats and their connectivity but also their dynamics, which depend on both the seasonal environmental variability and the evolution of fish needs as they grow. By identifying the most attractive environments for different species and at different juvenile stages, our work provides valuable information on the microhabitat types to be targeted to preserve and improve the quality of Mediterranean lagoons as fish nursery sites. In this regard, our results highlight the primary importance of microhabitats with either high sediment (MI, SW, NE) or high macrophyte (SE, NW) cover. Indeed, all the main resident species of commercial interest in the lagoon (*A. boyeri*, *P. marmoratus*, and *P. microps*) and most of the migratory ones (e.g., *S. aurata*, *A. anguilla*, *D. sargus*, *D. labrax*, *S. solea*, *L. aurata*, *L.* ramada, and *L. saliens*) were found to use them preferentially, at least during one stage of their juvenile life. As these two types of habitats are common in Mediterranean lagoons, where they usually spread over a significant part of the surface area (Menu et al. 2019), it is likely that they highly contribute to the lagoon's overall importance for the successful recruitment of coastal fishes (Sogar and Able 1991; Adams et al. 2004; Verdiell-Cubedo et al. 2013). In fish, the earliest juvenile stage is the most vulnerable, and many species tend to settle at sites of high structural complexity where they can easily hide from predators (Tupper and Boutilier 1995; Caddy 2008). However, as observed in the present work, this does not apply to species like gobiids or flatfishes whose protection and feeding rely on bare substrates (Le Luherne et al. 2016). Given the diversity of feeding guilds and the high number of species exploiting the same resources in the fish assemblage of the Prévost lagoon (Table 5), the overall diversity of the microhabitats and the high global productivity in this typical Mediterranean lagoon probably both contribute to reducing competition for food and sustaining high juvenile growth and body condition (Willemsem 1980; Isnard et al. 2015). However, even for a given species, the growth and body condition of the juveniles can vary greatly depending on their spatial distribution within the lagoons due to marked differences in the quality or quantity of local resources (Escalas et al. 2015). Furthermore, fish microhabitat preferences do not necessarily allow identification of where the best conditions for their growth are found. Indeed, fish distribution results from a mix of abiotic factors but also from complex inter- and intra-specific interactions. As shown for *A. boyeri* (Maci and Basset 2010), the earliest stages in fish can be preferentially observed at lagoon sites where environmental conditions (e.g., extreme salinities) exclude some predators but lower body conditions. Therefore, once preferred microhabitats are identified for a given species, we suggest that physiological stress and body condition should also be assessed against food availability, environmental parameters, and predation rates to conclude their potential quality as nursery sites for fish.

The results of the present work also highlight that the microhabitats of lagoon ecosystems are largely intertwined when considering their use as fish nurseries. This connectivity results both from the temporal variability in the extent and spatial location of microhabitat types within each lagoon and from ontogenetic changes in microhabitat preference during the juvenile life of fish. Given the economic importance of fish (e.g., Emiroglu and Tolon 2003) and the primary ecological role of their juveniles in lagoon food webs, the potential impact of human intervention in lagoons (even if minor and localized) on the overall quality of these ecosystems for juvenile fish should be carefully considered for the sustainable management of lagoons but also of coastal fisheries. For example, even in large lagoons, the mere creation of some sandy beaches along the shores has been shown to result in a significant loss of overall lagoon fish diversity, through the resulting homogenization of the environment and the reduction of the structural complexity of key shallow habitats (Pérez-Ruzafa et al. 2006; Verdiell-Cubedo et al. 2007). Meanwhile, the construction of breakwaters may locally increase the abundance and diversity of fish but alter the quality of the water and sediments in their area of influence (Pérez-Ruzafa et al. 2006). This calls for particularly high caution when planning the development and positioning of human activities in coastal lagoons. From another point of view, the local creation of artificial habitats adapted to the needs of juvenile fish but not adding pressure on the ecosystem could be considered, especially when the restoration of natural habitats is impossible or slow (Mercader et al. 2017). All these actions should be carried out considering local temporal fluctuations in the spatial extent and location of lagoon microhabitat types and their successive use at different ontogenetic stages by several fish species.

Conclusion

The present study provides valuable insights into the role of microhabitat diversity and variability in coastal lagoons in determining the final value of these heterogeneous ecosystems as nursery sites for fish. In particular, it highlights that even within small lagoons, differences in environmental characteristics are not only marked but also dynamic, with important consequences for the attractiveness of each lagoon area for young fish. Although an overall preference for lagoon areas with substantial macrophyte cover and three-dimensional habitat structure was observed, microhabitat preferences were found to be both species and ontogenetic stage dependent, with more contrasting environmental requirements in early juveniles. These findings are in line with recent clarifications of the fish nursery concept, which stress the importance of considering each nursery area as a landscape of (micro)habitats with potentially different but complementary ecological functions for juvenile fish (Nagelkerken et al. 2015; Litvin et al. 2018). For a full understanding of the value of coastal lagoons as nursery sites for fish, the information gathered here needs to be further developed by comparing the microhabitat preferences of juvenile fish between different lagoons, or even different types of coastal ecosystems, in the Mediterranean and beyond. This research should consider the effects of global change, as the impact of increasing climatic and anthropogenic pressures in the littoral zone threatens many coastal environments and will probably affect their quality as nursery sites for juvenile fish.

Appendix

Annex 1 Total length (mm) at first maturity for resident fish species

Species	Total length (mm)	Location	References
Atherina boyeri	45	Prévost lagoon	Kohler (1976) and Tomasini et al. (1996)
Gobius niger	43	Maugio lagoon	Joyeux et al. (1992)
Pomatoschistus marmoratus	28	Venice lagoon	Mazzoldi and Rasotto (2001)
Pomatoschistus microps	27	Maugio lagoon	Bouchereau et al. (1993)
Salaria pavo	44	Maugio lagoon	Ruchon (1995)
Syngnathus abaster	57	Maugio lagoon	Tomasini et al. (1991)

Acknowledgements This work is part of the NURSE project funded by Office Français de la Biodiversité and Ifremer. M. Iotti was financially supported by the "Ministère de l'Agriculture et de l'Alimentation". The authors would like to thank the LERLR team for their participation in field sampling, and the "Compagnons de Maguelone" for allowing access to the Prevost lagoon. The authors also thank the two anonymous referees whose comments greatly contributed to the improvement of the manuscript.

References

Abdi, H., and L.J. Williams. 2010. Principal component analysis. *Wiley Interdisciplinary Reviews: Computational Statistics* 2: 433–459. https://doi.org/10.1002/wics.101.

Adams, A.J., J.V. Locascio, and B.D. Robbins. 2004. Microhabitat use by a post-settlement stage estuarine fish: Evidence from relative abundance and predation among habitats. *Journal of Experimental Marine Biology and Ecology* 299: 17–33. https://doi.org/10.1016/j.jembe.2003.08.013.

Albertini-Berhaut, J. 1974. Biologie des stades juveniles de Teleosteens Mugilidae *Mugil auratus* Risso 1810, *Mugil capito* Cuvier 1829 et *Mugil saliens* Risso 1810. *Aquaculture* 4: 13–27. https://doi.org/10.1016/0044-8486(74)90015-5.

Aldanondo, N., U. Cotano, and E. Etxebeste. 2011. Growth of young-of-the-year European anchovy (*Engraulis encrasicolus*, L.) in the Bay of Biscay. *Scientia Marina* 75: 227–235.

Aliaume, C., C. Monteiro, M. Louis, T. Lam Hoai, and G. Lasserre. 1993. Organisation spatio-temporelle des peuplements ichtyologiques dans deux lagunes cotières: Au Portugal et en Guadeloupe. *Oceanologica Acta* 16: 291–301.

Alongi, D.M. 1998. *Coastal ecosystem processes*. New York: CRC Press.

Aminot, A., and R. Kérouel. 2004. Hydrologie des écosystèmes marins. Paramètres et analyses. Éd. Ifremer, 336p

Anne-Marie, E., G. Sundmark, and S. Thorman. 1980. The identification of Pomatoschistus pictus, P. microps, and P. minutus (Gobiidae, Pisces). *Sarsia* 65. Taylor & Francis: 239–242. https://doi.org/10.1080/00364827.1980.10431485.

Arias, A.M., and P. Drake. 1990. *Estados juveniles de la ictiofauna en los caños de las salinas de la bahía de Cádiz. Acuicultura Intermareal*. Cádiz: Consejo Superior de Investigaciones Científicas.

Bacha, M., and R. Amara. 2009. Spatial, temporal and ontogenetic variation in diet of anchovy (*Engraulis encrasicolus*) on the Algerian coast (SW Mediterranean). *Estuarine, Coastal and Shelf Science* 85: 257–264. https://doi.org/10.1016/j.ecss.2009.08.009.

Bachelet, G., X. De Montaudouin, I. Auby, and P.-J. Labourg. 2000. Seasonal changes in macrophyte and macrozoobenthos assemblages in three coastal lagoons under varying degrees of eutrophication. *ICES Journal of Marine Science* 57: 1495–1506.

Baras, E., D. Jeandrain, B. Serouge, and J .C. Philippart. 1998. Seasonal variations in time and space utilization by radio-tagged yellow eels *Anguilla anguilla* (L.) in a small stream. In *Advances in Invertebrates and Fish Telemetry*, ed. Claireaux G. Lagardère JP., Anras ML.B., 187–198. Dordrecht: Springer. https://doi.org/10.1007/978-94-011-5090-3_22.

Barnes, R.S.K. 1980. *Coastal lagoons: The natural history of a neglected habitat*. Cambridge: Cambridge University Press.

Beck, M.W., K.L. Heck, K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, et al. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.

Beitinger, T.L., and L.C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. *American Zoologist* 19: 319–329. https://doi.org/10.1093/icb/19.1.319.

Bertolini, C., E. Royer, and R. Pastres. 2021. Multiple evidence for climate patterns influencing ecosystem productivity across spatial gradients in the Venice lagoon. *Journal of Marine Science and Engineering* 9: 363. https://doi.org/10.3390/jmse9040363.

Bodinier, C., E. Sucré, L. Lecurieux-Belfond, E. Blondeau-Bidet, and G. Charmantier. 2010. Ontogeny of osmoregulation and salinity tolerance in the gilthead sea bream *Sparus aurata*. *Comparative Biochemistry and Physiology Part a: Molecular & Integrative Physiology* 157: 220–228. https://doi.org/10.1016/j.cbpa.2010.06.185.

Borme, D., V. Tirelli, S.B. Brandt, S. Fonda Umani, and E. Arneri. 2009. Diet of *Engraulis encrasicolus* in the northern Adriatic Sea (Mediterranean): Ontogenetic changes and feeding selectivity. *Marine Ecology Progress Series* 392: 193–209. https://doi.org/10.3354/meps08214.

Bouchereau, J-L., J.P. Quignard, J.C. Joyeux, and J.A. Tomasini. 1993. Structure du stock des géniteurs de la population de *Pomatoschistus microps* (Kroyer, 1838)(Gobiidae), dans la lagune de Mauguio, France. *Cybium* 17: 3–15.

Bouchereau, J.-L., O. Guelorget, Y. Vergne, and J.-P. Perthuisot. 2000. The fish fauna in the biological organization of a lagoonar paralic system: The Prevost-Arnel lagoonal complex (Languedoc, France). *Vie Milieu* 50: 19–27.

Bouchoucha, M., C. Aliaume, Y. Baldi, I. Lebel, Y. Abdallah, L. Thieulle, A. Sofianos, A. Courrat, and M. Lepage. 2012. *Suivi des peuplements ichtyologiques dans les eaux de transition du bassin Rhône-Méditerranée et Corse : Campagne 2010 & 2011*. IFREMER.

Bruno, D.O., S.A. Barbini, J.M. Díaz de Astarloa, and P. Martos. 2013. Fish abundance and distribution patterns related to environmental factors in a choked temperate coastal lagoon (Argentina). *Brazilian Journal of Oceanography* 61. SciELO Brasil: 43–53.

Bryan, M.D., and D.L. Scarnecchia. 1992. Species richness, composition, and abundance of fish larvae and juveniles inhabiting natural and developed shorelines of a glacial Iowa lake. *Environmental Biology of Fishes* 35: 329–341. https://doi.org/10.1007/BF00004984.

Bureau du Colombier, S., P. Lambert, and A. Bardonnet. 2008. Is feeding behaviour related to glass eel propensity to migrate? *Estuarine, Coastal and Shelf Science* 80: 323–329. https://doi.org/10.1016/j.ecss.2008.08.015.

Caddy, John F. 2008. The importance of "cover" in the life histories of demersal and benthic marine resources: a neglected issue in fisheries assessment and management. *Bulletin of Marine Science* 83. University of Miami-Rosenstiel School of Marine and Atmospheric Science: 7–52.

Cardona, L. 2006. Habitat selection by grey mullets (Osteichthyes: Mugilidae) in Mediterranean estuaries: The role of salinity. *Scientia Marina* 70: 443–455. https://doi.org/10.3989/scimar.2006.70n3443.

Cattin, M.F., G. Blandenier, C. Banasek-Richter, and L.F. Bersier. 2003. The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. *Biological Conservation* 113 (2): 179–188.

Chaoui, L., P.-A. Gagnaire, B. Guinand, J.P. Quignard, C. Tsigenopoulos, M.H. Kara, and F. Bonhomme. 2012. Microsatellite length variation in candidate genes correlates with habitat in the gilthead sea bream *Sparus aurata*. *Molecular Ecology* 21. Wiley Online Library: 5497–5511.

Charrad, M., N. Ghazzali, V. Boiteau, and A. Niknafs. 2014. NbClust : An R Package for determining the relevant number of clusters in a data set. *Journal of Statistical Software* 61: 1–36.

Chervinski, J. 1977. Adaptability of *Chelon labrosus* (Risso) and *Liza saliens* (Risso) (Pisces, Mugilidae) to fresh water. *Aquaculture* 11: 75–79.

Christensen, M.S. 1978. Trophic relationships in juveniles of three species of sparid fishes in the south african marine littoral. *Fishery Bulletin* 76: 389–401.

Christia, C., and E.S. Papastergiadou. 2007. Spatial and temporal variations of aquatic macrophytes and water quality in six coastal lagoons of western Greece. *Belgian Journal of Botany*. JSTOR: 39–50.

Cimiterra, N., L. Massinelli, L. Dijoux, J. Oheix, and V. Derolez. 2020. *Diagnostic du compartiment macrophyte dans 17 masses d'eau de transition lagunaires en 2016, 2017 et 2018*. IFREMER.

Colombano, D.D., A.D. Manfree, T.A. O'Rear, J.R. Durand, and P.B. Moyle. 2020. Estuarine-terrestrial habitat gradients enhance nursery function for resident and transient fishes in the San Francisco Estuary. *Marine Ecology Progress Series* 637: 141–157. https://doi.org/10.3354/meps13238.

Como, S., C. Lefrancois, E. Maggi, F. Antognarelli, and C. Dupuy. 2014. Behavioral responses of juvenile golden gray mullet *Liza aurata* to changes in coastal temperatures and consequences for benthic food resources. *Journal of Sea Research* 92: 66–73. https://doi.org/10.1016/j.seares.2013.10.004.

Como, S., and P. Magni. 2009. Temporal changes of a macrobenthic assemblage in harsh lagoon sediments. *Estuarine, Coastal and Shelf Science* 83: 638–646. https://doi.org/10.1016/j.ecss.2009.05.024.

Compaire, J.C., R. Cabrera, C. Gómez-Cama, and M.C. Soriguer. 2016. Trophic relationships, feeding habits and seasonal dietary changes in an intertidal rockpool fish assemblage in the Gulf of Cadiz (NE Atlantic). *Journal of Marine Systems* 158: 165–172. https://doi.org/10.1016/j.jmarsys.2016.02.006.

Costalago, D., I. Palomera, and V. Tirelli. 2014. Seasonal comparison of the diets of juvenile European anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* in the Gulf of Lions. *Journal of Sea Research* 89: 64–72. https://doi.org/10.1016/j.seares.2014.02.008.

Cuadros, A., J. Moranta, L. Cardona, P. Thiriet, J. Pastor, N.L. Arroyo, and A. Cheminée. 2017. Seascape attributes, at different spatial scales, determine settlement and post-settlement of juvenile fish. *Estuarine, Coastal and Shelf Science* 185: 120–129. https://doi.org/10.1016/j.ecss.2016.12.014.

Crean, S.R., J.T.A. Dick, D.W. Evans, R.S. Rosell, and R.W. Elwood. 2005. Survival of juvenile European eels (*Anguilla anguilla*), transferred among salinities, and developmental shifts in their salinity preference. *Journal of Zoology* 266: 11–14. https://doi.org/10.1017/S0952836905006539.

Dahlgren, C.P., and D.B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81: 2227–2240. https://doi.org/10.1890/0012-9658(2000)081[2227:EPUOHS]2.0.CO;2.

Dendrinos, P., and J.P. Thorpe. 1985. Effects of reduced salinity on growth and body composition in the European bass *Dicentrarchus labrax* (L.). *Aquaculture* 49: 333–358. https://doi.org/10.1016/0044-8486(85)90090-0.

Derolez, V., B. Bec, D. Munaron, A. Fiandrino, R. Pete, M. Simier, P. Souchu, T. Laugier, C. Aliaume, and N. Malet. 2019. Recovery trajectories following the reduction of urban nutrient inputs along the eutrophication gradient in French Mediterranean lagoons. *Ocean & Coastal Management* 171: 1–10. https://doi.org/10.1016/j.ocecoaman.2019.01.012.

Diehl, S., and R. Kornijów. 1998. The influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In *The structuring role of submerged macrophytes in Lakes*, ed. Ecological Studies (Analysis and Synthesis), 24–46. New York: Springer. https://doi.org/10.1007/978-1-4612-0695-8_2.

Dolédec, S., and D. Chessel. 1994. Co-inertia analysis: An alternative method for studying species-environment relationships. *Freshwater Biology* 31: 277–294. https://doi.org/10.1111/j.1365-2427.1994.tb01741.x.

Drake, P., and A.M. Arias. 1991. Ichthyoplankton of a shallow coastal inlet in south-west Spain: Factors contributing to colonization and retention. *Estuarine, Coastal and Shelf Science* 32: 347–364. https://doi.org/10.1016/0272-7714(91)90048-G.

Dufour, V., M. Cantou, and F. Lecomte. 2009. Identification of sea bass (*Dicentrarchus labrax*) nursery areas in the north-western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* 89: 1367–1374. https://doi.org/10.1017/S0025315409000368.

Dufrène, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Elliott, M., and F. Dewailly. 1995. The structure and components of European estuarine fish assemblages. *Netherlands Journal of Aquatic Ecology* 29: 397–417. https://doi.org/10.1007/BF02084239.

Elliott, M., and K. Hemingway. 2002. *Fishes in estuaries*. Oxford: Blackwell Science.

Embarek, R., and R. Amara. 2017. Fish assemblage structure in shallow waters of the Mellah Lagoon (Algeria): Seasonal and spatial distribution patterns and relation to environmental parameters. *Acta Ichthyologica Et Piscatoria* 47: 133–144. https://doi.org/10.3750/AIEP/02080.

Emiroglu, D., and T. Tolon. 2003. Fish production and marketing in the Mediterranean coastal lagoons. *New Medit* 2 (4): 59–62.

Escalas, A., F. Ferraton, C. Paillon, G. Vidy, F. Carcaillet, C. Salen-Picard, and F. Le Loc'h, P. Richard, and A.M. Darnaude. 2015.

Spatial variations in dietary organic matter sources modulate the size and condition of fish juveniles in temperate lagoon nursery sites. *Estuarine, Coastal and Shelf Science* 152: 78–90. https://doi.org/10.1016/j.ecss.2014.11.021.

European Commission DG Environment. 2013. *Interpretation manual of European Union Habitats-EUR 28*. Brussels.

Farrugio, H. 1975. *Les muges (poissons, téléosteens) de Tunisie-Répartition et pêche-Contribution à leur étude systématique et biologique*. Thesis: Université des Sciences et Techniques du Languedoc.

Félix-Hackradt, F.C., C.W. Hackradt, J. Treviño-Otón, A. Pérez-Ruzafa, and J.A. García-Charton. 2014. Habitat use and ontogenetic shifts of fish life stages at rocky reefs in South-western Mediterranean Sea. *Journal of Sea Research* 88: 67–77. https://doi.org/10.1016/j.seares.2013.12.018.

Ferrari, I., and A.R. Chieregato. 1981. Feeding habits of juvenile stages of *Sparus auratus* L., *Dicentrarchus labrax* L. and Mugilidae in a brackish embayment of the Po River delta. *Aquaculture* 25: 243–257.

Ferrari, R., H.A. Malcolm, M. Byrne, A. Friedman, S.B. Williams, A. Schultz, R. Al, and Jordan, and W.F. Figueira. 2018. Habitat structural complexity metrics improve predictions of fish abundance and distribution. *Ecography* 41: 1077–1091. https://doi.org/10.1111/ecog.02580.

Fiandrino, A., A. Giraud, S. Robin, and C. Pinatel. 2012. Validation d'une méthode d'estimation des volumes d'eau échangés entre la mer et les lagunes et définition d'indicateurs hydrodynamiques associés.

Fiandrino, A., V. Ouisse, F. Dumas, F. Lagarde, R. Pete, N. Malet, S. Le Noc, and R. de Wit. 2017. Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. *Marine Pollution Bulletin* 119: 132–144. https://doi.org/10.1016/j.marpolbul.2017.03.006.

Fouda, M.M. 1995. Life history strategies of four small-size fishes in the Suez Canal. *Egypt. Journal of Fish Biology* 46: 687–702. https://doi.org/10.1111/j.1095-8649.1995.tb01104.x.

Franco, T.P., L.M. Neves, and F.G. Araújo. 2019. Better with more or less salt? The association of fish assemblages in coastal lagoons with different salinity ranges. *Hydrobiologia* 828: 83–100. https://doi.org/10.1007/s10750-018-3804-8.

Franco, A., P. Franzoi, S. Malavasi, F. Riccato, and P. Torricelli. 2006a. Fish assemblages in different shallow water habitats of the Venice Lagoon. *Hydrobiologia* 555: 159–174. https://doi.org/10.1007/s10750-005-1113-5.

Franco, A., P. Franzoi, S. Malavasi, F. Riccato, P. Torricelli, and D. Mainardi. 2006b. Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. *Estuarine, Coastal and Shelf Science* 66. Elsevier: 67–83. https://doi.org/10.1016/j.ecss.2005.07.020.

Franco, A., P. Franzoi, and P. Torricelli. 2008. Structure and functioning of Mediterranean lagoon fish assemblages: A key for the identification of water body types. *Estuarine, Coastal and Shelf Science* 79: 549–558. https://doi.org/10.1016/j.ecss.2008.05.011.

Franco, A., R. Fiorin, M. Zucchetta, P. Torricelli, and P. Franzoi. 2010. Flounder growth and production as indicators of the nursery value of marsh habitats in a Mediterranean lagoon. *Journal of Sea Research* 64: 457–464. https://doi.org/10.1016/j.seares.2010.01.006.

Franco, A., A. Pérez-Ruzafa, H. Drouineau, P. Franzoi, E.T. Koutrakis, M. Lepage, D. Verdiell-Cubedo, et al. 2012. Assessment of fish assemblages in coastal lagoon habitats: Effect of sampling method. *Estuarine, Coastal and Shelf Science* 112: 115–125. https://doi.org/10.1016/j.ecss.2011.08.015.

Franzoi, P., R. Maccagnani, R. Rossi, and V.U. Ceccherelli. 1993. Life cycles and feeding habits of *Syngnathus taenionotus* and *S. abaster* (Pisces, Syngnathidae) in a brackish bay of the Po River Delta (Adriatic Sea). *Marine Ecology Progress Series* 97: 71–81. https://doi.org/10.3354/meps097071.

García-Rubies, A., and E. Macpherson. 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. *Marine Biology* 124: 35–42. https://doi.org/10.1007/BF00349144.

Gordo, L., and H. Cabral. 2001. The fish assemblage structure of a hydrologically altered coastal lagoon: The Óbidos lagoon (Portugal). *Hydrobiologia* 459: 125–133. https://doi.org/10.1023/A:1012510608231.

Grati, F., G. Scarcella, P. Polidori, F. Domenichetti, L. Bolognini, R. Gramolini, C. Vasapollo, et al. 2013. Multi-annual investigation of the spatial distributions of juvenile and adult sole (*Solea solea* L.) in the Adriatic Sea (northern Mediterranean). *Journal of Sea Research* 84: 122–132. https://doi.org/10.1016/j.seares.2013.05.001.

Heather, F.J., D. Childs, A.M. Darnaude and J. Blanchard. 2018. Using an integral projection model to assess the effect of temperature on the growth of gilthead seabream *Sparus aurata*. *PloS ONE* 13(5): e0196092.

Holmquist, J.G. 1997. Disturbance and gap formation in a marine benthic mosaic: Influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. *Marine Ecology Progress Series* 158: 121–130. https://doi.org/10.3354/meps158121.

Ifremer. 2014. *Réseau de Suivi Lagunaire du Languedoc-Roussillon : Bilan des résultats 2013*. IFREMER.

Isnard, E., J. Tournois, D.J. McKenzie, F. Ferraton, N. Bodin, C. Aliaume, and A.M. Darnaude. 2015. Getting a good start in life? A comparative analysis of the quality of lagoons as juvenile habitats for the gilthead seabream *sparus aurata* in the Gulf of Lions. *Estuaries and Coasts* 38: 1937–1950. https://doi.org/10.1007/s12237-014-9939-6.

Joyeux, J-C., J.A. Tomasini, and J-L. Bouchereau. 1992. Modalités de la reproduction de *Gobius niger* (Teleostei, Gobiidae) dans une lagune méditerranéenne. *Vie et Milieu/Life & Environment* 1–13.

Kara, M.H., and J.P. Quignard. 2018a. *Les poissons des lagunes et des estuaires de Méditerranée 2: Les poissons sédentaires*. Great Britain: ISTE Group.

Kara, M.H., and J.P. Quignard. 2018b. *Les poissons des lagunes et des estuaires de Méditerranée 3A: Les poissons migrateurs*. Great Britain: ISTE Group.

Kara, M.H., and J.P. Quignard. 2018c. *Les poissons des lagunes et des estuaires de Méditerranée 3B: Les poissons migrateurs*. Great Brtitain: ISTE Group.

Kara, M.H, and J.P. Quignard. 2018d. *Les poissons des lagunes et des estuaires de Méditerranée 1: Diversité, bio-écologie et exploitation*. Great Britain: ISTE Group.

Kemp, J.O.G. 2009. Effects of temperature and salinity on resting metabolism in two south african rock pool fish: The resident *Gobiid caffrogobius* caffer and the transient sparid *Diplodus sargus capensis*. *African Zoology* 44: 151–158. https://doi.org/10.3377/004.044.0203.

Kennish, M.J., M.J. Brush, and K.A. Moore. 2014. Drivers of change in shallow coastal photic systems: An introduction to a special issue. *Estuaries and Coasts* 37: 3–19. https://doi.org/10.1007/s12237-014-9779-4.

Kennish, M.J., and H.W. Paerl. 2010. *Coastal lagoons: Critical habitats of environmental change*. Boca Raton: CRC Press.

Kiener, A., and C.J. Spillmann. 1969. Contribution à l'étude systématique et écologique des athérines des côtes françaises. *Mémoires du Muséum national d'Histoire naturelle. Série a, Zoologie* 60: 33–74.

Kingsford, M.J., and J.H. Choat. 1985. The fauna associated with drift algae captured with a plankton-mesh purse seine net. *Limnology and Oceanography* 30: 618–630. https://doi.org/10.4319/lo.1985.30.3.0618.

Kohler, A. 1976. Observations biologiques et biometriques sur *Atherina boyeri* Risso dans l'étang du Prévost à Palavas (Hérault). *Vie et milieu* 26: 157–174.

Koussoroplis, A.-M. 2010. *Sources de carbone et d'acides gras essentiels pour les juvéniles de Liza saliens (Pisces, Mugilidae) dans le réseau trophique d'une lagune côtière méditerranéenne : Approches in situ par biomarqueurs lipidiques et isotopiques*. Thesis: Université Blaise Pascal-Clermont-Ferrand II.

Koutrakis, E.T., A.I. Sinis, and P.S. Economidis. 1994. Seasonal occurrence, abundance and size distribution of gray mullet fry (Pisces, Mugilidae) in the Porto-Lagos lagoon and lake Vistonis (Aegean sea, Greece). *Israeli Journal of Aquaculture/bamidgeh* 46: 182–196.

Koutrakis, E.T., A.C. Tsikliras, and A.I. Sinis. 2005. Temporal variability of the ichthyofauna in a Northern Aegean coastal lagoon (Greece). *Influence of Environmental Factors. Hydrobiologia* 543: 245–257. https://doi.org/10.1007/s10750-004-7891-3.

Kovačić, M. 2020. Checklist of gobies (Teleostei: Gobiidae) of the Mediterranean Sea and a key for species identification. *Zootaxa* 4877: 75–101. https://doi.org/10.11646/zootaxa.4877.1.3.

Kristiansen, T., K.F. Drinkwater, R.G. Lough, and S. Sundby. 2011. Recruitment variability in North Atlantic cod and match-mismatch dynamics. *PLoS ONE* 6: e17456. https://doi.org/10.1371/journal.pone.0017456.

Kyprianou, T.-D., H.O. Pörtner, A. Anestis, B. Kostoglou, K. Feidantsis, and B. Michaelidis. 2010. Metabolic and molecular stress responses of gilthead seam bream *Sparus aurata* during exposure to low ambient temperature: An analysis of mechanisms underlying the winter syndrome. *Journal of Comparative Physiology B* 180: 1005–1018. https://doi.org/10.1007/s00360-010-0481-y.

Labelle, M., and J.R. Nursall. 1985. Some aspects of the early life history of the redlip blenny, *Ophioblennius atlanticus* (Teleostei: Blenniidae). *Copeia*: 39–49.

Laffaille, P., E. Feunteun, A. Baisez, T. Robinet, A. Acou, A. Legault, and S. Lek. 2003. Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment. *Ecology of Freshwater Fish* 12: 254–264. https://doi.org/10.1046/j.1600-0633.2003.00021.x.

Lagardère, F., R. Amara, and L. Joassard. 1998. Vertical distribution and feeding activity of metamorphosing sole, *Solea solea*, before immigration to the Bay of Vilaine nursery (northern Bay of Biscay, France). In *When do fishes become juveniles?*, ed. Hensel K. Copp G.H., Kováč V., 213–228. Dordrecht: Springer. https://doi.org/10.1007/978-94-017-3678-7_15.

La Mesa, M., F. Donato, G. Giannetti, and E. Arneri. 2009. Growth and mortality rates of European anchovy (*Engraulis encrasicolus*) in the Adriatic Sea during the transition from larval to juvenile stages. *Fisheries Research* 96: 275–280. https://doi.org/10.1016/j.fishres.2008.12.011.

Lasserre, P., and J.-L. Gallis. 1975. Osmoregulation and differential penetration of two grey mullets, *Chelon labrosus* (Risso) and *Liza ramada* (Risso) in estuarine fish ponds. *Aquaculture* 5: 323–344. https://doi.org/10.1016/0044-8486(75)90053-8.

Le Luherne, E., E. Réveillac, A. Ponsero, A. Sturbois, S. Ballu, M. Perdriau, and O. Le Pape. 2016. Fish community responses to green tides in shallow estuarine and coastal areas. *Estuarine, Coastal and Shelf Science* 175: 79–92. https://doi.org/10.1016/j.ecss.2016.03.031.

Lecomte-Finiger, R., and J. Bruslé. 1984. L'*Anguilla anguilla* des lagunes du Languedoc-Roussillon: Intérêt biologique et valeur halieutique. *Vie Et Milieu* 34: 185–194.

Lee, J.Y., and C. Juge. 1965. Observations morphologiques et biologiques sur les anchois (Engraulis encrasicholus) du golfe du Lion. *Rapports Et Procès-Verbaux Des Réunions De La Commission Internationale Pour L'exploration Scientifique De La Mer Méditerranée* 18: 221–224.

Le Fur, I., R. De Wit, M. Plus, J. Oheix, M. Simier, and V. Ouisse. 2018. Submerged benthic macrophytes in Mediterranean lagoons: Distribution patterns in relation to water chemistry and depth. *Hydrobiologia* 808: 175–200. https://doi.org/10.1007/s10750-017-3421-y.

Leitão, R., F. Martinho, J.M. Neto, H. Cabral, J.C. Marques, and M.A. Pardal. 2006. Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. *Estuarine, Coastal and Shelf Science* 66: 231–239. https://doi.org/10.1016/j.ecss.2005.08.012.

Leruste, A., N. Malet, D. Munaron, V. Derolez, E. Hatey, Y. Collos, R. De Wit, and B. Bec. 2016. First steps of ecological restoration in Mediterranean lagoons: Shifts in phytoplankton communities. *Estuarine, Coastal and Shelf Science* 180: 190–203. https://doi.org/10.1016/j.ecss.2016.06.029.

Levin, L.A., D.F. Boesch, A. Covich, C. Dahm, C. Erséus, K.C. Ewel, R.T. Kneib, et al. 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4: 430–451. https://doi.org/10.1007/s10021-001-0021-4.

Litvin, S.Y., M.P. Weinstein, M. Sheaves, and I. Nagelkerken. 2018. What makes nearshore habitats nurseries for nekton? An emerging view of the nursery role hypothesis. *Estuaries and Coasts* 41: 1539–1550. https://doi.org/10.1007/s12237-018-0383-x.

Maci, S., and A. Basset. 2009. Composition structural characteristics and temporal patterns of fish assemblages in non-tidal Mediterranean lagoons: A case study. *Estuarine Coastal and Shelf Science* 83 (4): 602–612. https://doi.org/10.1016/j.ecss.2009.05.007.

Maci, S., and A. Basset. 2010. Spatio-temporal patterns of abundance, size structure and body condition of *Atherina boyeri* (Pisces: Atherinidae) in a small non-tidal Mediterranean lagoon. *Estuarine, Coastal and Shelf Science* 87: 125–134. https://doi.org/10.1016/j.ecss.2010.01.002.

Madeira, D. 2016. *Effects of ocean warming throughout the life cycle of Sparus aurata : A physiological and proteomic approach*. Thesis: Universidade Nova de Lisboa.

Madeira, D., L. Narciso, H.N. Cabral, and C. Vinagre. 2012. Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. *Journal of Sea Research* 70: 32–41. https://doi.org/10.1016/j.seares.2012.03.002.

Madeira, D., L. Narciso, H.N. Cabral, C. Vinagre, and M.S. Diniz. 2013. Influence of temperature in thermal and oxidative stress responses in estuarine fish. *Comparative Biochemistry and Physiology Part a: Molecular & Integrative Physiology* 166: 237–243. https://doi.org/10.1016/j.cbpa.2013.06.008.

Malavasi, S., R. Fiorin, A. Franco, P. Franzoi, A. Granzotto, F. Riccato, and D. Mainardi. 2004. Fish assemblages of Venice Lagoon shallow waters: An analysis based on species, families and functional guilds. *Journal of Marine Systems* 51: 19–31. https://doi.org/10.1016/j.jmarsys.2004.05.006.

Malavasi, S., A. Franco, R. Fiorin, P. Franzoi, P. Torricelli, and D. Mainardi. 2005. The shallow water gobiid assemblage of the Venice Lagoon: Abundance, seasonal variation and habitat partitioning. *Journal of Fish Biology* 67: 146–165. https://doi.org/10.1111/j.0022-1112.2005.00919.x.

Malavasi, S., A. Franco, F. Riccato, C. Valerio, P. Torricelli, and P. Franzoi. 2007. Habitat selection and spatial segregation in three pipefish species. *Estuarine, Coastal and Shelf Science* 75: 143–150. https://doi.org/10.1016/j.ecss.2007.02.022.

Manzo, C., C. Brugnano, A. Fabbrocini, L. Roselli, and R. D'adamo. 2011. Recruitment dynamics of young-of-the-year marine fish in the coastal lagoon of Lesina. In *Marine Research at CNR*, DTA/06–201, 2099–2114. Roma.

Manzo, C., A. Fabbrocini, L. Roselli, and R. D'Adamo. 2016. Characterization of the fish assemblage in a Mediterranean coastal lagoon: Lesina Lagoon (central Adriatic Sea). *Regional Studies in Marine Science* 8: 192–200. https://doi.org/10.1016/j.rsma.2016.04.003.

Mariani, S. 2001. Can spatial distribution of ichthyofauna describe marine influence on coastal lagoons? A central Mediterranean case study. *Estuarine, Coastal and Shelf Science* 52: 261–267. https://doi.org/10.1006/ecss.2000.0746.

Mariani, S. 2006. Life-history- and ecosystem-driven variation in composition and residence pattern of seabream species (Perciformes: Sparidae) in two Mediterranean coastal lagoons. *Marine Pollution Bulletin* 53. Elsevier: 121–127. https://doi.org/10.1016/j.marpolbul.2005.09.019.

Marshall, S., and M. Elliott. 1998. Environmental influences on the fish assemblage of the Humber estuary, U.K. *Estuarine, Coastal and Shelf Science* 46: 175–184. https://doi.org/10.1006/ecss.1997.0268.

Martinho, F., R. Leitão, J.M. Neto, H. Cabral, F. Lagardère, and M.A. Pardal. 2008. Estuarine colonization, population structure and nursery functioning for 0-group sea bass (*Dicentrarchus labrax*), flounder (*Platichthys flesus*) and sole (*Solea solea*) in a mesotidal temperate estuary. *Journal of Applied Ichthyology* 24: 229–237. https://doi.org/10.1111/j.1439-0426.2007.01049.x.

Mazzoldi, C., and M. B. Rasotto. 2001. Extended breeding season in the marbled goby, *Pomatoschistus marmoratus* (Teleostei: Gobiidae), in the Venetian Lagoon. *Environmental Biology of Fishes* 61: 175–183

McDevitt-Irwin, J.M., J.C. Iacarella, and J.K. Baum. 2016. Reassessing the nursery role of seagrass habitats from temperate to tropical regions: A meta-analysis. *Marine Ecology Progress Series* 557: 133–143. https://doi.org/10.3354/meps11848.

Menu, M., S. Vaz, T. Bajjouk, V. Derolez, A. Fiandrino, A. Giraud, P. Grillas, and V. Ouisse. 2019. *Rapport final du projet CHAMILA (Cartographie des habitats en milieu lagunaire méditerranéen)*. IFREMER.

Mercader, M., A. Mercière, G. Saragoni, A. Cheminée, R. Crec'hriou, J. Pastor, M. Rider, et al. 2017. Small artificial habitats to enhance the nursery function for juvenile fish in a large commercial port of the Mediterranean. *Ecological Engineering* 105: 78–86. https://doi.org/10.1016/j.ecoleng.2017.03.022.

Minos, G., G. Katselis, I. Ondrias, and I.J. Harrison. 2002. Use of melanophore patterns on the ventral side of the head to identify fry of grey mullet (Teleostei: Mugilidae). *The Israeli Journal of Aquaculture - Bamidgeh* 54: 12–26.

Mistri, M., E.A. Fano, G. Rossi, K. Caselli, and R. Rossi. 2000. Variability in macrobenthos communities in the Valli di Comacchio, northern Italy, a hypereutrophized lagoonal ecosystem. *Estuarine, Coastal and Shelf Science* 51: 599–611. https://doi.org/10.1006/ecss.2000.0697.

Munaron, D., N. Tapie, H. Budzinski, B. Andral, and J.-L. Gonzalez. 2012. Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: Results from a pilot survey using passive samplers. *Estuarine, Coastal and Shelf Science* 114: 82–92. https://doi.org/10.1016/j.ecss.2011.09.009.

Murrel, M.C., and E.M. Lores. 2004. Phytoplankton and zooplankton seasonal dynamics in a subtropical estuary: Importance of cyanobacteria. *Journal of Plankton Research* 26: 371–382. https://doi.org/10.1093/plankt/fbh038.

Nagelkerken, I., M. Sheaves, and Ronald. Baker, and R.M. Connolly. 2015. The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries* 16: 362–371. https://doi.org/10.1111/faf.12057.

Neveu, A. 1981. Densité et microrépartition des différentes espèces de poissons dans la Basse-Nivelle, petit fleuve côtier des Pyrénées Atlantiques. *Bulletin Français de Pisciculture*: 86–102. https://doi.org/10.1051/kmae:1981021.

Nohrén, E., and E. Odelgård. 2010. Response of epibenthic faunal assemblages to varying vegetation structures and habitat patch size. *Aquatic Biology* 9: 139–148. https://doi.org/10.3354/ab00247.

Nunn, A.D., L.H. Tewson, and I.G. Cowx. 2012. The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries* 22: 377–408.

Orlando-Bonaca, M., and L. Lipej. 2007. Microhabitat preferences and depth distribution of combtooth blennies (Blenniidae) in the Gulf of Trieste (North Adriatic Sea). *Marine Ecology* 28: 418–428. https://doi.org/10.1111/j.1439-0485.2007.00185.x.

Pérez-Ruzafa, A., and C. Marcos. 2012. Fisheries in coastal lagoons: An assumed but poorly researched aspect of the ecology and functioning of coastal lagoons. *Estuarine, Coastal and Shelf Science* 110: 15–31. https://doi.org/10.1016/j.ecss.2012.05.025.

Pérez-Ruzafa, A., C. Marcos, I.M. Pérez-Ruzafa, E. Barcala, M.I. Hegazi, and J. Quispe. 2007a. Detecting changes resulting from human pressure in a naturally quick-changing and heterogeneous environment: Spatial and temporal scales of variability in coastal lagoons. *Estuarine, Coastal and Shelf Science* 75: 175–188. https://doi.org/10.1016/j.ecss.2007a.04.030.

Pérez-Ruzafa, A., J.A. García-Charton, E. Barcala, C. Marcos. 2006. Changes in benthic fish assemblages as a consequence of coastal works in a coastal lagoon: The Mar Menor (Spain Western Mediterranean). *Marine Pollution Bulletin* 53(1-4): 107–120. https://doi.org/10.1016/j.marpolbul.2005.09.014.

Pérez-Ruzafa, A., J.I. Quispe-Becerra, J.A. Garcia-Charton, and C. Marcos. 2004. Composition, structure and distribution of the ichthyoplankton in a Mediterranean coastal lagoon. *Journal of Fish Biology* 64: 202–218. https://doi.org/10.1111/j.1095-8649.2004.00301.x.

Pérez-Ruzafa, A., M.C. Mompeán, and C. Marcos. 2007b. Hydrographic, geomorphologic and fish assemblage relationships in coastal lagoons. *Hydrobiologia* 577: 107–125. https://doi.org/10.1007/s10750-006-0421-8.

Peterson, M.S., C.F. Rakocinski, B.H. Comyns, and G.L. Fulling. 2000. Laboratory growth responses of juvenile Mugil sp. to temperature and salinity: Delineating optimal field growth conditions. *Proceedings of the Gulf and Caribbean Fisheries Institute* 51: 341–352.

Petitgas, P., A.D. Rijnsdorp, M. Dickey-Collas, G.H. Engelhard, Myron A. Peck, John K. Pinnegar, K. Drinkwater, M. Huret, and R.D.M. Nash. 2013. Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography* 22: 121–139. https://doi.org/10.1111/fog.12010.

Pichavant, K. 2001. Comparative effects of long-term hypoxia on growth, feeding and oxygen consumption in juvenile turbot and European sea bass. *Journal of Fish Biology* 59. Wiley Online Library: 875–883. https://doi.org/10.1006/jfbi.2001.1702.

Plaut, I. 1998. Comparison of salinity tolerance and osmoregulation in two closely related species of blennies from different habitats. *Fish Physiology and Biochemistry* 19: 181–188. https://doi.org/10.1023/a:1007798712727.

Podani, J., and B. Csányi. 2010. Detecting indicator species: Some extensions of the IndVal measure. *Ecological Indicators* 10. Elsevier: 1119–1124. https://doi.org/10.1016/j.ecolind.2010.03.010.

Post, P., E. Blom, C. Chen, L.J. Bolle, and M.J. Baptist. 2017. Habitat selection of juvenile sole (*Solea solea* L.): Consequences for shoreface nourishment. *Journal of Sea Research* 122. https://doi.org/10.1016/j.seares.2017.02.011.

Potter, I.C., P.N. Claridge, and R.M. Warwick. 1986. Consistency of seasonal changes in an estuarine fish assemblage. *Marine Ecology Progress Series* 32: 217–228.

Pulcini, D., C. Costa, J. Aguzzi, and S. Cataudella. 2008. Light and shape: A contribution to demonstrate morphological differences in diurnal and nocturnal teleosts. *Journal of Morphology* 269: 375–385. https://doi.org/10.1002/jmor.10598.

QGIS.org. 2021. QGIS Geographic Information System. QGIS Association.

Quignard, J.-P., A. Man-Wai, and R. Vianet. 1984. Les poissons de l'étang de Mauguio (Hérault, France) inventaire, structure du peuplement, croissance et polymorphisme des tailles. *Vie Et Milieu/life & Environment* 34: 173–183.

Redolfi Bristol, S. 2019. *Nursery function of coastal lagoons: Implications of habitat connectivity for the management of lagoon habitats*. Thesis: Università Ca'Foscari Venezia.

Ribeiro, J., G.M. Carvalho, J.M. Gonçalves, and K. Erzini. 2012. Fish assemblages of shallow intertidal habitats of the Ria Formosa lagoon (South Portugal): Influence of habitat and season. *Marine Ecology Progress Series* 446: 259–273. https://doi.org/10.3354/meps09455.

Rigal, F., T. Chevalier, C. Lorin-Nebel, G. Charmantier, J.-A. Tomasini, F. Aujoulat, and P. Berrebi. 2008. Osmoregulation as a potential factor for the differential distribution of two cryptic gobiid species, *Pomatoschistus microps* and *P. marmoratus* in French Mediterranean lagoons. *Scientia Marina* 72: 469–476. https://doi.org/10.3989/scimar.2008.72n3469.

Říha, M., J. Kubečka, T. Mrkvička, M. Prchalová, M. Čech, V. Draštík, J. Frouzová, et al. 2008. Dependence of beach seine net efficiency on net length and diel period. *Aquatic Living Resources* 21: 411–418. https://doi.org/10.1051/alr:2008061.

Rodríguez-Climent, S., N. Caiola, and C. Ibáñez. 2013. Salinity as the main factor structuring small-bodied fish assemblages in hydrologically altered Mediterranean coastal lagoons. *Scientia Marina* 77: 37–45. https://doi.org/10.3989/scimar.03698.26B.

Rooper, C.N., D.R. Gunderson, and D.A. Armstrong. 2006. Evidence for resource partitioning and competition in nursery estuaries by juvenile flatfish in Oregon and Washington. *Fishery Bulletin* 104: 616.

Rosecchi, E. 1987. L' alimentation de *Diplodus annularis*, *Diplodus sargus*, *Diplodus vulgaris* et *Sparus aurata* (Pisces, Sparidae) dans le Golfe du Lion et les lagunes littorales. *Revue Des Travaux De L'institut Des Pêches Maritimes* 49: 125–141.

Rountree, R.A., and K.W. Able. 2007. Spatial and temporal habitat use patterns for salt marsh nekton: Implications for ecological functions. *Aquatic Ecology* 41: 25–45. https://doi.org/10.1007/s10452-006-9052-4.

Ruchon, F. 1995. *Lipophrys pavo* (Risso 1810)(Pisces, Blenniidae). Biologie d'une population lagunaire (stratégies et tactiques adaptatives). Thesis: Univ Aix-Marseille.

Sadler, K. 1979. Effects of temperature on the growth and survival of the European eel, *Anguilla anguilla* L. *Journal of Fish Biology* 15: 499–507. https://doi.org/10.1111/j.1095-8649.1979.tb03633.x.

Selfati, M., N. El Ouamari, A. Franco, P. Lenfant, G. Lecaillon, A. Mesfioui, P. Boissery, and H. Bazairi. 2019. Fish assemblages of the Marchica lagoon (Mediterranean, Morocco): Spatial patterns and environmental drivers. *Regional Studies in Marine Science* 32: 100896. https://doi.org/10.1016/j.rsma.2019.100896.

Sfriso, A., A. Buosi, C. Facca, and A.A. Sfriso. 2017. Role of environmental factors in affecting macrophyte dominance in transitional environments: The Italian Lagoons as a study case. *Marine Ecology* 38: e12414. https://doi.org/10.1111/maec.12414.

Shahriari Moghadam, M., B. Abtahi, S. Mosafer Khorjestan, and M.A. Bitaab. 2013. Salinity tolerance and gill histopathological alterations in *Liza aurata* Risso, 1810 (Actinopterygii: Mugilidae) fry. *Italian Journal of Zoology* 80: 503–509. https://doi.org/10.1080/11250003.2013.853326.

Sogard, S.M., and K.W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine, Coastal and Shelf Science* 33: 501–519. https://doi.org/10.1016/0272-7714(91)90087-R.

Souchu, P., B. Bec, V.H. Smith, T. Laugier, A. Fiandrino, L. Benau, V. Orsoni, Y. Collos, and A. Vaquer. 2010. Patterns in nutrient limitation and chlorophyll a along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 743–753. https://doi.org/10.1139/F10-018.

Steendam, C., P. Verhelst, S. Van Wassenbergh, and J. De Meyer. 2020. Burrowing behaviour of the European eel (*Anguilla anguilla*): Effects of life stage. *Journal of Fish Biology* 97: 1332–1342. https://doi.org/10.1111/jfb.14481.

Stoll, S., P. Fischer, P. Klahold, N. Scheifhacken, H. Hofmann, and K.-O. Rothhaupt. 2008. Effects of water depth and hydrodynamics on the growth and distribution of juvenile cyprinids in the littoral zone of a large pre-alpine lake. *Journal of Fish Biology* 72: 1001–1022. https://doi.org/10.1111/j.1095-8649.2007.01780.x.

Tagliapietra, D., M. Sigovini, and A.V. Ghirardini. 2009. A review of terms and definitions to categorise estuaries, lagoons and associated environments. *Marine and Freshwater Research* 60: 497–509. https://doi.org/10.1071/MF08088.

Thiel, R., A. Sepulveda, R. Kafemann, and W. Nellen. 1995. Environmental factors as forces structuring the fish community of the Elbe Estuary. *Journal of Fish Biology* 46: 47–69. https://doi.org/10.1111/j.1095-8649.1995.tb05946.x.

Thiriet, P. 2014. *Comparison of fish assemblage structure and underlying ecological processes, between Cystoseira forests and less structurally complex habitats in North-Western Mediterranean rocky subtidal rocky reefs*. Thesis: Université Nice Sophia Antipolis.

Tomasini, J.A., D. Collart, and J.P. Quignard. 1996. Female reproductive biology of the sand smelt in brackish lagoons of southern France. *Journal of Fish Biology* 49 : 594–612.

Tomasini, J.A, J.P. Quignard, C. Capapé, and J-L. Bouchereau. 1991. Facteurs du succès reproductif de *Syngnathus abaster* Risso, 1826 (Pisces, Teleostei, Syngnathidae) en milieu lagunaire méditerranéen (lagune de Maugio, France). *Acta oecologica* 12: 331–355.

Tsikliras, A.C., E. Antonopoulou, and K.I. Stergiou. 2010. Spawning period of Mediterranean marine fishes. *Reviews in Fish Biology and Fisheries* 20: 499–538. https://doi.org/10.1007/s11160-010-9158-6.

Tupper, M., and R. G. Boutilier. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 52. NRC Research Press Ottawa, Canada: 1834–1841.

Van Halder, I., L. Barbaro, E. Corcket, and H. Jactel. 2007. Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. In: Brockerhoff E.G., Jactel H., Parrotta J.A., Quine C.P., Sayer J., Hawksworth D.L. (eds) Plantation Forests and Biodiversity: Oxymoron or Opportunity? Topics in Biodiversity and Conservation, vol 9. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-2807-5_12.

Vasconcelos, R.P., P. Reis-Santos, V. Fonseca, A. Maia, M. Ruano, S. França, V. Vinagre, M.J. Costa, and H. Cabral. 2007. Assessing anthropogenic pressures on estuarine fish nurseries along the Portuguese coast: A multi-metric index and conceptual approach. *Science of the Total Environment* 374 (2–3): 199–215. https://doi.org/10.1016/j.scitotenv.2006.12.048.

Vasconcelos, R.P., P. Reis-Santos, A. Maia, V. Fonseca, S. França, N. Wouters, M.J. Costa, and H.N. Cabral. 2010. Nursery use patterns of commercially important marine fish species in estuarine systems along the Portuguese coast. *Estuarine, Coastal and Shelf Science* 86: 613–624. https://doi.org/10.1016/j.ecss.2009.11.029.

Velasco, E.M., M.C. Gómez-Cama, J.A. Hernando, and M.C. Soriguer. 2010. Trophic relationships in an intertidal rockpool fish assemblage in the gulf of Cádiz (NE Atlantic). *Journal of Marine Systems* 80: 248–252. https://doi.org/10.1016/j.jmarsys.2009.10.014.

Ventura, D., G. Jona Lasinio, and G. Ardizzone. 2014. Temporal partitioning of microhabitat use among four juvenile fish species of the genus Diplodus (Pisces: Perciformes, Sparidae). *Marine Ecology* 36: 1013–1032. https://doi.org/10.1111/maec.12198.

Verdiell-Cubedo, D. 2009. *Ictiofauna de las zonas someras litorales del Mar Menor (SE Península Ibérica): Parámetros de su biología y relaciones con el hábitat*. Thesis: Universidad de Murcia.

Verdiell-Cubedo, D., F.J. Oliva-Paterna, A. Ruiz-Navarro, and M. Torralva. 2013. Assessing the nursery role for marine fish species in a hypersaline coastal lagoon (Mar Menor, Mediterranean Sea). *Marine Biology Research* 9: 739–748. https://doi.org/10.1080/17451000.2013.765580.

Verdiell-Cubedo, D., F. Oliva Paterna, M. Andreu Soler, and M. Torralva Forero. 2007. Characterisation of the nursery areas for YOY Sparidae fish species in a Mediterranean coastal lagoon (SE Iberian Peninsula). *Anales de Biología*: 3–11.

Verdiell-Cubedo, D., F.J. Oliva Paterna, A. Egea Serrano, and M. Torralva Forero. 2008. Biología poblacional y asociaciones con el hábitat de las especies de peces bentónicas en las áreas someras de una laguna costera mediterránea (SE Península Ibérica). *Scientia Marina* 72: 319–328. https://doi.org/10.3989/scimar.2008.72n2319.

Vigliola, L., and M. Harmelin-Vivien. 2001. Post-settlement ontogeny in three Mediterranean reef fish species of the genus Diplodus. *Bulletin of Marine Science* 68: 271–286.

Ward, J.H. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58: 236–244. https://doi.org/10.1080/01621459.1963.10500845.

Westerberg, H., J. Haamer, and I. Lagenfeldt. 1993. A new method for sampling elvers in the coastal zone. In *ICES, C.M. Anadromous and Catadromous Fish Committee 1993*, M:5:10.

Whitehead, P.J.P. 1988. *FAO species catalogue: An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings*, vol. 7. Rome: Food & Agriculture Org.

Whitfield, A.K. 1999. Ichthyofaunal assemblages in estuaries: A South African case study. *Reviews in Fish Biology and Fisheries* 9: 151–186. https://doi.org/10.1023/A:1008994405375.

Whitfield, A.K. 2017. The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries* 27: 75–110. https://doi.org/10.1007/s11160-016-9454-x.

Whitfield, A.K., R.H. Taylor, C. Fox, and D.P. Cyrus. 2006. Fishes and salinities in the St Lucia estuarine system—A review. *Reviews in Fish Biology and Fisheries* 16: 1–20. https://doi.org/10.1007/s11160-006-0003-x.

Wilkins, H.K.A., and A.A. Myers. 1992. Microhabitat utilisation by an assemblage of temperate Gobiidae (Pisces: Teleostei). *Marine Ecology Progress Series* 90: 103–112.

Willemsen, J. 1980. Fishery-aspects of eutrophication. *Hydrobiological Bulletin* 14. Springer: 12–21.

Woodland, R.J., F.Y. Warry, Y. Zhu, R. Mac Nally, P. Reich, G.P. Jenkins, D. Brehm, and P.L.M. Cook. 2019. Role of benthic habitat structure and riverine connectivity in controlling the spatial distribution and ecology of estuarine fish. *Marine Ecology Progress Series* 630: 197–214. https://doi.org/10.3354/meps13116.

Yáñez-Arancibia, A., A.L. Lara-Dominguez and D. Pauly. 1994. Coastal lagoons as fish habitats, Chapter 12:363–376 in Coastal Lagoon Processes, Oceanography Series 60, ed B. Kjerve (Amsterdam: Elsevier Science B.V.), 578

Science of the Total Environment 732 (2020) 139292

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Fifty years of ecological changes: Regime shifts and drivers in a coastal Mediterranean lagoon during oligotrophication

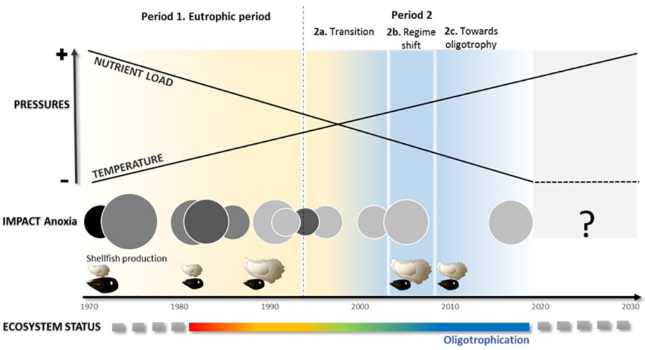
Valérie Derolez[a],*, Nathalie Malet[b], Annie Fiandrino[a], Franck Lagarde[a], Marion Richard[a], Vincent Ouisse[a], Béatrice Bec[c], Catherine Aliaume[c]

[a] MARBEC, Univ Montpellier, CNRS, IRD, Ifremer, Sète, France
[b] Ifremer LERPAC/CO, 20600 Bastia, France
[c] MARBEC, Univ Montpellier, CNRS, IRD, Ifremer, Montpellier, France

HIGHLIGHTS

- This 5-decades study explains the oligotrophication trajectory of a coastal lagoon.
- The decrease in nutrient inputs resulted in ecological changes in pelagic & benthic communities.
- A eutrophic period, a transition phase & a regime shift characterised recovery.
- The main triggers of summer anoxia were air temperature and eutrophication status.
- Oligotrophication has made the ecosystem more resistant to the threat of heat waves.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 26 February 2020
Received in revised form 6 May 2020
Accepted 6 May 2020
Available online 11 May 2020

Editor: Ashantha Goonetilleke

Keywords:
Eutrophication
Resilience
Anoxia
Climate change
Shellfish
Thau

ABSTRACT

Thau lagoon is a large Mediterranean coastal lagoons and it supports traditional shellfish farming activities. It has been subject to eutrophication leading to major anoxic events associated with massive mortalities of shellfish stocks. Since the 1970s, improvements have been made to wastewater treatment systems, which have gradually led to oligotrophication of the lagoon. The aim of our study was to determine how the decrease in nutrient inputs resulted in major ecological changes in Thau lagoon, by analysing five decades of time-series (1970–2018) of observations on pelagic and benthic autotrophic communities. We were able to identify two periods during the oligotrophication process. Period 1 (1970–1992) was considered a eutrophic period, characterised by the shift from seagrass dominance to dominance of red macroalgae. Period 2 (1993–2018), characterised by improved eutrophication status, was further divided into three: a transition phase (1993–2003) during which the water column continued to recover but the benthic community lagged behind in recovery and in partial resilience; a regime shift (2003–2006), after which the water column became oligotrophic and seagrass began to recover (2007–2018). Considering anoxia crises as indicators of ecosystem resilience and resistance, we used a generalised linear model to analyse meteorological and environmental data with the aim of identifying the triggers of summer anoxia over the study period. Among the meteorological variables studied, air temperature had the strongest positive effect, followed by the period and wind intensity (both negative effects) and by rainfall in

---

* Corresponding author.
E-mail address: valerie.derolez@ifremer.fr (V. Derolez).

https://doi.org/10.1016/j.scitotenv.2020.139292

July (positive effect). The risk of triggering anoxia was lower in period 2, evidence for the increasing resistance of the ecosystem to climatic stress throughout the oligotrophication process. At the ecosystem scale and in the long term perspective, the ecological gains related to oligotrophication are especially important in the context of climate change, with more frequent and severe heat waves predicted.

1. Introduction

Eutrophication is one of the most severe anthropic pressures faced by coastal ecosystems (de Jonge and Elliott, 2001; Nixon, 1995). Coastal lagoons are particularly exposed to anthropogenic eutrophication because of their relative isolation from the sea, their close links with watersheds, and their geomorphological features which enable high biological productivity (Newton et al., 2014; Pérez-Ruzafa et al., 2019b; Zaldívar et al., 2008). Anoxia is triggered by eutrophication and by hydro-climatic factors such as high temperatures, and can seriously affect ecosystem functioning and the provision of ecosystem services (Iriarte et al., 2014; Jager et al., 2018; Newton et al., 2018) as they lead to the collapse of aquatic communities (Elliott and Quintino, 2007; Friedrich et al., 2014).

Thau lagoon is one of the largest Mediterranean coastal lagoons and supports traditional fishery and shellfish farming and, more recently, tourism and recreational activities (Deslous-Paoli et al., 1998; Gangnery et al., 2001). At the beginning of the 20th century, Thau lagoon was dominated by seagrass beds associated with gastropods, while bare bottom areas were dominated by bivalves (Calvet, 1910). Since the 1960s, facing the exponential growth of the human population in the French Mediterranean coastal region and the resulting increase in anthropogenic inputs, Thau lagoon has suffered eutrophication and degradation of water quality (La Jeunesse and Elliott, 2004; Picot et al., 1990; Souchu et al., 2010). Among the ecological and socio-economic impacts of this degradation, eutrophication caused major anoxic events leading to massive mortality of shellfish stocks with significant economic impacts (Chapelle et al., 2000a; Souchu et al., 1998a).

In the 1970s, improvements were made to waste-water treatment systems in the watershed. Ever since, a decrease in nutrient inputs to Thau lagoon has been recorded (Deslous-Paoli et al., 1998; La Jeunesse et al., 2002), reinforced in the late 2000s by the European regulations (EC, 1991a, 1991b, 2000), which gradually led to the oligotrophication of the ecosystem (Bec et al., 2011; Collos et al., 2009). In our study, “oligotrophication” refers to the process associated with the depletion of nutrient in aquatic ecosystems, as used in other studies analysing the process of recovery of coastal or freshwater ecosystems after a decrease in nutrient loads (De Wit et al., 2020; Kamenir and Morabito, 2009; Mozetič et al., 2010). The recovery of the ecosystem was associated with a significant decrease in phytoplankton biomass, linked to a decrease in diatom abundance, and to a taxonomic shift in the microphytoplankton community, raising shellfish farmers' concerns about the limit of the lagoon's carrying capacity (Gowen et al., 2015; Derolez et al., 2020). In parallel, climate forcings in the Mediterranean region changed between the 1970s to the 2010s, with an increase in mean air temperature and in the frequency of summer heat waves, and a decrease in the frequency of wet years (Derolez et al., 2020; Jouzel et al., 2014). This raised the hypothesis that the shift in phytoplankton communities could be the result of the effects of a reduction in nutrient inputs combined with climatic-related variables.

Oligotrophication has only recently been characterised in coastal lagoons and existing studies mainly focus on a single community of primary producers: phytoplankton (Collos et al., 2009; Derolez et al., 2020; Leruste et al., 2016) or macrophytes (Le Fur et al., 2019; Tsiamis et al., 2013). Some of these studies showed that oligotrophication can lead to significant community shifts: from the dominance of diatoms to that of Chlorella-like algae and dinophytes (Leruste et al., 2016) and from the dominance of opportunistic species to that of perennial macrophyte species (Le Fur et al., 2019; Tsiamis et al., 2013). However, few studies have described coastal lagoons at the ecosystem level and over a long period to identify ecological changes (Pasqualini et al., 2017; Pérez-Ruzafa et al., 2019a). In coastal lagoons, assessing ecological status regarding eutrophication requires data on both pelagic and benthic compartments, as recommended by several authors (Newton et al., 2003; Zaldívar et al., 2008), most of which are identified in the Water Framework Directive (WFD) (EC, 2000): nutrients in the water column, phytoplankton biomass and abundance, macrophyte abundance and composition, and finally nutrients and organic matter in the sediment. However, regarding the dynamics of ecosystems recovery under global change, integrated long-term studies are needed to better understand the trajectories of lagoons focused on (i) changes in the ecosystem status, (ii) the capacity of ecosystems to withstand changes during environmental stresses (hereafter referred to as “resistance”), and (iii) their ability to return to predisturbance levels (hereafter referred to as “resilience”) (Elliott et al., 2007; Gladstone-Gallagher et al., 2019).

The aim of the present study was first to determine how the decrease in nutrient inputs has resulted in ecological changes in the Thau lagoon ecosystem, by analysing five decades of time-series (1970–2018) of observations of the pelagic (nutrients and phytoplankton in the water column) and benthic (macrophytes and sediment) compartments. We hypothesise that the process of oligotrophication has led to ecosystem regime shifts and to changes in the drivers of summer anoxia, making the ecosystem more resistant to the threat of climate change. Considering anoxia crises as indicators of ecosystem resilience and resistance, we then analysed meteorological data, eutrophication status and shellfish production to identify the triggers of summer anoxia over the 49-year period.

2. Materials and methods

2.1. Study site

Thau lagoon is a microtidal restricted coastal lagoon, connected to the Mediterranean Sea through two permanent inlets, one of which is the Sète channel located in the north-east, which is responsible for 90% of sea water exchanges (Fig. 1) (Fiandrino et al., 2017). The lagoon covers an area of 68 km^2, its mean depth is 4 m (Fiandrino et al., 2017). A depth gradient is observed from the south-west (mean depth: 3.3 m) to the north-east (mean depth: 5.2 m) of the lagoon (Souchu et al., 2001). The Thau watershed covers 280 km^2 and is drained by tributaries with intermittent flows and two permanent rivers (La Jeunesse et al., 2015). Approximately half the watershed's permanent population (103,500 inh. in 2015, INSEE 2016) is located in the city of Sète (La Jeunesse et al., 2015).

Shellfish farming structures cover 20% of the lagoon surface in three cultivation zones (Fig. 1). The shellfish reared are mussels *Mytilus galloprovincialis* (*M. galloprovincialis*) and Pacific oyster, *Crassostrea gigas* (*C. gigas*), whose production accounted for about 10% of total French oyster production in the 2000s (Gangnery et al., 2003).

2.2. Biological and meteorological monitoring

The biological and meteorological data used in our study, the associated spatial and temporal strategy and the references when available, are described in detail in Table A1.

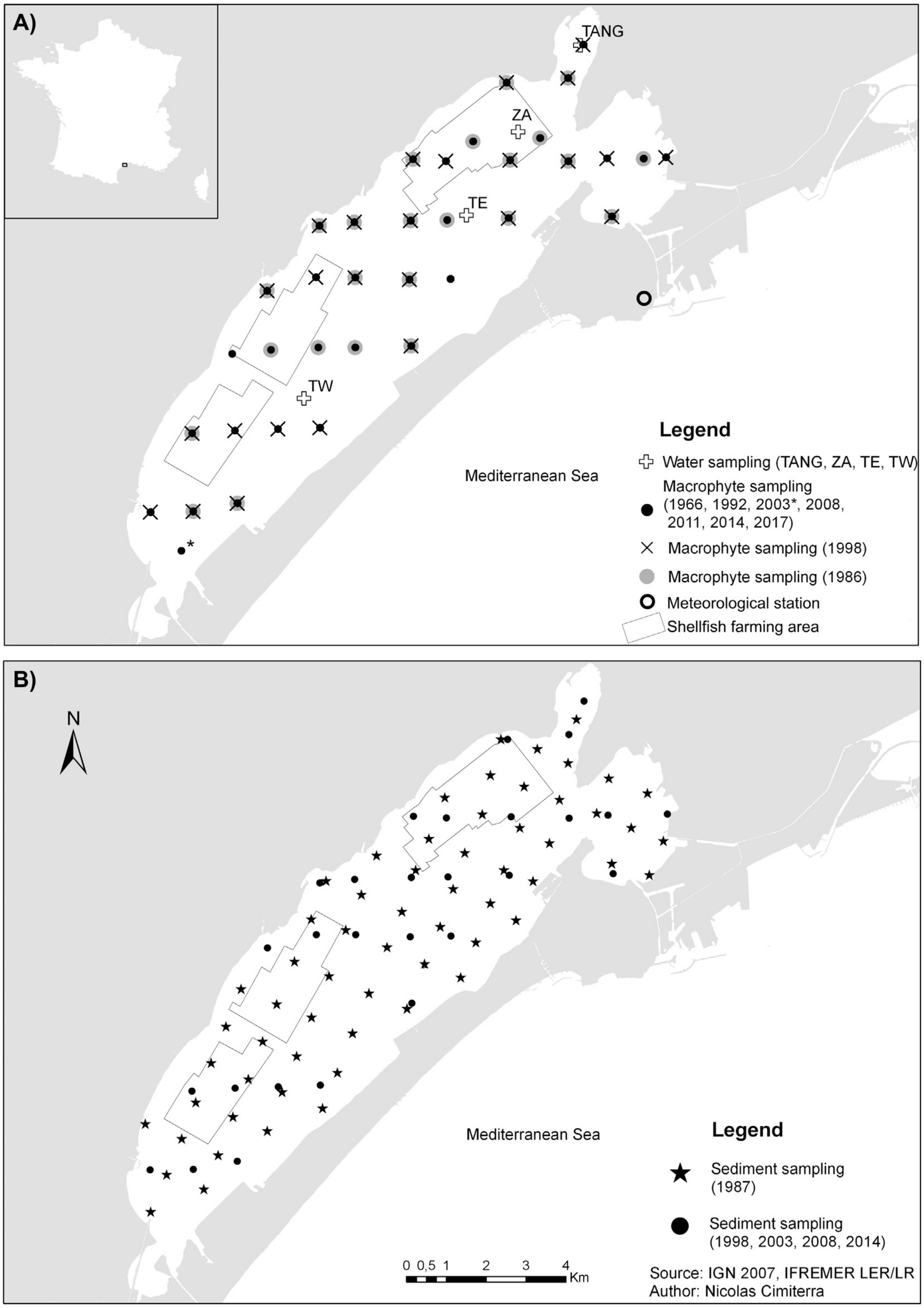


Fig. 1. A) Location of Thau lagoon and of water and macrophyte sampling stations (*the macrophyte station not sampled in 2003). B) Location of sediment sampling stations. The three shellfish farming areas are represented by polygons.

2.2.1. Hydrological, nutrients and phytoplankton time series

From 1999 to 2018, water samples were collected monthly in summer (June, July and August), which is the maximum primary production period in Mediterranean lagoons (Bec et al., 2011; Souchu et al., 2010), at three stations: TANG, TE and TW (Fig. 1A). Samples were collected a minimum of three days after any period when wind speed exceeded 12.5 m s^{-1} to allow sediments to stabilise. Temperature (*TEMP*, °C), salinity (*SAL*) and dissolved oxygen (*O2*, mg L^{-1}) were recorded in situ with field sensors. At each station, on each sampling occasion, one water sample was collected in a 1 L polypropylene bottle 1 m below the surface for laboratory analyses, according to Souchu et al. (2010).

Laboratory analyses were carried out to measure dissolved and total nutrient concentrations (μM): dissolved inorganic phosphorus (*DIP*), dissolved inorganic nitrogen ($DIN = NH_4^+ + NO_3^- + NO_2^-$), total nitrogen (*TN*) and total phosphorus (*TP*). Nutrients were analysed using the standard protocols (Aminot and Kérouel, 2007) described in Souchu et al. (2010). Turbidity (*TURB*, NTU) was measured in the laboratory with a HACH 2100 N IS sensor according to ISO 7027.

From 1972 to 1993, DIP was analysed in water samples collected monthly in summer at ZA station, located in the shellfish farming area in the north-east part of the lagoon (Fig. 1A) (Collos et al., 2009; Derolez et al., 2020; Souchu et al., 1998a).

Phytoplankton analyses were performed according to Bec et al. (2011). Chlorophyll *a* concentrations (*CHLA*, μg Chl *a* L^{-1}) were measured by spectrofluorimetry (Neveux and Lantoine, 1993) with a Perkin-Elmer L650. Based on cytometric analyses, different size classes of phytoplankton were identified and counted with a FACSCalibur flow cytometer: autotrophic picoeukaryotes (≤3 μm) and nanophytoplankton (>3 μm) abundances (*PEUK* and *NANO*, 10^{-6} cells L^{-1}). Phycoerythrin-rich picocyanobacteria (<1 μm, *PE-CYAN*, 10^{-6} cells L^{-1}) were distinguished from other photosynthetic organisms by their strong orange fluorescence and light-scattering properties.

2.2.2. Macrophyte and sediment time series

Soft bottom macrophytes were monitored five times in June from 2003 to 2017 at 36 stations (Fig. 1A, Table A1). Data from four older samplings (1966 to 1998), collected using different sampling protocols and monitoring methods, were added to the macrophyte time series. Table A1 summarises the years of observation, the formats of the data and the sampling methods used for all macrophyte data. In the case of sampling carried out over several years to cover the entire surface of the lagoon, it was decided to refer to the year corresponding to the middle of the period (i.e. year 1966 for the sampling period 1963–1968, and year 1992 for the sampling period 1988–1994) in the results Section 2.3.2. The methods applied in 1998 and from 2003 to 2017 are detailed in Le Fur et al. (2017).

Sediment was sampled at 28 stations in late spring or early summer in 1998, 2003, 2008 and 2014 (Fig. 1B). The top layer (0–5 cm) of sediment was collected with a sediment corer and then sifted through a 2-mm sieve (see Le Fur et al. (2019) for details). Mud content (%) corresponded to the fraction with a diameter of less <50 μm. Organic matter content (*OM*, expressed as % of dry sediment weight), total nitrogen (*TN*) and total phosphorus (*TP*) were analysed and were expressed in g kg^{-1} and mg kg^{-1} of dry sediment, respectively.

Data on Kjeldahl-N (*KN*) and TP concentrations, analysed in sediment samples collected in 1987 at 30 stations, were taken from Péna and Picot (1991) and added to the sediment time series.

2.2.3. Shellfish production

Total annual oyster production, mussel production and total shellfish production data (in 10^3 t y^{-1}) were collected by the Departmental Direction of Maritime Affairs and gathered by Comps (2000) and Gangnery (1998, 1999) for the period 1970–2000. Data for the years 2001, 2002 and 2003 were collected by Gangnery (2003). Production data for the period 2004 to 2018, were provided by the Departmental Directorate of Territories and the Sea (French acronym DDTM). The mussel species remained the same throughout the study period (*M. galloprovincialis*), but the oyster species changed in 1973 after the epizootic linked to an iridovirus which resulted in the disappearance of the Portuguese oyster *Crassostrea angulata*, which was replaced by the Pacific oyster (*C. gigas*) (Grizel and Héral, 1991).

Given that anoxia events can cause significant mortality of the shellfish cultivated in the lagoon, the total shellfish production of the preceding year was used to estimate the stock exposed to anoxia in the summer of any given year (*Q_shellfish_1*). Data were transformed into binary variables with the following values: *shellfish* = 1 for low production rates (≤10,000 t) and *shellfish* = 2 for higher production (>10,000 t).

2.2.4. Meteorological data

Daily data on rainfall (mm), air temperature (°C) and wind intensity (m s^{-1}) from 1970 to 2018 were collected from the Sète meteorological station (Météo-France station n°34301002) (Fig. 1A).

Summer air temperatures and wind intensities were averaged by month (June, July and August) (*air_M*, *wind_M*). Wind intensities were then standardised according to four periods determined by shifts in the raw time series corresponding to modifications to the sensors identified by Météo-France (January 1972, August 1996, January 2008) (*wind_ST*).

Rainfall was cumulated in June, July and August (*rainfall_6*, *rainfall_7*, *rainfall_8*) corresponding to the summer months when anoxia occurs, and from January to May (*rainfall_1–5*) corresponding to the winter and spring months preceding anoxia.

2.3. Data processing and analyses

2.3.1. Hydrological, nutrient and phytoplankton time series

Data collected in summer from 1999 to 2018 at the three stations TANG, TE and TW were averaged per year before performing an explanatory PCA analysis with nine variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*, *PE-CYAN* and *O2*) (ade4 package in R). The phytoplankton variables were $\log_{10}$ transformed to normalise the data and reduce the effect of very high values. The three hydrological parameters (*TEMP*, *SAL* and *TURB*) were considered as illustrative variables in the PCA. K-means cluster analysis was then applied to identify years and stations with similar eutrophication patterns (vegan package in R). The optimal number of clusters was estimated based on the Calinski-Harabasz index (Calinski and Harabasz, 1974).

For the hydrological and phytoplankton variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*, *PE-CYAN*, *O2*, *TEMP*, *SAL*, *TURB* and the ratio *PE-CYAN/PEUK*), Mann-Kendall tests (MK) were performed on the means calculated for each year from 1999 to 2018 to characterise the monotonic trends. To eliminate the effect of serial correlations on the MK test, we used the modification by effective sample size, computed with significant serial correlation coefficients (Hamed and Rao (1998), modified mk package in R). If the test was significant (i.e. *p*-values < 0.05), the Theil-Sen's slope estimator was calculated (Sen, 1968). The correlation between water temperature and *PE-CYAN* was tested using Spearman's test.

In Thau lagoon, DIP is not considered to be the main limiting nutrient (Fouilland et al., 2002; Souchu et al., 2010) and its concentrations in water are well correlated with the inputs from human activities in the watershed (La Jeunesse and Elliott, 2004). Moreover, in summer, it has been shown that in deeper lagoons such as Thau, P loads from sediments are enhanced by high temperatures through the benthic remineralization process (Chapelle et al., 2000b; Souchu et al., 1998a; Zilius et al., 2015). Finally, shellfish farming is known to contribute to summer remineralization (Chapelle et al., 2000a; Mazouni et al., 1996). For all these reasons, the summer concentration of DIP in the water column is a good indicator of eutrophication in the Thau lagoon. To analyse the changes in summer DIP concentrations in the water of Thau lagoon from 1970 to 2018, we pooled the data collected in summer at ZA and TE stations, located in the same well mixed zone according to Millet (1989) and Fiandrino et al. (2017). To avoid the impact of high temperatures and anoxia on DIP due to increased discharge from sediment (Chapelle et al., 2000b; Mazouni et al., 1996), data collected in the late summer (July and August) were removed from the dataset. Thus, DIP data collected in June (*DIP_6*) were modelled using LOESS (polynomial degree = 2, smoothing degree = 0.75). The first derivative of the modelled data was first used to identify the breaking points characterising changes in the slope in the curve. Then, the measured concentrations of DIP in June were compared with the threshold of the good status for DIP according to the WFD (DIP ≤ 1 μM; MTES, 2018), in order to identify the year after which this threshold was no longer exceeded. These two criteria were used to divide the time series into two contrasting periods in terms of eutrophication status: *period 1* and *period 2*. We performed MK tests on the total time series and for both periods to characterise monotonic trends.

2.3.2. Macrophyte community

The phylum taxonomic scale was chosen to enable us to compare macrophyte data from the nine available surveys conducted between 1966 and 2018 (Table A1). The macrophytes were distributed in four groups: red algae (Rhodophyta), green algae (Chlorophyta), brown algae (Ochrophyta) and seagrass (Tracheophyta). An additional group corresponding to bare sediment was created for stations with no vegetation. For data whose measurements were sporadic, the percentage of cover or biomass was calculated for each group of macrophytes. The group with the highest percentage of cover was selected as "dominant". When the difference in the percentages between the first two groups was ≤2%, both groups were considered to be dominant. This pretreatment enabled comparison of data on dominant groups shown on the maps collected from 1966 to 1992. The first two most frequent genera in each group are given for each survey.

The spatial representation of the macrophyte was homogenised over the nine vegetation surveys in order to retrieve the data corresponding to the 36 benthic stations monitored in the five most recent surveys (Fig. 1). Concerning the three surveys conducted between 1986 and 1998, the macrophyte data were retrieved from 100 m buffer zones created around the 36 stations projected onto the three available maps. The publications used to construct the map of the 1960s consisted of a description of macrophyte distribution in the literature, without precise spatial coordinates. Consequently, we localised the information on the dominant species in the locations described in the literature. In the surveys carried out before 2003, it was not possible to collect information from all 36 stations. The number of stations used for each survey is given in Table A1.

Finally, the proportion of stations with bare sediment (i.e. without vegetation) or dominated by each group of macrophytes was calculated for each period as follows: Proportion of stations dominated by group *i* = number of stations dominated by group *i* ÷ total number of stations considered.

2.3.3. Sediments

To characterise the monotonic trends of sediment variables we performed Mann-Kendall tests on the medians calculated for each survey (1998, 2003, 2008 and 2014 for mud, OM and TN and 1987, 1998, 2003, 2008 and 2014 for TP).

2.3.4. Occurrence and intensity of anoxia events, meteorological and environmental conditions

Information on the frequency and intensity of the summer anoxic crises which occurred between 1970 and 2018 was collected from the scientific and grey literature (Hamon et al., 2003; Troussellier and Deslous-Paoli, 2001; Ifremer, 2004; Ifremer, 2007; Lagarde, 2018). Since the spatial and temporal strategies of O_2 monitoring did not remain the same over the study period, we defined the occurrence of anoxia based on presence of white water caused by sulphur bacteria reoxidising the sulphur released in the water column (Minghelli-Roman et al., 2011), or on the presence of at least one measurement of O_2 concentration < 0.05 mg L^{-1}. The intensity of the anoxia crises was characterised according to their duration in months (≤1 to 3) and to their maximum spatial extent: 1 (one of the shellfish farming areas), 2 (two of the shellfish farming areas), 3 (all three shellfish farming areas), 5 (the whole lagoon).

Out of the total of 147 summer months in the 1970–2018 period, 12 months were characterised by the onset of an anoxia crisis (*anoxia* = 1) and 135 months had no anoxia onset (*anoxia* = 0). In order to identify the meteorological and environmental conditions involved in the triggering of anoxia, a binomial generalised linear model (glm) (McCullagh and Nelder, 1989) was built with the following eight variables:

- meteorological variables: *air_M* and *wind_ST* (summer monthly averages), *rainfall_6*, *rainfall_7*, *rainfall_8* and *rainfall_1–5* (cumulative rainfalls);
- eutrophication status: *period* (1 or 2);
- shellfish production: *shellfish* (1: low or 2: high).

The Akaike information criterion (AIC) was used to select the significant variables and the odds ratios (OR) were calculated ($OR_x = e^{\beta x}$, with β_x the estimated coefficient for variable x) to evaluate the probability of triggering anoxia versus the probability of not triggering anoxia when modifying variables independently. The odds ratios provide information on the strength and direction of the association between the dependent and explanatory variables (OR > 1: increases the probability, 0 ≤ OR < 1: decreases the probability) (Schwarz, 1978, ggeffects in R). The performance of the glm was assessed by cross validation (70% for calibration, 30% for validation). The test datasets consisted of 100 observations randomly drawn from the 135 months with no anoxia; and from the 12 months characterised by the onset of anoxia. The receiver operating characteristic (ROC), which depends on specificity and sensitivity, and the area under the curve (AUC) were calculated for the 50 test datasets drawn randomly to estimate the average and standard deviation of this criterion (DeLong et al., 1988, Presence-Absence in R). According to AUC, a model is considered as not contributing (AUC = 0.5), not very informative (0.5 ≤ AUC < 0.7), moderately informative (0.7 ≤ AUC < 0.9), very informative (0.9 ≤ AUC < 1) or perfect (AUC = 1) (Swets, 1988).

In addition, Kruskal-Wallis tests were performed on the following variables to identify significant differences in the characteristics of the two periods: *air_M*, *wind_ST*, *rainfall_6*, *rainfall_7*, *rainfall_8*, *rainfall_1–5*, *DIP_6* and *Q_shellfish_1*.

3. Results

3.1. Change in trophic status from eutrophication to oligotrophication

3.1.1. Water column

The average summer concentrations of dissolved phosphorus measured in water ranged from 6.7 μM in 1972 to 0.04 μM in 2016–2017, with a median value of 0.9 μM, and they decreased monotonically and significantly over the study period (MK $p < 0.001$, Theil-Sen's slope = −0.1 μM y^{-1}) (Fig. 2).

When focusing on June observations, the concentrations of dissolved phosphorus ranged from 5.2 μM in 1974 to 0.04 μM in 2015–2017, with a median value of 0.3 μM, and they decreased monotonically and significantly over the study period (MK $p < 0.001$, Theil-Sen's slope = −0.1 μM y^{-1}) (Fig. 2, black dots). The slope of the time series modelled with LOESS revealed two breaks: the first in June 1991 and the second in June 1993. Moreover, the threshold of good status according to WFD (DIP ≤ 1 μM) was no longer exceeded after June 1993, which made it possible to identify two contrasting periods based on the eutrophication status: period 1, from 1970 to 1992 and period 2, from 1993 to 2018. When considering data for each period separately, DIP concentrations also decreased significantly, but the median and the slope were higher in the first period (respectively, median = 2.3 μM, MK $p < 0.001$ and Theil-Sen's slope = −0.3 μM y^{-1}; median = 0.1 μM, MK $p = 0.002$ and Theil-Sen's slope = −0.005 μM y^{-1}).

PCA analysis of the data was performed on nine variables (*DIN*, *DIP*, *TP*, *TN*, *CHLA*, *PEUK*, *NANO*, *PE-CYAN* and *O2*) collected from 1999 to 2018, corresponding to PERIOD 2 defined based on eutrophic status. The PCA of this water column time series showed that the two first axes accounted for 52.6% of total variability (33.9% and 18.6% for axis 1 and axis 2, respectively). The third axis, accounted for 14.4% of the

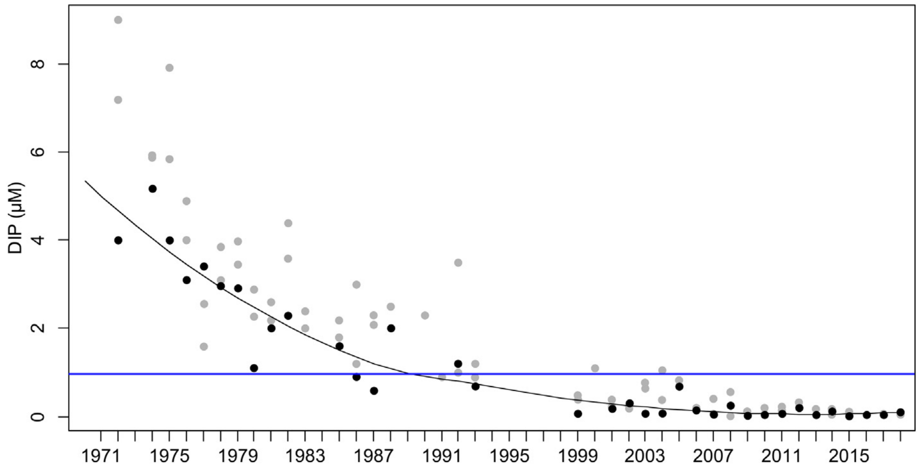


Fig. 2. Changes in summer DIP concentrations (µM) in the water in Thau lagoon from 1972 to 2018 at ZA station (1972–1993) and TE station (1999–2018). Data for June are represented by black dots and the LOESS curve in DIP in June by a black line. Data for July and August are represented by grey dots. The blue line represents the threshold of the good status according to the WFD (DIP ≤ 1 µM; MTES, 2018).

variability and was positively correlated with O2 and negatively correlated with TN (Fig. A1.A). The first axis revealed a clear temporal structure, contrasting the earliest and the most recent years (Fig. 3B). This first axis was negatively correlated mainly with TP, DIP, PEUK, CHLA and DIN (Fig. 3A). The second axis was mainly defined by PE-CYAN abundances, with a high contribution of the years 2006 and 2003 (Fig. 3A). The temperature, considered as an illustrative variable in the PCA analysis, was correlated with the second axis and consequently with PE-CYAN. The third axis isolated the samples collected at TANG station (Fig. A1.C).

Among the three clusters identified by the Calinski-Harabasz index on the PCA, a first group, located on the left side of the PCA, grouped 23 samples collected from 1999 to 2008, with the years 1999 to 2001 and 2003 to 2005 only found in this cluster (Fig. 3B). On the right side of the PCA, the second cluster (29 samples) was characterised by low levels of nutrient and phytoplankton biomass and abundance and isolated the samples collected exclusively from 2007 to 2018 (Fig. 3B). Finally, the third cluster was isolated according to the third axis and grouped seven samples collected at TANG station in 2002, 2006, 2008 to 2011 and 2018 (Fig. A1.B and A1.C).

From 1999 to 2018, the phytoplankton community was marked by changes in chlorophyll *a* biomass and pico- and nano-phytoplankton abundances at TW-TE stations (averaged data) and TANG stations (Fig. 4). A significant decreasing trend was found for chlorophyll *a* biomass from 1999 to 2018 (respectively MK $p = 0.003$ and $p = 0.02$, Theil-Sen's slope $= -0.17$ µg L^{-1} and -0.15 µg L^{-1}). Moreover, two phases are identifiable in the evolution of CHLA: the period 1999–2006, when maximum values were reached (respectively 6.2 and 15.7 µg L^{-1} at TW-TE and TANG), and the period 2007–2018 characterised by lower values (<2 µg L^{-1}) (Fig. 4A).

Like chlorophyll *a*, picoeukaryote abundances revealed a decreasing trend (MK $p = 0.006$ and 0.001 and Theil-Sen's slope $= -1.6$ 10^6 L^{-1} and -2.8 10^6 cells L^{-1} at TW-TE and TANG stations respectively), with the exception of the maximum values reached in 2003 and 2004 (respectively 120 10^6 cells L^{-1} at TW-TE and 113 10^6 cells L^{-1} at TANG) (Fig. 4C). On the contrary, nanophytoplankton revealed no significant monotonic trend (MK $p > 0.05$). Nanophytoplankton levels peaked in 2006 (41.6 10^6 cells L^{-1} at TANG) and increased to reach a second maximum in 2011 (28.4 10^6 cells L^{-1} at TW-TE), then decreased and remained below 3.7 10^6 cells L^{-1} (Fig. 4B).

Changes in phycoerythrin-rich picocyanobacteria were contrasted, with no significant monotonic trend (MK $p > 0.05$). PE-CYAN abundances exhibited three peaks in 2003, 2006 and 2018 (respectively 283.7, 295 and 282.3 10^6 cells L^{-1} at TW-TE), associated with water temperatures above 25.6 °C (Fig. 4D). Water temperatures and PE-CYAN abundances were significantly correlated at TW-TE stations (Spearman $p = 0.002$, rho $= 0.65$) but not at TANG station. Finally, the PE-CYAN/PEUK ratio increased significantly, from 0.01 in 1999 to 15.7 in 2018 at TW-TE (MK $p < 0.001$ Theil-Sen's slope $= 0.16$), but not at TANG station.

Among the other hydrological parameters, decreasing monotonic trends were found for TP, DIP and DIN at TW-TE and TANG stations from 1999 to 2018 (Fig. A2.B, A2.D and A2.C) and for TN and O2 only at TW-TE stations (Fig. A2.A and A2.F). An increasing trend was found for TEMP only at TANG station (Fig. A2.H).

3.1.2. Benthic compartment

3.1.2.1. Macrophyte composition. The percentage of benthic stations not covered by soft bottom macrophytes tended to decrease from 1966 to 2017, with the highest percentages measured in the 1980s and 1960s (28.6 and 22%, respectively), and null values from 2011 on (Fig. 5).

The macrophyte community consisted mainly of seagrass beds in the 1960s, dominating coverage at 40% of the benthic stations (Fig. 5). Seagrass cover declined between the 1960s and the 1980s in favour of red algae, which became the second dominant group after seagrass in 1986 and 1992. The percentage of stations dominated by seagrass continued to decline until 2003, when it reached its minimum (11.4%), then increased from 15.4% in 2008 to 22.5% in 2011 and 2014. After dominance by seagrass, red algae dominated the macrophyte community from 1998 to 2017 (between 42.5% of benthic stations were dominated by this group in 2011 and 2014 and 55.6% in 2017).

Brown algae dominated 18% of the stations in 1966, but rarely dominated between 1986 and 2008 (0 to 15.4% of the benthic stations were dominated by this group); brown algae reached 22.5% to 25% between 2011 and 2017. The contribution of green algae to macrophyte cover was low to zero (in 2017) and did not change significantly over the study period (from 11.4% of benthic stations dominated by this group in 1966 and 2003 to 19.2% in 1999).

Regarding the composition of each group of macrophytes, seagrass beds were composed of two *Zostera* species: *Zostera noltei* and *Z. marina*, both species being observed in all samples collected from 1966 to 2017.

Red algae consisted of *Polysophonia* and *Halopitys* genera in 1966 (Dubois, 1972; Lauret, 1967, 1970). Then, *Halopitys* and *Gracilaria* genera were the two most frequent red algae observed in 1986, 1992 and 1998 (Gerbal and Verlaque, 1995; Lauret, 1990, 1994; Verlaque, 2000). *Gracilaria* and *Alsidium* were the most frequent red algae in 2003 and *Gracilaria* and *Polysiphonia* in 2008 (Ifremer, 2004, 2007).

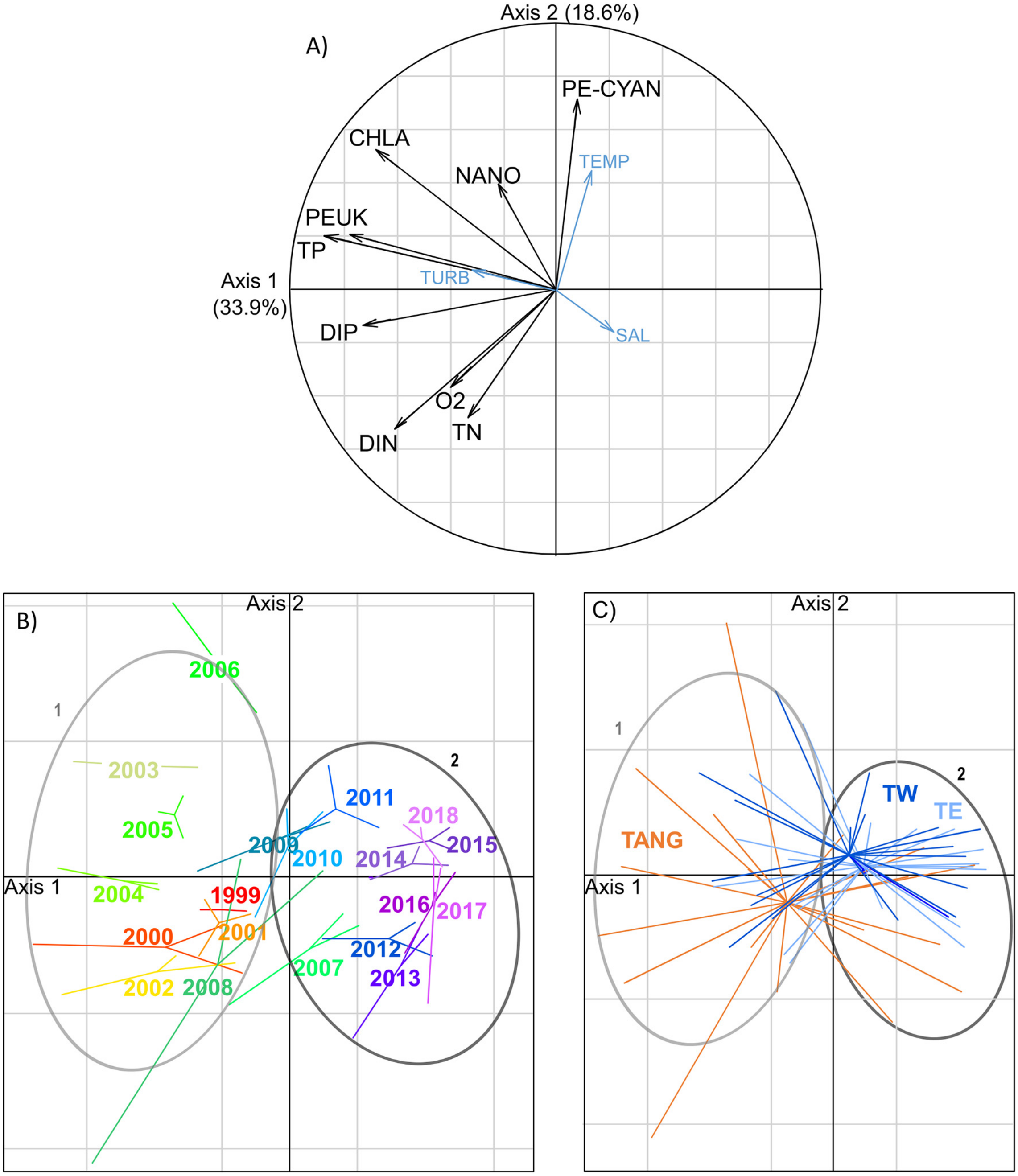


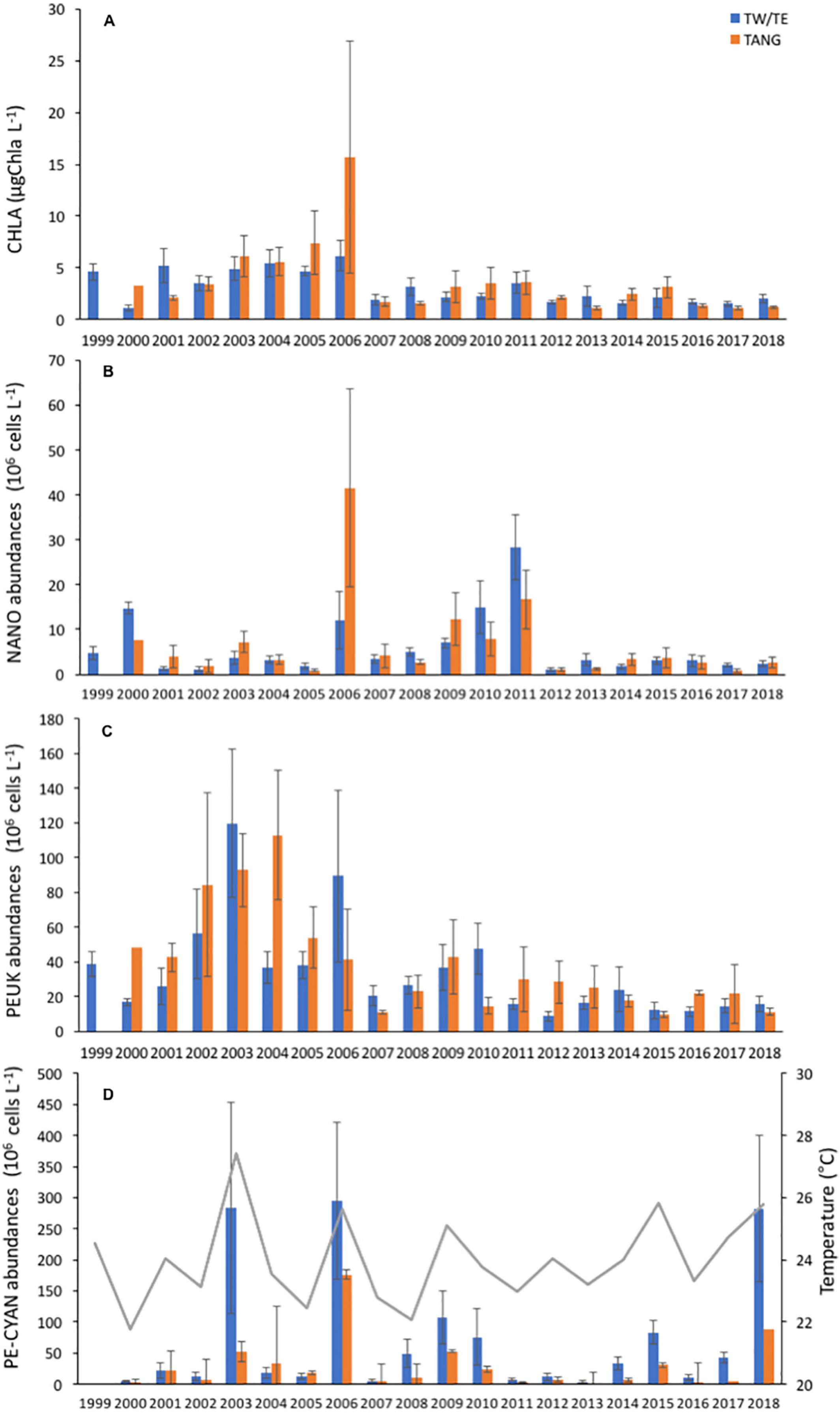
Fig. 3. Results of PCA analysis of water column parameters monitored from 1999 to 2018 at the three stations TW, TE and TANG. A) First and second axes for the nine environmental variables (dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), total phosphorus (TP), total nitrogen (TN), chlorophyll *a* (CHLA), autotrophic picoeukaryotes (PEUK), nanophytoplankton (NANO), phycoerythrin-rich picocyanobacteria (PE-CYAN) and dissolved oxygen (O2)). Illustrative hydrological variables (temperature (TEMP), salinity (SAL) and turbidity (TURB)) are in blue. B) Years and C) sampling stations on the plane defined by first and second axes accounted for 52.6% of the total variability. The first cluster is represented by a grey ellipse and the second cluster by a black ellipse.

Finally, from 2011 to 2017, *Gracilaria* and *Halopitys* again became the most frequent red algae, with a shift in dominance from *Gracilaria* to *Halopitys* in 2017 (Bouchoucha et al., 2019; Derolez et al., 2015; Ifremer, 2009, 2012).

Codium genera was the only green algae listed in 1966, while *Ulva* and *Monostroma* genera were the most frequently observed green algae in 1986 (Dubois, 1972; Gerbal and Verlaque, 1995; Lauret, 1967, 1970). *Ulva* and *Chaetomorpha* were the most frequent genera in 1992 (Lauret, 1990, 1994). Finally, the most frequent green algae were *Ulva* and *Cladophora* in 2008 and 2011 and *Chaetomorpha* and *Cladophora* in 1998, 2003 and 2014 (Derolez et al., 2015; Ifremer, 2004, 2009, 2012; Verlaque, 2000).

Cystoseira and *Sargassum* were the only brown algae genera listed in 1966 and 1998, respectively, whereas both genera were cited in 1986 (Dubois, 1972; Gerbal and Verlaque, 1995; Lauret, 1967, 1970). *Colpomenia* and *Cutleria* and *Colpomenia* and *Cystoseira* were the most frequently observed in 1998 and 2003, respectively, (Ifremer, 2004; Verlaque, 2000). Finally, *Dictyota* genera and the family *Ectocarpaceae* were the most frequent brown algae observed from 2008 to 2017 (Bouchoucha et al., 2019; Derolez et al., 2015; Ifremer, 2009, 2012).

3.1.2.2. Sediment. Median concentrations of mud and organic matter in the surface sediment ranged from 61.8% in 1998 to 83.5% in 2008 and from 6.6% in 1998 to 13% in 2014, respectively, but did not change


A
TW/TE
TANG
CHLA (µgChla L-1)
0
5
10
15
20
25
30
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018
B
NANO abundances (10⁶ cells L-1)
0
10
20
30
40
50
60
70
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018
C
PEUK abundances (10⁶ cells L-1)
0
20
40
60
80
100
120
140
160
180
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018
D
PE-CYAN abundances (10⁶ cells L-1)
0
50
100
150
200
250
300
350
400
450
500
Temperature (°C)
20
22
24
26
28
30
1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018

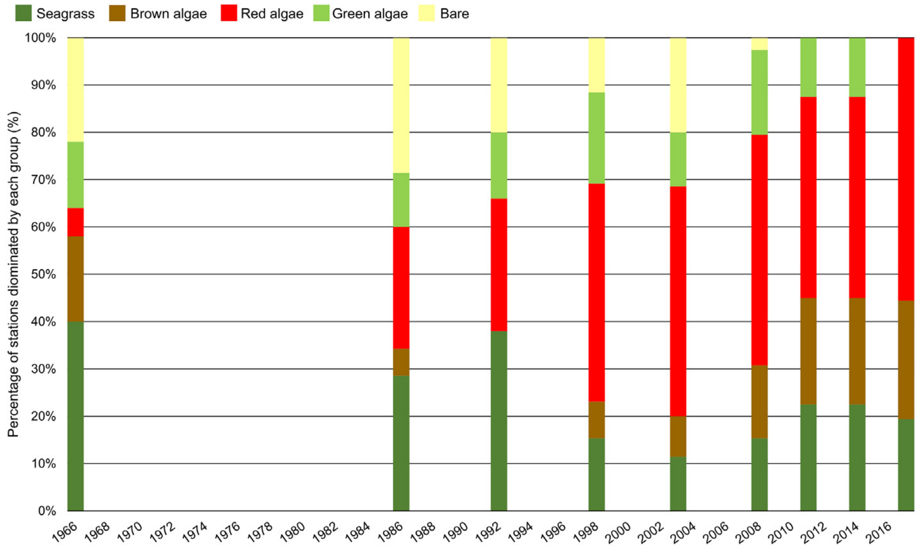


Fig. 5. Proportion of stations dominated by four groups of macrophytes (seagrass, brown algae, red algae and green algae) or bare sediment from 1966 to 2017 (data from Bouchoucha et al., 2019; Derolez et al., 2015; Dubois, 1972; Gerbal and Verlaque, 1995; Ifremer, 2004, 2009, 2012; Lauret, 1967, 1970, 1990, 1994; Verlaque, 2000). *NB: 1966 refers to the sampling period 1963–1968; 1992 refers to the sampling period 1988–1994.*

significantly from 1998 to 2014 (MK $p = 0.67$ and $p = 0.051$, respectively) (Fig. A3-A and A3-B). On the contrary, a significant increasing trend was revealed for total nitrogen from 1998 to 2014, with medians ranging from 2.8 to 4.7 g kg^{-1} (MK $p = 0.001$, Theil-Sen's slope = 0.54 g kg^{-1} y^{-1}) and confirmed from 1987 to 2014 when KN values measured in 1987 (2.7 g kg^{-1}) were included (MK $p < 0.001$, Theil-Sen's slope = 0.49 g kg^{-1} y^{-1}) (Fig. A3-C). In contrast to the other parameters, although the medians of total phosphorus did not show a monotonic trend from 1987 to 2014 (MK $p = 0.81$), the maximum was reached in 2003 (771 mg kg^{-1}) and the minimum in 2014 (577 mg kg^{-1}) (Fig. A3-D).

3.2. Changes in shellfish production

Shellfish production varied significantly between 1970 and 2018 (Fig. 7). Total annual production ranged from 6650 t in 1982 to 18,000 t in 2001 to 2003. Mussel production ranged from 1038 t in 1990 to 11,550 t in 1970 and dominated Thau shellfish production from 1970 to 1983 (45–93% of total production). From 1972 to the 1990s, mussel production declined in favour of oyster production (*Crassostrea angulata* until 1972 and *Crassostrea gigas* ever since). Thus, oyster production has accounted for most shellfish production since 1983 (53 to 90% of total production). Oyster production revealed two peaks: a first peak in 1994 (15,000 t) and a second peak during the period 2000–2008 (12,000 to 13,000 t). In 2009, oyster production declined sharply due to the OsHV-1 μvar epizootic (Pernet et al., 2012). It slowly increased from 2012 to 2017, while remaining below 8000 t. Finally in 2018, oyster production again decreased to 6030 t.

Fig. 6 also shows the years in which a summer anoxic event occurred (in grey). From 1970 to 2018, 12 anoxic events were recorded in the lagoon. About half of these crises occurred in the 1980s and 1990s. Some of these years were characterised by significant a decline in production (e.g. 1975, 1982, 1990, 1997, 2018), associated with shellfish mortalities.

3.3. Triggering factors of summer anoxia

Fig. 7 shows the duration and spatial extent of summer anoxia in Thau lagoon from 1970 to 2018. The 1970 anoxia event lasted three months and the 1983 and 1994 anoxia events each lasted two months. The anoxia events in 1975, 1982, and 1987 lasted six weeks and the other anoxia events, between 1990 and 2018 lasted one month or less. The most extensive anoxia event occurred in 1975, when the entire lagoon was under hypoxic conditions (Troussellier and Deslous-Paoli, 2001). The 1982, 1983, 1990, 2006 and 2018 anoxia events affected all three shellfish farming areas, while the others affected only one or two. The duration and spatial extent of the seven anoxia events which occurred in period 1 (from 1970 to 1992) were greater than those of the five last anoxia events which occurred in period 2 (from 1993 to 2018) (respective median duration ranged from four to six weeks and the median spatial extent from two to three areas).

The Kruskal-Wallis tests performed to differentiate the characteristics of *periods 1* and *2* were significant for the following variables (p-values < 0.05): mean monthly air temperature increased (*air_M*, median from 22.3 to 23.1 °C), rainfall from January to May and rainfall in June decreased (respectively *rainfall_1–5:* median from 253 mm to 219 mm, *rainfall_6*: median from 21 mm to 16 mm), the concentration of DIP in June decreased (*DIP_6*, median from 2.3 to 0.1 μM) and total annual shellfish production increased (*Q_shellfish_1*, median from 8.7 10^3 to 13.4 10^3 t y^{-1}). The other three variables (*wind_ST*, *rainfall_7*, *rainfall_8*) did not differ significantly between the two periods.

Among the eight variables included in the glm predicting the triggering of summer anoxia, four were considered as significant based on the AIC: summer monthly averages of air temperature and wind intensity, rainfall in July and the period determined according to the eutrophication status (*air_M*, *wind_ST*, *rainfall_7* and *period 2*). According to the AUC criterion, the performance of this glm was good (mean = 0.81, sd = 0.1), corresponding to moderately to very informative models. *Period 2* and *rainfall_7* were associated with, respectively, the highest and the lowest absolute values of the estimated coefficients in the glm (Table A2). Air temperature

Fig. 4. Changes in mean summer chlorophyll *a* biomass (μg Chla L^{-1}) (A), nanophytoplankton (B), picoeukaryote (C) and phycoerythrin-rich picocyanobacteria abundances (10^6 cells L^{-1}) with changes in water temperature (°C) (D) from 1999 to 2018 at TW and TE (averaged) and TANG stations (respectively in blue and orange).

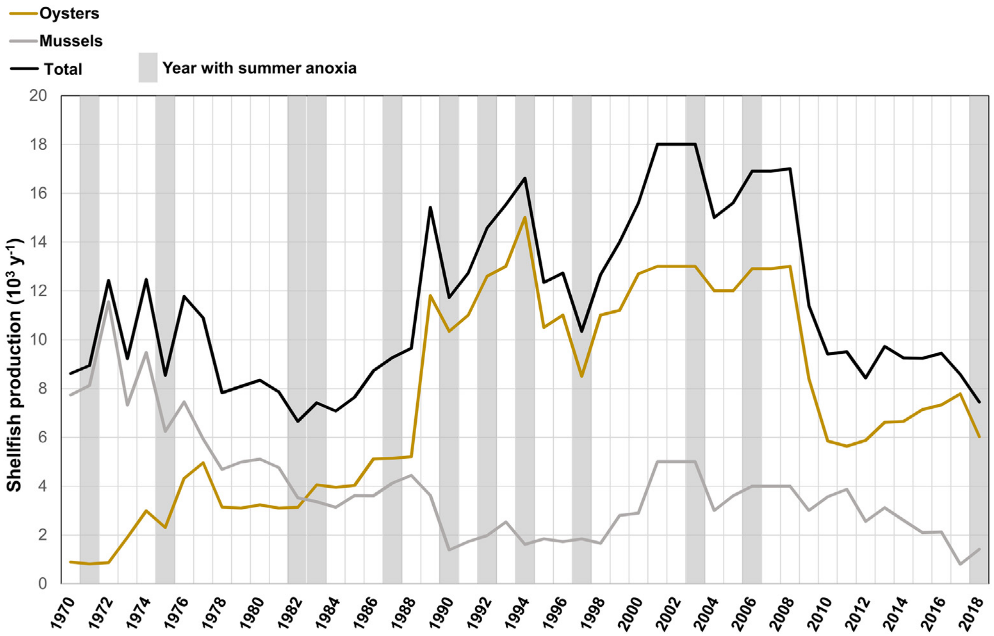


Fig. 6. Oyster (in brown), mussel (in grey) and total shellfish production (in black) in 10^3 t year^{-1} from 1970 to 2018 and the occurrence of summer anoxia events (vertical grey bands) in Thau lagoon.

and rainfall in July were associated with positive coefficients, in contrast to wind intensity and to the less eutrophic period (*period 2*: from 1993 to 2018). The odds ratio associated with the period corresponding to the eutrophication status is 0.17 ($e^{-1.78}$), meaning that the fact of being in period 2 divided the risk of triggering anoxia by 5.9 (1/0.17) compared to the risk in period 1. The odds ratio of the summer monthly average wind intensity was 0.27 ($e^{-1.32}$), meaning that an increase of 1 unit of wind intensity (the variable *wind_ST* being standardised) divided the risk by 3.7. The odds ratio associated with air temperature ($e^{1.03} = 2.8$) means that an 1 °C increase multiplies the risk of triggering anoxia by 2.8. Finally, the odds ratio of rainfall in July indicates that a 10 mm increase multiplies the risk by 1.5 ($e^{10*0.04} = 1.5$). Fig. 8 shows the predicted probabilities of triggering anoxia according to the three significant meteorological variables of the glm for period 1 and period 2, showing that the highest probabilities of the highest temperature were reached in period 1.

4. Discussion

4.1. Ecological changes and regime shifts during oligotrophication

Our results, based on long time series, show that the pelagic and benthic communities in Thau lagoon changed during the course of oligotrophication. Previous studies of the lagoon from the 1990s to the 2000s showed that the gradual decrease in nutrient inputs from the watershed resulted in a continuous decrease in nutrients and Chl *a* concentrations in the water column (Collos et al., 2009; Derolez et al., 2020; Deslous-Paoli et al., 1998a; Gowen et al., 2015). Our study revealed the continuation of oligotrophication over the past 20 years

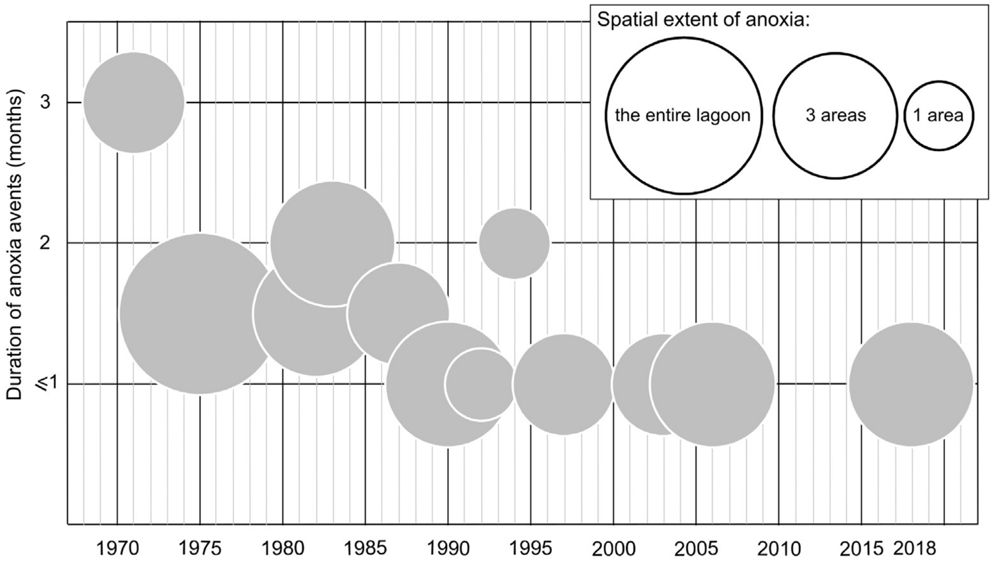


Fig. 7. Duration and intensity of summer anoxia crises from 1970 to 2018. The y-axis corresponds to the duration (months) of the crises and the size of the bubbles corresponds to the spatial extent of the anoxia.

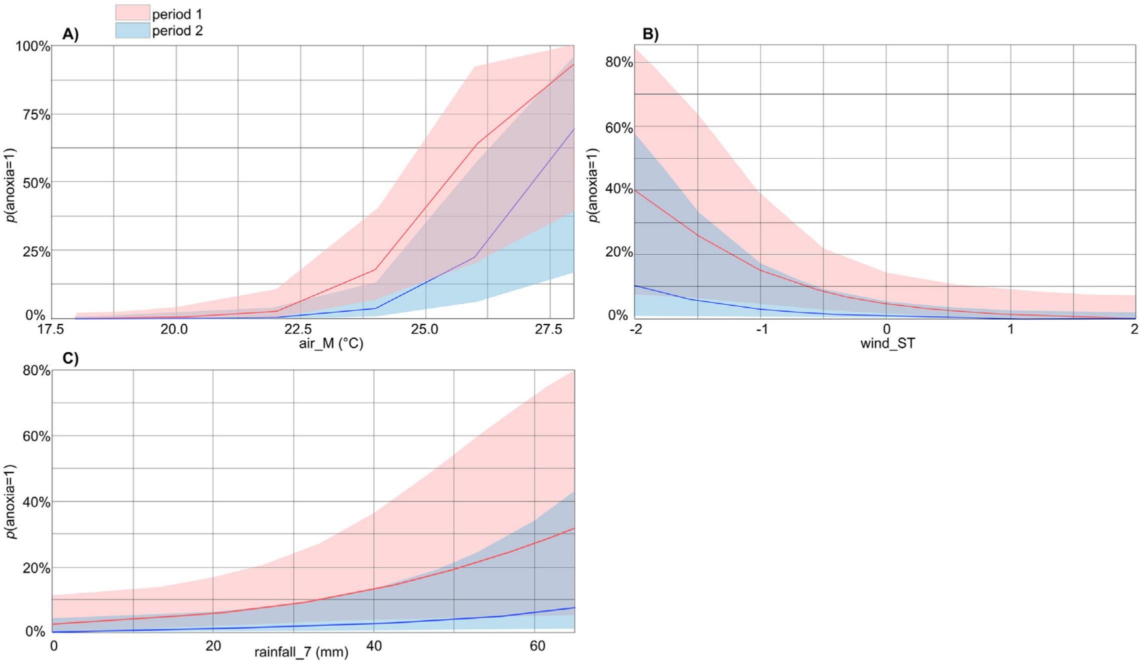


Fig. 8. Effects of the 3 meteorological variables included in the glm predicting the probability of triggering summer anoxia (%: mean and confidence interval): wind intensity (wind_ST, standardised unit), air temperature (air_M, °C), rainfall in July (rainfall_7, mm), based on the period determined according to the eutrophication status (period 1 or period 2).

(1999–2018), and the recovery of the ecosystem, through nutrient and phytoplankton parameters. Thus, based on changes in the summer concentration of DIP in the water, which is a good indicator of the eutrophication status of Thau lagoon (La Jeunesse and Elliott, 2004; Souchu et al., 1998a), we identified a progressive shift from a bad quality status to a high quality status, according to the thresholds of the WFD (MTES, 2018). Reaching the good DIP status (DIP < 1 µM, MTES, 2018), which was no longer exceeded after June 1993, divided the time series into two periods (1:1970–1992 and 2:1993–2018). At the same time, dissolved nitrogen concentrations also decreased significantly ($NO_3^- + NO_2^-$ in June: MK $p < 0.01$, slope $= -0.01$ µM y^{-1}). In period 2, when nutrient levels were already low, phytoplankton shifted with a time lag in year 2006. After 2006, the levels of Chl *a* biomass (<5 µg L^{-1}) and picoeukaryote abundances (<50 10^6 cells L^{-1}) corresponded to those reported in oligotrophic coastal waters of the Mediterranean (Massana, 2011). Coastal lagoons often host blooms of picophytoplankton that can continue for months to years (Glibert et al., 2010; Bec et al., 2011). In Thau lagoon, phycoerythrin-rich picocyanobacteria abundances did not increase significantly but their relative contribution (PE-CYAN/PEUK ratio) to picophytoplankton did. The numerical dominance of picocyanobacteria in summer may reflect the oligotrophic conditions of the lagoon linked to low phosphorus levels (Collos et al., 2009; Bec et al., 2011). We also found a positive correlation between temperature and the abundance of phycoerythrin-rich picocyanobacteria. Positive effects of temperature on the growth rate and abundance of picocyanobacteria have previously been demonstrated in Thau lagoon (Bec et al., 2005, 2011). These results confirmed the trends expected in coastal ecosystems under oligotrophication and global warming (Glibert, 2016; Pulina et al., 2018; Trombetta et al., 2019). This shift period observed in picophytoplankton in 2006 mirrors the shift in the microphytoplankton community identified in a previous study (decrease in diatom abundance and shift dominance from *Skeletonema-Chaetoceros* to *Chaetoceros-Pseudo-nitzschia* in the community between 2005 and 2008) (Derolez et al., 2020). Our results showed a rapid and significant response of the pelagic compartment to the decrease in nutrient loadings comparable to the responses observed in other coastal ecosystems (Boynton et al., 2013; Derolez et al., 2019; Leruste et al., 2016; Lie et al., 2011; Ní Longphuirt et al., 2016) and in lakes (Anneville et al., 2005; Jeppesen et al., 2007).

Decreases in nutrient concentrations and phytoplankton biomass and abundances were associated with a decrease in dissolved oxygen concentrations in summer from 1999 to 2018. This decrease could be induced by warming which is known to reduce the solubility of oxygen in water and to enhance microbial activity (Breitburg et al., 2018; Conley, 2000; Jager et al., 2018). Moreover, the respiration of shellfish coupled to the decrease in phytoplankton biomass could impact oxygen concentrations in water. Oligotrophication has also been shown to induce changes in trophic functioning, shifting from autotrophic regime to mixotrophic and heterotrophic regimes (Collos et al., 2009; Gowen et al., 2015; Lagarde et al., 2018), and thus leading to changes in oxygen balance.

Our results provide for the first time a long-term analysis of the benthic compartment of the Thau lagoon. In the sediments, total nitrogen concentrations increased significantly from the 1980s to the 2010s, suggesting that the benthic compartment stored these nutrients during the eutrophication period. In contrast, we found no significant trend in total phosphorus, whose maximum value was reached in 2003 and whose minimum value was reached in 2014. Such contrasted evolution has already been reported in coastal ecosystems, where the presence of sulphate reduces the efficiency retention of DIP by the sediments and favours recycling of DIP over that of DIN (Caraco et al., 1990; Conley, 2000; Lehtoranta et al., 2009). Moreover, high temperatures and anoxic conditions have a significant effect on benthic fluxes of NH_4^+ and DIP (Souchu et al., 1998a; Zilius et al., 2015). In Thau lagoon, we hypothesise that releases from the sediments, coupled with the decrease in inputs from the watershed - corresponding to internal and external nutrient loadings, respectively, (Chapelle et al., 2000b) - led to stabilisation, or even to the beginning of a decrease in the quantities of phosphorus in the sediments (lowest median of TP was observed in 2014).

Concerning the benthic macrophyte community, our results showed that the proportion of seagrass decreased in favour of red algae from the 1960s to the 1990s. This trend corresponds to the generic eutrophication trajectory described by many authors: a shift from dominance of seagrass and perennial macrophytes to dominance of macroalgae

(Schramm, 1999; Viaroli et al., 2008; Zaldívar et al., 2008). Seagrass meadows only started to slightly recover between 2003 and 2008, but their contribution to benthic vegetation did not reach the level observed in the 1960s, or the historical conditions describing Thau lagoon dominated by seagrass at the beginning of the 20th century (Calvet, 1910). Despite the significant and continuous decrease in nutrient inputs observed since the 1970s, the beginning of the recovery of the Thau lagoon macrophyte community lagged behind that of the phytoplankton community. This time lag and partial recovery suggest hysteresis during oligotrophication in the Thau lagoon and correspond to partial resilience observed in aquatic ecosystems (Borja et al., 2010; Duarte et al., 2009; Elliott et al., 2007). Continuous nutrient fluxes from sediments could promote phytoplankton or macroalgae growth and delay the recovery process of perennial macroalgae and seagrasses (Kosten et al., 2011). Accordingly, internal phosphorus loading from sediments has frequently been reported as a cause of hysteresis in lakes (Gulati and Van Donk, 2002; Jeppesen et al., 2007; Søndergaard et al., 2003) and more recently in coastal or estuarine ecosystems (Lillebø et al., 2007; Ní Longphuirt et al., 2016; Ratmaya et al., 2018; Riemann et al., 2016).

During five decades of changes from eutrophication to oligotrophication, contrasting periods in the pelagic and benthic compartments of the Thau lagoon were identified. This evolution is represented in the conceptual model (Fig. 9), showing the changes in several indicators of ecosystem status (DIP concentration in water, phytoplankton and macrophyte) in response to changes in the levels of pressures which affect the ecosystem (nutrient loads and temperature). Although the decrease in nutrient loads was accompanied by a decrease in nutrient concentrations and phytoplankton biomass in water, period 1 (1970–1992) can be considered as a eutrophic period due to the shift from seagrass to red macroalgae and to the frequent and critical anoxic crises during that period. Period 2 (1993–2018) was characterised by a better eutrophic status, less frequent and less intense anoxia crises and by the continuation of the recovery process. This second period can be divided into three steps: 2a) a transition phase (1993–2003) during which the pelagic compartment continued to recover from eutrophication with stabilisation of the benthic community; 2b) a regime shift between the year 2003, (before which seagrass continued to decline), and the year 2006, after which low chlorophyll *a* values were reached in the water column. Since the summers of 2003 and 2006 were both characterised by major heat waves and anoxias events, we hypothesise that this regime shift is the result of the combination of an internal oligotrophication process and external forces linked to high summer temperatures (Scheffer and Carpenter, 2003). After the regime shift, 2c) the ecosystem shifted to oligotrophy (2006–2018), the water column became characteristic of an oligotrophic state and the marine grass began to recover.

4.2. Triggers of anoxia, resistance and resilience of the ecosystem

To analyse the trajectory of Thau lagoon ecosystem over five decades, the effects of reduced nutrient inputs and of climatic-related variables, especially the gradual increase in temperature, which was evidenced in the Mediterranean and Thau regions (Bec et al., 2018; Cramer et al., 2018), need to be taken into account. Indeed, oligotrophication and warming may have combined effects on biodiversity and ecosystem functioning (Glibert, 2016; Kosten et al., 2011;

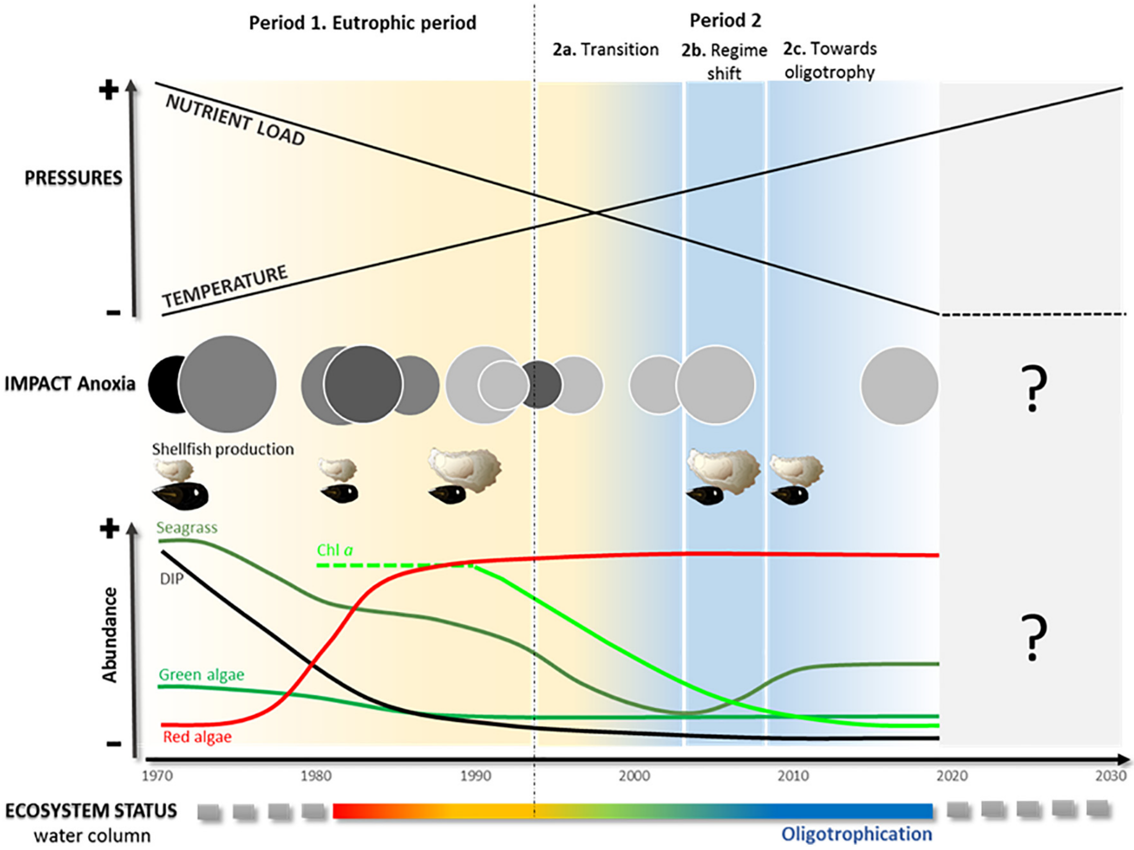


Fig. 9. Schematic synthesis of the oligotrophication process in Thau lagoon from 1970 to 2018 (period 1 and the 3 steps in period 2) and a possible scenario for the period 2020–2030 (stabilisation of the nutrient load and increase in temperature). Pressures: nutrient inputs from the watershed and climate driver (temperature). Impact: the size of the bubbles represents the spatial extent and the intensity of the colour grey the intensity of the summer anoxia crises. Changes in mussel and oyster production: the size of the shellfish represents the level of production. Abundance of DIP and Chl *a* in the lagoon water and the abundance of seagrass, green algae and red algae in the soft-bottom sediment. Ecosystem status: the eutrophication status of the water column according to the WFD thresholds determined for DIP in French coastal lagoons (MTES, 2018). All variables are represented within relative space.

Verbeek et al., 2018). Thus, we focused particularly on the occurrence and intensity of anoxia crises as indicators of ecosystem resilience and resistance and on what triggers these disturbances (Coffin et al., 2018).

The model used to predict the triggering of summer anoxia revealed that four variables were significant (three meteorological variables and one corresponding to the eutrophication status). The strongest effect was induced by air temperature, followed by the effect of the eutrophication period, by the negative effect of wind, and to a lesser extent by the positive effect of rainfall in July. These results highlight the effects of climate variables and confirmed a previous study underlying the effects of increasing temperature and decreasing winds on the probability of the occurrence of anoxia in the Thau lagoon (Harzallah and Chapelle, 2002). In coastal ecosystems, decreased wind speed could play an important role in triggering anoxia by decreasing vertical water mixing and oxygenation at the air-water interface (Chen et al., 2015; Du et al., 2018; Zilius et al., 2015). In northern temperate estuaries, increased frequency of extreme summer rainfall events could increase the frequency of anoxia events because floods can mobilize significant quantities of organic matter and suspended solids which are subsequently deposited in estuaries and/or due to more intense stratification (Iriarte et al., 2014; Oviatt et al., 2017).

We showed a 6-fold higher risk of triggering anoxia in the first period (1970–1992), considered to be the eutrophic period. It is known that anthropogenic nutrient inputs affect both the oxygen supply and uptake (Conley, 2000; Friedrich et al., 2014; Souchu et al., 1998a) and that eutrophication-related parameters (chlorophyll *a* biomass or nutrient concentrations or loadings) can trigger anoxia in coastal areas (Coffin et al., 2018; Du et al., 2018; Zilius et al., 2015). What is remarkable about our result is the marked effect of the eutrophication status, so that the oligotrophication process observed during our study period led to increasing resistance of the Thau lagoon ecosystem to climate stress. Among the climatic-related variables, the effect of air temperature on triggering anoxia was the strongest. Indeed, the functioning of the lagoon could be particularly threatened by warming since increases in the annual average temperature and in the frequency of summer heat waves were recorded in the Mediterranean region from the 1970s to the 2010s (Bec et al., 2018; Cramer et al., 2018). However, oligotrophication lead to the decreased risk of triggering anoxia in the Thau lagoon. This is consistent with a previous study in the mid-estuarine waters (Bilbao, Spain) showing that anthropogenic-mediated pollution mitigation was more important than climatic factors in driving inter-annual variations in dissolved oxygen saturation (Iriarte et al., 2014). In Narragansett Bay (USA), Oviatt et al. (2017) showed that a 60% reduction in nutrient concentrations resulted in a 34% reduction in summer hypoxia. In Chesapeake Bay (USA), authors suggested that reductions in nutrient loads would also reduce hypoxic volumes (Testa et al., 2014), but biological conditions (linked to nutrient loading) and physical conditions (vertical exchange and temperature) could play an equally important role in seasonal and inter-annual variations in the hypoxic condition of this ecosystem (Du et al., 2018). Among the climatic-related variables, we also showed a decrease in the rainfall levels from period 1 to period 2, due to the decrease in the occurrence of wet years recorded since 2005 (Bec et al., 2018). This trend may have facilitated the oligotrophication process by decreasing nutrient inputs resulting from watershed runoff (Bec et al., 2018).

With climate change trends already demonstrated by regional meteorological experts and predicted for the future (Jouzel et al., 2014), we would expect the effects of climate warming to slow down or even reverse the recovery process observed in the Thau lagoon. At regional scale, meteorological data revealed that 2003, 2017 and 2018 were the three hottest summers in the 1970–2018 period (Météo-France, 2018). In the present study, the last anoxia crisis occurred in 2018 when the water column was characteristic of an oligotrophic state (Fig. 9) and after a 12-years period without anoxic event. This support the conclusions drawn in the Mediterranean Basin where accelerated climate change could exacerbate existing environmental problems (Cramer et al., 2018). Similar results have been reported these limits in Lake Zurich, where, despite the success achieved in fighting eutrophication, a recent increase in hypoxia has been observed (Friedrich et al., 2014). In Chesapeake Bay, it has been shown that the expected climate changes will exacerbate physical conditions, which would also amplify the negative impact of human-induced eutrophication, requiring greater efforts to reduce nutrient inputs in order to reach a satisfactory level of water quality (Du et al., 2018). Finally, a recent study (Jager et al., 2018) reviewed ways to enhance the resilience of coastal aquatic ecosystems in the face of future, unnatural hypoxic regimes. In addition to efforts to slow climate change, the measures identified by these authors include: reducing nutrient and carbon loadings from rivers, restoring aquatic vegetation, increasing oxygen exchange in sediments and water clarity via the management of key species such as seagrass, or the protection of oyster and mussel beds (Jager et al., 2018). The restoration of the health of oyster reefs and the expansion of tidal marshes were also shown to reinforce the improvement of water and habitat quality along a restoration trajectory in Chesapeake Bay (Kemp et al., 2005). The choice of management options first requires the definition of a desirable state for the ecosystem. Jager et al. (2018) defined desired states as ecosystems with long trophic chains and slow nutrient and carbon dynamics that provide many ecosystem services. Other authors have shown that different levels of Mediterranean coastal lagoon restoration may be desired by society in terms of recovery of ecosystems, and that some discrepancies can be observed between social representations and ecological diagnoses (Audouit et al., 2017; de Wit et al., 2015).

4.3. Management of restoration and shellfish farming

In Thau lagoon, the significant efforts invested by public stakeholders and managers to mitigate eutrophication which began in the 1970s have succeeded in reducing the occurrence of anoxia events by increasing ecosystem resistance and achieved the good water column status targeted by the WFD. Official assessments of the biological quality elements in application of the WFD have only been carried out since 2009 in Thau lagoon. According to these diagnoses, the phytoplankton has reached the good status in 2009 and shifted to a high status in 2018 (Andral and Sargian, 2010; Bouchoucha et al., 2019). However, the macrophytes remained in a medium status from 2009 to 2018, although an improvement was observed, associated with the increase in the coverage of *Zostera* spp. The delay in reaching the WFD good status for macrophytes in comparison to phytoplankton is related to the time lag evidenced by several authors in the recovery of the benthic compartment (Borja et al., 2010; Le Fur et al., 2019). A recent study carried out on several French Mediterranean lagoons (Derolez et al., 2019) hypothesised that the level of recovery after the reduction of nutrient inputs could be affected by: (i) external drivers, such as completeness of nutrient reduction, marine connectivity, or climate change; (ii) internal factors such as physical traits, sediment nutrient stocks or the presence of residual seagrass patches or seed stocks; and interactions between the two drivers. Among the three strategies identified for the lagoons which have not fully achieved the objectives set by the European WFD ("Wait and see", "Go further", "Give a helping hand"), the first seems to be the most relevant for the Thau lagoon according to the importance of the works performed on the depuration system and their efficiency observed in the ecosystem. One could hypothesise that eutrophication pressure is now sufficiently low to allow the benthic compartment to recover its ecological functions and structure of the reference conditions, after a period of hysteresis.

However, it should be noted that in the 1990s, some authors mentioned the threat of reaching the limits of the trophic capacity of the Thau lagoon if the depuration works became too drastic (Deslous-Paoli et al., 1998; Souchu et al., 1998a). During the recovery, shellfish production in Thau lagoon has evolved due to changes in the main reared species from mussels to oysters from the 1970s to the 1990s for epizootic and economic reasons (Hamon and Tournier, 1984; Le

Brun, 1985); the removal of some shellfish structures located along the shoreline in the early 2000s following the recommendations of scientists made after the critical anoxia events of the 1990s (Deslous-Paoli et al., 1998; Souchu et al., 1998b); and changes in farming techniques following epizootics such as OsHV-1 in 2008 (Pernet et al., 2014). This last epizootic reduced oyster production by half. More recently, fishermen and shellfish farmers have been facing economic difficulties and they worry about the potential limiting capacity of the ecosystem (Derolez et al., 2020). In the context of emerging marine diseases related to climate change, recent studies have shown that the impact of oyster diseases can be limited by maintaining the good ecological status of coastal waters (Harvell et al., 1999; Pernet et al., 2018). To reach a satisfactory trade-off between uses, ecosystem services and maintaining biodiversity and ecological functions under global change, there is a need to use ecosystem-based models (Filgueira et al., 2015; Guyondet et al., 2014; McKindsey et al., 2006). Such a model has been developed for Thau lagoon and showed that lagoon productivity significantly depends on hydrometeorology, with higher oyster production in wet years than in dry years (Pete et al., 2020). Using a modelling approach based on scenario comparisons would help (i) disentangle the effects of anthropogenic forcings and of climate driven variables such as increasing temperature or decreasing rainfall and (ii) determine the limits of ecological tolerance. By testing different management and climate scenarios, this modelling approach would also help decision-makers better target their actions to improve the ecosystem's resistance to increasing climate pressure. It is will also be necessary to increase high-frequency oxygen measurements in real time (Friedrich et al., 2014; Schmidt et al., 2017) to help managers and shellfish farmers better anticipate the appearance of hypoxia/anoxia and design and apply mitigation actions (e.g. emersion of oysters at night) to mitigate environmental and economic impacts. Finally, in the context of global change, Breitburg et al. (2018) recommend an integrated framework, combining modelling, observations and experiments and involving all stakeholders (scientists, local governments, shellfish farmers) to facilitate the development and implementation of the most ecologically and economically effective management strategy to reduce anoxia.

5. Conclusions

The processes and consequences of oligotrophication have been poorly studied in coastal lagoons from a long-term perspective and at ecosystem scale. By analysing time series over 5 decades of observations on pelagic and benthic autotrophic communities, our study shows how the decrease in nutrient inputs led to major ecological changes in a Mediterranean coastal lagoon used for shellfish farming. Considering anoxia crises as indicators of ecosystem resilience and resistance, the combined analysis of meteorological data, eutrophication status and shellfish production over these 5 decades allowed us to identify air temperature and eutrophication status as the two main triggers of summer anoxia.

We identified successive periods in ecosystem functioning during the oligotrophication process: a eutrophic period characterised by a shift from dominance by seagrass to dominance by red macroalgae; a 3-step period characterised by a better eutrophication status i.e. a transition phase with a stable benthic community, a regime shift between two heat waves and anoxic crises; and finally the achievement of oligotrophic conditions. Our analyses also show that oligotrophication has led to changes in the drivers of summer anoxia, making the ecosystem more resistant to climatic stress caused by high summer temperatures.

However, with predicted climate change trends, we would expect the effects of climate warming to slow down or even to reverse the observed recovery process. The development and use of ecosystem-based models are now needed to better understand the functioning of the ecosystem and to help stakeholders find a trade-off between uses, ecosystem services and the maintenance of biodiversity and ecological functions in the context of global change.

Funding

This study was based on data collected during the projects “*Réseau de Suivi Lagunaire*” and Water Framework Directive, which received financial support from Ifremer, *Agence de l'Eau Rhône Méditerranée Corse*, *Région Languedoc-Roussillon*/*Occitanie et Cépralmar*. Historical data on macrophytes and sediment were collected during a project funded by the French Government, Herault Department and Region Languedoc-Roussillon (Lauret, 1990, 1994), by PIREN, Ifremer and the French Ministry of Environnement (ECOTHAU) (Gerbal and Verlaque, 1995; Péna and Picot, 1991) and by PNEC “*Lagunes Méditerranéennes*” (Verlaque, 2000).

CRediT authorship contribution statement

Valérie Derolez: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Writing - original draft, Writing - review & editing. **Nathalie Malet:** Writing - review & editing, Funding acquisition, Methodology, Validation, Project administration. **Annie Fiandrino:** Methodology, Validation, Writing - review & editing. **Franck Lagarde:** Validation, Writing - review & editing. **Marion Richard:** Validation, Writing - review & editing. **Vincent Ouisse:** Data curation, Validation, Writing - review & editing. **Béatrice Bec:** Formal analysis, Methodology, Writing - original draft, Writing - review & editing. **Catherine Aliaume:** Methodology, Validation, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This article is dedicated to the memory of Jocelyne Oheix.

The authors are extremely grateful to Grégory Messiaen, Elodie Foucault, Dominique Munaron, Martine Fortuné and Elise Hatey for nutrient and phytoplankton analyses and to Nicolas Cimiterra for producing the maps. We thank our colleagues at Ifremer LERLR for their help during field investigations. The authors would like to thank CIRAD for sediment analyses; Ms. Dubuisson, Ms. Guyon and Mr. Soubeyroux of DCSC Météo-France for meteorological data and expertise; Ludovic Cesmat (SMBT) for information on watershed inputs; DDTM/DML for data on shellfish production. We are particularly grateful to Michel Lauret, Jean-Louis Guillou, Thierry Laugier, Philippe Souchu, Marianela Pataccini-Alvarez, Anahita Marzin, Laury Dijoux and Hugo Daurin for their help with data collection and pre-processing; and to Dominique Soudant, Meïli Baragatti, Tarek Hattab and Grégoire Certain and Sandeep Kumar Patakamuri for their help with statistics.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.139292.

References

Aminot, A., Kérouel, R., 2007. Dosage automatique des nutriments dans les eaux marines. Quae ed. Versailles (188 pp).

Andral, B., Sargian, P., 2010. Directive Cadre Eau. District “Rhône et Côtiers Méditerranéens”. Contrôles de surveillance/opérationnel. (129 pp. Report in French). https://archimer.ifremer.fr/doc/00038/14923/.

Anneville, O., Gammeter, S., Straile, D., 2005. Phosphorus decrease and climate variability: mediators of synchrony in phytoplankton changes among European perialpine lakes. Freshw. Biol. 50, 1747–1771. https://doi.org/10.1111/j.1365-2427.2005.01429.x.

Audouit, C., Pasqualini, V., Wit, R. De, Flanquart, H., Deboudt, P., Ru, C., 2017. Comparing social representation of water quality in coastal lagoons with normative use of ecological indicators. Mar. Policy https://doi.org/10.1016/J.MARPOL.2017.08.023.

Bec, B., Husseini-Ratrema, J., Collos, Y., Souchu, P., Vaquer, A., 2005. Phytoplankton seasonal dynamics in a Mediterranean coastal lagoon: emphasis on the picoeukaryote community. J. Plankton Res. 27, 881–894. https://doi.org/10.1093/plankt/fbi061.

Bec, B., Collos, Y., Souchu, P., Vaquer, A., Lautier, J., Fiandrino, A., Benau, L., Orsoni, V., Laugier, T., 2011. Distribution of picophytoplankton and nanophytoplankton along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Aquat. Microb. Ecol. 63, 29–45. https://doi.org/10.3354/ame01480.

Bec, B., Derolez, V., Cesmat, L., Pete, R., Richard, M., 2018. Projet CAPATHAU: CAPAcité trophique de la lagune de THAU. Livrable 1. Evolution temporelle de l'état écologique de la lagune de Thau et des performances des coquillages en élevage au regard de la réduction des apports issus du bassin versant et des changements météorologiques. Rapport UMR MARBEC DLAL FEAMP. Report in French (157 pp).

Borja, A., Dauer, D.M., Elliott, M., Simenstad, C.A., 2010. Medium-and long-term recovery of estuarine and coastal ecosystems: patterns, rates and restoration effectiveness. Estuar. Coasts 33, 1249–1260. https://doi.org/10.1007/s12237-010-9347-5.

Bouchoucha, M., Derolez, V., Munaron, M., Cimiterra, N., Tomasino, C., 2019. Directive Cadre sur l'Eau. Bassin Rhône Méditerranée Corse - Année 2018. Report in French, 81 Ifremer. https://archimer.ifremer.fr/doc/00620/73224/.

Boynton, W.R., Hodgkins, C.L.S., O'Leary, C.A., Bailey, E.M., Bayard, A.R., Wainger, L.A., 2013. Multi-decade responses of a tidal creek system to nutrient load reductions: Mattawoman Creek, Maryland USA. Estuar. Coasts 37, 111–127. https://doi.org/10.1007/s12237-013-9690-4.

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Naqvi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., Zhang, J., 2018. Declining oxygen in the global ocean and coastal waters. Science 359 (6371). https://doi.org/10.1126/science.aam7240.

Calinski, T., Harabasz, J., 1974. A dendrite method for cluster analysis. Commun. Stat. 3 (1), 1–27.

Calvet, L., 1910. L'ostréiculture à Cette et dans la région de l'étang de Thau. Bull. la Société Cent. d'Aquaculture Pêche, pp. 1–107.

Caraco, N., Cole, J., Likens, G.E., 1990. A comparison of phosphorus immobilization in sediments of freshwater and coastal marine systems. Biogeochemistry 9, 277–290. https://doi.org/10.1007/BF00000602.

Chapelle, A., Lazure, P., Souchu, P., 2000a. Modelling anoxia in the Thau lagoon (France). Oceanol. Acta 24, S87–S97. https://doi.org/10.1016/S0304-3800(99)00206-9.

Chapelle, A., Ménesguen, A., Deslous-paoli, J., Souchu, P., 2000b. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon. Impact of oysters farming and inputs from the watershed. Ecol. Model. 127, 161–181.

Chen, X., Shen, Z., Li, Y., Yang, Y., 2015. Physical controls of hypoxia in waters adjacent to the Yangtze Estuary: a numerical modeling study. Mar. Pollut. Bull. 97, 349–364. https://doi.org/10.1016/j.marpolbul.2015.05.067.

Coffin, M.R.S., Courtenay, S.C., Pater, C.C., van den Heuvel, M.R., 2018. An empirical model using dissolved oxygen as an indicator for eutrophication at a regional scale. Mar. Pollut. Bull. 133, 261–270. https://doi.org/10.1016/j.marpolbul.2018.05.041.

Collos, Y., Bec, B., Jauzein, C., Abadie, E., Laugier, T., Lautier, J., Pastoureaud, A., Souchu, P., Vaquer, A., 2009. Oligotrophication and emergence of picocyanobacteria and a toxic dinoflagellate in Thau lagoon, southern France. J. Sea Res. 61, 68–75. https://doi.org/10.1016/j.seares.2008.05.008.

Comps, M.A., 2000. La qualité bactériologique des coquillages de l'étang de Thau. Analyse des données de colimétrie recueillies entre 1971 et 1998. Relations avec l'état de l'assainissement des communes du bassin versant 73 p. https://archimer.ifremer.fr/doc/00039/15012/.

Conley, D.J., 2000. Biogeochemical nutrient cycles and nutrient management strategies. Hydrobiologia 410, 87–96. https://doi.org/10.1023/A:1003784504005.

Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.-P., Iglesias, A., Lange, M.A., Lionello, P., Llasat, M.C., Paz, S., Peñuelas, J., Snoussi, M., Toreti, A., Tsimplis, M.N., Xoplaki, E., 2018. Climate change and interconnected risks to sustainable development in the Mediterranean. Nat. Clim. Chang. 8. https://doi.org/10.1038/s41558-018-0299-2.

De Wit, R., Leruste, A., Le Fur, I., Sy, M.M., Bec, B., Ouisse, V., Derolez, V., Rey-Valette, H., 2020. A multidisciplinary approach for restoration ecology of shallow coastal lagoons, a case study in South France. Front. Ecol. Evol. - Conserv. https://doi.org/10.3389/fevo.2020.00108.

DeLong, E.R., DeLong, D.M., Clarke-Pearson, D.L., 1988. Comparing areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. Biometrics 44 (3), 837–845. https://doi.org/10.2307/2531595.

Derolez, V., Oheix, J., Ouisse, V., Munaron, D., Fiandrino, A., Messiaen, G., Hubert, C., Lamoureux, A., Malet, N., Fortuné, M., Berard, L., Mortreux, S., Guillou, J.L., 2015. Suivi estival des lagunes méditerranéennes françaises. Bilan des résultats 2014. 86 pp. Report in French. https://archimer.ifremer.fr/doc/00273/38461/.

Derolez, V., Bec, B., Munaron, D., Fiandrino, A., Pete, R., Simier, M., Souchu, P., Laugier, T., Aliaume, C., Malet, N., 2019. Recovery trajectories following the reduction of urban nutrient inputs along the eutrophication gradient in French Mediterranean lagoons. Ocean Coast. Manag. 171, 1–10. https://doi.org/10.1016/j.ocecoaman.2019.01.012.

Derolez, V., Soudant, D., Malet, N., Chiantella, C., Richard, M., Abadie, E., Aliaume, C., Bec, B., 2020. Two decades of oligotrophication: evidence for a phytoplankton community shift in the coastal lagoon of Thau (Mediterranean Sea, France). Estuar. Coast. Shelf Sci. https://doi.org/10.1016/j.ecss.2020.106810.

Deslous-Paoli, J.-M., Souchu, P., Mazouni, N., Juge, C., Dagault, F., 1998. Relations milieu-ressources: impact de la conchyliculture sur un environnement lagunaire méditerranéen (Thau). Oceanol. Acta 21, 831–843. https://doi.org/10.1016/S0399-1784(99)80010-3.

Du, J., Shen, J., Park, K., Wang, Y.P., Yu, X., 2018. Worsened physical condition due to climate change contributes to the increasing hypoxia in Chesapeake Bay. Sci. Total Environ. 630, 707–717. https://doi.org/10.1016/j.scitotenv.2018.02.265.

Duarte, C.M., Conley, D.J., Carstensen, J., Sánchez-Camacho, M., 2009. Return to Neverland: shifting baselines affect eutrophication restoration targets. Estuar. Coasts 32, 29–36. https://doi.org/10.1007/s12237-008-9111-2.

Dubois, A., 1972. Le peuplement végétal du bassin de Thau. Rapp. Comm. Int. Mer Médit. 20, 495–497.

EC, 1991a. Council Directive 91/271/EEC Concerning Urban Waste-water Treatment.

EC, 1991b. Council Directive 91/676/EEC of 12 December 1991 Concerning the Protection of Waters against Pollution Caused by Nitrates from Agricultural Sources.

EC, 2000. Directive 200/60/EC of the European Parliament and of the Council of 23 October 2000 Establishing a Framework for Community Action in the Field of Water Policy.

Elliott, M., Quintino, V., 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar. Pollut. Bull. 54, 640–645. https://doi.org/10.1016/j.marpolbul.2007.02.003.

Elliott, M., Burdon, D., Hemingway, K.L., Apitz, S.E., 2007. Estuarine, coastal and marine ecosystem restoration: confusing management and science - a revision of concepts. Estuar. Coast. Shelf Sci. 74, 349–366. https://doi.org/10.1016/j.ecss.2007.05.034.

Fiandrino, A., Ouisse, V., Dumas, F., Lagarde, F., Pete, R., Malet, N., Le Noc, S., de Wit, R., 2017. Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. Mar. Pollut. Bull. 119, 132–144. https://doi.org/10.1016/j.marpolbul.2017.03.006.

Filgueira, R., Comeau, L.A., Guyondet, T., McKindsey, C.W., Byron, C.J., 2015. Modelling carrying capacity of bivalve aquaculture: a review of definitions and methods. Encyclopedia of Sustainability Science and Technology. Springer S, New York, pp. 1–33. https://doi.org/10.1007/978-1-4939-2493-6_945-1.

Fouilland, E., Descolas-Gros, C., Collos, Y., Vaquer, A., Souchu, P., Gasc, A., Bibent, B., Pons, V., 2002. Influence of nitrogen enrichment on size-fractionated in vitro carboxylase activities of phytoplankton from Thau Lagoon (Coastal Mediterranean Lagoon, France). Journal of Experimental Marine Biology and Ecology 275 (2), 147–171. https://doi.org/10.1016/S0022-0981(02)00235-6.

Friedrich, J., Janssen, F., Aleynik, D., Bange, H.W., Boltacheva, N., Çagatay, M.N., Dale, A.W., Etiope, G., Erdem, Z., Geraga, M., Gilli, A., Gomoiu, M.T., Hall, P.O.J., Hansson, D., He, Y., Holtappels, M., Kirf, M.K., Kononets, M., Konovalov, S., Lichtschlag, A., Livingstone, D.M., Marinaro, G., Mazlumyan, S., Naeher, S., North, R.P., Papatheodorou, G., Pfannkuche, O., Prien, R., Rehder, G., Schubert, C.J., Soltwedel, T., Sommer, S., Stahl, H., Stanev, E.V., Teaca, A., Tengberg, A., Waldmann, C., Wehrli, B., Wenzhöfer, F., 2014. Investigating hypoxia in aquatic environments: diverse approaches to addressing a complex phenomenon. Biogeosciences 11, 1215–1259. https://doi.org/10.5194/bg-11-1215-2014.

Gangnery, A., 1998. Estimation des stocks de bivalves en élevage et des épibiontes dans la lagune de Thau en 1998. Evolution depuis 1980. Rapport ENSAR/Ifremer, Palavas Les Flots (55 pp. Report in French).

Gangnery, A., 1999. Estimation des stocks de bivalves en élevage et des épibiontes dans la lagune de Thau et Modélisation de la dynamique des populations d'huitres creuses (*Crassostrea gigas*, Thunberg). Rapport de DEA. Université Paris VI/Ifremer/CREMA, Palavas Les Flots 38 pp. Report in French. https://archimer.ifremer.fr/doc/00443/55478/.

Gangnery, A., 2003. Etude et modélisation de la dynamique des populations de bivalves en élevage (*Crassostrea gigas* et *Mytilus galloprovincialis*) dans le bassin de Thau (Méditerranée, France) et des ascidies solitaires associées. (PhD thesis). Montpellier University (216 pp).

Gangnery, A., Bacher, C., Buestel, D., 2001. Assessing the production and the impact of cultivated oysters in the Thau lagoon (Mediterranee, France) with a population dynamics model. Can. J. Fish. Aquat. Sci. 58, 1012–1020. https://doi.org/10.1139/cjfas-58-5-1012.

Gangnery, A., Chabirand, J.M., Lagarde, F., Le Gall, P., Oheix, J., Bacher, C., Buestel, D., 2003. Growth model of the Pacific oyster, *Crassostrea gigas*, cultured in Thau Lagoon (Méditerranée, France). Aquaculture 215, 267–290. https://doi.org/10.1016/S0044-8486(02)00351-4.

Gerbal, M., Verlaque, M., 1995. Macrophytobenthos de substrat meuble de l'étang de Thau. Oceanol. Acta 18, 557–571.

Gladstone-Gallagher, R.V., Pilditch, C.A., Stephenson, F., Thrush, S.F., 2019. Linking traits across ecological scales determines functional resilience. Trends Ecol. Evol., 1–11 https://doi.org/10.1016/j.tree.2019.07.010.

Glibert, P.M., 2016. Margalef revisited: a new phytoplankton mandala incorporating twelve dimensions, including nutritional physiology. Harmful Algae 55, 25–30. https://doi.org/10.1016/j.hal.2016.01.008.

Glibert, P.M., Boyer, J.N., Heil, C.A., Madden, C., Sturgis, B., Wazniak, C.S., 2010. Blooms in lagoons: different from those of river-dominated estuaries. In: Kennish, M., Paerl, H. (Eds.), Coastal Lagoons: Critical Habitats of Environmental Change. CRC Press, Boca Raton, FL.

Gowen, R.J., Collos, Y., Tett, P., Scherer, C., Bec, B., Abadie, E., Allen, M., O'Brien, T., 2015. Response of diatom and dinoflagellate lifeforms to reduced phosphorus loading: a case study in the Thau lagoon, France. Estuar. Coast. Shelf Sci. 162, 45–52. https://doi.org/10.1016/j.ecss.2015.03.033.

Grizel, H., Héral, M., 1991. Introduction into France of the Japanese oyster (*Crassostrea gigas*). J. Cons. Int. Explor. Mer 47, 399–403. http://archimer.ifremer.fr/doc/00000/2760/.

Gulati, R.D., Van Donk, E., 2002. Lakes in the Netherlands, their origin, eutrophication and restoration: state-of-the-art review. Hydrobiologia 478, 73–106.

Guyondet, T., Comeau, L.a., Bacher, C., Grant, J., Rosland, R., Sonier, R., Filgueira, R., 2014. Climate change influences carrying capacity in a coastal embayment dedicated to shellfish aquaculture. Estuar. Coasts 38, 1593–1618. https://doi.org/10.1007/s12237-014-9899-x.

Hamed, K.H., Rao, A.R., 1998. A modified Mann-Kendall trend test for autocorrelated data. J. Hydrol. 204, 182–196. https://doi.org/10.1016/S0022-1694(97)00125-X.

Hamon, P.-Y., Tournier, H., 1984. Evolution de la biomasse de mollusques en élevage dans l'étang de Thau de 1980 à 1984. Rev. Trav. Inst. Pêches marit. 48, 33–44.

Hamon, P.Y., Vercelli, C., Pichot, Y., Lagarde, F., Le Gall, P., Oheix, J., 2003. Les malaïgues de l'étang de Thau. Tome 1. Description des malaïgues. Moyens de lutte, recommandations. (67 pp. Report in French). https://archimer.ifremer.fr/doc/00038/14951/.

Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J., Hofmann, E.E., Lipp, E.K., Osterhaus, A.D.M.E., Overstreet, R.M., Porter, J.W., Smith, G.W., Vasta, G.R., 1999. Emerging marine diseases - climate links and anthropogenic factors. Science 285, 1505–1510. https://doi.org/10.1126/science.285.5433.1505.

Harzallah, A., Chapelle, A., 2002. Contribution of climate variability to occurrences of anoxic crises "malaïgues" in the Thau lagoon (southern France). Oceanol. Acta 25, 79–86. https://doi.org/10.1016/S0399-1784(02)01184-2.

Ifremer, 2007. Réseau de Suivi Lagunaire du Languedoc-Roussillon : Bilan des résultats 2006. (506 pp. Report in French). http://archimer.ifremer.fr/doc/00118/22926/.

Ifremer, 2004. Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2003. 447 pp. Report in French. https://archimer.ifremer.fr/doc/00275/38591/.

Ifremer, 2009. Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2008. 366 pp. Report in French. https://archimer.ifremer.fr/doc/00118/22922/.

Ifremer, 2012. Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2011. 292 pp. Report in French. https://archimer.ifremer.fr/doc/00118/22913/.

Iriarte, A., Villate, F., Uriarte, I., Alberdi, L., Intxausti, L., 2014. Dissolved oxygen in a temperate estuary: the influence of hydro-climatic factors and eutrophication at seasonal and inter-annual time scales. Estuar. Coasts 38, 1000–1015. https://doi.org/10.1007/s12237-014-9870-x.

Jager, H.I., Novello, R.C., Dale, V.H., Villnas, A., Rose, K.A., 2018. Unnatural hypoxic regimes. Ecosphere 9, e02408. https://doi.org/10.1002/ecs2.2408.

Jeppesen, E., Søndergaard, M., Meerhoff, M., Lauridsen, T.L., Jensen, J.P., 2007. Shallow lake restoration by nutrient loading reduction. Some recent findings and challenges ahead. Hydrobiologia 584, 239–252. https://doi.org/10.1007/s10750-007-0596-7.

de Jonge, V.N., Elliott, M., 2001. Eutrophication. Encycl. Ocean Sci. 2, 852–870.

Jouzel, J., Ouzeau, G., Déqué, M., Jouini, M., Planton, S., Vautard, R., 2014. Le Climat de la France au XXIe siècle. Scénarios régionalisés: édition 2014 pour la métropole et les régions d'outre-mer. Rapports de la Direction générale de l'Energie et du Climat.

Kamenir, Y., Morabito, G., 2009. Lago Maggiore oligotrophication as seen from the long-term evolution of its phytoplankton taxonomic size structure. J. Limnol. 68, 146–161. https://doi.org/10.4081/jlimnol.2009.146.

Kemp, W.M., Boynton, W.R., Adolf, J.E., Boesch, D.F., Boicourt, W.C., Brush, G., 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. 303, 1–29.

Kosten, S., Jeppesen, E., Huszar, V.L.M., Mazzeo, N., Van Nes, E.H., Peeters, E.T.H.M., Scheffer, M., 2011. Ambiguous climate impacts on competition between submerged macrophytes and phytoplankton in shallow lakes. Freshw. Biol. 56, 1540–1553. https://doi.org/10.1111/j.1365-2427.2011.02593.x.

La Jeunesse, I., Elliott, M., 2004. Anthropogenic regulation of the phosphorus balance in the Thau catchment-coastal lagoon system (Mediterraean Sea, France) over 24 years. Mar. Pollut. Bull. 48, 679–687. https://doi.org/10.1016/j.marpolbul.2003.10.011.

La Jeunesse, I., Deslous-Paoli, J.M., Ximénès, M.C., Cheylan, J.P., Mende, C., Borrero, C., Scheyer, L., 2002. Changes in point and non-point sources phosphorus loads in the Thau catchment over 25 years (Mediterranean Sea - France). Hydrobiologia 475–476, 403–411. https://doi.org/10.1023/A:1020351711877.

La Jeunesse, I., Cirelli, C., Sellami, H., Aubin, D., Deidda, R., Baghdadi, N., 2015. Is the governance of the Thau coastal lagoon ready to face climate change impacts? Ocean Coast. Manag., 1–13 https://doi.org/10.1016/j.ocecoaman.2015.05.014.

Lagarde, F., 2018. Malaïgue sur la lagune de Thau, expertise de la température de l'eau de la lagune de Thau. Expertise for DDTM34/DML Sète (2018/08/13) (2 pp. Report in French).

Lagarde, F., Richard, M., Bec, B., Roques, C., Mortreux, S., Bernard, I., Chiantella, C., Messiaen, G., Nadalini, J.B., Hori, M., Hamaguchi, M., Pouvreau, S., Roque d'Orbcastel, E., Tremblay, R., 2018. Trophic environments influence size at metamorphosis and recruitment performance of Pacific oysters. Mar. Ecol. Prog. Ser. 602, 135–153. https://doi.org/10.3354/meps12666.

Lauret, M., 1967. Morphologie, phénologie, répartition des Polysiphonia marins du littoral languedocien 1. Section Oligosiphonia. Nat. Monspel. sér. Bot. 18, 347–387.

Lauret, M., 1970. Morphologie, phénologie, répartition des Polysiphonia marins du littoral languedocien. Nat. Monspel. sér. Bot. 21, 121–163.

Lauret, M., 1990. Les herbiers de zostères de l'étang de Thau. Campagne 1990 des Onglous à Mèze (11 pp. Report in French).

Lauret, M., 1994. Les herbiers de zostères de l'étang de Thau. Campagne 1994 de Mèze à la Crique de l'Angle. Bassin des Eaux Blanches. des Onglous à Mèze (13 pp. + maps. Report in French).

Le Brun, E., 1985. La conchyliculture dans le bassin de Thau: approche des exploitations conchylicoles (Rapport final. Report in French).

Le Fur, I., de Wit, R., Plus, M., Oheix, J., Simier, M., Ouisse, V., 2017. Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth. Hydrobiologia 808, 175–200. https://doi.org/10.1007/s10750-017-3421-y.

Le Fur, I., de Wit, R., Plus, M., Oheix, J., Derolez, V., Simier, M., Malet, N., Ouisse, V., 2019. Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons studied from 17-years' time-series. Mar. Ecol. Prog. Ser. 608, 13–32. https://doi.org/10.3354/meps12814MARINE.

Lehtoranta, J., Ekholm, P., Pitkänen, H., 2009. Coastal eutrophication thresholds: a matter of sediment microbial processes. Ambio 38, 303–308. https://doi.org/10.1579/09-A-656.1.

Leruste, A., Malet, N., Munaron, D., Derolez, V., Hatey, E., Collos, Y., de Wit, R., Bec, B., 2016. First steps of ecological restoration in Mediterranean lagoons: shifts in phytoplankton communities. Estuar. Coast. Shelf Sci. 180, 190–203. https://doi.org/10.1016/j.ecss.2016.06.029.

Lie, A.A.Y., Wong, C.K., Lam, J.Y.C., Liu, J.H., Yung, Y.K., 2011. Changes in the nutrient ratios and phytoplankton community after declines in nutrient concentrations in a semi-enclosed bay in Hong Kong. Mar. Environ. Res. 71, 178–188. https://doi.org/10.1016/j.marenvres.2011.01.001.

Lillebø, A.I., Teixeira, H., Pardal, M.A., Marques, J.C., 2007. Applying quality status criteria to a temperate estuary before and after the mitigation measures to reduce eutrophication symptoms. Estuar. Coast. Shelf Sci. 72, 177–187. https://doi.org/10.1016/j.ecss.2006.10.012.

Massana, R., 2011. Eukaryotic picoplankton in surface oceans. Annu. Rev. Microbiol. 65, 91–110. https://doi.org/10.1146/annurev-micro-090110-102903.

Mazouni, N., Gaertner, J.C., Deslous-Paoli, J.M., Landrein, S., Geringer D'Oedenberg, M., 1996. Nutrient and oxygen exchanges at the water-sediment interface in a shellfish farming lagoon (Thau, France). J. Exp. Mar. Bio. Ecol. 205, 91–113. https://doi.org/10.1016/S0022-0981(96)02594-4.

McCullagh, P., Nelder, J.A., 1989. Generalized linear models. Monographs on Statistics and Applied Probability. Chapman and Hall, London (526 p).

McKindsey, C.W., Thetmeyer, H., Landry, T., Silvert, W., 2006. Review of recent carrying capacity models for bivalve culture and recommendations for research and management. Aquaculture 261, 451–462. https://doi.org/10.1016/j.aquaculture.2006.06.044.

Météo-France, 2018. Bilan climatique de l'été 2018. http://www.meteofrance.fr/climat-passe-et-futur/bilans-climatiques/bilan-2018/bilan-climatique-de-l-ete-2018.

Millet, B., 1989. Fonctionnement hydrodynamique du bassin de Thau. Validation d'un modèle numérique de circulation (programme ECOTHAU). Ocean. Acta 12, 37–46.

Minghelli-Roman, A., Laugier, T., Polidori, L., Mathieu, S., Loubersac, L., Gouton, P., 2011. Satellite survey of seasonal trophic status and occasional anoxic "malaigue" cirses in the Thau lagoon using MERIS images. Int. J. Remote Sens. 32, 909–923.

Mozetič, P., Solidoro, C., Cossarini, G., Socal, G., Precali, R., Francé, J., Bianchi, F., De Vittor, C., Smodlaka, N., Fonda Umani, S., 2010. Recent trends towards oligotrophication of the northern Adriatic: evidence from chlorophyll a time series. Estuar. Coasts 33, 362–375. https://doi.org/10.1007/s12237-009-9191-7.

MTES, 2018. Arrêté du 27 juillet 2018 modifiant l'arrêté du 25 janvier 2010 relatif aux méthodes et critères d'évaluation de l'état écologique, de l'état chimique et du potentiel écologique des eaux de surface pris en application des articles R. 212-10, R. 212-11 et R. 212-18 du code de l'environnement. 76 p. JORF n°0199. https://www.legifrance.gouv.fr/eli/arrete/2018/7/27/TREL1819388A/jo/texte.

Neveux, J., Lantoine, F., 1993. Spectrofluorometric assay of chlorophylls and phaeopigments using the least squares approximation technique. Deep-Sea Res. Part I Oceanogr. Res. Papers 40, 1747–1765.

Newton, A., Icely, J.D., Falcao, M., Nobre, A., Nunes, J.P., Ferreira, J.G., Vale, C., 2003. Evaluation of eutrophication in the Ria Formosa coastal lagoon, Portugal. Cont. Shelf Res. 23, 1945–1961. https://doi.org/10.1016/j.csr.2003.06.008.

Newton, A., Icely, J., Cristina, S., Brito, A., Cardoso, A.C., Colijn, F., Riva, S.D., Gertz, F., Hansen, J.W., Holmer, M., Ivanova, K., Leppäkoski, E., Canu, D.M., Mocenni, C., Mudge, S., Murray, N., Pejrup, M., Razinkovas, A., Reizopoulou, S., Pérez-Ruzafa, A., Schernewski, G., Schubert, H., Carr, L., Solidoro, C., Viaroli, Pierluigi, Zaldívar, J.M., 2014. An overview of ecological status, vulnerability and future perspectives of European large shallow, semi-enclosed coastal systems, lagoons and transitional waters. Estuar. Coast. Shelf Sci. 140, 95–122. https://doi.org/10.1016/j.ecss.2013.05.023.

Newton, A., Brito, A.C., Icely, J.D., Derolez, V., Clara, I., Angus, S., Schernewski, G., Inácio, M., Lillebø, A.I., Sousa, A.I., Béjaoui, B., Solidoro, C., Tosic, M., Cañedo-Argüelles, M., Yamamuro, M., Reizopoulou, S., Tseng, H.-C., Donata, C., Roselli, L., Maanan, M., Cristina, S., Ruiz-Fernández, A.C., Lima, R., Kjerfve, B., Rubio-Cisneros, N., Pérez-Ruzafa, A., Marcos, C., Pastres, R., Pranovi, F., Snoussi, M., Turpie, J., Tuchkovenko, Y., Dyack, B., Brookes, J., Povilanskas, R., Khokhlov, V., 2018. Assessing, quantifying and valuing the ecosystem services of coastal lagoons. J. Nat. Conserv. https://doi.org/10.1016/j.jnc.2018.02.009.

Ní Longphuirt, S., Mockler, E.M., O'Boyle, S., Wynne, C., Stengel, D.B., 2016. Linking changes in nutrient source load to estuarine responses: an Irish perspective. Biol. Environ. Proc. R. Irish Acad. 116B, 295. https://doi.org/10.3318/bioe.2016.21.

Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia, 199–2019 https://doi.org/10.1080/00785236.1995.10422044.

Oviatt, C., Smith, L., Krumholz, J., Coupland, C., Stoffel, H., Keller, A., McManus, M.C., Reed, L., 2017. Managed nutrient reduction impacts on nutrient concentrations, water clarity, primary production, and hypoxia in a north temperate estuary. Estuar. Coast. Shelf Sci. 199, 25–34. https://doi.org/10.1016/j.ecss.2017.09.026.

Pasqualini, V., Derolez, V., Garrido, M., Orsoni, V., Baldi, Y., Etourneau, S., Leoni, V., Rébillout, P., Laugier, T., Souchu, P., Malet, N., 2017. Spatiotemporal dynamics of submerged macrophyte status and watershed exploitation in a Mediterranean coastal lagoon: understanding critical factors in ecosystem degradation and restoration. Ecol. Eng. 102, 1–14. https://doi.org/10.1016/j.ecoleng.2017.01.027.

Péna, G., Picot, B., 1991. Métaux traces dans les sédiments d'une lagune méditerranéenne: l'étang de Thau. Oceanol. Acta 14, 459–472.

Pérez-Ruzafa, A., Campillo, S., Fernández-Palacios, J.M., García-Lacunza, A., García-Oliva, M., Ibañez, H., Navarro-Martínez, P.C., Pérez-Marcos, M., Pérez-Ruzafa, I.M., Quispe-Becerra, J.I., Sala-Mirete, A., Sánchez, O., Marcos, C., 2019a. Long-term dynamic in nutrients, chlorophyll a, and water quality parameters in a coastal lagoon during a process of eutrophication for decades, a sudden break and a relatively rapid recovery. Front. Mar. Sci. 6, 1–24. https://doi.org/10.3389/fmars.2019.00026.

Pérez-Ruzafa, A., Pérez-Ruzafa, I.M., Newton, A., Marcos, C., 2019b. Coastal lagoons: environmental variability, ecosystem complexity, and goods and services uniformity. In: Wolanski, E., Day, J.W., Elliott, M., Ramachandran, R. (Eds.), Coasts and Estuaries. The Future, pp. 253–276. https://doi.org/10.1016/b978-0-12-814003-1.00015-0.

Pernet, F., Barret, J., Gall, P. Le, Corporeau, C., Dégremont, L., Lagarde, F., Pépin, J., Keck, N., 2012. Mass mortalities of Pacific oysters *Crassostrea gigas* reflect infectious diseases and vary with farming practices in the Mediterranean Thau lagoon, France. 2, 215–237. https://doi.org/10.3354/aei00041.

Pernet, F., Lagarde, F., Le Gall, P., Roque D'Orbcastel, E., 2014. Associations between farming practices and disease mortality of Pacific oyster *Crassostrea gigas* in a Mediterranean lagoon. Aquac. Environ. Interact. 5, 99–106. https://doi.org/10.3354/aei00096.

Pernet, F., Fuhrmann, M., Petton, B., Mazurié, J., Bouget, J.F., Fleury, E., Daigle, G., Gernez, P., 2018. Determination of risk factors for herpesvirus outbreak in oysters using a broad-scale spatial epidemiology framework. Sci. Rep. 8, 1–11. https://doi.org/10.1038/s41598-018-29238-4.

Pete, R., Guyondet, T., Bec, B., Derolez, V., Cesmat, L., Lagarde, F., Pouvreau, S., Fiandrino, A., Richard, M., 2020. A box-model of carrying capacity of the Thau lagoon in the context of ecological status regulations and sustainable shellfish cultures. Ecol. Model. 426. https://doi.org/10.1016/j.ecolmodel.2020.109049.

Picot, B., Péna, G., Casellas, C., Bondon, D., Bontoux, J., 1990. Interpretation of the seasonal variations of nutrients in a mediterranean lagoon: étang de Thau. Hydrobiologia 207, 105–113. https://doi.org/10.1007/BF00041446.

Pulina, S., Satta, C.T., Padedda, B.M., Sechi, N., Lugliè, A., 2018. Seasonal variations of phytoplankton size structure in relation to environmental variables in three Mediterranean shallow coastal lagoons. Estuar. Coast. Shelf Sci. 212, 95–104. https://doi.org/10.1016/j.ecss.2018.07.002.

Ratmaya, W., Soudant, D., Salmon-Monviola, J., Cochennec-Laureau, N., Goubert, E., Andrieux-Loyer, F., Barillé, L., Souchu, P., 2018. Reduced phosphorus loads from the Loire and Vilaine Rivers were accompanied by increasing eutrophication in Vilaine Bay (South Brittany, France). Biogeosci. Discuss., 1–29 https://doi.org/10.5194/bg-2018-406.

Riemann, B., Carstensen, J., Dahl, K., Fossing, H., Hansen, J.W., Jakobsen, H.H., Josefson, A.B., Krause-Jensen, D., Markager, S., Stæhr, P.A., Timmermann, K., Windolf, J., Andersen, J.H., 2016. Recovery of Danish coastal ecosystems after reductions in nutrient loading: a holistic ecosystem approach. Estuar. Coasts 39, 82–97. https://doi.org/10.1007/s12237-015-9980-0.

Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. 18, 648–656. https://doi.org/10.1016/j.tree.2003.09.002.

Schmidt, S., Bernard, C., Escalier, J.M., Etcheber, H., Lamouroux, M., 2017. Assessing and managing the risks of hypoxia in transitional waters: a case study in the tidal Garonne River (South-West France). Environ. Sci. Pollut. Res. 24, 3251–3259. https://doi.org/10.1007/s11356-016-7654-5.

Schramm, W., 1999. Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. J. Appl. Phycol. 11, 69–78.

Schwarz, G., 1978. Estimating the dimension of a model. Ann. Stat. 6, 461–464.

Sen, P.K., 1968. Estimates of the regression coefficient based on Kendall's tau. J. Am. Stat. Assoc. 63 (324), 1379–1389. https://doi.org/10.2307/2285891.

Søndergaard, M., Jensen, J.P., Jeppesen, E., 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506–509, 135–145. https://doi.org/10.1023/B:HYDR.0000008611.12704.dd.

Souchu, P., Gasc, A., Collos, Y., Vaquer, A., Tournier, H., Bibent, B., Deslous-Paoli, J., 1998a. Biogeochemical aspects of bottom anoxia in a Mediterranean lagoon (Thau, France). Mar. Ecol. Prog. Ser. 164, 135–146. https://doi.org/10.3354/meps164135.

Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Bibent, B., 2001. Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau lagoon. Mar. Ecol. Prog. Ser. 218, 141–152. https://doi.org/10.3354/meps218141.

Souchu, P., Abadie, E., Vercelli, C., Buestel, D., Sauvagnargues, J.C., 1998. La crise anoxique du bassin de Thau de l'été 1997. Bilan du phénomène et perspectives. (33 pp. Report in French). https://archimer.ifremer.fr/doc/00039/15010/.

Souchu, P., Bec, B., Smith, V.H., Laugier, T., Fiandrino, A., Benau, L., Orsoni, V., Collos, Y., Vaquer, A., 2010. Patterns in nutrient limitation and chlorophyll a along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Can. J. Fish. Aquat. Sci. 67, 743–753. https://doi.org/10.1139/F10-018.

Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science, 3 240 (4857), 1285–1293. https://doi.org/10.1126/science.3287615.

Testa, J.M., Li, Y., Lee, Y.J., Li, M., Brady, D.C., Di Toro, D.M., Kemp, W.M., Fitzpatrick, J.J., 2014. Quantifying the effects of nutrient loading on dissolved O_2 cycling and hypoxia in Chesapeake Bay using a coupled hydrodynamic–biogeochemical model. J. Mar. Syst. 139, 139–158. https://doi.org/10.1016/j.jmarsys.2014.05.018.

Trombetta, T., Vidussi, F., Mas, S., Parin, D., Simier, M., Mostajir, B., 2019. Water temperature drives phytoplankton blooms in coastal waters. PLoS One 14, 1–28. https://doi.org/10.1371/journal.pone.0214933.

Troussellier, M., Deslous-Paoli, J.M., 2001. La lagune de Thau: un site atelier pour l'acquisition, l'intégration et la valorisation des connaissances. Oceanis 27, 257–289.

Tsiamis, K., Panayotidis, P., Salomidi, M., Pavlidou, A., Kleinteich, J., Balanika, K., Küpper, F.C., 2013. Macroalgal community response to re-oligotrophication in Saronikos Gulf. Mar. Ecol. Prog. Ser. 472, 73–85. https://doi.org/10.3354/meps10060.

Verbeek, L., Gall, A., Hillebrand, H., Striebel, M., 2018. Warming and oligotrophication cause shifts in freshwater phytoplankton communities. Glob. Chang. Biol. 24, 4532–4543. https://doi.org/10.1111/gcb.14337.

Verlaque, M., 2000. Actualisation de la flore des macrophytes des étangs de Thau (Hérault) et de Salses-Leucate (Aude-Pyrénées-Orientales). PNEC "Lagunes Méditerranéennes", Thème 1, le compartiment "Macrophytes". GIS Posidonie - IFREMER Report, Marseille (64 p. + annexes. Report in French).

Viaroli, P., Bartoli, M., Giordani, G., Naldi, M., 2008. Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. Aquat. Conserv. Mar. Freshw. Ecosyst. 18, 105–117. https://doi.org/10.1002/aqc.

de Wit, R., Rey-Valette, H., Balavoine, J., Ouisse, V., Lifran, R., 2015. Restoration ecology of coastal lagoons: new methods for the prediction of ecological trajectories and economic valuation. Aquat. Conserv. Mar. Freshw. Ecosyst. 27, 137–157. https://doi.org/10.1002/aqc.2601.

Zaldívar, J.-M., Cardoso, A.C., Viaroli, P., Wit, R. De, Ibañez, C., Reizopoulou, S., Razinkovas, A., Basset, A., Holmer, M., Murray, N., 2008. Eutrophication in transitional waters: an overview. TWM, Transit. Waters Monogr. 1, 1–78. https://doi.org/10.1285/i18252273v2n1p1.

Zilius, M., Giordani, G., Petkuviene, J., Lubiene, I., Ruginis, T., Bartoli, M., 2015. Phosphorus mobility under short-term anoxic conditions in two shallow eutrophic coastal systems (Curonian and Sacca di Goro lagoons). Estuar. Coast. Shelf Sci. 164, 134–146. https://doi.org/10.1016/j.ecss.2015.07.004.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 20 May 2020
doi: 10.3389/fevo.2020.00108

A Multidisciplinary Approach for Restoration Ecology of Shallow Coastal Lagoons, a Case Study in South France

Rutger De Wit[1], Amandine Leruste[1], Ines Le Fur[1,2], Mariam Maki Sy[1], Béatrice Bec[1], Vincent Ouisse[2], Valérie Derolez[2] and Hélène Rey-Valette[3]*

[1] MARBEC, Université de Montpellier, CNRS, IRD, Ifremer, Montpellier, France, [2] MARBEC, Université de Montpellier, CNRS, IRD, Ifremer, Séte, France, [3] CEE-M, Université de Montpellier, CNRS, INRA, Montpellier SupAgro, Montpellier, France

Edited by:
Sofia Reizopoulou,
Hellenic Centre for Marine Research (HCMR), Greece

Reviewed by:
Christos Dimitrios Arvanitidis,
Hellenic Centre for Marine Research (HCMR), Greece
Sarah Faulwetter,
University of Patras, Greece

***Correspondence:**
Rutger De Wit
rutger.de-wit@umontpellier.fr

Specialty section:
This article was submitted to Conservation, a section of the journal Frontiers in Ecology and Evolution

Received: 23 July 2019
Accepted: 01 April 2020
Published: 20 May 2020

Citation:
De Wit R, Leruste A, Le Fur I, Sy MM, Bec B, Ouisse V, Derolez V and Rey-Valette H (2020) A Multidisciplinary Approach for Restoration Ecology of Shallow Coastal Lagoons, a Case Study in South France. Front. Ecol. Evol. 8:108. doi: 10.3389/fevo.2020.00108

By the end of the 20th century, many of the coastal lagoons along the French Mediterranean coast showed insufficient water quality and degraded ecosystem states due to anthropogenic impacts. Among these, nutrient over-enrichment, resulting in eutrophication, has been a major concern. The EU Water Framework Directive (WFD) has initiated public action to improve their water quality and ecosystem state using an approach rooted in restoration ecology. Here we analyze how this has been applied for the coastal lagoons in South France, considering eutrophication as an example of ecosystem degradation and oligotrophication as the corresponding trajectory for ecological restoration of the eutrophied coastal lagoons. Oligotrophication trajectories, initiated by the reduction of external nutrient loading, have resulted in a quick recovery (i.e., within 3 years) of integrative water column variables (Chlorophyll *a*, total N and P) and phytoplankton. Starting from hypertrophic systems, the oligotrophication trajectory is described by a sequence of three ecosystem states dominated respectively by (i) phytoplankton with bare non-vegetated sediments, (ii) opportunistic macroalgae, (iii) angiosperm and perennial macroalgae, punctuated by regime shifts between these ecosystem states. Nevertheless, the latter regime shift has not been observed for the most degraded ecosystems after 10-years oligotrophication. The N and P accumulated in sediments during eutrophication may also retard the ecological restoration. In shallow freshwater lakes, the phytoplankton-dominated and the angiosperm-dominated states are also characteristic for highly degraded and fully restored ecosystems states, respectively. In contrast, opportunistic macroalgae do not bloom in these systems. Hence, the alternative stable state model, used successfully for these lakes, cannot be applied straightforwardly for coastal lagoons. To be successful, ecological restoration should consider the legislative and societal questions as according the DPSIR framework it typically is a response of society. The conservation-oriented Habitats Directive systematically applies to coastal lagoons and the Birds Directive in some cases as well. The WFD approach is complementary to these more conventional nature conservation approaches. Collectively, local citizens and highly involved stakeholders strongly value the coastal lagoons and attribute very high importance to their regulating ecosystem services (ESs), while differences between stakeholder profiles are related to different perceptions and appreciations of cultural ESs. Hence, coastal lagoon ESs are very important for the different stakeholders and public policies aiming at the ecological restoration of these ecosystems may count on public support.

Keywords: restoration ecology, ecological restoration, water quality, WFD, ecosystem trajectories, DPSIR, conservation, ecological indices

INTRODUCTION

The EU Water Framework Directive 2000/60/EC (WFD) presents a highly integrated approach focused on water quality, which according Voulvoulis et al. (2017) is widely accepted as the most substantial and ambitious piece of European environmental legislation to date. Interestingly, the major aim of this directive is to improve the ecological status of water bodies, which calls for a pro-active approach rooted in the theory of restoration ecology. In general, a difference is made in the literature between restoration ecology and ecological restoration; the latter is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Society for Ecological Restoration International Science and Policy Working Group, 2004), The former, restoration ecology, is a scientific discipline, a field within ecology, focused on studying the concepts, experiences and practices of ecological restoration (Clewell and Aronson, 2013). Both restoration ecology and the WFD advocate that the approaches for ecological restoration should be based on (i) the identification of a reference state, (ii) a description of a desired state that is quite close to the reference state, and (iii) the development of a roadmap, which specifies how the ecosystem trajectory should converge toward that desired state. For restoration ecology, the reference state is a historical reference state referring to the ecosystem state before it was degraded by human impacts (Clewell and Aronson, 2013). The reference state according the WFD is the ecosystem state in conditions of minimal anthropogenic impact. Hence, for a degraded aquatic system considered for ecological restoration, this implies that such conditions of minimal anthropogenic impact occurred in the past and the reference state can thus be considered as a historical reference state *sensu* restoration ecology.

The Ecosystem state of many coastal lagoons worldwide has been degraded as a result of anthropogenic impacts comprising nutrient over-enrichment leading to eutrophication (Zaldívar et al., 2008), habitat destruction (De Wit, 2011; Newton et al., 2018), contaminant inputs (Covelli, 2012; Munaron et al., 2012). Environmental awareness of citizens, the practice of Integrated Coastal Zone Management (ICZM), and specific legislation derived from the EU, i.e., the WFD mentioned above together with the EU Habitats Directive 1992 (Council Directive 92/43/EEC) and the EU Birds Directive (2009) (Directive 2009/147/EC), have triggered public policies in the EU member states that value these ecosystems and aim to protect and improve their water quality, protect public health issues, conserve their biodiversity and develop their ecological potential for the delivery of ecosystem services. The WFD considers the ecological functioning of the aquatic ecosystems, including coastal lagoons, and formulates its main objectives as conserving and achieving "good ecological status" of water bodies. Therefore, the WFD is particularly important for biodiversity conservation in the EU and it has been stated that:

> "*the legislative framework in place to achieve the Biodiversity Strategy in aquatic ecosystems* (in the EU, *sic*) *can be linked to a complex array of interlinked policies, of which the most far-reaching ones are the Birds and Habitats Directives, Water Framework Directive, and Marine Strategic Framework Directive*"
>
> (Rouillard et al., 2017).

The latter has fewer implications for coastal lagoons, for which the water quality regulations are derived from the WFD. Coastal lagoons are listed as a priority habitat in the Habitats Directive and many coastal lagoons are particularly important for waterfowl and concerned by the Birds Directive (Dolbeth et al., 2016). Article 6 of the WFD requests member states to establish a register of areas which have been designated as requiring special protection under specific Community legislation for the conservation of habitats and species directly depending on water and WFD Annex IV explicitly links this requirement to the Natura 2000 sites designated according the Habitats and Birds Directives.

In this article, we use eutrophication as an example of ecosystem degradation, and oligotrophication as the corresponding trajectory for the ecological restoration of eutrophied lagoons. The many actions employed in South France to combat eutrophication of coastal lagoons and induce their oligotrophication thus represents an interesting study case for assessing ecological restoration according the theoretical framework of restoration ecology. We believe that such an analysis should particularly address the issues to which coastal lagoon managers are confronted in their daily practice. Therefore, first we propose a conceptualization placing the ecological restoration in societal context and adapt the conceptual scheme in such a way to accommodate the specificities of the WFD. Secondly, our study includes an analysis of the technical and natural science aspects of the ecological restoration practice as well as important questions concerning the societal context. Therefore, we have formulated the following three main questions (**Figure 1**):

1. Do scientific concepts and theories provide guidance for the ecological restoration practice and are their theoretical predictions of ecosystem trajectories supported by empiric ecological knowledge?

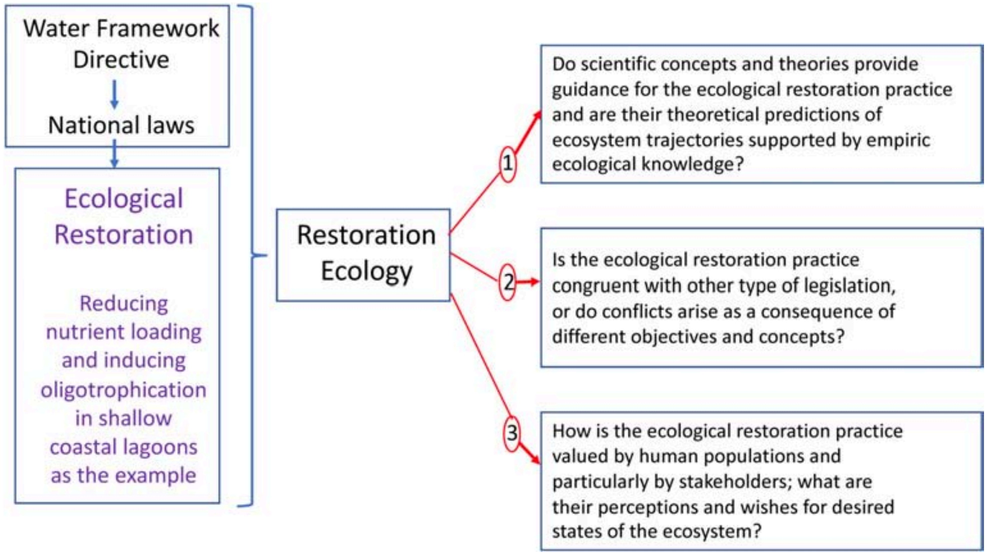


FIGURE 1 | The Water Framework Directive (2000/60/EC) through its transposition into national laws [in France: Loi n° 2006–1772 du 30 décembre 2006 sur l'eau et les milieux aquatiques (French law)] has resulted in South France in ecological restoration practice to improve the ecological status of coastal lagoons. A particular focus has been on reducing nutrient loading to combat eutrophication and thus induce oligotrophication of coastal lagoons. In this article this practice has been analyzed according the theoretical framework of restoration ecology and three main questions have been formulated for this assessment.

2. Is the ecological restoration practice congruent with other type of legislation, or do conflicts arise as a consequence of different objectives and concepts?
3. How is the ecological restoration practice valued by human populations and particularly by stakeholders; what are their perceptions and wishes for desired states of the ecosystem?

Ecological restoration of coastal lagoons has started around 2000 and is, therefore, quite novel in contrast to the ecological restoration of water quality in freshwater lakes initiated since the 1980s (Marsden, 1989; Gulati and Van Donk, 2002; Jeppesen et al., 2002). For providing scientific guidance for the technical aspects, we consider if the lessons learned from the ecological restoration of freshwater lakes can be applied to the brackish to saline coastal lagoons located at the interface between the land and the sea. A general model of alternative stable states was developed originally for shallow freshwater lakes (Scheffer et al., 1993), with a transparent water state dominated by submerged aquatic vegetation (SAV) and a turbid state dominated by phytoplankton. Hence, here we evaluate whether this model can also be applied to shallow coastal lagoons. In addition, we consider the sediment compartment as a possible internal source for nitrogen and phosphorus that could retard the oligotrophication process as has been observed in shallow freshwater lakes (Marsden, 1989; Søndergaard et al., 2003; Jeppesen et al., 2005). We report the different approaches for coastal lagoons in the WFD and the Habitats Directive and discuss the challenges faced by the managers of these ecosystems to cope simultaneously with the requirements of both directives. Concerning the social aspects, we study whether the normative approach for water quality imposed by the WFD is accepted by the local populations and stakeholders by studying their perceptions of water quality and their preferences for ecosystem services.

STUDY SITES AND METHODS

The study sites comprise the shallow coastal lagoons (average depth <2 m, surface >50 ha) along the Mediterranean coastlines of continental France and the island of Corsica, which are shown in **Figure 2**. Deeper coastal lagoons (average depth >2 m, in gray in **Figure 2**) have been excluded from this analysis as deeper water bodies show different ecological structure and functioning. In addition, deep lagoons are often complex systems comprising both shallow and deeper parts that may interact in a complex way. The terminology based on their salinities follows the Venice System (1958) and was described based on monitored salinity values in Le Fur et al. (2018). The shallow lagoons in **Figure 2** cover 396 km^2. Coastal lagoons occupy about 50% of the coastline along the Gulf of Lion, are numerous in the delta of the Rhône River and less common on the Côte d'Azur. In Corsica, coastal lagoons are located on the Eastern littoral facing the Tyrrhenian Sea.

Coastal lagoons are characterized by permanent or temporary connections with the adjacent sea, via one or several inlets (Kjerfve, 1994). Today, very few of the shallow lagoons shown in **Figure 2** have natural moving inlets (i.e., La Palme, Ayrolle, Biguglia), which only for La Palme lagoon close off completely every year (Larue and Rouquet, 2016). The natural inlet of Biguglia also tends to fill in, although it is regularly dredged to keep a permanent connection with the sea. In many cases, inlets have been modified by humans by construction of hard-substrate artificial inlet banks and are being dredged regularly.

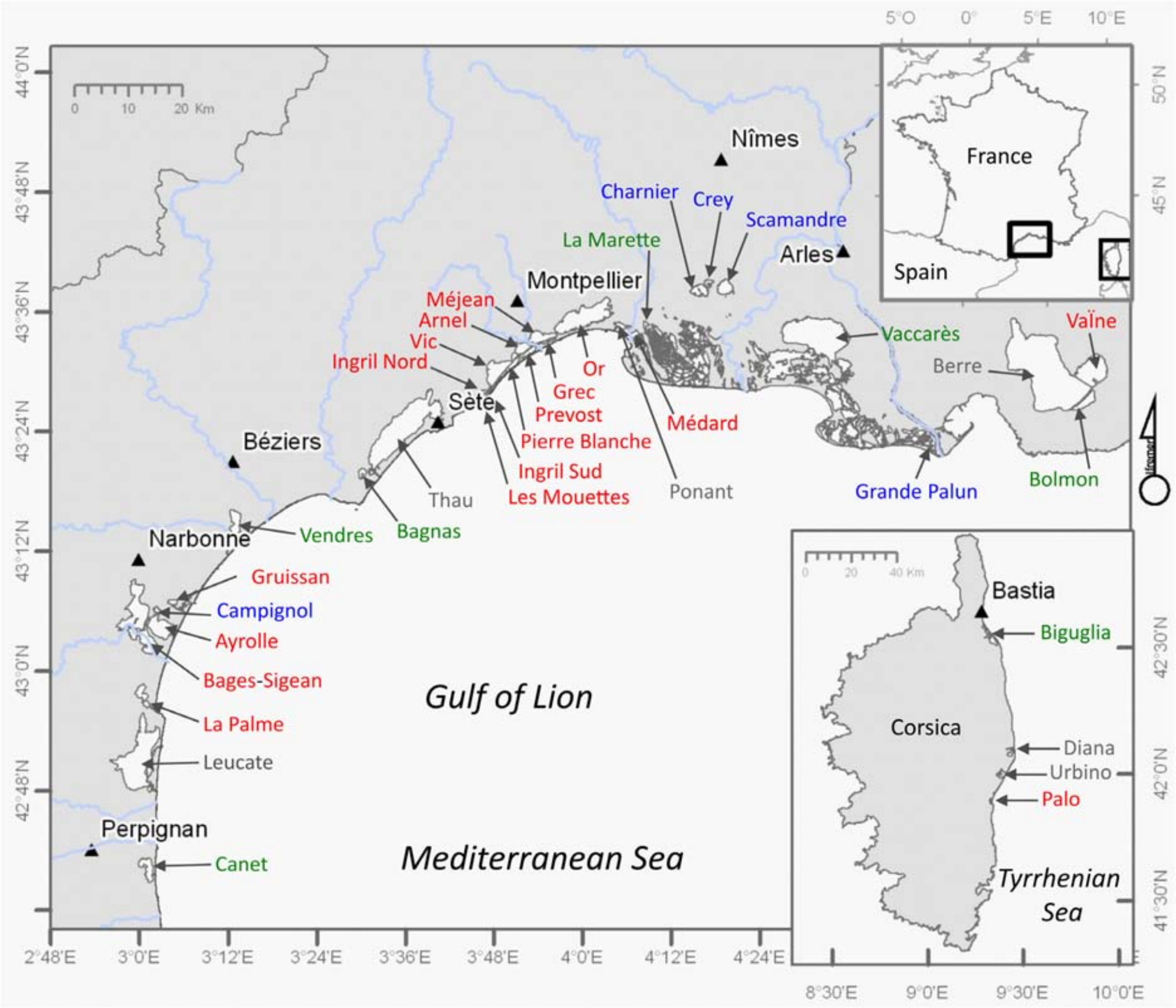


FIGURE 2 | Distribution of coastal lagoons, recognized for the WFD implementation in France, along the Mediterranean coastlines of continental France and the island of Corsica. In gray: deep lagoons (>2 m) not considered in this study. In blue: shallow (<2 m) oligohaline lagoons; in green: shallow (<2 m) mesohaline lagoons; in red: shallow (<2 m) poly- and euhaline lagoons. Triangles represent main urban centers (>40,000 inhabitants) in the proximity of the coastal lagoons.

This has fixed the locations of the inlets and resulted in a permanent connection of the lagoons with the sea. In some areas artificiality is even more striking. Some of the permanent lagoons in the deltaic setting have been separated from the sea several km's by the progression of the delta; the connections with the sea are maintained through artificial canals (Scamandre, Crey, Charnier) or through a wetland complex protected by a dike (Vaccarès). The Palavas lagoon complex (PLC) (in French: complexe lagunaire Palavasien) close to the city of Montpellier currently comprises eight lagoons (Ingril Nord, Ingril Sud, Vic, Pierre Blanche, Prévost, Arnel, Méjean, Grec) that have been created through the compartmentalization of the original "lagune de Mergueil." The creation of the Rhône-to-Sète canal since the 18th century has separated four permanent lagoons (Ingril Nord, Vic, Arnel, Méjean) from the coastline and exchanges of these lagoons with the sea occur through this canal.

To address the questions listed in **Figure 1** and described in section "Introduction" we use a combination of studies. The natural science information in this article is based on reviewing and synthesizing our previous studies (see **Table 1**), literature review including some gray literature that has been complemented with some additional unpublished data from three Ph.D. thesis (Leruste, 2016; Le Fur, 2018; Sy, 2019) and additional monitoring data from monitoring programs extracted from the French data bases "Banque Hydro[1]," Naïade[2], and "Surval," which among others hosts the data of the Réseau Suivi Lagunaire (RSL) monitoring program (Ifremer[3]). In the RSL, the total Nitrogen (TN) and Total Phosphorus (TP) data of the top 5 cm of the sediment (sampled at 6-year intervals) were expressed

---

[1] http://www.hydro.eaufrance.fr/

[2] http://www.naiades.eaufrance.fr/acces-donnees

[3] https://wwz.ifremer.fr/surval/

TABLE 1 | Scientific papers used to synthesize and review the information, which served to create the knowledge base about eutrophication gradients and oligotrophication trajectories in shallow Mediterranean coastal lagoons in South France.

Type of data used[1]	Period	Geographic area[2]	Subject	Biological (physico-chemical) compartment(s)	References
Monitoring (RSL)	1999–2001	G-Lion, Corsica	Eutrophication gradient	TN and TP as proxy for phytoplankton biomass, nutrient stochiometry	Souchu et al., 2010
Monitoring (RSL)	1998–2002	G-Lion, Corsica	Eutrophication gradient	Phytoplankton taxa and biomass	Bec et al., 2011
Monitoring (RSL)	1998–2015	G-Lion, Rhône-d, C-azur, Corsica	Eutrophication gradient	Benthic macrophytes taxa	Le Fur et al., 2018
Historical observations	1970–2014	Biguglia (Corsica)	Eutrophication gradient and hydrological changes	Phytoplankton biomass and benthic macrophyte taxa	Pasqualini et al., 2017
Monitoring (RSL)	2000–2013	Palavas lagoon complex (G-Lion)	Oligotrophication	Phytoplankton biomass and taxa	Leruste et al., 2016
Monitoring (RSL)	2001–2014	G-Lion, Corsica	Oligotrophication	Phytoplankton biomass, water column nutrients	Derolez et al., 2019
Monitoring (RSL)	1998–2015	G-Lion, Corsica	Oligotrophication (poly and euhaline lagoons)	Benthic macrophytes	Le Fur et al., 2019
Experimental	2013–2014	Biguglia (Corsica)	Bioassay to detect nutrient limitation of phytoplankton	phytoplankton taxa and cell sizes, water column nutrients	Leruste et al., 2019a
Experimental	2014	Méjean, Ingril N, Ayrolle (G-Lion)	Bioassay to detect nutrient limitation of phytoplankton	Phytoplankton taxa and cell sizes, water column nutrients	Leruste et al., 2019b

[1] RSL, Réseau Suivi Lagunaire monitoring program. [2] G-Lion, Gulf of Lion; Rhône-d, Rhône delta; C-azur, Côte d'Azur.

as N and P contents in g/kg dry weight of sediments. Due to variable water contents and densities of the sediments it is not possible to convert these values to an aerial basis. These values were converted to mmol/kg for a stoichiometric analysis.

The question of the congruencies between WFD and Habitats directives has been based on analysis of legal texts and technical documents of the European Commission. In addition to the previous studies on citizens and stakeholder perceptions and opinions reviewed in this article, it also includes new results from citizen workshops organized in 2017 and 2018 at two different places in the eastern and western vicinity of the PLC. Forty-three randomly selected citizens working or recreating in both parts of the lagoon complex participated in the workshops (see **Supplementary Tables S1, S2** for details of the survey). The methodology was based on Sy et al. (2018) using Q-method to analyze consensus and diverging preferences of local citizens for ecosystem services provided by these lagoons. The results obtained for the citizens were compared with those obtained for the highly involved stakeholders (Sy et al., 2018).

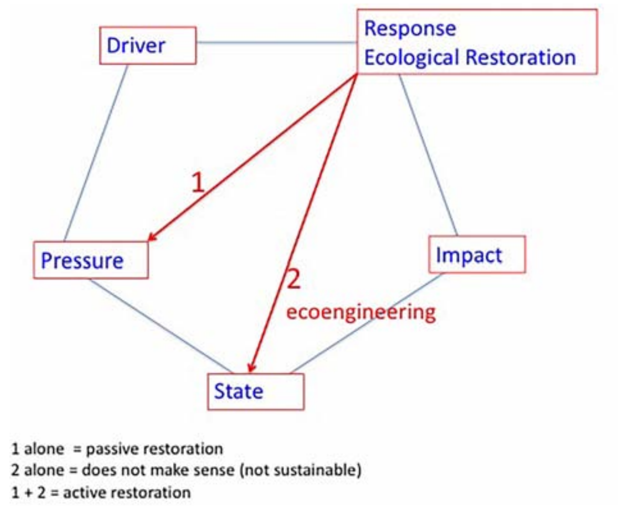


FIGURE 3 | Placing the Ecological Restoration practice in the D (drivers), P (pressures), S (state), I (impact), and R (response) framework. Accordingly, Ecological Restoration clearly is a societal response that targets 1) reducing the pressure on the ecosystem and 2) interfering directly with the ecosystem state through eco-engineering.

RESULTS AND DISCUSSION

Concept of Ecological Restoration in the Frame of the WFD

Ecological Restoration is a human action focused on degraded ecosystems that can thus be taken into account by the DPSIR framework, as this framework aims at analyzing the interactions between humans and ecosystems. Accordingly, ecological restoration should be considered as a Response (see **Figure 3**). In general, responses in DPSIR can potentially target D (drivers), P (pressures), S (state), and I (impact), although for ecological restoration it is clear that drivers and impacts are not really pertinent targets. Acting on major drivers is beyond the scope of action for ecological restoration *sensu stricto*; i.e., increasing urbanization and intensification of agriculture are drivers that could potentially be changed by spatial planning and agricultural policies, respectively, but not directly by ecological restoration. As ecological restoration has the ambition to repair degraded ecosystems it does not make sense to target the impacts; this would correspond to combating the symptoms and thus completely neglects the major objectives set for ecological restoration. Hence, ecological restoration could target the P (pressures) and the S (state).

For the problem of eutrophication of coastal lagoons, the pressure corresponds most often to nutrient over-enrichment mainly caused by nutrient loadings from their watershed. Hence, targeting the pressure thus corresponds to reducing the nutrient loading into the coastal lagoons. This action induces the reverse of eutrophication, i.e., oligotrophication. However, there is some debate about terminology, e.g., the term re-oligotrophication has been coined to describe the trajectories for lakes (Jeppesen et al., 2002) and coastal lagoons (Le Fur et al., 2019). This latter term seems to imply that the eutrophied systems were originally oligotrophic and that the trajectory should lead to full oligotrophic conditions. As not all coastal lagoons were originally oligotrophic (Nixon, 2009), it is preferable to use the more neutral term oligotrophication, which designates a process of moving toward more oligotrophic conditions. Moreover, in some cases the term de-eutrophication has been used.

An example of targeting the state (**Figure 3**) is seeding or planting marine angiosperms (Orth et al., 2012, MEPS thematic section, Van Katwijk et al., 2016), which are indicator species for good ecological conditions in coastal lagoons. Nevertheless, it is obvious that such eco-engineering activities alone without tackling the pressures on the system is not sustainable and would most likely result in failure in the short or mid-term (Van Katwijk et al., 2009; Cunha et al., 2012), a conclusion that has been confirmed in a recent study (Van Katwijk et al., 2016). We differentiated between passive and active ecological restoration (De Wit et al., 2017). Accordingly, passive ecological restoration is defined by action focused on reducing and combating the pressure (1 alone in **Figure 3**) and relies on the spontaneous ecological processes in the ecosystem for a trajectory toward improved conditions. Active ecological restoration implies a combination of reducing the pressure on the ecosystem in conjunction with eco-engineering *in situ* to improve the state of the ecosystem directly. A pertinent example for active ecological restoration in coastal lagoons is to combine a reduction of nutrient loading with seeding or planting marine angiosperms.

Figure 4 is the conceptual presentation derived from restoration ecology (Clewell and Aronson, 2013) that can be used as a roadmap and has been adapted to accommodate the specific requirements of the WFD. In the WFD, ecological status is measured using indicators and calculated as an ecological quality ratio (EQR; Zaldívar et al., 2008), with EQR being equal to one for the reference state. Hence, the EQR measures the deviation from reference conditions. The reference state is then taken as the ideal target for the ecological restoration, which is considered according WFD as high ecological quality status. Nevertheless,

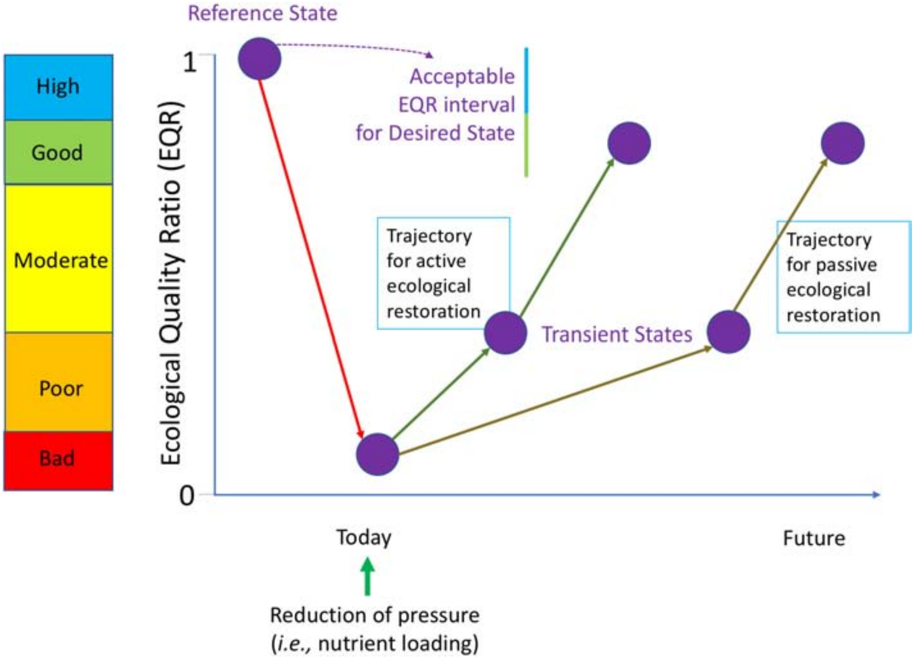


FIGURE 4 | Roadmap for ecological restoration applied in the frame of the WFD. The ecosystem states are characterized by a set of biological quality elements (BQE, e.g., phytoplankton, macrophytes) used as indicators and expressed as an Ecological Quality Ratio (EQR) represented on the Y-axis, with their qualifications for the corresponding ecological status (color coding). A historical ecosystem state not impacted by human pressures is taken as the reference condition for the ecological restoration. The WFD allows a small deviation from these reference conditions by targeting good or high ecological status for the Desired State of the coastal lagoons. After reduction of the pressure it is presumed that the degraded ecosystem (in the example currently in bad ecological status) will move gradually toward the Desired State, probably passing through one or multiple transient states (passive restoration). The recovery can be speed up by combining the reduction of the pressure with additional eco-engineering measures (active restoration, cf. **Figure 3**).

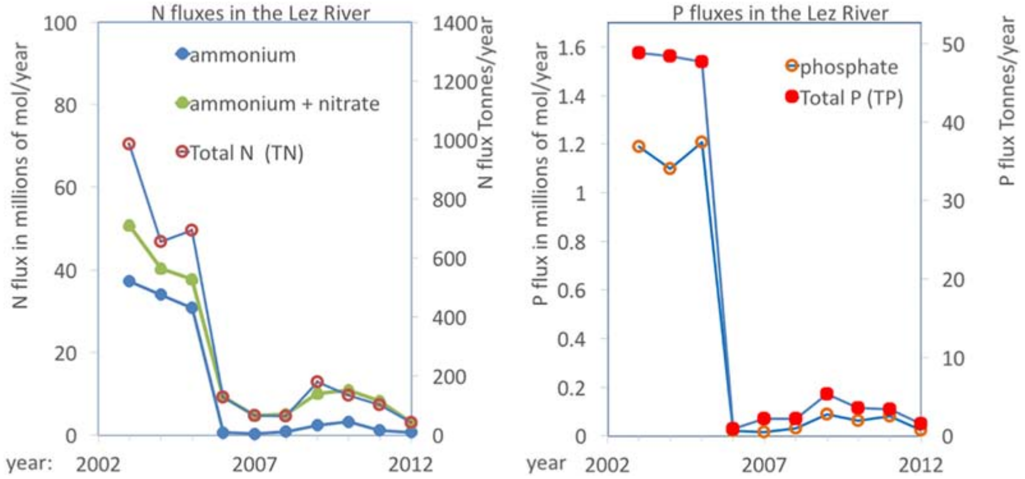


FIGURE 5 | Annual fluxes of N and P compounds in the Lez River. Values can be read on both scales (left in millions of mols/year; right in metric tonnes/year for N and P, respectively). Source: "Banque Hydro" and "Naïade" (réseau de données eaufrance, DCE).

the WFD is flexible and for achieving the target allows "*low levels of distortion resulting from human activity*," which "*deviate only slightly from those normally associated with the surface water body type under undisturbed conditions*" (WFD, Annex V) and ecological quality status are characterized as good for these conditions. Hence good or high ecological status correspond to the "Desired state" of the system that should be achieved in the future before a given deadline. After reduction of the pressure it is presumed that the system will move gradually toward this desired state, probably passing through one or multiple transient states. The recovery can be speed up by combining the reduction of the pressure with additional eco-engineering measures. The trajectories in the context of this study correspond to the different oligotrophication trajectories for the different scenarios. Hence, scientific knowledge of oligotrophication processes in coastal lagoons is of paramount importance for managers.

Can Scientific Knowledge of Eutrophication and Oligotrophication Trajectories in Mediterranean Coastal Lagoons Be Used to Provide Guidance for Ecological Restoration Actions?

Nutrient Loading Into Coastal Lagoons

In general, the demographic developments in the coastal zone since the 1950s and the resulting increased urbanization with insufficient sanitation and sewage treatments were the main drivers for the nutrient over-enrichment in the shallow coastal lagoons, particularly for those close to the cities of Montpellier, Narbonne, and Perpignan (cf. **Figure 2**). The urbanization to the south of Bastia accelerated later and particularly increased during the first decade of the 21st century (Pasqualini et al., 2017). Subsequently, action has been undertaken in these areas to reduce the nutrient loadings by improved sanitation (Leruste et al., 2016; De Wit et al., 2017; Pasqualini et al., 2017; Derolez et al., 2019; Le Fur et al., 2019). The case of the PLC is described in more detail. In the coastal lagoons of this complex, the bulk of the nutrient inputs originated from the urban waste-water treatment plant (WWTP) of the Montpellier agglomeration that discharged its effluents in the Lez River. As a result, most nutrients entered these lagoons via the Lez River and the Rhône-to-Sète canal. In 2005, a major investment was realized of 150 Million€ to upgrade the waste-water treatment facility in Montpellier, and create an off-shore outfall (Leruste et al., 2016; De Wit et al., 2017). All eight lagoons of the PLC benefited from this investment. In 2009, the WWTP of the city of Palavas (a smaller facility) was connected to the main WWTP in Montpellier, which resulted in an additional major reduction of nutrient loading into the Grec lagoon (Le Fur et al., 2019).

The annual fluxes of N and P carried by the Lez River are presented in **Figure 5**. This complete charge does not enter the lagoons as part flows through the river mouth directly into the Mediterranean Sea. Nevertheless, the Lez River represent the major tributary to the coastal lagoons of the PLC and this **Figure 5** gives therefore a good indication of the nutrient enrichment pressure on the system. From the Lez River, some water directly leaks into the Méjean and Arnel lagoons, but most enters the lagoons through the Rhône-to-Sète canal. As a result, the lagoon complex showed in the early 2000s an interesting gradient ranging from hypertrophic conditions in the lagoons close to the intersection of the Lez River and the canal to mesotrophic conditions in the two Ingril lagoons located farthest away (Bec et al., 2011; Souchu et al., 2010; Leruste et al., 2016; De Wit et al., 2017). Comparing the periods before (2003–2005) and after (2007–2012) showed decreases of 75 and 87% of total N and P, respectively (see **Figure 5**). Considering all other sources together with the major contribution from the Lez River it has been estimated that the intervention resulted in a reduction of the nutrient loadings from the watershed into the PLC of 83 and 73%, for total N and total P, respectively (Meinesz et al., 2013). Moreover, in the Lez River there was a strong shift in the relative proportions of NH_4^+ and NO_3^-, with NH_4^+ representing 79 and 20% of dissolved inorganic nitrogen (DIN), before and after, respectively. Before, organic nitrogen, i.e., the sum of dissolved and particulate organic nitrogen (DON and PON, respectively), represented 23% of total N and dropped to virtually 0 after the intervention (**Figure 5**).

What Can Be Learned From Shallow Lakes for Succession Patterns of Primary Producers in Mediterranean Coastal Lagoons?

Decades before tackling the eutrophication problems in coastal lagoons, the ecological restoration of aquatic systems started with the oligotrophication of shallow freshwater lakes. Therefore, it is inspiring to review freshwater lake oligotrophication and tempting to use it as a guideline for the ecological restoration of coastal lagoons. Scheffer (2001) stated "*Ponds and shallow lakes can be very clear with abundant submerged plants, or very turbid due to a high concentration of phytoplankton and suspended sediment particles*." This statement has been related to the alternative stable state theory (Scheffer et al., 1993). Accordingly, two attractors exist for these type of ecosystems, i.e., the SAV stable state attractor and the turbid stable state attractor, which dominate at very low and very high nutrient loadings, respectively. At intermediate nutrient loadings both attractors coexist and mathematically the ecosystem shows these two alternative stable states, which are each stabilized by a mixture of positive and negative feedback loops (Scheffer et al., 1993). Hence, a window of environmental conditions exists with alternative stable states in these aquatic ecosystems, where the actually occurring ecosystem state depends on the history of the system. Following the Scheffer model for shallow lakes, for environmental conditions within the window, the system can remain in the SAV state during increasing eutrophication until it reaches a critical turbidity, which is imposed by the minimum light requirements for growth and survival of the SAV. Above this threshold, the aquatic ecosystem shows a forward regime shift toward the turbid state. On the other hand, when nutrient loading is reduced in a turbid eutrophic lake, the system remains in the turbid state until the phytoplankton densities have decreased to such low values with a corresponding turbidity below the threshold. Hence, the model provides one possible explanation for hysteresis during eutrophication/oligotrophication trajectories. In addition, it can predict vulnerability of ecosystems states to perturbation, as for conditions within the window of two alternative stable states a perturbation may act to induce a regime shift (Beisner et al., 2003), e.g., a perturbation that causes a sudden die-back of SAV could result in a regime shift into the turbid state.

We may now ask the question, whether these two attractors and corresponding ecosystem states also exist for coastal lagoons? In general, the above-mentioned statement of Scheffer (2001) is pertinent for coastal lagoons as well. The clear water SAV dominated state in eu- and polyhaline lagoons is found under oligotrophic conditions and corresponds to the marine angiosperms, *Zostera noltei* Hornemann, 1832, *Ruppia cirrhosa* (Petagna) Grande, 1918, *Ruppia maritima* Linnaeus, 1753, *Cymodocea nodos*a (Ucria) Ascherson, 1870 and some slow-growing perennial macroalgae as e.g., *Acetabularia acetabulum* (Linnaeus) P. C. Silva, 1952, and *Valonia aegagropila* C. Agardh, 1823 (Le Fur et al., 2018, 2019). On the other hand, the highly turbid state is characterized by dense phytoplankton blooms often dominated by small phytoplankton (Bec et al., 2011; Leruste et al., 2016), belonging to picophytoplankton (<3 μm size; Bec et al., 2011) and ultraphytoplankton (>3 μm and <5 μm size; Li, 1995), with Chlorophyll *a* (Chl *a*) concentrations that may achieve several hundreds of mg/m^3. Clear examples of the latter are Or lagoon and before 2005 Méjean lagoon as well. Both ecosystem states have similar positive and negative feedback loops as those observed for their freshwater counterparts that stabilize these ecosystem states (Maxwell et al., 2017; Le Fur et al., 2019).

The succession patterns of primary producers with increasing eutrophication in Mediterranean coastal lagoons (Le Fur et al., 2018) are different from that of freshwater lakes. Accordingly, Le Fur et al. (2018) observed that poly- and euhaline lagoons follow the same general pattern as described by Schramm (1999) for the shallow coastal zone; i.e., with increasing eutrophication four stages have been observed, comprising successively (i) healthy marine angiosperms and perennial macroalgae, (ii) declining angiosperms with increasing loads of epiphytes, (iii) opportunistic macroalgae, and (iv) phytoplankton and bare non-vegetated sediment. In contrast, oligohaline coastal lagoons are dissimilar, because no blooms of macroalgae do develop. Hence, shallow oligohaline coastal lagoons are more similar to freshwater lakes. The dominant SAV in the Mediterranean oligohaline lagoons are charophytes and the angiosperm *Stuckenia pectinata* (Linnaeus) Börner, 1912 (formerly *Potamogeton pectinatus*). The latter species form long stems allowing an important proportion of its leaves to float at the surface of the water. This way, this species escapes from competition with planktonic algae for light. Mesohaline coastal lagoons are intermediate between the oligohaline on one side and the poly- and euhaline lagoons on the other side. As in poly- and euhaline lagoons, opportunistic macroalgae develop at intermediate eutrophication levels. On the other side, *Ruppia* species are characteristic angiosperms in mesohaline lagoons, which like *S. pectinata* form long stems with floating leaves (Le Fur et al., 2018).

In conclusion, in meso-, poly-, and euhaline lagoons, the Scheffer model for shallow freshwater lakes is not directly applicable as a third group, i.e., opportunistic macroalgae, can dominate primary producer communities and as a rather persistent community represent a third stable state in addition to the angiosperms and planktonic algae stable states. By comparison, the stage of declining angiosperms with increasing loads of epiphytes appears as a transient state, that is not stable because the developing epiphytes weaken their own support. It thus appears that the opportunistic macroalgae occupy a niche in the window where bistability of the two end members could occur. However, so far no clear mathematical analysis allows to determine whether the opportunistic macroalgal states completely overrules the theoretical window of bistability, or whether multiple stability domains exist in coastal lagoons. Increasing eutrophication in these coastal lagoons is correctly characterized by regime shifts according to the Schramm scheme (Le Fur et al., 2018). Nevertheless, threshold effects and regime shifts do not necessarily imply multiple stable states, as very steep but continuous shifts in equilibrium states are also possible (Petraitis and Hoffman, 2010). Viaroli et al. (2008) suggested two possible mechanisms for the regime shift from angiosperms to floating macroalgae, i.e., either as the conventional mechanism based on continuous shift or on a so-called dynamic shift implying a domain of bi-stability. One conclusion from their work, i.e., "*The alternative states which occur through the transition from pristine to modified primary producer communities can also be viewed as a sequence of stable states.......*" (Viaroli et al., 2008) is a bit ambiguous in this respect. We think that modified primary producer communities along eutrophication gradients in coastal lagoons should indeed be viewed as a sequence of stable states, but that it remains so far, uncertain whether these represent continuous shifts in equilibrium states or whether it hides multiple stable state domains.

Oligotrophication Trajectories

Eight-year to seventeen-year time series from monitoring programs have been used to study the oligotrophication trajectories in the French Mediterranean coastal lagoons, which allowed to make comparisons before and after nutrient reduction measures (Leruste et al., 2016; Derolez et al., 2019; Le Fur et al., 2019). In addition, a longer time series of more heterogeneous observations was available for Biguglia lagoon (Pasqualini et al., 2017). The monitoring effort was concentrated during summer and based on three samplings in June, July, and August, successively. Water column variables, including nutrients (NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, silicates), TN, TP, Chl *a*, and the pico- and nanophytoplankton cell abundances in 16 lagoons, including shallow and deeper lagoons, have been analyzed by a between-station principal component analysis (PCA). The trajectories of 14-year time series for some selected stations in shallow lagoons (Ayrolle, Bages, Méjean) have been plotted in the PCA plane (Derolez et al., 2019). The first axis of this PCA, which explained 81% of the variation, correlated mainly with Chl *a*, TN, TP, and dissolved inorganic phosphorus (DIP, i.e., PO_4^{3-}), and was clearly interpreted as the main eutrophication axis. The second axis (11% of variance explained) was correlated to DIN. The station in Méjean lagoon, which was hypertrophic before 2005, moved toward oligotrophy, although it was still eutrophic in 2014. The station in Bages, which was eutrophic before 2004 also moved toward oligotrophy, albeit less abruptly than the station in Méjean. It was concluded that integrative water column variables (Chl *a*, TN, and TP) recover quickly, i.e., within 1–3 years after nutrient reduction measures (Derolez et al., 2019).

Changes in phytoplankton communities following nutrient reduction measures were studied for the coastal lagoons of the PLC (Leruste et al., 2016). The Chl *a* concentrations in the hypertrophic Méjean were 185 ± 131 μgL^{-1} before and dropped on average by one order of magnitude after the nutrient input reduction (cf. **Figure 5**), with a concomitant drop of autotrophic picoeukaryotes cell numbers. There was a shift from small diatoms that still dominated in 2006 to green algae. The other lagoons of the PLC also showed significant decreases in Chl *a* after nutrient input reduction and increases in the proportions of peridin-containing dinophytes (Leruste et al., 2016), probably related to their mixotrophic capacities (phagocytosis and osmotrophy). Oligotrophication in shallow freshwater lakes also results in a drop of Chl *a* concentrations and phytoplankton abundance with the species composition shifting toward diatoms, cryptophytes and chrysophytes (Jeppesen et al., 2005). It has been observed that summer phytoplankton communities in the Mediterranean coastal lagoons in South France are clearly limited by P under oligotrophic conditions and with increasing eutrophication level change through P/N co-limitation to N-limitation (Souchu et al., 2010). It appears that this tendency is maintained during the oligotrophication trajectories and perhaps even strengthened. Hence, during the summer of 2014, bioassay experiments showed that the phytoplankton community in Méjean lagoon was clearly N-limited. The ambient concentrations of DIN and DIP were around 1 and 2.5 μM, respectively, showing excess of DIP. In contrast, a co-limitation by N and P was observed in the eutrophic Biguglia, the mesotrophic Ingril and the oligotrophic Ayrolle lagoons (**Figure 2**); the latter was studied for comparisons. In the PLC, the phytoplankton communities of the Ingril and Méjean lagoons strongly responded to the experimental nutrient pulses, suggesting that despite their oligotrophication trajectories, these lagoons were still vulnerable to occasional eutrophication events (Leruste et al., 2019a,b).

The impact of the oligotrophication process on the macrophyte assemblages was studied in 21 poly- and euhaline lagoons, by comparing the taxonomic composition of the macrophytes sampled at different stations in the lagoons with variables characterizing the water column using 17 years of observations (Le Fur et al., 2019). The observations were again restricted to the summer period. The data comprised a series of paired data tables, i.e., for species and the other for the water column environmental conditions. Two axes were considered for the multivariate analysis (STATICO factor map); the first axis (88.5% of total variability explained) correlated with Chl *a* concentrations, turbidity, TN and TP, and was again interpreted as the main eutrophication axes. The second axis (9.5% of total variability explained) correlated with DIN and DIP concentrations. A general scheme was inferred for the changes in macrophyte assemblages during the oligotrophication process. Hence, when placing hypertrophic and oligotrophic conditions end to end, the oligotrophication trajectories were described by a sequence of three ecosystem states dominated by (i) phytoplankton with bare non-vegetated sediments, (ii) opportunistic macroalgae, (iii) seagrass and perennial macroalgae, punctuated by regime shifts between these ecosystem states. The regime shift from the phytoplankton-dominated state to opportunistic macroalgae was observed in Méjean lagoon, where *Ulva rigida* C. Agardh, 1823, dominated in 2009 after a strong decrease in Chl *a* (see above), followed by more diverse communities since 2012 with among others different *Gracilaria* spp. and *Chaetomorpha aerea* (Dillwyn) Kützing, 1849. However, during the 10-year period following the reduction of the nutrient loading, Méjean lagoon did not achieve the oligotrophic

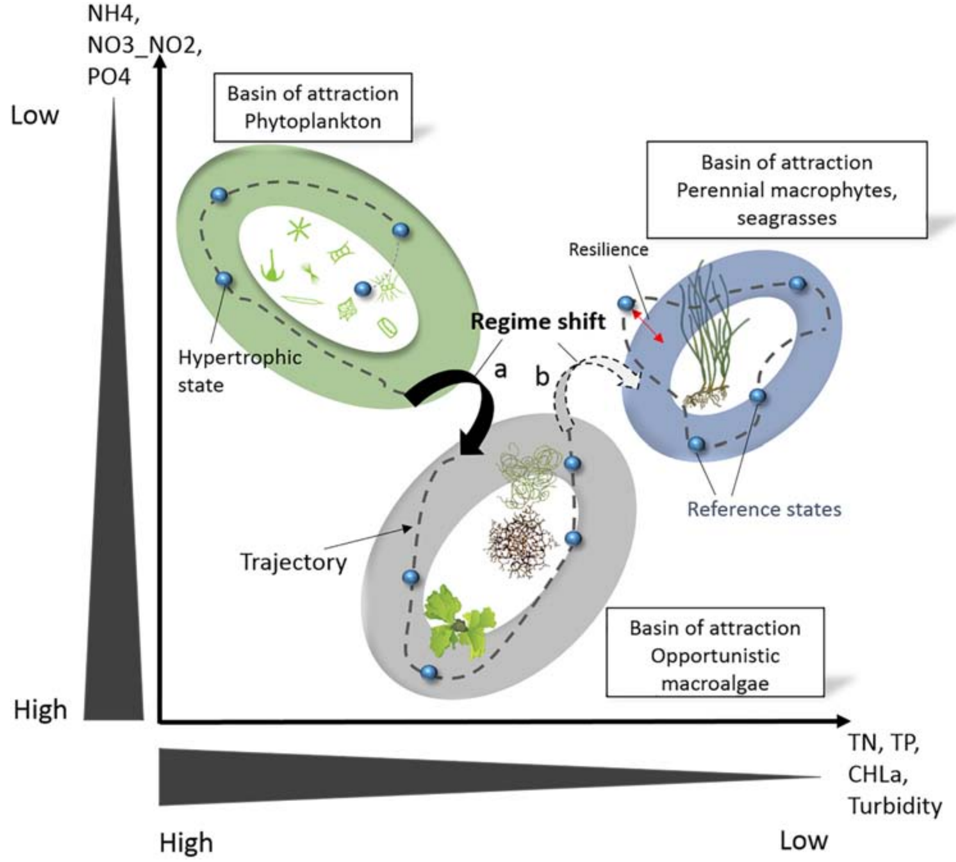


FIGURE 6 | Illustration of ecosystem states and regime shifts along oligotrophication trajectories in Mediterranean coastal lagoons. The ellipses represent the three basins of attraction that were identified, i.e., three ecosystem states dominated by (i) phytoplankton with bare non-vegetated sediments, (ii) opportunistic macroalgae, and (iii) seagrass and perennial macroalgae. The small blue spheres represent the different ecosystem states and the stippled lines their trajectory according their chronology. Small pictograms courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Creative Commons license, reproduced from Le Fur et al. (2019).

state dominated by seagrass and perennial macroalgae (Le Fur et al., 2019).

Interestingly, for primary producers, the oligotrophication trajectories in poly- and euhaline lagoons appear as the inverse of the eutrophication trajectories (cf. above, Schramm, 1999), with the exception of the transitional state occurring during eutrophication of angiosperms perishing under a high coverage of epiphytes. Again, during oligotrophication, opportunistic macroalgae, including *Ulva intestinalis* Linnaeus, 1753, *U. rigida*, *C. aerea*, and *Gracilaria* spp., occupy an intermediate domain between the two end members, i.e., ecosystem states dominated by (i) phytoplankton and (ii) seagrass and perennial macroalgae, at the hypertrophic and oligotrophic extremes, respectively. We have assumed that these three ecosystem states are the result of attraction basins reinforced by positive and negative feedback loops. Hence, these three attraction basins and the oligotrophication trajectories have been plotted graphically (**Figure 6**) and compared with the STATICO factor map (Le Fur et al., 2019). Despite representing the hypertrophic state, the attraction basin for phytoplankton-dominated systems is projected at low DIN and DIP levels, related to the high affinity uptake capacities of phytoplankton.

Sediment N and P

Figure 7 shows that the sediments of the oligotrophic lagoons La Palme and Ayrolle are characterized by low TP and low TN contents of approximately 7 and 50–80 mmol/kg, respectively. These values are roughly four times higher in the hypertrophic Méjean lagoon. The geometric mean regression shows for the poly- and euhaline lagoons a N/P molar ratio of 19.3, which is close to the Redfield ratio of 16. This suggests that during eutrophication, the sediments become enriched in N and P, probably largely due to the accumulation of organic matter. The regression line shows that on average 5.8 mmol/kg TP is predicted for TN = 0. Hence, even in the absence of organic matter, phosphorus is expected to be present, which can be explained by the presence of inorganic mineral forms like phosphoapatites and P sorbed on iron compounds. Søndergaard et al. (2003) stated that "*Internal P loading originates from a pool accumulated in the sediment at high external loading, and significant amounts of phosphorus in lake sediments may*

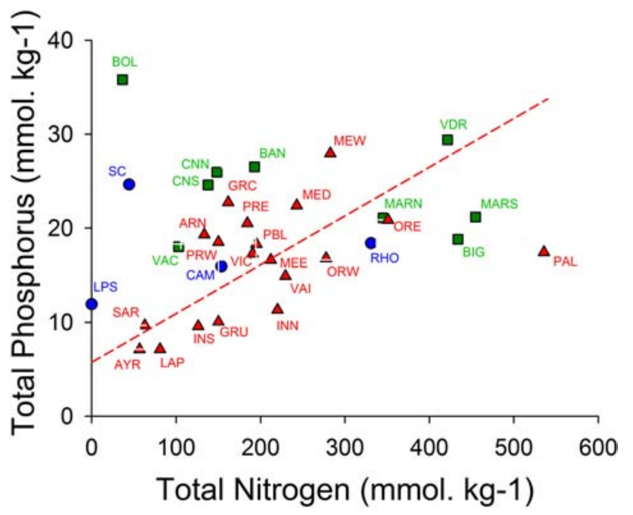


FIGURE 7 | Graph of total nitrogen (TN) and total phosphorus (TP) contents of the top 5 cm of the sediments expressed per dry weight (DW) of sediments. Oligohaline lagoons in blue circles, mesohaline lagoons in green squares and poly- and euhaline lagoons in red triangles (cf. **Figure 2**). A geometric mean regression was calculated for the poly- and euhaline lagoons and depicted as a broken red line (TP = 0.0519 × TN + 5.752 (mol · kg^{-1}), $r = 0.494$), corresponding to a N/P molar ratio of 19.27. Codes for sampling stations: AYR, Ayrolle; ARN, Arnel; BAN, Bagnas; PBL, Pierre Blanche; BIG, Biguglia; BOL, Bolmon; CAM, Campignol; CNN, CNS, Canet North and South stations, respectively; GRC, Grec; GRU, Gruissan; INN, Ingril Nord; INS, Ingril Sud; LAP, La Palme; LPS, La Palissade; MARN, La Marette; MED, Médard; MEE, MEW, Méjean, East and West stations, respectively; ORE, ORW, Or East and West stations, respectively; PAL, Palo; PRE, PRW, Prévost, East and West stations, respectively; RHO, Rhône de Saint Romans; SC, Scamandre; VAI, Vaïne; VDR, Vendres.

be bound to redox-sensitive iron compounds or fixed in more or less labile organic forms." In addition, the mineralization of the organic matter in the sediment provide inorganic N and P that could sustain a flux of DIN and DIP across the sediment-water interface, which represents thus another internal source for the water column.

Coastal Lagoons in the Habitats Directive and Links With WFD Approaches

The scientific literature about coastal lagoons in Europe comprises numerous studies on the implications of the WFD, but to our knowledge very few studies have assessed the consequences of its co-implementation with the Habitats and Birds Directives for these ecosystems. While the WFD explicitly links the WFD with the Habitats and Birds Directives (WFD, Annex VI) in common day practice, coastal lagoon managers in the EU are systematically confronted with co-implementation of WFD and Habitats Directive, in some cases even together with the Birds Directive.

Coastal lagoons are considered in the WFD as transitional water bodies (TWB) together with river mouth ecosystems (water bodies in estuaries and deltas). For the WFD application in the French Mediterranean water basin, the coastal lagoons are considered as a subcategory within TWB, i.e., Mediterranean lagoons, which are non-tidal or nano-tidal. Moreover, the "Comité de Bassin Rhône Méditerranée" decided in 2009 to exclude ephemeral coastal lagoons as well as permanent coastal lagoons smaller than 50 ha. The Habitats Directive recognizes coastal lagoon as a priority habitat 1150, which has been defined (European Commission DG Environment, 2013) as "*expanses of shallow coastal salt water, of varying salinity and water volume, wholly or partially separated from the sea by sand banks or shingle, or, less frequently, by rocks. Salinity may vary from brackish water to hypersalinity depending on rainfall, evaporation and through the addition of fresh seawater from storms, temporary flooding of the sea in winter or tidal exchange. With or without vegetation from Ruppietea maritimae, Potametea, Zosteretea, or Charetea (CORINE 91: 23.21 or 23.22).*" The latter are vegetation units defined by phytosociology. Hence, the coastal lagoons listed in **Figure 2** all belong to the priority habitat 1150 of the Habitats directive and have been included in Natura 2000 sites. In France, many temporal saline ponds along the Mediterranean coastline have also been included in the priority habitat 1150. In some cases, the temporal ponds are coastal lagoons according the definition of Kjerfve (1994), i.e., with a temporal inlet connecting with the sea. In such cases, during summer the inlet closes and the lagoon dries out completely. However, many of the temporal ponds that function as endorheic systems without direct connection to the sea, have also been included in habitat 1150. Nonetheless, such an approach is fully acceptable according the Interpretation Manual of European Union Habitats – EUR28 (European Commission DG Environment, 2013) as "*the salt basins and salt ponds may also be considered as lagoons, providing they had their origin on a transformed natural old lagoon or on a saltmarsh, and are characterized by a minor impact from exploitation.*" Many of the former salt-ponds in abandoned Salinas typically represent such a case (De Wit et al., 2019). In the PLC two Salinas have been abandoned, i.e., the Salins de Frontignan and Villeneuve, which have been included as peripheral wetlands in the Natura 2000 site of the "etangs Palavasiens" (FR9101410). In the Mediterranean climate, these temporal ponds are typically filled with water from rain and run-off after heavy rainfall in autumn and tend to dry out during late spring or the summer period. The salinity of the ephemeral water column, which originates in the endorheic systems from dissolving the salt in the soils, varies strongly during the year. The aquatic plants in these ephemeral ponds comprise species of the association of the angiosperm *Althenia filiformis* Petit, 1928 and the charophyte *Lamprothamnium papulosum* (K. Wallroth) J. Groves, 1916.

The Natura 2000 network is a network of protected areas designated according the Habitats directive [Site of Community Interest (SCI)] and the Birds Directive [Special Protection Areas (SPA)]. The member states have an obligation to report on the conservation status of habitats within Natura 2000 sites. It is a major challenge to combine the management and surveillance monitoring for the "ecological status" according the WFD with that for the "conservation status" of habitats and species according the Habitats Directive and extent these to the temporal lagoons.

Communication With Coastal Lagoon Stakeholders, Their Values, Perceptions, and Opinions

The normative approach of the WFD is based on the use of EQRs calculated for different biological quality elements (BQE, e.g., phytoplankton, macrophytes). Based on the EQR values classes are attributed using the qualifications Bad, Poor, Moderate, Good, and High, based on the deviation from the reference state corresponding to conditions of minimal anthropogenic impact. However, an aggregated qualification is attributed based on the principle "one out all out," which means that the BQE with the lowest EQR determines the overall EQR and quality class, thus overruling all the others.

These aggregated qualifications are often restituted to the managers, policy makers and general public by using a color code. Accordingly, **Figure 8** presents the color coding for the ecological status of the water column in the PLC restituted every year by the Lagoon monitoring network "RSL" (IFREMER, 2014).

Figure 8 shows that in general the water quality has improved from 2000 to 2013 for the lagoons of the PLC, although in 2013 only two (Ingril Nord and Ingril Sud) of eight lagoons had achieved "good" ecological status for the water column, while the rest was reported as poor or moderate. Social representation of water quality by the local populations was identified and compared to the water quality assessment carried out according to the French surveillance monitoring system (Audouit et al., 2019). More than half of the interviewees in the PLC considered water quality as moderate (40%) or good (26%). In 2013, only Ingril Nord and Ingril Sud lagoons were in a good status. Hence, social representation gave a higher score than the surveillance monitoring. Partly this difference could be attributed to the conservative scoring used in the WFD based on the principle "one out all out" (Audouit et al., 2019). Nevertheless, both the surveillance monitoring and the social perception of water quality explain a perception in society of the failure of achieving WFD goals for a large number of coastal lagoons. Interestingly, the social representation of the biodiversity of the coastal lagoons was much more positive than that of water quality, with 40% valuing as high and 40% valuing as good for the lagoons of the PLC. In general, interviewees judged that the current situation was better

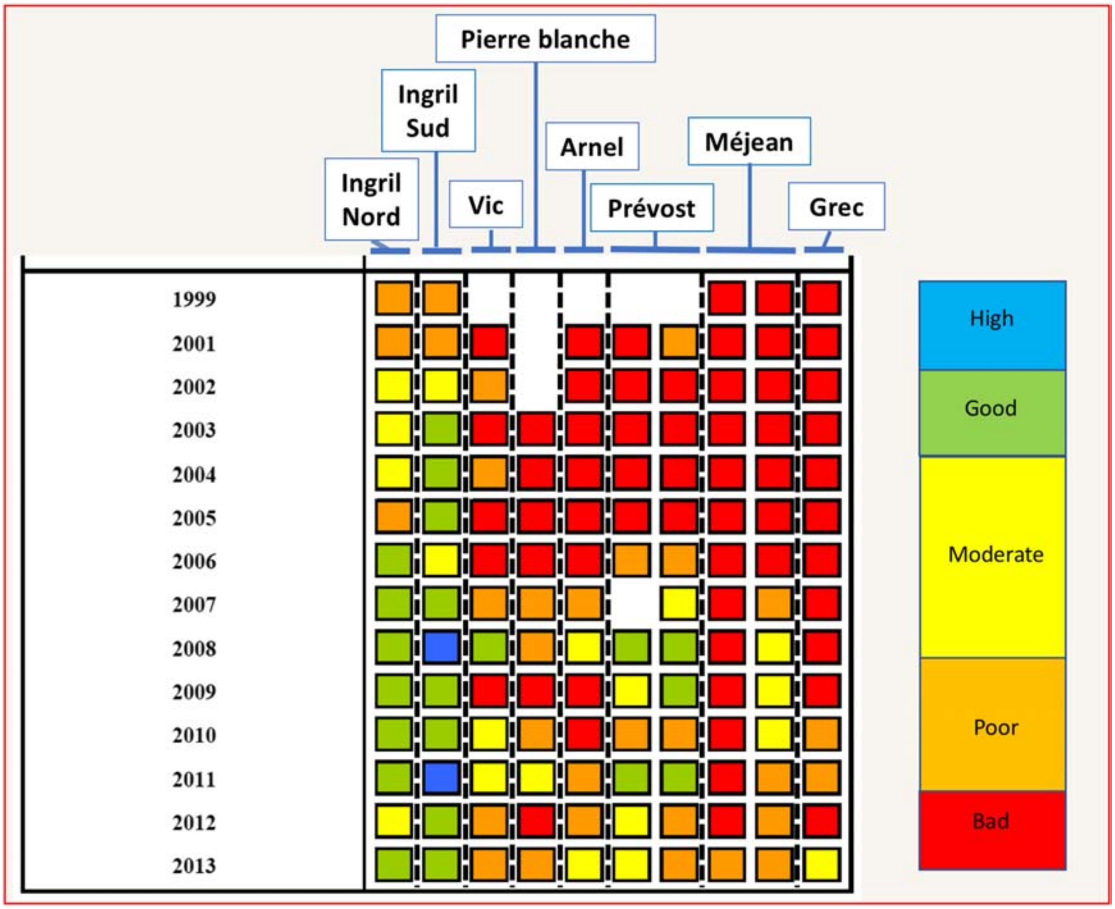


FIGURE 8 | Color coding restitution of water quality by the Lagoon Monitoring Network for the lagoons of the PLC from 1999–2013 (Figure designed using Tableau 11.2, page 175 of IFREMER, 2014, Courtesy Ifremer).

than in the past (Audouit et al., 2019), meaning that some positive impact of public policy and management has been perceived by the general public.

The lack of full restoration of water quality and of other aspects for qualifying as good ecosystem state (e.g., benthic macrophytes) raised the question whether the reduction of the nutrient loading should not be combined with additional eco-engineering measures (cf. **Figures 3, 4**, active restoration). Therefore, the hypertrophic Méjean and the mesotrophic Ingril Sud lagoons were compared. While it was considered that Ingril Sud lagoon was already on a trajectory for spontaneous recovery after the nutrient reduction (passive restoration), additional measures for active restoration were considered for Méjean lagoon. These measures comprise a first phase based on collection of macroalgae and their exportation from the lagoon followed by a second phase based on planting marine angiosperms. Based on these suggestions, four scenarios were defined for Méjean lagoon, ranging from passive to a high level of active ecological restoration and questionnaires were designed for residents and tourists and face-to-face interviews were performed. More than 85% of both residents and tourists expressed that they have a positive perception of the ecological and societal importance of coastal lagoons and of their ecological restoration. A willingness to pay for active restoration (i.e., additional costs for the eco-engineering measures on top of the 150 Million€ engaged for the improvement of the water quality, see above) was expressed by 70 and 60% of the resident and tourists' respondents, respectively. The residents were willing to pay each about 25€ a year for the highest level of ecological restoration and willing to allocate a much smaller amount of about 5€ for the improvement of the infrastructure for visiting the site (De Wit et al., 2017).

The study of how stakeholders perceive ecosystem services of coastal lagoons and how they value them it is important to understand the benefits people obtain from these ecosystems and get insights on their expectations for the future. Hence, such an assessment of ecosystem services is very instrumental for ecological restoration projects to assess whether the project corresponds to the expectations and perceptions of the stakeholders. Monetary valuations of ecosystem services may present an obvious advantage for ecological restoration projects as it allows a straightforward cost-benefit analysis (De Groot et al., 2013; De Wit et al., 2017). Nevertheless, monetary approaches can be problematic when working with stakeholders as most of the ecosystem services provided by the coastal lagoons areas are non-market services and, stakeholders in general, tend to reject the monetary approaches. Therefore, we turned to non-monetary approaches and used the Q-method (Sy et al., 2018), which is based on a serious card game that allows to capture levels of consensus and divergence among participants. Thirty-one ecosystem services provided by the lagoons were selected by a focus group (see **Table 2**) and highly involved stakeholders were asked to rank these ecosystem services. The highly involved stakeholders were characterized by their strong involvement in following the management process and many of them were members of the Natura 2000 committee. They were grouped in seven categories, i.e., local government, private sector, NGOs, scientists, public and para-public sectors, managers, and local residents. Statistical analysis was improved by bootstrapping in order to obtain additional and more detailed measures of variability and thus help to better understand the data and the outcomes. Accordingly, three groups of these stakeholders, each sharing similar point of views the group, were extracted (Sy et al., 2018). Here, we complement this study with new data obtained through citizen workshops for local citizens (see **Supplementary Table S2** for their sociodemographic composition). These local citizens can thus be considered as less-involved stakeholders (e.g., García-Nieto et al., 2015).

Forty-three citizens actively participated in these citizen workshops and completed the Q-method ranking of the same 31 ecosystem services (**Table 2**), ranked earlier by the highly involved stakeholders (Sy et al., 2018). The analyses again extracted three different groups which are listed in **Table 3** with their most salient results (more detail in **Supplementary Figures S1, S2**). All three groups attributed high level of priority to regulation and maintenance services. Consensus among these citizens was particularly striking for providing protection against flooding and other extreme natural events. Biodiversity and nursery, water purification capacity and microclimate regulation were among the top of priorities for two or one of the groups, but the overlapping variability of the bootstrapped estimates indicated still a certain degree of consensus of their importance. There was also consensus on the most unimportant side, which was most likely based on mere rejection, i.e., for camping. Two of the three groups also seemed to reject waterfowl hunting. Group #1, which gave an absolute priority to regulation and maintenance services, was quite similar to the preferences of group #2 of the highly involved stakeholders of the PLC, characterized as "environmental and territorial approach" (Sy et al., 2018). Group #2 had a clearly naturalist profile, giving among the regulating services the highest priority to biodiversity and nursery services with strong preferences for cultural services as bird watching and esthetic value of species and habitats. This result was rather similar to group #1's preferences ("environmental and hedonic vision" identified for the highly involved stakeholders (Sy et al., 2018). The hedonist aspect is also reflected by the importance group #2 attached to the sentiment of relaxation. A very small group #3 comprising only four persons, among which three from the eastern part of the PLC, was atypical, because it valued two provisioning services very high, i.e., (i) shellfish farming, developed in the Prévost lagoon and (ii) commercial inland navigation, related to traffic on the Rhône-to-Sète canal running through the lagoon complex. This group was hardly interested in naturalistic aspects, although it valued the esthetic value of the landscape very high. Perhaps this is related to a sensitivity for heritage aspects.

GENERAL DISCUSSION AND SYNTHESIS

Restoration ecology of coastal lagoons should integrate solid knowledge of the biodiversity of the communities and ecosystem functioning. But, as it studies a human activity, i.e., ecological restoration, we argue that it should also take into account

TABLE 2 | Modified from Sy et al. (2018).

ES category	ES subcategory	Ecosystem service	General definition
Provisioning services	Food provision	Shellfish resources Biomass for grazing Crops Shellfish farming Fish resources ***Fish farming***	The provision of biomass for human consumption and the conditions to grow it. It mostly relates to cropping, animal husbandry, and fisheries.
	Water provision	Commercial inland navigation	The provision of water for human consumption and for other uses.
	Biotic materials and biofuels	Non-food products	The provision of biomass or biotic elements for non-food purposes.
Regulation and maintenance services	Water purification	Purification capacity	Biochemical and physicochemical processes involved in the removal of wastes and pollutants from the aquatic environment.
		Wastes decomposition	
	Coastal protection	Flooding and other extreme events regulation and protection	Protection against floods, droughts, hurricanes, and other extreme events. Also, erosion prevention in the coast.
		Banks reinforcement	
	Climate regulation	Microclimate regulation	Regulation of greenhouse and climate active gases. The most common proxies are the uptake, storage, and sequestration of carbon dioxide.
	Life cycle maintenance	Nursery and biodiversity maintenance	Biological and physical support to facilitate the healthy and diverse reproduction of species.
Cultural services	Symbolic and esthetic values	Esthetic value of landscapes Local identity Esthetic value of habitats or species Historical sites	Exaltation of senses and emotions by landscapes, habitats, or species.
	Recreation and tourism	Recreational boat navigation Non-motorized water sports Bird watching Cycling Horse riding Waterfowl hunting Sentiment of relaxation Camping Recreational hiking and walking Recreational fishing	Opportunities that the natural environment provide for relaxation and amusement.
	Cognitive effects	Artistic inspiration Research opportunity Environmental education	Trigger of mental processes like knowing, developing, perceiving, or being aware resulting from natural landscapes or living organisms.

The Ecosystem Services (ESs) supplied by the coastal lagoons of the Palavas lagoon complex have been categorized according to the classification designed for coastal and marine ESs by Liquete et al. (2013), which has recently been included in CICES version 5.1 (Haines-Young and Potschin, 2018). These 31 ESs (Q-set) were ranked according Q methodology by both the highly-involved stakeholders (Sy et al., 2018) and the local citizens in citizens' workshops. The Ecosystem service in italics, i.e., Fish farming, is currently not exploited in these lagoons.

the pertinent aspects of legislation, as well as socio-economic aspects concerning perceptions by local stakeholders and their expectations for the future desired state of the ecosystems. Hence, restoration ecology, in addition to sound ecological knowledge, thus has to establish multidisciplinary collaborations with social sciences. In this study, we analyzed by such an integrated multidisciplinary approach, the practice of ecological restoration to combat eutrophication, which has been achieved by reducing the external nutrient loading to shallow Mediterranean coastal lagoons in South France. This action has resulted in oligotrophication of formerly eutrophied coastal lagoons.

When the reduction of nutrient loadings to shallow coastal lagoons was initiated in the early 2000s through the WFD, little scientific knowledge was available for predicting the ecosystem trajectories of shallow coastal lagoons during oligotrophication and ideas were inspired by the experience obtained for the oligotrophication of shallow freshwater lakes that had been initiated two decades earlier. The experience in South France was followed by intensive surveillance monitoring (RSL) and

TABLE 3 | Most salient results from analyzing the Q-sorts of the 43 participants in citizen workshops.

		Group #1	**Group #2**	**Group #3**	**Bootstrap results**
		Environmental and territorial approach	**Naturalist**	**Environmental utilitarian – local identity**	**Groups with overlapping variability, *all three groups different $p < 0.05$**
Most important (score type: + + = 4 or + = 3)					
Regulating and maintenance	Protection against flooding	++	+	+	1, 2, 3
	Biodiversity + nursery	+	++		1, 2, 3
	Purification capacity	++		++	1, 2, 3
	Waste decomposition	+			2, 3
	Microclimate regulation	+			1, 2, 3
Cultural services	Sentiment of relaxation		++		1, 2, 3
	Bird watching		+		1, 3
	Esthetic value species and habitats		+		*
	Esthetic value of landscape			++	*
Provisioning	Commercial inland navigation			+	*
	Shellfish farming			+	*
Most unimportant (score type: −− = −4)					
Cultural services	Camping	−−	−−	−−	1, 2, 3
	Waterfowl hunting	−−	−−		1, 2, 3
	Esthetic value species and habitats			−−	*
Composition of the groups					
Home of resident	Number of respondents				
Eastern part of PLC	10	4	3	3	
Western part of PLC	17	11	6	0	
Montpellier	11	6	5	0	
Others	5	3	1	1	
Total – number	43	24	15	4	
Total		56%	35%	9%	

Statistical analysis was improved by bootstrapping and groups with overlapping variability for a given ES are indicated. The analysis meaningfully extracted three factors allowing to identify three corresponding groups. The representative Q-sorts for the different groups are provided in ***Supplementary Figure S2****. This table resumes the services selected for most important and less important and provides the geographic position of the home address of the respondents.*

PLC, Palavas lagoon complex; eastern part PLC, municipalities of Pérols, Palavas, Lattes, Villeneuve-les-Maguelone; western part of PLC, municipalities of Mireval, Vic-la-Gardiole, Frontignan; Others, other municipalities close to the lagoon complex.

scientific studies (cf. **Table 1**) focused on improving the understanding of the eutrophication (Souchu et al., 2010, Bec et al., 2011; Le Fur et al., 2018) and of oligotrophication trajectories (Leruste et al., 2016; Pasqualini et al., 2017; Derolez et al., 2019; Le Fur et al., 2019). From this we have obtained a large body of understanding and empirical knowledge to guide the ecological restoration practice. We hereby summarize the main findings. Coastal lagoons show similar attractors at both extremes along the eutrophication gradient as described for freshwater lakes (cf. Scheffer, 2001). At the oligotrophic side, shallow poly- and euhaline lagoons show transparent water and are home to meadows of the marine angiosperms, *Z. noltei*, *Ruppia* spp. and *C. nodosa* together with some slow-growing perennial macroalgae as e.g., *A. acetabulum* (Le Fur et al., 2018). At the hypertrophic extreme, shallow poly- and euhaline lagoons show turbid water with dense phytoplankton (Bec et al., 2011; Leruste et al., 2016). However, in contrast to freshwater lakes, massive blooming of opportunistic macroalgae represents a third ecosystem state in shallow coastal lagoons (Valiela et al., 1997; De Wit et al., 2001; Viaroli et al., 2008; Le Fur et al., 2018, 2019) in between both extremes. The importance of this third attractor, implies that the attractive bistability scheme proposed by Scheffer for freshwater lakes does not apply straightforwardly for coastal lagoons. Nevertheless, for the poly- and euhaline lagoons, oligotrophication trajectories from hypertrophy to oligotrophy have now been described as a sequence from (i) phytoplankton with bare non-vegetated sediments, (ii) opportunistic macroalgae, and (iii) seagrass and perennial macroalgae, punctuated by regime shifts between the ecosystem states (Le Fur et al., 2019). At present, in these systems, it remains unclear whether domains of multiple stable states occur for the eutrophication – oligotrophication pathways or whether all the regime-shifts represent steep but continuous shifts in equilibrium states. The shift from the phytoplankton-dominated state to the macroalgal-dominated state occurs very quickly upon reduction of the external nutrient loading, i.e., within one or a couple of years (Le Fur et al., 2019), and it has been argued that water-column showed little hysteresis (Derolez et al., 2019). In contrast, ten years of oligotrophication of the hypertrophic lagoons did not yet result in the second regime shift from a macroalgal-dominated state into the SAV state (Le Fur et al., 2019), suggesting strong hysteresis for this final part of the trajectory. Such hysteresis may in part be explained by a time lag to re-establish the positive feedbacks (Maxwell et al., 2017) and mutualistic networks (Van der Geest et al., 2020) in the seagrass systems. Another source of hysteresis during oligotrophication may be due to time lags caused by internal loading from the biogeochemical sinks for nutrients accumulated during the eutrophication phase. Indeed, the poly- and euhaline lagoons showed concomitant increase of N and P with increasing eutrophication (see **Figure 7**) most likely related to the increase of the organic matter content (average N/P molar ratio of 19.3, which is close to the Redfield ratio). Benthic fluxes of N and P need to be measured (Ouisse et al., 2013) to provide more information on the role of internal loading in delaying oligotrophication. Inertia caused by internal loadings have also been described for the oligotrophication of shallow freshwater lakes, although the focus has been on P alone (Jeppesen et al., 2002), while for the lagoons we show that both N and P play a role.

We can conclude that scientific knowledge and empirical observations are nowadays operational for providing guidance for ecological restoration of the poly- and euhaline Mediterranean coastal lagoons. Nevertheless, insufficient knowledge is still available for the oligo- and mesohaline lagoons. The specific behavior of the aquatic angiosperms forming floating leaves (*S. pectinata* in oligohaline and *Ruppia* sp. in mesohaline lagoons) has to be taken into account. Another source of problem is the fact that for hypertrophic poly- and euhaline lagoons it is still not possible to predict whether a complete oligotrophication trajectory will occur and how long it may take. Many of these formerly hypertrophic lagoons appear to remain stuck in the macroalgal stage, even after 10 years of oligotrophication. This raises the question whether in such cases, the ecological restoration should become an active approach by combining the nutrient reduction with the active planting and seeding of the angiosperms (Orth et al., 2012; De Wit et al., 2017). Currently, such an approach is undertaken in Venice lagoon (Sfriso et al., 2019).

Ecological restoration is a human activity that is clearly identified as a Response in the DPSIR framework (see **Figure 3**). The link between DPSIR and ecological restoration has been invoked in studies focusing on the ecological restoration of rivers (Song and Frostell, 2012; Lalande et al., 2014) although their focus has been more upstream underscoring the importance of identifying drivers and pressures for designing ecological restoration rather than analyzing what is actually targeted by the different practices of ecological restoration. Collectively, these studies together with our study highlight the paramount importance of clearly identifying the pressures on aquatic ecosystems and that ecological restoration should target a reduction of these pressures in the first place. Hence improved sanitation and appropriate management of non-point sources of nutrient in watersheds is paramount for the ecological restoration of eutrophied lagoons. Ecological restoration measures only targeting the state of the ecosystems are not efficient without acting on the pressures.

Surveillance monitoring is a key aspect to follow the state of the ecosystem (S in the DPSIR). The principle "one out all out" was designed for surveillance monitoring of the ecological status of aquatic ecosystems in the WFD, particularly to check if a system is and remains in better than moderate, i.e., good or high conditions. The application of this principle is probably a reason why (i) the perception of local populations is more optimistic than that of WFD, (ii) the assessment systems have been judged by 8% of the interviewed managers as "*overly strict to define success*" (Carvalho et al., 2019), and (iii) it appears as particularly problematic for assessing the impact of specific actions as ecological restoration. For example, it does not identify correctly if variables move in the right direction (the aggregated score only moves until the worst valued has also moved in the positive direction). Thus, the surveillance monitoring that has been used in the frame of the WFD is very conservative and does not give a sufficient indication of minor to major advances in ecological status. Hence, it is important to introduce specific action monitoring for following the impact of ecological restoration that should be designed to detect more responsively (i) whether the ecosystem state moves in the right direction, (ii) identify possible transient states, and (iii) assess whether the different targets for the ecological restoration project have been achieved.

For the conservation and management of coastal lagoons, there is a clear need to study the juxtaposition particularly of the WFD and Habitats Directives, as well as the Birds Directive in some cases. Hence, complementarities and possible incongruences between these Directives should be identified and solutions proposed. For protected areas, the WFD approach has clear advantages with respect to more conventional nature conservation approaches, because it adopts the concept of the aquatic continuum, underscores importance of land-use in the watershed for ecological processes in the lagoon, explicitly considers chemical pollutants and provides a framework that accommodates the concepts of restoration ecology. This approach works well for addressing water quality and the aquatic biota. However, the WFD does not consider the terrestrial habitats as the coastal barrier with beaches and dune systems, the salt marshes and wetlands in its immediate surroundings, as part of the lagoon ecosystem. Moreover, in addition to nutrient reduction targeting oligotrophication, ecological restoration in coastal lagoons includes an array of different actions, e.g., including restoring the freshwater-salt water ecoclines and ecotones through hydrological measures

(Yáñez-Arancibia et al., 2013; Feola et al., 2018), restoration of dune vegetation on the coastal barrier (Buisson et al., 2014) and the restoration of meadows of submerged marine angiosperms (Sfriso et al., 2019). In these cases, the Natura 2000 network offers workable sites comprising different habitats to pursue such management actions and the Life program a funding mechanism for ecological restoration demonstration projects. Hence, the ecological restoration projects that are being developed in coastal lagoon territories have to adapt to the Habitats Directive and for the aquatic compartment also to the WFD. This may represent a challenge as in the Habitats Directive, the assessment of the conservation status of priority habitats is very much rooted in phytosociological approaches, and the possibilities offered by more modern ecological approaches like restoration ecology need to be included more explicitly. While, the WFD promotes a highly integrated vision and is explicitly linked to the Habitats Directive, the differences of approaches and implementation by different public bodies in member states can result in rather sectorial approaches. Hence, WFD is not fully congruent with the Habitats Directive as a consequence of different objectives and concepts. Both have their advantages and inconveniences and an intelligent application of both should be based on integrative non-sectorial application of national legislation and pragmatic management. The active restoration of angiosperm meadows and ecological restoration of aquatic connectivity are examples where co-implementation of both Directives is particularly beneficial. We also recommend the integration of some of the valuable concepts of the WFD into the conservation management of temporal and smaller (i.e., in France <50 ha) lagoons requested by the Habitats Directive.

Knowledge of social representation of the ecosystem and perceptions of management actions are of paramount importance for managers engaged in ecological restoration projects. In fact, public understanding and appreciation lead to more legitimate and accepted public policies such as coastal lagoon ecological restoration projects. In contrast, a low level of congruency will imply a high risk of conflict for implementing such policies. Nevertheless, the results of our studies are encouraging as the ecological restoration practice is highly valued by human populations and stakeholders. Stakeholders have a positive perception of the ecological and societal importance of coastal lagoons and of the need of their ecological restoration, i.e., more than 85% of both residents and tourists close to Montpellier expressed this point of view (De Wit et al., 2017). However, the social representation of the lagoons is more focused on biodiversity aspects than on water quality *sensu stricto* (Audouit et al., 2019). There is consensus among both the highly involved stakeholders (Sy et al., 2018) and among the local residents, who participated in our citizen workshops, on giving highest importance to the regulation and maintenance ecosystem services. While primarily characterized by the consensus on the role of regulating services, stakeholder profile groups' preferences mainly varied based on cultural services and more rarely on provisioning services. Many stakeholders have a sort of collective appreciation of the importance of these regulation and maintenance services for the local surrounding of the lagoons (territorial approach). Other enjoyments as a personal experience provided by contemplating nature, are also important wishes as e.g., the coastal lagoons should contribute to the sentiment of relaxation, the esthetics of species and landscapes, and possibilities for birdwatching. Some groups showing a more naturalist type of profile (citizens) compared to others with a more environmentalist profile (highly involved stakeholders). These studies allow to conclude that coastal lagoons ecosystem services are very important for the stakeholders and that public policies aiming at the ecological restoration of these fragile ecosystems may count on public support.

NOMENCLATURE

Taxonomic nomenclature followed AlgaeBase (Guiry and Guiry, 2016) and World Register of Marine Species (WoRMS Editorial Board, 2016).

DATA AVAILABILITY STATEMENT

This article was based on review of the ecological publications listed in **Table 1** and social science data (publications cited in the text). The ecological monitoring data are available in the French data bases "Banque Hydro" (http://www.hydro.eaufrance.fr/), Naïade (http://www.naiades.eaufrance.fr/acces-donnees), and "Surval," which among others hosts the data of the Réseau Suivi Lagunaire (RSL) monitoring program (Ifremer, https://wwz.ifremer.fr/surval/). Data of the citizens' workshop are available in **Supplementary Material**.

ETHICS STATEMENT

The citizen workshop was based on voluntary participation and the data have been treated anonymously in compliance with the EU General Data Protection Regulation (GDPR).

AUTHOR CONTRIBUTIONS

AL, IL, MS, BB, VO, VD, and RD contributed to the field and laboratory work, and ecological data compilation and interpretation. VD hold responsibilities for the Lagoon Monitoring Network "RSL," and Water Framework Directive (WFD) monitoring programs. MS, HR-V, and RD organized the citizen workshops. MS analyzed the data. BB, VO, HR-V, and RD contributed to supervising the Ph.D. thesis of AL, IL, and MS. RD wrote this publication with the help of all co-authors.

FUNDING

Ecological data used in this article have been collected through (1) the Lagoon Monitoring Network (RSL), financed by Région LR, AERMC, Ifremer, (2) the Water Framework Directive (WFD) financed by AERMC and Ifremer, (3) the DRIIHM LabEx (ANR-11-LABX-0010_DRIIHM), "Device for Interdisciplinary Research on human-environments Interactions" within the framework of the Human-environment observatory "Mediterranean coastline," (4) Ph.D. studies at the University of Montpellier, and (5) additional studies (PNEC, INTERREG II/PNOC, and RLC programs). The DRIIHM LabEx supported the studies with the citizens' workshops. The Laboratory for Excellence project (DRIIHM LabEx) was supported by the program "Investment in the future" (ANR). AL, IL, and MS were supported by Ph.D. fellowships by the Doctoral School in Montpellier, Ifremer and AERMC, and the DRIIHM Labex, respectively.

ACKNOWLEDGMENTS

Philippe Souchu, Thierry Laugier, Nathalie Malet, Annie Fiandrino, Dominique Munaron, Jocelyne Oheix, Martine Fortuné, Grégoire Messiaen, Elise Hatey, and Michel Lauret are thanked for their major contributions to the Lagoon Monitoring Network "RSL." The staff of the Ifremer LER laboratories (LER "Languedoc Roussillon" and LER "Provence Azur Corse") are thanked for their contributions to field work and laboratory analysis. The Cépralmar provided logistic help for the RSL. Many coastal lagoon managers in South France are thanked for their interest and contribution to discussions. We thank the reviewers for their constructive comments and suggestions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00108/full#supplementary-material

REFERENCES

Audouit, Ch, Pasqualini, V., De Wit, R., Flanquart, H., Deboudt, Ph, and Rufin-Soler, C. (2019). Comparing social representation of water quality in coastal lagoons with normative use of ecological indicators. *Mar. Polic.* 101, 137–146. doi: 10.1016/j.marpol.2017.08.023

Bec, B., Collos, Y., Souchu, P., Vaquer, A., Lautier, J., Fiandrino, A., et al. (2011). Distribution of picophytoplankton and nanophytoplankton along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. *Aqua. Microb. Ecol.* 63, 29–45. doi: 10.3354/ame01480

Beisner, B. E., Haydon, D. T., and Cuddington, K. (2003). Alternative stable states in ecology. *Front. Ecol. Environ.* 1:376–382.

Buisson, E., Bravet, P., Mieusset, J., Baillot, N., Dubreucq, C., Sadonès, L., et al. (2014). Plant communities of a coastal lagoon foredune: definition of the reference and restoration after compaction. *Acta Bot. Gall.* 161, 277–286. doi: 10.1080/12538078.2014.919875

Carvalho, L., Mackay, E. B., Cardoso, A. C., Baattrup-Pedersen, A., Birk, S., Blackstock, K. L., et al. (2019). Protecting and restoring Europe's waters: an analysis of the future development needs of the water framework directive. *Sci. Total Environ.* 658, 1228–1238. doi: 10.1016/j.scitotenv.2018.12.255

Clewell, A. F., and Aronson, J. (2013). *Ecological Restoration, Principles, Values, and Structure of an Emerging Profession*. 2nd Edn. Washington, DC: Island Press.

Covelli, S. (2012). The MIRACLE Project: an integrated approach to understanding biogeochemical cycling of mercury and its relationship with lagoon clam farming. *Estuar. Coast. Shelf Sci.* 113, 1–6. doi: 10.1016/j.ecss.2012.08.011

Cunha, A. H., Marbá, N., Van Katwijk, M., Pickerell, C., Henriques, M., Bernard, G., et al. (2012). Changing paradigms in seagrass restoration. *Restor. Ecol.* 20, 427–430. doi: 10.1111/j.1526-100x.2012.00878.x

De Groot, R., Blignaut, J., Van der Ploeg, S., Aronson, J., Elmqvist, T., and Farley, J. (2013). Benefits of investing in ecosystem restoration. *Conserv. Biol.* 27, 1286–1293. doi: 10.111/cobi.12158

De Wit, R. (2011). "Biodiversity of coastal lagoon ecosystems and their vulnerability to global change," in *Ecosystems Biodiversity*, eds O. Grillo and G. Venore (London: InTech Open Access Publisher), 29–40.

De Wit, R., Rey-Valette, H., Balavoine, J., Ouisse, V., and Lifran, R. (2017). Ecological restoration of coastal lagoons; prediction of ecological trajectories and economic valuation. *Aqua. Conserv.* 27, 137–157. doi: 10.1002/aqc.2601

De Wit, R., Stal, L. J., Lomstein, B. A., Herbert, R. A., Van Gemerden, H., Viaroli, P., et al. (2001). ROBUST: The ROle of BUffering capacities in STabilising coastal lagoon ecosystems. *Cont. Shelf Res.* 21, 2021–2041.

De Wit, R., Vincent, A., Foulc, L., Klesczewski, M., Scher, O., Loste, C., et al. (2019). Seventy-year chronology of Salinas in southern France: coastal surfaces managed for salt production and conservation issues for abandoned sites. *J. Nat. Conserv.* 49, 95–107. doi: 10.1016/j.jnc.2019.03.003

Derolez, V., Bec, B., Munaron, D., Fiandrino, A., Pete, R., Simier, M., et al. (2019). Recovery trajectories following the reduction of urban nutrient inputs along the eutrophication gradient in French Mediterranean lagoons. *Ocean Coast. Manag.* 171, 1–10. doi: 10.1016/j.ocecoaman.2019.01.012

Dolbeth, M., Stålnacke, P., Alves, F. L., Sousa, L. P., Gooch, G. D., Khokhlov, V., et al. (2016). An integrated Pan-European perspective on coastal Lagoons management through a mosaic-DPSIR approach. *Sci. Rep.* 6:19400. doi: 10.1038/srep19400

EU Birds Directive (2009). *Directive 2009/147/EC of the European Parliament and of the Council on the conservation of wild birds (the first version of this Directive was adopted in 1979 as Directive 79/409/EEC that was amended in 2009)*. Brussels: EU.

EU Habitats Directive (1992). *Directive 92/43/EEC of the European Parliament and of the Council on the Conservation of Natural Habitats and of Wild Fauna and Flora*. Available online at: http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm (accessed February 26, 2020).

EU Water Framework Directive (2000). *Directive 2000/60/EC of the European Parliament and of the Council Establishing a Framework for the Community Action in the Field of Water Policy*. Available online at: http://ec.europa.eu/environment/water/water-framework/ (accessed February 26, 2020).

European Commission DG Environment (2013). *The Interpretation Manual of European Union Habitats - EUR28*. Available online at: http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf (accessed February 26, 2020).

European Environment Agency (1999). *Technical Report No 25, Environmental Indicators: Typology and Overview*. Copenhague: European Environment Agency.

Feola, A., Bonometto, A., Ponis, E., Cacciatore, F., Oselladore, F., Matticchio, B., et al. (2018). *LIFE LAGOON REFRESH. Ecological restoration in Venice Lagoon (Italy): Concrete Actions Supported by Numerical Modeling and Stakeholder Involvement*. Available online at: http://www.lifelagoonrefresh.eu/file/pubblicazioni/COWM_2018_Extendedabstract.pdf (accessed February 26, 2020).

García-Nieto, A. P., Quintas-Soriano, C., García-Llorente, M., Paloma, I., Montes, C., and Martín-López, B. (2015). Collaborative mapping of ecosystem services : the role of stakeholders' profiles. *Ecosyst. Serv.* 13, 141–152. doi: 10.1016/j.ecoser.2014.11.006

Guiry, M. D., and Guiry, G. M. (2016). *AlgaeBase. World-wide electronic publication*. Galway: National University of Ireland.

Gulati, R. D., and Van Donk, E. (2002). Lakes in the Netherlands, their origin, eutrophication and restoration: state-of-the-art review. *Hydrobiologia* 478, 73–106. doi: 10.1007/978-94-017-1335-1_5

Haines-Young, R., and Potschin, M. B. (2018). *Common International Classification of Ecosystem Services (CICES) V5.1 and Guidance on the Application of the Revised Structure*. Brussel: European Environment Agency.

IFREMER (2014). *Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2013*. Issy-les-Moulineaux: IFREMER.

Jeppesen, E., Jensen, J. P., and Søndergaard, M. (2002). Response of phytoplankton, zooplankton, and fish to re-oligotrophication: an 11 year study of 23 Danish lakes 31-43. *Ecosyst. Health Manag.* 5, 31–43. doi: 10.1080/14634980260199945

Jeppesen, E., Søndergaard, M., Jensen, J. P., Havens, K. E., Anneville, O., Carvalho, L., et al. (2005). Lake responses to reduced nutrient loading—an analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.* 50, 1747–1771. doi: 10.1111/j.1365-2427.2005.01415.x

Kjerfve, B. (1994). "Coastal lagoons," in *Coastal Lagoon Processes*, ed. B. Kjerfve (Amsterdam: Elsevier Oceanographic Series), 1–8. doi: 10.1016/s0422-9894(08)70006-0

Lalande, N., Cernesson, F., Decherf, A., and Tournoud, M.-G. (2014). Implementing the DPSIR framework to link water quality of rivers to land use: methodological issues and preliminary field test. *Int. J. River Basin Manag.* 12, 201–217.

Larue, J. P., and Rouquet, J. (2016). La lagune de La Palme (Aude, France) face au comblement et à l'eutrophisation. *Physiol. Géol.* 10, 45–60. doi: 10.4000/physio-geo.4761

Le Fur, I. (2018). *Rôle Des Macrophytes Dans la Restauration Des Milieux Lagunaires : Successions Écologiques*. Montpellier: Université de Montpellier, 210.

Le Fur, I., De Wit, R., Plus, M., Oheix, J., Derolez, V., Simier, M., et al. (2019). Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. *Mar. Ecol. Progr. Ser.* 608, 13–32. doi: 10.3354/meps12814

Le Fur, I., De Wit, R., Plus, M., Oheix, J., Simier, M., and Ouisse, V. (2018). Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth. *Hydrobiologia* 808, 175–200. doi: 10.1007/s10750-017-3421-y

Leruste, A. (2016). *Trajectoires D'évolution des Communautés Phytoplanctoniques au Cours du Processus de Restauration Écologique des Milieux Lagunaires Méditerranéens*. Montpellier: Université de Montpellier, 314.

Leruste, A., Guilhaumon, F., De Wit, R., Malet, N., Collos, Y., and Bec, B. (2019a). Phytoplankton strategies to exploit nutrients in coastal lagoons with different eutrophication status and involved in a re-oligotrophication process. *Aqua. Microb. Ecol.* 83, 131–146. doi: 10.3354/ame01906

Leruste, A., Pasqualini, V., Garrido, M., Malet, N., De Wit, R., and Bec, B. (2019b). Physiological and behavioral responses of phytoplankton communities to nutrient availability in a disturbed Mediterranean coastal lagoon. *Estuar. Coast. Shelf Sci.* 219, 176–188. doi: 10.1016/j.ecss.2019.02.014

Leruste, A., Malet, N., Munaron, D., Derolez, V., Hatey, E., Collos, Y., et al. (2016). First steps of ecological restoration in Mediterranean lagoons: shifts in phytoplankton communities. *Estuar. Coast. Shelf Sci.* 180, 190–203. doi: 10.1016/j.ecss.2016.06.029

Li, W. K. W. (1995). Composition of ultraphytoplankton in the central North Atlantic. *Mar. Ecol. Progr. Ser.* 122, 1–8. doi: 10.3354/meps122001

Life programme (2020). Available online at: https://ec.europa.eu/easme/en/life (accessed February 28, 2020).

Liquete, C., Piroddi, C., Drakou, E. G., Gurney, L., Katsanevakis, S., Charef, A., et al. (2013). Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PLoS One* 8:e67737. doi: 10.1371/journal.pone.0067737

Marsden, M. (1989). Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. *Freshw. Biol.* 21, 139–162.

Maxwell, P. S., Eklof, J. S., Van Katwijk, M. M., O'brien, K. R., De La Torre-Castro, M., Bostrom, C., et al. (2017). The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems - a review. *Biol. Rev.* 92, 1521–1538. doi: 10.1111/brv.12294

Meinesz, C., Derolez, V., and Bouchoucha, M. (2013). *Base de Données "Pressions Sur Les Lagunes Méditérranéennes" - Analyse des liens état - pression. Report in French*. Montpellier: Agence de l'Eau Rhône-Méditeranée-Corse.

Munaron, D., Tapie, N., Budzinski, H., Andral, B., and Gonzalez, J. L. (2012). Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: results from a pilot survey using passive samplers. *Estuar. Coast. Shelf Sci.* 114, 82–92. doi: 10.1016/j.ecss.2011.09.009

Newton, A., Brito, A. C., Icely, J. D., Derolez, V., Clara, I., Angus, S., et al. (2018). Assessing, quantifying and valuing the ecosystem services of coastal lagoons. *J. Nat. Conserv.* 44, 50–65. doi: 10.1016/j.jnc.2018.02.009

Nixon, S. W. (2009). Eutrophication and the macroscope. *Hydrobiologia* 629, 5–19. doi: 10.1007/978-90-481-3385-7_2

Orth, R. J., McGlathery, K. J., and Heck, K. L. Jr. (eds) (2012). Theme section: eelgrass recovery induces state changes in a coastal bay system. *Mar. Ecol. Progr. Ser.* 434, 171–301.

Ouisse, V., Fiandrino, A., De Wit, R., and Malet, N. (2013). *Restauration des écosystèmes lagunaires : évaluation du rôle du sédiment et des herbiers à phanérogames. Rapport Final du Contrat n 2012 1835*. Report in French. France: Agence de l'Eau Rhône-Méditeranée-Corse.

Pasqualini, V., Derolez, V., Garrido, M., Orsoni, V., Baldi, Y., Etourneau, S., et al. (2017). Spatiotemporal dynamics of submerged macrophyte status and watershed exploitation in a Mediterranean coastal lagoon: understanding critical factors in ecosystem degradation and restoration. *Ecol. Eng.* 102, 1–14. doi: 10.1016/j.ecoleng.2017.01.027

Petraitis, P. S., and Hoffman, C. (2010). Multiple stable states and relationship between thresholds in processes and states. *Mar. Ecol. Progr. Ser.* 413, 189–200. doi: 10.3354/meps08691

Rouillard, J. J., Lago, M., Roeschel, L., Abhold, K., Kafyeke, T., Klimmek, H., et al. (2017). Protecting and restoring aquatic biodiversity: is the existing EU policy framework fit for purpose? *Environ. Policy Gov.* 28, 114–128. doi: 10.1002/eet.1793

Scheffer, M. (2001). Alternative attractors of shallow lakes. *Sci. World* 1, 254–263. doi: 10.1100/tsw.2001.62

Scheffer, M., Hosper, S. H., Meijer, M.-L., Moss, B., and Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8, 275–279. doi: 10.1016/0169-5347(93)90254-m

Schramm, W. (1999). Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. *J. Appl. Phycol.* 11, 69–78.

Sfriso, A., Buosi, A., Tomio, Y., Juhmani, A.-S., Facca, C., Sfriso, A. A., et al. (2019). Aquatic angiosperm transplantation: a tool for environmental management and restoring in transitional water systems. *Water* 11:2135. doi: 10.3390/w11102135

Society for Ecological Restoration International Science and Policy Working Group (2004). *The SER International Primer on Ecological Restoration*. Available online at: https://www.ctahr.hawaii.edu/littonc/PDFs/682_SERPrimer.pdf (accessed July 11, 2019).

Søndergaard, M., Jensen, J. P., and Jeppesen, E. (2003). Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 50, 135–145. doi: 10.1023/b:hydr.0000008611.12704.dd

Song, X., and Frostell, B. (2012). The DPSIR framework and a pressure-oriented water quality monitoring approach to ecological river restoration. *Water* 4, 670–682. doi: 10.3390/w4030670

Souchu, P., Bec, B., Smith, V. H., Laugier, T., Fiandrino, A., Benau, L., et al. (2010). Patterns in nutrient limitation and chlorophyll a along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. *Can. J. Fish. Aqua. Sci.* 67, 743–753. doi: 10.1139/F10-018

Sy, M. M. (2019). *Evaluation Des Services Écosystémiques Fournis Par les Complexes Lagunaires Dans un Processus de Restauration Écologique*. Montpellier: Université de Montpellier, 175.

Sy, M. M., Rey-Valette, H., Simier, M., Pasqualini, V., Figuières, Ch, and De Wit, R. (2018). Identifying consensus on coastal lagoons ecosystem services and conservation priorities for an effective decision making: A Q approach. *Ecol. Econ.* 154, 1–13. doi: 10.1016/j.ecolecon.2018.07.018

Valiela, I., McLelland, J., Hauxwell, J., Behr, P. J., Hersh, D., and Foreman, K. (1997). Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* 42, 1105–1118. doi: 10.4319/lo.1997.42.5_part_2.1105

Van der Geest, M., Van der Heide, T., Holmer, M., and De Wit, R. (2020). First field-based evidence that the seagrass-lucinid mutualism can mitigate sulfide stress in seagrasses. *Front. Mar. Sci.* 7:11. doi: 10.3389/fmars.2020.00011

Van Katwijk, M. M., Bos, A. R., De Jonge, V. N., Hanssen, L. S. A., Hermus, D. C. R., and De Jong, D. J. (2009). Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. *Mar. Pollut. Bull.* 58, 179–188. doi: 10.1016/j.marpolbul.2008.09.028

Van Katwijk, M. M., Thorhaug, A., Marba, N., Orth, R. J., Duarte, C. M., Kendrick, G. A., et al. (2016). Global analysis of seagrass restoration: the importance of large-scale planting. *J. Appl. Ecol.* 53, 567–578. doi: 10.1111/1365-2664.12562

Venice System. (1958). The Venice system for the classification of marine waters according to salinity. *Limnol. Oceanogr.* 3, 346–347. doi: 10.4319/lo.1958.3.3.0346

Viaroli, P., Bartoli, M., Giordano, G., Naldi, M., Orfanidis, S., and Zaldivar, J. M. (2008). Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. *Aqua. Conserv.* 18, 105–117. doi: 10.1002/aqc.956

Voulvoulis, N., Arpon, K. D., and Giakoumis, T. (2017). The EU Water Framework Directive: from great expectations to problems with implementation. *Sci. Total Environ.* 575, 358–366. doi: 10.1016/j.scitotenv.2016.09.228

WoRMS Editorial Board (2016). *World Register of Marine Species*. doi: 10.14284/170 Available online at: http://www.marinespecies.org at VLIZ (accessed July 23, 2019).

Yáñez-Arancibia, A., Day, J. W., Sánchez-Gil, P., Day, J. N., Lane, R. R., Zárate-Lomelí, D., et al. (2013). Ecosystem functioning: the basis for restoration and management of a tropical coastal lagoon, Pacific coast of Mexico. *Ecol. Eng.* 65, 88–100. doi: 10.1016/j.ecoleng.2013.03.007

Zaldívar, J.-M., Cardoso, A. C., Viaroli, P., Newton, A., De Wit, R., Ibañez, C., et al. (2008). Eutrophication in transitional waters: an overview. *Trans. Waters Monogr.* 2, 1–78.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Hydrobiologia
DOI 10.1007/s10750-017-3421-y

PRIMARY RESEARCH PAPER

Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth

Ines Le Fur · Rutger De Wit · Martin Plus · Jocelyne Oheix · Monique Simier · Vincent Ouisse

Received: 2 May 2017 / Revised: 11 October 2017 / Accepted: 23 October 2017

Abstract A large spectrum of coastal lagoon types with a wide range of environmental conditions is observed along the French Mediterranean coast. These comprise wide trophic and salinity gradients, ranging from oligotrophic to hypertrophic status, and from nearly freshwater to slightly above marine Mediterranean Sea water salinities, respectively. The statistical analysis of a long-term dataset, including water column variables and observations of macrophyte genera, showed that salinity, depth, and then trophic status, were important factors explaining the distribution of benthic macrophytes for the soft-bottom sediments in the 34 studied French Mediterranean lagoons. Based on this, we assumed that the vegetation succession along the eutrophication gradient was different according to the lagoon salinity ranges. Euhaline and polyhaline lagoons follow the well-known Schramm schematic model, where aquatic angiosperm such as seagrasses dominate under oligotrophic conditions, and opportunistic macroalgae and phytoplankton dominate under eutrophic and hypertrophic conditions. In oligohaline and mesohaline lagoons, the succession is probably an intermediate scheme between the successions observed in small temperate lakes and in marine coastal ecosystems due to the presence of both brackish and freshwater

Handling editor: Pierluigi Viaroli

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10750-017-3421-y) contains supplementary material, which is available to authorized users.

I. Le Fur (✉) · J. Oheix · V. Ouisse
Ifremer, UMR MARBEC (IRD, Ifremer, Université de Montpellier, CNRS), Station Ifremer, avenue Jean Monnet, CS 30171, 34203 Sète Cedex, France
e-mail: ines.le.fur@ifremer.fr;
ines.le.fur@gmail.com

I. Le Fur · J. Oheix · V. Ouisse
Ifremer, Laboratoire Environnement Ressources Languedoc Roussillon (LER LR), avenue Jean Monnet, CS 30171, 34203 Sète Cedex, France

R. De Wit
CNRS, UMR MARBEC (IRD, Ifremer, Université de Montpellier, CNRS, Université de Montpellier), Place Eugène Bataillon, 34095 Montpellier Cedex 5, France

M. Simier
IRD, UMR MARBEC, (IRD, Ifremer, Université de Montpellier, CNRS), Station Ifremer, avenue Jean Monnet, CS 30171, 34203 Sète, France

M. Plus
Ifremer, Laboratoire d'écologie pélagique (DYNECO-PELAGOS), Centre Bretagne, ZI Pointe du Diable, CS 10070, 29280 Plouzané, France

species. We thus propose a conceptual scheme for the oligohaline and mesohaline lagoons.

Keywords French coastal lagoons · Submerged aquatic vegetation (SAV) · Eutrophication · Salinity · Depth · Canonical correspondence analysis (CCA)

Introduction

Coastal lagoons are generally defined as shallow water bodies, separated from the sea by a barrier and connected to the sea by one or more restricted inlets (Barnes, 1980; Kjerfve, 1994). They occupy around 13% of the coastline worldwide and about 5.3% of the European coast, where they are particularly abundant around the Mediterranean Sea (Cromwell, 1971). Coastal lagoons rank among the most productive ecosystems in the world and provide a wide range of ecosystem services and resources (Kennish & Paerl, 2010). They support important fisheries and are also used for aquaculture exploitation, recreation, and tourism (Pérez-Ruzafa et al., 2011). Located at the interface between the continental coastal zone and the sea, they support strong physical and ecological gradients. They are influenced by both marine and freshwater inputs from the catchment area; indeed, the salinity can vary from nearly freshwater to hypersaline water, depending on the hydrological balance (Kjerfve, 1994). Variation in salinity and other environmental factors can also be observed within a lagoon, both spatially and temporally. Since coastal lagoons are often subdivided into different rather homogenous hydrological basins (Tagliapietra & Ghirardini, 2006; Fiandrino et al., 2017), different ecological conditions can be met even in neighboring basins.

Hence, despite their common features, coastal lagoons present a wide variability of their environmental conditions. These depend particularly on freshwater inputs from their watershed and the magnitude of water exchanges with the sea, which are the main driver of the hydrological processes within the different basins, as well as on their geomorphology and human activities. Although depth in coastal lagoons generally averages less than 2 m, deeper waters may be encountered according to their geomorphological origin. Hence, coastal lagoons with a tectonic origin, like Diana, Urbino (Corsica), or Thau (South of France), are deeper than brackish lagoons with a deltaic (e.g., Camargue in Rhône delta in France, Po and Ebro delta in Italy and Spain, respectively) or sedimentary origin (e.g., Palavasian lagoons, south of France (Guerlorget & Perthuisot, 1992; Schramm & Nienhuis, 1996; De Wit, 2011). A great number of Mediterranean coastal lagoons are more strongly influenced by waves than by tides and wind direction and speed are key elements for the genesis of waves. Microtidal (< 2 m) conditions predominate in many coastal lagoons (Eisma, 1998). The Mediterranean coast of continental South of France and Corsica are subjected to tidal ranges below 0.5 m and lagoons can be defined as nanotidal, as suggested by Tagliapietra & Ghirardini (2006). Tidal range determines the morphology and grain size distribution of sediment; in nanotidal lagoons, the deepest zones tend to be in the center of the basin (Tagliapietra & Ghirardini, 2006). The majority of the bottoms in coastal lagoons are composed of soft-bottom sediments.

Because of their shallowness, local meteorological conditions strongly influence water temperature and other physical and chemical parameters in coastal lagoons. Under Mediterranean climates (characterized by warm to hot dry summers and mild to cool winters), coastal lagoons support a high variability of seasonal events (such as precipitations, high temperature). All these features would make lagoons vulnerable to global climatic change. Sea level, temperature, precipitations, and storms are expected to impact coastal lagoons (Anthony et al., 2009; De Wit, 2011). Furthermore, coastal lagoons have been subjected to development of human activities on their watershed and thus, an increase in nutrient and chemical contaminant inputs (e.g., urban sewage, waste water treatment plants, agricultural effluents) have often occurred (Barnes, 1980; Castel et al., 1996; Kennish & Paerl, 2010; Munaron et al., 2012). Their restricted water exchanges with the sea, confinement, long water residence times, and their potential to accumulate elevated levels of nutrients supplied from their watersheds and internal loading make coastal lagoons particularly sensitive to eutrophication processes (Barnes, 1980; Kjerfve, 1994; Glibert et al., 2014).

Both the natural and anthropogenic perturbations mentioned above may affect the diversity as well as the physiological and ecological adaptation of the species inhabiting coastal lagoons. They can highly influence not only the composition and size structure of phytoplankton communities (Bec et al., 2011; Leruste et al., 2016) but also the sessile organisms such as benthic fauna and macrophytes (Sfriso et al., 1992; Charpentier et al., 2005). Submerged macrophytes, composed of macroalgae and aquatic angiosperms, are of particular interest in coastal lagoons, because these are important primary producers. Many species can be considered as ecosystem engineers by creating habitats for aquatic organisms and birds (Duarte & Cebrián, 1996; Levin et al., 2001; Vizzini & Mazzola, 2008) and by structuring the physical environments in coastal ecosystems (Hartvig et al., 2009; Thomaz & da Cunha, 2010). Benthic macrophytes form highly productive (Agostini et al., 2003) and extensive meadows in many coastal lagoons. Hence, in coastal lagoons, macrophytes play an important role not only in benthic oxygen and nutrient fluxes (Viaroli et al., 1996), in biogeochemical cycles (Plus et al., 2003) but also in driving sediment microbial processes (Hansen et al., 2000).

Knowledge on the ecology of macrophytes is paramount both for the fundamental knowledge of the ecosystem functioning in coastal lagoons as well as for more applied aspects, including their use as ecological indicators of environmental health and ecological status (Sfriso et al., 2009; Sargian et al., 2013; Orfanidis et al., 2014). Accordingly, in the European Water Framework Directive (WFD) (European Commission (EC), 2000), macrophytes are recognized as important biological quality elements for determining the ecological status of transitional waters, including coastal lagoons.

Growth and distribution of macrophytes in coastal ecosystems are influenced by both biotic (e.g., grazing, competition) and abiotic factors such as nutrients and light availability (Dennison, 1987; Duarte, 1991, 1995), pattern of currents (Fonseca & Kenworthy, 1987), temperature (Larkum et al., 2006; Hurd et al., 2014), and salinity (Lirman et al., 2008; Steinhardt & Selig, 2011). In Mediterranean lagoons, many species start growing in spring and often form the densest biomass late spring or during the summer (Menéndez & Comín, 2000; Agostini et al., 2003; Sfriso & Facca, 2007; Obrador & Pretus, 2010). Angiosperms and macroalgae are sensitive to anthropogenic stress (Orth et al., 2006), particularly to excessive nutrient inputs (Cloern, 2001; de Jonge et al., 2002; McGlathery et al., 2007). Both macroalgae and submerged aquatic angiosperms such as seagrasses and Potamogetonaceae take up nutrients directly from the water column, whereas, in addition, aquatic angiosperms can also take up nutrients from the sediment through their roots. Submerged macrophytes have morphological, physiological, and ecological adaptations to face environmental fluctuations (e.g., variations of salinity, water level, temperature, and light) (Littler & Littler, 1984; Brock, 1986). Under low nutrient and clear water conditions, seagrasses or other angiosperms are dominant on soft bottoms and perennial macroalgae on hard substrata. In contrast, under high nutrient and high turbidity conditions, macrophyte community compositions shift from aquatic angiosperms and perennial macroalgae to fast-growing opportunistic macroalgae and phytoplankton. Finally, under hypertrophic conditions, phytoplankton becomes the main primary producer (Schramm, 1999; Viaroli et al., 2008). This scheme, representing the changes of macrophyte communities along a eutrophication gradient, is known as the "Schramm schematic model" (Schramm, 1999). It has been used as a framework for the use of macrophytes as indicators of water quality in coastal ecosystems (Sfriso et al., 2009; Sargian et al., 2013; Orfanidis et al., 2014). Expert judgment has been used to create the French macrophyte index (examination tool for coastal lagoon macrophyte ecological status, EXCLAME) developed for the Water Framework Directive (WFD) (Ifremer et al., 2011; Sargian et al., 2013) and a slightly different macrophytes index was used in the Lagoon Monitoring Network (RSL, Réseau de Suivi Lagunaire, Ifremer, 2007). After almost two decades of intensive monitoring of macrophyte communities and hydrological parameters in coastal lagoons, it is now possible to study, in a statistically rigorous way, the link between environmental conditions and the occurrence of macrophyte taxa in coastal lagoons and check the general validity of the Schramm scheme (Schramm, 1999).

In this paper, we test the hypothesis that water chemistry and depth of the coastal lagoons determine the communities of aquatic macrophytes that dominate during late spring and early summer on the soft bottoms of the coastal lagoons. Particularly, we aim to disentangle the impacts of the eutrophication status, depth, and the salinity on these communities. Therefore, we study 34 French Mediterranean coastal lagoons, comprising different salinities, depths, and trophic status and use the data from different monitoring programs such as the RSL, the WFD, and smaller lagoon monitoring projects pursued by lagoon managers. These were compiled in a coherent large and single database. Hence, the aims of this study were i) to determine and rank the main environmental factors driving the distribution of these macrophytes in Mediterranean coastal lagoons characterized by large trophic and salinity gradients, ranging from oligotrophic to hypertrophic status, and from nearly freshwater to slightly above Mediterranean sea water salinities, ii) to investigate the distribution patterns of macrophyte communities in these Mediterranean lagoons.

Methods

Study sites

In the French Mediterranean area, most coastal lagoons are located in the Gulf of Lions (NW Mediterranean Sea), where these systems constitute more than 50% of the coastline. In addition, coastal lagoons occur along the coasts of the Côte d'Azur and the Tyrrhenian Sea (E. Corsica). This study covered 34 lagoons from these different areas (Fig. 1) belonging to the administrative regions of Occitanie, Provence-Alpes-Côte d'Azur and Corse. Some lagoons were divided into sectors corresponding to hydrodynamic sub-basins empirically defined on the basis of their bathymetry in order to individualize sectors belonging to the same lagoon but displaying significant differences (Souchu et al., 2010). Hence, a total of 43 sectors were defined for 34 lagoons. General morphometric data on the studied coastal lagoons are provided in Table 1, together with the identified sectors and occurrence of shellfish farming within the lagoons and additional information on freshwater tributaries from their watersheds. In general, the studied lagoons are shallow water bodies (mean depth smaller than 2 m); only six lagoons have a mean depth higher than 2 m: Berre (BER, VAI), Diana (DIA), Leucate (the south part LES), Thau (TW, TE), and Urbino (URB) (Table 1).

Many lagoons in the South of France still have the typical geomorphological features including narrow sandy barriers and one or several restricted inlets (Table 1), although many inlets have been highly modified by humans. In addition, a significant proportion of the coastal lagoons have been very strongly modified by humans and have either lost their inlets or lost a natural connection to their watersheds (e.g., freshwater inflows through channels). In addition, some of the lagoons in the deltaic settings nowadays occur inland, several kms separated from the sea, because of accretion of the delta, while still communicating with the sea through an artificial canal (Table 1). Other lagoons have been compartmentalized by humans into a complex of several adjacent lagoons. This is the case for the Palavasian lagoons (close to Montpellier city) where a navigation canal—the Rhône to Sète canal—was built through the former Melgueil lagoon running parallel to the coastline. Together with other types of human interventions and natural infilling, this has resulted in creating five "seafront" lagoons and four "inland" lagoons (Fig. 1). The "seafront" lagoons have an inlet, but are separated from their watershed by the Rhône to Sète canal; the "inland" lagoons are separated from the sea by this canal from which they receive seawater indirectly (Leruste et al., 2016).

Data collection

Environmental variables

We used water column data collected through the Lagoon Monitoring Network (RSL) and the Water Framework Directive (WFD) (Ifremer, Quadrige data bank). We considered nine variables from these databases: depth, turbidity, salinity, concentrations of chlorophyll *a*, total nitrogen, total phosphorus, and concentrations of ammonium, nitrate plus nitrite, and phosphate. Samplings were carried out during late spring and summer periods between 1998 and 2015 (Table S1 in Supplementary Material). Water was sampled at a single station per lagoon sector three times per year, i.e., once a month from June to August. No water samplings were available for Les Mouettes (MOU). This lagoon communicated directly with the adjacent Ingril Sud (INS) lagoon; therefore, Ingril Sud (INS) water column data were taken as a proxy for Les Mouettes (MOU). Water samples were collected (1) through a Niskin bottle or (2) with 2 l polypropylene bottles according to the accessibility of lagoons. Samples for total nitrogen and phosphorus, as well as Chl *a* were transported at 4°C and filtered in the

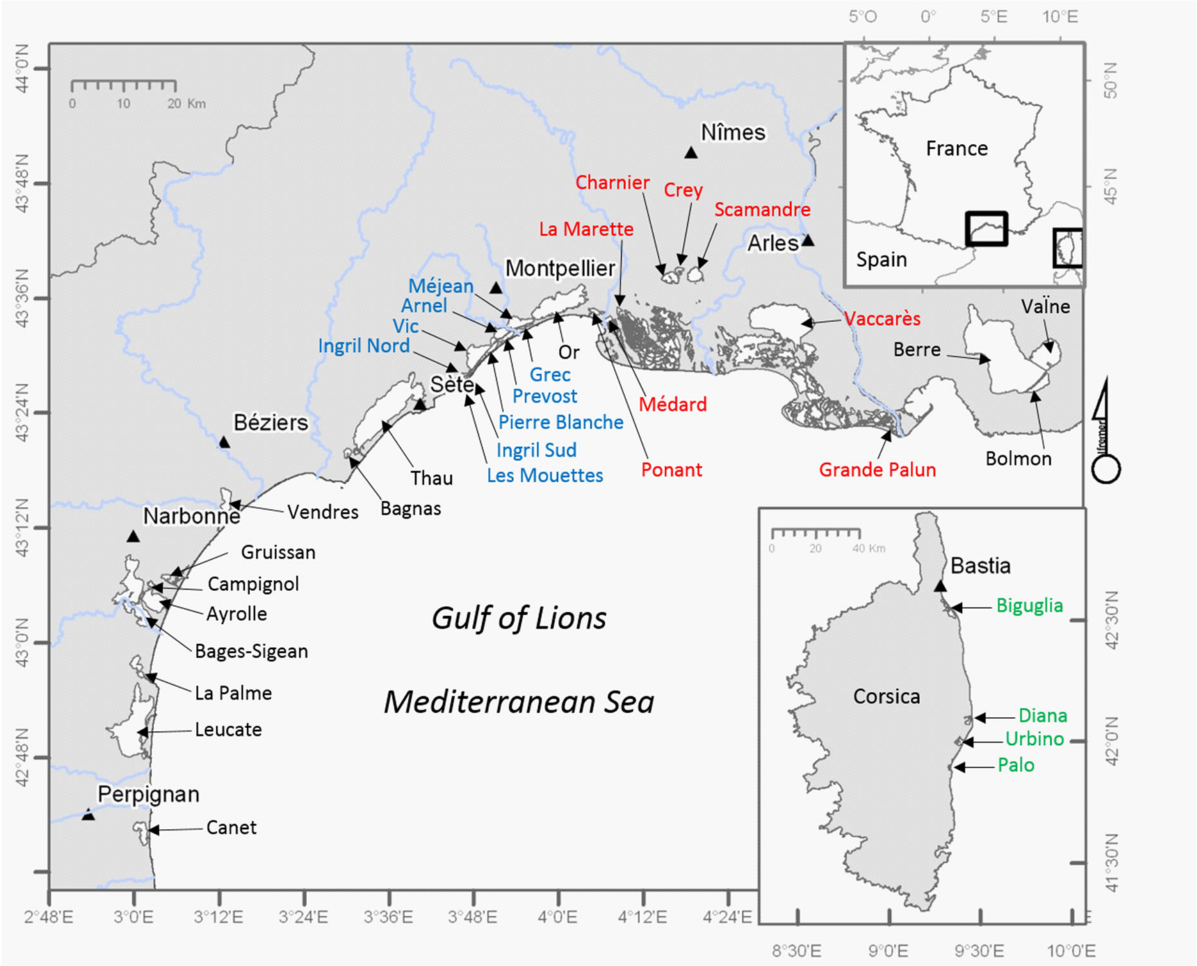


Fig. 1 Overview of the study area showing the 34 lagoons studied. In blue: lagoons from the Palavasian complex, in red: Camargue lagoons, in green: Corsican lagoons. In this study, some lagoons were divided into sectors corresponding to hydrodynamic sub-basins. The number and the names of sectors corresponding to each lagoon are presented in Table 1

laboratory within 3 h after sampling. Inorganic nutrients samples were pre-filtered (1) directly in the field or (2) in the laboratory through 20-µm nylon filters. Salinity was recorded with a WTW LF 197 field sensor. Turbidity was measured at the laboratory with an optic turbidimeter (2100N IS turbidimeter ISO 7027). Chlorophyll *a* concentration, used as a proxy for phytoplankton biomass, was measured by spectrofluorimetry (Neveux & Lantoine, 1993). The analytical protocols of nutrients have been described in detail by Souchu et al. (2010) and details of filtration, conservation, and analysis of phytoplankton have been described by Bec et al. (2011).

Benthic sampling

The data were obtained from different monitoring networks: the RSL and WFD database (Ifremer/Quadrige) and data collected by lagoon managers for the Berre (BER) and Vaccarès (VAC) lagoons. The monitoring surveys were conducted between 1998 and 2015. Macrophyte samplings were performed at benthic stations. To cope with the spatial heterogeneity of the benthos, 1–54 benthic sampling stations were chosen in the studied lagoon sectors depending on the surface of the sector (see Supplementary Material). However, macrophyte samplings were only performed every 2–4 years. The number of benthic stations and the years of macrophyte sampling in the different lagoon

Table 1 Characteristics of the 34 studied lagoons along the French Mediterranean coast comment

Lagoon	Label of the sector	Lagoon Area (km^2)	Mean depth by sector (m)	Connection to the sea through an inlet	Main freshwater tributary	Shellfish farming
Canet	CNN, CNS	6.5	0.6–0.6	np^2	River	
Leucate	LEN, LES	52.7	1.6–2.2	p	Karst	×
La Palme	LAP	6.1	0.7	np^1	Karst	
Bages-Sigean	BGN, BGM, BGS	37.7	1.5–1.5–1.2	p	River	
Ayrolle	AYR	13.4	0.7	p	Wetland	
Campignol	CAM	1.0	0.7	–	Canal	
Gruissan	GRU	1.4	0.7	p	Canal	
Vendres	VDR	6.6	0.6	–	Indirectly to the river	
Bagnas	BAN	1.7	0.6	–	Canal	
Thau	TE, TW	68.0	5.2–3.3	p	River, Canal (RSC)	×
Palavasian complex: (in blue in Fig. 1)						
Les Mouettes	MOU	0.4	0.8	–	Connected to Ingril Sud	
Ingril Nord	INN	3.2	0.7	–	Canal (RSC)	
Ingril Sud	INS	3.6	0.8	p	Canal (RSC)	
Pierre Blanche	PBL	3.3	0.6	–	Canal (RSC)	
Vic	VIC	12.0	1	–	Canal (RSC)	
Prevost	PRE, PRW	2.4	0.9–0.7	p	Canal (RSC)	×
Arnel	ARN	5.9	0.6	–	Canal (RSC)	
Mejean	MEE, MEW	7.2	0.7–0.7	–	Canal (RSC)	
Grec	GRC	1.2	0.5	–	Canal (RSC)	
Or	ORE, ORW	31.8	1.1–1.2	np^2	Canal (RSC)	
Camargue: (in red in Fig. 1)						
Ponant	PON	1.9	2.6	p	River	
Medard	MED	1.4	0.7	–	Canal (RSC)	
La Marette	MARN, MARS	1.3	0.7–0.6	–	Canal	
Vaccares	VAC	101.3	1.4	np^2	Canal	
Grande Palun	GP	3.0	0.6	–	River	
Scamandre	SC	5.5	1.2	–	Canal	
Charnier	CH	5.2	0.9	–	Canal	
Crey	CR	1.7	0.9	–	Canal	
Berre	BER, VAI	132.5	4.9	p	River, Canal	
Bolmon	BOL	6.0	1.3	–	River, Canal	
Corsica: (in green in Fig. 1)						
Biguglia	BIG	13.8	1.5	np^1	River, Canal	
Diana	DIA	5.4	3.5	p	River	×
Urbino	URB	7.6	4.2	np^1	River	×
Palo	PAL	1.1	0.8	np^1	Wetland, Stream	

Legend (p) permanent connection to the sea through an inlet; (np) non-permanent connection to the sea, natural (1) or artificial (2); (−) lagoons without inlets, indirectly connected to the sea through an artificial canal or another lagoon. × indicates the presence of shellfish farming. RSC is the Rhône to Sète canal sectors are shown in Table S1 (see the Supplementary Material). The macrophyte sampling campaigns were generally carried out in late spring or early summer, during the maximal growth and production rates. Unlike water column data, the protocol and the macrophyte sampling methods can be different according to the monitoring program and the sampling date. These methods are identified in Table S1 and described in the Supplementary Material. Only stations with soft bottoms were considered in this study.

In each lagoon, the depth was measured at each benthic station. In the deepest stations, the depth was measured with a depth gauge by SCUBA divers, whereas in the shallowest lagoons, the depth was measured with a graduated ruler. The mean depth was calculated for each lagoon sector.

Macrophyte taxonomy

The taxonomic resolution of macrophyte determinations was heterogeneous among and within the monitoring programs, ranging from the species to the genus level. To homogenize and standardize the data, all the statistical analyses were carried out at the genus level. Taxonomic nomenclature followed AlgaeBase (Guiry & Guiry, 2016) and World Register of Marine Species (WoRMS Editorial Board, 2016).

Data analyses

The water column data were not normally distributed; therefore median values and interquartile ranges (IQR) were calculated.

A canonical correspondence analysis (CCA) (Ter Braak, 1986, 1987) was used to explore the relationship among macrophyte genera and environmental variables in the lagoons. CCA aims to visualize a pattern of community variation and the main features of species distribution along environmental variables (Ter Braak, 1987), based on unimodal taxon–environment relationships. CCA can be considered as the constrained form of a correspondence analysis (CA) in which the axes are linear combinations of the environmental variables. CCA results are displayed by an ordination diagram in which the taxa scores (represented by points) and the environmental variables (represented by arrows), together reflect the taxa distributions along the different environmental variables (Ter Braak, 1986), with further details about its interpretation provided by Ter Braak (1987).

CCA produces two kind of site scores (Ter Braak, 1986; Palmer, 1993; McCune, 1997): linear combination (LC) scores which are linear combinations of constraining variables and weighted averages (WA) scores which are weighted averages of species scores. Some controversy exists regarding the choice of the site scores (Palmer, 1993; Ter Braak, 1994; McCune, 1997; Oksanen, 2016). According to Graffelman & Tuft, (2004) WA and LC, scores have different properties that are pertinent for the interpretation of results. We chose the LC scores because these have been reported to give better results in simulation (Palmer, 1993; Ter Braak, 1994) and they are interpretable with respect to both taxa and variable markers (Graffelman & Tuft, 2004).

The CCA involved 34 lagoons representing 43 different sectors, 50 genera (after removing rare genera, i.e., genera that have a frequency of occurrence $< 1\%$), and nine environmental variables: Chlorophyll a (CHLa), salinity (SALINITY), turbidity (TURB), depth (DEPTH), total nitrogen (TN), total phosphorus (TP), nitrate plus nitrite (NO3_NO2), ammonium (NH4), and phosphate (PO4). Table 2 list all observed macrophyte taxa and indicates which genera have been used for the CCA analyses. Samplings with non-determined taxa or without macrophytes were removed before the analysis because CCA cannot cope with missing or zero values. Due to the heterogeneity of the macrophyte sampling methods, only the presence–absence data were used. All 43 studied sectors comprised different numbers of benthic stations (see above and Table S1). This allowed us to calculate at each sampling date the relative frequency of occurrence for each taxon in the different sectors by dividing the number of occurrences by the total number of benthic stations in the lagoon sector. This relative frequency of each taxon per sector was used in the CCA.

All abiotic variables were inspected for outliers and the asymmetry and the normality of their distributions were tested (Shapiro–Wilk normality test). All variables, except salinity, have a right-skewed distribution. To improve the distribution of these abiotic variables (make them closer to the normal distribution), with the exception of salinity, all other environmental variables were transformed either as log (x) or as log (x + 1) (i.e., TP, PO4 and NO3_NO2, because

Table 2 List of macrophytes recorded in the 34 studied lagoons

Phylum	Genus	Code used in CCA	Species	Author citation
Charophyta	*Chara*	Cha	*Chara aspera*	C.L. Willdenow, 1809
			Chara galioides	A.P. De Candolle, 1813
			Chara hispida	Linnaeus, 1753
			Chara tomentosa	Linnaeus, 1753
	Lamprothamnium	Lam	*Lamprothamnium papulosum*	(K. Wallroth) J.Groves, 1916
Chlorophyta	*Acetabularia*	Ace	*Acetabularia acetabulum*	(Linnaeus) P.C.Silva, 1952
	Bryopsis	Bry	*Bryopsis hypnoides*	J.V. Lamouroux, 1809
			Bryopsis muscosa	J.V. Lamouroux, 1809
			Bryopsis plumosa	(Hudson) C. Agardh, 1823
	Chaetomorpha	Che	*Chaetomorpha aerea*	(Dillwyn) Kützing, 1849
			Chaetomorpha linum	(O.F.Müller) Kützing, 1845
	Cladophora	Cla	*Cladophora albida*	(Nees) Kützing, 1843
			Cladophora battersii	van den Hoek, 1963
			Cladophora coelothrix	Kützing, 1844
			Cladophora glomerata	(Linnaeus) Kützing, 1843
			Cladophora lehmanniana	(Lindenberg) Kützing, 1843
			Cladophora liniformis	Kützing, 1849
			Cladophora pellucida	(Hudson) Kützing, 1843
			Cladophora socialis	Kützing, 1849
			Cladophora vadorum	(Areschoug) Kützing, 1849
			Cladophora vagabunda	(Linnaeus) van den Hoek, 1963
	Codium	Cod	*Codium fragile*[1]	(Suringar) Hariot, 1889
			Codium tomentosum	Stackhouse, 1797
	Monostroma	Mon	*Monostroma grevillei*	(Thuret) Wittrock, 1866
	Spirogyra	Spi *		Link, 1820
	Ulva	Ulv	*Ulva clathrata*	(Roth) C. Agardh, 1811
			Ulva compressa	Linnaeus, 1753
			Ulva intestinalis	Linnaeus, 1753
			Ulva lactuca	Linnaeus, 1753
			Ulva linza	Linnaeus, 1753
			Ulva rigida	C. Agardh, 1823
			Ulva rotundata	Bliding, 1968
	Ulvaria	Ulr	*Ulvaria obscura*[1]	(Kützing) P. Gayral ex C. Bliding, 1969
	Valonia	Val	*Valonia aegagropila*	C. Agardh, 1823
			Valonia utricularis	(Roth) C. Agardh, 1823
Ochrophyta	*Aglaozonia*	Agl *	*Aglaozonia melanoidea*	Sauvageau, 1899
			Aglaozonia parvula	(Greville) Zanardini, 1843
	Chorda	Cho	*Chorda filum*[1]	(Linnaeus) Stackhouse, 1797
	Cladosiphon	Cld *	*Cladosiphon mediterraneus*	Kützing, 1843
	Cladostephus	Cls	*Cladostephus spongiosus*	(Hudson) C. Agardh, 1817
	Colpomenia	Col	*Colpomenia peregrina*[1]	Sauvageau, 1927
			Colpomenia sinuosa	(Mertens ex Roth) Derbès & Solier, 1851
	Cutleria	Cut	*Cutleria adspersa*	(Mertens ex Roth) De Notaris, 1842
			Cutleria multifida	(Turner) Greville, 1830

Table 2 continued

Phylum	Genus	Code used in CCA	Species	Author citation
	Cystoseira	Cys	*Cystoseira barbata*	(Stackhouse) C. Agardh, 1842
			Cystoseira compressa	(Esper) Gerloff & Nizamuddin, 1975
	Desmarestia	Des	*Desmarestia viridis*[1]	(O.F.Müller) J.V. Lamouroux, 1813
	Dictyota	Dic	*Dictyota dichotoma*	(Hudson) J.V. Lamouroux, 1809
			Dictyota spiralis	Montagne, 1846
	Feldmannia	Fel *	*Feldmannia irregularis*	(Kützing) G.Hamel, 1939
	Halopteris	Hao *	*Halopteris filicina*	(Grateloup) Kützing, 1843
	Padina	Pad *	*Padina pavonica*	(Linnaeus) Thivy, 1960
	Sargassum	Sar	*Sargassum muticum*[1]	(Yendo) Fensholt, 1955
	Scytosiphon	Scy *	*Scytosiphon lomentaria*	(Lyngbye) Link, 1833
	Sphacelaria	Sph		Lyngbye, 1818
	Sphaerotrichia	Spe *	*Sphaerotrichia divaricata*[1]	(C. Agardh) Kylin, 1940
	Stictyosiphon	Sti	*Stictyosiphon adriaticus*	Kützing, 1843
	Taonia	Tao *	*Taonia atomaria*	(Woodward) J. Agardh, 1848
	Vaucheria	Vau		A.P de Candolle, 1801
Rhodophyta	*Acrochaetium*	Acc *		Nägeli, 1858
	Agardhiella	Aga	*Agardhiella subulata*[1]	(C. Agardh) Kraft & M.J. Wynne, 1979
	Aglaothamnion	Ago *	*Aglaothamnion pseudobyssoides*	(P.L. Crouan & H.M. Crouan) Halos, 1965
	Ahnfeltiopsis	Ahn	*Ahnfeltiopsis flabelliformis*[1]	(Harvey) Masuda, 1993
	Alsidium	Als	*Alsidium corallinum*	C. Agardh, 1827
	Antithamnion	Ant *	*Antithamnion cruciatum*	(C. Agardh) Nägeli, 1847
	Callithamnion	Cal	*Callithamnion corymbosum*	(J.E. Smith) Lyngbye, 1819
			Callithamnion tetragonum	(Withering) S.F.Gray, 1821
	Centroceras	Cen	*Centroceras clavulatum*	(C. Agardh) Montagne, 1846
	Ceramium	Cer	*Ceramium codii*	(H. Richards) Feldmann-Mazoyer, 1938
			Ceramium comptum	Børgesen, 1924
			Ceramium diaphanum	(Lightfoot) Roth, 1806
			Ceramium strictum	(Kützing) Rabenhorst, 1847
			Ceramium tenerrimum	(G. Martens) Okamura, 1921
			Ceramium tenuissimum	(Roth) J. Agardh, 1851
			Ceramium virgatum	Roth, 1797
	Chondracanthus	Chc	*Chondracanthus acicularis*	(Roth) Fredericq, 1993
	Chondria	Chn	*Chondria capillaris*	(Hudson) M.J. Wynne, 1991
			Chondria simplisiuscula	Weber-van Bosse, 1913
	Chondrus	Chd	*Chondrus giganteus*[1]	Yendo, 1920
	Chrysymenia	Chr	*Chrysymenia wrightii*[1]	(Harvey) Yamada, 1932
	Chylocladia	Chy	*Chylocladia verticillata*	(Lightfoot) Bliding, 1928
	Corallina	Cor *	*Corallina elongata*	J.Ellis & Solander, 1786
	Dasya	Das	*Dasya hutchinsiae*	Harvey, 1833
			Dasya pedicellata	(C. Agardh) C. Agardh, 1824

Table 2 continued

Phylum	Genus	Code used in CCA	Species	Author citation
			Dasya sessilis[1]	Yamada, 1928
	Falkenbergia	Fal	*Falkenbergia rufolanosa*	(Harvey) F. Schmitz, 1897
	Gelidium	Gel *	*Gelidium crinale*	(Hare ex Turner) Gaillon, 1828
	Gracilaria	Gra	*Gracilaria bursa-pastoris*	(S.G. Gmelin) P.C. Silva, 1952
			Gracilaria dura	(C. Agardh) J. Agardh, 1842
			Gracilaria gracilis	(Stackhouse) M. Steentoft, L.M. Irvine & F. Farnham, 1995
	Gracilariopsis	Grc	*Gracilariopsis longissima*	(S.G.Gmelin) M. Steentoft, L.M. Irvine & F. Farnham, 1995
	Grateloupia	Grt	*Grateloupia doryphora*	(Montagne) M. Howe, 1914
			Grateloupia filicina[1]	(J.V. Lamouroux) C. Agardh, 1822
	Griffithsia	Gri	*Griffithsia corallinoides*[1]	(Linnaeus) Trevisan, 1845
	Gymnogongrus	Gym	*Gymnogongrus griffithsiae*	(Turner) Martius, 1833
	Halopithys	Hal	*Halopithys incurva*	(Hudson) Batters, 1902
	Halymenia	Hay	*Halymenia floresii*	(Clemente) C. Agardh, 1817
	Hypnea	Hyp *	*Hypnea valentiae*[1]	(Turner) Montagne, 1841
	Laurencia	Lau	*Laurencia coronopus*	J. Agardh, 1852
			Laurencia microcladia	Kützing, 1865
			Laurencia obtusa	(Hudson) J.V. Lamouroux, 1813
	Lomentaria	Lom	*Lomentaria clavellosa*	(Lightfoot ex Turner) Gaillon, 1828
	Lophosiphonia	Lop	*Lophosiphonia obscura*	(C. Agardh) Falkenberg, 1897
			Lophosiphonia subadunca	(Kützing) Falkenberg, 1901
	Nitophyllum	Nit *	*Nitophyllum punctatum*	(Stackhouse) Greville, 1830
	Osmundea	Osm	*Osmundea hybrida*	(A.P. de Candolle) K.W. Nam, 1994
			Osmundea pinnatifida	(Hudson) Stackhouse, 1809
	Polysiphonia	Pol	*Polysiphonia denudata*	(Dillwyn) Greville ex Harvey, 1833
			Polysiphonia elongata	(Hudson) Sprengel, 1827
			Polysiphonia mottei	Lauret, 1967
			Polysiphonia opaca	(C. Agardh) Moris & De Notaris, 1839
			Polysiphonia scopulorum	Harvey, 1855
			Polysiphonia sertularioides	(Grateloup) J. Agardh, 1863
			Polysiphonia setigera	Kützing, 1849
	Pterosiphonia	Pte	*Pterosiphonia parasitica*	(Hudson) Falkenberg, 1901
			Pterosiphonia pennata	(C. Agardh) Sauvageau, 1897
	Radicilingua	Rad	*Radicilingua thysanorhizans*	(Holmes) Papenfuss, 1956
	Rytiphlaea	Ryt	*Rytiphlaea tinctoria*	(Clemente) C. Agardh, 1824
	Solieria	Sol	*Solieria chordalis*	(C.Agardh) J. Agardh, 1842
			Solieria filiformis[1]	(Kützing) P.W. Gabrielson, 1985
	Sphaerococcus	Sph	*Sphaerococcus coronopifolius*	Stackhouse, 1797
	Spyridia	Spy	*Spyridia filamentosa*	(Wulfen) Harvey, 1833

Table 2 continued

Phylum	Genus	Code used in CCA	Species	Author citation
Tracheophyta	*Ceratophyllum*	Cea *	*Ceratophyllum demersum*	Linnaeus, 1753
	Cymodocea	Cym	*Cymodocea nodosa*	(Ucria) Ascherson, 1870
	Myriophyllum	Myr	*Myriophyllum spicatum*	Linnaeus, 1753
	Potamogeton	Pot*	*Potamogeton crispus*	Linnaeus, 1753
	Stuckenia	Stu	*Stuckenia pectinata*	(Linnaeus) Börner, 1912
	Ruppia	Rup	*Ruppia cirrhosa*	(Petagna) Grande, 1918
			Ruppia maritima	Linnaeus, 1753
	Zostera	Zos	*Zostera marina*	Linnaeus, 1753
			Zostera noltei	Horneman, 1832

Species with (1) are introduced species (Verlaque 2000, 2001, 2002). Genus codes marked with an asterisk represent the rare genera with a frequency of occurrence $< 1\%$; these rare genera have been removed before the CCA analysis

of the presence of zero values). The water column samples were usually collected during the late spring and mid-summer period, whereas macrophyte samples were collected during late spring or early summer, generally in May–June. Thus, it would not be correct to directly associate the macrophyte data with the environmental variables. Moreover, we assumed that the presence–absence of macrophytes in a site is not exclusively explained by the environmental condition of the year of sampling "*y*," but also by the conditions prevailing during the previous years (particularly for perennial species). Therefore, the macrophyte samplings of the year "*y*" were associated with the mean of each environmental variable integrated over a period of 3 years (y, $y-1$, and $y-2$). The statistical significance of the relationship between the species and the whole set of environmental variables was evaluated with a permutation test (Monte Carlo).

An agglomerative hierarchical clustering (AHC) was done after the CCA analysis using the Ward's aggregation method in order to identify groups of lagoons according to the environmental variables and macrophytes composition. The *K*-means method using the Calinski–Harabasz criterion (Calinski & Harabasz, 1974) was used to determine the number of clusters in the AHC.

The CCA analysis and all statistical tests were implemented using the R software version 3.1.1 (R development team, 2016), ade4 package (Dray & Dufour, 2007), and vegan package (Oksanen et al., 2016).

Results

Environments

Salinity

The salinity in the different sectors of the coastal lagoons shown in Fig. 2 ranged from oligohaline (salinity between 0.5 and 5) to hyperhaline (salinity > 40). The majority (65%) of the lagoon sectors had a median in the polyhaline and euhaline ranges, 33% in oligohaline to mesohaline range, and 2% in the hyperaline range. Only five lagoons had oligohaline waters, i.e., Campignol (CAM) and the Camargue lagoons Grande Palun (GP), Scamandre (SC), Charnier (CH), and Crey (CR). The Lowest and highest median salinities (0.9 and 41.6) were recorded in the Grande Palun lagoon (GP) and in the western sector of the Pierre-Blanche lagoon (PBW), respectively (Fig. 2). Salinity showed important between-year fluctuations in the Canet lagoon sectors (CNN, CNS), whereas deeper lagoon sectors with a greater marine influence such as Thau (TW, TE), Diana (DIA), and Urbino (URB) showed minor salinity fluctuations. For Scamandre (SC), Charnier (CH), and Crey (CR), the salinity was only recorded in 2013. A north–south salinity gradient was observed in Bages lagoon with a lowest median salinity recorded in the north part of the lagoon (BGN, 15.5), whereas the highest median salinity was recorded in the south part (BGS, 29.6), which is connected to sea by an inlet. In

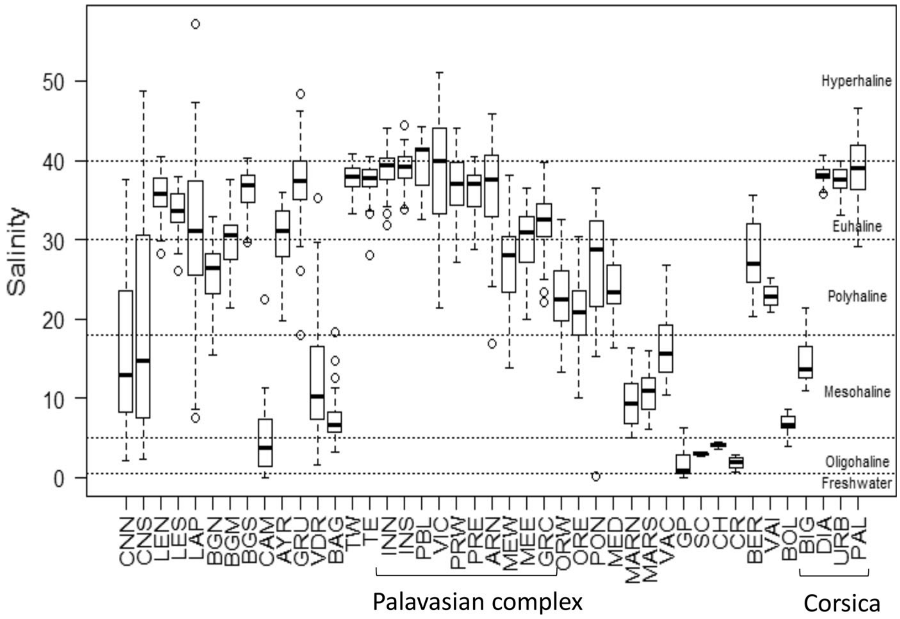


Fig. 2 Distribution of the salinity in the 43 Mediterranean lagoon sectors ordered geographically from west to east along the French Mediterranean coast. Box and whiskers plots from data (June, July, and August) between years: the whiskers represent the 5th and the 95th percentiles, the outer edges of the boxes represent the 25th and 75th percentiles, and the horizontal line within the boxes represents the median. Salinity range from oligohaline and hyperhaline was defined according to the Venice System (1958)

Table 3 Overall median values and ranges (minimum, maximum) of the environmental variables. The codes and transformations used in the CCA are also indicated

Quantitative variables	Median	Min	Max	Code used in CCA	Transformation used in CCA
Salinity	33.9	0.1	47.8	Salinity	
Turbidity (NTU)	3.4	0.5	211	Turb	Log
Depth (m)	1.5	0.5	5.2	Depth	Log
Chlorophylle a ($\mu g.l^{-1}$)	3.9	0.2	397	Chl *a*	Log
Total nitrogen (μM)	39.4	6.03	463	TN	Log
Total phosphorus (μM)	1.33	0.13	57.3	TP	Log ($x + 1$)
Nitrate + nitrite (μM)	0.23	0.00	71.9	NO3_NO2	Log ($x + 1$)
Ammonium (μM)	0.58	0.00	107	NH4	Log
Phosphate (μM)	0.18	0.00	27.3	PO4	Log ($x + 1$)

the Palavasian lagoons, higher salinities were recorded in the west part (INN, INS, VIC, and PBL) than in the east part (PRW, PRE, MEW, MEE, and GRC). Among the Corsican lagoons studied, only Biguglia (BIG) had mesohaline water, the other Corsican lagoons (DIA, URB, PAL) had euhaline waters.

Nutrient, Chlorophyll a, and turbidity

Table 3 shows the overall median, minimum and maximum values recorded for the nutrients, the turbidity, and the Chl *a* concentrations in the lagoon sectors. The mesohaline Canet lagoon (CNN), close to the Pyrenees (Fig. 1) showed the highest concentrations in PO4 (16.4 μM, IQR = 11.3 μM) and TP (30.5 μM, IQR = 14.0 μM), combined with high median values for Chl *a* concentrations and turbidity. PO4 and TP concentrations were 91- and 23-fold higher, respectively, than their corresponding grand median values for all lagoons together (cf., 0.18 μM for PO4 and 1.33 μM for the TP see Table 3). High concentrations of TP (> 5 μM) were also recorded in Vendres (VDR), Bolmon (BOL), Or (ORW, ORE), and in the east part of the Palavasian complex (MEW, MEE, and GRC). The Camargue lagoons (SC, CH, CR), Vendres (VDR), and Or (OR, ORE) lagoons had the highest concentrations in TN, Chl *a*, and turbidity with median values higher than

130 μM for TN, 50 μg l^{-1} for the Chl *a* and 20 NTU for the turbidity. The turbidity was also high (29.9 NTU, IQR = 22.4 NTU) in the Grande Palun lagoon (GP), whereas the TN concentration (37.2 μM, IQR = 14.8 μM) and Chl *a* (14.5 μg l^{-1}, IQR = 6.55 μg l^{-1}) were lower than those observed in other oligohaline lagoons from the Camargue area. An east–west gradient was observed along the Palavasian complex with higher turbidity, Chl *a*, and TN concentrations recorded in the east part (PRW, PRE, ARN, MEW, MEE, and GRC) than the west part (INN, INS, VIC, PBL). Furthermore, all the values recorded for these three parameters were higher in the Palavasian complex than the grand median values calculated for all lagoons studied (Table 3). The lowest median values for all the parameters were recorded in lagoons such as Ayrolle (AYR, i.e., PO4 < 0.07 μM, NO3_NO2 = 0.10 μM, TURB < 1.5 NTU), Leucate (LEN, LES), and the Corsican lagoons Urbino (URB) and Diana (DIA). The latter showed the lowest median values for TP (TP < 0.5 μM), while the lowest TN was observed in Diana (12.7 μM).

Macrophytes

A total of 127 species belonging to 76 genera were observed in the 43 lagoon sectors during the study period (Table 2). Fifty-one percent of the genera belonged to the phylum Rhodophyta, 25% to Ochrophyta, 13% to Chlorophyta, 8% to Tracheophyta (vascular plants), and 3% to the phylum Charophyta (*Chara* and *Lamprothamnium* genera). The six Tracheophyta belonged to the genera *Ceratophyllum*, *Myriophyllum*, *Cymodocea*, *Stuckenia*, *Zostera*, and *Ruppia.* Three different species of seagrasses "sensu stricto" according to (Larkum et al., 2006), were found, i.e., *Zostera marina* Linnaeus, *Zostera noltei* Horneman, and *Cymodocea nodosa* (Ucria) Ascherson, and two species belonging to the Potamogetonaceae, i.e., *Ruppia cirrhosa* (Petagna) Grande, and *Stuckenia pectinata* (Linnaeus) Börner. Figure 3

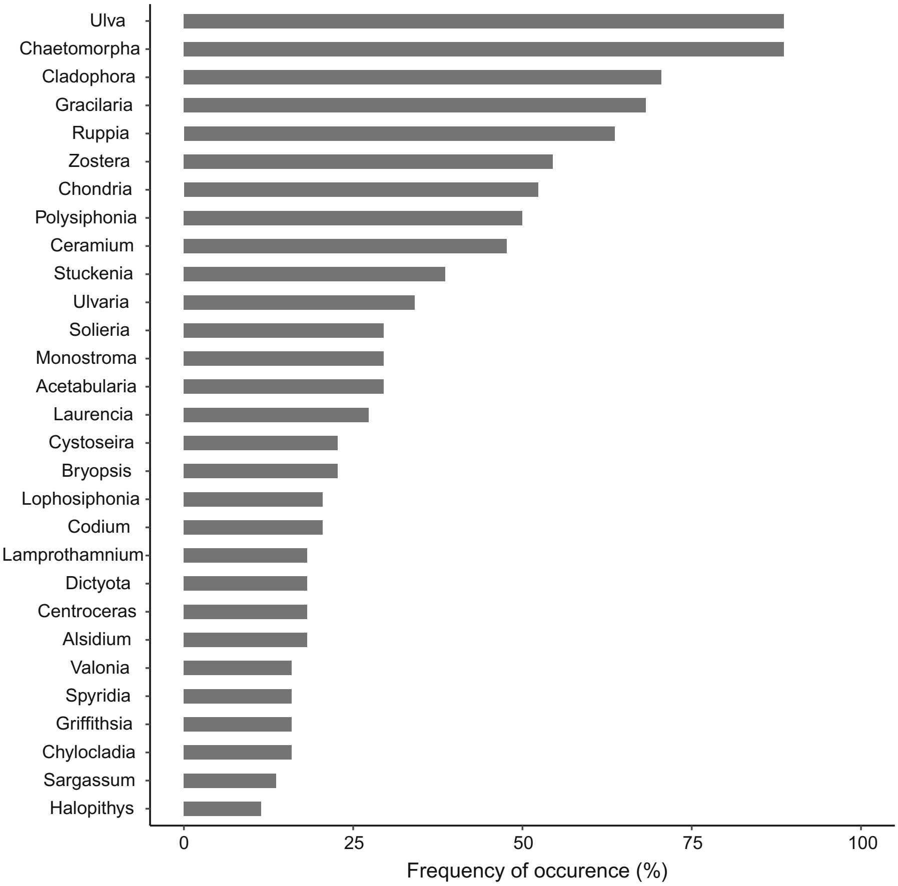


Fig. 3 Frequency of occurrence of the genera in the 43 lagoon sectors. Only genera with a frequency of occurrence > 10% are presented

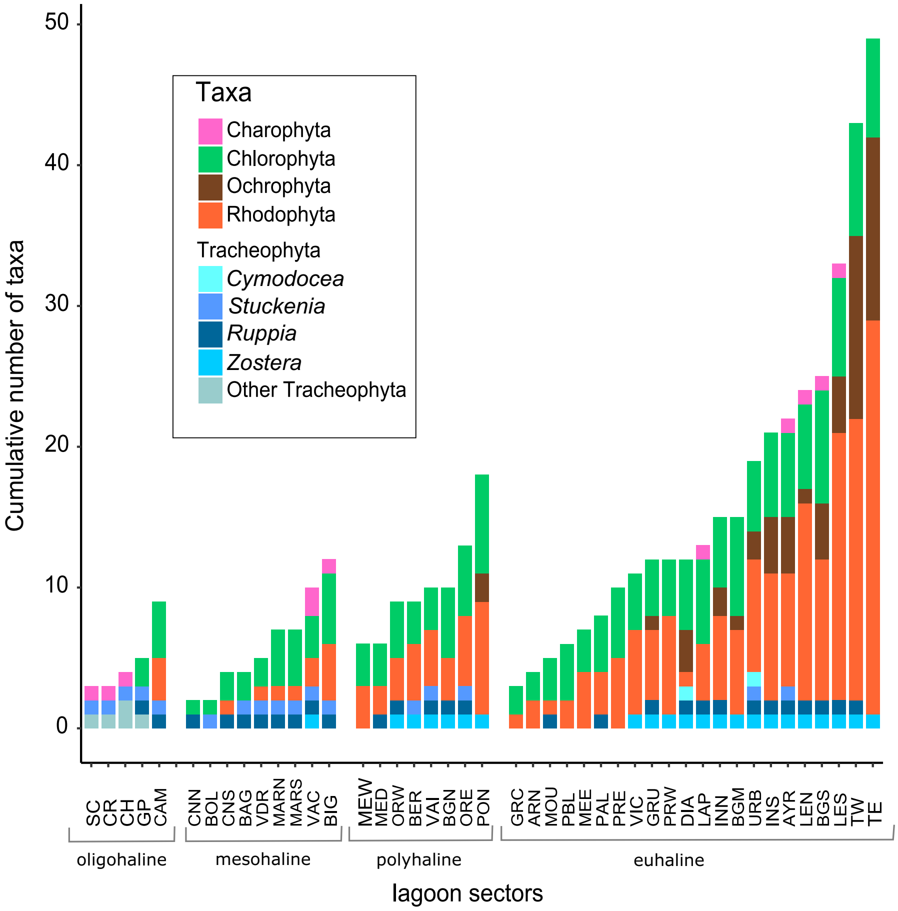


Fig. 4 Cumulative number of genera over the study periods in lagoon sectors. Sectors are grouped according to the salinity classification (see Fig. 2). The number of genera per phylum is represented as well as the main angiosperms (*Cymodocea*, *Stuckenia*, *Ruppia*, *Zostera*) belonging to the phylum Tracheophyta

shows the frequency of occurrence of the different macroalgal genera in the 43 Mediterranean lagoon sectors studied. The three most commonly occurring genera were the green algae *Ulva*, *Chaetomorpha*, and *Cladophora*. These taxa were found in more than 70% of the lagoon sectors. The Tracheophyta *Ruppia* and *Zostera*, as well as the red algae *Gracilaria, Chondria*, and *Polysiphonia* were present in more than 50% of the sectors (Fig. 3).

The cumulative numbers of taxa (at the genus level) observed throughout the study period in the different sectors are shown in Fig. 4. This maximum varied between 2, both in Bolmon (BOL) and in the North part of Canet (CNN), and 49 in the east part of the Thau lagoon (TE, Fig. 4). Lagoons with less than five genera observed were Bagnas (BAG), Arnel (ARN), Canet (CNN, CNS), Grec (GRC), Scamandre (SC), Charnier (CH), and Crey (CR). In contrast, Thau (TW, TE), Leucate (LEN, LES), Bages sud (BGS), Ayrolle (AYR), and Ingril sud (INS) had more than 20 genera observed. On average, oligohaline and mesohaline sectors had lower maximum genera numbers than polyhaline and euhaline sectors. However, large variation was observed in the euhaline group, where the maximum number of genera ranged from 3 in Grec (GRC) to 49 in the east part of the Thau lagoon (TE).

Only nine lagoons presented genera belonging to the phylum Charophyta: the species *Lamprothamnium papulosum* (K. Wallroth) J. Groves was present in Leucate (LES, LEN), Bages sud (BGS), Ayrolle (AYR), La Palme (LAP), Biguglia (BIG), Vaccarès (VAC); different species from the genus *Chara* were present in the Camargue lagoons Scamandre (SC), Charnier (CH), Crey (CR), and Vaccarès (VAC). The brown algae were present in nine lagoons: Thau (TW, TE), Leucate (LEN, LES), Bages (BGS, BGM), Ayrolle (AYR), Gruissan (GRU), Ingril nord (INN), Ingril sud (INS), Ponant (PON), Urbino (URB), and Diana (DIA). Genera from the phylum Tracheophyta were present in all the lagoons except in the eastern part of the Palavasian complex in Arnel (ARN), Prevost (PRE), Pierre Blanche (PBL), Méjean (MEW, MEE), and Grec (GRC). The seagrass *C. nodosa* was only observed in the Corsican lagoons Urbino (URB) and Diana (DIA). In the oligohaline Camargue lagoons, Scamandre (SC), Charnier (CH), and Crey (CR) no genera belonging to the Chlorophyta nor to the Rhodophyta phylum were observed (Fig. 4).

Relationship between macrophytes and environment

The CCA included the 43 lagoons sectors, the 50 genera, and the nine environmental variables listed above. The first three axes were highly significant ($P < 0.001$, 999 permutation) and accounted for 43.9, 17.7, and 14.7% of the total inertia, respectively (Table 4).

The ordination diagram of CCA shows, in an approximate way, the centers of the genera distributions along each environmental variable (Fig. 5) and the position of the sites (Fig. 6). The first axis was highly positively correlated with salinity and negatively with turbidity and TN (Table 4). Genera on the left side of axis 1 were found at lower salinities, higher turbidities, and higher TN concentrations (Fig. 5a). The genera *Chara* and *Myriophyllum* were mainly found in oligohaline lagoons such as Scamandre (SC), Charnier (CH), and Crey (CR) (Figs. 5a, 6a). *Stuckenia* was mainly found in oligohaline and mesohaline lagoons such as Grande Palun (GP), Bagnas (BAG), Bolmon (BOL), or Biguglia (BIG). Genera on the right side of axis 1 were mainly found in polyhaline and euhaline lagoon sectors. The second axis reflected a depth gradient (Fig. 5b), with taxa located on the lower side such as *Halopithys*, *Griffithsia*, or *Rytiphlaea* related to deeper euhaline lagoons sectors such as Thau (TW, TE), Leucate (LES), Urbino (URB), and Diana (DIA). Some taxa were only present in one single lagoon: *Grateloupia*, *Colpomenia*, *Cutleria*, and *Chorda* were only found in the Thau lagoon (TW, TE), whereas the seagrass *Cymodocea nodosa* was only found in the Corsican lagoons Urbino (URB) and Diana (DIA) (Figs. 5b, 6). Genera located in the upper part of the second axis, such as *Lamprothamnium* and *Acetabularia* were found mainly in shallow lagoons such as Ayrolle (AYR) and La Palme (LAP). Finally, the third axis reflects TP, Chl *a*, and PO4 gradients (Table 4; Fig. 5c). This axis can be defined as a gradient of trophic status. According to the level of eutrophication, two groups of lagoon sectors can be distinguished on this third axis (Fig. 6b). Lagoon sectors with lower Chl *a*, TP, and PO4 concentrations as in Ayrolle (AYR), La Palme (LAP), or Bages (BGN, BGM, and BGS) were projected on the positive part of the third axis (Fig. 6b). In these lagoons, taxa such as *Acetabularia*, *Zostera*, *Valonia*, *Centroceras*, *Lamprothamnium*, or *Spyridia* were observed (Fig. 5d). On the negative part of axis 3, lagoon sectors from the Palavasian complex (e.g., GRC, MEW, MEE, PBL, ARN) were characterized by higher Chl *a*, TP, and PO4 concentrations and by the genera *Ulva*, *Gracilaria*, or *Solieria* (Figs. 5d, 6b). *Ulva*, *Gracilaria*, and *Solieria*, located on the lower central part of the diagram are ubiquist genera present in many lagoons. However, they were mainly present in the most eutrophicated sectors with high concentrations of Chl *a* and TP and PO4.

Following the CCA analysis, the clustering allowed to classify the lagoon sectors according to the presence of genera and environmental parameters (Fig. 6a, b). Thus, five groups were identified according to the Calinski–Harabasz criterion: one group comprising oligohaline and mesohaline sectors, one intermediate

Table 4 Percentage of variation, relative eigenvalues, and correlation coefficients between environmental variables and the first three CCA axes

	Axis 1	Axis 2	Axis 3
Variation (%)	43.90	17.73	14.69
Eigenvalues	0.43	0.17	0.14
Salinity	0.84	0.24	−0.08
Turb	−0.73	−0.02	−0.54
Depth	0.55	−0.78	0.12
Chl *a*	−0.58	−0.33	−0.70
TN	−0.72	0.09	−0.51
TP	−0.54	−0.02	−0.77
NO3_NO2	−0.31	0.02	−0.28
NH4	−0.34	0.07	−0.39
PO4	−0.24	0.05	−0.70

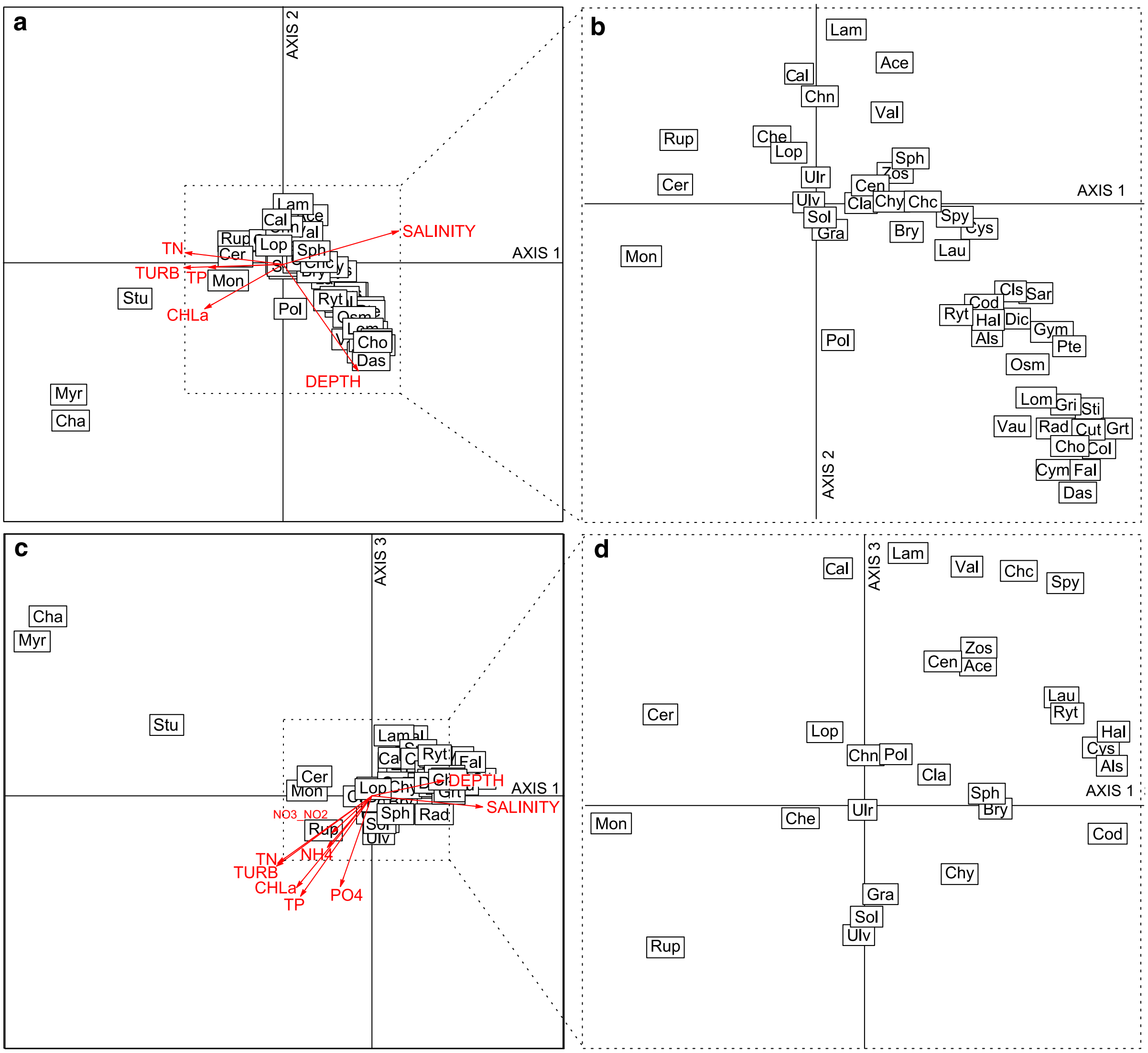


Fig. 5 CCA biplots with the genera (in boxes) and environmental variables (red arrows) in the factorial planes 1–2 (**a**, **b**) and 1–3 (**c**, **d**). Arrows are drawn for the most important variables only. See Table 2 for the environmental variable abbreviations. The dotted line squares (**b**, **d**) represent a zoom of the biplots offering a more detailed view of the genera. The names of the genus codes are defined in Table 3. Rare genera (< 1%) were not included in the analysis

group mainly comprising mesohaline sectors but also some oligohaline and polyhaline sectors during certain periods, and three groups among the polyhaline and euhaline sectors i.e., (i) deep lagoon sectors, (ii) oligotrophic and mesotrophic sectors, and (iii) eutrophic to hypertrophic lagoon sectors (Fig. 6a, b). Hence, water column depth and trophic status clearly impact the macrophyte community composition in the polyhaline and euhaline lagoons. Large variations of nutrient concentrations occurred both among oligohaline and mesohaline lagoons. Nevertheless for the oligohaline and mesohaline sectors, the CCA did not show the very strong differences in macrophyte genera in relation to the variable nutrient concentrations, as observed in polyhaline and euhaline sectors. In addition, the oligohaline and mesohaline lagoons studied were all shallow (< 1.5 m), which did not allow us to study depth as a structuring factor for these lagoons. Hence, in our analysis, neither depth, nor nutrient concentrations were clearly discernable as

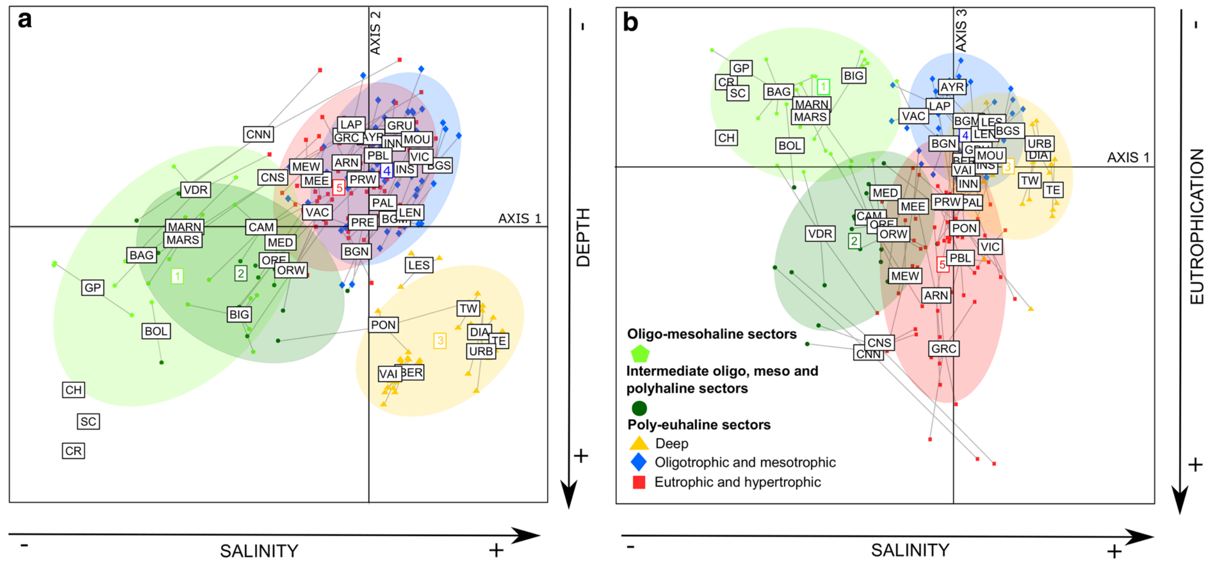


Fig. 6 Visualization of the CCA diagram showing the spatial ordination of lagoon sectors in the factorial planes 1–2 (**a**) and 1–3 (**b**). Points associated to each sector by a line represent a sampling date. In the factorial plane 1–2 (**a**), the hierarchical clustering reveals 2 main groups according to the salinity along the first axis: oligohaline and mesohaline groups (in light green polygons and dark green circles), polyhaline and euhaline groups (blue diamonds, red squares, and yellow triangles). The second axis is related to depth and deeper sectors are represented by yellow squares. On the third axis (**b**), lagoon sectors are distributed along an eutrophication gradient, separating oligotrophic and mesotrophic sectors (blue diamonds) from eutrophic and hypertrophic sectors (red squares). Ellipse contains 95% of points

structuring factors for the macrophyte communities in oligohaline and mesohaline lagoons.

Discussion

The French Mediterranean lagoons located in the adjacent Gulf of Lion, Côte d'Azur and Tyrrhenian Sea (E. Corsica), for which we studied 43 lagoon sectors in 34 lagoons, represent a large spectrum of lagoon types and a wide range of environmental conditions. Our hypothesis that water chemistry and depth determine the communities of aquatic macrophytes in these coastal lagoons is clearly supported by our analysis of the long-term dataset, as we were able to explain 76.3% of the variability of aquatic macrophyte communities in the CCA by the selected factors. Our study, however, focused on the macrophyte communities during late spring or early summer, and, therefore, we have overlooked some cold-loving species that may develop in autumn or winter as e.g., Ochrophyta. Another drawback in our study is that the water chemistry was only sampled from June to August, which does not give a full description of the annual fluctuations of nutrient concentrations and salinities, although this period of sampling provides a very good indicator for the eutrophication status (Souchu et al., 2010). Salinities are maximal during summer. Nevertheless, we checked our classification of salinity classes with the classification based on annual salinity measurements (Bec et al., 2011; Sanchez & Grillas, 2012) and generally found good agreement. Thus, we found that the observed salinity was the main variable driving the distribution of submerged macrophytes in late spring and summer, explaining more than 40% of the variance. Collectively, the environmental and macrophyte data allowed to identify four different groups of lagoon sectors. Two major groups of lagoon sectors were separated according to the salinity gradient. Nested within the group of euhaline and polyhaline sectors, we identified a group of deep lagoon sectors and two groups of shallow lagoon sectors distributed along a eutrophication gradient. In the following discussion, we aim to disentangle the impacts of salinities and the eutrophication status on these communities.

Salinity

CCA analysis showed that salinity was the main variable explaining the distribution of submerged macrophytes (43.9% of the variance). This is in agreement with many studies that have shown that the distribution and abundances of macrophytes are related to the tolerated salinity range (Vaquer & Heurteaux, 1989; Adams et al., 1992; Menéndez et al., 2002; Greve & Binzer, 2004; Vincent et al., 2006; Casagranda & Boudouresque, 2007; Christia & Papastergiadou, 2007; Lirman et al., 2008; Obrador & Pretus, 2008; Schubert et al., 2011; Antunes et al., 2012). Along this gradient, two main groups emerged from the CCA, i.e., a group comprising oligohaline and mesohaline sectors and another group comprising polyhaline and euhaline sectors. In addition, an intermediate group emerged, mainly comprising mesohaline sectors with high salinity variability. Oligohaline and mesohaline sectors harbor freshwater macrophytes tolerant to brackish conditions. One characteristic example is *Stuckenia pectinata*, which tolerates brackish waters with salinity up to 10 (Van Wijk, 1988). This species is highly productive at salinities of 0 and 5 (Teeter, 1965; Borgnis & Boyer, 2016). Although it is less productive at a salinity of 10, it is able to double in biomass and increase the shoot number. In addition, a previous study found that a salinity of 15 reduced production or proved fatal for many plants (Teeter, 1965). Inversely, polyhaline and euhaline lagoon sectors harbor both brackish and marine taxa.

Furthermore, the CCA analysis also showed that the presence of the genera in oligohaline lagoon sectors was also related to higher turbidity and total nitrogen content. In coastal lagoons, nutrient inputs and eutrophication can lead to an increase of the turbidity in the water column. Although increasing turbidity is often caused by phytoplankton growth due to nutrient inputs, turbidity could also be due to sediment resuspension. In fact, in shallow coastal lagoons, type of substrate, sediment resuspension due to the wind (Lawson et al., 2007; Millet et al., 2010), and bioturbation (Scheffer et al., 1993) can increase the amount of suspended solids in the water column. Moreover, turbidity is more persistent in oligohaline lagoons due to very low settling velocity of suspended solids (at salinity < 5), thus reducing light availability for plants (Charpentier et al., 2005). Hence, frequent natural windy conditions, which are common in the South of France favor sediment resuspension that persists in oligohaline lagoons for longer periods (Sanchez & Grillas, 2013).

Turbidity impacts the abundance and the distribution of submerged macrophytes in aquatic environments (Scheffer et al., 1992; Obrador & Pretus, 2008; Zaldívar et al., 2008). However, taxa such as *Stuckenia pectinata* have a specific strategy of extended stem growth thus locating its leaves just below the water surface in a floating canopy. This strategy allows this species to use light resources more efficiently (Van Wijk, 1988). As observed in other regions of the Mediterranean sea (Verhoeven, 1980; Christia & Papastergiadou, 2007; Prado et al., 2013), *S. pectinata* can coexist in oligohaline lagoons with taxa such as *Myriophyllum spicatum* Linnaeus and charophytes, i.e., *Chara aspera* C.L Willdenow, *Chara tomentosa* Linnaeus, and *Chara hispida* Linnaeus. *S. pectinata* is therefore a better competitor for light compared with submerged macrophytes such as the bottom-covering *Chara* species (den Berg et al., 1999; Bakker et al., 2010). In oligohaline lagoons, most of charophytes are sensitive to eutrophication and have a low tolerance to turbidity (Blindow, 1992; Coops, 2002; Mouronval & Baudouin, 2010). *M. spicatum* is a very competitive freshwater species which can develop in turbid and eutrophicated waters (Mouronval & Baudouin, 2010), this fast-growing species often forms a thick canopy shading out other aquatic plants. Because *S. pectinata* is more salt tolerant than *M. spicatum,* it is a better competitor at the salinities occurring in oligohaline lagoons. Moreover, *S. pectinata* is also dominant in mesohaline lagoons. These species co-exists with brackish and marine taxa such as *R. cirrhosa* and *Z. noltei*. However, a suite of life history traits makes *S. pectinata* more competitive than *R. cirrhosa* at lower salinity (< 10) and at lower water transparency (Verhoeven, 1980; Van Wijk, 1988; Menéndez & Comín, 1989; Prado et al., 2013). In the same way, seagrasses, such as *Zostera*, are well adapted to sudden changes and could grow at salinities ranging between 5 and 45 (Greve & Binzer, 2004), but they are less competitive than *S. pectinata* in oligo-mesohaline waters.

Remane (1934) showed a minimum of diversity for invertebrates along the salinity gradient and a critical salinity zone (5–8) was defined by Kinne (1971) where species number was lower. Recently, Telesh et al.

(2013) showed that such a critical salinity zone also exist for macrophytes. The same trend was observed in oligo-mesohaline lagoons where the number of taxa was generally lower than in poly-euhaline lagoons (Fig. 4).

The macrophyte distribution in polyhaline and euhaline lagoons was explained by two other factors, i.e., depth (17.7% of the variance in the CCA) and eutrophication level (14.7% of the variance). Hereafter, the macrophyte distribution patterns are sequentially discussed for these two factors.

Depth

Depth is also an important structuring factor in the distribution of aquatic macrophytes (Vincent et al., 2006; Christia & Papastergiadou, 2007). In most of the deepest lagoon sectors e.g., Thau (TW, TE), south part of Leucate (LES), Diana (DIA), Urbino (URB), a higher salinity (euhaline) was observed, with less fluctuation than in shallowest sectors. Due to their higher volume, and their connection to the sea, these lagoons are less affected by salinity variations. Deep lagoons, in particular Thau lagoon, have a higher number of taxa than other lagoons: the seagrasses *Z. marina* and *Z. noltei*, marine macroalgae such as the red algae *Halopithys incurva* (Hudson) Batters, *Alsidium corralinum* C. Agardh, and also marine exotic species such as *Griffithsia corralinoides* (Linnaeus), Trevisan, *Sargassum muticum* (Yendo) Fensholt, or *Codium fragile* (Suringar), Hariot. *H. incurva* often associated with *Zostera*, *Rytiphlaeae tinctoria* (Clemente),C. Agardh, and *A. corallinum* constituted a permanent group in the west part of this lagoon (Dubois & Lauret, 1991; Gerbal & Verlaque, 1995).

Both quality and quantity of light change with depth. Irradiance decreases with depth and water strongly absorbs the red radiations of the light spectrum. For most submerged aquatic vegetation, light defines the lower limit of their depth distribution (Greve & Binzer, 2004). Hence, some macrophytes and most red algae are more adapted to lower irradiance and usually thrive best in deeper water (Häder & Figueroa, 1997). Seagrasses are able to colonize down to the depth receiving, on the average 11% of the surface light (Duarte, 1991). *Zostera noltei* generally found in shallow waters was observed at 7.5-m deep in TE, whereas *Zostera marina* was found in deeper sites until 9-m deep (Gerbal & Verlaque, 1995). In the Thau lagoon (TE, TW), the red algae *Solieria chordalis* (C. Agardh), J. Agardh, characteristic of deep areas (Gerbal & Verlaque, 1995), was mainly present in depth higher than 4 m. Nevertheless, this species was also found in eutrophicated lagoon sectors with high turbidity levels such as Arnel (ARN), Méjean (MEW, MEE), and Prévost (PRW, PRE).

In addition, deep lagoons showed high proportion of exotic species. This is probably not only related to depth as an ecological driver, but rather the result of the fact that most of the deeper lagoons are used for shellfish farming. Verlaque (2001) described the Thau lagoon as a hot spot of marine species introduction in Europe. More than 20% of the macrophytes species of the Thau lagoon were introduced through shellfish farming. The majority (43 genera) may originate from the Pacific region; the transfer of oysters is a highly probable vector of macrophytes introduction, particularly for those genera that develop on hard substrates. Although many introduced species in Thau and Leucate lagoons have been mainly reported for hard substrates (Verlaque, 2000), we observed some exotic species on soft-bottom substrate (Table 3).

Eutrophication

A third major gradient corresponding to the eutrophication level (14.7% of the variance in the CCA) divided the polyhaline and euhaline lagoon sectors into two groups: on one hand, hypertrophic and eutrophic sectors, and on the other hand, mesotrophic and oligotrophic sectors. Our study showed that lagoons with a low nutrient and Chl *a* concentrations e.g., Ayrolle (AYR), La Palme (LAP), were characterized by the presence of perennial macrophytes such as *Zostera* (*Z. marina* and *Z. noltei*), the Charophyte *Lamprothamnium papulosum* (the only representative of this phylum in these lagoons), and macroalgae such as *Acetabularia acetabulum* (Linnaeus) P.C. Silva or *Centroceras clavulatum* (C. Agardh) Montagne. Inversely, sectors with higher turbidity, Chl *a* and nutrient concentrations in the water column e.g., east part of the Palavasian complex: Méjean (MEW, MEE), Prévost (PRW, PRE), Grec (GRC), Arnel (ARN) were characterized by the presence of opportunistic algae from the genus *Ulva*, *Gracilaria*, or *Solieria*. The high level of eutrophication in these lagoon sectors is due to excess nutrient inputs over the last decades (Leruste et al., 2016). Hence, our results confirm and illustrate the schematic model of Schramm (Schramm & Nienhuis, 1996; Schramm, 1999) and observations made by several authors in lagoons and coastal ecosystems (Sand-Jensen & Borum, 1991; Duarte, 1995; Schramm & Nienhuis, 1996; Burkholder et al., 2007; Viaroli et al., 2008; Zaldívar et al., 2008) where under low nutrient and clear water conditions, extensive meadows of perennial seagrass species dominate, whereas increasing nutrient inputs enhance the growth of phytoplankton, fast-growing epiphytic macroalgae, and finally floating ephemeral macroalgae which alternate with phytoplankton communities. Under hypertrophic conditions, phytoplankton becomes the dominant primary producer and macroalgae disappear.

This community shift results not only in a loss of ecosystem components, but also in an impoverishment of the ecosystem complexity and organization (Viaroli et al., 2008). Our results showed a lower diversity in the most eutrophicated lagoon sectors with only few genera observed (e.g., *Gracilaria*, *Ulva*, *Solieria*) and the absence of brown algae and angiosperms (Fig. 4). However, macroalgal blooms involve relatively few taxa. Among these taxa, we can cite the opportunistic, free floating macroalgae: *Gracilaria* and *Ulva* which indicate a degraded-eutrophic status which is characterized by high nutrient conditions. These taxa outcompete with benthic perennial macrophytes because they are more adapted to high turbidity, lower irradiance, and nutrient supply. *Ulva* and *Gracilaria* are nitrophilic species (Gerbal & Verlaque, 1995) and the rate of growth of these fast-growing macroalgae increases with increasing dissolved inorganic nitrogen supply (Teichberg et al., 2010). Hence, *Ulva* and red algae such as *Gracilaria* or *Solieria* outcompete other primary producers due to their ability to store nitrogen and phosphorus, but also in the case of the *Gracilaria* to lower light intensity requirement. In our results, the excess of DIP and the high TP concentrations in the most eutrophicated lagoons (e.g., MEW, GRC), suggest that P was not limiting the primary production as described by Souchu et al. (2010). These authors conclude in a studied of 20 coastal French Mediterranean lagoons, that increase of DIP along the eutrophication gradient is explained by the P content of lagoon sediments and that recycling processes strongly affect inorganic nutrient concentrations in the water column. The nitrogen limitation in eutrophicated lagoons is thus related to high TP and PO4 concentrations in the water column. The primary growth limiting nutrient may shift from P alone in oligotrophic lagoons to N alone as eutrophication proceeds (Souchu et al., 2010).

We showed that the vegetal succession along a eutrophication gradient described by Schramm (Schramm & Nienhuis, 1996; Schramm, 1999) is clearly applicable for the shallow polyhaline and euhaline coastal lagoons (Fig. 7), at least for the NW Mediterranean region. The submerged aquatic vegetation under oligotrophic conditions comprises seagrasses and slow-growing algae (Orfanidis et al. 2008), while opportunistic macroalgae and phytoplankton dominate under eutrophic and hypertrophic conditions, respectively (see Fig. 7d). Viaroli et al. (2008) argue that the two successional stages, i.e., the rooted angiosperms and the opportunistic macroalgae, represent two alternative stable states. Nevertheless, our analysis did not allow us to show that these two stages represented coexisting attraction basins representing clearly alternative states for a given window of environmental conditions. In contrast, for the oligohaline and mesohaline lagoons, the Schramm scheme does not fully comply. This is related to the predominance of members from the Potamogetonaceae in these lagoons that have a particular growth form capable of extended stem growth with many floating leaves (Van Wijk, 1988). This strategy allows these species to expose their leaves to the high light intensities in the surface layer of the lagoon and thus, to escape from the shading caused by dense phytoplankton and floating macroalgae. This way, these Potamogetonaceae species are able to coexist with the latter and can, therefore, persist at higher levels of eutrophication than the typical seagrass species in the polyhaline and euhaline lagoons. Therefore, we hypothesize that the succession of primary producer's along a eutrophication gradient in oligohaline and mesohaline lagoons (Fig. 7b, c) resembles the scheme described by (Sand-Jensen & Borum, 1991) for small temperate lakes, which is depicted in Fig. 7a. In agreement with our results and observations, we assume that in oligohaline and mesohaline lagoons, smaller submerged bottom dwelling macrophytes (e.g., particularly Charophytes in oligohaline lagoons) dominate in the oligotrophic status, although often coexisting with small populations of *S. pectinata*. With increasing eutrophication level, this Potamogetonaceae increase in biomass in concert with

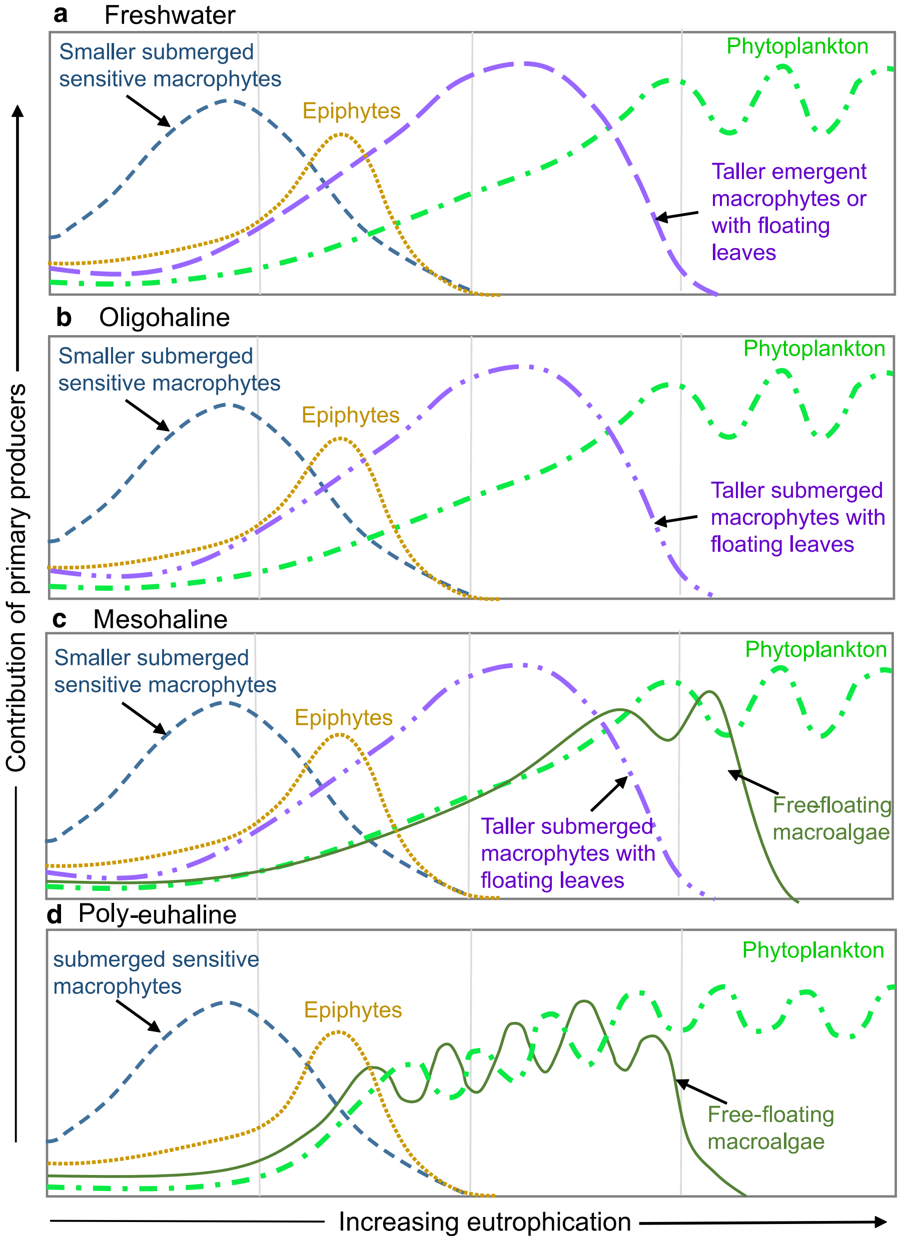


Fig. 7 Conceptual representation of the relative succession of primary producers along an increasing eutrophication gradient in (**a**) shallow temperate lakes [modified from Sand-Jensen (1980), Sand-Jensen and Borum (1991)], (**b**) oligohaline and (**c**) mesohaline lagoons [this study],(**d**) polyhaline and euhaline lagoons [modified from Schramm (Schramm & Nienhuis, 1996)]

phytoplankton and with opportunistic macroalgae, the latter particularly in mesohaline lagoons (Fig. 7c). The fact that *S. pectinata* are present over a very wide range of eutrophication levels explains why in our CCA analysis we could not discern the impact of eutrophication levels as a structuring driver for the macrophyte community composition in the oligohaline and mesohaline lagoons. The conceptual scheme we propose in Fig. 7 needs to be validated by more data on biomass and coverage of macrophyte taxa in oligohaline and mesohaline lagoons with contrasting trophic levels.

The general trend of macrophyte taxa suggested in Fig. 7 is probably more adapted in the French lagoons or Mediterranean lagoons with nanotidal conditions and less pertinent for the microtidal Italian lagoons in the Norther Adriatic Sea. However, nanotidal conditions are widespread in the Mediterranean and tides exceeding 50 cm only occur in the Northern Adriatic and the Gulf of Gabès (Tunisia). Nevertheless, the coexistence of Charophytes and *S. pectinata* has also been observed in a Western Greek lagoon by Christia & Papastergiadou (2007) under low salinity and small fluctuation of this parameter. However, more biogeographic data are needed to extrapolate our findings to the ensemble of nanotidal lagoons in the whole Mediterranean Sea.

Other factors

Even though a significant portion of the macrophyte distribution could be attributed to salinity, depth, and trophic status, yet a portion (24% of the CCA) remains unexplained. The two main reasons for undetermined variation are the lack of other relevant explanatory variables and stochastic variations in taxa distribution. Stochastic fluctuations are impossible to quantify and remain unexplained in a statistic analysis (Borcard et al., 1992). Other abiotic and biotic factors may drive the macrophyte community structure. These may include, other factors related to water chemistry as e.g., oxygen, pH, and chemical contaminants. In this respect, pH and oxygen are subject to strong diurnal fluctuations related to the community metabolism in the lagoon and we were, therefore, unable to take these into account due to the large variability of sampling in our database. Non-chemical factors include hydrodynamics, physical exposure, substratum, grazing, interspecific, and intraspecific competition. Among these factors, hydrodynamics play an important role in spatial and temporal distribution of macroalgae, transporting plants and influencing chemical characteristics in the water column and in the sediment (Flindt et al., 1999), impacting the connectivity between the adjacent Mediterranean sea and the lagoons (Fiandrino et al., 2017). Furthermore, coastal lagoons can be highly impacted by chemical contaminants (Munaron et al., 2012) and some of these compounds can impact the photosynthesis and the growth of macrophytes (Haynes et al., 2000; Chesworth et al., 2004). Future studies need to focus on the impact of these factors on the macrophyte communities.

Acknowledgements This study was supported by a Ph.D. Grant for Ines Le Fur, financed by Ifremer and the French Water Agency (Agence de l'Eau Rhône Méditerranée Corse). The authors thank the staff of the Ifremer laboratory in Languedoc-Roussillon and PACA, the Tour du Valat institute, lagoons managers of the GIPREB and of the Réserve Nationale de Camargue and all surveyors involved in the collection of the data on which this article is based.

References

Adams, P., J. C. Thomas, D. M. Vernon, H. J. Bohnert & R. G. Jensen, 1992. Distinct cellular and organismic responses to salt stress. Plant and Cell Physiology 33: 1215–1223.

Agostini, S., G. Pergent & B. Marchand, 2003. Growth and primary production of *Cymodocea nodosa* in a coastal lagoon. Aquatic Botany 76: 185–193.

Anonymous, 1958. The Venice System for the classification of marine waters according to salinity. Limnology and Oceanography 3: 346–347.

Anthony, A., J. Atwood, P. August, C. Byron, S. Cobb, C. Foster, C. Fry, A. Gold, K. Hagos, L. Heffner, D. Kellogg, K. Lellis-Dibble, J. Opaluch, C. Oviatt, A. Pfeiffer-Herbert, N. Rohr, L. Smith, T. Smythe, J. Swift & N. Vinhateiro, 2009. Coastal lagoons and climate change: ecological and social ramifications in U.S. Atlantic and Gulf Coast ecosystems. Ecology and Society 14: 8.

Antunes, C., O. Correia, J. M. da Silva, A. Cruces, M. Conceição Freitas & C. Branquinho, 2012. Factors involved in spatiotemporal dynamics of submerged macrophytes in a Portuguese coastal lagoon under Mediterranean climate. Estuarine, Coastal and Shelf Science 110: 93–100.

Bakker, E. S., E. Van Donk, S. A. J. Declerck, N. R. Helmsing, B. Hidding & B. A. Nolet, 2010. Effect of macrophyte community composition and nutrient enrichment on plant biomass and algal blooms. Basic and Applied Ecology 11: 432–439.

Barnes, R. S. K., 1980. Coastal Lagoons; the Natural History of a Neglected Habitat. Cambridge University Press, Cambridge.

Bec, B., Y. Collos, P. Souchu, A. Vaquer, J. Lautier, A. Fiandrino, L. Benau, V. Orsoni & T. Laugier, 2011. Distribution of picophytoplankton and nanophytoplankton along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Aquatic Microbial Ecology 63: 29–45.

den Berg, M. S. V., M. Scheffer, E. V. Nes & H. Coops, 1999. Dynamics and stability of *Chara* sp. and *Potamogeton pectinatus* in a shallow lake changing in eutrophication level. Hydrobiologia 408–409: 335–342.

Blindow, I., 1992. Decline of charophytes during eutrophication: comparison with angiosperms. Freshwater Biology 28: 9–14.

Borcard, D., P. Legendre & P. Drapeau, 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055.

Borgnis, E. & K. E. Boyer, 2016. Salinity tolerance and competition drive distributions of native and invasive submerged aquatic vegetation in the upper San Francisco estuary. Estuaries and Coasts 39: 707–717.

Brock, M. A., 1986. Adaptation to fluctuations rather than to extremes of environmental parameters. In Deckker, P. D. & W. D. Williams (eds), Limnology in Australia. Springer, Netherlands: 131–140.

Caliński, T. & J. Harabasz, 1974. A dendrite method for cluster analysis. Communications in Statistics 3: 1–27.

Burkholder, J. M., D. A. Tomasko & B. W. Touchette, 2007. Seagrasses and eutrophication. Journal of Experimental Marine Biology and Ecology 350: 46–72.

Casagranda, C. & C. F. Boudouresque, 2007. Biomass of *Ruppia cirrhosa* and *Potamogeton pectinatus* in a Mediterranean brackish lagoon, Lake Ichkeul, Tunisia. Fundamental and Applied Limnology 168: 243–255.

Castel, J., P. Caumette & R. Herbert, 1996. Eutrophication gradients in coastal lagoons as exemplified by the Bassin d'Arcachon and the Étang du Prévost. Hydrobiologia 329: ix–xxviii.

Charpentier, A., P. Grillas, F. Lescuyer, E. Coulet & I. Auby, 2005. Spatio-temporal dynamics of a Zostera noltii dominated community over a period of fluctuating salinity in a shallow lagoon, Southern France. Estuarine, Coastal and Shelf Science 64: 307–315.

Chesworth, J. C., M. E. Donkin & M. T. Brown, 2004. The interactive effects of the antifouling herbicides Irgarol 1051 and Diuron on the seagrass Zostera marina (L.). Aquatic Toxicology (Amsterdam, Netherlands) 66: 293–305.

Christia, C. & E. S. Papastergiadou, 2007. Spatial and temporal variations of aquatic macrophytes and water quality in six coastal lagoons of western Greece. Belgian Journal of Botany 140: 39–50.

Cloern, J. E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series 210: 223–253.

Coops, H., 2002. Ecology of charophytes: an introduction. Aquatic Botany 72: 205–208.

Cromwell, J. E., 1971. Barrier coast distribution: a world-wide survey. Second National Coastal Shallow Water research Conference. Baton Rouge, LA: 50.

de Jonge, V. N., M. Elliott & E. Orive, 2002. Causes, historical development, effects and future challenges of a common environmental problem: eutrophication. Hydrobiologia 475–476: 1–19.

De Wit, R., 2011. Chapter 2. Biodiversity of coastal lagoon ecosystems and their vulnerability to global change. Ecosystems Biodiversity: 29–40.

Dennison, W. C., 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquatic Botany 27: 15–26.

Dray, S. & A.-B. Dufour, 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22: 1–20.

Duarte, C. M., 1991. Seagrass depth limits. Aquatic Botany 40: 363–377.

Duarte, C. M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41: 87–112.

Duarte, C. M. & J. Cebrián, 1996. The fate of marine autotrophic production. Limnology and Oceanography 41: 1758–1766.

Dubois, A. & M. Lauret, 1991. Macroflore benthique. In ECOTHAU, synthèse des résultats, D.Jouffre et M.Amanieu éditeurs. Laboratoire d'Hydrologie marine et continentale, Université Montpellier II: 115–118

Eisma, D., 1998. Intertidal Deposits: River Mouths, Tidal Flats, and Coastal Lagoons. CRC Press, Boca Raton.

European Commission (EC), 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework community actions in the field of water policy. Official Journal of the European Communities L327,1-73.22.12.2000.

Fiandrino, A., V. Ouisse, F. Lagarde, R. Pete, S. Le Noc & R. de Wit, 2017. Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. Marine Pollution Bulletin 119: 132–144.

Flindt, M. R., M. A. Pardal, A. I. Lillebø, I. Martins & J. C. Marques, 1999. Nutrient cycling and plant dynamics in estuaries: a brief review. Acta Oecologica 20: 237–248.

Fonseca, M. S. & W. J. Kenworthy, 1987. Effects of current on photosynthesis and distribution of seagrasses. Aquatic Botany 27: 59–78.

Gerbal, M. & M. Verlaque, 1995. Macrophytobenthos de substrat meuble de l'étang de Thau (France, Méditerranée) et facteurs environnementaux associés. Oceanologica Acta 18: 557–571.

Glibert, P. M., D. C. Hinkle, B. Sturgis & R. V. Jesien, 2014. Eutrophication of a Maryland/Virginia coastal lagoon: a tipping point, ecosystem changes, and potential causes. Estuaries and Coasts 37: 128–146.

Graffelman, J. & R. Tuft, 2004. Site scores and conditional biplots in canonical correspondence analysis. Environmetrics 15: 67–80.

Greve, T. M. & T. Binzer, 2004. Which factors regulate seagrass growth and distribution? In Borum, J et al. (ed.), European Seagrasses: An Introduction to Monitoring and Management.

Guerlorget, O. & J. P. Perthuisot, 1992. Paralic ecosystems. Biological organization and functioning. Vie Milieu 42: 215–251.

Guiry, M. D. & G. M. Guiry, 2016. AlgaeBase. World-wide electronic publication. National University of Ireland, Galway [available on internet at http://www.algaebase.org].

Häder, D. & F. L. Figueroa, 1997. Photoecophysiology of marine macroalgae. Photochemistry and Photobiology 66: 1–14.

Hansen, J. W., J. W. Udy, C. J. Perry, W. C. Dennison & B. A. Lomstein, 2000. Effect of the seagrass Zostera capricorni on sediment microbial processes. Marine Ecology Progress Series 199: 83–96.

Hartvig, C., N. Kjell Magnus & F. Stein, 2009. Macrophytes as habitat for fauna. Marine Ecology Progress Series 396: 221–233.

Haynes, D., P. Ralph, J. Prange & B. Dennison, 2000. The impact of the herbicide diuron on photosynthesis in three species of tropical seagrass. Marine Pollution Bulletin 41: 288–293.

Hurd, C. L., P. J. Harrison, K. Bischof & C. S. Lobban, 2014. Seaweed Ecology and Physiology. Cambridge University Press, Cambridge, NY.

Ifremer, 2007. Réseau de Suivi Lagunaire du Languedoc-Roussillon: Bilan des résultats 2006.

Ifremer, Cepralmar, Agence de l'Eau RMC, & Région Languedoc-Roussillon, 2011. Guide de reconnaissance et de suivi des macrophytes des lagunes du Languedoc-Roussillon.

Kennish, M. J. & H. W. Paerl, 2010. Coastal Lagoons: Critical Habitats of Environmental Change. CRC Press, Boca Raton.

Kinne, O., 1971. Salinity: animals-invertebrates. Marine Ecology 1: 821–995.

Kjerfve, B., 1994. Chapter 1. Coastal lagoons. In Kjerfve, B. (ed.), Elsevier Oceanography Series. Elsevier, Amsterdam: 1–8.

Larkum, A., R. J. Orth & C. M. Duarte, 2006. Seagrasses: Biology, Ecology and Conservation. Springer, The Netherland.

Lawson, S. E., P. L. Wiberg, K. J. McGlathery & D. C. Fugate, 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. Estuaries and Coasts 30: 102–112.

Leruste, A., N. Malet, D. Munaron, V. Derolez, E. Hatey, Y. Collos, R. De Wit & B. Bec, 2016. First steps of ecological restoration in Mediterranean lagoons: shifts in phytoplankton communities. Estuarine, Coastal and Shelf Science 180: 190–203.

Levin, L. A., D. F. Boesch, A. Covich, C. Dahm, C. Erséus, K. C. Ewel, R. T. Kneib, A. Moldenke, M. A. Palmer, P. Snelgrove, D. Strayer & J. M. Weslawski, 2001. The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4: 430–451.

Lirman, D., G. Deangelo, J. Serafy, A. Hazra, D. S. Hazra, J. Herlan, J. Luo, S. Bellmund, J. Wang & R. Clausing, 2008. Seasonal changes in the abundance and distribution of submerged aquatic vegetation in a highly managed coastal lagoon. Hydrobiologia 596: 105.

Littler, M. M. & D. S. Littler, 1984. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. Journal of Experimental Marine Biology and Ecology 74: 13–34.

McCune, B., 1997. Influence of noisy environmental data on canonical correspondence analysis. Ecology 78: 2617–2623.

McGlathery, K. J., K. Sundbck & I. C. Anderson, 2007. Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. Marine Ecology Progress Series 348: 1–18.

Menéndez, M. & F. A. Comín, 1989. Seasonal patterns of biomass variation of *Ruppia cirrhosa* (Petagna) Grande and *Potamogeton pectinatus* L. in a coastal lagoon. Scientia Marina 53: 633–638.

Menéndez, M. & F. A. Comín, 2000. Spring and summer proliferation of floating macroalgae in a Mediterranean coastal lagoon (Tancada Lagoon, Ebro Delta, NE Spain). Estuarine, Coastal and Shelf Science 51: 215–226.

Menéndez, M., O. Hernandez & F. A. Comin, 2002. Spatial distribution and ecophysiological characteristics of macrophytes in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 55: 403–413.

Millet, B., C. Robert, P. Grillas, C. Coughlan & D. Banas, 2010. Numerical modelling of vertical suspended solids concentrations and irradiance in a turbid shallow system (Vaccares, Se France). Hydrobiologia 638: 161–179.

Mouronval, J.-B. & S. Baudouin, 2010. Plantes aquatiques de Camargue et de Crau. Paris.

Munaron, D., N. Tapie, H. Budzinski, B. Andral & J.-L. Gonzalez, 2012. Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: results from a pilot survey using passive samplers. Estuarine, Coastal and Shelf Science 114: 82–92.

Neveux, J. & F. Lantoine, 1993. Spectrofluorometric assay of chlorophylls and phaeopigments using the least squares approximation technique. Deep Sea Research Part I: Oceanographic Research Papers 40: 1747–1765.

Obrador, B. & J. L. Pretus, 2008. Light regime and components of turbidity in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 77: 123–133.

Obrador, B. & J. L. Pretus, 2010. Spatiotemporal dynamics of submerged macrophytes in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 87: 145–155.

Oksanen, J., 2016. Design decisions and implementation details in vegan. Vignette of the package vegan. R package version 2.4-1.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2016. Vegan: Community Ecology Package. R package version 2.4-1.

Orfanidis, S., M. Pinna, L. Sabetta, N. Stamatis & K. Nakou, 2008. Variation of structural and functional metrics in macrophyte communities within two habitats of eastern Mediterranean coastal lagoons: natural versus human effects. Aquatic Conservation: Marine and Freshwater Ecosystems 18: S45–S61.

Orfanidis, S., K. Dencheva, K. Nakou, S. Tsioli, V. Papathanasiou & I. Rosati, 2014. Benthic macrophyte metrics as bioindicators of water quality: towards overcoming typological boundaries and methodological tradition in Mediterranean and Black Seas. Hydrobiologia 740: 61–78.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott & S. L. Williams, 2006. A global crisis for seagrass ecosystems. BioScience 56: 987–996.

Palmer, M. W., 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215–2230.

Pérez-Ruzafa, A., C. Marcos & I. M. Pérez-Ruzafa, 2011. Mediterranean coastal lagoons in an ecosystem and aquatic resources management context. Physics and Chemistry of the Earth, Parts A/B/C 36: 160–166.

Plus, M., A. Chapelle, P. Lazure, I. Auby, G. Levavasseur, M. Verlaque, T. Belsher, J.-M. Deslous-Paoli, J.-M.Zaldívar & C. N. Murray, 2003. Modelling of oxygen and nitrogen cycling as a function of macrophyte community in the Thau lagoon. Continental Shelf Research 23: 1877–1898.

Prado, P., N. Caiola & C. Ibáñez, 2013. Spatio-temporal patterns of submerged macrophytes in three hydrologically altered Mediterranean coastal lagoons. Estuaries and coasts 36: 414–429.

R development team, 2016. R: a language and environment for statistica computing. R foundation for Statistical Computing. Vienna, Austria, http://www.R-project.org.

Remane, A., 1934. Die Brackwasserfauna. Verhandlungen Der Deutschen Zoologischen Gesellschaft 36: 34–74.

Sanchez, A. & P. Grillas, 2012. Indicateur macrophytes dans les lagunes oligo-halines et mésohalines. Université Aix-Marseille, Tour du valat: 71.

Sanchez, A. & P. Grillas, 2013. Mise au point d'un indicateur DCE compatible pour les lagunes oligo et mésohalines. Tour du Valat: 66.

Sand-Jensen K., 1980. Balancen mellem autotrofe komponenter i tempererede soer med forskellig neringsbelastnig. Vatten 2: 80–89

Sand-Jensen, K. & J. Borum, 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. Aquatic Botany 41: 137–175.

Sargian, P., B. Andral, & V. Derolez, 2013. Réseaux de surveillance DCE-Campagne 2012-District "Rhône et côtiers méditerranéens". Ifremer.

Scheffer, M., M. R. de Redelijkheid & F. Noppert, 1992. Distribution and dynamics of submerged vegetation in a chain of shallow eutrophic lakes. Aquatic Botany 42: 199–216.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. Trends in Ecology & Evolution 8: 275–279.

Schramm, W., 1999. Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. Journal of applied Phycology 11: 69–78.

Schramm, W. & P. Nienhuis, 1996. Marine Benthic Vegetation: Recent Changes and the Effects of Eutrophication. Springer, NewYork.

Schubert, H., P. Feuerpfeil, R. Marquardt, I. Telesh & S. Skarlato, 2011. Macroalgal diversity along the Baltic Sea salinity gradient challenges Remane's species-minimum concept. Marine Pollution Bulletin 62: 1948–1956.

Sfriso, A. & C. Facca, 2007. Distribution and production of macrophytes and phytoplankton in the lagoon of Venice: comparison of actual and past situation. Hydrobiologia 577: 71–85.

Sfriso, A., C. Facca & P. F. Ghetti, 2009. Validation of the macrophyte quality index (MaQI) set up to assess the ecological status of Italian marine transitional environments. Hydrobiologia 617: 117–141.

Sfriso, A., B. Pavoni, A. Marcomini & A. A. Orio, 1992. Macroalgae, nutrient cycles, and pollutants in the Lagoon of Venice. Estuaries 15: 517.

Souchu, P., B. Bec, V. H. Smith, T. Laugier, A. Fiandrino, L. Benau, V. Orsoni, Y. Collos & A. Vaquer, 2010. Patterns in nutrient limitation and chlorophyll a along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Canadian Journal of Fisheries and Aquatic Sciences 67: 743–753.

Steinhardt, T. & U. Selig, 2011. Influence of salinity and sediment resuspension on macrophyte germination in coastal lakes. Journal of Limnology 70: 11–20.

Tagliapietra, D. & A. V. Ghirardini, 2006. Notes on coastal lagoon typology in the light of the EU Water Framework Directive: Italy as a case study. Aquatic Conservation: Marine and Freshwater Ecosystems 16: 457–467.

Teeter, J. W., 1965. Effects of sodium chloride on the sago pondweed. The Journal of Wildlife Management 29: 838–845.

Teichberg, M., S. E. Fox, Y. S. Olsen, I. Valiela, P. Martinetto, O. Iribarne, E. Y. Muto, M. A. V. Petti, T. N. Corbisier, M. Soto-Jiménez, F. Páez-Osuna, P. Castro, H. Freitas, A. Zitelli, M. Cardinaletti & D. Tagliapietra, 2010. Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with Ulva spp. Global Change Biology 16: 2624–2637.

Telesh, I., H. Schubert & S. Skarlato, 2013. Life in the salinity gradient: discovering mechanisms behind a new biodiversity pattern. Estuarine, Coastal and Shelf Science 135: 317–327.

Ter Braak, C. J. F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.

Ter Braak, C. J. F., 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69–77.

Ter Braak, C. J. F., 1994. Canonical community ordination. Part I: basic theory and linear methods. Écoscience 1: 127–140.

Thomaz, S. M. & E. R. da Cunha, 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. Acta Limnologica Brasiliensia 22: 218–236.

Van Wijk, R. J., 1988. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions. Aquatic Botany 31: 211–258.

Vaquer, A. & P. Heurteaux, 1989. Modifications récentes de la végétation aquatique de l'étang du Vaccarès (Camargue, France) liées aux perturbations anthropiques. Annales de Limnologie 25: 25–38.

Verhoeven, J. T. A., 1980. The ecology of Ruppia-dominated communities in Western Europe. II. Synecological classification. Structure and dynamics of the macroflora and macrofauna communities. Aquatic Botany 8: 1–85.

Verlaque, M., 2000. Actualisation de la flore des macrophytes des étangs de Thau (Hérault) et de Salses-Leucate (Aude-Pyrénées-Orientales). In: PNEC "Lagunes Méditerranéennes", Thème 1, le compartiment "Macrophytes". GIS Posidonie - IFREMER Report, Marseille.

Verlaque, M., 2001. Checklist of the macroalgae of Thau Lagoon (Hérault, France), a hot spot of marine species introduction in Europe. Oceanologica Acta 24: 29–49.

Viaroli, P., M. Bartoli, C. Bondavalli, R. R. Christian, G. Giordani & M. Naldi, 1996. Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. Hydrobiologia 329: 105–119.

Viaroli, P., M. Bartoli, G. Giordani, M. Naldi, S. Orfanidis & J. M. Zaldivar, 2008. Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. Aquatic Conservation: Marine and Freshwater Ecosystems 18: S105–S117.

Vincent, C., D. Mouillot, M. Lauret, T. D. Chi, M. Troussellier & C. Aliaume, 2006. Contribution of exotic species, environmental factors and spatial components to the macrophyte assemblages in a Mediterranean lagoon (Thau lagoon, Southern France). Ecological Modelling 193: 119–131.

Vizzini, S. & A. Mazzola, 2008. The fate of organic matter sources in coastal environments: a comparison of three Mediterranean lagoons. Hydrobiologia 611: 67–79.

WoRMS Editorial Board, 2016. World Register of Marine Species [available on internet at http://www.marinespecies.org at VLIZ. Accessed 16 Nov 2016. doi: http://doi.org/10.14284/170.

Zaldívar, J.-M., P. Viaroli, A. Newton, R. De Wit, C. Ibañez, S. Reizopoulou, F. Somma, A. Razinkovas, A. Basset, M. Holmer & N. Murray, 2008. Eutrophication in transitional waters: an overview. Transitional Waters Monographs 2: 1–78.

Vol. 608: 13–32, 2019
https://doi.org/10.3354/meps12814

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 3

Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series

Ines Le Fur[1,*], Rutger De Wit[2], Martin Plus[3], Jocelyne Oheix[1], Valérie Derolez[1], Monique Simier[1], Nathalie Malet[4], Vincent Ouisse[1]

[1]MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, CS 30171, 34203 Sète, France
[2]MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, CC093, 34095 Montpellier, France
[3]Ifremer, Laboratoire d'écologie pélagique (DYNECO-PELAGOS), Centre Bretagne, ZI Pointe du Diable, CS 10070, 29280 Plouzané, France
[4]Ifremer, Laboratoire Environnement Ressources Provence-Azur-Corse, station de Corse, Immeuble Agostini, Z.I. Furiani, 20600, Bastia, France

---

ABSTRACT: Since the mid-20th century, Mediterranean lagoons have been affected by eutrophication, leading to significant changes in primary producers. In the early 2000s, management actions have been implemented to reduce nutrient inputs with the aim to achieve a good ecological status as requested by the EU water framework directive. As a result of these actions, a sharp decline in nutrient loads has been recorded in several lagoons leading to an oligotrophication of the water column. The analyses of a long-term data set (1998–2015) of 21 polyhaline and euhaline lagoons with contrasting trophic status allowed us to infer a general scheme for the changes in macrophyte assemblages during the oligotrophication process. Placing hypertrophic and oligotrophic conditions end to end, we inferred that the general pattern for the re-oligotrophication trajectory in Mediterranean coastal lagoons is described by the following sequence, with regime shifts between each state: (1) bare non-vegetated sediments, phytoplankton-dominated state; (2) opportunistic macroalgae; (3) seagrass and perennial macroalgae dominated state. However, we did not observe the latter regime shift for the most eutrophicated lagoons, which, so far, remained stuck in the opportunistic macroalgae state. So far, the shift from dominance of opportunistic macroalgae to a system dominated by seagrasses was only observed in a single lagoon where seagrasses had never completely disappeared, which possibly relates to resilience. More generally, the conditions favoring regime shifts from opportunistic macroalgae to seagrasses are still poorly understood. In conclusion, we describe a generic pattern for re-oligotrophication of Mediterranean coastal lagoons, although a full recovery from highly eutrophied to oligotrophic conditions may require more than a decade and may include conditions that remain so far poorly recognized.

KEY WORDS: Submerged aquatic vegetation · Recovery · Nutrient reduction · Restoration · Long-term data series · Resilience · Regime shift · Coastal lagoon

---

1. INTRODUCTION

Marine benthic macrophyte communities, including seagrasses and macroalgae, play a major structural and functional role in shallow coastal ecosystems such as estuaries and coastal lagoons. Marine macrophytes are among the most productive habitats on earth (Mann 1973) and play an important role in the ocean carbon budget (Duarte 1995, Duarte & Cebrián 1996) and in other biogeochemical processes, e.g. nutrient cycles (Rysgaard et al. 1996, Flindt et al. 1999, Human et al. 2015). Furthermore, by reducing wave energy and water flow, submerged aquatic vegetation, particularly seagrasses,

*Corresponding author: ines.le.fur@gmail.com

Publisher: Inter-Research · www.int-res.com

increases the deposition of suspended matter and improves sediment stability (van der Heide et al. 2007 and references therein). Hence, submerged aquatic vegetation contributes to increase water transparency. Moreover, the uptake of nutrients, and the production of oxygen and its release into the water column (Romero et al. 2006), may reduce potential anoxic events. Macrophytes also represent an important food source and provide nurseries and foraging habitats for many species (e.g. invertebrates, fish, and birds). Hence, macrophytes create complex habitats and influence the physical, chemical and biological parameters of coastal environments by acting as ecological engineers and providing many ecosystem services (Costanza et al. 1997, Orth et al. 2006, Barbier et al. 2011).

Since the mid-20th century, human population growth, urbanization, agricultural and industrial expansion has led to significant nutrient over-enrichment of coastal ecosystems worldwide (Cloern 2001, de Jonge et al. 2002). This excess of nutrient loading has led to eutrophication, which has become a widespread phenomenon impacting water quality and ecological processes of marine coastal ecosystems (Nixon 1995). The major impacts of eutrophication include changes in the structure and functioning of marine ecosystems, reduction of biodiversity, as well as changes in the composition and size structure of phytoplankton communities (Bec et al. 2011) and sessile organisms such as benthic fauna (Lloret & Marín 2011) and macrophytes. Concerning the latter point, the change of submerged aquatic vegetation along eutrophication gradients and its consequences on ecosystem functioning is well known (Harlin 1995, Valiela et al. 1997, Schramm 1999, Viaroli et al. 2008, Le Fur et al. 2018). During the eutrophication process, ephemeral epiphytic macroalgae and fast growing opportunistic macroalgae (e.g. *Ulva, Chaetomorpha, Cladophora*) gradually replace seagrasses and perennial macroalgae. Finally, under hypertrophic conditions, phytoplankton becomes the main primary producer, drastically reducing the available light for benthic photosynthesis (Duarte 1995, Schramm 1999, Viaroli et al. 2008). Phytoplankton and macroalgal blooms not only affect natural coastal communities and ecosystem functions (Duarte 1995), but have also high economic consequences for recreational and commercial uses (Charlier & Lonhienne 1996, Dion & Bozec 1996, Lyons et al. 2014).

Due to the widespread degradation of aquatic ecosystems, a number of policies have been implemented to mitigate the ecological and economic effects of eutrophication and to restore aquatic ecosystems by reducing anthropogenic nutrient inputs. In Europe, several directives have been adopted in order to reduce eutrophication and other anthropogenic pressures: the nitrate directive (91/676/EEC, in 1991); the urban wastewater treatment directive (91/271/EEC, in 1991); the water framework directive (WFD, 2000/60/EC, in 2000); and the marine strategy framework directive (MSFD, 2008/56/EC, in 2008). The aim of the WFD is to achieve a good ecological status of groundwater and surface waters (rivers, lakes, transitional and coastal waters; the latter 2 include the coastal lagoons) by 2021.

Management actions have been implemented to reduce nutrient loadings into coastal ecosystems in order to induce a re-oligotrophication trajectory and eventually restore the coastal ecosystems. The oligotrophication process, which is considered as the inverse of the eutrophication process, is defined as the response of the ecosystem to a reduction of nutrient loadings. The term 're-oligotrophication trajectory' is coined here for describing the trajectory of an ecosystem during the oligotrophication process following a previous eutrophication phase. During the last decades, the recovery of coastal ecosystems after nutrient reduction has received a growing interest in scientific studies (e.g. Tsiamis et al. 2013, Riemann et al. 2016, Leruste et al. 2016, Pasqualini et al. 2017, Lefcheck et al. 2018). Nevertheless, our understanding of re-oligotrophication trajectories remains limited. In addition, to quote the review of estuarine and coastal systems by Duarte et al. (2015, p. 1210):

> … partial recovery prevails, degradation and recovery typically follow different pathways as buffers act to maintain the degraded state, and recovery trajectories can depend on the nature of the pressure as well as the connectivity of ecosystems and can differ among ecosystems components and among ecosystems …

According to McCrackin et al. (2017), lakes and coastal marine areas only achieved 34 % and 24 % of baseline conditions decades after cessation or partial reduction of nutrients, respectively. In some cases no changes or worsened conditions were observed, suggesting that achieving baseline conditions may not be possible in all cases. Moreover, recovery times after cessation of nutrient inputs can vary from less than a year to nearly a century (Borja et al. 2010, McCrackin et al. 2017).

Due to their location between land and sea, their shallow depth and their relatively weak exchange with the open sea, coastal lagoons are particularly vulnerable to eutrophication (Barnes 1980, Kjerfve 1994, Kennish & Paerl 2010). Ecological restoration of coastal lagoons following the reduction of nutrient loading is recent and studies of this process are still scarce (Facca et al. 2014, Leruste et al. 2016, Pasqualini et al. 2017). Due to the high variability and dynamics of these systems, restoration trajectories are expected to be variable and complex. During the oligotrophication process in Mediterranean lagoons, a decline in phytoplankton biomass is observed, accompanied by a shift in community structure and composition (Leruste et al. 2016). In non-eutrophicated conditions, shallow lagoons tend to be dominated by benthic primary producers, such as seagrasses, macroalgae and benthic microalgae rather than phytoplankton (Lloret & Marín 2009, Le Fur et al. 2018).

Studying the dynamics of changes in submerged aquatic vegetation requires large spatial scale and long-term observations that allow the description of trajectories in the ecosystem state space (Tett et al. 2013). In Southern France, nutrient reduction has been pursued in lagoon watersheds as part of public policy for the past 10 to 15 yr. We hypothesize that the reduction of nutrient availability causes a decrease in the phytoplankton biomass followed by a dynamic macrophyte succession pattern. This study, based on environmental and macrophyte data, aims (1) to determine the general patterns of the relationships between environmental conditions and macrophyte assemblages in Mediterranean lagoons, and (2) to study how the assemblages changed over time together with the environmental conditions, in order to gain a better understanding of the ecosystem state trajectories for the aquatic vegetation.

2. MATERIALS AND METHODS

2.1. Study sites

Our study covered 21 French Mediterranean coastal lagoons with salinities ranging from polyhaline to euhaline (Venice System, 1958). Most of these lagoons are located in the Gulf of Lion (NW Mediterranean Sea) and 3 of them are located along the east coast of Corsica (Tyrrhenian Sea) (Fig. 1). The studied lagoons are shallow water bodies; only 4 lagoons have a mean depth >2 m: Leucate (the southern part), Thau, Diana, and Urbino (see Souchu et al. 2010, Bec et al. 2011 and Le Fur et al. 2018 for a

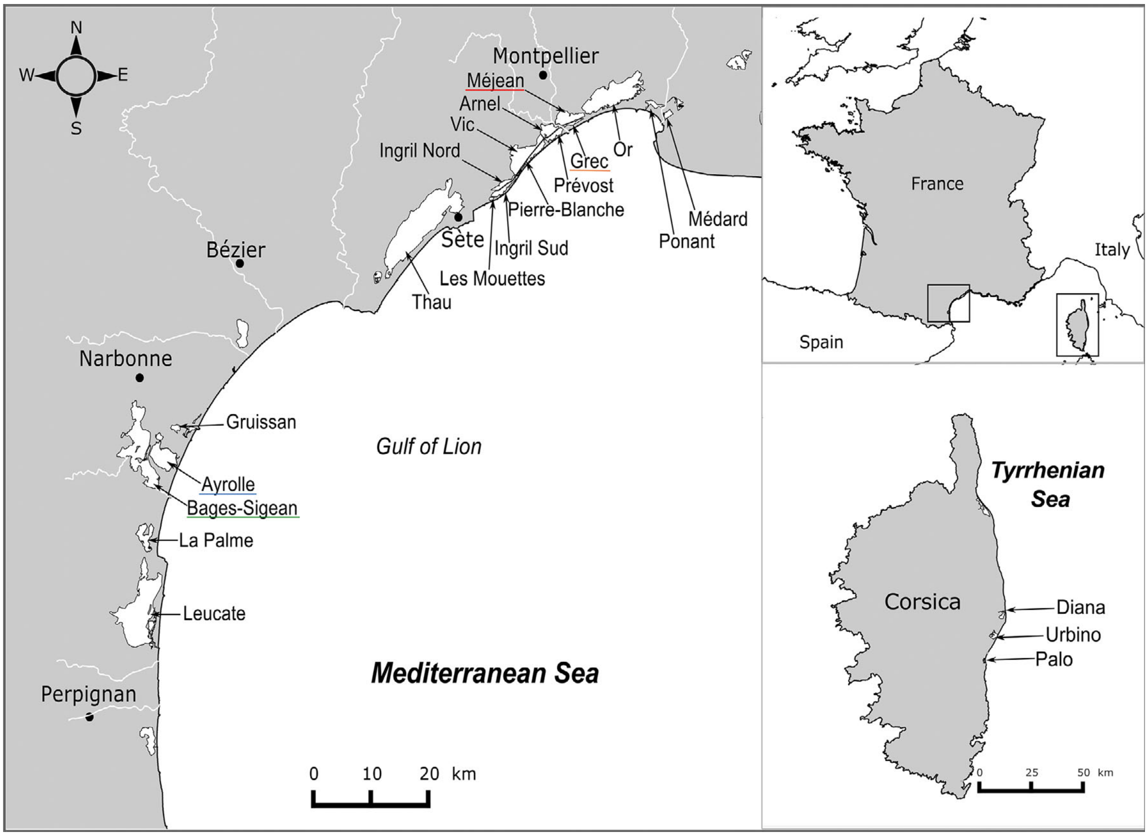


Fig. 1. Overview of the study area, showing the 21 polyhaline and euhaline lagoons of the French Mediterranean coast. Lagoons used to illustrate our study are underlined (Bages in green, Ayrolle in blue, Méjean in red and Grec in orange)

more detailed overview of the catchment area characteristics of these lagoons). Some of these lagoons (i.e. Leucate, Bages, Thau, Prévost, Méjean, Or) were divided into hydrodynamically homogeneous sectors corresponding to sub-basins empirically defined on the basis of their bathymetry (Souchu et al. 2010). Hence, a total of 27 homogeneous sectors were defined within these 21 coastal lagoons. Over time, the 27 lagoon sectors experienced different trophic statuses ranging from oligotrophic to hypertrophic (Souchu et al. 2010, Le Fur et al. 2018).

Based on the analyses of the results, a set of lagoons was selected to study re-oligotrophication trajectories in more detail. The criteria for this selection of lagoons were the following: (1) lagoons showing clear re-oligotrophication trends when their starting conditions were hypertrophic to eutrophic; (2) lagoons where specific management has been implemented for the reduction of nutrient loading, or oligotrophic lagoons that had been minimally impacted by anthropogenic nutrient loading; (3) lagoons collectively representing a set of conditions ranging from hypertrophic to oligotrophic. The objective was to describe a generic trajectory from hypertrophy to oligotrophy during re-oligotrophication.

2.2. Sampling methods

2.2.1. Water column

Sampling methodology and analyses of the water column variables were consistent throughout the entire monitoring period 1998–2015. We considered 7 variables from the database: the turbidity (TURB), the concentrations of chlorophyll *a* (chl *a*), total nitrogen (TN), total phosphorus (TP), and the concentrations of ammonium (NH_4), sum of nitrate plus nitrite (NO_3+NO_2) and phosphate (PO_4). TN and TP include dissolved organic and inorganic nitrogen and phosphorus, respectively, plus their particulate forms. Sampling was carried out 3 times (i.e. once per month from June to August) every year at 1 station per lagoon sector (see Table S1 in Le Fur et al. 2018). On each date, water was collected with 2-l polypropylene bottles. Turbidity was measured in the laboratory with an optic turbidimeter (2100N IS turbidimeter ISO 7027). Chl *a* concentration, used as a proxy for phytoplankton biomass, was measured by spectrofluorimetry (Neveux & Lantoine 1993). Filtration, conservation and analysis of chl *a* concentrations were performed following the methods described in Bec et al. (2011), and nutrients concentrations were measured following the analytical protocols described in Souchu et al. (2010).

2.2.2. Sediment

Sediment cores were taken by scuba diving (in late spring or early summer) at each benthic station with a frequency of once every 5 or 6 yr from 1999 to 2012. The first centimeters (0–5 cm) of the sediment were collected with a sediment core and then sifted through a 2 mm sieve (Ifremer et al. 2000). Organic matter content (OM, expressed as % of dry sediment weight) was calculated as the loss of weight on ignition of 20 ml of dry sediment placed into a muffle furnace at 450°C for 12 h. Total nitrogen in the sediment (TNsed) was analyzed with a Thermoquest CN 2100. Total phosphorus in the sediment (TPsed) was measured through colorimetry as phosphate (Souchu et al. 2010) after dissolution and hydrolysis. For this, sediment samples were mixed with a solution of nitric, hydrofluoric and perchloric acids. The solution obtained was then evaporated and dissolved in hydrochloric acid. TNsed and TPsed concentrations were expressed in g kg^{-1} and mg kg^{-1} dry sediment, respectively, with a precision of 5%.

2.2.3. Benthic vegetation

All 27 lagoon sectors were monitored for benthic vegetation from 1998 to 2015 using a sampling frequency of once every 3 or 4 yr. For further details about the monitoring surveys, see the supplementary material in Le Fur et al. (2018).The macrophyte samplings were performed at benthic stations; the number of benthic stations and sampling frequency for each lagoon is available in Le Fur et al. (2018), Table S1 of the supplementary material. Macrophyte sampling campaigns were carried out in late spring or early summer during the maximal growth and production rates. The benthic stations were located following a regular systematic grid with 1 station for every 100 ha for large lagoons (surface area exceeding 1000 ha) and 1 station for every 50 ha for smaller lagoons. The benthic stations of the deepest lagoons were sampled by scuba diving, and those of the shallowest lagoons were sampled by snorkeling. Total vegetation cover was estimated visually by the diver at each benthic station. The method to estimate the proportional abundance of the different species in the assemblages changed during the monitoring program. Thus, from 1998 to 2006, the biomasses of the different species were measured in the laboratory as dry weight. From 2007 onwards, the species cover was visually estimated directly in the field by divers (see Le Fur et al. 2018 for more details of the methodology). These different methods were intercalibrated in the first year after the change. The comparison of the results made it possible to show an equivalence of the lists of species recorded by both methods. More details of the methodology are provided in Le Fur et al. (2018).

At each benthic station, macrophyte samples were collected and identified in the laboratory. Macrophytes were sorted and identified using a binocular microscope and a light microscope. The taxonomic resolution of macrophyte determinations was at species level when possible. Taxonomic nomenclature followed AlgaeBase (Guiry & Guiry 2016) and World Register of Marine Species (WoRMS Editorial Board 2016).

2.3. Statistical analysis

2.3.1. Data format

The data used in this study were extracted from the French database 'Quadrige' (Ifremer, http://quadrige.eaufrance.fr/). Data concerning the water column are available via the open data file: www.seanoe.org/data/00361/47248/.

Presence–absence data for each species were used for the macrophytes, due to the heterogeneity of the sampling methods. In addition, a supplementary variable labelled as 'bare sediment' was introduced to characterize sediment without macrophytes. The relative frequencies for the different species (and bare sediment) were calculated by dividing the number of occurrences by the total number of benthic stations in each lagoon sector for each sampling year.

The water column samples were not collected exactly at the same period as the macrophyte samples, and thus it would not have been correct to directly associate the macrophyte data with the environmental variables. We assumed that the presence–absence of a given species in a sector is not exclusively explained by the environmental condition of the sampling year 'k', but also by the conditions prevailing during the previous 2 yr (particularly for perennial species). Therefore, the macrophyte samplings of the year 'k' were associated with the mean summer values of each environmental variable integrated over a period of 3 yr (k, $k - 1$, $k - 2$).

2.3.2. Multivariate STATICO analysis and other tests

The objective of the present study was to establish a statistically meaningful link between environmental conditions and the presence of macrophyte species and their variations over time. The structure of the data comprised a series of paired data tables (see Fig. 2), i.e. one table with the presence–absence of species, and another table with the environmental conditions. These can be analyzed pairwise through different techniques including canonical correspondence analysis (CCA), redundancy analysis (RDA) or the multitable analysis method STATICO (Simier et al. 1999, Thioulouse et al. 2004). Among these, we chose STATICO as it represented the following advantages. Firstly, STATICO does not require an *a priori* model describing the relationship between the occurence of the different species and environmental conditions, which is assumed to be unimodal in CCA and linear in RDA. Secondly, STATICO maximizes the covariance instead of calculating a correlation. Thus, the information of the sampling data is explicitly maintained in the analyses. Thirdly, STATICO is capable of giving different weights to pairs of tables and is thus able to weight down tables with minor contributions to the main patterns. These advantages are related to the mathematical optimality theorems of STATICO (Thioulouse et al. 2004). STATICO thus calculates a species–environment relation for each sampling occasion and is, therefore, very well suited for describing long-term changes in the species environment relationships (Mendes et al. 2012).

To implement the STATICO analysis we created for each sampling year (k ranging from 1 to 16, from 1998 to 2015; K = total number of years equal to 16), a pair of 2 tables, i.e. a table (Y) with columns for the 7 environmental variables and another table (X) with columns for the 105 species and the additional variable 'bare sediment'. Both environment and species tables have 27 rows, which correspond to the number of lagoon sectors (Fig. 2). STATICO analysis was performed on the set of $K = 16$ pairs of tables (X and Y). The STATICO method involves 3 steps (Fig. 2): (1) each table is first analyzed using a principal component analysis (PCA) for the environmental tables and a correspondence analysis (CA) for the species tables; (2) each pair of tables is linked by a co-inertia analysis (Dolédec & Chessel 1994) which provides an image of the common structure (resulting in species–variables cross table Z) for each year; (3) partial triadic analysis (PTA) is used to analyze the series of K cross tables. The PTA itself is a 3-step procedure: (i) the interstructure; (ii) the compromise factor map;

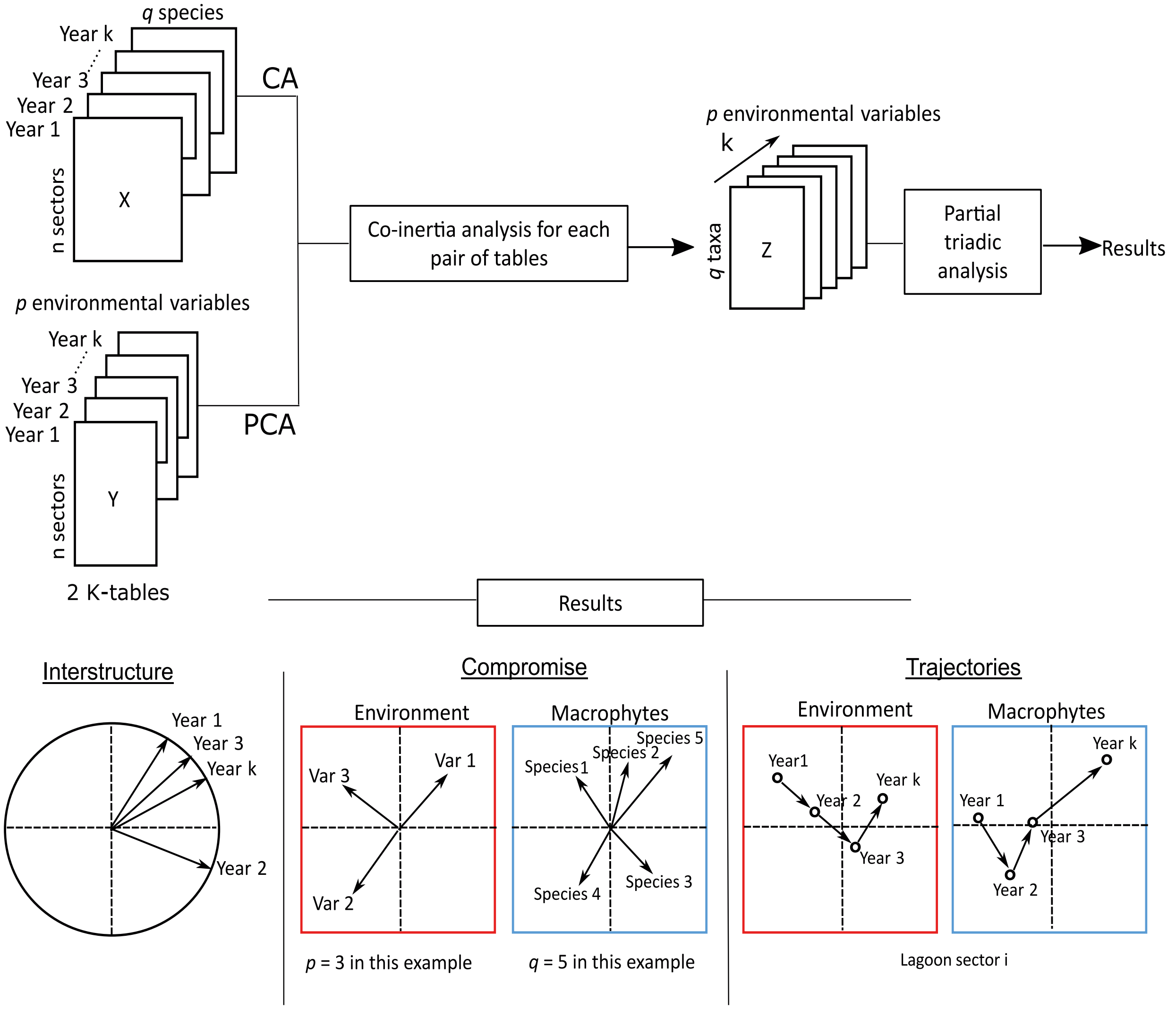


Fig. 2. STATICO diagram, the data structure is a sequence of *k* pairs of ecological tables. The *X* and *Y* are the tables of the species and environmental variables, respectively. *Z* indicates the cross tables, n the number of lagoon sectors, *q* the number of species, *p* the number of environmental variables. Lagoon sector i is one sector out of n. Figure modified from Kidé et al. (2015)

and (iii) the trajectories analysis. The interstructure step summarizes the global structure and the relationship between the *K* cross tables and computes coefficients characterizing the importance of each table. The next step computes a weighted mean of the *K* cross tables (using the coefficients computed at the interstructure step) and gives an image of their common structure. This is presented as the STATICO compromise factor map, an *n*-dimensional space. This compromise factor map can thus be considered as a factorial representation of the ecosystem state space for the collection of coastal lagoon sectors included in the analysis. Species assemblages and environmental variables corresponding to the different samplings can then be plotted in the compromise factor map, allowing an analysis of trajectories for the different lagoon sectors. Hence, the temporal dynamics of the species-environment co-structure (trajectories) can be interpreted in terms of changes of the ecosystem state. Sediment data were not included in the STATICO analysis due to a lower sampling frequency.

The trajectories of the selected lagoons (see criteria for selection in 'Study site') are depicted together in the compromise factor map. The 7 water column parameters of the selected lagoon sectors were compared before and after implementation of the main management actions using the non-parametric Wilcoxon test. For the sediment, Kruskal-Wallis and pairwise Wilcoxon tests were used to identify significant differences of OM, TNsed, and TPsed between lagoon sectors and between periods, respectively.

2.3.3. Software

All analyses were performed using R software (version 3.1.1; R Core Team 2018). Calculations and graphs shown for the STATICO analyses were done using the ade4 package (Dray & Dufour 2007).

3. RESULTS

3.1. Relationships between environment and macrophyte assemblages and their change over time

The 17 most frequently occurring species (occurrence >5% in the grand ensemble of all samples) are presented in Table 1 and comprised 10 species of Chlorophyta (3 species of *Ulva*, 2 species of *Cladophora*, 2 species of *Chaetomorpha*, and 3 others), 4 species of Rhodophyta (among these 3 *Gracilaria* species), and 3 Tracheophyta. The latter are rooted angiosperms and included the 2 seagrasses *Zostera noltei* and *Z. marina*, and the spiral ditch grass *Ruppia cirrhosa*.

The interstructure step of the STATICO analyses showed that the first 2 axes of the interstructure represented 29.6% and 17.0% of the total variability, respectively (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m608p013_supp.pdf). The 16 tables were positively correlated, i.e. all the years were on the same side along the first axis. The construction of the compromise factor map was thus justified. Among the 16 years, 2002, 2004, 2006 and 2013 were the most important (highest $\cos^2$ and weights; Fig. S1) for defining the compromise factor map. This means that the relationship between environmental variables and assemblages of macrophyte species were strongest during those years (see Fig. S1 for further details).

The findings of the interstructure step thus allowed us to calculate a weighted mean of the relationship between species and environmental conditions among dates, i.e. the compromise factor map of the STATICO analysis shown in Fig. 3. The scree plot indicating the eigenvalues for the different factors is shown in Fig. 3c, which shows that the first axis was clearly dominant, explaining 88.5% of the total variability, the second axis still explained 9.5% of the total variability, while the following axes could be neglected (i.e. less than 2% of the total variability explained). Hence, hereafter, we will only use the first 2 axes and represent the STATICO space as a plane.

The projection of the environmental variables and the macrophyte species in the assemblage are shown in Fig. 3a and 3b, respectively. TN, TP, chl *a* and turbidity variability are shown along the first axis of the analysis (see Fig. 3a), with high values located on the left side and low values on the right side of this axis. This first axis represents, therefore, a trophic gradient with hypertrophic conditions on the left and oligotrophic conditions on the right. Dissolved inorganic nutrient variability is shown on the second axis, with higher concentrations towards the bottom of the graph.

The projection of the species in the compromise factor map (Fig. 3b) shows that macrophyte species

Table 1. Species and their abbreviations used in the multivariate analysis (STATICO)

Phylum	Genus	Species	Abbreviation	Taxonomist
Chlorophyta	*Acetabularia*	*Acetabularia acetabulum*	*A. acetabulum*	(Linnaeus) P. C. Silva, 1952
	Chaetomorpha	*Chaetomorpha aerea*	*C. aerea*	(Dillwyn) Kützing, 1849
		Chaetomorpha linum	*C. linum*	(O. F. Müller) Kützing, 1845
	Cladophora	*Cladophora glomerata*	*C. glomerata*	(Linnaeus) Kützing, 1843
		Cladophora vagabunda	*C. vagabunda*	(Linnaeus) van den Hoek, 1963
	Ulva	*Ulva clathrata*	*U. clathrata*	(Roth) C. Agardh, 1811
		Ulva intestinalis	*U. intestinalis*	Linnaeus, 1753
		Ulva rigida	*U. rigida*	C. Agardh, 1823
	Ulvaria	*Ulvaria obscura*	*U. obscura*	(Kützing) P. Gayral ex C. Bliding, 1969
	Valonia	*Valonia aegagropila*	*V. aegagropila*	C. Agardh, 1823
Rhodophyta	*Chondria*	*Chondria capillaris*	*C. capillaris*	(Hudson) M. J. Wynne, 1991
	Gracilaria	*Gracilaria bursa-pastoris*	*G. pastoris*	(S. G. Gmelin) P. C. Silva, 1952
		Gracilaria dura	*G. dura*	(C. Agardh) J. Agardh, 1842
		Gracilaria gracilis	*G. gracilis*	(Stackhouse) M. Steentoft, L. M. Irvine & F. Farnham, 1995
Tracheophyta	*Ruppia*	*Ruppia cirrhosa*	*R. cirrhosa*	(Petagna) Grande, 1918
	Zostera	*Zostera marina*	*Z. marina*	Linnaeus, 1753
		Zostera noltei	*Z. noltei*	Horneman, 1832

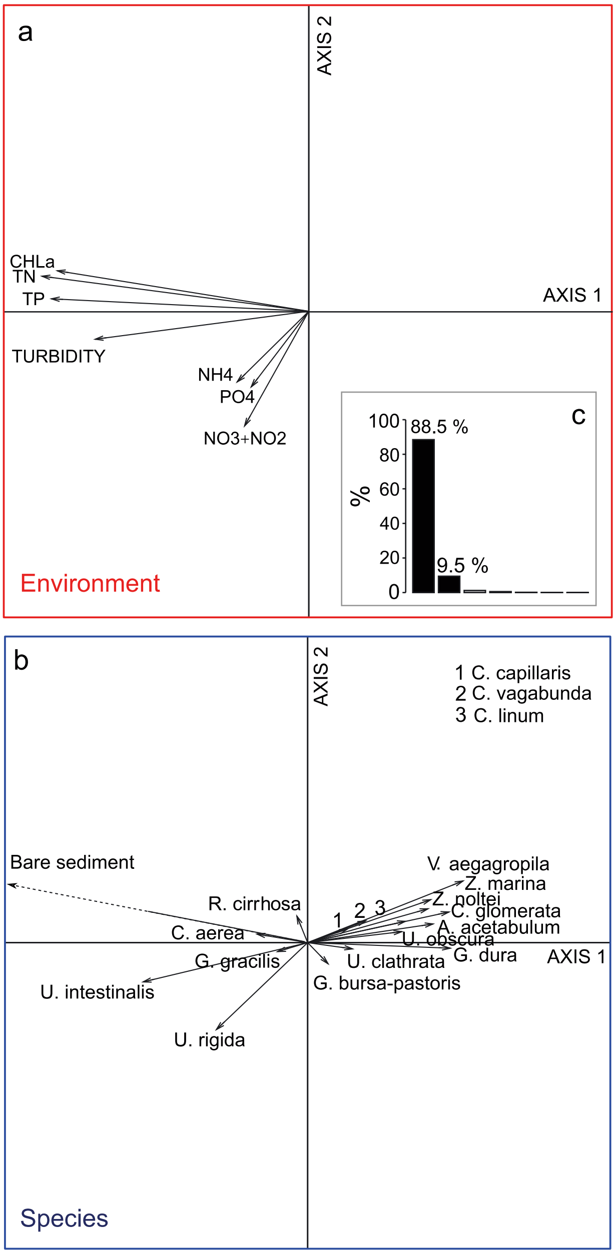


Fig. 3. Compromise factor map of the STATICO analysis taking into account the 27 lagoon sectors. (a) Projection of the environmental variables (variable codes are given in 'Materials and methods'), and (b) projection of the macrophyte species. (c) Scree plot of eigenvalues for the different factors. The superimposition of the 2 maps provides information about the stable part of the relationships between environmental variables and macrophytes species. Note that (b) has been enlarged in order to give a better view of the species

were distributed along a trophic gradient. The green algae *Ulva intestinalis*, *U. rigida*, *Chaetomorpha aerea*, and the red algae *Gracilaria gracilis* were projected on the graph's left side, corresponding to high TN, TP, chl *a* concentrations and a high turbidity level, whereas species such as the macroalgae *Acetabularia acetabulum*, *Valonia aegagropila*, and the seagrasses *Z. marina* and *Z. noltei* were projected on the right side, corresponding to lagoon sectors with low nutrient and chl *a* concentrations as well as low turbidities (Fig. 3b). The position of *U. rigida* (lower left) corresponded to eutrophic environments with high levels of dissolved inorganic nutrient concentrations. The position of the variable 'bare sediment' on the far-left of axis 1 indicates the absence of macrophytes and corresponded to hypertrophic conditions characterized by the highest levels of TN and TP, chl *a* and turbidity (Fig. 3a,b).

3.2. Trajectories of lagoons

The projection of the trajectories over time in the compromise factor map, both for the environmental conditions and the species compositions of the macrophyte assemblages, are shown for all studied lagoon sectors in the Supplement (Fig. S2). We classified these trajectories into 5 different categories (Table 2). seven lagoons showed clear trajectories while other lagoons showed few dynamics. A stable trophic status has been attributed to the latter set of lagoons. Hence, we found a stable oligotrophic status for 7 lagoons, a mesotrophic status for 4 lagoons and an eutrophic status for 1 lagoon. In 2015, none of the lagoons showed a hypertrophic status. Seven lagoons showed well-defined dynamics: 6 lagoons (Méjean, Grec, the northern basin of Bages [BGN], Ingril, Arnel and Ponant) showed a trajectory from left to right, a re-oligotrophication trajectory, and only 1 lagoon (Pierre-Blanche) from right to left, a eutrophication trajectory. Among these lagoons with well-defined dynamics, 2 (Méjean and Grec) showed hypertrophic conditions in the early 2000s and showed improvement, without achieving oligotrophic status in 2015.

3.3. Re-oligotrophication trajectories of selected lagoons plotted in the compromise factor map

Based on criteria, 3 lagoons (Méjean, Grec and Bages) were selected to illustrate re-oligotrophication trajectories. The oligotrophic Ayrolle lagoon (AYR), little exposed to anthropogenic pressure, was selected as a reference lagoon. These 4 lagoons were plotted together in the compromise factor map (Fig. 3). The context of the selected lagoons was described (Table 3), and average values and 2-way comparisons for water column variables before and after the implementation of the management actions targeting nutrient reduction were provided (Table 4). Before their implementation, the western part of Méjean lagoon (MEW) and Grec lagoon (GRC) were among the most heavily degraded lagoons on the French Mediterranean coast and classified as hypertrophic (Souchu et al. 2010). The northern sector of the Bages lagoon (BGN) is hydrodynamically confined (Fiandrino et al. 2017) and used to be exposed to high nutrient loading from wastewater discharges and was classified as eutrophic (Ifremer 2007). Since the end of 2005 both Méjean and Grec lagoons have benefitted from the improvement of the waste water treatment plant (WWTP) of the Montpellier urban area and the diversion of its effluents through an offshore outfall (Leruste et al. 2016). Moreover, stopping the discharge from the WWTP of the village of Palavas (a smaller facility) into Grec lagoon in 2009, led to an additional improvement for this lagoon. For Méjean and Grec lagoons together, the estimated reductions of nitrogen and phosphorus loadings were 92% and 95%, respectively. In Bages lagoon improvement has progressed since 2003, resulting in a reduction of nitrogen (85%) and phosphorus (90%) loadings between 2002 and 2009 (Table 4).

Fig. 4 shows hypertrophic conditions for Grec (GRC) and Méjean West (MEW), and eutrophic conditions for Bages North (BGN) at the beginning of the observation period, and re-oligotrophication since the implementation of management actions. During the entire monitoring period, Ayrolle lagoon (AYR) showed the lowest values for all variables (TN, TP, chl *a*, NO_3+NO_2, NH_4, PO_4, Turbidity), confirming that this lagoon can be used as an oligotrophic reference state.

The possibility of combining the different re-oligotrophication trajectories to deduce a generic pattern will be discussed in the 'Discussion' section. Here-

Table 2. Classification of lagoon sector trajectories according to the STATICO analysis. Note that Diana (DIA) was excluded from the table because of incoherent trajectory between environmental conditions and species

Category	Sector(s)
Re-oligotrophication trajectory	Bages Northern basin (BGN), Ingril (INN, INS), Arnel (ARN), Méjean (MEW, MEE), Grec (GRC), Ponant (PON)
Eutrophication trajectory	Pierre-blanche (PBL)
Oligotrophic status	Ayrolle (AYR), La Palme (LAP), Bages Southern basin (BGM, BGS), Leucate (LEN, LES), Thau (TW, TE), Mouettes (MOU), Urbino (URB)
Mesotrophic status	Gruissan (GRU), Vic (VIC), Prévost (PRW, PRE), Palo (PAL)
Eutrophic status	Or (ORW, ORE)

Table 3. Characteristics of the 4 lagoons used to illustrate our study. The trophic status at the beginning of the study period is specified from Souchu et al. 2010. *: In Bages lagoon, nutrients (N, P) from a waste water treatment plant (WWTP) were estimated in 2002 and 2009 by the Parc Naturel Régional de la Narbonnaise (PNR 2011); in MEW and GRC nutrients from a WWTP were estimated from French Water Agency in 2003 (Cépralmar et al. 2006) and 2010 (Meinesz et al. 2013)

	Lagoon sector			
	Méjean West	Grec	Bages North	Ayrolle
Code	MEW	GRC	BGN	AYR
Initial trophic status (before management actions)	Hypertrophic	Hypertrophic	Eutrophic	Oligotrophic
Watershed area (km^2)	661.9	661.9	466.8	34.7
Lagoon area (km^2)	7.2	1.2	37.7	13.4
Volume (10^6 m^3)	4.1	0.7	48.2	9.9
Mean depth (m)	0.7	0.5	1.5	0.7
Connection to the sea	Indirect	Indirect	Direct: permanent inlet	Direct: natural permanent inlet
Main freshwater sources	Canal	River, canal	Intermittent streams, canals	Temporary resurgence, wetland
Major management actions	2005	2005	2003	
Minor management actions		2009	2005, 2009	
Estimation of domestic nutrient inputs*:				
N (t N × yr^{-1}) before and (after) management actions	1436 (118)		291 (43)	0
P (t P × yr^{-1}) before and (after) management actions	123 (6.6)		47 (4.5)	0

Table 4. Statistics of water column variables during the study period (1999–2015) for 4 representative lagoon sectors (Ayrolle [AYR], Bages North [BGN], Grec [GRC], and Méjean West [MEW]). The values before (B) and after (A1, A2) management actions were tested with a Wilcoxon-Mann-Whitney test between 2 groups. In GRC, to compare the differences between the 3 management action periods, a Kruskal-Wallis test followed by a pairwise Wilcoxon test was used. Letters in the p-value column indicate between which periods a significant difference was observed. TN: total nitrogen (µM); TP: total phosphorus (µM); chl *a*: chlorophyll *a*; NH_4: ammonium (µM); NO_3+NO_2: nitrate + nitrite (µM); PO_4: phosphate (µM); TURB: turbidity (NTU). $^*p < 0.05$

Variable and lagoon sector	Period before/ after MA		Mean	SD	N	p
TN						
AYR			31.9	11.1	49	
BGN	1999–2003	B	54.4	15.0	12	<0.001*
	2004–2015	A1	38.7	8.07	36	
GRC	1999–2005	B	216	80.9	19	<0.001*
	2006–2009	A1	142	120	11	B–A1, B–A2, A1–A2
	2010–2014	A2	55.6	21.6	15	
MEW	2000–2005	B	334	110	16	<0.001*
	2006–2015	A1	104	69.2	30	
TP						
AYR			0.69	0.26	49	
BGN	1999–2003	B	3.22	1.93	12	<0.001*
	2004–2015	A1	1.34	0.60	36	
GRC	1999–2005	B	12.0	6.58	19	<0.001*
	2006–2009	A1	6.21	6.49	11	B–A1, B–A2
	2010–2014	A2	3.47	2.17	15	
MEW	2000–2005	B	19.2	1.58	16	<0.001*
	2006–2015	A1	7.87	5.41	30	
Chl *a*						
AYR			1.07	0.83	49	
BGN	1999–2003	B	7.16	5.56	12	0.004*
	2004–2015	A1	3.58	3.42	36	
GRC	1999–2005	B	128	85.3	19	<0.001*
	2006–2009	A1	52.3	106	11	B–A1, B–A2
	2010–2014	A2	7.08	6.63	15	
MEW	2000–2005	B	185	131	16	<0.001*
	2006–2015	A1	19.8	28.1	30	
NH_4						
AYR			0.49	0.29	49	
BGN	1999–2003	B	0.85	0.99	12	0.125
	2004–2015	A1	0.61	0.84	36	
GRC	1999–2005	B	20.7	24.1	19	0.002*
	2006–2009	A1	36.0	42.7	11	B–A2, A1–A2
	2010–2014	A2	1.12	1.53	15	
MEW	2000–2005	B	1.90	3.40	16	0.230
	2006–2015	A1	1.68	3.23	30	
NO_3+NO_2						
AYR			0.14	0.12	49	
BGN	1999–2003	B	0.45	0.76	12	0.453
	2004–2015	A1	0.38	0.45	36	
GRC	1999–2005	B	4.68	5.06	19	<0.001*
	2006–2009	A1	5.20	5.42	11	B–A2, A1–A2
	2010–2014	A2	0.22	0.19	15	
MEW	2000–2005	B	0.41	1.58	16	0.390
	2006–2015	A1	0.28	0.32	30	
PO_4						
AYR			0.10	0.15	49	
BGN	1999–2003	B	1.47	1.61	12	0.005*
	2004–2015	A1	0.29	0.49	36	
GRC	1999–2005	B	2.25	5.06	19	0.007*
	2006–2009	A1	0.63	1.21	11	A1–A2
	2010–2014	A2	1.17	1.23	15	
MEW	2000–2005	B	1.59	6.36	16	0.090
	2006–2015	A1	2.41	1.69	30	
TURB						
AYR			1.53	1.26	49	
BGN	1999–2003	B	2.74	1.41	12	0.088
	2004–2015	A1	3.52	1.80	36	
GRC	1999–2005	B	22.4	12.2	19	0.003*
	2006–2009	A1	23.3	32.3	11	B–A2
	2010–2014	A2	8.26	5.49	15	
MEW	2000–2005	B	27.1	12.8	16	0.001*
	2006–2015	A1	15.0	11.6	30	

after, the trajectories of the 4 lagoons (GRC, MEW, BGN, AYR) will be assessed in more detail, illustrating them by time-series of their water column variables, vegetation cover and biomasses (Figs. 5 & 6). The position of the oligotrophic AYR in the compromise factor map was systematically in the upper right part, with positive coordinates for axes 1 and 2 (Fig. 4), with low mean concentrations of nutrients, low turbidity, and low chl *a* concentrations (Fig. 5, Table 4). Among the years, the positions of the environmental variables and species compositions of the submerged macrophyte communities at AYR showed minor movements in the compromise factor map, suggesting stable environmental variables and species assemblages with only small fluctuations over the study period (1999–2015). Such minor fluctuations were indeed confirmed by very low standard deviations (SD) of water column variables (Table 4). The species composition was constant, dominated by *Z. noltei* and *A. acetabulum*, although total vegetation cover showed significant fluctuations (Fig. 6a). A minimum vegetation cover of 41% was observed in 2005, corresponding to a biomass (mean ± SD) of *Z. noltei* of 62.2 ± 76.7 g m^{-2}, compared to a biomass of *Z. noltei* of 767 ± 492 g m^{-2} observed in 1999. Furthermore, *Z. marina* presence strongly fluctuated: it was observed at 86% (12 out of 14) of the benthic stations in 2002 and was only observed at 2 stations in 2005 and 1 station in 2007 (out of 14 stations). In the following study years (2010 and 2013), the total vegetation cover (see Fig. 6a for total cover before and after 2005) and the frequency of occurrence of *Z. marina* returned to values observed before 2005.

Before 2003, BGN was qualified as eutrophic (see Tables 3 & 4). In the compromise factor map, this lagoon sector moved from slightly eutrophic conditions towards oligotrophic conditions close to those observed in AYR. Before 2003, nutrient concentrations in BGN were low compared to those observed in MEW and GRC. Since the implementation of management actions for sewage treatment in 2003 on the Bages watershed, levels of TN, TP, and

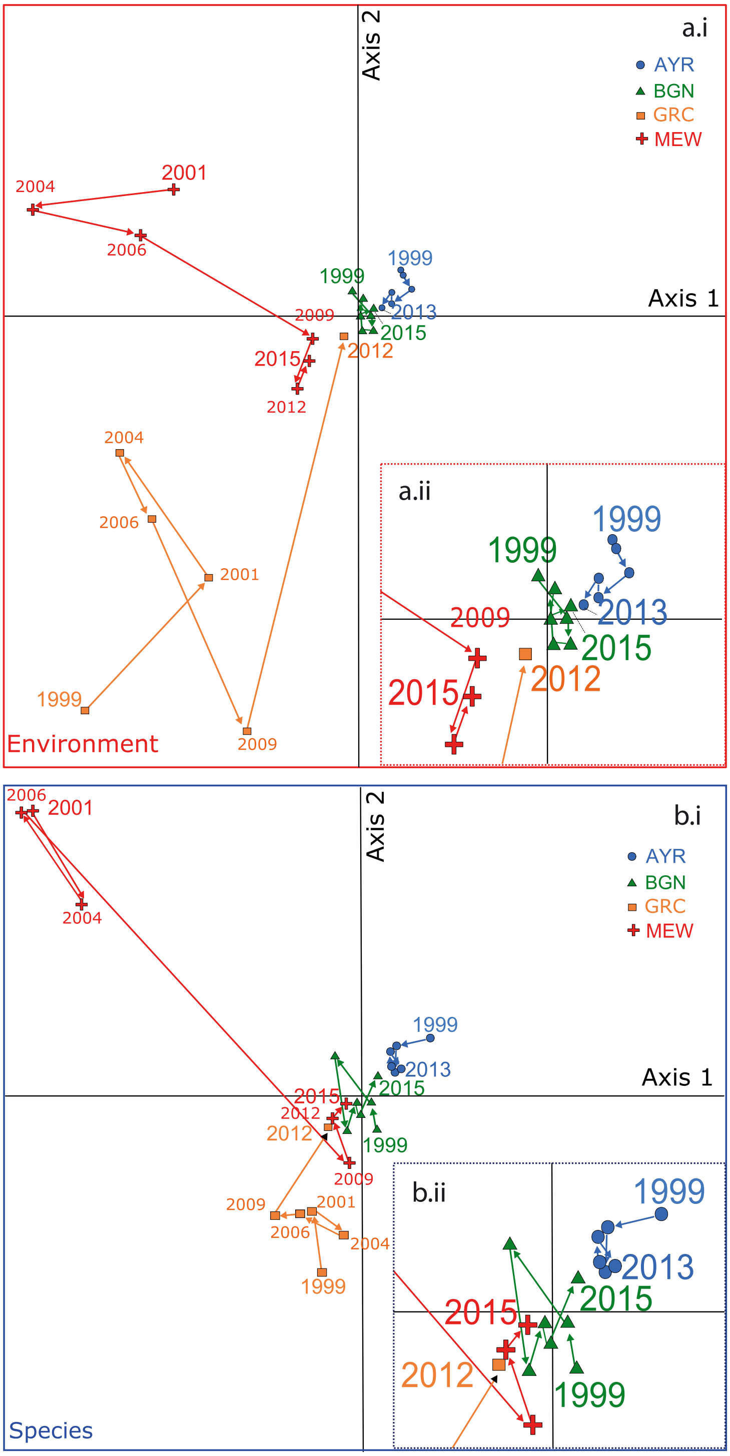


Fig. 4. Trajectories of the STATICO analysis showing the temporal dynamics of (a.i) the environmental parameters and (b.i) macrophyte species in the sectors of Ayrolle (AYR, blue dots), Bages North (BGN, green triangles), Grec (GRC, orange squares) and Méjean West (MEW, red crosses) in the compromise factor map. For each sector, the sampling dates are linked by arrows indicating the direction of the trajectory over time. The inserts (a.ii) and (b.ii) show enlargements focusing on the trajectories close to the origin of the compromise factor map

PO_4 in BGN decreased significantly (Wilcoxon test, $p < 0.05$), by 29%, 58% and 80%, respectively. Simultaneously, chl *a* decreased significantly by 50% (Wilcoxon test, $p < 0.05$) (Fig. 5, Table 4). In contrast, dissolved inorganic nitrogen and turbidity showed no significant differences before and after the implementation of management actions. Concomitant with the changes in the water column, we observed a change in the macrophyte community composition over the study period. From 1999 to 2005, the vegetation of BGN was dominated by the species *U. rigida*, *G. gracilis*, *G. bursa-pastoris* and *C. vagabunda*. The mean (±SD) total vegetation cover decreased from 89.1 ± 13.6% in 2002 to 68.5 ± 34.8% in 2005 (Fig. 6b). In 2005, *G. gracilis* represented the highest average biomass of the sector (117 ± 154 g m^{-2}) compared with *C. vagabunda* (6.1 ± 5.1 g m^{-2}) and *Z. noltei* (4.8 ± 15.1 g m^{-2}). In the same year, the seagrass *Z. noltei* declined strongly and *Z. marina* disappeared. In addition, a lack of vegetation was observed in some benthic stations. In 2007, a recovery of *Z. marina* was observed in 2 stations and the occurrence of *Zostera* spp. started to increase and finally, in 2013, this genus was found at all the benthic stations. In 2013 and 2015, the mean total vegetation cover reached more than 70% (Fig. 6b). Furthermore, the species richness increased from 4 to 12 species between 2005 and 2015.

Before 2005, MEW and GRC were clearly qualified as hypertrophic. The first sampling years of MEW and GRC were projected to the left-most side of the compromise factor map both for environment and species composition (Fig. 4). Nevertheless, a strong difference was observed between MEW and GRC. This difference was related to the absence of submerged aquatic vegetation (i.e. bare sediments), to higher concentration of chl *a* in MEW before 2006, and to particularly high values of dissolved inorganic nitrogen in GRC (Figs. 3 & 5). Both MEW and GRC trajectories for environment parameters moved toward the center of the compromise factor map (Fig. 4). After 2005, in both sectors, TN, TP, and chl *a* dropped significantly (Wilcoxon test, $p < 0.05$) by more than 55%, ~60% and >79%, respectively (Table 4). The turbidity levels also showed a significant change after

Fig. 5. Time courses of (a) total nitrogen (TN), (b) total phosphorus (TP), (c) chlorophyll *a* (chl *a*), (d) ammonium (NH_4), (e) nitrate plus nitrite (NO_3+NO_2) and (f) phosphate (PO_4), between the summers of 1999 and 2015 for Ayrolle (AYR, blue dots), Bages North (BGN, green triangle), Grec (GRC, orange squares), and Méjean West (MEW, red crosses). For each graph, the LOESS regression line for each lagoon sector is shown

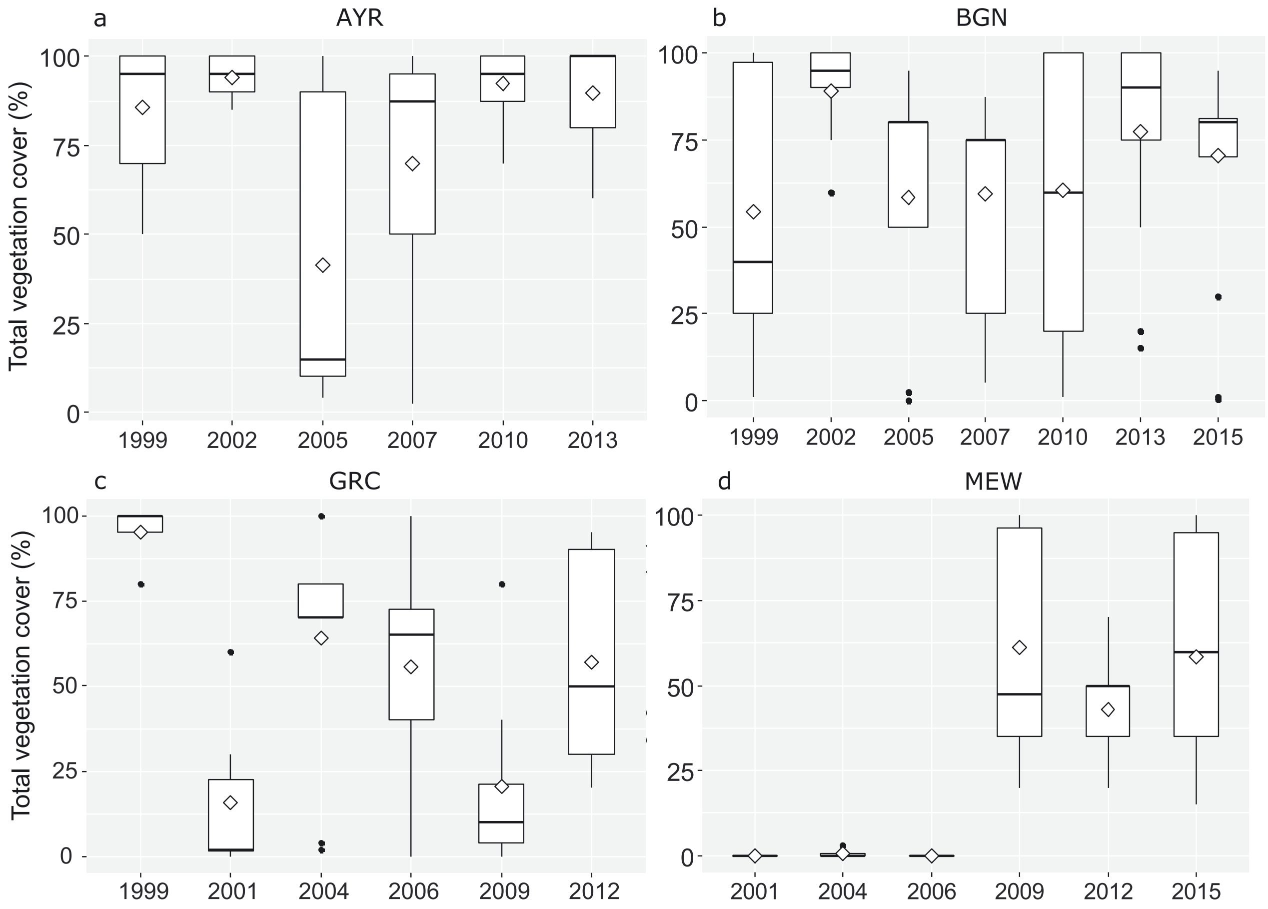


Fig. 6. Time course of the mean total vegetation cover in (a) Ayrolle (AYR), (b) Bages North (BGN), (c) Grec (GRC) and (d) Méjean West (MEW). Box and whiskers plots from spring data in all benthic stations. The whiskers represent the 5th and the 95th percentiles, the outer edges of the boxes represent the 25th and 75th percentiles, and the horizontal line within the boxes represents the median. The diamond symbols represent the means

2005 with a decline from 22.4 NTU and 27.1 NTU, in GRC and MEW, respectively, to ~15 NTU (Wilcoxon test, $p < 0.05$).

In MEW the trajectory of species (Fig. 4b) showed a change from non-vegetated (bare sediment) to a macroalgal community comprising algae of the genera *Ulva*, *Gracilaria* and *Chaetomorpha* (Fig. 7a). No submerged vegetation was observed in 2001 and 2006, only some thalli of *U. clathrata* and *G. gracilis* were present in 1 station in 2004 (Fig. 7a). In 2009, an emergence of species was observed with a mean total vegetation cover higher than 60% (Fig. 6d). *U. rigida* was the dominant species followed by *G. gracilis* (Fig. 7a). From 2009 to 2015, the mean cover of *U. rigida* declined by more than 90%. In 2012 and 2015, *Gracilaria* spp. and *C. aerea* became the dominant species. The red algae *C. capillaris* and *Solieria chordalis* (C. Agardh) J. Agardh also emerged in 2015. In 2015, macroalgae species were present at all benthic stations. Between 2009 and 2015, the species richness increased from 5 to 9 species.

For the GRC sector, the trajectory of species also moved toward the center of the compromise factor map. Submerged aquatic vegetation was present during the entire monitoring period. From 1999 to 2009, the green algae *U. rigida* and *U. clathrata* were the only species observed in GRC (Fig. 7b). During this period, important fluctuations of the mean vegetation cover *Ulva* spp. (Figs. 6c & 7b) and biomass were observed. In 1999, the mean vegetal cover of *U. rigida* was 95.0 ± 8.7% for all benthic stations associated with a high average biomass (141 ± 118 g m^{-2}). Afterwards, the mean total dropped in 2009 to reach 20.4 ± 27.1% (Fig. 7b). Important reductions of nutrient loads were realized in 2 steps, i.e. in 2005 and in 2009. An important change of the macrophytes community was observed in 2012 with the decline of *U. rigida* (mean cover: 3.2 ± 6.3% in 2012) and the appearance of 3 new species: the red algae *G. bursa-*

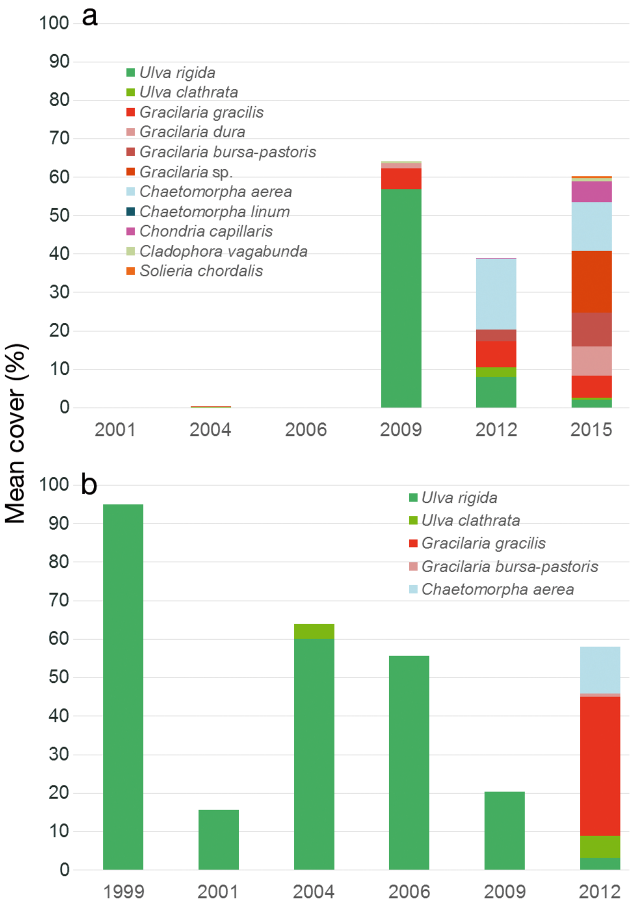


Fig. 7. Change in the mean cover (%) of macrophyte species over time in (a) Méjean West (MEW) and (b) Grec (GRC)

pastoris, *G. gracilis* and the green algae *C. aerea* (Fig. 7b). In 2012, *G. gracilis* and *C. aerea* were dominant with a mean cover of 36.2 ± 22.6% and 12.2 ± 6.3%, respectively.

3.4. Variation of organic matter and N and P contents in sediments

Averaged over the entire period OM content (mean ± SD) was lowest in AYR and highest in GRC, 3.0 ± 1.6% and 11.0 ± 2.0%, respectively (Kruskal-Wallis test, $p < 0.05$). TNsed and TPsed were lowest in AYR, 0.81 ± 0.53 g kg^{-1} and 268 ± 79.5 mg kg^{-1}, respectively, and highest in MEW, 3.9 ± 0.89 g kg^{-1} and 869 ± 99.6 mg kg^{-1}, respectively (Kruskal-Wallis test, $p < 0.05$). Between 1999 and 2010, we observed a 25–30% TPsed decrease in AYR and BGN from 314 ± 78.2 mg kg^{-1} to 221 ± 79.3 mg kg^{-1}, and from 519 ± 111 mg kg^{-1} to 385 ± 86.3 mg kg^{-1}, respectively (Wilcoxon tests, $p < 0.05$). During the entire study period, OM content and TNsed did not vary significantly in the 4 studied lagoons and TPsed showed no significant variation in MEW and GRC.

4. DISCUSSION

In this study, we aimed to describe a general pattern for re-oligotrophication trajectories for the macrophyte communities all the way from hypertrophy to oligotrophy. Such a complete trajectory that was not observed for a single lagoon in our database, can be inferred by combining trajectories observed in the compromise factor map for different lagoons (Fig. 4). Hence, after nutrient reduction, the trajectories of the 2 hypertrophic lagoons (Méjean and Grec) and the eutrophic lagoon (North Bages) were all directed towards the oligotrophic conditions as observed in Ayrolle lagoon (Fig. 4). Placed hypertrophic and oligotrophic conditions end to end, we postulate that the general pattern for re-oligotrophication trajectories in Mediterranean coastal lagoons is described by the following sequence, each punctuated by a regime shift: (1) bare non-vegetated sediments, phytoplankton-dominated state; (2) opportunistic macroalgae; (3) seagrass and perennial macroalgae dominated state (Fig. 8). However, we did not observe the second regime shift for Méjean and Grec lagoons, which remained in the macroalgal dominated state. The studied 10-yr re-oligotrophication trajectory was probably not long enough for these lagoons, which had been very strongly impacted by nutrient over-enrichment for multiple decades.

4.1. Relationships between water column variables and macrophyte assemblages

Under oligotrophic conditions, Mediterranean lagoons are characterized by high species richness and dominated by perennial macrophytes such as the macroalgae *A. acetabulum* and *V. aegagropila* and the seagrasses *Z. marina* and/or *Z. noltei*. Thanks to their ability to absorb nutrients in the sediment with their root system, seagrasses are particularly adapted to low nutrient levels in the water column (Romero et al. 2006). Under more eutrophic and in nearly hypertrophic conditions, these lagoons are dominated by free-floating macroalgae such as *Ulva* spp., *Gracilaria* spp. and *C. area*. Worldwide, these species bloom in response to increased anthropogenic nutrient inputs to coastal waters worldwide (Schramm & Nienhuis 1996, Kennish & Paerl 2010, Le Fur et al.

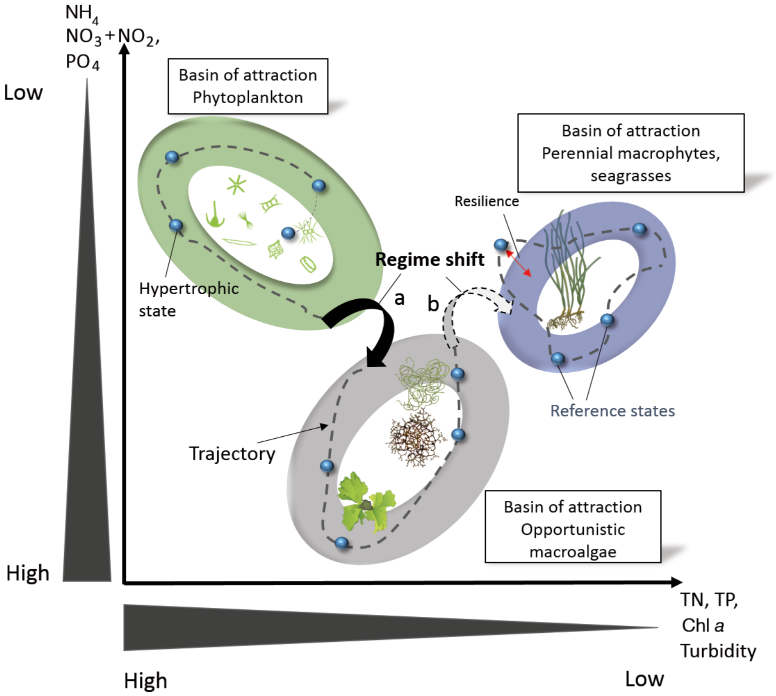


Fig. 8. Illustration of ecosystem states and regime shifts along re-oligotrophication trajectories in coastal lagoons. The ellipses represent the 3 basins of attraction that we identified, i.e. the 3 states dominated by (1) phytoplankton with non-vegetated sediments, (2) opportunistic macroalgae, and (3) perennial macroalgae and angiosperms. Within an attraction basin the vegetation assemblages may vary in terms of species composition and densities due to variations of environmental conditions. The small blue spheres represent the different ecosystem states and the stippled lines their trajectories according to the temporal sequence of these states. The sphere moves between basins of attraction following changes in nutrient concentration. The sequence during re-oligotrophication is characterized by (a, black arrow) a shift from phytoplankton to opportunistic macroalgae; (b, dashed grey arrow) a shift from opportunistic macroalgae to perennial macrophytes. The second regime shift was not observed in our study. Inspired by Tett et al. (2013). Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

2018). The high affinity of *Ulva* spp. for nitrate and ammonium and their high growth rates give them a competitive advantage compared with more slowly growing species such as seagrasses (Pedersen & Borum 1997). Under hypertrophic conditions with continuously high nutrient inputs, phytoplankton is often the main primary producer, preventing macroalgal growth due to shading (Sand-Jensen & Borum 1991, Duarte 1995). This was clearly the case for the Méjean lagoon before 2006. Hence, this is also consistent with the schematic model of Schramm (Schramm & Nienhuis 1996, Schramm 1999) and *in situ* observations made by several authors in lagoons, and more generally in coastal ecosystems (Sand-Jensen & Borum 1991, Duarte 1995, Burkholder et al. 2007, Viaroli et al. 2008, Le Fur et al. 2018). Nevertheless, intense eutrophication is not always associated with macroalgal decline (De Vries et al. 1996, Cebrian et al. 2014). For example, in more shallow lagoons, the effect of shading by phytoplankton is reduced and high flushing in lagoons with short residence times may restrict the accumulation of phytoplankton biomass. The former appears to be the case for the shallow Grec lagoon, where hypertrophic conditions co-occur with a predominance of macroalgae.

4.2. Linking re-oligotrophication trajectories of macrophytes with ecosystem theory

Ecosystem theory predicts that different ecosystem states are the result of attraction basins that result from feedback loops between the biocenosis and the environmental conditions, when these include both positive and negative feedbacks (Walker et al. 2004). The shifts from one attraction basin to another, which is induced by forcing above a threshold level, are known as regime shifts in ecosystem theory. Thus, we recognize 3 major states for the lagoon ecosystem, each as attraction basins characterized by different assemblages of primary producers that can be plotted in the ecosystem state space. The re-oligotrophication trajectories can thus be described as regime shifts between these states, which are explained hereafter. The conditions in the hypertrophic Méjean lagoon before the reduction of the nutrient loading, were characterized by bare non-vegetated sediments and high phytoplankton densities reflected by high chl *a*, TN and TP concentrations and high turbidity. This corresponds clearly to an attraction basin (Fig. 8), as it has been described for hypertrophic lakes by Scheffer et al. (1993), where high turbidity in the water column results in insufficient light for benthic macrophytes. On the oligotrophic side, an attraction basin based on rooted angiosperms (seagrasses) and perennial macroalgae such as *A. acetabulum* and *V. aegagropila* (Fig. 8) is exemplified by Ayrolle lagoon (AYR). This lagoon exhibited small fluctuations both for water column variables and macrophyte composition. Stronger fluctuations occurred for vegetation cover, particularly for *Zostera* spp., showing a decline of the coverage between 2002 and 2005 followed by a rapid recovery (Fig. 6). These variations show that the concept of an attraction basin describes the ecosystem state better for these oligotrophic conditions than stable equilibrium. The variations may be linked to natural changes (e.g. climatic variability) or to occasional and short-term pressure on this lagoon. Shortly after the reduction of the nutrient loadings, a regime shift was observed for the hypertrophic Méjean lagoon from the bare non-vegetated sediments, phytoplankton-dominated state to a dominance of opportunistic macroalgae. The decrease of chl *a* concentration by 1 order of magnitude we observed (Table 4) may have been concomitant to changes of phytoplankton composition from picoeukaryotic diatoms towards green algae dominance (e.g. small *Chlorella*-like algae) and dinophytes, which have been described by Leruste et al. (2016). The first species to proliferate after this regime shift was *U. rigida* succeeded later by other species such as *Gracilaria* spp., *Chaetomorpha* spp., *Chondria capillaris* and *S. chordalis* (Fig. 7). In the shallow hypertrophic Grec lagoon, *U. rigida* was present, albeit at fluctuating densities, throughout the entire 14-yr period (Fig. 7). Hence, a third basin of attraction in these coastal lagoons corresponds to a dominance of opportunistic macroalgae. However, the factors driving macroalgal species blooms are still unclear. Thus, it is uncertain whether or not different secondary attraction basins exist within the macroalgal attraction basin. Studies on nitrogen nutrition and growth of *Ulva* and *Gracilaria* species, however, indicate differences between these genera. *Ulva* species have higher photosynthetic and growth rates and take up nitrogen more rapidly than *Gracilaria* (Fujita 1985, Anderson et al. 1996). *Ulva* has a limited capacity to store nitrogen and depends on a constant high ambient concentration to sustain high growth rates. Conversely, *Gracilaria* maintains a high growth rate even when ambient nitrogen levels are low: it can store nitrogen for longer periods and can persist when nitrogen levels are low or only sporadically high. But, its maximal growth rate under optimal conditions is lower than that of *Ulva* (Ryther et al. 1981, Bird et al. 1982, Rosenberg & Ramus 1982, Anderson et al. 1996). Futhermore, the increasing PO_4 availability could also favour *Gracilaria* as it may increase its photosynthetic rate (García Sánchez et al. 1996). Thus, with its ability to take up lower levels of nitrogen and to store it for long periods, *Gracilaria* may have a competitive advantage over *Ulva* when the nitrogen concentrations are frequently depleted and, thus, become a limiting factor for *Ulva*.

During our study period, we did not observe a regime shift in Méjean and Grec lagoons towards oligotrophic angiosperms. In 2015, these lagoons remained in the macroalgae-dominated state. The studied 10-yr re-oligotrophication trajectory was probably not long enough for these lagoons, which had been very strongly impacted by nutrient over-enrichment for multiple decades, with the sediment acting as an internal source of nutrients. Furthermore, the absence of seagrasses during the very long period of eutrophication could have resulted in a lack of propagules to facilitate recovery. In contrast, in the north sector of the Bages lagoon (BGN), we observed a shift from an opportunistic macroalgae assemblage (e.g. *Gracilaria* spp., *Ulva* spp.) before 2005 to a system dominated by *Zostera* species. In this sector, *Z. noltei* had never completely disappeared and, therefore, one could argue that this is indicative of the resilience of the seagrass dominated state than a regime shift.

When a system is resilient, it tends to stay in its attraction basin if the threshold of forcing or disturbance is not exceeded. An ecosystem can be resilient both in its degraded and non-degraded states. In this study, we observed a case of resilience of the angiosperm-dominated state for 2 lagoons (AYR and BGN). The rapid recovery of seagrass in these lagoons was probably due to the persistence of seagrasses, their dispersal characteristics as well as the protected nature of these lagoons. Similar examples of resilience have been observed in Thau lagoon (Plus et al. 2003) and Biguglia lagoon (Pasqualini et al. 2017), where the aquatic angiosperms naturally recovered within 1 yr after a dystrophic crisis (so-called 'malaïgue' in the Mediterranean lagoons), and relatively shortly (4–5 yr) after improvements in sewage treatment and hydrological management, respectively. Moreover, after previous declines seagrasses have shown rapid recovery in a number of cases, as long as propagules (seeds) are available.

On the other hand, the macroalgal-dominated state also appears to be very resilient both with respect to shifts towards the phytoplankton-dominated state and the angiosperm-dominated state, forced by eutrophication and oligotrophication, respectively.

4.3. Recovery process, factors causing delay, and difficulties for achieving ecological quality targets

The definition of 'recovery' has been well defined for management purposes as a return towards undisturbed system state once the pressure has been reduced or eliminated (Tett et al. 2013). Recovery is

> … *the process of an ecosystem regaining its composition, structure and function relative to the levels identified for the reference ecosystem*

(McDonald et al. 2016, p. 20). As noted by Lotze et al. (2011, p. 596),

> … *the aim might be to recover a population or an ecosystem to pre-disturbance conditions or its 'natural' state before human disturbance*

However, in many studies, including the present one, the historical baseline is not known owing to a lack of historical data. In our study, we thus assumed that we could use the oligotrophic Ayrolle lagoon as a reference site as a recovery target. Therefore, management is currently aimed at pursuing re-oligotrophication trajectories. However, we have to be careful with the choice of this recovery target because, since according to the trophic classification of Nixon (1995), some coastal lagoons fall within the range of eutrophic, mesotrophic or oligotrophic conditions based on their natural conditions of nutrient inputs and residence times. Therefore, some lagoons will probably never reach oligotrophic conditions. Nonetheless, for those lagoons where a return to oligotrophic conditions is possible, the recovery of perennial macrophytes will probably be a long process. Hence, long-term monitoring is still needed to see if the system is able to recover by itself after reduction of nutrient loading, without additional measures (De Wit et al. 2017). However, several authors have suggested that most ecosystems have shown partial recovery and that time lag or hysteresis can delay the recovery response even after the reduction or suppression of the environmental pressure (see Duarte et al. 2015).

Nutrient reduction plans have often failed to return coastal ecosystems to the pre-disturbance state due to hysteresis and shifting baselines (Duarte et al. 2015). As our results show, high internal nutrient loads have accumulated in the sediment during the previous eutrophication periods. However, we only observed a reduction of TP, but not of TN in the sediment over the study period. The continuing nutrient fluxes from the sediment represent an internal load that may support phytoplankton growth (Richardson & Jørgensen 1996) or macroalgal growth during re-oligotrophication trajectories, thus delaying the recovery process. However, following the reduction of external nutrient loading, the decrease of phytoplankton biomass increases the light availability for benthic primary producers. Therefore, macrophytes become important once again and can accelerate the recovery process by re-oxygenating the sediment, intercepting the sediment–water column nutrient flux and temporarily retaining nutrients in plant biomass (McGlathery et al. 2007).

According to Duarte et al. (2015), recovery is believed to be dependent also on the connectivity between the degraded recovering and adjacent healthy ecosystems. Connectivity would allow the supply of propagules and colonizers (Pratt 1994) and will also impact other functional aspects through its influence on the resilience of ecosystems (Elliott et al. 2007).

In addition to internal loading and the lack of connectivity with healthy ecosystems, other factors can also limit the recovery, such as nutrient inputs from diffuse sources (e.g. agriculture), for which it is still difficult to assess the importance and which are difficult to manage effectively to achieve reduction. Hence, these diffuse nutrient sources may still contribute to maintain eutrophic conditions in several Mediterranean lagoons. In addition, Grec and Méjean lagoons are not directly connected to the sea but receive nutrient-rich waters from a canal ('Rhône to Sète' canal), which will hinder the quick recovery of these lagoons. Furthermore, coastal lagoons can be strongly affected by chemical contaminants (Munaron et al. 2012) and some of these compounds can impact the photosynthesis and the growth of macrophytes (Haynes et al. 2000, Chesworth et al. 2004). Physical factors such as sediment resuspension can also limit the recovery, by maintaining low water transparency and limiting light availability for macrophytes. Dense seagrass meadows stabilize the sediment by dissipating wave energy and promoting particle trapping, and hence improve water clarity (Widdows et al. 2008, Carr et al. 2010, Maxwell et al. 2017). But in the absence of vegetation, the sediment resuspension and consecutive high turbidity will limit the reestablishment of these rooted angiosperms. In addition, the historical states of the Méjean and Grec lagoons are not known. We do not know if rooted macrophytes were initially present at all stations in these lagoons. A recent study tested the potential presence of *Z. noltei* in the Méjean lagoon, by simulating oligotrophic conditions of the water column. This study showed that several areas of this lagoon were not able to harbor this species due to wind conditions and bottom shear stress (Ouisse et al. 2014). This highlights that, when the historical state of an ecosystem is unknown, the desired state may not be reached due to natural conditions even when pressures have been removed.

Acknowledgements. This study was supported by a PhD grant for I.L.F., financed by Ifremer and the French Water Agency (Agence de l'Eau Rhône-Méditerranée-Corse). The authors thank the staff of the Ifremer laboratory (LER/LR) and all the people involved in the collection of the data on which this article is based. All the data used in this paper have been collected through the Lagoon Monitoring Network and the Water Framework Directive (WFD) monitoring, and additional studies (PNEC, INTERREG II/PNOC and RLC programs) carried out from 1998 to 2015.

LITERATURE CITED

Anderson RJ, Monteiro PMS, Levitt GJ (1996) The effect of localised eutrophication on competition between *Ulva lactuca* (Ulvaceae, Chlorophyta) and a commercial resource of *Gracilaria verrucosa* (Gracilariaceae, Rhodophyta). Hydrobiologia 326–327:291–296

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193

Barnes RSK (1980) Coastal lagoons, the natural history of a neglected habitat. Cambridge University Press, Cambridge

Bec B, Collos Y, Souchu P, Vaquer A and others (2011) Distribution of picophytoplankton and nanophytoplankton along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Aquat Microb Ecol 63:29–45

Bird KT, Habig C, DeBusk T (1982) Nitrogen allocation and storage patterns in *Gracilaria tikvahiae* (Rhodophyta). J Phycol 18:344–348

Borja Á, Dauer DM, Elliott M, Simenstad CA (2010) Medium- and long-term recovery of estuarine and coastal ecosystems: patterns, rates and restoration effectiveness. Estuaries Coasts 33:1249–1260

Burkholder JM, Tomasko DA, Touchette BW (2007) Seagrasses and eutrophication. J Exp Mar Biol Ecol 350:46–72

Carr J, D'Odorico P, McGlathery K, Wiberg P (2010) Stability and bistability of seagrass ecosystems in shallow coastal lagoons: role of feedbacks with sediment resuspension and light attenuation. J Geophys Res Biogeosci 115:G03011

Cebrian J, Corcoran D, Lartigue J (2014) Eutrophication-driven shifts in primary producers in shallow coastal systems: implications for system functional change. Estuaries Coasts 37:180–197

Cépralmar (2006) Défi eutrophisation des lagunes littorales du Languedoc-Roussillon—Etude réalisée dans le cadre du 8ème programme de l'Agence de l'Eau Rhône-Méditerranée et Corse. Cépralmar, Montpellier

Charlier RH, Lonhienne T (1996) The management of eutrophicated waters. In: Schramm W, Nienhuis PN (eds) Marine benthic vegetation. Springer, Berlin, p 45–78

Chesworth JC, Donkin ME, Brown MT (2004) The interactive effects of the antifouling herbicides Irgarol 1051 and Diuron on the seagrass *Zostera marina* (L.). Aquat Toxicol 66:293–305

Cloern JE (2001) Our evolving conceptual model of the coastal eutrophication problem. Mar Ecol Prog Ser 210: 223–253

Costanza R, d'Arge R, de Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

De Vries I, Philippart CJM, De Groodt EG, van der Tol MWM (1996) Coastal eutrophication and marine benthic vegetation: a model analysis. In: Schramm W, Nienhuis PN (eds) Marine benthic vegetation. Ecol Stud, Vol 123. Springer Science & Business Media, Berlin, p 79–113

De Wit R, Rey-Valette H, Balavoine J, Ouisse V, Lifran R (2017) Restoration ecology of coastal lagoons: new methods for the prediction of ecological trajectories and economic valuation. Aquat Conserv 27:137–157

Dion P, Bozec SL (1996) The French Atlantic coasts. In: Schramm W, Nienhuis P (eds) Marine benthic vegetation: recent changes and the effects of eutrophication. Ecol Stud, Vol 123. Springer Science & Business Media, Berlin, p 251–264

Dolédec S, Chessel D (1994) Co-inertia analysis: an alternative method for studying species–environment relationships. Freshw Biol 31:277–294

Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. J Stat Softw 22:1–20

Duarte CM (1995) Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41:87–112

Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. Limnol Oceanogr 41:1758–1766

Duarte CM, Borja A, Carstensen J, Elliott M, Krause-Jensen D, Marbà N (2015) Paradigms in the recovery of estuarine and coastal ecosystems. Estuaries Coasts 38:1202–1212

Elliott M, Burdon D, Hemingway KL, Apitz SE (2007) Estuarine, coastal and marine ecosystem restoration: confusing management and science—a revision of concepts. Estuar Coast Shelf Sci 74:349–366

Facca C, Ceoldo S, Pellegrino N, Sfriso A (2014) Natural recovery and planned intervention in coastal wetlands: Venice lagoon (northern Adriatic Sea, Italy) as a case study. Sci World J 2014:968618

Fiandrino A, Ouisse V, Dumas F, Lagarde F and others (2017) Spatial patterns in coastal lagoons related to the hydrodynamics of seawater intrusion. Mar Pollut Bull 119:132–144

Flindt MR, Pardal MÂ, Lillebø AI, Martins I, Marques JC (1999) Nutrient cycling and plant dynamics in estuaries: a brief review. Acta Oecol 20:237–248

Fujita RM (1985) The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. J Exp Mar Biol Ecol 92:283–301

García Sánchez MJ, Fernández JA, Niell FX (1996) Photosynthetic response of P deficient *Gracilaria tenuistipitata* under two different phosphate treatments. Physiol Plant 96:601–606

Guiry MD, Guiry GM (2016) AlgaeBase. World-wide electronic publication. National University of Ireland, Galway. www.algaebase.org/ www.algaebase.org/

Harlin MM (1995) Changes in major plant groups following nutrient enrichment. In: McComb AJ (ed) Eutrophic shallow estuaries and lagoons. CRC Press, Boca Raton, FL, p 173–187

Haynes D, Ralph P, Prange J, Dennison B (2000) The impact of the herbicide Diuron on photosynthesis in three species of tropical seagrass. Mar Pollut Bull 41:288–293

Human LRD, Snow GC, Adams JB, Bate GC, Yang SC (2015) The role of submerged macrophytes and macroalgae in nutrient cycling: a budget approach. Estuar Coast Shelf Sci 154:169–178

Ifremer (2007) Réseau de suivi lagunaire du Languedoc-Roussillon. Bilan des résultats 2006. Rapport RSL-07/2007. https://archimer.ifremer.fr/doc/00118/22926/

Kennish MJ, Paerl HW (2010) Coastal lagoons: critical habitats of environmental change. CRC Press, Boca Raton, FL

Kidé SO, Manté C, Dubroca L, Demarcq H, Mérigot B (2015) Spatio-temporal dynamics of exploited groundfish species assemblages faced to environmental and fishing forcings: insights from the Mauritanian exclusive economic zone. PLOS ONE 10:e0141566

Kjerfve B (1994) Coastal lagoons. In: Kjerfve B (ed) Coastal lagoon processes. Elsevier Oceanogr Ser, Vol 60. Elsevier Science, Amersterdam, p 1–8

Le Fur I, De Wit R, Plus M, Oheix J, Simier M, Ouisse V (2018) Submerged benthic macrophytes in Mediterranean lagoons: distribution patterns in relation to water chemistry and depth. Hydrobiologia 808:175–200

Lefcheck JS, Orth RJ, Dennison WC, Wilcox DJ and others (2018) Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. Proc Natl Acad Sci USA 115:3658–3662

Leruste A, Malet N, Munaron D, Derolez V and others (2016) First steps of ecological restoration in Mediterranean lagoons: shifts in phytoplankton communities. Estuar Coast Shelf Sci 180:190–203

Lloret J, Marín A (2009) The role of benthic macrophytes and their associated macroinvertebrate community in coastal lagoon resistance to eutrophication. Mar Pollut Bull 58:1827–1834

Lloret J, Marín A (2011) The contribution of benthic macrofauna to the nutrient filter in coastal lagoons. Mar Poll Bull 62:2732–2740

Lotze HK, Coll M, Magera AM, Ward-Paige C, Airoldi L (2011) Recovery of marine animal populations and ecosystems. Trends Ecol Evol 26:595–605

Lyons DA, Arvanitidis C, Blight AJ, Chatzinikolaou E and others (2014) Macroalgal blooms alter community structure and primary productivity in marine ecosystems. Glob Change Biol 20:2712–2724

Mann KH (1973) Seaweeds: their productivity and strategy for growth. Science 182:975

Maxwell PS, Eklöf JS, van Katwijk MM, O'Brien KR and others (2017) The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems — a review. Biol Rev Camb Philos Soc 92: 1521–1538

McCrackin ML, Jones HP, Jones PC, Moreno-Mateos D (2017) Recovery of lakes and coastal marine ecosystems from eutrophication: a global meta-analysis. Limnol Oceanogr 62:507–518

McDonald T, Jonson J, Dixon KW (2016) National standards for the practice of ecological restoration in Australia. Restor Ecol 24:S4–S32

McGlathery KJ, Sundbäck K, Anderson IC (2007) Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. Mar Ecol Prog Ser 348:1–18

Meinesz C, Derolez V, Bouchoucha M (2013) Base de données « pressions sur les lagunes méditérranéennes » — analyse des liens état-pression. https://archimer.ifremer.fr/doc/00154/26496/24607.pdf

Mendes S, Fernández-Gómez MJ, Pereira MJ, Miranda Azeiteiro U, Galindo-Villardón MP (2012) An empirical comparison of canonical correspondence analysis and STATICO in the identification of spatio-temporal ecological relationships. J App Stat 39:979–994

Munaron D, Tapie N, Budzinski H, Andral B, Gonzalez JL (2012) Pharmaceuticals, alkylphenols and pesticides in Mediterranean coastal waters: results from a pilot survey using passive samplers. Estuar Coast Shelf Sci 114:82–92

Neveux J, Lantoine F (1993) Spectrofluorometric assay of chlorophylls and phaeopigments using the least squares approximation technique. Deep Sea Res I 40:1747–1765

Nixon SW (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41: 199–219

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. Bioscience 56:987–996

Ouisse V, Perron C, Fiandrino A, Rochette S (2014) Rôle des macrophytes dans la restauration des milieux lagunaires: distribution spatiale de *Zostera noltei* (MARES1). ODE/UL/LERLR 14-21. Ifremer, Sète

Pasqualini V, Derolez V, Garrido M, Orsoni V and others (2017) Spatiotemporal dynamics of submerged macrophyte status and watershed exploitation in a Mediterranean coastal lagoon: understanding critical factors in ecosystem degradation and restoration. Ecol Eng 102:1–14

Pedersen MF, Borum J (1997) Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. Mar Ecol Prog Ser 161:155–163

Plus M, Deslous-Paoli JM, Dagault F (2003) Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. Aquat Bot 77:121–134

PNR (Parc Naturel Régional de la Narbonnaise en Méditerranée) (2011) Bulletin de l'observatoir du parc naturel régional. Spécial suivi des stations d'épuration- étang de Bages-Sigean Résultats 2009. No. 7, January 2011. www.parc-naturel-narbonnaise.fr/actions-parc/environnement/lagunes-zones-humides/observatoire-des-etangs

Pratt JR (1994) Artificial habitats and ecosystem restoration: managing for the future. Bull Mar Sci 55:268–275

R Core Team (2018) R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna. www.R-project.org/

Richardson K, Jørgensen BB (1996) Eutrophication: definition, history and effects. In: Jørgensen BB, Richardson K (eds) Eutrophication in coastal marine ecosystems. American Geophysical Union, Washington, DC, p 1–19

Riemann B, Carstensen J, Dahl K, Fossing H and others (2016) Recovery of danish coastal ecosystems after reductions in nutrient loading: a holistic ecosystem approach. Estuaries Coasts 39:82–97

Romero J, Lee KS, Perez M, Mateo MA, Alcoverro T (2006) Nutrient dynamics in seagrass ecosystems. In: Larkum AWD, Orth RJ, Duarte C (eds) Seagrasses: biology, ecology and conservation, Vol 16. Springer, Dordrecht, p 227–254

Rosenberg C, Ramus J (1982) Ecological growth strategies in the seaweeds *Gracilaria foliifera* (Rhodophyceae) and *Ulva* sp. (Chlorophyceae): soluble nitrogen and reserve carbohydrates. Mar Biol 66:251–259

Rysgaard S, Risgaard-Petersen N, Sloth NP (1996) Nitrification, denitrification, and nitrate ammonification in sediments of two coastal lagoons in Southern France. Hydrobiologia 329:133–141

Ryther JH, Corwin N, DeBusk TA, Williams LD (1981) Nitrogen uptake and storage by the red alga *Gracilaria tikvahiae* (McLachlan, 1979). Aquaculture 26:107–115

Sand-Jensen K, Borum J (1991) Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. Aquat Bot 41:137–175

Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. Trends Ecol Evol 8:275–279

Schramm W (1999) Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. J Appl Phycol 11:69–78

Schramm W, Nienhuis P (1996) Marine benthic vegetation: recent changes and the effects of eutrophication. Ecol Stud, Vol 123. Springer Science & Business Media, Berlin

Simier M, Blanc L, Pellegrin F, Nadris D (1999) Approche simultanée de *K* couples de tableaux: application à l'étude des relations pathologie végétale-environnement. Rev Stat Appl 47:31–46

Souchu P, Bec B, Smith VH, Laugier T and others (2010) Patterns in nutrient limitation and chlorophyll *a* along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. Can J Fish Aquat Sci 67:743–753

Tett P, Gowen RJ, Painting SJ, Elliott M and others (2013) Framework for understanding marine ecosystem health. Mar Ecol Prog Ser 494:1–27

Thioulouse J, Simier M, Chessel D (2004) Simultaneous analysis of a sequence of paired ecological tables. Ecology 85:272–283

Tsiamis K, Panayotidis P, Salomidi M, Pavlidou A, Kleinteich J, Balanika K, Küpper FC (2013) Macroalgal community response to re-oligotrophication in Saronikos Gulf. Mar Ecol Prog Ser 472:73–85

Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K (1997) Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol Oceanogr 42:1105–1118

van der Heide T, van Nes EH, Geerling GW, Smolders AJP, Bouma TJ, van Katwijk MM (2007) Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems 10:1311–1322

Venice System (1958) The venice system for the classification of marine waters according to salinity. Limnol Oceanogr 3:346–347

Viaroli P, Bartoli M, Giordani G, Naldi M, Orfanidis S, Zaldivar JM (2008) Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. Aquat Conserv 18:S105–S117

Walker B, Holling CS, Carpenter S, Kinzig A (2004) Resilience, adaptability and transformability in social–ecological systems. Ecol Soc 9:5

Widdows J, Pope ND, Brinsley MD, Asmus H, Asmus RM (2008) Effects of seagrass beds (*Zostera noltii* and *Z. marina*) on near-bed hydrodynamics and sediment resuspension. Mar Ecol Prog Ser 358:125–136

WoRMS Editorial Board (2016) World register of marine species. Available from www.marinespecies.org at VLIZ. (accessed 16 November 2016)

Editorial responsibility: Morten Pedersen,
Roskilde, Denmark

Submitted: January 15, 2018 ; Accepted: November 4, 2018
Proofs received from author(s): December 13, 2018

AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. (2015)

DOI: 10.1002/aqc.2601

Restoration ecology of coastal lagoons: new methods for the prediction of ecological trajectories and economic valuation

RUTGER DE WIT[a,*], HELENE REY-VALETTE[b], JULIETTE BALAVOINE[a,c], VINCENT OUISSE[d] and ROBERT LIFRAN[b]
[a] *Centre for Marine Biodiversity, Exploitation and Conservation (MARBEC), IRD, Ifremer, Université de Montpellier, Montpellier, France*
[b] *UMR LAMETA, INRA, Université de Montpellier, Montpellier, France*
[c] *Plan Bleu pour la Méditerranée, PAM/PNUE Regional Activity Centre, Valbonne, France*
[d] *Centre for Marine Biodiversity, Exploitation and Conservation (MARBEC), IRD, Ifremer, Université de Montpellier, Sète, France*

ABSTRACT

1. Conservation of the seven lagoons of the Palavas complex (southern France) has been severely impaired by nutrient over-enrichment during at least four decades. The effluents of the Montpellier wastewater treatment plant (WWTP) represented the main nutrient input. To improve the water quality of these lagoons, this WWTP was renovated and upgraded and, since the end of 2005, its effluents have been discharged 11 km offshore into the Mediterranean (total investment €150 M).

2. Possibilities of ecosystem restoration as part of a conservation programme were explored by a focus group of experts. Their tasks were: (i) to evaluate the impact of the reduction of the nutrient input; (ii) if necessary, to design additional measures for an active restoration programme; and (iii) to predict ecosystem trajectories for the different cases. Extension of Magnoliophyta meadows can be taken as a proxy for ecosystem restoration as they favour the increase of several fish (seahorse) and bird (ducks, swans, herons) species, albeit they represent a trade-off for greater flamingos. Additional measures for active ecosystem restoration were only recommended for the most impaired lagoon Méjean, while the least impaired lagoon Ingril is already on a trajectory of spontaneous recovery.

3. A multiple contingent valuation considering four different management options for the Méjean lagoon was used in a pilot study based on face-to-face interviews with 159 respondents. Three levels of ecosystem restoration were expressed in terms of recovery of Magnoliophyta meadows, including their impact on emblematic fish and avifauna. These were combined with different options for access (status quo, increasing access, increasing access with measures to reduce disturbance). The results show a willingness of local populations to pay per year about €25 for the highest level of ecological restoration, while they were only willing to allocate about €5 for additional footpaths and hides.

Received 30 May 2014; Revised 5 August 2015; Accepted 30 August 2015

KEY WORDS: coastal lagoon; seagrass meadow; marine and brackish Magnoliophyta; phytoplankton; ecosystem services; willingness to pay (WTP); ecosystem trajectory' nutrient enrichment; oligotrophication; sediment N and P contents; Water Framework Directive

---

*Correspondence to: Rutger De Wit, Centre for Marine Biodiversity, Exploitation and Conservation (MARBEC), IRD, Ifremer, Université de Montpellier, CNRS, Place Eugène Bataillon, Université de Montpellier, Case 093, F-34095 Montpellier Cedex 5, France. Email: rutger.de-wit@umontpellier.fr

INTRODUCTION

Coastal lagoons occupy about 13% of the world's coastlines (Barnes, 1980) and about 5.5% of the European coast (Razinkovas *et al*., 2008), where they are particularly abundant around the Mediterranean Sea and the south-eastern Baltic coasts. Their surroundings represent attractive sites for human development and lagoons are exploited for different uses including fisheries, aquaculture, recreation and tourism (Anthony *et al*., 2009; Kuhfuss *et al*., 2010). Water quality and biodiversity in coastal lagoons are particularly vulnerable to high nutrient and contaminant loadings from their watersheds and, in general, coastal lagoons suffer from increasing demographic and economic developments in the coastal zone. Hence, despite the fact that conservation measures including designations as natural parks, regional nature reserves, 'Natura 2000' and 'Ramsar' sites have been applied to many coastal lagoon sites in Europe, many of these ecosystems have been degraded by anthropogenic pressures, among which eutrophication has been particularly important (Zaldivar *et al*., 2008).

In coastal lagoons the impact of eutrophication on ecosystem structure and functioning is characterized by regime shifts that are well documented in the scientific literature (Nixon 1995, Valiela *et al*., 1997; Schramm, 1999; De Wit *et al*., 2001; Orfanidis *et al*., 2003; Viaroli *et al*., 2008). The different stages are described briefly. Oligotrophy in coastal lagoons, which typically represents the pristine situation for many of them, is characterized by low water column turbidity resulting from low phytoplankton densities. In the South of France it has been shown that phytoplankton growth in oligotrophic lagoons is limited by phosphorus supply (Souchu *et al*., 2010). The low water turbidity favours a submerged aquatic vegetation (SAV) of Magnoliophyta, comprising seagrasses in polyhaline and mixoeuhaline lagoons, while freshwater and brackish species may occur in oligohaline and mesohaline lagoons. At a low level of nutrient loading the Magnoliophyta grow vigorously. However, as loading increases, a first intermediate stage is characterized by heavy growth of epiphytes on the leaves and stems of the Magnoliophyta, which may induce a shading stress for the latter. As nutrient loading further increases, the system may flip over into another state dominated either by opportunistic macroalgae or by a dense phytoplankton bloom. Macroalgal-dominated systems are susceptible to development of dystrophic crises during summer with water column hypoxia following a sudden crash of the algal blooms (Valiela *et al*., 1997; De Wit *et al*., 2001; Viaroli *et al*., 2008). Extremely high loading often results in primary producer communities dominated by phytoplankton species, i.e. often picoeukaryotes in hypertrophic Mediterranean lagoons (Bec *et al*., 2011) and filamentous cyanobacteria in oligohaline systems (Pilkaitytė and Razinkovas, 2006; Chomérat *et al*., 2007). Insufficient light availability close to the bottom is a key factor explaining the absence of SAV in coastal systems, illustrated by the fact that the depth limit for the establishment of SAV decreases with increasing eutrophication (Duarte, 1991).

The general aim of improving the water quality and ecological conditions in surface waters as requested in the European Union by the Water Framework Directive (Council of the European Communities, 2000) thus clearly converges with the objective of the conservation of valuable aquatic ecosystems such as coastal lagoons. Before 2000, interventions to reduce the stress caused by eutrophication in Mediterranean coastal lagoons included: (i) macroalgal harvesting (Guyoneaud *et al*., 1998; Lenzi *et al*., 2003); and (ii) measures for improving water exchange with the adjacent sea. Nowadays, it is considered that the reduction of nutrient loading to coastal lagoons is of primary importance to combat eutrophication and prevent dystrophic crises in coastal lagoons. Therefore, a lot of effort has been spent in upgrading sewage collection systems and wastewater treatment plants (WWTP) and in some cases the output of the WWTP bypasses the lagoon and is discharged into the open sea, as is the case for the Bassin d'Arcachon (De Wit *et al*., 2005) and for the Mediterranean lagoons of the Palavasian complex close to Montpellier (see detail below).

Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Society for Ecological Restoration International Science and Policy Working Group, 2004). Hence, human intervention focused on reducing the pressures on ecosystems with the aim of recovering the earlier existing ecosystem structure and functioning is clearly part of ecological restoration. It remains, however, an open question whether suppression of the main pressure, i.e. nutrient over-enrichment, is sufficient for a return to historical ecosystem conditions. Borja *et al*. (2010) review marine and coastal systems where a reduction of the main pressure was realized and evaluates if, and how quickly, the ecosystem returns to its state before its degradation. Ecosystem trajectories for return may show hysteresis with respect to their degradation, particularly when regime shifts are based on existence of multiple stable states. It has also been questioned whether marine and coastal ecosystems can return per se to their pristine conditions (Elliott *et al*., 2007; Duarte *et al*., 2009). In the context of this paper, passive restoration is defined as the suppression of the external pressure that caused the degradation without taking additional measures. It assumes that after the pressure is relieved, a trajectory to recovery of good ecological conditions is based on spontaneous natural processes. For comparison, active restoration implies that the suppression of the causative pressure is accompanied by additional management measures based on direct interventions. Attempts to restore seagrass meadows in coastal lagoons based on actively planting or seeding is a clear example of such an intervention. A specific theme section of the journal *Marine Ecology Progress Series* has been devoted to large-scale operations for seagrass recovery in the coastal lagoons of Maryland and Delaware (Orth *et al*., 2012) and a first pilot experiment has been performed in the south of France (Hebert *et al*., 2012). While, reducing the external pressures on water bodies clearly is the objective of a general water policy (Council of the European Communities, 2000), the additional measures applied locally in the lagoons should typically be included in the local Master Plans for the conservation and management of lagoons.

The concept of ecosystem services, which has been defined as the benefits that people obtain from ecosystems (Millennium Ecosystem Assessment, 2005), appears appropriate for evaluating how society may benefit from ecosystem conservation and restoration measures. To our knowledge there are very few studies where ecosystem services have been considered for coastal lagoons as an entity. A major database that is now available from case studies on values of ecosystem services of different biomes (De Groot *et al*., 2012) does not include lagoons as a specific entry, and only one of the cited studies concerns coastal lagoons (Nunes *et al*., 2004). Similarly, the review of Barbier *et al*. (2011) concerning the value of ecosystem services in the coastal zone does not deal with lagoons specifically. In the study by De Groot *et al*. (2012), some habitats that are typical for coastal lagoons, such as seagrass meadows and intertidal flats, have been confounded within the biomes of coastal systems and coastal wetlands, respectively. Regionally, in southern France, an inventory of the ecosystem services of coastal lagoons in the Languedoc-Roussillon region has been compiled using a slight modification of the typology used by the Millennium Ecosystem Assessment (2005), which has served to create a typology of human uses of lagoons (Kuhfuss *et al*., 2010). Ecosystem services and human capital has also been a key concept for studying the possibilities of ecosystem restoration of the Etang de Berre lagoon close to Marseille, which has been degraded by excessive input of fresh water from an electric powerplant (Aronson *et al*., 2012).

It is not the aim to determine the total economic value of the ecosystem services (De Groot *et al*., 2012), which is very demanding and controversial (Norgaard, 2010). In contrast, the main interest was to assess the marginal economic value, i.e. the value that could be gained by ecological restoration and thus represents the difference between the total economic values of the ecosystem services after and before ecological restoration. Therefore, different options for the restoration of coastal lagoons have been considered as part of a more comprehensive conservation strategy. Using valuation methods for ecosystem services, the marginal value has been related to the costs of the restoration of ecosystems and been assessed using so-called 'Cost based Methods' (De Groot *et al.*, 2012). These take into account the total amount spent for a realized restoration project, or consider a realistic budget for a planned restoration. Another approach, known as contingent valuation, is to submit a single scenario for a future restoration project, without a clearly established budget, to the general public and ask them their willingness to pay for this project (Ahtiainen *et al.*, 2013). However, a single scenario is often not satisfactory, as stakeholders often want to consider different alternatives. Hence, participation of stakeholders and the general public during the planning phase of a restoration project is obviously most important for its success. Thus, different planning and management options can be developed and proposed to the general public. Ideally, the costs associated with different options have been clearly identified before proposing them to the public. If that is the case, a choice experiment can be used (Westerberg *et al.*, 2010; Jaeck and Lifran, 2013). Unfortunately, so far, it has not been possible to calculate the budgets related to the different restoration options because the data on restoration costs are scarce and highly variable, and each restoration involves specific investments. Therefore, it was decided to prepare four different scenarios for ecosystem restoration and management, and each of these four scenarios has been used simultaneously for contingent valuation, referred to as a multiple contingent valuation (MCV).

This study focused on the coastal lagoons of the Palavasian complex, close to Montpellier. The seven coastal lagoons of this complex have suffered from different degrees of eutrophication, particularly between 1960 and 2005, when the population densities of the Montpellier agglomeration increased by 260%. The nutrient-rich effluents from the WWTP of this urban agglomeration used to be discharged into Lez River, which communicates with the lagoons. In 2005, the WWTP was renovated and upgraded and a 20 km blast pipe was built to implement an offshore outfall system located on the sea bed 11 km from the coast. The total costs of this operation were €150 million and it resulted in a reduction of 83% of N and 70% of P inputs into the lagoon (Meinesz *et al.*, 2013).

In this study natural sciences and socio-economic research were integrated to develop a novel approach. A focus group of experts was formed that concentrated their analyses on two selected lagoons. Based on the knowledge synthesized and recommendations for active restoration scenarios by the focus group a socio-economic questionnaire was designed and used for a multiple contingent valuation (MCV). The objective of this study was to test this new methodology. Hence, it was aimed to synthesize the currently available scientific information in order to predict ecosystem trajectories resulting from nutrient reduction alone (i.e. passive restoration), and how these could be influenced by additional measures (active restoration). The second aim was to analyse the perception of the local populations of ecological restoration of the coastal lagoons and to study their willingness to pay for it.

STUDY AREA

The lagoons of the Palavasian lagoon complex occur along the SW–NE oriented Mediterranean coastline to the south of the city of Montpellier and are located between 3.76 and 3.96°E and between 43.43 and 43.57°N (decimal degrees, IGN maps Geoportail http://www.geoportail.gouv.fr). The complex consists of seven lagoons, from west to east, respectively, Etang d'Ingril, Etang de Vic, Etang de Pierre Blanche, Etang d'Arnel, Etang du Prévost, Etang du Méjean and Etang du Grec (Figure 1). The word '*Etang*' is used instead of '*lagune*' both in the vernacular language and in the official geographic denomination, despite the fact that it formally translates into English as 'lake' or 'pond'. Hereafter, the word 'Etang' is replaced by the English word 'lagoon'; hence, e.g. Etang d'Ingril will be referred to as Ingril lagoon. These different lagoons have been created by compartmentalization of the original 'lagune de Melgueil' starting from the late 17th century due to building of the Canal de Rhône à Sète, canalization of the Lez River, and later by building roads to gain access to the beaches. The

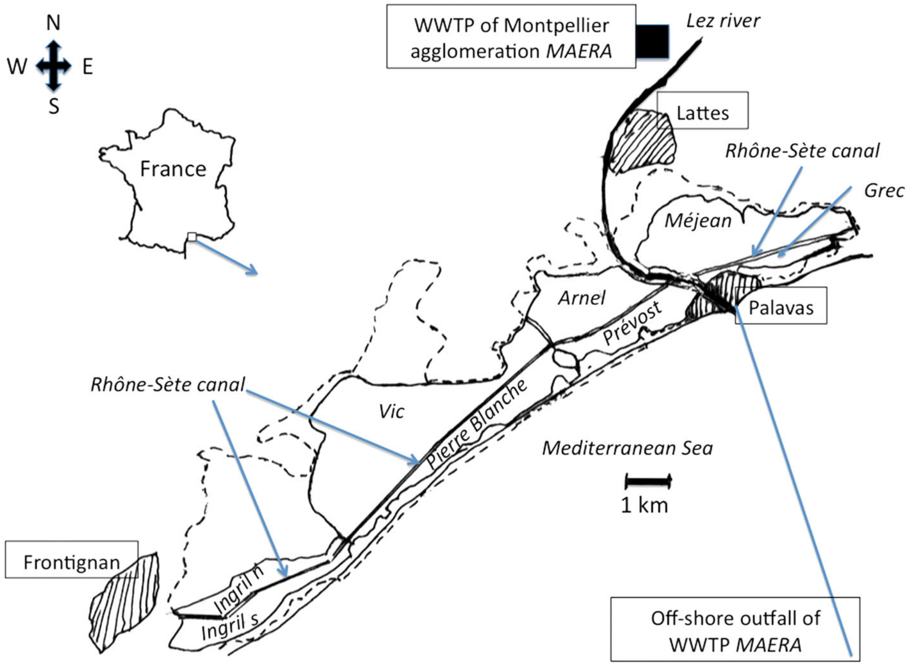


Figure 1. Map of the seven lagoons of the Palavas lagoon complex indicating the boundary of the Natura 2000 protected area (broken line) and of the geographic location of the WWTP of the Montpellier agglomeration (450 000 inhabitants) and its outfall 11 km offshore in the Mediterranean Sea.

main WWTP of the Montpellier agglomeration is located on the coastal plain between the city and the lagoons and close to the western shore of the Lez River. The original WWTP, which was called La Cereirede, discharged its nutrient-rich effluents directly into the Lez River. As a result, the Méjean, Grec, Prévost and Arnel lagoons have been particularly affected by the nutrient over-enrichment, while the Ingril lagoon, further away, has been less affected (Ifremer, 2007). Thanks to the new WWTP facility MAERA with its offshore outfall system located 11 km from the coast (Figure 1), all seven have benefited at the same time from reduction of their nutrient loading. This presented a unique opportunity, as the seven lagoons of the Palavasian complex represented a clear eutrophication gradient in 2005 (Ifremer, 2007) it is possible to assess how ecosystem trajectories during restoration are influenced by the prior eutrophication state of the system. Hence, for this study the Méjean lagoon and the Ingril lagoon were selected as specific cases, representing a hypertrophic and a less degraded lagoon, respectively. Méjean lagoon has a surface of 5.6 km^2 and an average depth of 0.73 m and belongs to the municipalities of Lattes and Pérols. Salinity fluctuates between 10 and 30 with some occasional values of 5 after heavy rainfall. Ingril lagoon has a surface of 6.2 km^2 and an average depth of 0.66 m and is separated into two parts by the Canal de Rhône à Sète.

METHODS

Discussion of ecosystem trajectories by a focus group and proposals for active restoration

The major difficulties in this study were to obtain a comprehensive view of ecosystem restoration and the different management issues and share the language and methods between ecologists and socio-economists. The collective approach that was adopted is depicted in Figure 2 and described in detail below.

Most ecologists are specialists in a certain field, e.g. microbial ecologist, botanists, benthologists, ornithologists, and none of them has a comprehensive view of the restoration of lagoon ecosystems. Therefore, it was important to bring these experts around a table, to share their views with the authors of this paper (three ecologists, two socio-economists) and provide expert

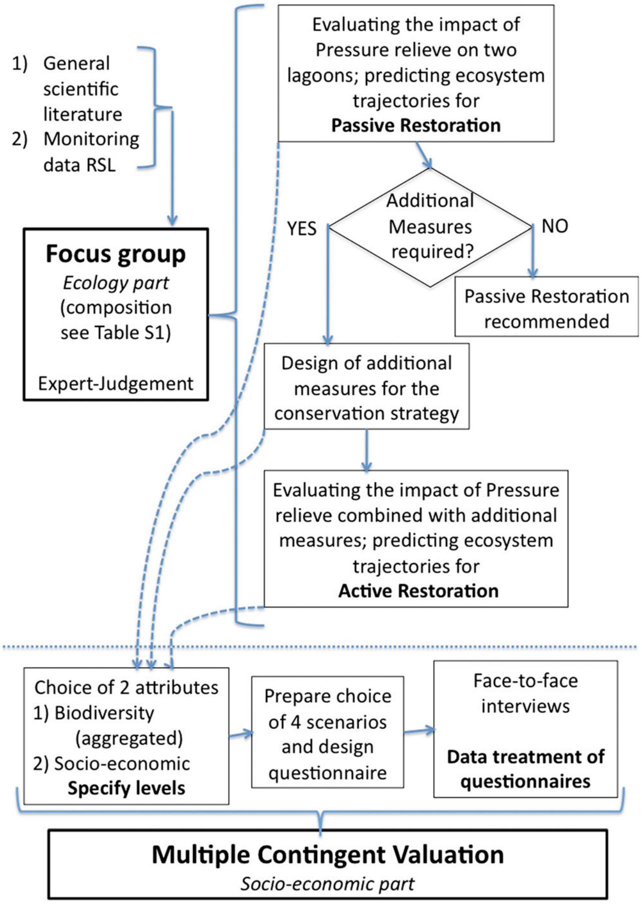


Figure 2. Flow diagram of the procedures followed for the integrated ecological socio-economic study, showing the different tasks for the focus group and for the socio-economic part of the study.

judgement in a collective and integrative way. Hence, 15 experts in ecology were invited, of whom seven actively participated in a focus group meeting organized on 15 May 2013 at the University of Montpellier (Table S1, Supplementary material). Those experts unable to participate in the meeting were visited afterwards.

To structure the discussion with the specialists it was decided to predict the ecosystem restoration trajectories by using selected ecosystem state variables. Hence, clear hypotheses were formulated and based on these hypotheses the trajectories were predicted. As an input, the experts used their general knowledge of the scientific literature and were provided access to the data collected within the frame of the '*Réseau de Suivi Lagunaire*' (RSL) monitoring programme, which was operated from 2000–2013 by Ifremer, The Regional Council of the Languedoc-Roussillon Region and The Agence de l'Eau Rhône-Méditerranée-Corse (Ifremer, 2002, 2005, 2007, 2010, 2013, 2014; '*Réseau de Suivi Lagunaire*' (RSL), 2014). It focused on monitoring the ecosystem state of the lagoons with respect to eutrophication; every year, i.e. during summer the water chemistry (concentrations of NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, total dissolved and suspended nitrogen TN and total dissolved and suspended phosphorus TP), and chlorophyll *a* concentrations, as a proxy for phytoplankton biomass, were measured. In addition, macrophytes (both macroalgae and Magnoliophyta) and sediment features (total N and P contents in the top 5 cm and granulometry) were monitored every 3 and 6 years, respectively. Reported observations between 2006 and 2012 (Ifremer, 2007, 2010, 2013) were used to confront predictions with reality. Predictions at longer decadal scales, i.e. expected to occur after 2012, could obviously not be tested. In addition, some formal biodiversity inventories (Direction Régionale de l'Environnement, de l'Aménagement et du Logement, DREAL, de la Région Languedoc-Roussillon, 2010) were used for this comparison, as well as the Masterplan (DOCOB) of the Natura 2000 site (Figure 1) and other specific reports prepared by the Syndicat mixte des étangs littoraux (2009 a, b; 2010). The predictions are presented graphically and are discussed critically for each ecosystem variable. This approach was, however, problematic for the socio-economic colleagues, who suggested that the information should be presented on a conservation quality scale and the ensemble of the ecosystem state variables should be aggregated in a single attribute that could be understood in terms of 'biodiversity' or 'environmental quality' by the general public. As a first approach, it was decided to conceptually rescale the selected ecosystem variables along a scale ranging from bad (B), through poor (P), moderate (M), and good (G), to high (H) as is currently used for the RSL and WFD monitoring programmes. In practice this meant that ecosystem state variables where high values indicate low environmental quality, e.g. the biomass densities of phytoplankton and opportunistic macroalgae, were inverted on the graphic ordinate to range from high value (poor quality) to a low value (high quality). Other state variables, where high values corresponded to high quality, e.g. the extension of marine Magnoliophyta meadows, were represented on the ordinate as usual. The aggregation of these variables for a single attribute was decided collectively and the process is described in the section below.

Multiple contingent valuation and preparation of a questionnaire

The economic valuation was based on contingent valuation, which belongs to the 'stated preference' methods. In a standard contingent valuation (CV), only a single scenario is exposed to the public that is compared with a reference situation (Ahtiainen *et al.*, 2013) and respondents are asked for their acceptance and willingness to pay (WTP) for the scenario. The format recommended for the questionnaire is a type of referendum, one prior cost being associated to the unique scenario. The outcome of the survey is then a distribution of willingness to pay for that scenario. As a consequence, the results do not support variations in restoration beside the main scenario, nor do they give any empirical evidence about the weight of a project's characteristics in the preferences of respondents. To overcome these limitations, a CV survey with four scenarios was designed, in order to obtain more variability in the project's attributes and, thus be able to estimate their impact on the acceptability and the WTP of respondents. The questionnaires were designed largely based on the results from the focus group (cf. Figure 2) that are described in the Results section. Considering two attributes, i.e. (i) biodiversity (an aggregation of different ecosystem state variables), and (ii) socio-economic issues, and three levels for each attribute, results in nine possible combinations. Out of these, four combinations were selected to present at the same time contrasting situations with realistic combinations (see Results for choice). This approach, which is intermediate between a standard contingent valuation and a choice experiment, is referred to as a multiple contingent valuation (MCV).

The Hérault department has a total population of 1.1 million inhabitants of which about 450 000 live in the urban agglomeration of Montpellier, including 265 000 inhabitants of the municipality of Montpellier. In addition, during summertime the Mediterranean coastline of the lagoons is an important tourist destination with Palavas and Frontignan-Plage as the main holiday resorts. Therefore, two different versions of the questionnaires were prepared, i.e. for residents and tourists, respectively. The questionnaires were designed in four modules and were presented to the interviewees in two steps. First, questions focused on the origin of the respondents and the modes and frequencies of them using the lagoon. The survey included questions that checked respondents' perceptions and how they valued the different ecosystem services of the lagoons as per three of the four main types used in the Millennium Ecosystem Assessment (2005). As the study targeted the general public rather than specific user groups, such as professional fishermen or hunters, provisioning services were excluded. Subsequently, using graphic illustrations (Appendices S1 and S2), the context was presented to the respondents comprising geographic information and uses of the lagoons. The interviewer presented the four selected scenarios for active ecosystem restoration for the Méjean lagoon. The other modules were focused respectively on willingness to pay and accompanying questions on the perception and main societal issues, and the socio-economic characteristics of the respondents. Face-to-face interviews were carried out during July and August 2013 in three different municipalities, i.e. Montpellier (Esplanade de l'Europe and close to the railway station), Lattes (central plaza in town) and Palavas les Flots (on the sea beach). On average, the duration of the interview was about 20 min.

RESULTS

Description of the ecosystem state since 2000 and developments until 2013 for the lagoons of the Palavas complex

At the beginning of the 21st century, the seven lagoons of the Palavas complex showed a clear eutrophication gradient and the RSL quality scores were systematically better in the south-west than in the north-east. For example, between 2001 and 2006, the scores in Ingril lagoon fluctuated between Poor and Moderate with occasionally Good scores, while Méjean lagoon presented systematically Bad quality scores (Réseau de Suivi Lagunaire, 2014). The experts decided to focus their analyses on these two contrasting lagoons.

The annual monitoring during summer periods showed that phytoplankton densities responded very quickly to the reduction of nutrient inputs after 2006. Hence in Méjean lagoon, summertime Chl *a* concentrations in the water column fluctuated between 100 and 400 $\mathrm{mg\,m^{-3}}$ before 2006, and afterwards dropped by one to two orders of magnitude to fluctuate between 1 and 25 $\mathrm{mg\,m^{-3}}$. The phytoplankton community in this lagoon was dominated by diatoms and green microalgae. In Ingril lagoon, before 2006 the summertime Chl *a* concentrations fluctuated between 5 and 20 $\mathrm{mg\,m^{-3}}$, and afterwards between 0.6 and 3 $\mathrm{mg\,m^{-3}}$.

At the start of the lagoon monitoring by the RSL in 2000, no meadows of Magnoliophyta occurred in the Méjean lagoon, and up to 2012 only relicts have been observed in the form of very small patches (Direction Régionale de l'Environnement, de l'Aménagement et du Logement (DREAL) de la Région Languedoc-Roussillon, 2010). Extended macrophyte surveys have been conducted in the Méjean lagoon at 13 stations (seven in the western and six in the eastern part) in 2001, 2004, 2006, 2009, and 2012. For all of these surveys, Magnoliophyta were never observed, while the first three surveys (2001, 2004 and 2006) showed virtually no (i.e. $<$ 0.5% coverage of the lagoon bed) macroalgae (Ifremer, 2002, 2005, 2007). In contrast, the surveys in 2009 and 2012 showed lagoon bed coverages of macroalgae of 44 ± 37%, and 49 ± 39%, respectively (Ifremer, 2010, 2013). The dominant populations included *Ulva* spp. and *Chaetomorpha* spp. and more occasionally the red alga *Chondria capilaris*, which during the summer of 2009 covered about 30% of the lagoon bed in the eastern part.

During the early 2000s Ingril lagoon did not contain well-developed Magnoliophyta prairies, although some patches of *Ruppia* sp. occurred before 2006. Between 2006 and 2012 a recolonization of the Magnoliophyta prairies was observed. By 2012 in the southern part of the Ingril lagoon there were dense but sparsely distributed meadows covering about one-third of the sediment surface. *Zostera noltei* was the main species although at several stations it coexisted with *Ruppia cirrhosa* (Syndicat mixte des étangs littoraux (SIEL) and P2A Développement SARL, 2012).

The sedimentary concentrations of total N and total P in the top 5 cm at the monitoring stations in the Palavasian lagoons between 1999 and 2012 are shown in Figure 3. Among the stations from the seven lagoons, the western station in the Méjean lagoon contained the highest concentrations of N and P, around 4 $\mathrm{g\,kg^{-1}}$ and 0.9 $\mathrm{g\,kg^{-1}}$, respectively. The southern station in the Ingril lagoon contained the lowest values at around 1–2 $\mathrm{g\,kg^{-1}}$ and 0.4 $\mathrm{g\,kg^{-1}}$ for N and P, respectively. The eastern station in Méjean lagoon was intermediate between these extremes for both N and P values. The northern station in Ingril lagoon was as low in P as the southern station in this lagoon, but recorded a higher level of N, i.e. around 3 $\mathrm{g\,kg^{-1}}$ (Ouisse *et al.*, 2013).

Hypothesis and predicted ecosystem trajectories for the Méjean and Ingril lagoons

The focus group agreed on the four following hypotheses:

H1

Phytoplankton densities respond very quickly to a decrease of the external N- and P-loading to the lagoon.

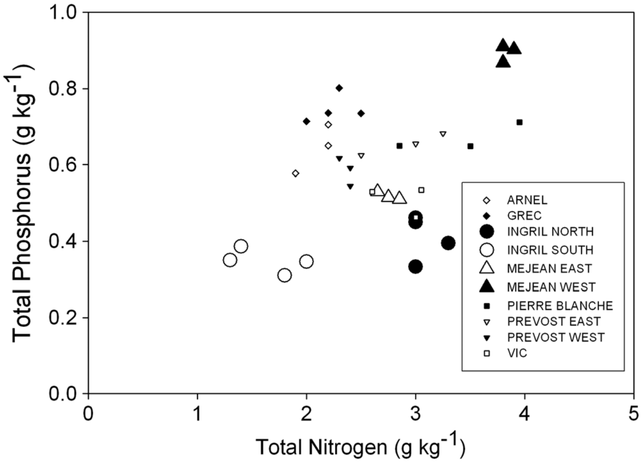


Figure 3. Sedimentary contents (top 5 cm) of total N and P in the sediments of the seven lagoons from the Palavas complex (sampled in 1999. 2001, 2006, and 2012).

H2
Lagoon sediments that have historically been enriched in N and P during the eutrophication phase will show a net efflux of N and P from the sediment during the re-oligotrophication phase. The total N and P contents of the sediment are the main drivers for these N and P effluxes, respectively. As a result of these effluxes, the sediments will progressively decrease their N and P content during re-oligotrophication.

H3
Opportunistic macroalgae benefit from a decrease of phytoplankton in the water column as this results in higher light availability; since these macroalgae are located on average closer to the sediment surface than phytoplankton, they may benefit from N and P release from the sediment.

H4
Recovery of marine Magnoliophyta can occur as a spontaneous process, when these plants are released from competition for light with both phytoplankton and macroalgae. The recovery rate may, however, be limited by low availability of seed banks in the lagoon and by low connectivity with potential source populations in nearby lagoons.

Predicted ecosystem trajectories based on these hypotheses and considering the different states of the two lagoons before reduction of the nutrient loading are shown in Figure 4. For the less degraded Ingril lagoon, it was predicted that Magnoliophyta would be able to recolonize the lagoon concomitantly with a decrease in phytoplankton biomass densities and decreasing N and P contents of the sediment. A process in two phases was described based on the prediction that ecosystem restoration in the northern part of Ingril would lag behind that occurring in the southern part. For this lagoon, it was predicted that the densities of opportunistic macroalgae would remain low. Except for phytoplankton trajectories, a very different chronology was described for the highly impaired Méjean lagoon. Thus, it was predicted that marine Magnoliophyta would not

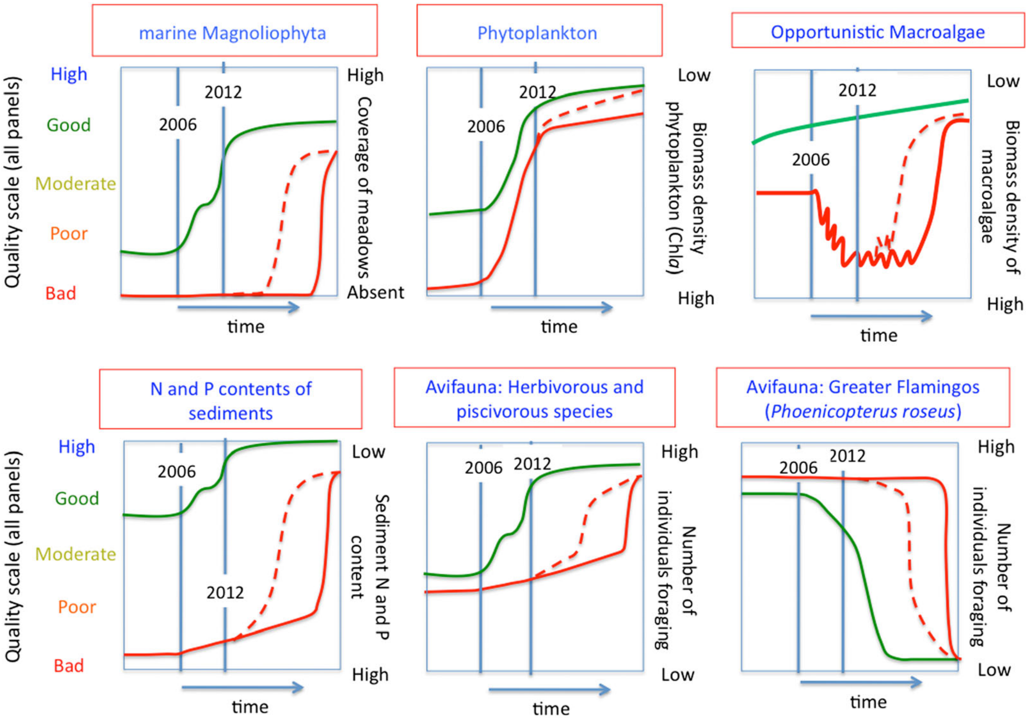


Figure 4. Predicted ecosystem trajectories for Ingril (green line) and Méjean (red line) lagoons according to the focus group and additional experts based on the three hypothesis and the monitoring observations between 2006 and 2012. The broken red line indicates the predicted impact of the additional measures proposed for the project of active restoration of the Méjean lagoon.

be able to colonize the lagoon for a very long time, concomitantly with a very slow rate of improvement of the quality indices for the sediment. While the phytoplankton quality index was expected to improve rapidly after the reduction of the external loading, following hypothesis H3, it was predicted that opportunistic macroalgae would increasingly proliferate. The monitoring observations in 2009 and 2012 indeed showed the appearance of macroalgae during the early stage on the Méjean trajectory after reduction of nutrient loading (see above). The abundance of the macroalgae was considered as characteristic for a transient phase, while macroalgal densities were expected to fluctuate strongly within and between years. After some time, however, it was expected that the lagoon would leave the transient state when concomitantly with an accelerated improvement of the sediment and the water column DIN and DIP quality indices, the macroalgal densities would decrease systematically. This would allow colonization by the Magnoliophyta and move towards the final ecologically restored state. Nevertheless, it is still difficult to predict the duration of the macroalgal-dominated transient state.

The focus group also evaluated the impact of these different trajectories on avifauna. Hence, it was predicted that colonization of the lagoon by the Magnoliophyta would be beneficial for herbivorous and piscivorous bird species, e.g. ducks and herons, respectively. In contrast, greater flamingos (*Phoenicopterus roseus*) use non-vegetated sediments for foraging and were, therefore, expected to decrease in number within the lagoons with increasing coverage of Magnoliophyta.

Active restoration as an option for conservation management in the Méjean lagoon and the impact on its ecosystem trajectories

The high coverage of macroalgae observed during the surveys in the summers of 2009 and 2012 (see above, cf. Figure 4) was highlighted as an interesting phenomenon and it was recommended to make use of it during the first part of the restoration process. Hence, harvesting the macroalgae and extracting them from the lagoon will export the N and P contained in their biomass from the lagoon. Once, the good conditions for Magnoliophyta growth are established again it can be expected to further accelerate the process by seeding and/or transplantation. The broken lines in Figure 4 depict the impact of the additional measures on the trajectories of the different variables in Méjean lagoon. The quality indices associated with most of the ecosystem variables show an acceleration of their improvement, with the exceptions of the negative impact on greater flamingos and an almost negligible impact on phytoplankton. It is not possible, however, to predict the length of the macroalgal-dominated transient phase for the passive or the active ecological restoration trajectories.

Consensus and controversy among the experts

There was a remarkable degree of consensus among the experts concerning the predicted trajectories (Figure 4), although most experts highlighted that the timescale of the processes is still difficult to assess. It requires gaining experience in the field combined with careful monitoring of a couple of case studies, although estimates could be derived from ecosystem modelling using a coupled biogeochemical–ecological model.

However, there were some areas of controversy such as the reference state chosen as the target for a desired state of the ecosystem. In the Ayrolle lagoon the *Z. noltei* coverage typically exceeds 80% of the lagoon bed, and this has often been used as a reference site for these Mediterranean lagoons (Ifremer, 2014). While comparable in mean depth (i.e. Méjean lagoon 0.73 m, Ingril lagoon 0.66 m, Ayrole lagoon 0.64 m) it is believed that besides eutrophication levels there are numerous other physical differences between the lagoons that mean it is not appropriate to adopt the Ayrole lagoon as a reference site.

A second controversy related to the techniques of transplanting the Magnoliophyta. Some argue that proliferation of the plants simply depends on the ecological conditions and if these conditions are fulfilled the Magnoliophyta will proliferate regardless. In contrast, when the ecological conditions are not fulfilled, transplantation is generally unsuccessful and plants die within a few months, thus it is a waste of money developing such techniques. Others agreed to caution against trying to transplant or seed areas when conditions are clearly unfavourable, but, nevertheless, recognized that this may be a useful technique when conditions have improved in systems where plants are known to have occurred previously and where their proliferation may be limited owing to depletion of the seed banks and distances (connectivity) from a potential source population are too large.

A third controversy was generated regarding the concept of ‘iconic’, ‘charismatic’ or ‘emblematic’ species when communicating with the public. Emblematic is the term most commonly used in France. When introducing the questionnaire to the general public and seeking their participation the use of emblematic species makes the subject more easily recognizable for them. However, the concept of emblematic species may be confounded with the concept of patrimonial species, a concept often used by French practitioners of nature conservation and environmental management. It is also important to aggregate variables to create a limited number of attributes for the questionnaires. Hence, it was proposed to take the surface coverage of Magnoliophyta in the lagoon as exemplary of an ensemble of ecosystem variables including avifauna and fishes, particularly the presence of seahorses (*Hippocampus guttulatus*). Some experts doubted whether *H. guttulatus* could recolonize all the lagoons and suggested that such a process depended on connectivity with source populations and on ecological conditions in the lagoon, e.g. salinity fluctuations.

Design of the questionnaire for the Multiple Contingent Valuation

Based on the preparatory work of the focus group and interviews with other specialists it was concluded that the least affected lagoon Ingril is already on a satisfactory trajectory for ecosystem restoration and, therefore, no additional measures have been recommended. In contrast, additional measures were recommended for active restoration for the most degraded lagoon Méjean and, therefore, the socio-economic study was focused on this lagoon only (cf. Figure 2). The attribute ‘biodiversity’ (see methods) was created based on an aggregation of several ecosystem variables (cf. Figure 4) that were represented by the surface coverage of Magnoliophyta in the lagoon. The surface coverage of Magnoliophyta is positively linked with good quality indices for water column and sediment and biodiversity, as exemplified by herbivorous and piscivorous birds (Figure 4) and by fishes (including the emblematic *H. guttulatus*, see above). Hence, surface coverage of Magnoliophyta is a good proxy for good ecological conditions in coastal lagoons (*sensu* WFD) and indeed also reflects a high degree of biodiversity. Nevertheless, the negative trade-off between surface area of Magnoliophyta and foraging greater flamingos (see above, cf. Figure 4) was explicitly taken into account and clearly presented to the interviewees. Hence, the three levels for the surface coverage of Magnoliophyta in the lagoon were described for the interviewees as follows:

1. Status quo: 0 to 10% Magnoliophyta coverage implying high numbers of flamingos foraging in the lagoon, no swans, no emblematic seahorses (*H. guttulatus*), and bad water quality indices.
2. 40% Magnoliophyta coverage implying intermediate numbers of flamingos foraging in the lagoon, no swans, but some herbivorous duck species, e.g. Eurasian wigeon (*Anas penelope*), low number of emblematic seahorses (*H. guttulatus*), and water quality indices improved.
3. 70% Magnoliophyta coverage or higher implying a large decrease in the numbers of flamingos foraging in the lagoon, high number of swans and herbivorous duck species, e.g. the Eurasian wigeon (*A. penelope*), high number of emblematic seahorses (*H. guttulatus*), and a good to high quality status for the water quality indices.

Public policy often aims to accompany conservation and ecological restoration measures with increasing access to the site. Currently, cycling paths follow the western shoreline (4 km) and a small section (0.5 km) of the easternmost shoreline of the lagoon, while footpaths have been created through the peripheral marshes bordering the NW sector of the lagoon. Hence, more footpaths could be created to increase accessibility to the site, while at the same time care should be taken that hikers do not disturb the waterfowl. Therefore, access to the site was added as an additional attribute and based on this attribute, three different options for spatial planning of the access have been proposed:

1. Status quo for this attribute: maintenance of the existing walking and cycling paths as the only access to the zone.
2. Increase the number of footpaths, but without hides and other additional measures to reduce the disturbance of waterfowl by hikers.
3. Increase the number of footpaths, combined with hides and other additional measures to reduce the disturbance of waterfowl by hikers.

The two different versions of the questionnaire, for residents and tourists, are provided in Appendix S1 and Appendix S2, respectively, with their illustrative material used in interviews. From the nine possible combinations four were selected (see Methods) comprising:

I Magnoliophyta level 1, footpaths level 2 (scenario 1 - M1-F2)
II Magnoliophyta level 2, footpaths level 1 (scenario 2 – M2-F1)
III Magnoliophyta level 2, footpaths level 3 (scenario 3 – M2-F3)
IV Magnoliophyta level 3, footpaths level 3 (scenario 4 – M3-F3)

Descriptive statistics of the sample

The 159 interviews conducted comprised 94 residents and 65 tourists. The socio-economic profile of the sample is shown in Table 1, and Tables S2 and S3. Gender distribution was almost equal with males only slightly more numerous representing 52% and 54% for the residents and tourists, respectively. Among the residents, the age class 18 – 30 years was most represented by about 40%, although it was slightly lower than for the urban area of Montpellier altogether (43.6% see Table 1).

Attitudes, perceptions and recreative uses of lagoons

Among the respondents, 40% and 69% of the residents and tourists, respectively, replied that they do not visit the lagoons. Among the users, walking, bird watching and enjoying nature was the major recreational activity pursued by 47% and 23% of the resident and tourist respondents, respectively. Cycling was also popular, representing 31% and 15% of the resident and tourist respondents, respectively; while nautical sports, horse and pony trekking, and fishing were the other main activities. Several respondents indicated that they pursued multiple activities, which is reflected by a total sum of activities exceeding 100% Table 2).

Among the non-users, the fact that they were unfamiliar with the lagoons was most often invoked, representing 26% and 58% of the

Table 1. Demographic and sociological profiles of the respondents and of the urban area of Montpellier (Agglomération de Montpellier). 68 of the resident respondents (72%) lived in the municipality of Montpellier (year of the census in parenthesis)

	N	Gender	Age-class(years)				Region of birth	Marital status		Children		
		male/female	18-30	31-45	45-65	>65	Languedoc-Roussillon	single, widow, divorced	married or living in couple	None	1 or 2	>2
Residents	**94**	**49/45** 52.1%/47.8%	**38** 40.4%	**15** 16.0%	**26** 27.7%	**15** 16.0%	**35** 37.2%	**54** 57.4%	**40** 42.6%	**49** 52.1%	**30** 31.9%	**15** 16.0%
Tourists	**65**	**35/30** 53.8%/46.2%	**23** 35.4%	**17** 26.2%	**18** 27.7%	**7** 10.8%	**11** 16.9%	**37** 56.9%	**28** 43.1%	**50** 76.9%	**12** 18.5%	**3** 4.6%
Urban Area of Montpellier	**406 139** (2006)		43.6%	43.7%		13.8%	Not informed	54.0%	46.0%	67.6%	28.6%	3.8%

Table 2. Uses of the lagoons by the interviewees. Percentages standardized to number of respondents (n = 94 , and n = 65 for residents and tourists, respectively

	Residents		Tourists	
Do not visit lagoons and do not use them	**38**	40.4%	**45**	69.2%
Walking, bird watching, enjoying nature	**44**	46.8%	**15**	23.1%
Cycling	**29**	30.9%	**10**	15.4%
Nautical sports (kayak, kite surf, etc.)	**7**	7.4%	**1**	1.5%
Walking with a dog	**4**	4.3%	**0**	0.0%
Horse and pony trekking	**3**	3.2%	**1**	1.5%
Fishing	**1**	1.1%	**0**	0.0%
Total*		134.0%		110.8%

*Note total sums above 100% because certain respondents indicated multiple uses.

residents and non-user tourists, respectively. There was a more equal distribution of responses among resident non-users compared with tourists. The total of responses summed slightly above 100% indicating a very limited number of multiple responses (Table 3). Among the residents interviewed, those born in the Languedoc-Roussillon region visited the lagoons more frequently than residents born in other regions.

The supporting service provided by biodiversity was identified most often as the most important ecosystem service provided by the lagoons, i.e. by 52% and 60% of the resident and tourist respondents, respectively (Table 4). More than 80% of both groups recognized this service among their top two priorities. The second largest group identified the regulating services as the top priority. Only about 10% of both resident and tourist respondents considered cultural services as the top priority, nevertheless, a large proportion indicated these as their second priority. As a result about half the resident and tourist respondents recognized cultural services among the top two priorities for lagoons. In addition, a very large majority, i.e. 87% and 85% of residents and tourists, respectively, fully agreed with the statement 'the lagoons represent an important natural heritage asset and should be conserved for future populations' and entirely disagreed with the statement that 'it is useless to restore the ecosystems as sooner or later these will disappear due to sea-level rise'. A slightly smaller proportion, i.e. 80% and 68% of residents and tourists, respectively, entirely disagreed with the statement that 'there is too much priority for restoring lagoon ecosystems compared to other societal issues'.

Table 3. Reasons invoked for not visiting the lagoons, percentages have been standardized to the subsamples of non-users of lagoons, i.e. n = 38 and n = 45 for residents and tourists, respectively

	residents		tourists	
I don't know the lagoons	**10**	26%	**26**	58%
The lagoons are too far away	**9**	24%	**6**	13%
I am not interested in the lagoons	**8**	21%	**4**	9%
The lagoons are polluted and smell badly	**6**	16%	**2**	4%
Other reasons	**4**	11%	**8**	18%
No response	**4**	11%	**2**	4%
Total*		108%		107%

*Note total sum of reasons invoked exceeds 100% as some respondents invoked multiple reasons.

Preferences for scenarios and willingness to pay

Among the respondents, 77% and 71% of the residents and tourists, respectively, preferred scenario 4, which combines the highest degree of ecosystem restoration (M3) with construction of additional footpaths, combined with hides and other additional measures to reduce the disturbance of waterfowl by hikers (F3). Sixty-six (70%) and 43 (66%) interviewed residents and tourists, respectively, explicitly confirmed their willingness to contribute financially to an active restoration programme for the Méjean lagoon (Table 5). This proportion is lower than the above-mentioned 85% of respondents that recognized the need for ecosystem restoration. The main reasons why respondents were reluctant to contribute financially were because either: (i) they are not willing to pay additional taxes (17% and 26% of residents and tourists, respectively); or (ii) they thought that it was not their responsibility to pay for the restoration (11% and 5% of residents and tourists, respectively) (Table 5). A small proportion were not confident and doubted whether their financial contribution would be effectively allocated to the restoration of the Méjean lagoon and were suspicious that it might be used for other public spending. Willingness to pay for the four different options is highly variable both

Table 4. Identification of top priorities by the respondents among the selected ecosystem services proposed in the survey. These proposed ecosystem services have been grouped according to three of the four major types of services used in the Millenium Ecosystem Assesment (2005). Note that the type of provisioning services has not been proposed to the interviewees and that for the top two priorities the total percentages sum to 200% of respondents as each respondent registered two priorities

	Top priority				**Cited among the first top two priorities**			
	residents		tourists		residents		tourists	
Supporting services	**49**	**52.1%**	**39**	**60.0%**	**78**	**83.0%**	**56**	**86.2%**
Biodiversity	49	52.1%	39	60.0%	78	83.0%	56	86.2%
Regulating services	**36**	**38.3%**	**19**	**29.2%**	**61**	**64.9%**	**43**	**66.2%**
Flood regulation	15	16.0%	7	10.8%	23	24.5%	13	20.0%
Water purification	21	22.3%	12	18.5%	38	40.4%	30	46.2%
Cultural services	**9**	**9.6%**	**7**	**10.8%**	**49**	**52.1%**	**31**	**47.7%**
Enjoying landscape	5	5.3%	5	7.7%	18	19.1%	17	26.2%
Recreational fishing	1	1.1%	0	0.0%	4	4.3%	1	1.5%
Hunting	0	0.0%	0	0.0%	1	1.1%	0	0.0%
Walking, leisure	3	3.2%	2	3.1%	26	27.7%	13	20.0%
Sum		100%		100%		200%		200%

Table 5. Different opinions adopted by the respondents corresponding to their willingness to financially contribute to the active restoration of the Méjean lagoon (n = 94, and n = 65 for residents and tourists, respectively)

	Residents		**Tourists**	
I am not opposed to contribute financially	**66**	70.2%	**43**	66.2%
I don't want to pay a new tax	**16**	17.0%	**17**	26.2%
I don't believe that my contribution will be effectively used for the restoration of the Etang de Méjean	**15**	16.0%	**4**	6.2%
It is not up to me to finance the restoration project	**10**	10.6%	**3**	4.6%
Total:	**107**	113.8%	**67**	103.1%

Note total sums above 100% as certain respondents indicated multiple reasons that motivated their reluctance to pay.

among residents and tourists, respectively (Figures 5 and 6). Nevertheless, the highest mean and median values were observed for scenario 4, which is consistent with the preferences expressed by the respondents.

Data processing and econometric estimation of willingness to pay

The 159 questionnaires produced 795 responses for willingness to pay (WTP) corresponding to five specific combinations of levels of restoration of Magnoliophyta prairies and access facilities, i.e. the four studied scenarios as well as a business as usual (BAU) scenario, which corresponds to (M1 – F1) plus. These five scenarios were coded as a combination of dichotomous variables, and the individual data were duplicated five times to get a panel structure.

Before proceeding to econometric estimation, some questionnaires were discarded because 20 questionnaires had the same positive WTP for the four scenarios, and 11 respondents provided four null values. This expresses a strategic bias, either in favour or against restoration. The answers were crosschecked against the two questions 'I would not pay an additional tax' and 'It's not my duty to pay for the restoration' (Table 5). In the first case, the refusal is clear, and even if the respondent provided a value for a scenario, that is not a real WTP. In the second case, the given value expresses the value given to the scenario, to be paid by someone else, but not the own WTP of the respondent. In all, 24 questionnaires were discarded for residents and WTP estimation proceeded with 70 respondents (i.e. 350 observations). The same procedure was used for the tourists, resulting in 45 respondents and 225 observations (cf. Figures 5 and 6, showing the frequency distributions for the four different scenarios of the WTP for residents and tourists, respectively).

The monetary variables related to the level of ecosystem restoration (roughly WTP) increase with the level of seagrass bed restoration, ranging from €11.3 up to €29.45 per year, and from €3.37 up to €10 per week, for residents and tourists, respectively (cf. Table S4 for detail on econometric calculations). Estimates do not

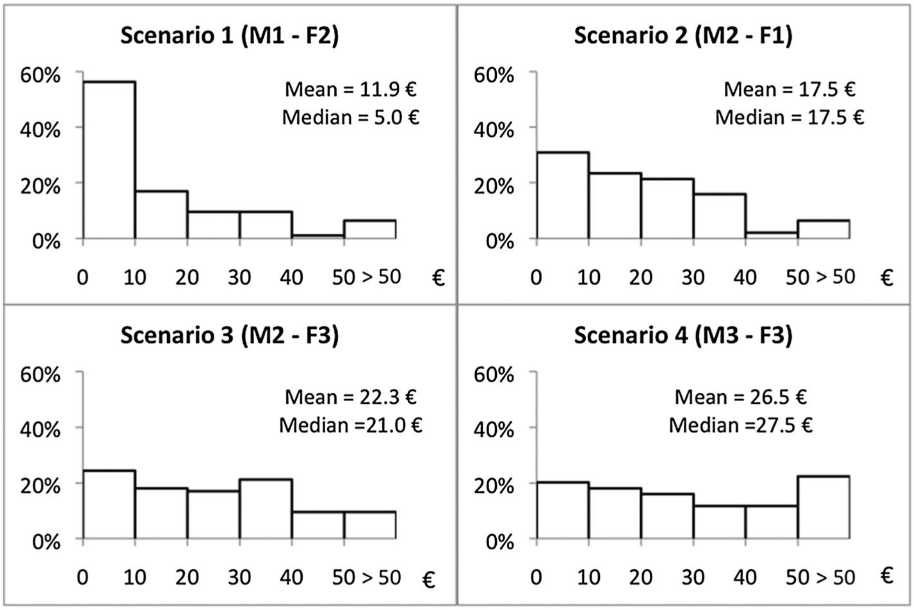


Figure 5. Frequency of WTP by residents for the four different scenarios. Values expressed per year.

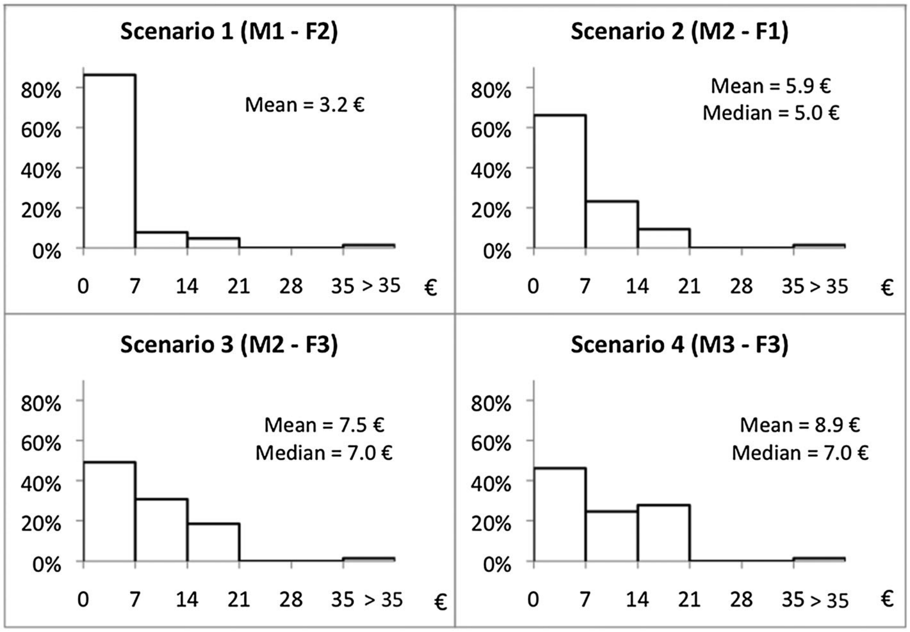


Figure 6. Frequency of WTP by tourists for the four different scenarios. Values expressed per week.

exhibit any trade-off in preferences between the biodiversity state attached to low and high levels of restoration. The variable for income is low, not significant for residents, but significant for tourists. WTP increases with age, more so for tourists than for residents. Variable estimates are used to compute the average WTP by the residents: for a high level of restoration (M3) the WTP is €25.00 per year, for a medium level of restoration (M2) it is €16.58 per year, and for a low-level (M1) it is €6.55 per year. The WTP for creating additional footpaths and hides for observing birds without disturbing them was much lower, i.e. only €5 per year. Some respondents replied that such new structures would damage their perception of ‘naturalness’ of the site and thus jeopardize their feeling of enjoying nature.

DISCUSSION

Ecological restoration as part of the conservation management of coastal lagoons

In this study, a framework for a transdisciplinary study has been developed for addressing the ecological and socio-economic issues of the ecological restoration of coastal lagoons (Figure 2) through a collective learning process. A focus group was used to synthesize the pertinent ecological knowledge and develop future ecosystem trajectories. A study on the restoration ecology of Berre lagoon (S. France) also used a focus group, whose aim was to characterize the natural capital of the historical reference states and achieve consensus for selecting one of them as a model for the desired state of this specific lagoon (Aronson *et al*., 2012). In this present study, the focus group was used to rationalize the thinking about possible future ecosystem trajectories.

The ecological restoration of coastal lagoons is still in its infancy compared with that for freshwater lakes. However, in both cases, the improvement of water transparency and return of SAV are often the major objectives, particularly when the objective is to revert the eutrophication process, which can be considered as a re-oligotrophication. For lakes the potential role of the sediments in retarding restoration has been underscored (Eppesen *et al*., 2005) and this phenomenon also appears to be relevant for coastal lagoons. A remarkable degree of consensus existed among the experts for predicting the sequence of events during re-oligotrophication (Figure 4), although it has to be highlighted that the timescale of this process is subject to a very high degree of uncertainty. More detailed studies of the biogeochemistry and hydrodynamics of the lagoons are required and a coupled ecological—biogeochemical—hydrological model could provide the basis for more quantitative predictions concerning the time frame. Nevertheless, the six years of summer observations since the nutrient reduction occurred provided support for hypothesis H1 (decrease of phytoplankton densities in both lagoons) and partial support for H2 (cf. Figure 3, Ouisse *et al*., 2013) in both lagoons. However, based on splitting the sediment samples into two groups, i.e. sediment samples before 2006 and between 2006 and 2012, a predicted decrease in N and P content due to benthic fluxes was not statistically significant (Welch test, $P > 0.05$ for total N and total P in both Ingril and Méjean lagoons, $n = 13$). The low frequency of observations may explain that such a predicted trend is not yet visible. Partial support for H3 (appearance of macroalgae during a transient state) and H4 (spontaneous recovery of Magnoliophyta) were obtained for Méjean and Ingril lagoons, respectively. In Ingril lagoon, observations of increasing *Z. noltei* and *R. cirrhosa* meadows are in agreement with predictions (cf. Figure 4) that return of Magnoliophyta may be a fast process for lagoons that have been affected by eutrophication to a lesser degree only. Although, future scientific studies should be focused on testing the general validity of the hypothesis H1–H4 forwarded in this study.

Hence, it clearly appears that for less-degraded lagoons, e.g. Ingril lagoon, a return to good ecological conditions may occur spontaneously and quite rapidly following the reduction of nutrient loading. In contrast, ecological restoration of the Méjean coastal lagoon without any further additional measures would take a very long time, probably decades (Ouisse *et al*., 2013). Thus, while reduction of nutrient loading is of paramount importance in all cases, ecological restoration within a reasonable time frame of the more heavily degraded lagoon requires additional measures, which is characterized as active restoration.

Additional measures may thus speed up the restoration project in Méjean lagoon and a draft for an active restoration project has been designed that comprises two steps. The first step entails macroalgal removal. In the past, removal of *Ulva* spp. has been used to combat the symptoms of severe eutrophication and prevent dystrophic crises in the nearby Prévost lagoon (Guyoneaud *et al.*, 1998). Macroalgal growth close to the sediment surface will intercept DIN and DIP effluxes from the sediment (hypothesis H3) and thus contribute to lower DIN and DIP concentrations in the water column. During 2012, benthic effluxes of 3–6 mmol N m^{-2} day^{-1} and 0.05 to 0.5 mmol P m^{-2} day^{-1} have been measured in the Méjean lagoon (Ouisse *et al.*, 2013). By increasing the concentration gradient from the sediment to the overlying water it appears very likely that macroalgal growth will increase the driving force for the benthic efflux of N and P from the sediment. Hence, macroalgal growth could accelerate the decrease of total N and P contents of the sediment in a sustainable way, provided that its biomass is exported from the lagoon. The results of the first phase of the active restoration management need to be monitored in order to decide when it becomes appropriate to start the replanting or seeding of the Magnoliophyta. However, there was no general concensus for actively planting Magnoliophyta. In general, it was agreed that after a transient state, when there is a simultaneous increase of the quality indices for the water column DIN and DIP and the total N and P contents of the sediments, conditions may become favourable for recolonization by Magnoliophyta. A recent opinion paper based on experiences throughout Europe confirms that priority should be given to enhancing the natural restoration potential for seagrass habitats (Cunha *et al.*, 2012). A fictive ecological restoration project was proposed for Méjean lagoon in order to provide an understandable context for the socio-economic questionnaires. According to this project, removal of macroalgae from the lagoon would be pursued for a period of 5 years. The planting or seeding of the selected Magnoliophyta would start only after this initial 5 year period and be pursued for an additional period of 5 years. Thus this fictive project proposed to the interviewed public would be for 10 years, which was considered sufficiently short for the public to feel themselves involved with the project and willing to contribute to this study.

Active restoration designed with the original aim of improving the water quality is clearly compatible with a proactive conservation strategy. Increasing Magnoliophyta meadows in coastal lagoons, in addition to its positive impact on water quality, will promote an increase of herbivores and piscivorous bird species (ducks, e.g. *A. penelope*; swans, e.g. *Cygnus olor*; and herons, *Egretta garzetta* and *Ardea cinerea*), and several fish species would also increase in abundance. Fish assemblages associated with *Z. noltei* meadows in the close-by Thau lagoon have been described in Villéger *et al.* (2012), which include sygnate *Sygnathes abaster* and the emblematic *H. guttulatus*. On the other hand, the disappearance of non-vegetated sediments at the expense of Magnoliophyta meadows has a negative impact for greater flamingos (*Phoenicopterus roseus*), which sieve the bare sediment to collect small macrofauna. The latter are emblematic species in south France, with 800 individuals regularly observed in the Méjean lagoon. While, the latter shows that not all species will benefit from the ecosystem changes during restoration, in general it seems reasonable to use Magnoliophyta coverage as an aggregate attribute in socio-economic studies as it is a proxy for many biodiversity values. In addition, it correlates with a high level for the water quality index and is thus useful for finding a convergence between objectives for conservation (e.g. Habitats Directive) and water quality management (WFD).

Perceptions by the residents and tourists of ecological restoration of lagoons and econometric estimation of their willingness to pay for it

The 159 interviews undertaken in this study were sufficient for this pilot study, particularly for testing the new approach described in Figure 2. Nevertheless, the size of the sample is not sufficient for use as support in public policy development as more statistical precision would be needed to avoid any possible bias. In this respect, the sample of interviewed residents corresponded quite well to the socio-economic profile of the inhabitants of the urban area of Montpellier except that unemployed and students were over-represented with respect to intermediate and high-level employees (cf. Tables 1 and S2). Such a check is, however, not possible for the sample of tourists. Nevertheless, it has been possible to put human perceptions and WTP in perspective with a scientific expert analysis of lagoon ecological status and trajectories and how these respond to passive or active ecological restoration. Based on several provocative questions, it was concluded that among the interviewed residents and tourists more than 85% have positive perceptions both of the ecological and societal importance of coastal lagoons as well as of the ecological restoration. The high perception of the ecological and societal importance of lagoons appeared to be based mainly on the recognition by the respondents of the importance of supporting and regulating ecosystem services in coastal lagoons. Their cultural ecosystem services were also highly appreciated by a minority, mainly for walking, leisure and enjoying landscape (cf. Table 4). The fact that this was a minority probably reflects that high proportions of residents and tourists, 40% and 69%, respectively, did not use the lagoons for their own leisure activities (cf. Table 3).

Hence, there was general support for the active ecological restoration proposed for Méjean, which implies specific management actions in addition to the €150 M invested in 2005. This large sum was invested to improve the Montpellier WWTP and achieve a large reduction in nutrient loadings to all seven lagoons of the Palavas complex. The public support is reflected by the 70% and 66% of the resident and tourist respondents, respectively, who declared a willingness to contribute financially for the ecological restoration of lagoons. However, this is lower than the more than 85% of respondents that recognize the importance of coastal lagoons and the need for their ecological restoration. The difference was explained by the fact that some are reluctant to pay (cf. Table 5). Willingness to pay was quite variable, more so within the sample of residents than among the interviewed tourists. However, the clearly stated preference for scenario 4 was coherent with the highest median and mean WTP values (cf. Figures 5 and 6). This latter scenario was based on achieving the highest level for Magnoliophyta meadows. The ecological restoration of Magnoliophyta meadows is indeed favourable for biodiversity in general, although not all emblematic species will benefit from it. Nevertheless, the trade-off of Magnoliophyta for greater flamingos, which was clearly indicated to the respondents, appeared to play no part in their response.

It was important for this study to propose the four different scenarios and submit each to a classical contingent valuation to collectively become a multiple contingent valuation (MCV). To the best of our knowledge, this is the first study to apply such a MCV. By asking for multiple responses, a panel structure was obtained for the two project attributes, comprising 350 and 225 observations, for residents and tourists, respectively. With such a panel the impact of project attributes and individual characteristics on the WTP were assessed, as in a choice experiment (see Hanley *et al.*, 2001 for a comparison of a choice experiment with contingent valuation). The results were statistically robust (Table S4) and showed for the resident respondents a WTP of about €25 per year for the highest level of ecological restoration, while they were only willing to allocate about €5 per year for additional footpaths and hides. Hence, the residents, but also the tourists, clearly showed a higher sensibility towards ecosystem quality and were less interested in improving access for hiking and bird observations. Some of them even disapproved of such infrastructure.

The survey showed that strong support exists for active ecosystem restoration among the residents from the Montpellier urban area and the tourists. Thus, for the most degraded lagoons, in addition to the €150 M investment that was necessary to relieve the over-enrichment pressure, it makes sense to develop an active ecosystem restoration management strategy as part of a conservation plan for these coastal lagoons. In general, while reduction of nutrient loading is of paramount importance, for the most degraded lagoons this should be accompanied by additional measures. As clear estimates of the real costs of active ecological restoration of lagoons are lacking so far, it is still too early to make a cost–benefit analysis for conservation of the different restoration scenarios (De Groot *et al.*, 2013).

In conclusion, the rationalized thinking about possible future ecosystem trajectories and consensus building within the focus group allowed for a clear dialogue with the socio-economic colleagues to develop the novel methodology for coupling ecology with a socio-economic study of the perception of lagoon restoration projects and of the willingness to pay for them by residents and tourists. This study clearly addresses some of the key questions in the area of restoration ecology that needs to cope with questions about technical feasibility based on sound ecological knowledge as well as with questions about human acceptability based on perceptions and costs. Hence, this transdisciplinary approach and novel methodology could be applied more widely to the restoration ecology of aquatic coastal ecosystems.

ACKNOWLEDGEMENTS

This study was orally presented during the 6th Eurolag conference that took place in Lecce (Italy) from 16–19 December 2012 in the session 5 ‘Conservation and Management of Coastal Lagoons’. The authors thank Hamédy Diop for undertaking the majority of the interviews and all the experts (listed in Table S1) for their valuable contributions. Special thanks are due to Juliette Picot and Sebastien Pollet of the Syndicat Mixte des Etangs Littoraux (SIEL) and the Natura-2000 committee of the Palavasian lagoon complex, the municipality of Lattes and the Conservatoire du Littoral for their interest in this study. This study was financed by the Agence National de la Recherche through its Labex ‘Dispositif de Recherche Interdisciplinaire pour les Interactions Hommes-Milieux (DRIIHM)’, programme ‘OHM Littoral méditterranéen’.

REFERENCES

Ahtiainen H, Artell J, Czajkowski M, Hasler B, Hasselström L, Hyytiäinen K, Meyerhoff J, Smart JCR, Söderqvist T, Khaleeva J, *et al*. 2013. Public preferences regarding use and condition of the Baltic Sea – an international comparison informing marine policy. *Marine Policy* **42**: 20–30.

Anthony A, Atwood J, August P, Byron C, Cobb S, Foster C, Fry C, Gold A, Hagos K, Heffner L, *et al*. 2009. Coastal lagoons and climate change: ecological and social ramifications in US Atlantic and Gulf coast ecosystems. *Ecology and Society* **14**: 8 [online] URL: http://www.ecologyandsociety.org/vol14/iss1/art8/

Aronson J, Claeys F, Westerberg V, Picon P, Bernard G, Bocognano J-M, De Groot R. 2012. Towards sustainability and tools for restoring natural capital: Etang de Berre (Southern France) case study. In *Sustainability Science*, Weinstein MP, Turner RE (eds). Springer: New York; 111–138.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* **81**: 169–193.

Barnes RSK. 1980. *Coastal Lagoons; the Natural History of a Neglected Habitat*, Cambridge University Press: Cambridge.

Bec B, Collos Y, Souchu P, Vaquer A, Lautier J, Fiandrino A, Benau L, Orsoni V, Laugier T. 2011. Distribution of picophytoplankton and nanophytoplankton along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. *Aquatic Microbial Ecology* **63**: 29–45.

Borja A, Dauer DM, Elliott M, Simenstad CA. 2010. Medium- and long-term recovery of estuarine and coastal ecosystems: patterns, rates and restoration effectiveness. *Estuaries and Coasts* **33**: 1249–1260.

Chomérat N, Garnier R, Bertrand CA, Cazaubon A. 2007. Seasonal succession of cyanoprokaryotes in a hypereutrophic oligo-mesohaline lagoon from the South of France. *Estuarine, Coastal and Shelf Science* **72**: 591–602.

Council of the European Communities. 2000. Directive 2000/60/EC of the European Parliament and the Council of 23rd October 2000. *Establishing a framework for community action in the field of water policy. Official Journal of the European Communities* **L327**: 1–72.

Cunha AH, Marbá NN, Van Katwijk MM, Pickerell C, Henriques M, Bernard G, Ferreira MA, Garcia S, Garmendia JM, Manent P. 2012. Changing paradigms in seagrass restoration. *Restoration Ecology* **20**: 427–430.

De Groot R, Brander L, Van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, *et al*. 2012. Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* **1**: 50–61.

De Groot R, Blignaut J, Van der Ploeg S, Aronson J, Farley J, Elmqvist T. 2013. Benefits of investing in ecosystem restoration. *Conservation Biology* **27**: 1286–1293.

De Wit R, Stal LJ, Lomstein BA, Herbert RA, van Gemerden H, Viaroli P, Ceccherelli VU, Rodríguez-Valera F, Bartoli M, Giordani G, *et al*. 2001. ROBUST: The ROle of BUffering capacities in STabilising coastal lagon ecosystems. *Continental Shelf Research* **21**: 2021–2041.

De Wit R, Leibreich J, Vernier F, Delmas F, Beuffe H, Maison P, Chossat J-C, Laplace-Treyture C, Laplana R, Clavé V, *et al*. 2005. Relationship between land-use in the agro-forestry system of les Landes, nitrogen loading to and risk of macro-algal blooming in the Bassin d’Arcachon coastal lagoon (SW France). *Estuarine Coastal Shelf Science* **62**: 453–465.

Direction Régionale de l’Environnement, de l’Aménagement et du Logement (DREAL) de la Région Languedoc-Roussillon. 2010. Modernisation de l’inventaire ZNIEFF : ZNIEFF de type I n° 0000–3013 Etang du Méjean-Pérols. 7p. http://irlr-app.dreal-languedoc-roussillon.fr/~addsd/ZNIEFF/pdf/znieff_0000-3014.pdf [14 October 2014]

Duarte CM. 1991. Seagrass depth limits. *Aquatic Botany* **40**: 363–377.

Duarte CM, Conley DJ, Carstensen J, Sánchez-Camacho M. 2009. Return to neverland: shifting baselines affect eutrophication restoration targets. *Estuaries and Coasts* **32**: 29–36.

Elliott M, Burdon D, Hemingway KL, Apitz SE. 2007. Estuarine, coastal and marine ecosystem restoration: Confusing management and science: a revision of concepts. *Estuarine, Coastal and Shelf Science* **74**: 349–366.

Eppesen R, Søndergaard M, Jensen JP, Havens KE, Anneville O, Carvalho L, Coveney MF, Deneke R, Dokulil M, Foy B, *et al*. 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. *Freshwater Biology* **50**: 1747–1771.

Guyoneaud R, De Wit R, Matheron R, Caumette P. 1998. Impact of macroalgal dredging on dystrophic crises and phototrophic bacterial blooms (red waters) in a brackish coastal lagoon (Prévost lagoon, France). *Oceanologica Acta* **21**: 551–561.

Hanley N, Mourato S, Wright RE. 2001. Choice modelling approaches: a superior alternative for environmental valuation? *Journal of Economics Surveys* **15**: 435–462.

Hebert M, Dupré N, Barral M, Messiaen G, Oheix J, Deslous-Paoli J-M, Roque d'Orbcastel E, Laugier T. 2012. Programme de réimplantation d'herbiers de phanérogames (*Zostera noltii/ Ruppia cirrhosa*) dans les lagunes de Bages, Ingril et Thau (Languedoc-Roussillon – France), Rapport Cépralmar: 07–2012. Report in French: http://archimer.ifremer.fr/doc/00089/20062/17703.pdf

Ifremer. 2002. Réseau de Suivi Lagunaire du Languedoc-Roussillon : Bilan des résultats 2001. Chapitre 11 Etangs Palavasiens http://rsl.cepralmar.com/doc/RSL-01-11.pdf

Ifremer. 2005. Réseau de Suivi Lagunaire du Languedoc-Roussillon : Bilan des résultats 2004. Chapitre 11 Etangs Palavasiens. http://rsl.cepralmar.com/doc/RSL-04-11.pdf

Ifremer. 2007. Réseau de Suivi Lagunaire du Languedoc-Roussillon : Bilan des résultats 2006. http://archimer.ifremer.fr/doc/00118/22926/

Ifremer. 2010. Réseau de Suivi Lagunaire du Languedoc-Roussillon : Bilan des résultats 2009. http://archimer.ifremer.fr/doc/00118/22919/ Ifremer. 2013. Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan de résultats 2012. http://archimer.ifremer.fr/doc/00148/25940/

Ifremer. 2014. Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2013. http://archimer.ifremer.fr/doc/00210/32154/

Jaeck M, Lifran R. 2013. Farmers' preferences for production practices: a choice experiment study in the Rhone river delta. *Journal of Agricultural Economics* **65**: 112–130.

Kuhfuss L, Rey-Valette H, Sourisseau E. 2010. Typologie des systèmes lagunaires en Languedoc-Roussillon en fonction des types de services rendus. *Revue de l'économie méridionale (REM)* **58**(n°229–230): 9–24.

Lenzi M, Palmieri R, Porrello S. 2003. Restoration of the eutrophic Orbetello lagoon (Tyrrhenian Sea, Italy): water quality management. *Marine Pollution Bulletin* **46**: 1540–1548.

Meinesz C, Derolez V, Bouchoucha M. 2013. Base de données 'pressions sur les lagunes méditérranéennes' - Analyse des liens état - pression. Report in French. Agence de l'Eau Rhône-Méditeranée-Corse, Montpellier, France.

Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Synthesis*. Island Press: Washington, DC. http://www.millenniumassessment.org/documents/document.356.aspx.pdf

Nixon SW. 1995. Coastal marine eutrophication – a definition, social causes, and future concerns. *Ophelia* **41**: 199–219.

Norgaard RB. 2010. Ecosystem services: from eye-opening metaphor to complexity blinder. *Ecological Economics* **69**: 1219–1227.

Nunes PALD, Rossetto L, De Blaeij A. 2004. Measuring the economic value of alternative clam fishing management practices in the Venice Lagoon: results from a conjoint valuation application. *Journal of Marine Systems* **51**: 309–320.

Orfanidis S, Panayotidis P, Stamatis N. 2003. An insight to the ecological evaluation index (EEI). *Ecological Indicators* **3**: 27–33.

Orth RJ, McGlathery KJ, Heck KL Jr (eds). 2012. Theme section: eelgrass recovery induces state changes in a coastal bay system. *Marine Ecology Progress Series* **434**: 171–301 http://www.int-res.com/articles/theme/m448_ThemeSection.pdf

Ouisse V, Fiandrino A, De Wit R, Malet N. 2013. Restauration des écosystèmes lagunaires : évaluation du rôle du sédiment et des herbiers à phanérogames Rapport final du Contrat n° 2012 1835. Report in French, Agence de l'Eau Rhône-Méditeranée-Corse, Montpellier, France: http://archimer.ifremer.fr/doc/00166/27774/

Pilkaitytė R, Razinkovas A. 2006. Factors controlling phytoplankton blooms in a temperate estuary: nutrient limitation and physical forcing. *Hydrobiologia* **555**: 41–48.

Razinkovas A, Gasiūnaitė Z, Viaroli P, Zaldívar J-M. 2008. European lagoons – need for further comparison across spatial and temporal scales. *Hydrobiologia* **611**: 1–179.

'*Réseau de Suivi Lagunaire*' (RSL). 2014. http://rsl.cepralmar.com/sites/c09/2005.html (in French, a menu option allows to check for different years and the site provides the possibility to download more detailed reports in French) [14 October 2014]

Schramm W. 1999. Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. *Journal of Applied Phycology* **11**: 69–78.

Society for Ecological Restoration International Science & Policy Working Group. 2004. The SER International Primer on Ecological Restoration. www.ser.org and Tucson : Society for Ecological Restoration International: http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration#3 [28 July 2015]

Souchu P, Bec B, Smith VH, Laugier T, Fiandrino A, Benau L, Orsoni V, Collos Y, Vaquer A. 2010. Patterns in nutrient limitation and chlorophyll a along an anthropogenic eutrophication gradient in French Mediterranean coastal lagoons. *Canadian Journal of Fisheries and Aquatic Sciences* **67**: 743–753.

Syndicat mixte des étangs littoraux (SIEL). 2009a. DOCOB Natura 2000 des sites « Etangs palavasiens et étang de l'Estagnol » Tome II, Atlas Cartographique. Villeneuve-lès-Maguelone, France.

Syndicat mixte des étangs littoraux (SIEL). 2009b. DOCOB Natura 2000 des sites « Etangs palavasiens et étang de l'Estagnol » Tome III : concertation et fiches habitats naturels et espèces d'intérêt communautaire. Villeneuve-lès-Maguelone, France.

Syndicat mixte des étangs littoraux (SIEL), 2010. DOCOB Natura 2000 des sites « Etangs palavasiens et étang de l'Estagnol » Tome I, Rapport du DOCOB. Villeneuve-lès-Maguelone, France.

Syndicat mixte des étangs littoraux (SIEL) and P2A Développement SARL. 2012. Réalisation d'un état de référence des herbiers à phanérogames sur les étangs d'Ingril Sud et des Mouettes. Rapport in French, Villeneuve-lès-Maguelone, France.

Valiela I, McLelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* **42**: 1105–1118.

Viaroli P, Bartoli M, Giordano G, Naldi M, Orfanidis S, Zaldivar JM. 2008. Community shifts, alternative stable states, biogeochemical controlsand feedbacks in eutrophic coastal lagoons: a brief overview. *Aquatic Conservation: Marine Freshwater Ecosystems* **18**: 105–117.

Villéger S, Ferraton F, Mouillot D, De Wit R. 2012. Nutrient recycling by coastal macro-organisms: intra vs. interspecific differences. *Marine Ecology Progress Series* **452**: 297–303.

Westerberg VH, Lifran R, Olsen SB. 2010. To restore or not? A valuation of social and ecological functions of the Marais des Baux wetland in Southern France. *Ecological Economics* **69**: 2383–2393.

Zaldívar J-M, Cardoso AC, Viaroli P, Newton A, De Wit R, Ibañez C, Reizopoulou S, Somma F, Razinkovas A, Basset A, *et al*. 2008. Eutrophication in transitional waters: an overview. *Transitional Waters Monographs* **2**: 1–78.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.

Vol. 437: 79–87, 2011
doi: 10.3354/meps09274

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 15

Community-level carbon flux variability over a tidal cycle in *Zostera marina* and *Z. noltii* beds

Vincent Ouisse[1,2,*], Aline Migné[1,2], Dominique Davoult[1,2]

[1]UPMC Univ Paris 06, UMR7144, Roscoff, France
[2]CNRS, UMR 7144, Equipe Réseaux Trophiques et Production Benthique, Station Biologique, Place Georges Teissier, BP 74, 29682, Roscoff Cedex, France

ABSTRACT: Abiotic parameters such as light, temperature, nutrient availability and inorganic carbon source are known to vary widely between immersion and emersion. We measured gross community productivity (GCP) and community respiration (CR) over spring tidal cycles in intertidal *Zostera marina* and *Z. noltii* communities. CO_2 fluxes during emersion and inorganic carbon fluxes during immersion were assessed using closed benthic chambers. GCP and CR rates were significantly higher during immersion than during emersion for both communities. In July, GCP rates were 3- and 5-fold higher and CR rates were 2.5- and 9-fold higher during immersion for the *Z. marina* and *Z. noltii* communities, respectively. This trend was confirmed in the *Z. noltii* community at different periods of the year (February, April and November). Neither photoinhibition nor desiccation was measured during emersion, but shading might have greatly limited the GCP rates. Higher CR during immersion could be explained by enhanced bacterial and infaunal activity.

KEY WORDS: Production · Primary productivity · Respiration · Seagrass · Intertidal · Temporal variability · Metabolism

INTRODUCTION

In temperate areas, research has emphasised the pronounced influence of temperature, light, inorganic carbon and nutrient availability on both leaf photosynthesis and community metabolism in seagrasses (see Lee et al. 2007 for review). However, little attention has been given to the response of intertidal seagrasses to these parameters when exposed to air. It is known that abiotic parameters such as temperature, light and nutrients vary greatly between immersion and emersion, creating important modifications to the plants' environment. During emersion, light intensity is always higher than during immersion. Temperature can also be higher, while nutrient availability sources are reduced to pore water in sediment. Intertidal seagrasses are also exposed to varying concentrations of inorganic carbon such as gaseous CO_2 during emersion and dissolved CO_2, bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) during immersion.

Zostera marina and *Z. noltii*, temperate seagrasses that inhabit the low intertidal zone, can be exposed to air for several hours, particularly during spring tides. Several studies have highlighted the important effect of light on primary production of *Z. marina* (e.g. Drew 1979, Mazzella & Alberte 1986) and *Z. noltii* (e.g. Jiménez et al. 1987) during immersion. Desiccation tolerance has been studied in both species at the scale of leaves using pulse-amplitude modulation (PAM) methods (Shafer et al. 2007) or CO_2 gas analysers (Leuschner & Rees 1993, Leuschner et al. 1998). Over the course of a tidal cycle, Silva et al. (2005) measured a lower photosynthetic response during immersion than emersion using PAM methods and explained this result by the rapid air–water CO_2 diffusion in the thin water film on leaves exposed to the air. However, these measurements were conducted only on leaves and overlooked interactions at the community scale. Seagrasses are just one component of a highly diverse

*Email: ouisse@sb-roscoff.fr

system that also includes significant biomass contributions from other primary producers such as benthic microalgae, macroalgae and epiphytes (McRoy & McMillan 1977), which create large interspecific interactions.

Some measurements have been performed at the community scale in *Zostera marina* beds under immersion (Martin et al. 2005) and in *Z. noltii* beds under both immersion (Plus et al. 2001) and emersion (Ouisse et al. 2010). A direct comparison of aerial and underwater carbon metabolism has only been documented on a *Z. noltii* bed in the Banc d'Arguin, Mauritania (Clavier et al. 2011), and investigations at the community scale over tidal cycles are still needed. In this context, the aim of the present study was to measure the variation in community metabolism at the scale of a tidal cycle in *Z. marina* and *Z. noltii* beds.

MATERIALS AND METHODS

Study site

This study was carried out on 2 intertidal seagrass communities near Roscoff (western English Channel, France), where the maximal tidal amplitude is approximately 9 m. The *Zostera marina* (48° 44.299 N, 3° 58.390 W) and *Z. noltii* beds (48° 41.735 N, 3° 57.653 W) are located below 1.8 and 3.3 m (above chart datum—lowest astronomical tide), respectively. During spring tide, emersion occurs at approximately mid-day and the *Z. noltii* community is exposed to the air for several hours, whereas the *Z. marina* community is exposed for less than 2 h.

In situ measurements of abiotic parameters

Temperature (°C) and photosynthetically available radiation (PAR; µmol quanta m^{-2} s^{-1}) were measured in air next to the study sites with a Vaisala HMP45C (for temperature) and a Skye SKP215 flat sensor (for ambient light), and were recorded every 15 min throughout the year. In seawater, temperature, depth and PAR were measured in each *Zostera* community next to the benthic chamber (approximately 10 cm above the sediment surface) using ultra-miniature MDS-MKV sensors (Alec Electronics™), and were recorded at 1 min intervals during carbon flux measurements. A PAR conversion factor (0.571, $R^2 = 0.868$, $p < 0.001$, $n = 1769$) was estimated from simultaneous flat and spherical sensor measurements in order to convert underwater light to flat surface measurements (µmol quanta m^{-2} s^{-1}).

Benthic carbon flux measurements

Benthic chambers (surface area = 0.071 m^2) were pushed down to 10 cm sediment depth, sealed with clear (for net community productivity [NCP] measurements) or dark (for community respiration [CR] measurements) acrylic hemispheres to trap a known volume (ca. 11 l, depending on the core insertion into the sediment) of seawater or air (for immersion or emersion, respectively). Gross community productivity (GCP) was then calculated by correcting NCP by CR with the assumption that CR rates are equivalent under light and dark conditions. During immersion, the seawater inside the chambers was mixed by autonomous stirrers. Seawater was collected from inside the benthic chambers using 100 ml syringes at the beginning and end of incubations (duration of incubations was ca. 40 to 60 min) and then passed through cellulose acetate membrane filters (0.8 µm) for potentiometric laboratory determination of total alkalinity (Millero et al. 1993), which was performed the following day on 3 subsamples of 20 ml. The pH of seawater samples was measured immediately after sampling. The inorganic carbon concentration of seawater was calculated from the pH, total alkalinity (TA), temperature and salinity according to Strickland & Parsons (1972) and using the formula given in Oviatt et al. (1986). The inorganic carbon fluxes were then calculated using the difference between the final and initial concentrations and expressed in carbon units for the community (mg C m^{-2} h^{-1}). During emersion, inorganic carbon fluxes were measured in the benthic chambers using closed air circuits for CO_2 analysis (see Migné et al. 2002 for the method). Changes in air CO_2 concentration (ppm) were measured in the chamber with CO_2 infrared gas analysers (LiCor Li-800). Gas exchange was monitored for 10 to 30 min to ensure the linearity of the measurements. Data were recorded with data loggers (LiCor Li-1400) at 15 s intervals. CO_2 fluxes were then calculated from the recorded data using the slope of CO_2 concentration (µmol mol^{-1}) against time (min). Results were expressed in carbon units for the bulk benthic community (mg C m^{-2} h^{-1}), assuming a molar volume of 22.4 l at standard temperature and pressure. Carbon fluxes are measured from the community to the environment, and are positive when respiration is greater than carbon fixation and negative when carbon fixation by the community is greater than respiration.

Sampling procedure

Carbon fluxes were measured *in situ* during spring tide cycles in July and October 2009 and February 2010 for the *Zostera marina* community and in April, July and November 2009 and February 2010 for the *Z. noltii* community. On each occasion, 3 benthic chambers were positioned approximately 2 m apart to account for spatial variability. Successive underwater incubations (up to 5) were performed at ambient light during ebb tide. When emersion occurred, successive incubations (up to 6) were then performed in air on the same communities, first at ambient light and then in darkness. Finally, 1 dark incubation was performed during immersion on the subsequent rising tide. The benthic chambers were opened for at least 10 min between successive incubations to restore ambient conditions. For the *Z. marina* community, measurements during both immersion and emersion periods were made only once (on July 24).

To characterise the relationship between photosynthesis (GCP) and light, carbon fluxes were also measured as a function of varying irradiance during air exposure for the *Zostera marina* community (April and September 2008, March and June 2009 and February 2010), and for the *Z. noltii* community (April, June, August and September 2008, March, June and November 2009 and January 2010). For each date, 1 benthic chamber was covered with a series of neutral density filters under ambient light to create an artificial range of light intensities from maximum ambient daylight to darkness.

After each carbon flux measurement, *Zostera* spp. leaves and associated epiphytes, benthic macroalgae and 3 sediment cores (16 mm inner diameter, 10 mm depth) for benthic microalgae were collected inside each benthic chamber to determine the biomass of primary producers.

Primary producer biomass

Chlorophyll *a* (chl *a*) was extracted from the sediment cores in 90% acetone, gently mixed, stored at 6°C for 4 h and centrifuged at 4000 rpm for 15 min. Chl *a* content was determined by spectrophotometry (see Jeffrey & Humphrey 1975 for the method) and expressed in units per sediment area (mg chl *a* m^{-2}). Finally, the benthic microalgae biomass inside the benthic chamber was expressed as g C m^{-2} using a C:chl *a* ratio of 40.8 according to de Jonge (1980). *Zostera* spp. leaves plus associated epiphytes and macroalgae were dried separately at 60°C to a constant weight (dry weight, DW), and the carbon portion of the DW was estimated from CHN analysis using a Flash EA CN analyser. Biomass of primary producers was then expressed as g C m^{-2} using a carbon portion of DW of 43.5% for *Z. noltii* plus associated epiphytes, 40.1% for *Z. marina* plus associated epiphytes, 33.7% for perennial macroalgae (small red algae) and 35.2% for ephemeral macroalgae (*Ulva* spp.).

Statistical treatment and analyses

The highest GCP of each condition was used to compare immersion and emersion rates. Considering the different dates of measurements (1 date in *Zostera marina* and 4 dates in *Z. noltii* beds, 3 benthic chambers at each experiment) as replication, groups of 15 paired (immersion–emersion) observations are available for each process (highest GCP and CR). The normality of these pooled data was verified (Shapiro test, $p > 0.05$), and paired *t*-tests were applied to test for differences between immersion and emersion rates.

Photosynthetic parameters of community (maximum GCP, GCP_{max}, and the saturation onset parameter, I_k) during emersion were estimated for each sampling date by fitting GCP and mean recorded PAR during measurements with the mathematical model of Webb et al. (1974):

$$GCP = GCP_{max}\left[1 - \exp^{\left(-\frac{I}{I_k}\right)}\right] \qquad (1)$$

where GCP and GCP_{max} are in units of mg C m^{-2} h^{-1}, and I (light intensity) and I_k are in units of µmol quanta m^{-2} s^{-1}.

GCP_{max} and I_k were estimated by minimisation of an ordinary least-square criterion performed by a simplex algorithm (Nelder & Mead 1965). The relationship between photosynthesis (GCP) and light was then tested with an *F*-test using SPSS Systat 11© software.

RESULTS

Underwater versus aerial carbon fluxes

Carbon fluxes measured over a tidal cycle varied with exposure to air and light. In the *Zostera marina* community (24 July; Fig. 1a) under the lowest ambi-

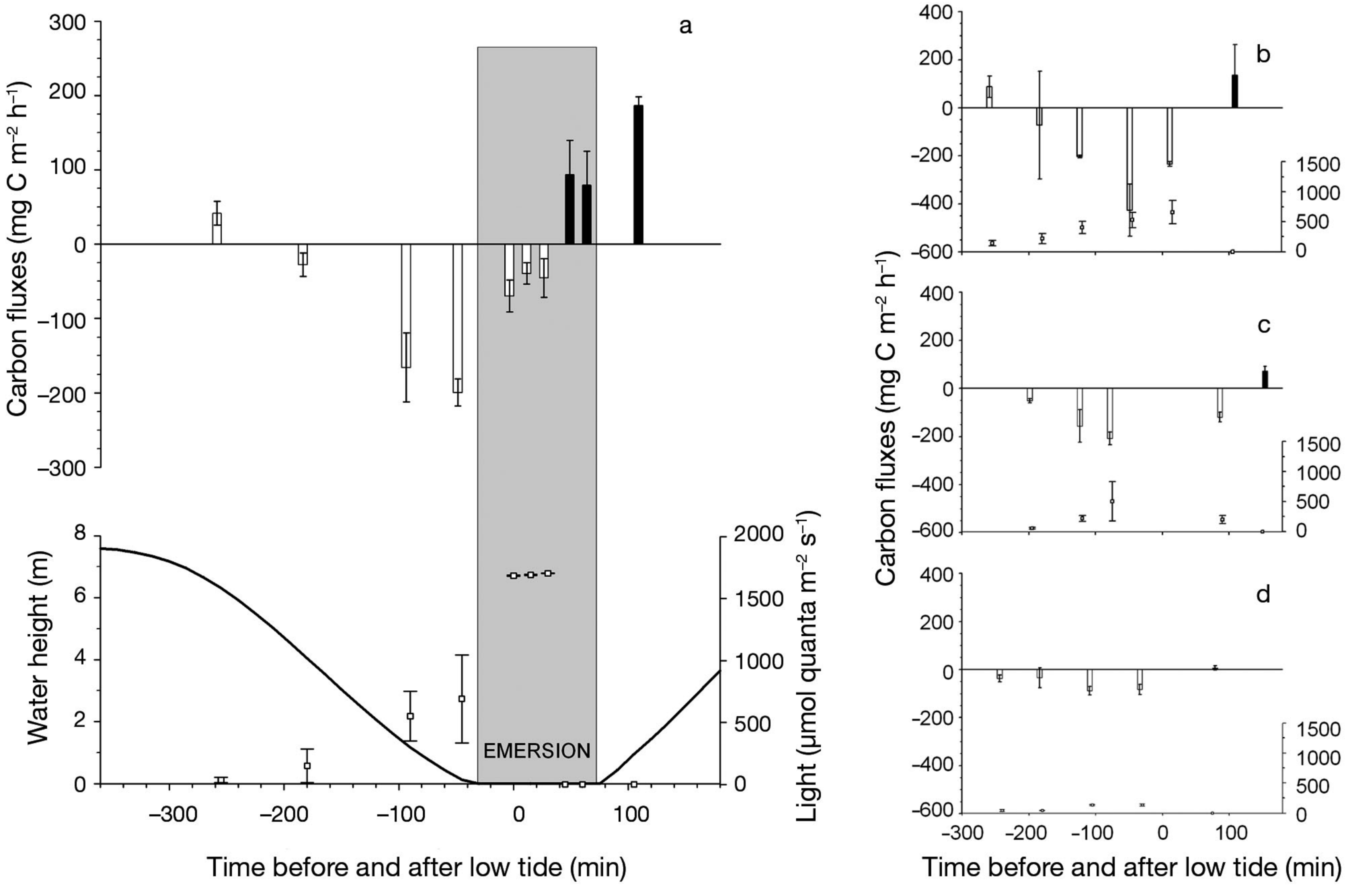


Fig. 1. Mean (±SD) carbon flux (mg C m^{-2} h^{-1}), water height (solid line in panel a, m) and ambient light (open square, µmol quanta m^{-2} s^{-1}) during light (white bars) and dark (dark bars) incubations in the *Zostera marina* community over a tidal cycle on (a) 24 July 2009, (b) 9 July 2009, (c) 19 October 2009 and (d) 17 February 2010. The grey shaded area corresponds to the emersed condition (data only available for 24 July 2009)

ent light (38 ± 22 µmol quanta m^{-2} s^{-1}), community carbon fluxes were positive (41.54 ± 16.06 mg C m^{-2} h^{-1}), which indicated that photosynthesis did not compensate for CR. During the ebb tide, community carbon fluxes increased in absolute value with a maximum just before emersion (−199.52 ± 18.16 mg C m^{-2} h^{-1}), corresponding to maximum ambient light in water (690 ± 356 µmol quanta m^{-2} s^{-1}). During emersion, ambient light was high (1684 ± 5 to 1706 ± 2 µmol quanta m^{-2} s^{-1}) but community carbon fluxes were smaller (−39.31 ± 14.32 to −69.68 ± 21.54 mg C m^{-2} h^{-1}) than during immersion. CR was 2.5 ± 1.6-fold higher during immersion (186.34 ± 12.17 mg C m^{-2} h^{-1}) than during emersion (79.14 ± 45.87 to 93.36 ± 46.28 mg C m^{-2} h^{-1}) at a similar temperature (17.8°C in seawater and 17.2°C in air; Table 1). The highest GCP calculated from correcting NCP by CR was approximately 3 times higher during immersion than during emersion (Fig. 2a,b, respectively).

For the same period, in the *Zostera noltii* community (27 July; Fig. 3a), carbon fluxes were always negative in daylight and varied during immersion from −22.14 ± 13.22 to −142.60 ± 44.19 mg C m^{-2} h^{-1}, reaching their maximum (in absolute value) just before emersion when the ambient light was the highest in water (639 ± 174 µmol quanta m^{-2} s^{-1}). Community carbon fluxes were smaller during emersion (−23.41 ± 4.71 to −30.42 ± 0.77 mg C m^{-2} h^{-1}) than during immersion whereas light was higher (1457 ± 6 to 1532 ± 102 µmol quanta m^{-2} s^{-1}). The CR was extremely variable among chambers during immersion (109.08 ± 77.96 mg C m^{-2} h^{-1}), and was more than 9 times higher as compared with emersion (8.29 ± 1.25 to 10.92 ± 3.52 mg C m^{-2} h^{-1}; Fig. 2c,d, respectively), although the mean temperature varied only from 17.6°C in seawater to 16.6°C in air (Table 1). The highest GCP was 5 times higher during immersion than emersion. As observed in July, carbon fluxes in

Table 1. Mean (±SD) primary producer biomass in the benthic chambers (PPB), maximum mean light and temperature during light (T_{NCP}) and dark (T_{CR}) incubations measured over a tidal cycle in July 2009 (9th and 24th), October 2009 and February 2010 in the *Zostera marina* community and in April, July and October 2009 and February 2010 in the *Zostera noltii* community. NCP: net community productivity; CR: community respiration

Sampling date	PPB ($g C m^{-2}$)	Immersion Light ($\mu mol quanta m^{-2} s^{-1}$)	Immersion T_{NCP} (°C)	Immersion T_{CR} (°C)	Emersion Light ($\mu mol quanta m^{-2} s^{-1}$)	Emersion T_{NCP} (°C)	Emersion T_{CR} (°C)
Zostera marina							
9 Jul 2009	99.7 ± 25.48	529 ± 127	15.5	16.7			
24 Jul 2009	163.08 ± 46.68	690 ± 356	17.7	17.8	1694 ± 5	17.0	17.2
Oct 2009	69.91 ± 26.17	502 ± 327	15.3	15.1			
Feb 2010	12.74 ± 2.77	133 ± 13	8.3	8.6			
Zostera noltii							
Apr 2009	19.42 ± 8.8	275 ± 79	12.9	14.9	1215 ± 220	17.8	18.7
Jul 2009	30.24 ± 16.53	639 ± 174	17.9	17.6	1532 ± 102	16.5	16.6
Nov 2009	28.49 ± 7.91	131 ± 74	12.6	13.1	829	13.1	13.2
Feb 2010	5.84 ± 1.98	305 ± 100	7.4	8.8	1017 ± 128	7.5	7.9

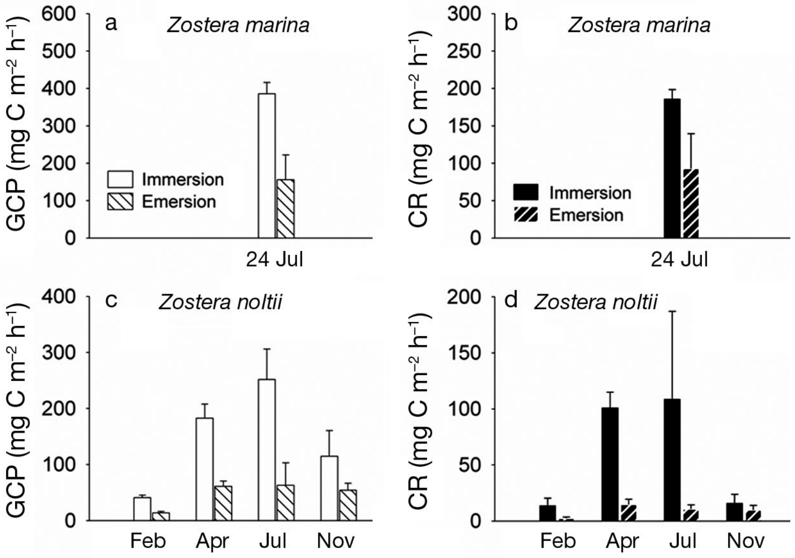


Fig. 2. Mean (±SD) highest (a,c) gross community productivity (GCP) and (b,d) community respiration (CR) in the *Zostera marina* community on 24 July 2009 and the *Z. noltii* community on 27 July 2009, 24 April 2009, 17 November 2009 and 16 February 2010, respectively, during immersion (solid bars) and emersion (hatched bars)

the *Z. noltii* community always reached their maximum during immersion, just before low tide (Fig. 3).

Considering all data (Fig. 2), the highest measured GCP and CR were significantly higher during immersion than during emersion (paired *t*-test on grouped data, GCP, $p < 0.001$, $n = 15$; CR, $p < 0.001$, $n = 15$).

Carbon fluxes under immersion over the year

In the *Zostera marina* community, the CR and maximal GCP during immersion were lowest in February and highest in July (Fig. 1). Conversely, the ratio between GCP and primary producer biomass (PPB) during immersion was lowest in July (2.51 ± 0.78 mg C g^{-1} C h^{-1}) and highest in February (7.60 ± 1.67 mg C g^{-1} C h^{-1}). In the *Z. noltii* community, the GCP was lowest in February and high in April, July and November. The GCP:PPB ratio was highest in April (10.43 ± 3.50 mg C g^{-1} C h^{-1}) and lowest in February (4.08 ± 1.14 mg C g^{-1} C h^{-1}; Fig. 2c). CR also reached its minimum in February and its maximum in July (Fig. 2d).

Carbon fluxes as a function of irradiance under air exposure

Photosynthetic parameters calculated on additional carbon flux measurements under artificial decreasing light during emersion for both communities also varied over the course of the year. GCP$_{max}$ of the *Zostera marina* community reached its maximum in September 2008 and its minimum in April 2008 (Table 2). In the *Z. noltii* community, GCP$_{max}$ was the lowest in January 2010 and the highest in September 2008 (Table 2). The saturation onset parameter (I_k) was higher in summer (in June 2009 for *Z. marina* and in August 2008 for *Z. noltii*) and lower in March 2009 and in January 2010 for the *Z. marina* and *Z. noltii* communities, respectively.

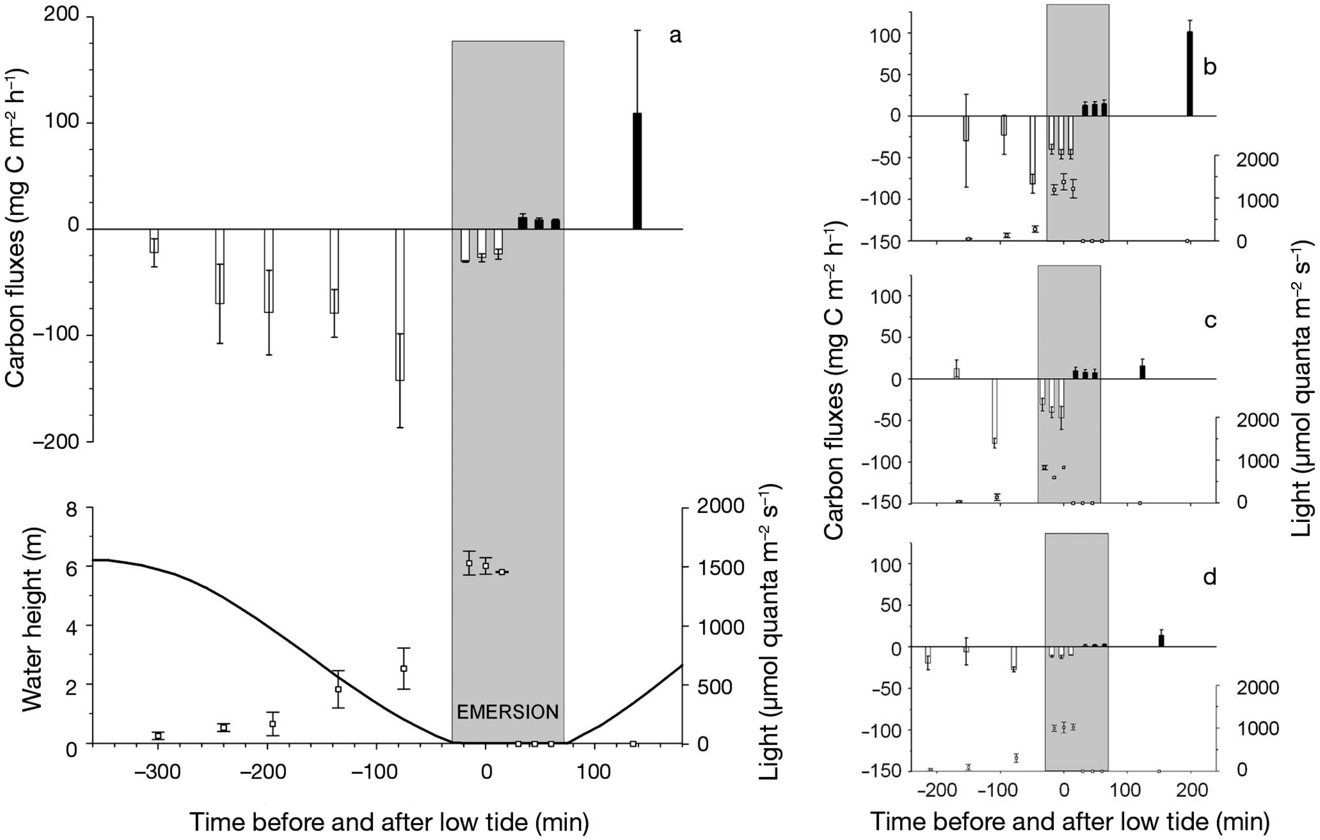


Fig. 3. Mean (±SD) carbon fluxes (mg C m^{-2} h^{-1}), water height (solid line in panel a, m) and ambient light (open square, µmol quanta m^{-2} s^{-1}) during light (white bars) and dark (dark bars) incubations in the *Zostera noltii* community over a tidal cycle on (a) 27 July 2009, (b) 24 April 2009, (c) 17 November 2009 and (d) 16 February 2010. The grey shaded area corresponds to the emersed condition

Table 2. Mean temperature during incubations (T), primary producer biomass in the benthic chamber (PPB), and parameters estimated from the model of Webb et al. (1974): maximal gross community productivity (GCP$_{max}$), saturation onset parameter (I_k). R^2 and p-values are presented for the fit of the Webb et al. model to each chamber under emersed conditions in the *Zostera marina* community in February 2010, March 2009, April 2008, June 2009, September 2008 and the *Z. noltii* community in January 2010, March 2009, April 2008, June 2008, June 2009, August 2008, September 2008 and November 2009. n: number of incubations

Sampling date	T (°C)	PPB (g C m^{-2})	CR (mg C m^{-2} h^{-1})	GCP$_{max}$ (mg C m^{-2} h^{-1})	I_k (µmol quanta m^{-2} s^{-1})	n	R^2	p
Zostera marina								
Feb 2010	7.7	56.34	16.92	42.65	91.79	7	0.915	0.002
Mar 2009	16.1	14.60	17.24	36.75	86.88	7	0.876	<0.001
Apr 2008	7.9	18.17	15.93	24.75	90.74	6	0.966	<0.001
Jun 2009	16.4	15.30	15.78	41.04	140.81	6	0.968	<0.001
Sep 2008	15.8	63.51	57.54	141.63	124.37	7	0.995	<0.001
Zostera noltii								
Jan 2010	3.4	17.34	4.12	37.38	79.95	6	0.945	<0.001
Mar 2009	9.9	8.85	9.32	47.28	129.32	7	0.998	<0.001
Apr 2008	8.3	12.32	22.28	79.49	86.47	8	0.996	<0.001
Jun 2008	14.4	24.41	20.98	62.91	201.89	9	0.922	<0.001
Jun 2009	15.9	47.55	42.42	80.64	132.57	8	0.986	<0.001
Aug 2008	19.6	87.11	51.39	115.43	204.45	8	0.973	<0.001
Sep 2008	16.1	52.15	49.53	125.89	148.82	9	0.962	<0.001
Nov 2009	14.6	18.92	8.75	47.23	128.29	6	0.983	<0.001

DISCUSSION

CR and GCP rates measured during immersion over the course of the year were within the range previously reported in the literature for both *Zostera marina* (Murray & Wetzel 1987, Barranguet & Alliot 1995, Martin et al. 2005) and *Z. noltii* communities (Vermaat & Verhagen 1996, Viaroli et al. 1996, Plus et al. 2001). During emersion, CR and GCP rates were low but consistent with studies conducted on the same communities during 2008, when CR varied from 13.8 to 82.8 mg C m^{-2} h^{-1} and GCP from 43.9 to 251.5 mg C m^{-2} h^{-1} in the *Z. marina* community (authors' unpubl. data) and CR varied from 3.2 to 49.1 mg C m^{-2} h^{-1} and GCP from 22.4 to 120.4 mg C m^{-2} h^{-1} in the *Z. noltii* community (Ouisse et al. 2010).

In the present study, immersion rates were significantly higher than emersion rates for both communities across different time periods. This main result confirms the observation made only once for a *Zostera noltii* community on the northwest coast of Mauritania (Clavier et al. 2011). More generally, a higher CR rate during immersion than emersion has been observed in previous studies of temperate mudflats (Gribsholt & Kristensen 2003, Cook et al. 2004, Migné et al. 2009). In soft sediment, CR can be mainly ascribed to heterotrophic organisms (del Giorgio & Williams 2005), and higher CR during immersion might be explained by enhanced bacterial and infaunal activity. This phenomenon might be amplified in seagrass beds, as bacterial metabolism in sediment and on seagrass leaves (Wittmann et al. 1981) is particularly enhanced due to the high organic matter inputs from plants (Holmer & Nielsen 1997). In the present study, the GCP rate was much higher at the end of immersion than during emersion for both communities, whereas light intensity was always lower during immersion. This certainly cannot be explained by the contribution of planktonic organisms, which can be assumed to be negligible (see for example Santos et al. 2004, who measured a plankton contribution of approximately 0.01 % to the metabolism of a *Z. noltii* community). *Zostera* spp. communities are also subjected to drastic HCO_3^- and CO_2 concentration changes. Because of its high constant concentration in seawater, HCO_3^- is used directly or indirectly as a major source of inorganic carbon by *Zostera* spp. (Hellblom et al. 2001), whereas CO_2 contributes only marginally to photosynthesis during immersion (Sand-Jensen & Gordon 1984, Beer & Rehnberg 1997). During emersion, the majority of carbon has to be supplied by atmospheric CO_2 that passes through the thin water film remaining on the leaves (Leuschner & Rees 1993). Considering the high affinity of plants to CO_2 (see Touchette & Burkholder 2007 for review) and the high availability of CO_2 in the air, the seagrasses might not be limited by inorganic carbon needs during emersion. Measurements of photosynthesis versus irradiance during emersion for both communities highlighted the lack of a decrease in GCP under high irradiance (Fig. 4), and thus no photoinhibition. This is in accordance with previous studies on *Z. marina* (Mazzella & Alberte 1986) and *Z. noltii* leaves (Jiménez et al. 1987); therefore, the low GCP observed during emersion cannot be ascribed to photoinhibition. During emersion, the leaves are flattened and only one side of the leaves can receive the incident light. In addition, the superimposition of leaves of the same shoot limits the exposure to light solely to external leaves.

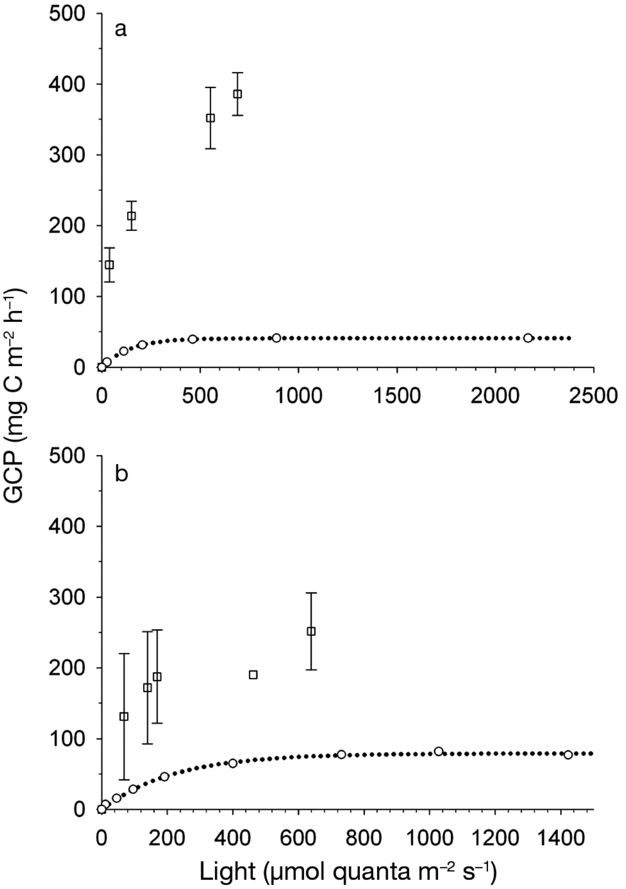


Fig. 4. Relationship between gross community productivity (GCP, mg C m^{-2} h^{-1}) and irradiance (µmol quanta m^{-2} s^{-1}) in the (a) *Zostera marina* and (b) *Z. noltii* communities under emersed conditions in June 2009 and August 2008, respectively, according to the model of Webb et al. (1974) (open circles and dotted lines). Also shown is mean (± SD) GCP under immersed conditions in July 2009 (open squares; see 'Materials and methods')

Finally, in the case of *Z. marina*, leaves cover the rest of the community and can decrease the incident light available to the other primary producers. Thus, the shading might have reduced GCP for both communities.

NCP decreased immediately at the beginning of emersion and did not vary throughout the air exposure period. Although the limitation of metabolism by desiccation has been described at the scale of both the plant (Björk et al. 1999) and the leaf (Shafer et al. 2007), the present study did not highlight any desiccation effect at the community scale. An important superficial cover of *Zostera* spp. kept the rest of the community moist and limited the evaporation from the sediment into the air.

At the annual scale, maximum underwater GCP rates for both communities varied with PPB (Table 1). However, the ratio between GCP and PPB for the *Zostera marina* community was lowest in summer. During this season, shading created by the superimposition of leaves in the small benthic chamber artificially reduced the light available for leaves and, as a consequence, decreased the GCP. The GCP:PPB ratio for *Z. noltii* community was highest in April. In winter and early spring, leaves did not grow much, allowing a high level of epiphyte colonization. In spring, epiphyte biomass was still high and the *Z. noltii* leaves started to grow. This could enhance the GCP at the community scale, as previously supposed based on results obtained for the same community during emersion (Ouisse et al. 2010).

In summary, the main explaination for the lower GCP during emersion than during immersion is the large effect of self-shading of the community by seagrass leaves. The leaf superimposition protected the community from high desiccation but decreased available light. No photoinhibition was demonstrated during emersion in either community. Even though there are clear *Zostera noltii* and *Z. marina* community distribution patterns in the intertidal zone, the present study did not find any clear difference in the metabolism responses to tidal cycle between these communities. This study highlights the importance of studying carbon fluxes at the community scale in order to take into account the complex interactions among species, especially as community-scale results sometimes contradict those obtained at the plant scale. In addition, tidal and seasonal variations need to be taken into account in order to estimate the role of *Zostera* spp. communities in the carbon cycle of the coastal zone.

Acknowledgements. This study forms part of the PhD thesis of V.O. and was financially supported by the 'Ministère de l'Enseignement Supérieur et de la Recherche'. The authors thank the Service Mer et Observation of the Station Biologique de Roscoff, A. Bonnefoy and S. Martin for their participation in field experiments and L. Noël and A. Cahill for editing and improving the English. They also thank the 3 anonymous referees, whose comments greatly contributed to the improvement of the manuscript.

LITERATURE CITED

Barranguet C, Alliot E (1995) Spatial and temporal variations of benthic fluxes (oxygen and ammonia) and microphytic biomass in a shellfish cultivation area of Thau Lagoon (France). J Rech Oceanogr 20:15–26

Beer S, Rehnberg J (1997) The acquisition of inorganic carbon by the seagrass *Zostera marina*. Aquat Bot 56: 277–283

Björk M, Uku J, Weil A, Beer S (1999) Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. Mar Ecol Prog Ser 191:121–126

Clavier J, Chauvaud L, Carlier A, Amice E and others (2011) Aerial and underwater carbon metabolism of a *Zostera noltii* seagrass bed in the Banc d'Arguin, Mauritania. Aquat Bot 95:24–30

Cook PLM, Butler ECV, Eyre BD (2004) Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. I. Benthic metabolism. Mar Ecol Prog Ser 280:25–38

de Jonge VN (1980) Fluctuation in the organic carbon to chlorophyll *a* ratios for estuarine benthic diatom populations. Mar Ecol Prog Ser 2:345–353

del Giorgio PA, Williams PJ (2005) Respiration in aquatic ecosystems. Oxford University Press, Oxford

Drew EA (1979) Physiological aspects of primary production in seagrasses. Aquat Bot 7:139–150

Gribsholt B, Kristensen E (2003) Benthic metabolism and sulfur cycling along an inundation gradient in a tidal *Spartina anglica* salt march. Limnol Oceanogr 48: 2151–2162

Hellblom F, Beer S, Björk M, Axelsson L (2001) A buffer sensitive inorganic carbon utilisation system in *Zostera marina*. Aquat Bot 69:55–62

Holmer M, Nielsen SL (1997) Sediment sulfur dynamics related to biomass–density patterns in *Zostera marina* (eelgrass) beds. Mar Ecol Prog Ser 146:163–171

Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls *a*, *b*, c_1 and c_2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanz 167:191–194

Jiménez C, Niell FX, Algarra P (1987) Photosynthetic adaptation of *Zostera noltii* Hornem. Aquat Bot 29:217–226

Lee KS, Park SR, Kim YK (2007) Effects of irradiance, temperature, and nutrient on growth dynamics of seagrasses: a review. J Exp Mar Biol Ecol 350:144–175

Leuschner C, Rees U (1993) CO_2 gas exchange of two intertidal seagrass species, *Zostera marina* L. and *Zostera noltii* Hornem., during emersion. Aquat Bot 45:53–62

Leuschner C, Landwehr S, Mehlig U (1998) Limitation of carbon assimilation of intertidal *Zostera noltii* and *Zostera marina* by desiccation at low tide. Aquat Bot 62: 171–176

Martin S, Clavier J, Guarini JM, Chauvaud L and others

(2005) Comparison of *Zostera marina* and maerl community metabolism. Aquat Bot 83:161–174

➤ Mazzella L, Alberte RS (1986) Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. J Exp Mar Biol Ecol 100:165–180

McRoy CP, McMillan C (1977) Production ecology and physiology of seagrasses. In: McRoy CP, Helfferich C (eds) Seagrass ecosystems: a scientific perspective. Dekker, New York, NY, p 53–81

➤ Migné A, Davoult D, Spilmont N, Menu D, Boucher G, Gattuso JP, Rybarczyk H (2002) A closed-chamber CO_2-flux method for estimating intertidal primary production and respiration under emersed conditions. Mar Biol 140: 865–869

➤ Migné A, Spilmont N, Boucher G, Denis L and others (2009) Annual budget of benthic production in Mont Saint-Michel Bay considering cloudiness, microphytobenthos migration, and variability of respiration rates with tidal conditions. Cont Shelf Res 29:2280–2285

➤ Millero FJ, Zhang JZ, Lee K, Campbell DM (1993) Titration alkalinity of seawater. Mar Chem 44:153–165

➤ Murray L, Wetzel RL (1987) Oxygen production and consumption associated with the major autotrophic components in two temperate seagrass communities. Mar Ecol Prog Ser 38:231–239

Nelder VA, Mead R (1965) A simplex method for function minimization. Comput J 7:308–313

➤ Ouisse V, Migné A, Davoult D (2010) Seasonal variations of community production, respiration and biomass of different primary producers in an intertidal *Zostera noltii* bed (western English Channel, France). Hydrobiologia 649: 3–11

➤ Oviatt CA, Rudnick DT, Keller AA, Sampou PA, Almquist GT (1986) A comparison of system (O_2 and CO_2) and C-14 measurements of metabolism in estuarine mesocosms. Mar Ecol Prog Ser 28:57–67

➤ Plus M, Deslous-Paoli JM, Auby I, Dagault F (2001) Factors influencing primary production of seagrass beds (*Zostera noltii* Hornem.) in the Thau Lagoon (French Mediterranean coast). J Exp Mar Biol Ecol 259:63–84

➤ Sand-Jensen K, Gordon DM (1984) Differential ability of marine and freshwater macrophytes to utilize HCO_3^- and CO_2. Mar Biol 80:247–253

➤ Santos R, Silva J, Alexandre A, Navarro N, Barrón C, Duarte C (2004) Ecosystem metabolism and carbon fluxes of a tidally-dominated coastal lagoon. Estuaries 27:977–985

➤ Shafer DJ, Sherman TD, Wyllie-Echeverria S (2007) Do desiccation tolerances control the vertical distribution of intertidal seagrasses? Aquat Bot 87:161–166

➤ Silva J, Santos R, Calleja ML, Duarte CM (2005) Submerged versus air-exposed intertidal macrophyte productivity: from physiological to community-level assessments. J Exp Mar Biol Ecol 317:87–95

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis. Bull Fish Res Board Can 167:1–311

➤ Touchette BW, Burkholder JM (2007) Carbon and nitrogen metabolism in the seagrass, *Zostera marina* L.: environmental control of enzymes involved in carbon allocation and nitrogen assimilation. J Exp Mar Biol Ecol 350: 216–233

➤ Vermaat JE, Verhagen FCA (1996) Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem.: coupling demographic and physiological patterns. Aquat Bot 52: 259–281

➤ Viaroli P, Bartoli M, Bondavalli C, Christian RR, Giordani G, Naldi M (1996) Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. Hydrobiologia 329:105–119

➤ Webb WL, Newton M, Starr D (1974) Carbon dioxide exchange of *Alnus rubra*. Oecologia 17:281–291

Wittmann KL, Mazzella L, Fresi E (1981) Age specific patterns of leaf growth: their determination and importance for epiphytic colonization in *Posidonia oceanica* (L.) Delile. Rapp Comm Int Mer Medit 27:187–191

Editorial responsibility: William Kemp,
Maryland, USA

Submitted: July 14, 2010; Accepted: June 29, 2011
Proofs received from author(s): September 8, 2011