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Drivers and fates of jellyfish blooms

The case study of *Aurelia coerulea* in the Thau lagoon (North Western Mediterranean)

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RAQUEL FONSECA DA SILVA MARQUES

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RÉSUMÉ EN FRANÇAIS

Introduction générale

Les méduses sont un groupe très diversifié d'organismes qui partagent la caractéristique d'être composés principalement d'eau, ce qui leur confère un aspect gélatineux. Dans cette thèse, le terme «méduse» sera utilisé pour désigner le groupe des cnidaires médusozoaires (*i.e.* Scyphozoa, Hydrozoa et Cubozoa, Schiariti et al. 2018) et en particulier les Scyphozoaires, puisqu' *Aurelia coerulea* appartient à cette classe.

Le cycle de vie de la plupart des scyphozoaires est complexe et comprend un stade benthique et un stade pélagique. Les méduses ont, au stade pélagique, une reproduction sexuée, produisant des larves ciliées (les planules) qui, une fois atteint le bon substrat benthique, s'y fixent et se métamorphosent en scyphistomes (ou polypes). Chaque scyphistome est capable de se reproduire de manière asexuée, contrôlant la densité de la population benthique (Lucas 2001; Lucas et al. 2012; Schiariti et al. 2014). Enfin, dans des conditions environnementales favorables, les scyphistomes libèrent un grand nombre d'éphyrules au cours d'un processus appelé strobilation. Les éphyrules se développent ensuite en méduses, bouclant ainsi le cycle de vie. Les fortes densités de certaines méduses, associées à leur croissance rapide, conduisent à l'accumulation de biomasses importantes appelées proliférations ou*"blooms"* (Boero et al. 2008). Après leur reproduction sexuée, les méduses souvent meurent et l'épisode de prolifération disparait (Pitt et al. 2014). Malgré leur coté éphémère, les proliférations de méduses interfèrent, directement ou indirectement, avec plusieurs activités humaines (Purcell et al. 2007; Richardson et al. 2009; Purcell 2012) et peuvent avoir des impacts importants, qu'ils soient négatifs ou positifs, sur le fonctionnement des écosystèmes (*e.g.* Pitt et al. 2009b; Doyle et al. 2014; Graham et al. 2014). Par exemple, la forte pression de prédation exercée par les méduses sur les niveaux trophiques inférieurs au cours de leur croissance, ou la dégradation de leur biomasse en fin de bloom, peut avoir des conséquences dramatiques sur les réseaux trophiques et les cycles biogéochimiques (*e.g.* Pitt et al. 2009; Ramirez-Romero et al. 2018). La prolifération de méduses peut aussi affecter de nombreuses activités humaines (comme la pêche, l'aquaculture, les installations de l'industrie côtière et le tourisme) entraînant des pertes économiques parfois très élevées (Graham et al. 2014). Cependant, les proliférations de méduses peuvent également avoir des impacts positifs. En effet, elles contribuent à la séquestration du carbone dans les océans, servant de nourriture pour certains prédateurs marins, sont exploitées pour la consommation humaine, ou pour la fabrication de multiples bioproduits destinés à être utilisés en médecine et en biotechnologie (Doyle et al. 2014; Brotz et al. 2017).

L'augmentation des épisodes de prolifération de méduses, du moins dans certaines régions du monde (Brotz et al. 2012; Condon et al. 2012), est souvent associée à des pressions anthropogéniques accrues sur le milieu marin (Purcell 2012). Le changement climatique, la surpêche, l'artificialisation des habitats, l'eutrophisation et l'introduction d'espèces exotiques (*e.g.* Purcell et al. 2007; Duarte et al. 2012; Boero 2013) ont été désignés comme les principaux promoteurs de ces épisodes de prolifération. Cependant, notre manque de connaissances de base sur les facteurs environnementaux qui affectent la dynamique des populations de méduses entrave nos efforts pour prédire l'évolution future des proliférations de méduses et leurs impacts, que ce soit sur les écosystèmes ou sur les activités humaines.

L'étang de Thau dans le sud de la France (Méditerranée NO) présente la particularité rare d'abriter une population résidente d'*Aurelia coerulea*, l'une des espèces qui forme le plus de proliférations dans le monde. Tout le cycle de vie de cette méduse se déroule dans cet étang et la dynamique de la population pélagique, ainsi que la distribution spatiale du stade benthique ont déjà été étudiées dans la lagune (Bonnet et al. 2012; Marques et al. 2015b; a). Par conséquent, l'Étang de Thau est le site idéal pour étudier l'écologie de *A. coerulea* comprendre l'origine de ses blooms et fournir des indices sur leurs impacts potentiels sur le fonctionnement des écosystèmes. Ainsi, cette thèse vise à identifier les facteurs environnementaux responsables des proliférations de *A. coerulea* dans l'étang et à préciser le devenir de la matière organique ainsi produite chaque année.

Facteurs contrôlant les proliférations de méduses

Introduction

Le processus de prolifération des méduses résulte du cycle de vie complexe de ces organismes et de facteurs environnementaux agissant à chaque étape de ce cycle de vie. Dans l'étang de Thau, la dynamique de population des stades pélagiques d'*A. coerulea* a déjà été décrite, révélant l'importance de la température et de la disponibilité de la nourriture pour la croissance des méduses. Cependant, alors que la distribution spatiale et les habitats préférentiels des scyphistomes de l'espèce sont connus dans la lagune (Marques et al. 2015b), les stratégies de reproduction asexuée et la dynamique de population des scyphistomes d'*A. coerulea* sont encore inexplorées. Compte tenu du rôle clé de la population benthique dans la production des méduses, il est urgent de mener des études approfondies sur sa dynamique temporelle et sur les facteurs environnementaux qui la contrôlent. L'importance des processus dit « bottom-up » au sein des réseaux trophiques pour la régulation des populations de méduses (Lucas 1996; Lucas et al. 1997; Uye 2011) a également montré la nécessité d'études approfondies sur l'écologie

trophique des deux phases (benthique et pélagique) du cycle de vie sur le terrain. De plus, en raison de la grande importance économique locale de la conchyliculture dans l'étang de Thau, il était également important de déterminer si les méduses et les scyphistomes d'*A. coerulea* entrent ou non en compétition pour la nourriture avec les huîtres produites dans la lagune ou s'ils peuvent être bénéfiques pour la production de bivalves via des contrôles indirects sur la communauté planctonique.

Cette thèse a permis de combler ce manque de connaissance. Pendant un an, des suivis bimensuels en utilisant des photoquadrats sous-marins, et l'observation en laboratoire de scyphistomes prélevés régulièrement sur le terrain, ont permis de décrire la dynamique de population du stade benthique d'*A. coerulea* dans Thau, sa stratégie de reproduction asexuée et les facteurs environnementaux qui les affectent. L'écologie trophique des scyphistomes et des méduses d'*A. coerulea* a également été précisée, en combinant l'analyse des contenus stomacaux des méduses et l'étude des variations mensuelles des signatures isotopiques en carbone et en l'azote des deux stades de vie d'*A. coerulea* et de leurs principales sources de matière organique potentielles. En outre, les niches isotopiques des scyphistomes et des méduses ont été comparées avec celles des huîtres produites dans la lagune, fournissant des informations sur la compétition trophique intra et interspécifique dans la lagune de Thau.

Dynamique de la population benthique d'A. coerulea (Article 1)

Dans Thau, la dynamique démographique annuelle des scyphistomes d'*A. coerulea* se caractérise par une densité maximale au printemps, suivie d'une diminution jusqu'à ce que des valeurs minimales soient atteintes (en été et en automne) et d'un rétablissement progressif des effectifs en hiver. Ces observations contrastent avec celles faites précédemment pour le genre *Aurelia* (Ishii and Katsukoshi 2010; Makabe et al. 2014; Hocevar et al. 2018), où les densités de scyphistomes sont généralement leur maximum à l'été et à leur plus bas niveau pendant l'hiver. La température, la salinité, la concentration en chlorophylle a et l'abondance du mésozooplancton ont été testés en tant que variables explicatives, mais seules la température et la salinité semblent avoir une influence significative sur la dynamique particulière de la population benthique d'*A. coerulea* dans Thau. Bien que la densité de scyphistomes soit positivement corrélée à la température, l'interaction des hautes températures et des salinités élevées en été semblé être préjudiciable pour les scyphistomes. Cependant, un impact fort des facteurs biotiques, comme la prédation, la compétition spatiale et trophique n'est pas à exclure. En effet, plusieurs prédateurs benthiques potentiels ont été identifiés dans les photoquadrats suivis, même si la consommation de scyphistomes par ces organismes n'a jamais été rapportée

à ce jour. La consommation indirecte de scyphistomes par prédation sur leurs substrats de fixation, pourrait aussi contribuer fortement à leur réduction démographique. En effet, les taux de recouvrement des scyphistomes et de certains organismes leur servant de substrat (e.g. *Peyssonnelia* sp.) étaient significativement corrélés, suggérant une réduction synchrone de ces deux paramètres. En outre, certaines espèces de poissons vivant dans la lagune se sont révélées pouvoir être d'importants consommateurs indirects des scyphistomes d'*A. coerulea* notamment pendant leur consommation de bivalves (Marques et al. 2016), qui sont le substrat préférentiel de fixation des polypes de l'espèce (Marques et al. 2015b).

Chez les méduses, la croissance des populations benthiques résulte à la fois de la production de bourgeons par reproduction asexuée, du désenkystement de podocystes et du recrutement de planules pélagiques sur des substrats (Schiariti et al. 2014). Dans Thau, le recrutement des planules et le désenkystement des podocystes semblent avoir peu contribué à l'augmentation de la densité des scyphistomes d'*A. coerulea*. En effet, pendant l'année de cette étude, la période de libération des planules a coïncidé avec le déclin de la population benthique. En fin, bien que le nombre de podocystes par scyphistomes ait été positivement corrélé à la densité des scyphistomes, il est impossible de vérifier la contribution des podocystes à l'augmentation de la population benthique tant que leur production, leur désenkystement et leur temps de résidence ne sont pas étudiés *in situ*.

La production de bourgeons, au contraire, pourrait être la principale responsable des augmentations de densité de scyphistomes observées. Bien que la production de bourgeons dans le temps et la densité de scyphistomes ne soient pas significativement corrélées (avec une inadéquation en été), la production estimée de bourgeons était élevée avant le pic de recouvrement en scyphistomes du mois d'avril (entre février et avril 2017, 15,0 ± 6,7 à 19,4 ± 5,2% des scyphistomes produisaient des bourgeons), avec un pic de 12 800 bourgeons m^{-2}. En la production de bourgeons a déjà été montrée comme étant stimulée par les températures élevées et la disponibilité de la nourriture (Han et al. 2010; Schiariti et al. 2014; Hubot et al. 2017; Ikeda et al. 2017). Cependant, dans cette étude aucune des variables environnementales testées ne semble expliquer cette production. Néanmoins, seule une partie des proies potentielles des scyphistomes d'*A. coerulea* a été étudiée dans ce travail (*e.g.* l'abondance du mésozooplancton) et, une étude plus conséquente prenant en compte les fluctuations temporelles de toutes leurs sources de matière organique aurait dû être développée. Cela a été fait par la suite, dans la deuxième partie de cette étude (voir ci-après).

Dans Thau, le début de la strobilation d'*A. coerulea* semble être déclenché par une chute de la température de l'eau (de 8,3 ºC) entre octobre et novembre, comme suggéré précédemment

(Holst 2012). Par conséquent, la strobilation débute et atteint son point culminant en novembre (33,1 ± 4,2% des scyphistomes strobilaient) mais elle se poursuit jusqu'au début du printemps (avril). Ce résultat confirme la période d'occurrence des éphyrules dans la lagune précédemment rapportée (Bonnet et al. 2012; Marques et al. 2015a) ainsi que les périodes de strobilation décrites jusqu'à présent dans d'autres zones pour *Aurelia* spp. (*e.g.* Miyake et al. 2002; Uye and Shimauchi 2005; Hocevar et al. 2018). Cépendant, en supposant une période de strobilation continue entre novembre et avril, le nombre total d'éphyrules libérées était estimé à 82 301 ind m^{-2}. La production d'éphyrules au cours de l'année étudiée a présenté un pic bref mais remarquable en novembre (estimé à 19 100 disques m^{-2}), mais était également élevée en février (estimé à 11 800 disques m^{-2}). Le pic de production d'éphyrules de novembre a été limité par la faible densité de scyphistomes en cette saison. Par conséquent, l'ampleur des blooms d'*A. coerulea* dans Thau est limitée, non seulement par la mortalité des éphyrules pendant l'hiver (Fu et al. 2014), mais également par l'importante mortalité des scyphistomes au cours de l'été. Étant donné que les étés chauds et secs devraient être plus fréquents dans la région méditerranéenne au cours des prochaines décennies (Dubrovský et al. 2014), le changement climatique dans la région pourrait contribuer à une diminution de la taille des populations benthiques d'*A. coerulea* et donc à une diminution de l'intensité de la prolifération de cette méduse, du moins dans Thau. Cependant, des investigations complémentaires, basées sur des études à long terme, sont encore nécessaires pour corroborer cette hypothèse.

Écologie trophique des deux stades de vie d'A. coerulea (Article II)

Ce travail de thèse a permis de fournir la première étude portant sur l'écologie trophique des deux stades de vie (benthique et pélagique) d'une même espèce de méduse en association avec la dynamique de sa population *in situ*. Nos résultats sont en accord avec les rapports précédents décrivant les méduses d'*Aurelia* sp. comme des organismes zooplanctivores (*e.g.* Hansson 2006; Malej et al. 2007; Lo and Chen 2008). Plus de 88% des proies identifiées étaient du mésozooplancton, tandis que le microzooplancton et le phytoplancton (identifiés seulement en avril et en mai) ne représentaient que 8% et 4% respectivement. La composition du bol alimentaire reflétait largement la composition de la communauté de plancton dans l'environnement au moment de l'échantillonnage. En effet, des pics remarquables d'abondance de phytoplancton ont été observés en janvier et mai, de microzooplancton en février, avril et septembre et de mésozooplancton en juin. Cependant, l'analyse du contenu stomacal conduit souvent à une surestimation de l'importance trophique des proies avec un exosquelette 'dur' qui sont plus résistantes à la digestion, comme le mésozooplancton (Hyslop 1980). L'utilisation

des isotopes stables comme approche complémentaire a permis de révéler les sources de matiere organique véritablement utilisées pour la croissance de scyphistomes et des méduses d'*A. coerulea* au cours de l'année.

Des changements temporels de signatures isotopiques ont été observés pour les deux stades biologiques, révélant des changements dans leurs niches trophiques au cours de l'année. Malgré cela, les différences de signatures en carbone et azote entre les deux stades du cycle de vie d'*A. coerulea* n'étaient jamais significatives pendant la période de présence des méduses dans Thau. Trois périodes de stabilité des signatures isotopiques au cours de l'année (périodes de niche isotopique stable, INP), similaires pour les deux stades ont été identifiées : de décembre à avril (INP 1), de juin à août (INP 2) et de septembre à novembre (INP 3, pour les scyphistomes). Mai reflétait une période de transition rapide entre INP 1 et INP 2 et, par conséquent, n'a été inclus dans aucune INP.

Au cours de l'hiver et au début du printemps (INP 1), c'est-à-dire avant la prolifération des méduses d'*A. coerulea*, la matière organique particulaire (MOP, *i.e* l'ensemble du phyto- et du microzooplancton) était la principale source de nourriture des scyphistomes et des jeunes stades pélagiques d'*A. coerulea*. Ceci est particulièrement important car il s'agit d'une période critique pour la formation du bloom annuel. À cette période de l'année, l'abondance élevée du microzooplancton a probablement stimulé la production de bourgeons, augmentant la densité des scyphistomes dans la lagune et, finalement, leur production d'éphyrules (voir précédemment). Dans le même temps, la MOP a soutenu la survie et la croissance des jeunes stades pélagiques. En effet, même si les éphyrules n'ont été collectées qu'une seule fois au cours de la période d'étude (en janvier), elles montraient des valeurs de $\delta^{13}C$ et $\delta^{15}N$ similaires à celles des scyphistomes collectés au même moment, ce qui suggère qu'elles se nourrissent de la même source de nourriture. Un chevauchement intraspécifique des niches isotopiques a été observé pendant toute la période de cooccurrence des stades benthique et pélagique d'*A. coerulea* dans la lagune. Malgré cela, il est probable que compétition intraspécifique soit faible pendant l'INP1 en raison d'une disponibilité élevée de l'ensemble des proies consommées. Le contraire pourrait se produire pendant l'INP 2 (en juin-juillet), lorsque la niche trophique des méduses recouvre entièrement celles des scyphistomes. La compétition trophique intraspécifique pourrait ainsi contribuer à la baisse de densité de scyphistomes observée à cette époque de l'année. La matière organique sédimentaire et le mésozooplancton ont été identifiés comme des sources importantes de nourriture pour les deux stades de vie pendant l'INP 2, probablement à la suite de la remise en suspension des sédiments en mai et du pic d'abondance du mésozooplancton en juin. Au cours de la saison sèche suivante (de septembre à novembre),

la MOP redevient la principale source de matière organique pour les scyphistomes, probablement en raison de la forte abondance du microzooplancton, qui soutient le pic de reproduction asexuée observé en septembre et la strobilation en novembre, *i.e.* le début du prochain épisode de prolifération de méduses dans l'étang de Thau. Globalement, ces résultats montrent l'importance des contrôles trophiques de type « bottom-up » sur la formation de la prolifération annuelle d'*A. coerulea* dans la lagune de Thau.

En ce qui concerne la compétition trophique interspécifique, le chevauchement isotopique des niches trophiques entre les deux stades d'*A. coerulea* et les huîtres s'est révélé généralement limité, voir absent si l'on prend en compte la variabilité temporelle des signatures, (c'est-à-dire par INP). La compétition trophique faible entre les huitres et l'*A. coerulea* pourrait être liée à leurs mécanismes de filtration et de rétention des particules différents (Dubois et Colombo 2014). À la lumière des résultats obtenus, la prolifération des méduses d'*A. coerulea* pourrait même être avantageuse pour la production d'huîtres dans la lagune par un effet de cascade trophique qui pourrait *in fine* augmenter les biomasses de phytoplancton et de bactéries (Turk et al., 2008).

Le devenir de la matière organique

Introduction

Les études sur les méduses se concentrent depuis longtemps sur les facteurs responsables de la prolifération des méduses (*e.g.* Purcell 2012), tandis que les causes de leur mortalités des méduses et le devenir de la biomasse produite au cours de leurs proliférations sont encore mal connues (Purcell and Arai 2001; Pitt et al. 2009b, 2014). Ces informations sont toutefois fondamentales pour comprendre la dynamique des populations de méduses et les impacts potentiels de leurs blooms sur les écosystèmes et les activités humaines qui en dépendent.

Jusqu'à présent, les méduses étaient considérées comme des « impasses » dans les réseaux trophiques marins et, en raison de leur forte teneur en eau et de leur faible valeur nutritionnelle on ne leur connaissait que peu de prédateurs (Doyle et al. 2007). Cependant, ce paradigme a récemment été remis en question (Hays et al. 2018). Des techniques contemporaines ont permis d'identifier divers types de prédateurs de méduses, mais leur diversité est encore mal connue. Ceci est particulièrement évident en ce qui concerne la prédation sur les scyphistomes et les éphyrules, ce qui revêt une importance particulière en raison de leur effet potentiel sur la dynamique des populations de méduses (*e.g.* Ishii et al. 2004; Takao et al. 2014). Lorsqu'elles ne sont pas consommées par des prédateurs, les méduses

coulent rapidement sur le fond et causent d'importantes accumulations de biomasse dans les habitats benthiques (Lebrato et al. 2012). La dégradation des méduses mortes a des impacts potentiellement importants sur les cycles biogéochimiques et le fonctionnement des écosystèmes benthiques (*e.g.* Pitt et al. 2009; Sweetman et al. 2016).

Cette thèse a permis de mieux comprendre ces processus en étudiant la prédation des poissons sur les stades pélagiques et benthiques d'*A. coerulea* dans l'étang de Thau et la dégradation de ses méduses sur le fond de la lagune. Pour cela, les contenus stomacaux de différentes espèces de poissons d'importance commerciale ont été analysés par des techniques moléculaires afin d'identifier la présence d'ADN d'*A. coerulea* dans leurs tractus digestifs. Le devenir des méduses mortes sur le fond a été étudiée par différentes expériences *in situ* réalisées dans la lagune. Des carcasses de méduses ont été déposées sur le fond dans différents types d'habitats et leurs taux de décomposition ont été estimés. De plus, les modifications des communautés de macroorganismes benthiques ont été déterminées au fil du temps afin d'évaluer leur rôle potentiel dans le processus de recyclage de la biomasse produite par les proliférations de méduses.

Prédation des poissons sur A. coerulea (Article III)

La majorité des espèces de poissons d'intérêt commercial analysées dans cette étude (quatre sur cinq) ingèrent régulièrement des individus d'*A. coerulea*. Cela suggère que la diversité des poissons prédateurs de méduses a été jusqu'ici sous-estimée dans la lagune et que ces poissons pourraient jouer un rôle crucial dans le contrôle de la population locale d'*A. coerulea*. Pour certaines espèces, tous les individus testés possédaient de l'ADN d'*A. coerulea* dans leurs tractus digestifs, ce qui suggère que cette méduse pourrait être une source non négligeable de nourriture pour la croissance et la survie de ces bioressources exploitées dans la lagune. Parmi elles, les espèces les plus importantes sont l'anguille européenne et la dorade. Au cours de cette étude, toutes les anguilles testées ont montré des concentrations en ADN d'*A. coerulea* relativement élevées dans leur tube digestif. La consommation d'organismes gélatineux par les larves d'anguilles (leptocéphales) a déjà été rapportée (Riemann et al. 2010; Ayala et al. 2018) et il n'est donc pas étonnant que l'espèce conservent la capacité de se nourrir d'organismes gélatineux pendant le reste de sa vie. Il est possible que les anguilles aient mordu les ombrelles des méduses, profitant de la consistance molle de leur corps et de leur abondance élevée pendant les épisodes de proliférations. Des estimations théoriques révèlent qu'une méduse pourrait fournir suffisamment d'énergie pour maintenir le métabolisme standard d'une anguille pendant 51 jours. Même si une consommation importante de méduses est nécessaire

pour satisfaire ces besoins énergétiques (80,5% du poids d'anguille par jour), les taux rapides de digestion et de vidange des estomacs en cas de consommation de méduses (Arai et al. 2003) permettent aux poissons d'augmenter leurs taux d'ingestion. Ces résultats revêtent une grande importance, étant donné que l'anguille européenne est en danger de disparition et que les informations concernant son régime alimentaire sont encore limitées. La consommation d'*A. coerulea* au cours de ses proliférations a également été enregistrée pour la daurade avec, dans certains cas, une forte concentration d'ADN d'*A. coerulea* dans les tubes digestifs. Ce résultat n'est pas surprenant puisqu'il a été démontré en laboratoire que cette espèce peut consommer tous les stades de développement d'*A. coerulea* (Marques et al. 2016). L'ADN d'*A. coerulea* a également été détecté chez cette espèce lorsque ses stades pélagiques de la méduse étaient absents de la lagune, ce qui montre que des scyphistomes sont également ingérés par poissons dans Thau. En ce sens, la dorade royale pourrait être un important consommateur de scyphistomes d'*A. coerulea* et contrôle leur dynamique de population, mais par ingestion indirecte. En effet, les bivalves sont des proies préférentielles des daurades adultes (Pita et al. 2002; Tancioni et al. 2003; Russo et al. 2007). Ils sont très abondants dans la lagune de Thau et régulièrement recouverts par les polypes d'*A. coerulea* (Marques et al. 2015b). Ainsi, la consommation des scyphistomes de l'espèce *in situ* résulte probablement d'une ingestion non volontaire lorsque les daurades se nourrissent de bivalves. Ces résultats mettent en évidence l'impact probablement sous-estimé de la prédation de daurades sur la régulation de la densité de scyphistomes dans la lagune, qui pourrait expliquer la réduction de leurs densités en été et en automne, lorsque que la demande énergétique de l'espèce et son alimentation en lagune sont le plus intenses.

Dégradation des méduses mortes (Article IV)

Si les méduses présentes dans la colonne d'eau ne sont pas consommées de leur vivant, elles coulent sur le fond de la lagune lorsqu'elles meurent. La rareté des amas de méduses mortes sur les fonds de la lagune de Thau suggérait la consommation rapide des carcasses par les des prédateurs benthiques. Cependant, cela n'a pas été vérifié u cours de cette thèse. La dégradation *in situ* des méduses dans la lagune a été très rapide (99% de la biomasse des méduses ayant été reminéralisée en 1 à 6 jours), généralement plus rapidement que les valeurs indiquées pour d'autres sites ou espèces (*e.g*. Lebrato et al. 2011). On sait que les taux de décomposition varient en fonction des espèces de méduses, de leur taille, de la température ambiante et du type et de la composition des assemblages bactériens (Titelman et al. 2006; Lebrato et al. 2011, 2012). Dans Thau, l'effondrement de la prolifération d'*A. coerulea* coïncide

avec le pic des températures estivales (> 23 ºC), ce qui pourrait accélérer leur dégradation. De plus, les méduses d'*A. coerulea.* sont généralement plus petites dans la lagune de Thau (e.g. (Pitt 2000; Fuentes et al. 2011; Prieto et al. 2013) et leurs tissus sont très labiles (Jane et al. 2009; Pitt et al. 2009b), ce qui explique les résultats obtenus. De ce fait, la contribution des consommateurs benthiques à reminéralisation des méduses est probablement limitée dans Thau. Une seule espèce (*Tritia* sp., famille des Nassariidae) a montré une réponse significative à la présence de méduses mortes sur le fond marin au cours de notre étude. Bien que ces gastéropodes puissent consommer de grandes quantités de matière organique en peu de temps (Morton 2011), la disparition rapide des méduses sur le fond est probablement principalement le résultat d'une forte dégradation microbienne. Néanmoins, certains macroorganismes benthiques pourraient profiter de manière opportuniste de l'effondrement des blooms, par une augmentation de la disponibilité de nourriture directe (méduses) ou indirecte (microorganismes se nourrissant de méduses). Au final, le devenir des proliférations d'*A. coerulea* dans la lagune de Thau semble donc essentiellement reposer sur leur consommation par les poissons pélagiques ou sur la dégradation microbienne des méduses mortes, avec ou sans l'aide d'organismes benthiques opportunistes. L'omniprésence d'ADN d'*A. coerulea* dans les tractus digestifs de poissons de forte importance commerciale dans la lagune souligne les implications des blooms pour l'écologie des poissons et des méduses et pour les activités économiques locales. D'une part, la prédation directe sur les méduses ou la prédation indirecte sur les polypes pourrait contribuer à contrôler les épisodes de prolifération. D'autre part, la disponibilité et l'accessibilité des méduses pendant les épisodes de prolifération constituent une source de nourriture alternative pour les populations de poissons. De même, la dégradation rapide de la prolifération de méduses par la communauté microbienne pourrait avoir des impacts significatifs sur les cycles biogéochimiques dans la lagune, ainsi que ses réseaux trophiques. Il est donc urgent d'inclure l'ensemble des processus liés à la consommation et à la dégradation des méduses dans les modèles trophiques et biogéochimiques dans Thau et ailleurs.

Conclusion

Ce travail de thèse a mis en évidence l'interaction complexe de paramètres biotiques et abiotiques dans le contrôle de la dynamique des populations benthiques et pélagiques d'*A. coerulea*. Au-delà de la disponibilité d'habitat benthiques favorables pour la fixation des scyphistomes, la température, la salinité, la disponibilité de nourriture et la prédation semblent être les principaux processus écologiques contrôlant l'intensité des proliférations d'*A. coerulea*. Compte tenu de l'ensemble du cycle de vie d'*A. coerulea* dans la lagune, il a été possible

d'identifier deux périodes favorables et deux périodes défavorables à la dynamique des méduses. Les saisons favorables sont le début du printemps, en raison de la production de bourgeons favorisée par une disponibilité élevée en microzooplancton, et la fin d'automne, lors du passage du stade de bourgeonnement à celui de strobilation qui conduit à la libération d'une abondance élevée d'éphyrules dans la lagune. Les saisons défavorables sont l'été, en raison de la mortalité des scyphistomes, probablement due à une température et une salinité élevées, ainsi qu'à une prédation indirecte élevée par les poissons, et l'hiver, en raison de la mortalité des éphyrules, liée au faibles températures dans la lagune. Ces résultats fournissent quelques indices sur les conséquences potentielles du changement climatique sur le développement des proliférations d'*A. coerulea* dans l'étang de Thau et peut-être ailleurs. Cependant, en raison de la complexité de leur cycle de vie, ces organismes pourraient être en mesure de s'adapter à différentes conditions environnementales. L'impact du changement climatique sur leurs dynamiques de population reste donc à préciser.

Indépendamment de la réponse finale des populations d'*A. coerulea* au changement climatique prévu, la persistance ou l'augmentation possible de l'ampleur de leurs proliférations pourrait avoir des incidences écologiques importantes sur le fonctionnement de l'écosystème de la lagune. Pour la matière organique produite au cours des blooms, deux principaux devenirs ont peut être démontrés. Les méduses sont d'abord consommées par les prédateurs pélagiques, tels que les poissons. Cependant, lorsqu'elles meurent, elles peuvent également sédimenter et être principalement reminéralisées par la communauté microbienne. Cela a des impacts à la fois positifs et négatifs sur le fonctionnement de l'écosystème de la lagune de Thau. Par exemple, les méduses pourraient constituer une source non négligeable de nourriture pour les poissons locaux, contribuant potentiellement à la survie de leurs jeunes stades et à la productivité des pêcheries locales. En outre, la prédation des méduses sur le méso- et le microzooplancton pourrait augmenter l'abondance in situ du phytoplancton (Turk et al. 2008) ce qui pourrait, au moins périodiquement, avoir un impact bénéfique pour la conchyliculture dans la lagune. La dégradation microbienne des méduses mortes pourrait quant à elle avoir un impact négatif sur le fonctionnement de l'écosystème en réduisant les teneurs en oxygène dissous et en contribuant aux crises anoxiques estivales qui se produisent sur Thau.

Dans l'ensemble, bien que nous ayons obtenu dans cette thèse des informations sur les facteurs induisant les épisodes de proliférations d'*A. coerulea* à Thau ainsi que sur leur devenir, il conviendrait de poursuivre les recherches à l'aide de modèles afin de prévoir avec précision l'ampleur des proliférations d'*A. coerulea* et leurs conséquences sur le fonctionnement de l'écosystème.

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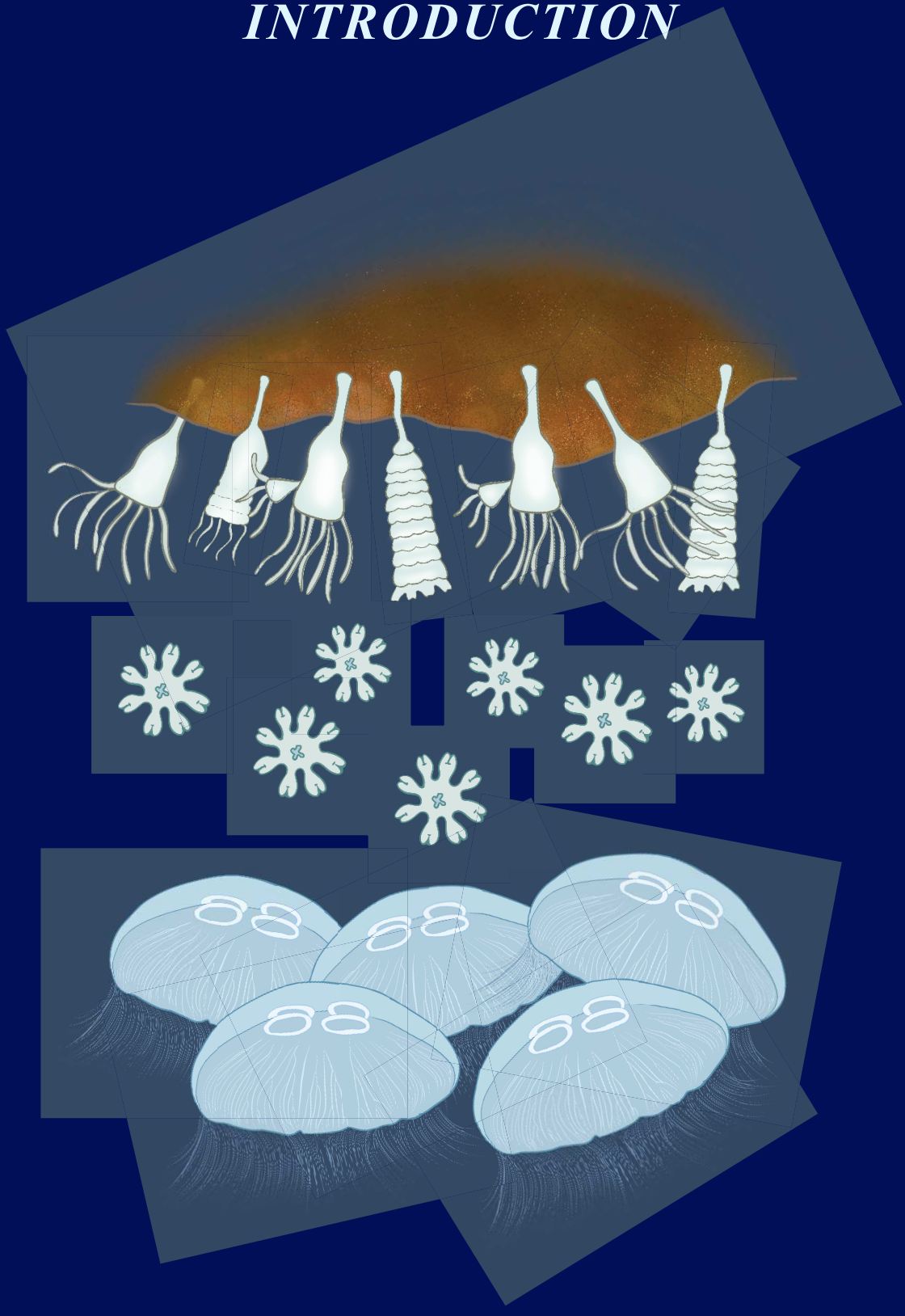
Paper II: Trophic ecology of the jellyfish *Aurelia coerulea* in a Mediterranean coastal lagoon (*in prep*) Marques R, Bonnet D, Roques C, Carré C, Darnaude AM

Paper III: Molecular approach indicates consumption of jellyfish by commercially important fish species in a coastal Mediterranean lagoon **(2019)** Marques R, Darnaude AM, Crochemore S, Bouvier C, Bonnet D. *Marine Environmental Research.* Doi: https://doi.org/10.1016/j.marenvres.2019.104787

Paper IV: Jellyfish degradation in a shallow coastal Mediterranean lagoon (*in prep*) Marques R, Rufino M, Darnaude AM, Carcaillet F, Meffre M, Bonnet D.

CHAPTER 1. GENERAL INTRODUCTION



1.1 JELLYFISH: WHAT ARE THEY?

The term "Jellyfish" is often imprecise. This term is a popular term describing what many authors call gelatinous zooplankton, a group of pelagic animals that share the characteristic of being composed mainly by water, which gives them a typical gelatinous appearance (Boero 2013). In fact, the gelatinous zooplankton comprises organisms that belong to very different phyla, such as Cnidaria, Ctenophora and some classes of the subphylum Tunicata (Boero 2013; Schiariti et al. 2018). Therefore, the term "jellyfish" has been used differently in the literature, often referring to specific components of the gelatinous zooplankton (*e.g.* Richardson et al. 2009; Purcell 2012; Boero 2013; Schiariti et al. 2018). This is the case in this thesis, where "jellyfish" will be used to refer to the group of medusozoan cnidarians (*i.e.* Scyphozoa, Hydrozoa and Cubozoa, Schiariti et al. 2018) with a special emphasis on the Scyphozoans (considered as the "true jellyfish", Lucas and Dawson, 2014), since *Aurelia coerulea* belongs to this class.

The life cycle of jellyfish is often complex and varies among species, even within the medusozoan group (Schiariti et al. 2018). The life cycle of most scyphozoan species though comprises four successive life stages (Fig. 1): a benthic one (called scyphistomae or polyps), and three pelagic ones (the ephyrae, the medusae and the planulae).

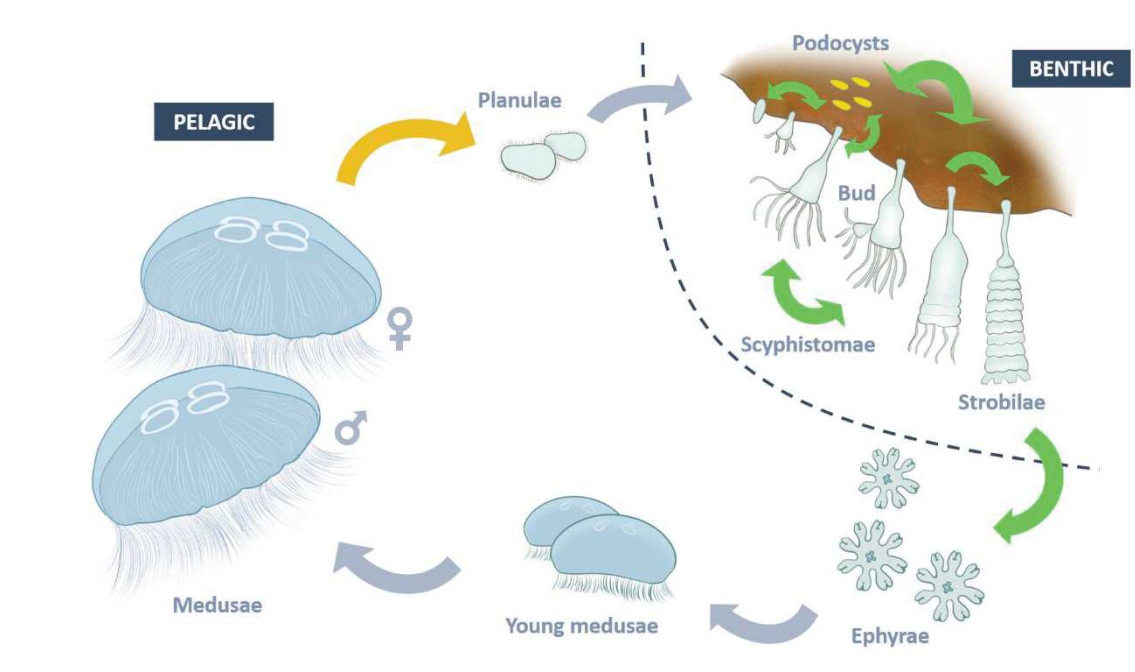


Fig. 1 Jellyfish life cycle (example of *Aurelia coerulea*). Arrows indicate the sense of life cycle development. The yellow and green arrows indicate sexual and asexual reproduction, respectively. Drawings by Justine Courboulès.

After the sexual reproduction, the female medusae release ciliate larvae called planulae (Fig. 2 A), which settle on hard benthic substrates and metamorphose into scyphistomae (Fig. 2 B-C). Each scyphistoma is capable to reproduce asexually thereby regulating the density of the benthic population (Lucas 2001; Lucas et al. 2012). Different species appear to use different asexual reproduction strategies (Schiariti et al. 2014), but the most common are typical lateral budding (Fig. 2 B, a), lateral budding by means of stolons and podocysts (Fig. 2 B, b). Under specific environmental conditions, large numbers of ephyrae are released by the scyphistomae, through a process called strobilation (Fig. 2 C). The ephyrae (Fig. 2 D) grow into medusae (*i.e.* the adult stage, Fig. 2 E), which, after sexual reproduction, releases new planulae, closing the life-cycle. The medusa stage is frequently short-lived, remaining in the water column for a few weeks or months, after which they rapidly disappear. Concurrent factors may lead to medusae mortality, among which food limitation, physiological stress, post-spawning mortality and predation are possibly the most common (Pitt et al. 2014).

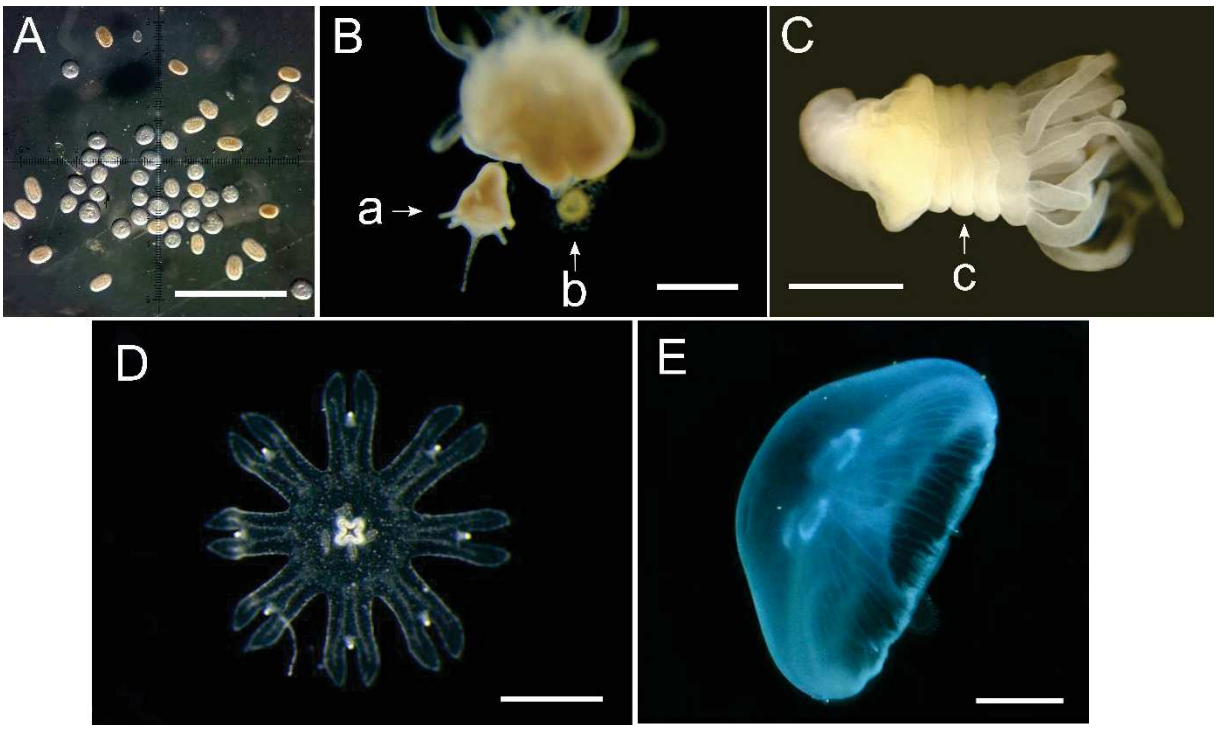


Fig. 2 The different stages of *A. coerulea* life cycle. A) planulae, B) scyphistomae, producing one bud (a) and one podocyst (b), C) strobila and its strobila disks (c), D) ephyrae and E) medusae. All white bars represent 1 mm, except in E where it represents 1 cm. Photographs taken by Raquel Marques.

This alternation between the planktonic and benthic stages, complicates the definition of the term "population" for jellyfish (Schiariti et al. 2018). Depending on the author, we might consider the existence of one (the organisms of the same species coexisting in a given area) or two populations of jellyfish (two life stages that inhabit different habitats). In this thesis, we

will consider the existence of two populations (benthic and pelagic), bearing in mind though, that the pelagic population is not self-sustaining, which is a condition that determines a population (Schiariti et al. 2018).

1.2 WHY SHOULD WE CARE?

Jellyfish are known for their sudden and dense aggregations, *i.e.* rapid increase in their abundance and biomass, referred to as *blooms* (Boero et al. 2008). Impressive blooms may exceed 10 tons of wet weight per 100 m^{-3} (Lilley et al. 2011) and increasing indications of the human-mediated stimulation of jellyfish blooms is promoting a rising concern related to the potential expansion of these outbreaks in the future. Indeed, many studies advocate that gelatinous organisms benefit from human-induced changes in aquatic ecosystems (Mills 1995, 2001; Arai 2001; Purcell et al. 2007; Pauly et al. 2009; Richardson et al. 2009; Purcell 2012; Boero 2013). Moreover, it was suggested that the frequency and magnitude of jellyfish blooms is currently increasing at least in some parts of the world (*e.g.* Brodeur et al. 1999; Lynam et al. 2006; Attrill et al. 2010; Brotz et al. 2012) which has led to a paradigm in which scientists predict a rise of gelatinous zooplankton in the world's oceans, due to the increasing impacts of climate change and anthropogenic pressures on the marine environment. This recent paradigm has been questioned though, due to a possible misinterpretation of the scientific findings (Sanz-Martín et al. 2016; Pitt et al. 2018) as systematic, long time monitoring data on jellyfish populations are sparse or non-existing (Condon et al. 2012, 2013). Still, since ongoing changes in the marine environment are expected to continue, the hypothesis of recurrent and greater jellyfish blooms in the future cannot be excluded (Purcell et al. 2007; Pauly et al. 2009; Richardson et al. 2009; Purcell 2012). This urgently calls for increasing research and monitoring efforts on jellyfish populations.

Jellyfish blooms interfere, directly or indirectly, with several human activities (*e.g.* Purcell et al. 2007; Richardson et al. 2009; Purcell 2012) and can have a great impact on ecosystem functioning (*e.g.* Pitt et al. 2009a; Richardson et al. 2009), with both negative and positive consequences regarding ecosystem services (*e.g.* Doyle et al. 2014; Graham et al. 2014).

On the negative side, jellyfish blooms can induce significant shifts in ecosystems structure and functioning (Fig. 3). Their predation, by diminishing particular components of the plankton community, might drive trophic cascades affecting the abundance of lower trophic levels and modifying energy transfer pathways within food webs (Pitt et al. 2007; Pauly et al.

2009; Robinson et al. 2014; Ramirez-Romero et al. 2018). In addition, the large accumulation of medusae and the typical subsequent collapse of their blooms might influence local biogeochemical cycles. Indeed, the significant amounts of organic and inorganic matter released in the environment surrounding jellyfish blooms (either by medusa excretion and mucus production or during dead jellyfish degradation) modify the productivity and composition of primary producer communities (Hansson and Norrman 1995; Pitt et al. 2009b; Sweetman et al. 2016). Moreover, when concentrations of dead jellyfish on the seabed are high, the organic matter decomposition might lead to localized hypoxic or anoxic conditions, with potentially drastic impacts on the benthic communities (Jane et al. 2009; Pitt et al. 2009b; Chelsky et al. 2016).

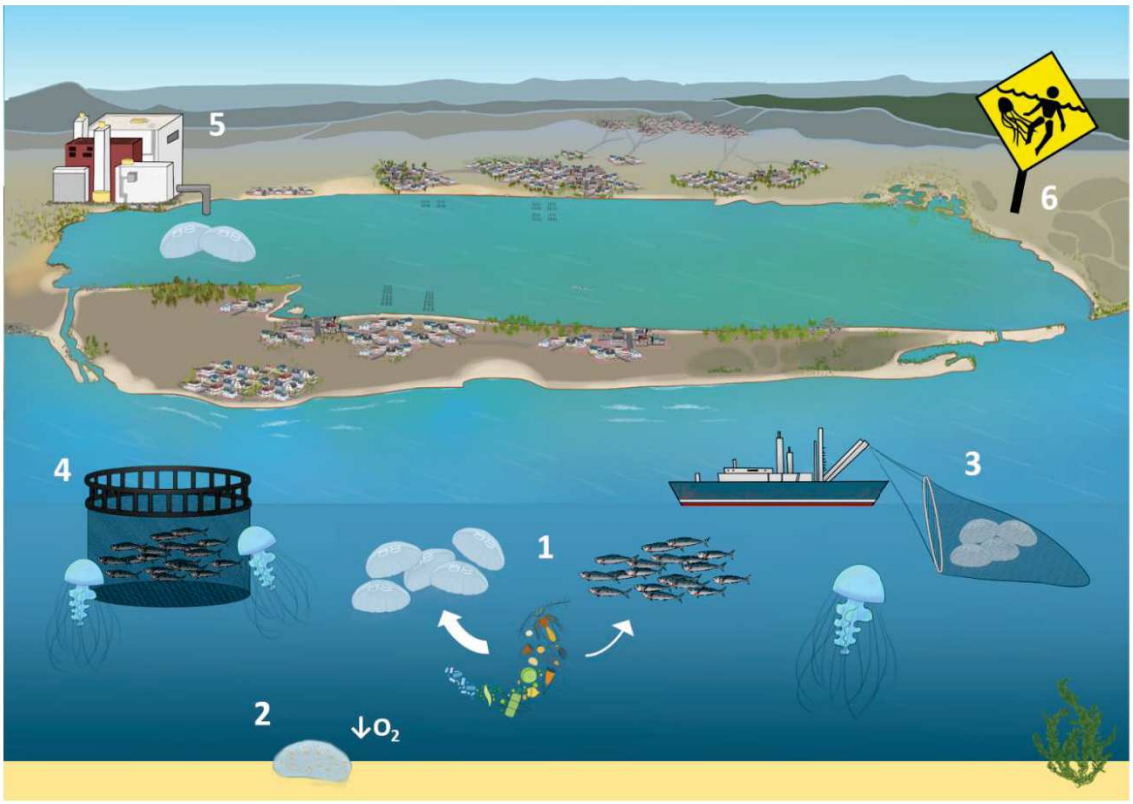


Fig. 3: Examples of the negative impacts of jellyfish blooms on the ecosystem functioning and ecosystem services. 1) reduction of food availability for zooplanktivorous fish, 2) decrease of dissolved oxygen during medusae degradation, 3) reduce fishing landings and damage of fishing gears, 4) mortality and/or illness of aquaculture products, 5) clogging coastal industry facilities, 6) reduce the attractiveness of touristic areas. Drawings by Justine Courboulès.

Among the human activities affected by jellyfish blooms, fishing is probably the most impacted one. Jellyfish may be simultaneously competitors of commercially important fish species and predators of their eggs and larvae, ultimately reducing fish stocks and landings (*e.g.* (Purcell and Arai 2001; Purcell and Sturdevant 2001; Brodeur et al. 2002; Hansson et al. 2005; Purcell et al. 2007; Graham et al. 2014). In addition, the local aggregation of jellyfish can

directly impact fishing and extensive aquaculture activities, by clogging or destructing nets, reducing the quality of catches or aquaculture products and even, occasionally, leading to the interdiction of fishing or production (reviewed by Purcell et al. 2007; Graham et al. 2014). Economic losses on the fishing activity due to jellyfish blooms may be up to $300 million (Uye 2011). Like fishing gears, cooling systems of power plants and industrial factories are also clogged by large aggregations of jellyfish (Dong et al. 2010), causing elevated economic losses all over the world (reviewed by Purcell et al. 2007; Graham et al. 2014). Finally, for numerous countries in the world, tourism is among the primary sources of income. Therefore, jellyfish blooms can have severe impacts on worldwide economy as episodes of jellyfish stings might raise healthcare issues, increase costs for warning and protection systems and cause indirect economical losses by the reduction of attractiveness of touristic coastal areas (Gershwin et al. 2010; Boero 2013). As human interactions with coastal ecosystems continue to increase, in parallel with possible intensification of jellyfish blooms, the negative impacts of these latter are expected to expand.

On the positive side though, jellyfish also provide a variety of ecosystem services (Doyle et al. 2014; Graham et al. 2014, Fig. 4).

Fig. 4: Examples of positive impacts of jellyfish blooms on the ecosystem functioning and ecosystem services: 1) contribution to carbon sequestration, 2) source of inorganic nutrients for phytoplankton and bacterial production, 3) source of food for various predators, 4) refugia for several organisms, 5) support jellyfish fishing industry, 6)

source of compounds used in biotechnology, medicine, pharmacy and cosmetics, 7) attractions in public aquariums, 8) food for humans. Drawings by Justine Courboulès.

First, they contribute to climate regulation through carbon sequestration (Doyle et al. 2014). Indeed, the sinking of large quantities of jellyfish biomass after the collapse of their blooms (*e.g.* Billett et al. 2006; Yamamoto et al. 2008; Lebrato et al. 2013) play an important role in the transfer of carbon from the surface waters to the seabed (Lebrato et al. 2012), by increasing the efficiency of carbon vertical transport, in comparison with the sinking of small-sized phytoplankton cells (Doyle et al. 2014; Graham et al. 2014). Second, jellyfish support some important ecosystem functioning processes (Doyle et al. 2014). Indeed, the products generated by their excretion, their mucus production and their degradation are all released in the water column. This provides inorganic nutrients (C, N and P) essential for both phytoplanktonic and bacterial productions (Pitt et al. 2009b), which can be determinant in particular locations or periods of nutrient limitation. Moreover, due to their frequent large dimensions, jellyfish often act as a pelagic refuge for juvenile fish, providing them with food (the fish might feed directly on the jellyfish, indirectly on their parasites, food remains or benefit from higher prey encounters) and shelter from predators (Purcell and Arai 2001; Lynam and Brierley 2007; Masuda 2009). Moreover, although jellyfish have long been considered as dead ends in aquatic food webs, due to their low nutritional value and high water content (Doyle et al. 2007), recent studies based on new techniques (*e.g.* stable isotopes, molecular approaches, animal-borne cameras) prompted a paradigm shift in their trophic importance (Hays et al. 2018). They are now recognised as a valuable source of organic matter for a large diversity of organisms (*e.g.* Ates 2017) and even for commercially exploited species (*e.g.* Cardona et al. 2012; Dunlop et al. 2017; Ayala et al. 2018). Thirdly, jellyfish might provide important provisioning services for humans (Doyle et al. 2014). They have been eaten in China for more than a thousand years and are very important in the gastronomy of other Asiatic countries (Hsieh et al. 2001; Omori and Nakano 2016). In addition, jellyfish can also provide a variety of molecules for multiple uses in biotechnology, medicine, pharmacy and cosmetics (Doyle et al. 2014). For instance, the jellyfish *Aequorea victoria* is responsible for the discovery and isolation of the Green Fluorescent Protein (GFP), which is now widely used in medicine and biotechnology (Zimmer 2009). This has led to a Nobel Prize in Chemistry award in 2008. The development of new ecological products based on jellyfish bioproducts, such as biodegradable tissues, fertilizers or feed for farmed animals, (among many other), are currently under research (see Brotz et al. 2017). As a result, the commercial demand for jellyfish products supports a growing global fishing industry with an estimated harvest of 420 918 metric tons in 2011, exceeding that of some commercially important species (Graham et al. 2014; Brotz et al. 2017).

Finally, jellyfish also provide important cultural services. For instance, in some places around the world, wild jellyfish are not viewed as threats, but instead, they can be a main touristic attraction supporting large local economic incomes, such as in Palau during the 90s (Dawson et al. 2001). Likewise, because of the beauty and peacefulness of their swim and the diversity in their colours and shapes, jellyfish are focal attractions in public aquariums and sustain the growing commercial sectors of ornamental aquariums and jellyfish pets (Doyle et al. 2014).

Under the potential scenario of jellyfish blooms intensification in the coming decades, the increase in value of their ecosystem services will be likely slower than that of the costs linked to their negative impacts (Graham et al. 2014). Irrespective of this, comprehensive studies on the drivers and fates of jellyfish blooms are urgently needed if we want to anticipate their ecological and economic consequences.

1.3 POSSIBLE DRIVERS OF JELLYFISH BLOOMS

The possible global intensification of jellyfish blooms apparently has multiple drivers, ranging from climate change and overfishing to habitat modification (Purcell et al. 2007; Richardson et al. 2009; Purcell 2012; Boero 2013).

Climate change has been claimed as one of the most important triggers of intense jellyfish blooms (Purcell, 2005). Higher temperatures, drier conditions and lower wind stress appears to amplify the magnitude and frequency of jellyfish outbreaks around the world (Molinero et al., 2005, 2009; Kogovšek et al., 2010; Licandro et al., 2010; Lynam et al., 2011), by direct effects on their population dynamics or indirect effects on ecosystem functioning. Temperature is one of the most important factors affecting jellyfish benthic stages as high temperatures and food availability conditions seem to boost scyphistomae asexual reproduction, in particular the production of buds (Han and Uye 2010; Lucas et al. 2012; Purcell 2012; Widmer et al. 2016; Hubot et al. 2017). However, this effect varies among species and populations, depending on jellyfish geographical distribution (Lucas et al. 2012). Climate change might also indirectly amplify jellyfish blooms by inducing shifts in the structure of zooplankton communities, through the dominance of small-sized zooplankton species, which favors gelatinous populations and simultaneously impair their competitors, *i.e.* the zooplanktivorous fishes (Molinero et al. 2005, 2009; Lynam et al. 2011; Reygondeau et al. 2015). However, among the *ca.* 3700 species of pelagic cnidarians (Daly et al. 2007) the responses may not be equal within and among species and further research at local/regional and global scales is required.

Overfishing has also been pointed out as a major driver of jellyfish blooms as it may positively affect jellyfish populations in two ways: by removing their predators, and by removing their competitors (Purcell et al. 2007; Richardson et al. 2009; Purcell 2012; Boero 2013). The role of fish predation in the regulation of jellyfish populations has been suggested (e.g. Pauly et al. 2009; Hays et al. 2018), but is still overlooked. Yet, the removal of fish by commercial exploitation might lead to increases in the abundance of jellyfish, by releasing them from predation pressure (Pauly et al. 2009). At the same time, the removal of their competitors, by fishing the stocks of zooplanktivorous fish species, likely opens an ecological niche, providing high food availability and promoting jellyfish blooms (Robinson et al. 2014). Indeed, the diet overlap of jellyfish and zooplanktivorous fish, co-occurring in the same area, have often been reported, stressing the potentially high level of trophic competition between them in some places around the world (*e.g.* Purcell & Sturdevant, 2001; Brodeur et al., 2002). Moreover, jellyfish outbreaks frequently occur after the collapse of local fish stocks (*e.g.* Shiganova, 1998; Daskalov, 2002; Lynam et al., 2006; Daskalov et al., 2007). Finally, since jellyfish may also prey on their own trophic competitors, by eating their eggs and larvae (Purcell 1985; Purcell et al. 1987; Hansson et al. 2005; Gordoa et al. 2013), the impact of jellyfish blooms on fish stocks might be accentuated, dropping the resilience of the already fragile fish stocks (Boero 2013).

Another important driver of the observed increases in the magnitude and geographical distributions of jellyfish outbreaks seems to be the expansion of human-made infrastructures in the coastal landscape. Indeed, the artificial infrastructures added in the water (e.g. breakwaters, jetties, seawalls, floating devices) provide suitable substrates for jellyfish planulae settlement and scyphistoma development, promoting their proliferation and ultimately boosting pelagic jellyfish abundances (Purcell et al. 2007; Duarte et al. 2012; Purcell 2012; Boero 2013; Gibbons and Richardson 2013). Thus, human-mediated changes of the marine ecosystem appear to have been crucial in the development of local jellyfish populations in various places (*e.g.* Makabe et al. 2014; Marques et al. 2015b; Dong et al. 2018a; b).

Eutrophication is also considered to promote jellyfish populations through rising food availability (Arai 2001; Purcell et al. 2007; Purcell 2012). The simplest and direct consequence of nutrients enrichment in coastal ecosystems is the enhancement of primary production (Nixon et al. 1995). However, eutrophication also results in food web changes, with usually observed shifts from large diatom-based pathways to small flagellate-based ones (Purcell et al. 2007). This type of phytoplankton community composition, may offer an inter-specific competitive advantage for jellyfish, since, unlike other organisms, they are capable of feeding on wide range of prey, from particulate organic matter to mesozooplankton (Bamstedt et al. 2001; Hansson

2006; Kamiyama 2011; McNamara et al. 2013; Morais et al. 2015). Eutrophication is also commonly associated with depleted oxygen levels, which are lethal to numerous organisms. However, jellyfish are tolerant to low oxygen concentrations (Purcell and Arai 2001; Purcell et al. 2001) and even capable of asexual reproduction under such conditions (Condon et al. 2001). With the possible expansion of eutrophic and hypoxic zones, as a consequence of human impacts (Diaz and Rosenberg 2008), it is likely that habitats suitable for jellyfish dominance will increase.

Finally, the introduction of jellyfish species in a new recipient environment might, in particular cases, boost the size of their populations. Their physiological, ecological and life-history traits (*i.e.* rapid growth, asexual propagation, intensive predation impact and morphological plasticity) make them perfectly suited as invasive organisms (Graham and Bayha 2008). If introduced in an already impacted environment, they might profit from the modified ecosystem conditions (for instance caused by overfishing and eutrophication) and proliferate, as observed for the ctenophore *Mnemiopsis leidyi* introduced in the Black Sea (e.g. Gucu 2002).

Addressing the real cause of jellyfish outbreaks is intricate, though. Interactions between gelatinous organisms and climate, overfishing, eutrophication, habitat modification and introduction of alien species are extremely problematical and predictions are difficult to make. Human impact on marine ecosystems is highly concentrated in coastal areas where those different parameters interfere with each other and may influence jellyfish ecology in a synergetic way (Arai 2001; Purcell et al. 2007; Purcell 2012). Moreover, our general lack of knowledge at the basic level, *i.e.* on the environmental drivers affecting species-specific jellyfish population dynamics, hampers the formulation of sustained conclusions.

1.4 CASE STUDY: *AURELIA COERULEA* IN THE THAU LAGOON

One of the big challenges in jellyfish research is the assessment of the concurrent environmental processes forcing the benthic and pelagic populations. This is mainly due to the typical obscured habitats of scyphistomae and/or to dispersion processes that physically disconnect the two life stages. This hampers comprehensive studies embracing all the processes affecting each and every stage of the jellyfish life cycle and the understating of the main drivers of jellyfish blooms. Furthermore, these blooms, often collapse rapidly sinking to the seabed, where large accumulations of dead medusae might have severe impacts on the benthic food webs and biogeochemical cycles. This study benefited from the rare opportunity provided by

the Thau lagoon to study the ecology and population dynamics of both the benthic scyphistomae and the pelagic medusae of the jellyfish *Aurelia coerulea* within this semi-enclosed coastal ecosystem. Indeed, Thau can be considered as a 'large scale mesocosm', due to its high level of confinement, which allows studying the complex ecosystem processes interacting with the population of *A. coerulea*. The presence of this jellyfish in the Thau lagoon is, therefore, a case study that might be used as a model to understand the development of the blooms, its impacts and provide primary information for other *Aurelia* spp. populations or for other jellyfish species.

1.4.1. *Aurelia* species in the world

A large number of jellyfish blooms in coastal areas are performed by scyphozoan species of the genus *Aurelia* (Mills 2001). *Aurelia* spp. inhabits nearshore waters, especially semi-enclosed basins, and occupy a great variety of habitats worldwide, such as coastal embayments, fjords and estuaries (Lucas 2001). For a long time, *Aurelia aurita*, the most studied jellyfish species, was considered as cosmopolitan, capable of local adaptation due to its phenotypic plasticity (Lucas 2001). However, recent studies have addressed the biogeography of the genus *Aurelia* and reported that is actually a species-complex embracing numerous locally adapted species (Dawson and Jacobs 2001; Dawson and Martin 2001; Schroth et al. 2002; Dawson 2003; Dawson et al. 2005; Ki et al. 2008), even within the Mediterranean area (Scorrano et al. 2016). The *Aurelia coerulea* (Fig. 5) used as the biological model in this study is distributed in many different places around the world, including Japan, China, California (USA), Australia, France and Italy (Dawson et al. 2005; Scorrano et al. 2016) and therefore, under a variety of climate regimes and site-specific environmental pressures.

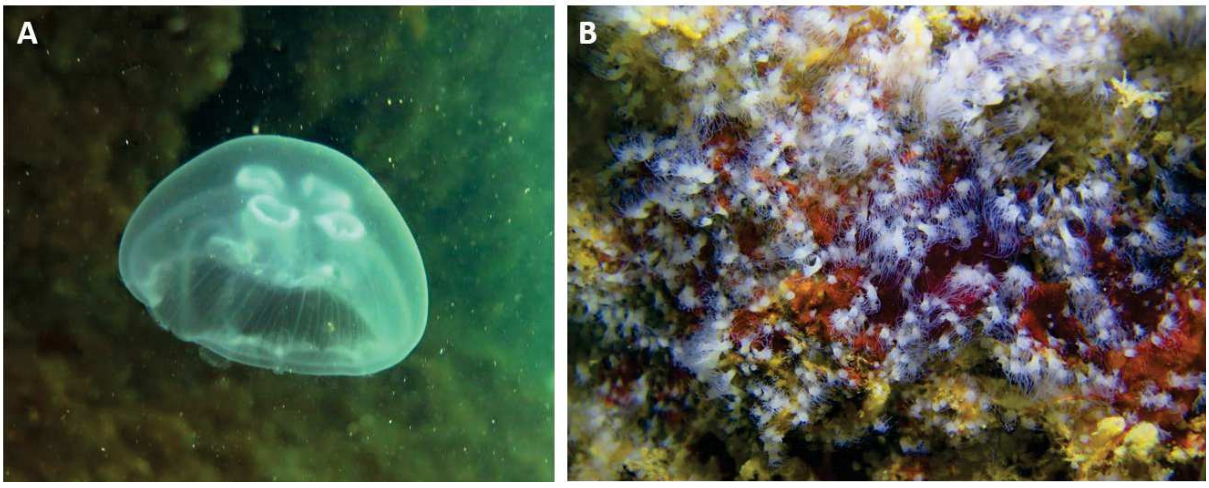


Fig. 5: *Aurelia coerulea* medusae (A) and scyphistomae (B). Photographs were taken in the Thau lagoon by Raquel Marques.

1.4.2. *Aurelia coerulea* in the Thau lagoon

The Thau lagoon is a semi-enclosed, marine coastal lagoon (43°23'59.10'' N 3°36'37.15'' E) which covers an area of 75 km^2 and is connected to the Mediterranean Sea by three narrow channels (Fig. 6). It is relatively shallow, with mean and maximum depths of 4 and 10 m, respectively (with the exception of a localized depression of 24 m). This lagoon has a weak tidal range (< 1m), which promotes a high residence time of water masses (1-4 months), and is highly influenced by seasonal strong wind events (Millet and Cecchi 1992; Fiandrino et al. 2012). The catchment area of the lagoon (290 km^2, Plus et al. 2006) is drained by small intermittent rivers that dry out between May and September and show occasional flush floods during the wet season (Tournoud et al. 2006). As a result, marine conditions prevail in the lagoon. Temperatures and salinities are lower in the winter (minimum of 5 and 32, respectively) and high in the summer (maximum of 27 ºC and 41, respectively; Marques et al. 2015a). Thau lagoon is under heavy human pressure, due to the vicinity of the touristic city of Sète, and to the many villages and agriculture fields that surround it. Tourism is an important economic activity in, on and around the lagoon, but the main source of income derived from Thau is shellfish farming (Mongruel et al. 2013). Shellfish farms cover around 20% of the lagoon surface area, mainly in its northern and north-western parts (Fig. 6), and are amongst the main suppliers of the Pacific Oyster *Crassostrea gigas* in France, representing around 10% of the national production (Pernet et al. 2012a).

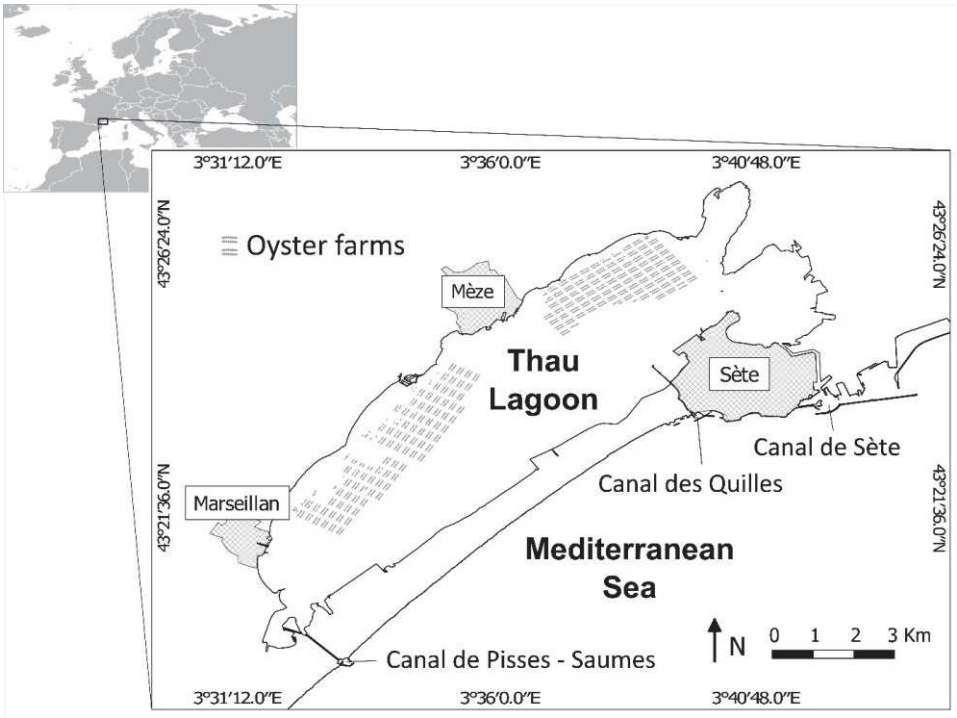


Fig. 6: Map of the Thau lagoon. Shaded areas represent urban areas and grey points represent oyster farms.

The Thau lagoon presents the rare particularity to harbor a complete resident population of *Aurelia coerulea* (Bonnet et al. 2012; Marques et al. 2015b). Molecular analysis of both the scyphistomae and medusae stages confirmed the presence of this species in the Thau lagoon (this study). Although Thau is connected to the sea, there is no advection of this species from and to the Mediterranean Sea (Bonnet et al. 2012), which implies that all stages of its life-cycle are produced, remain and ultimately die within the lagoon. The Thau lagoon thus offers an exceptional framework to understand the possible drivers and fates of the blooms of the jellyfish *A. coerulea* and to provide new insights on the potential processes that regulate jellyfish populations.

A. coerulea benthic polyps (scyphistomae) are widespread in the lagoon, usually forming aggregations (hereafter called "sub-populations") on the underside surface of hard substrates (Marques et al. 2015b, Fig. 7).

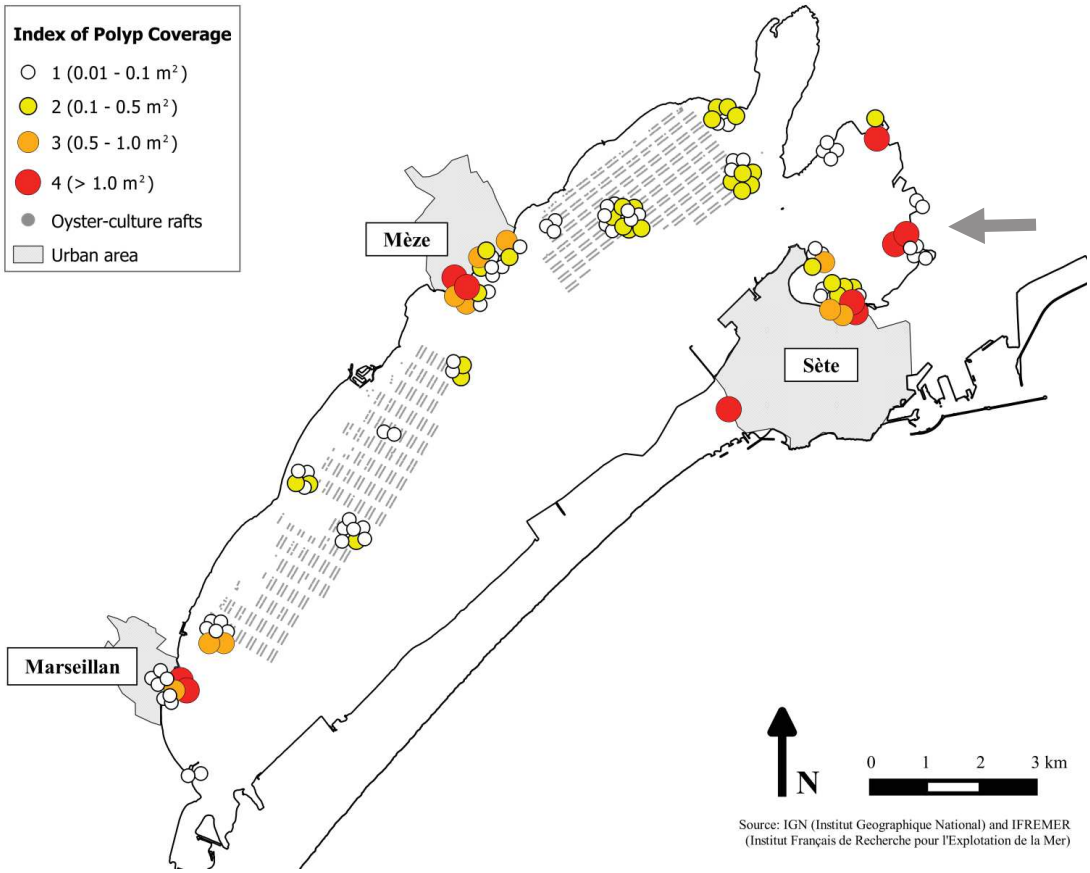


Fig. 7: Distribution of the sub-populations of *A. coerulea* scyphistomae in the Thau lagoon. A sub-population was defined as one or several patches of scyphistomae, covering the same continuous substrate type. The size of each sub-population was visually estimated according to a semi-quantitative index system (Index of Polyp Coverage, Marques et al. 2015b). The biggest aggregation ever observed in the lagoon was found on the underside of a submerged boat, near an old industrial concrete pontoon (grey arrow).

The highest densities of scyphistomae are found in areas under the heavy anthropogenic influence, where surfaces areas faced downwards, such as floating piers, pontoons and plastic debris provide suitable settling structures. The largest sub-population of *A. coerulea* found in the lagoon was fixed on a half-submerged fiberglass boat (Fig. 7). Biofouling organisms that grow on those structures appear to be critical as settling substrates (Fig. 8), especially oyster and mussel shells (86.6% of the sub-populations identified in the lagoon were settled on biofouling organisms, among which 90.4% were oysters, Marques et al. 2015b).

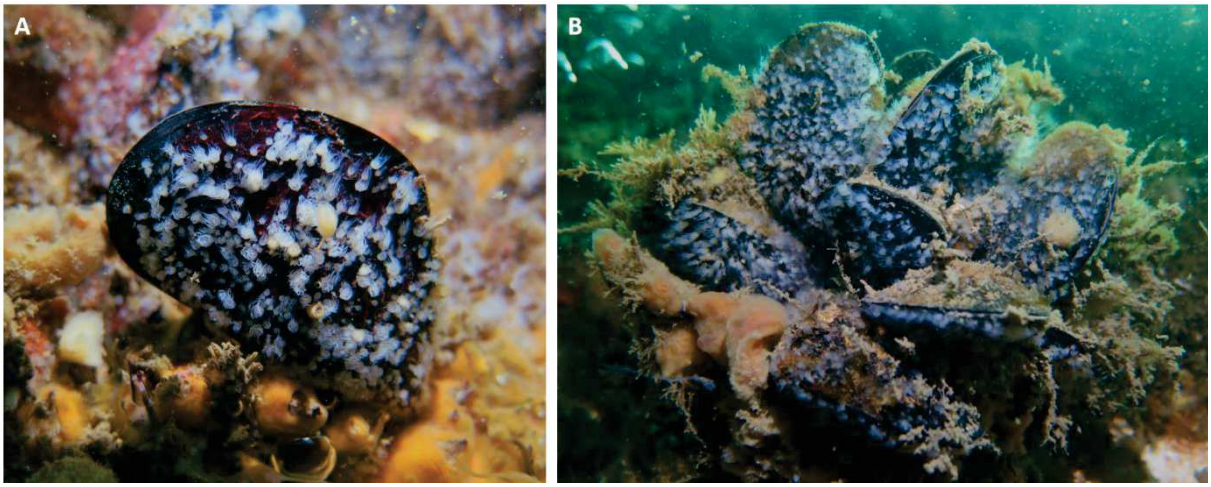


Fig. 8: *A. coerulea* scyphistomae fixed on mussel shells in the Thau lagoon. Photographs taken by Raquel Marques.

The population dynamics of the pelagic stages of *A. coerulea* have already been described in Thau lagoon (Bonnet et al. 2012; Marques et al. 2015a). The *A. coerulea* pelagic population in the Thau lagoon is univoltine (*i.e.* only one generation per year), with a life-span ranging from 7 to 8 months (Fig. 9). Ephyrae first appear in early winter (November) giving rise to adult medusae at the beginning of spring (April), when the temperature rises. Medusae remain in the lagoon until late spring (June), when sexual reproduction occurs and planulae are released in the water column. This precedes the drastic decline in abundance and the disappearance of the pelagic stages, which are absent from July to October.

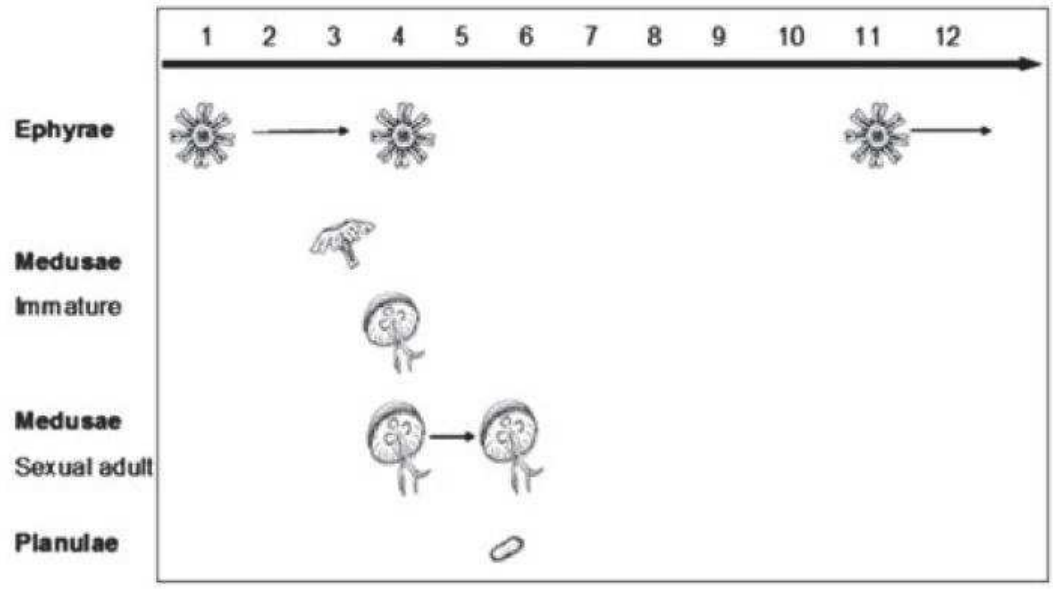


Fig. 9 Representation of the timing of occurrence of the different pelagic life stages of *A. coerulea* in the Thau lagoon. Numbers represent months (Bonnet et al. 2012).

The *A. coerulea* exhibits recurrent annual bloom in Thau (Marques et al. 2015a). Despite the high inter-annual variability in abundance, the maximum values for ephyrae (1472 ind.100m^{-3}) and for medusae (331 ind.100m^{-3}) were reported in February and May, respectively. After their release, ephyrae grows slowly until April (0.08 mm.day^{-1}), but the bell diameter suddenly increases then, with maximum growth rates (2.53 mm. d^{-1}on average) and bell diameters (22.38 cm on average) observed in May (Table 1, Fig. 10). Rises in temperature and food availability appear to promote the growth of medusae in the water column. In July, the medusae shrink and the bloom collapses within a few weeks.

Table 1: Ephyrae (< 1cm bell diameter) and medusae growth rates in the Thau lagoon between 2010 and 2014. The term "Medusae" is used to represent the time of exponential growth, while "Mature medusae" is used for the shrinking period. n is the number of individuals used to calculate growth rates. Max Bd is the maximum bell diameter registered in each year (data from Marques et al. 2015a).

Year	Growth rate (mm.d^{-1})			Max Bd (cm)
	Ephyrae (n)	Medusae (n)	Mature medusae (n)	
2010	0.08 (115)	2.02 (131)	- 0.56 (92)	17.07
2011	0.004 (158)	1.33 (14)	-	16.93
2013	0.01 (6)	2.53 (31)	- 1.02 (46)	22.38
2014	0.02 (350)	0.57 (6)	-	5.70*

* Larger medusae were observed in 2014 (7-8cm) but were not included in the analysis.

Fig. 10: *A. coerulea* bloom in the Thau lagoon. Photograph taken by Raquel Marques.

The annual blooms of *A. coerulea*, might have several impacts on ecosystem functioning in the Thau lagoon and directly or indirectly affect several local economic activities. On the negative side, the blooms might have a direct or indirect impact on the local fishing, aquaculture and tourism activity, which are central economic sectors in the region (Mongruel et al. 2013). When large abundances of medusae are attained, fishing nets and aquaculture equipments are frequently clogged, causing potentially high economic losses in cleaning and reparation operations (J. Fabrice, personal communication). Other negative impacts include damages on the exploited marine species, human physical injuries during professional and recreational activities (Bonnet 2009), which can result in non-negligible economic losses for local communities, as previously reported elsewhere in the Mediterranean (e.g. Palmieri et al. 2014; Ghermandi et al. 2015). The negative impacts of *A. coerulea* blooms in Thau might, however, also be indirect and often imperceptible. Indeed, jellyfish medusae are voracious predators with strong impacts on zooplankton communities (e.g. Ramirez-romero et al. 2018). This has been pointed out as a possible driver of the drastic reductions in mesozooplankton abundance in the lagoon (Bonnet et al. 2012) and might lead to food web modifications in the

lagoon decreasing food availability for higher trophic levels (e.g. Robinson et al. 2014). Considering that Thau is an important nursery area for several zooplanktivorous young stages of commercially important fish species (Kara and Quignard 2018a), the impact of the *A. coerulea* blooms might be, at best, temporarily significant for the survival of these organisms and their subsequent recruitment.

In this context, it is vital to elucidate the ecological role of *A. coerulea* in the Thau lagoon and the drivers and fate of its local blooms, not only to uncover the potential impacts of this species in the local ecosystem functioning but also to provide essential information on jellyfish ecology and blooms formation. This is critical if we want to forecast the potential response of jellyfish to climate change and anticipate the possible impacts of their blooms on the ecosystem functioning and services.

1.5 OBJECTIVES

The main goals of this PhD are to **identify the drivers and the fates of *A. coerulea* blooms within the Thau lagoon.** To do so, it was necessary to gather comprehensive knowledge and understanding on the biology and ecological role of both its benthic and pelagic life stages. Despite the information already available on the spatial distribution of the benthic population and the annual population dynamics of the pelagic stages, there are still big gaps of knowledge with this regard. To address them, this thesis was organised in two main chapters (Fig. 11). One (CHAPTER 2) investigating the main biotic and abiotic drivers of the *A. coerulea* blooms in the lagoon and one (CHAPTER 3) studying the local fates of *A. coerulea* biomass.

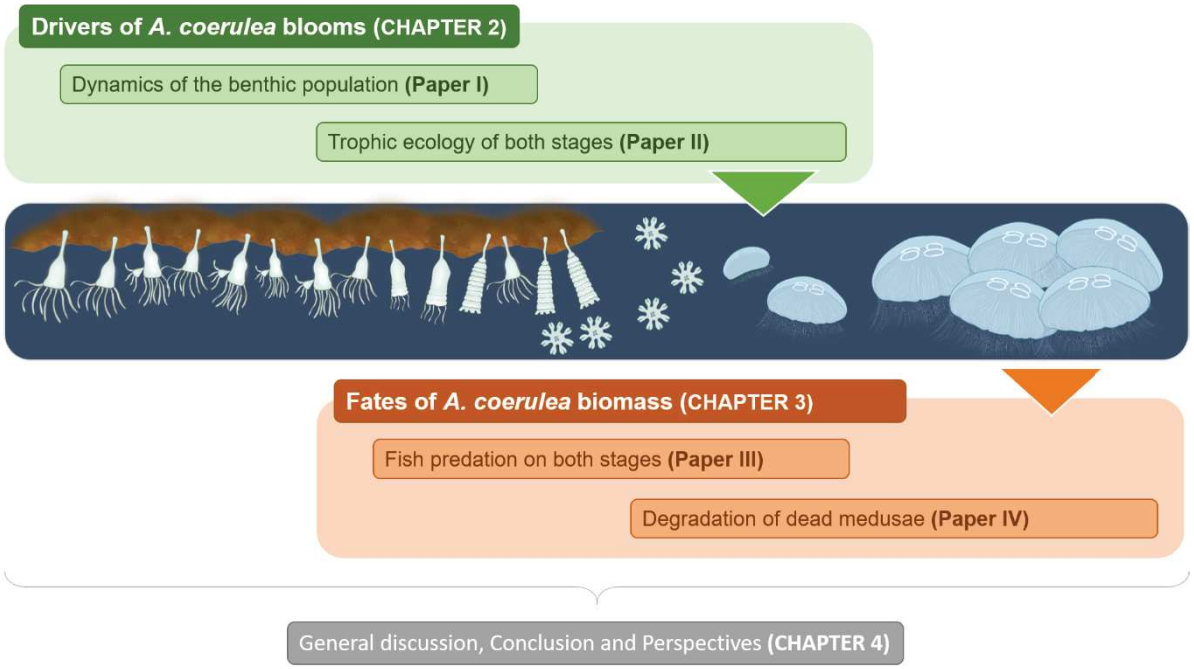


Fig. 11: Schematic representation of the organisation of this thesis.

1.5.1. CHAPTER 2: Drivers of *A. coerulea* blooms

Due to its complex life cycle, the understanding of the drivers of the blooms requires a complementary study addressing the different ecological processes acting at each and every stage of the *A. coerulea* life cycle. This knowledge is critical if we want to deliberate on the potential future responses of jellyfish to the predicted climate change and ongoing anthropogenic impacts on the marine ecosystems. Although much information has been gathered regarding the pelagic population of this species in the lagoon, their benthic population dynamics and its role in the development of the *A. coerulea* booms are largely overlooked. Therefore, this PhD first focused on the benthic population dynamics of the *A. coerulea*

scyphistomae, with the aim to describe the intra-annual demographic variation of its scyphistomae, assess their asexual reproduction strategy over the year and identify the main environmental factors regulating the observed population dynamics in the Thau lagoon **(Paper I)**. Matching this information with the known pelagic population dynamics allows to identify the main bottlenecks and boosting periods of the life cycle and understand what environmental factors are responsible for that. In addition, the comprehension of the development of the jellyfish blooms and their potential influence of the local food webs is not possible to achieve without the knowledge of their trophic interactions. Therefore, the trophic ecology of both stages was assessed **(Paper II)**, by investigating the intra-annual variation of the stable isotopic signatures of both the scyphistomae and the medusae stage of *A. coerulea* in the Thau lagoon. This provided information regarding temporal shifts of their isotopic niche and the potential organic matter sources responsible for the observed fluctuation. In addition, by comparing their isotopic niche with that from the oysters cultivated in the lagoon, it allowed addressing potential local intra- and interspecific trophic competition. Matching this information with the knowledge of the benthic and pelagic population dynamics, allowed to uncover the importance of bottom-up processes on critical periods of the *A. coerulea* life cycle and speculate regarding the possible impacts of the jellyfish blooms on the Thau lagoon's ecosystem functioning.

1.5.2. CHAPTER 3: Fates of *A. coerulea* biomass

Addressing the fates of the blooms is as much important as assessing its drivers, since this information is mandatory to identify the potential impacts of the blooms in the ecosystem functioning and uncover trophic interactions that might play a critical role in the regulation of *A. coerulea* in the lagoon. In this sense, this PhD first focused on the fish predation on *A. coerulea* in Thau **(Paper III).** Indeed, although generally ignored, one of the possible fates of their biomass is predation by top predators, like fish. Assess if fish actually consume *A. coerulea* in the Thau lagoon is critical to understand potential sources of control of their populations, the impact of this jellyfish on the local trophic food web, as well as their importance as a source of food for fish. Fishing is an important economic activity for the local communities and therefore, the investigation of this trophic interaction is fundamental to understand the ecology of both the *A. coerulea* and fish species inhabiting the lagoon. If the *A. coerulea* medusae are not predated in the water column, the medusae die and sink to the bottom. In this sense, the last section of this chapter intended to study the degaradtion of dead medusae on the seabed, by estimating their decay rates and the potential role of the macrobenthic community on its degradation **(Paper IV)**. This information allows to identify the fate of the dead organic matter

and shed light on the potential impacts on the lagoon's biogeochemical cycle, local trophic webs and ecosystem functioning.

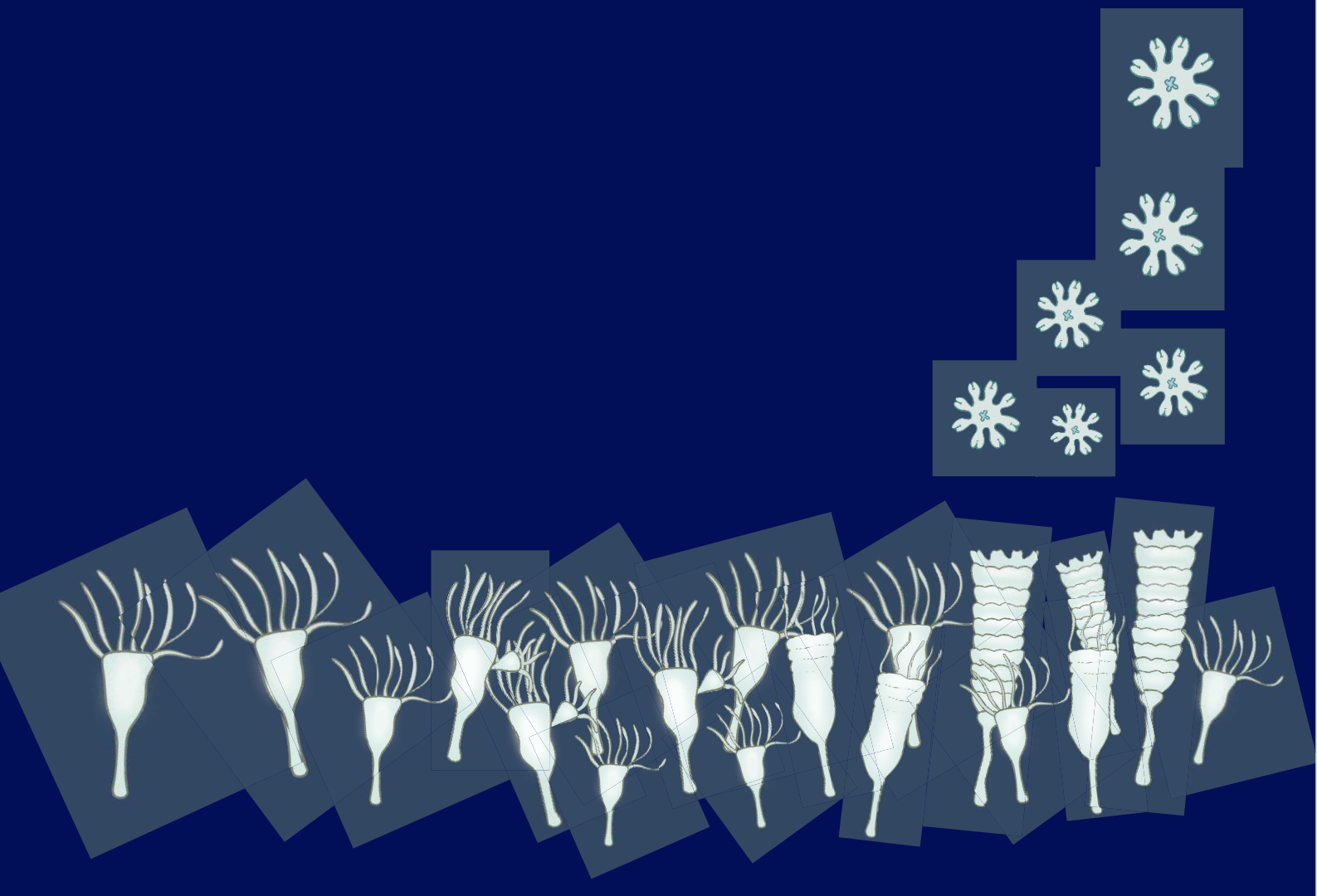
1.5.3. CHAPTER 4: General Discussion, Conclusion and Perspectives

Combining all the results gathered during this work and discussing them allowed to highlight the main factors controlling the benthic and pelagic population dynamics of *A. coerulea* and provided essential ecological information on the formation of their blooms. Likewise, identifying the main fates of the *A. coerulea* biomass, dead or alive, in the lagoon allowed to discuss the control of the local populations of this jellyfish and its potential role in the lagoon's food web. The valuable knowledge acquired in this study supports further discussion on the potential evolution of jellyfish blooms worldwide, as well as on their potential impacts on ecosystem functioning and services.

CHAPTER 2. DRIVERS OF A. COERULEA BLOOMS

Paper I: Dynamics of *A. coerulea* benthic population

Paper II: Trophic ecology of both *A. coerulea* stages



2.1 DYNAMICS OF *A. COERULEA* BENTHIC POPULATION (PAPER I)

The development of jellyfish blooms is tightly dependent on the dynamics of its benthic population. Therefore, this section of the PhD aimed to describe the intra-annual demographic variability of the scyphistomae population and the main environmental factors regulating it. For that, the benthic population of the *A. coerulea* was surveyed during one year using complementary underwater image analysis and sample observation in the Thau lagoon. This provided information regarding the main environmental drivers controlling the growth and decline of the scyphistomae population and their asexual reproduction strategy. This allowed understanding the role of the benthic population on the regulation of *A. coerulea* blooms in the lagoon and shed light on the potential evolution of jellyfish blooms under future climate conditions.

This section was presented at the 8th European Coastal Lagoons Symposium in March 2018 and published in *Marine Biology* Journal in 2019

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ORIGINAL PAPER

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Dynamics and asexual reproduction of the jellyfish *Aurelia coerulea* benthic life stage in the Thau lagoon (northwestern Mediterranean)

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2.1.1. Abstract

For many jellyfish, the magnitude and timing of medusae blooms are recognized to result from the benthic stage dynamics. However, information on the scyphistomae of jellyfish populations in the wild remains scarce. Here, bi-mensual underwater photoquadrat surveys were combined with scyphistomae sampling and observation to describe the annual (February 2017 - January 2018) benthic stage dynamics and asexual reproduction strategy of *Aurelia coerulea* in the Thau lagoon (43°25'31.1"N; 03°42'0.9"E). Our results revealed unexpected seasonal patterns of variation: scyphistoma coverage peaked in the spring (11.6 ± 3.7% on April 21st) and was minimal in the summer and autumn (1.4 ± 1.3% on October 10th). The increase in scyphistoma coverage mainly resulted from an intense production of buds between February and April during the spring rise in water temperature (peak of 12 800 buds per m^2 on April 21st), but scyphistoma coverage appeared to be negatively influenced by the interaction of high summer temperatures and salinities. Strobilation was observed from November to April. It peaked on November 17th, with 33.1 % of the scyphistomae strobilating and an average production of 19 100 strobila disks per m^2. However, the low scyphistoma coverage at this time of the year (< 2%) likely limited the intensity of ephyrae liberation and the subsequent medusae bloom. The final population size of *A. coerulea* thus results from a complex interaction of abiotic and biotic factors. Our results bring into question how the different populations of *Aurelia* spp. will respond to the predicted global warming scenarios.

2.1.2. Introduction

Seeming increases in the frequency of jellyfish blooms in some areas of the world (Richardson et al. 2009; Brotz et al. 2012), together with their negative consequences on several marine or littoral economic activities (Graham et al. 2014), have stimulated the scientific interest on jellyfish ecology and bloom formation.

Climate change, overfishing, eutrophication, the introduction of alien species and habitat modifications have all been pointed out as factors that might boost jellyfish blooms (Purcell et al. 2007; Richardson et al. 2009; Purcell 2012; Boero 2013). However, many blooming jellyfish, mostly scyphozoans, have a complex life cycle, which complicates the identification of the factors controlling the magnitude of their blooms. Previous studies suggested that ocean warming might boost jellyfish benthic stage densities by increasing asexual reproduction and scyphistoma survival, especially for temperate species (Purcell 2005, 2012; Purcell et al. 2007; Richardson et al. 2009), which might originate larger and more frequent blooms.

Jellyfish from the *Aurelia* genus, are among the most common scyphozoans that form blooms (Dawson and Martin 2001; Mills 2001). They are widely distributed in the Mediterranean, where they occur mainly in coastal areas and semi-enclosed seas (Mills 2001). Their life cycle comprises a sexual reproductive pelagic stage and an asexual reproductive benthic stage (hereafter referred to as pelagic and benthic populations, respectively). The adult medusae reproduce sexually, releasing planulae that settle on natural and artificial hard substrates (Holst and Jarms 2007; Hoover and Purcell 2009). After settlement, the planulae metamorphose into scyphistomae which can display different asexual reproduction modes, including different budding types (motile and non-motile) and podocysts (see Schiariti et al. 2014 for details). Under specific environmental conditions, scyphistomae produce and release great numbers of pelagic ephyrae, through the process of strobilation. These ephyrae grow in the pelagic environment until they reach the adult medusa stage, ultimately causing pelagic population pulses, which can sometimes result in outbreaks or the so-called jellyfish blooms (Schiariti et al. 2014). The timing and magnitude of the *Aurelia* spp. blooms are therefore dependent on the dynamics of their benthic populations and the environmental factors that control it. Yet, this critical stage of the life cycle has been little investigated so far and very few studies were performed on wild benthic populations of *Aurelia* spp. (Gröndahl 1988; Willcox et al. 2008; Purcell et al. 2009; Malej et al. 2012; Hocevar et al. 2018). Moreover, the *Aurelia* genus comprises a complex of species, even within the Mediterranean (Dawson and Jacobs 2001; Dawson and Martin 2001; Scorrano et al. 2016). Among them, *Aurelia coerulea* has been

reported to occur in Japan, China, California, Australia, France and Italy (Dawson et al. 2005; Scorrano et al. 2016). However, information on its wild populations is scarce (Watanabe and Ishii 2001; Miyake et al. 2002; Ishii and Katsukoshi 2010; Makabe et al. 2014).

The Thau lagoon (NW Mediterranean) presents the rare particularity to harbor a complete resident population of *Aurelia coerulea*, seemingly isolated from the Mediterranean Sea (Bonnet et al. 2012; Marques et al. 2015b). In this lagoon, ephyrae first appear in the early winter, to give rise to adult individuals at the beginning of spring, when temperature increases (Marques et al. 2015a). Medusae remain in the water column until the late spring, when they reproduce sexually before disappearing from the system. The benthic scyphistomae of *A. coerulea* are found mainly on biofouling organisms covering man-made hard substrates. Their local spatial distribution and preferential habitats in the Thau lagoon have been described thoroughly (Marques et al. 2015b). However, their local seasonal population dynamics and their asexual reproduction strategy are still unexplored.

Changes in jellyfish scyphistoma population size are regulated by the balance between population growth (*i.e.* the increase in scyphistoma coverage and/or density) and mortality. Population growth might result from the benthic recruitment of planulae, the excystment of podocysts, the production of new scyphistomae by asexual reproduction and the dispersion of detached scyphistomae or motile bud-like tissue particles (Lucas et al. 2012; Schiariti et al. 2015). Scyphistomae mortality might be induced by predation, inter- and intra-specific interactions and physiological stress (Lucas et al. 2012). The influences of varied environmental factors on planulae settlement and scyphistomae asexual reproduction have been studied for several species of the *Aurelia* genus, mainly in laboratory experiments (*e.g.* Han and Uye 2010; Purcell et al. 2012; Schiariti et al. 2014; Sokołowski et al. 2016; Hubot et al. 2017). The latter studies suggest that temperature and food availability are likely critical factors controlling benthic population dynamics in *Aurelia* spp., through an influence on the intensity of scyphistoma asexual reproduction. However, the impacts of biotic and abiotic factors on the wild benthic population dynamics of these jellyfish are complex and still poorly known (Willcox et al. 2008; Malej et al. 2012; Hocevar et al. 2018). Density dependent factors, predation and interspecific space competition were also stressed as important potential drivers of scyphistoma densities, both from *in situ* (Miyake et al. 2002; Willcox et al. 2008; Feng et al. 2017; Dong et al. 2018a) and laboratory studies (Hoover et al. 2012; Takao et al. 2014).

In this context, the present study aimed to (1) describe the seasonal dynamics of the benthic population of *A. coerulea* and its annual asexual reproduction strategy in the Thau lagoon and (2) link it with the annual variation of the main biotic and abiotic factors known to

affect jellyfish scyphistoma densities and physiology. This would allow identifying the main drivers of *A. coerulea* scyphistoma population size in this lagoon and the importance of its benthic population dynamics on the timing and intensity of its local pelagic medusae blooms.

2.1.3. Material and Methods

2.1.3.1 Study site and sampling

The Thau lagoon is a semi-enclosed, marine coastal lagoon which covers an area of 75 km^2 and is connected to the Mediterranean Sea by three narrow channels (Fig. 1). It is relatively shallow, with mean and maximum depths of 4 and 10 m, respectively (with the exception of a localized depression of 24 m). The monitoring area chosen for this study (43°25'31.1"N; 03°42'0.9"E) is among those with the biggest shaded continuous surfaces (underside surface of a half-submerged fiberglass boat) and, therefore, highest coverage of *A. coerulea* scyphistomae in Thau (Marques et al. 2015b). It is located in the eastern part of the lagoon, where the maximum depth is of 7 m. Seasonal changes in the dynamics and asexual reproduction strategy of the scyphistomae of *Aurelia coerulea* were studied there over one entire year, by 23 SCUBA diving surveys, scheduled every two weeks from February 2017 to January 2018.

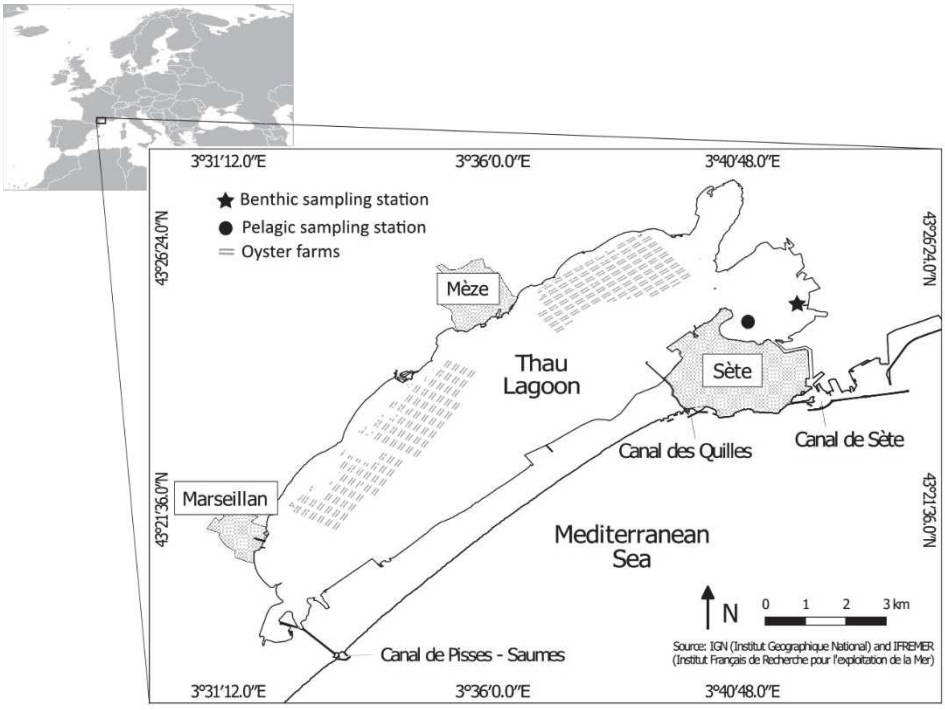


Fig. 1 Map of the Thau lagoon showing the location of the benthic (star) and pelagic (circle) sampling sites for this study. Shaded areas represent urban areas

2.1.3.2 Environmental parameters

For each sampling date, environmental parameters (temperature, salinity, chlorophyll *a* concentration and mesozooplankton abundance) were monitored. Temperature and salinity were measured with a probe (EC 300 VWR international/ WTW model 350i), right above the scyphistoma monitoring site, at about 0.5 m depth. Chlorophyll *a* concentration and mesozooplankton abundance were determined from samples collected at a nearby site (43º23'59.1''N; 03º36'37.2''E, Fig. 1). Chlorophyll *a* concentration was measured from 150 ml water samples, collected in triplicate. Water was filtered on Whatman GF/F filters and stored at -30ºC until pigment extraction in acetone and chlorophyll *a* concentration measurement by spectrofluorimetry (LS 50B Perkin Elmer). Mesozooplankton samples were collected near the surface, by horizontal towing, using a modified WP2 plankton net (1.2 m long, 50 cm opening area and 200-µm mesh). Samples were immediately preserved in 4% buffered formaldehyde until further analysis in the laboratory. Mesozooplankton abundance was determined by visual counting of organisms under a dissecting microscope (Olympus SZX7 – ILLT).

2.1.3.3 Dynamics of the benthic stage

The temporal dynamics of the benthic stage of *A. coerulea* on the study site was estimated at a depth of 2 – 4 m, by measuring the scyphistoma coverage (%) using an underwater photoquadrat method. For this, four distinct zones of 15 × 15 cm (hereafter called photoquadrats) were selected on the surface of the wreck, according to four criteria: a minimum distance of 2 m between photoquadrats and, within each of them, a flat surface area, the absence of large biofouling organisms (*e.g.* mussels, oysters, sponges, etc.) and the presence of at least a small patch of *A. coerulea* scyphistomae. Their respective positions were identified by scratching the surface of the wreck. Underwater photographs of all four zones were taken at each survey date using a Canon PowerShot G16 camera with Ikelite Canon G16 Compact Housing non-TTL case and a Riff TL-WW light. For this, a PVC structure forming a square of 15 × 15 cm was adapted to the camera case in order to keep a constant distance between the camera and the analysed surface. Only the same central square area of 11 × 11 cm (121 cm^2) was analysed in each photoquadrat to avoid shaded areas. Photographs were pre-treated with Gimp 2.8.22 to improve contrast and analysed using a purpose-built image analysis software in MATLAB (IZS: Image Zone Selector, Tremblay, unpublished). The IZS uses the different colour channels of the images in order to identify, select and determine the percent coverage of the scyphistomae (Fig. 2). All images were also visually inspected and corrections were made when necessary.

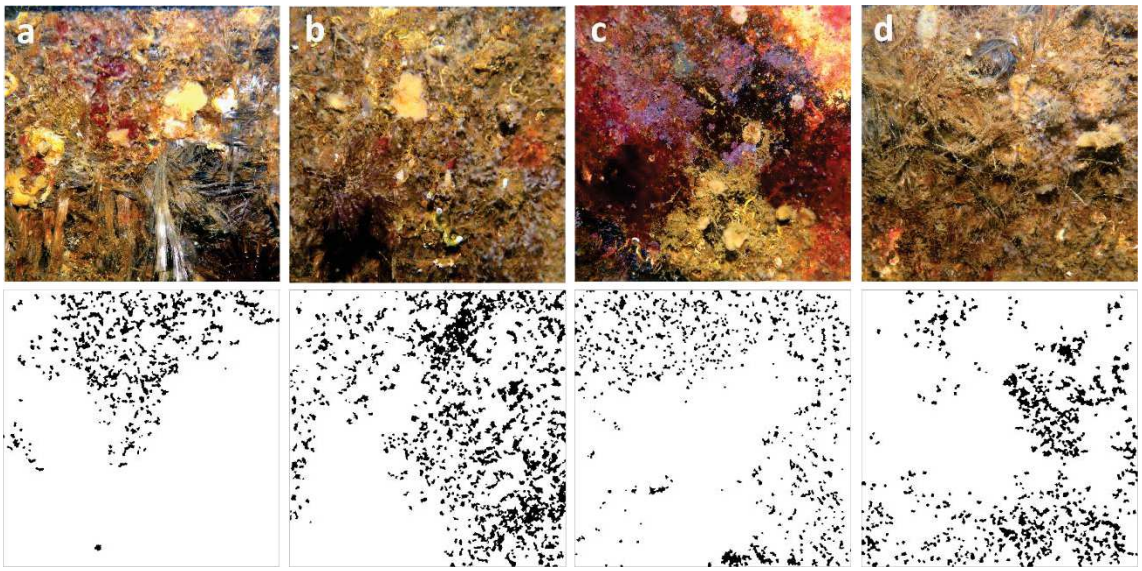


Fig. 2 Example of the photoquadrats (top) and the respective IZS output (bottom). a) photoquadrat 1 (6.10 % coverage), b) photoquadrat 2 (16.1 % coverage), c) photoquadrat 3 (6.64 % coverage), c) photoquadrat 4 (9.93 % coverage).

To avoid the bias linked to software limitations in individual scyphistomae identification, six photographs per photoquadrat, from different times of the year (embracing minimum, maximum and intermediate values of scyphistoma coverage), were re-analysed and scyphistomae were visually counted. The number of scyphistomae in the photographs was plotted against the corresponding value for scyphistoma coverage and a linear regression line was fitted (Fig. 3). The regression equation was used to estimate the number of scyphistomae in all photographs. Scyphistoma densities (in ind cm^{-2}) in each photoquadrat (121 cm^2), were then estimated over the entire study period following the equation

(eq.1) $$Density = \frac{88.5 + 6542.1 * Scyphistoma\ coverage\ (\%) * 100^{-1}}{121}$$

Where 88.5 and 6542.1 are the *y*-intercept and slope of the regression line, respectively.

When determining scyphistoma coverage by image analysis, one biofouling species, the red algae *Peyssonnelia* sp., was identified as an important substrate for scyphistoma fixation, with potential influence on the dynamics of the benthic population of *A. coerulea.* Therefore, the IZS was also used to assess its coverage (%), by changing the values of the colour channels. All images were visually inspected and corrected when necessary.

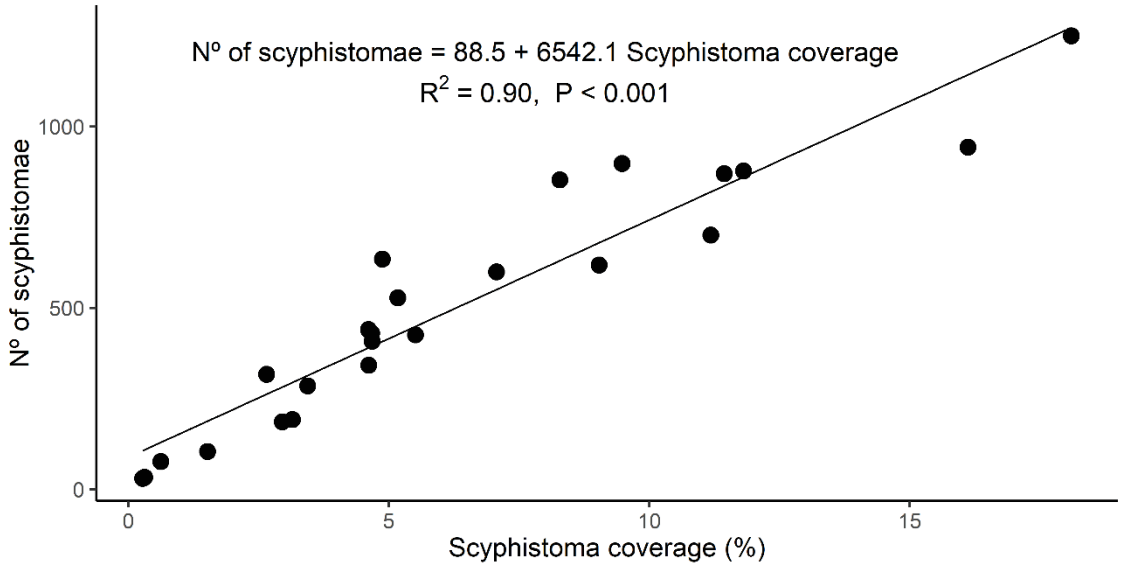


Fig. 3 Relationship between the number of scyphistomae and scyphistoma coverage (%) in the photoquadrats (121 cm^{-2}). The resulting equation was used to estimate scyphistoma density in the study site (eq. 1)

2.1.3.4 Asexual reproduction strategies

To investigate the reproductive activity of the benthic population of *A. coerulea* at each survey date, three samples of scyphistomae, attached to the underside surface of oyster or mussel shells, were collected in the monitoring site. Sampling was done on the same half-submerged fiberglass boat, at depths between 2 and 6 m, a few meters away from the photoquadrats. Scyphistomae were brought alive to the laboratory and counted under a dissecting microscope (Olympus SZ40; Olympus KL 1500 LCD), using a small mesh net (mesh 0.65 cm^2) as a counting grid. Since density dependent effects were previously demonstrated to influence population growth of *Aurelia* scyphistomae (*e.g.* Melica et al. 2014; Schiariti et al. 2015), the effect of density was reduced by selecting only the most dense area of each sample for asexual reproduction assessment (*i.e.* 3 to 22 sections of the counting grid with a mean density of 44.4 ± 16.6 scyphistomae cm^{-2}, to obtain a minimum of 100 scyphistomae per sample). Asexual reproduction modes were identified after Schiariti et al. (2014), using needles to inspect each individual scyphistoma and recording the following data for each sample: the total number of scyphistomae, their density (ind cm^{-2}), the percentage of non-reproductive scyphistomae, the percentage of scyphistomae producing non-motile buds (NMB, specifying the percentage of scyphistomae producing 1, 2 or more buds), the number of podocysts per scyphistoma, the percentage of strobilae and the number of disks per strobila. The percentage of scyphistomae producing non-motile buds (NMB) comprises three reproductive modes: typical lateral budding, lateral budding by means of stolons and reproduction from parts of

stolons/stalks (see Schiariti et al. 2014 for details). We pooled them since their distinction is often difficult in wild samples and they have an equivalent impact on scyphistomae population dynamics (Schiariti et al. 2014), as they all produce sessile buds right beside the mother scyphistoma and appear to respond to the same environmental clues (Schiariti et al. 2015).

2.1.3.5 Asexual reproduction effort

The asexual production (*AP*) of buds or strobila disks per surface area (m^2) was estimated for each sampling date (t_i) as:

(eq.2) $$AP(t_i) = \frac{p * n * d * 10^3}{100}$$

Where p is the percentage of the scyphistomae exhibiting each asexual reproduction strategy (*i.e.* production of NMB or strobilation), n is the mean number of reproductive outputs (*i.e*. buds or strobila disks) produced per scyphistoma and d is the mean density of scyphistomae estimated from the four photoquadrats (eq.1). The total number of ephyrae released (ind m^{-2}) from the study site during the whole study period (assuming a continuous strobilation period between November and April), was estimated based on Ishii and Katsukoshi (2010) and Makabe et al. (2014). The ephyrae liberation at each sampling date (EL_{t_i}, ind m^{-2}) was calculated as:

(eq.3) $$EL_{t_i} = AP(t_i) * R^{-1}$$

Where R is the residence time of ephyrae (days). R is dependent on temperature (T) and was estimated based on *in situ* temperatures in Thau, using the equation obtained by laboratory experiments on *A. coerulea* from Japan, performed by Makabe et al. (2014), as:

(eq.4) $$R = 109 * e^{-0.221 * T}$$

The number of ephyrae released (ind m^{-2}) from the study site between t_0 and t_1 was then estimated as:

(Eq.5) $$EL_1 = (EL_{t0} + EL_{t1}) * (t_1 - t_0) * 2^{-1}$$

And that during the whole study period was estimated as:

(Eq.6) $$TEL = EL_1 + EL_2 + \cdots + EL_n$$

2.1.3.6 Statistical analysis

For biological variables (scyphistoma coverage, percentage of scyphistomae adopting each reproductive strategy, number of buds and disks produced per scyphistoma and number of podocysts per scyphistoma) differences among sampling months and photoquadrats (for scyphistoma coverage) were tested by one-way ANOVAs, when variables presented normal

distribution and homogeneity of variances (tested by Shapiro and Bartlett tests). Otherwise, Kruskal-Wallis tests were used and *post hoc* tests were carried out using Dunn's test for multiple comparisons. Temporal and spatial autocorrelations were tested by examination of ACF plots and by Mantel tests from ade4 package (Dray and Dufour 2007). Although scyphistoma coverage of *A. coerulea* differed significantly between the four photoquadrats (ANOVA, F (3, 83) = 5.33, P = 0.002), temporal or spatial autocorrelations were not detected so the data from all photoquadrats was grouped for temporal trend analyses. Generalized linear models (GLM, using linear and logistic regressions) were employed to assess the contribution of temperature, salinity, chlorophyll *a* concentration and mesozooplankton abundance (explanatory variables) on the scyphistoma coverage, NMB and podocysts per scyphistoma (response variables). The minimal adequate model was achieved by a stepwise deletion of the least significant terms from the maximal model, with interactions included. For each fitted model, we calculated AIC and selected the model presenting the lowest AIC. The final models were validated by examination of plots of residuals versus fitted values for the entire model (Harrison et al. 2018). The influence of the environmental parameters on the strobilation activity was assessed by Hurdle models from pscl package (Zeileis et al. 2008), due to the presence of many zeros in the dataset. Spearman correlations tests were used to investigate the relationship between the scyphistoma percent coverage with the NMB and the number of podocysts per scyphistoma. The presence of the red algae was observed in photoquadrats 1, 2 and 3. The relationship between scyphistoma and red algae coverages in these three photoquadrats was studied by Pearson correlation test. All statistical analyses were performed using the software R Studio Version 1.0.143 (R Core Team 2017) and taking $\alpha < 0.05$ as the limit for statistical significance.

2.1.4. Results

2.1.4.1 Environmental conditions in the Thau lagoon

The annual pattern of temperature variation in Thau followed the normal trend in temperate regions, with lower values in the winter and higher values in the summer (Fig. 4). During the study period, the temperature at the study site ranged from 7.6 ºC (on December 13th 2017 and January 29th 2018) to 25.8 ºC on June 27th 2017. Salinity varied between 35.0 (on February 24th 2017) to 39.6 (on November 09th 2017), with a drastic decrease at the end of the study period, where salinity dropped to 33.9 (on January 29th 2018). The concentration of chlorophyll *a* and the abundance of mesozooplankton were highly variable over the year.

Chlorophyll *a* concentration ranged from 0.5 µg L^{-1} (on January 10th 2018) to 2.8 µg L^{-1} (on February 24th 2017) without any clear seasonal pattern, while mesozooplankton abundance varied between 94 and 166 607 ind m^{-3} (on April 21st 2017 and June 27th 2017, respectively), with an intermediate peak of abundance at 10 524 ind m^{-3} (on March 10th 2017). Due to logistic constraints, chlorophyll *a* concentration and mesozooplankton abundance were not measured in August 2017.

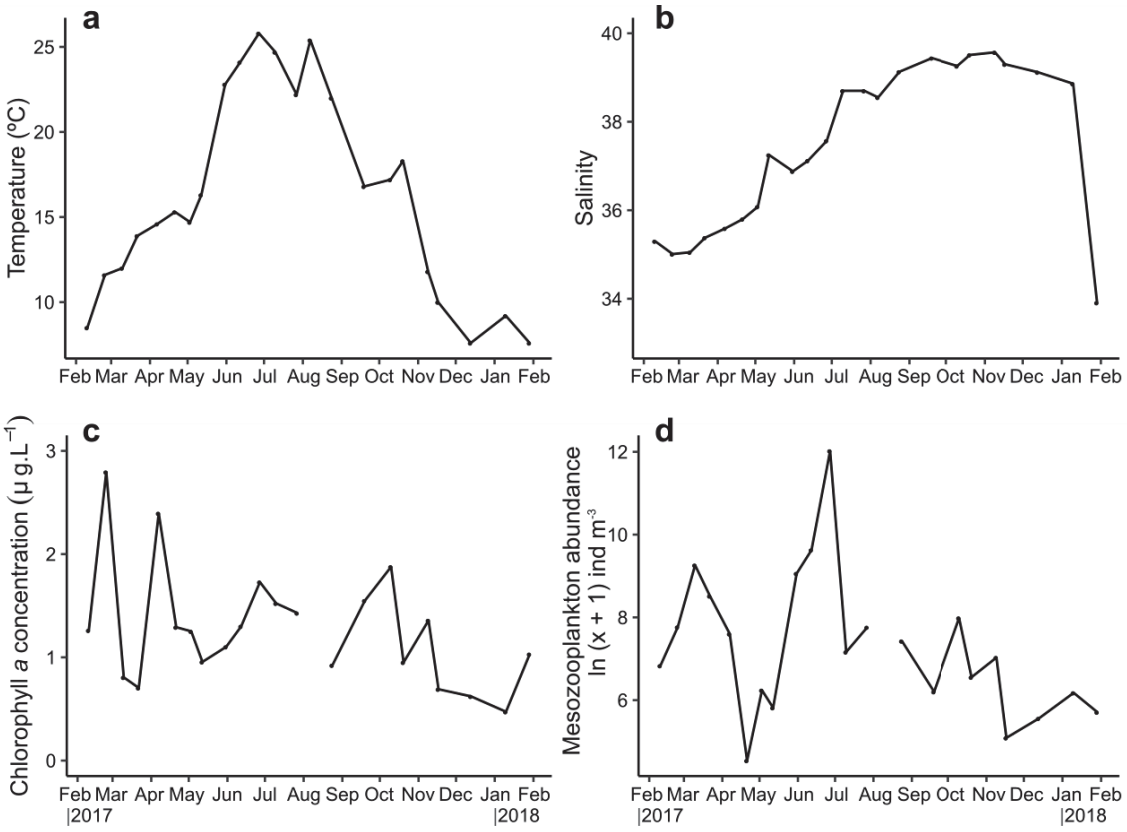


Fig. 4 Variation of the environmental variables in the Thau lagoon, during the study period: a) temperature, b) salinity, c) chlorophyll *a* concentration and d) mesozooplankton abundance

2.1.4.2 Dynamics of the benthic stage

Scyphistoma coverage in the photoquadrats varied between a minimum of 0.3% and a maximum of 18% of the photographed area (both observed in photoquadrat 2, Fig. 5), which corresponds to a range in density of 0.25 to 10.3 scyphistomae cm^{-2}. The overall mean of scyphistoma coverage on the study site fluctuated significantly during the study period (ANOVA, F (1, 21) = 11.2, P = 0.003), with a minimum average value (1.4 ± 1.3%, n = 4) on October 10th 2017 and a maximum one (11.6 ± 3.7%, n = 4) on April 21st 2017. Temporal variations differed slightly among photoquadrats: scyphistoma coverage peaked in April in photoquadrats 1, 3 and 4 and in May – June in photoquadrat 2. However, all photoquadrats

presented low scyphistoma coverage between September and November. Scyphistoma coverage for this period was below 1%, with the exception of photoquadrat 4, where it remained above 3% during the study period.

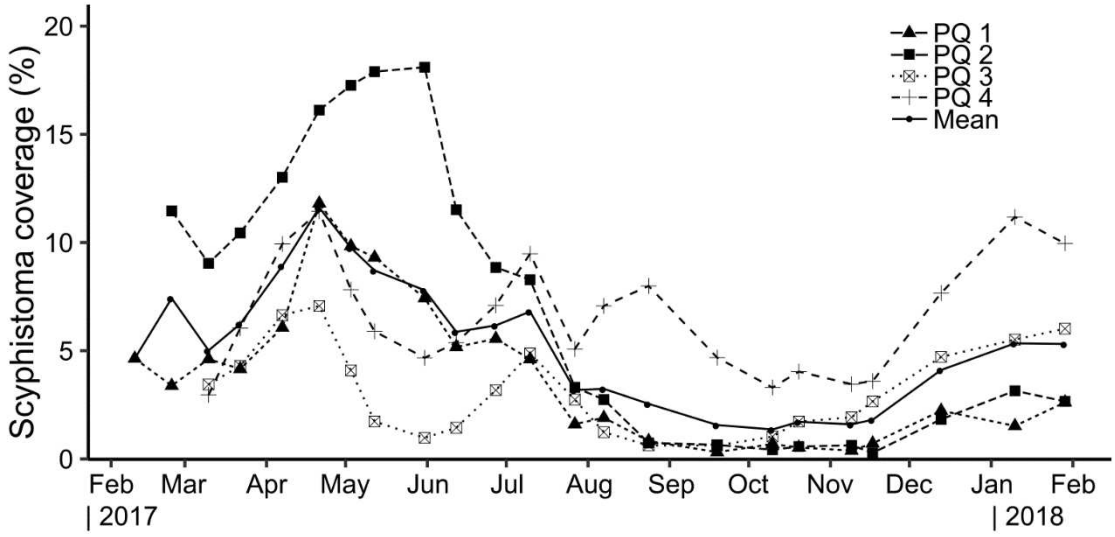


Fig. 5 Variation of *A. coerulea* scyphistoma coverage in each photoquadrats (PQ) and the mean of all photoquadrats, during the study period

2.1.4.3 Asexual reproduction strategy

During the whole study period, the mean percentage of scyphistoma reproducing asexually varied between 2.2 ± 1.5 to 33.5 ± 4.9 % (n=3, per sampling date) (Fig. 6). Scyphistoma-to-scyphistoma reproduction (NMB) was the most important asexual reproduction mode observed. The percentage of scyphistomae producing buds varied between sampling dates (Kruskal-Wallis test, $H24 = 53.5$, $P < 0.001$). It was maximum between March and May 2017, when 15.0 ± 6.7 to 19.4 ± 5.2 % (n = 3, per sampling date) of the scyphistomae were producing buds. The asexual production (AP_{ti}) of buds was higher in this period, with a peak on April 21st when 12 800 buds m^{-2} were produced (Fig. 7). The percentage of scyphistomae producing buds was then highly variable until November (4.6 ± 1.1 to 25.2 ± 7.3 %, n = 3, per sampling date), with noticeable peaks above 19% in July, September and October (Fig. 6). During the study period, most of the budding scyphistomae (92.8 ± 17.3%, n = 69) produced just one bud at a time, but the simultaneous production of several buds per scyphistoma was observed all year round (except in January 2018). The maximum number of buds observed for a given scyphistoma (4), was registered in September. However, the production of buds observed per scyphistoma was highest in October: among the budding scyphistoma, 13.7 ± 5.3% (n = 3, per sampling date) produced two buds and 4.2 ± 4.5% (n = 3,

per sampling date) produced 3 or more buds. In November, the percentage of scyphistomae producing buds decreased sharply and reached its lowest value (0.4 ± 0.7%, n = 3) on November 17th, when the production of buds was also minimum (70 ind m^{-2}, Fig. 7). This percentage remained low (< 9%) until the end of the study period (in January 2018).

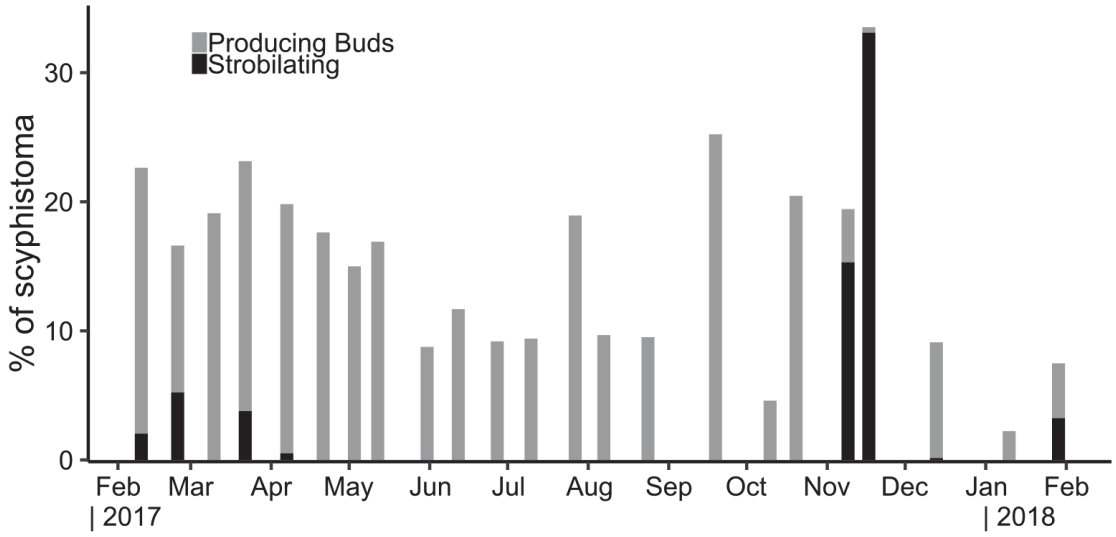


Fig. 6 Annual asexual reproduction strategy of *A. coerulea* scyphistoma in the Thau lagoon over the study period. Each bar represents the percentage of the population producing non-motile buds (grey) and strobilating (black) at each sampling time

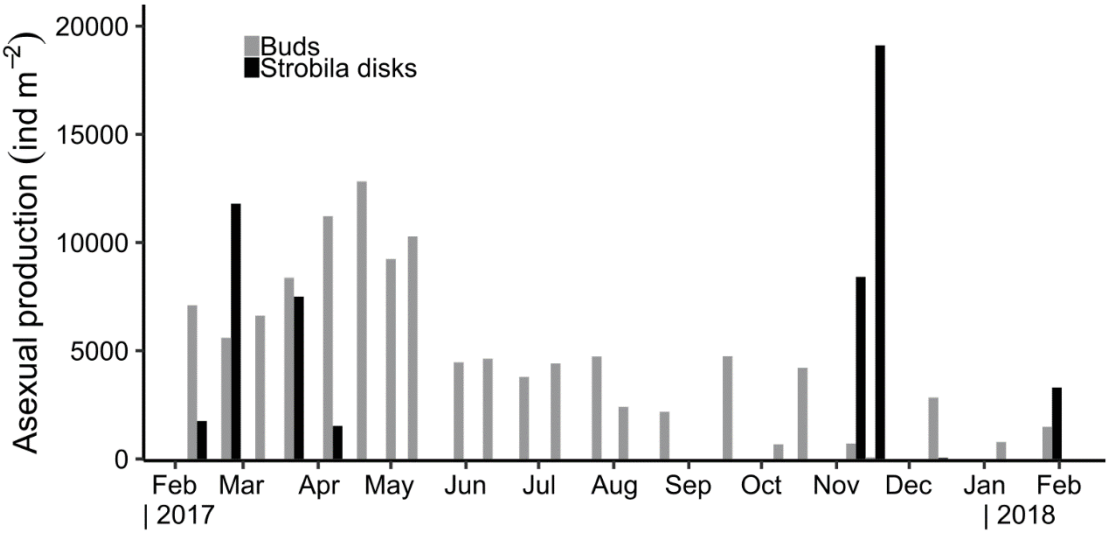


Fig. 7 Asexual Production (AP_{ti}) in the Thau lagoon over the study period. Each bar represents the estimated production of non-motile buds (grey) and strobila disks (black) by the population of *A. coerulea* scyphistoma, at each sampling time (t_i), at the study site

The average number of podocysts per scyphistoma ranged from 0 to 0.5 ± 0.4 (n = 3, per sampling date), showing high variability between samples from the same date. No

significant difference was observed among sampling dates for this reproduction mode (Kruskal-Wallis test, $H22 = 24.8$, $P = 0.3$).

Strobilation was observed from February to April 2017 and from November 2017 to January 2018 suggesting that ephyrae production by *A. coerulea* scyphistoma likely occurs from late autumn to early spring in the Thau lagoon (Fig. 6). During this period, the percentage of scyphistomae strobilating varied significantly between sampling dates (Kruskal-Wallis test, $H24 = 56.7$, $P < 0.001$): less than 5.5% of the population strobilated irrespective of the month, except in November when this percentage increased to 33.1 ± 4.2% (n= 3, on November 17th). During the strobilation period, the maximum number of disks produced per strobila was of 11, with a general mean of 3.7 ± 1.4 (n= 16) disks per scyphistoma. No significant differences between sampling dates were recorded in the number of disks formed per scyphistoma (Kruskal-Wallis test, $H7 = 9.9$, $P = 0.2$). As a result, the estimated asexual production (AP_{ti}) of strobila disks presented a short but conspicuous peak in November 17th 2017 (19 100 disks m^{-2}), but was also high in spring, due to high scyphistoma density (Fig. 7). During this season, it peaked at 11 800 disks m^{-2} on February 24th 2017 and decreased afterwards to 1 500 disks m^{-2} on April 7th 2017, in parallel with an increase of buds production. Assuming a continuous strobilation period between November and April, the total number of ephyrae liberated (TEL) from the study site during the whole study period was estimated at 82 301 ind m^{-2}.

2.1.4.4 Drivers of the dynamics and asexual reproduction

Scyphistoma coverage was positively influenced by temperature (GLM, $P = 0.03$) but responded negatively to joint increases in temperature and salinity (GLM, $P = 0.03$) (Table 1). No significant correlation was found with the other environmental variables tested. The coverage of *A. coerulea* scyphistomae and that of the red algae (*Peyssonnelia* sp.) were positively correlated (Pearson correlation, $t\ 19 = 5.06$, $P < 0.01$).

With regards asexual reproduction modes, scyphistoma coverage was significantly correlated only with the number of podocysts per scyphistoma (Spearman correlation, $S = 853.7$, $P = 0.004$), which was similarly affected by temperature (positive correlation, GLM, $P = 0.02$) and by the interaction of temperature and salinity (negative correlation, GLM, $P = 0.02$) (Table 1). Although NMB was the highest before April, *i.e.* before the peak of scyphistoma coverage, it was not correlated with the latter variable (Spearman correlation, $S = 1746$, $P = 0.53$). Indeed, scyphistoma coverage dropped from spring to summer, while NMB remained high and even peaked when scyphistoma coverage was at its minimum. Moreover, none of the environmental variables tested was significantly correlated with the variability in NMB.

Strobilation intensity was found to be affected only by temperature (Zero Hurdle model, $P = 0.046$), with the probability of a scyphistoma to strobilate increasing by 0.75 times for each decreasing ºC (Table 2). Indeed, the high peak of strobilation observed in November followed a sharp decrease in temperature (of 8.3 ºC) from October 20th to November 17th (Fig. 4).

Table 1 Parameters of the final General Linear Models used to assess correlations between each of the biological variables (scyphistoma coverage, percentage of scyphistomae producing non-motile buds (NMB) and podocysts per scyphistoma) and environmental variables in the lagoon. Temp: temperature (ºC), Sal: salinity; Chla: chlorophyll *a* concentration (µg L^{-1}), logZAb: mesozooplankton abundance (ln (x + 1) ind m^{-3}). Significant correlations ($P < 0.05$) are indicated in bold.

Scyphistoma coverage (%)	Estimate	Std. Error	t value	*P*
(Intercept)	-1.78	1.22	-1.46	0.17
Temp	0.23	0.09	2.47	**0.03**
Sal	0.05	0.03	1.50	0.16
logZAb	0.21	0.19	1.09	0.29
Temp:Sal	-0.01	0.00	-2.43	**0.03**
Temp:logZAb	-0.02	0.01	-1.62	0.13
Sal:logZAb	-0.01	0.01	-1.12	0.28
Temp:Sal:logZAb	0.00	0.00	1.62	0.13
NMB (%)				
(Intercept)	179.57	221.44	0.81	0.42
Temp	-12.97	14.69	-0.88	0.38
Sal	-5.32	5.80	-0.92	0.36
MChla	-231.26	240.37	-0.96	0.34
logZAb	-20.53	28.22	-0.73	0.47
Temp:Sal	0.37	0.38	0.96	0.34
Temp:MChla	13.17	15.31	0.86	0.39
Sal:MChla	6.63	6.35	1.04	0.30
Temp:logZAb	1.46	1.88	0.78	0.44
Sal:logZAb	0.61	0.74	0.83	0.41
MChla:logZAb	28.57	31.26	0.91	0.36
Temp:Sal:MChla	-0.37	0.40	-0.92	0.36
Temp:Sal:logZAb	-0.04	0.05	-0.86	0.39
Temp:MChla:logZAb	-1.53	1.99	-0.77	0.44
Sal:MChla:logZAb	-0.83	0.83	-1.00	0.32
Temp:Sal:MChla:logZAb	0.04	0.05	0.83	0.41
Podocysts per scyphistoma				
(Intercept)	-2.56	1.47	-1.75	0.10
Temp	0.29	0.11	2.61	**0.02**
Sal	0.07	0.04	1.76	0.09
Temp:Sal	-0.01	0.00	-2.54	**0.02**

Table 2 Hurdle model coefficients used to assess the influence of environmental variables on strobilation intensity. Temp: temperature (ºC), Sal: salinity; Chla: chlorophyll *a* concentration (µg L^{-1}), logZAb: mesozooplankton abundance (ln (x + 1) ind m^{-3}). Significant correlations ($P < 0.05$) are indicated in bold.

Count model coefficients (truncated negbin with log link):	Estimate	Std. Error	z value	*P*
(Intercept)	-1.79	11.73	-0.15	0.88
Temp	0.27	0.47	0.57	0.57
Sal	0.19	0.30	0.64	0.52
Chla	0.10	0.60	0.17	0.87
logZAb	-0.62	0.89	-0.71	0.48
Log(theta)	-0.19	0.60	-0.31	0.76
Zero hurdle model coefficients (binomial with logit link):				
(Intercept)	-2.23	12.40	-0.18	0.86
Temp	-0.29	0.15	-2.00	**0.05**
Sal	0.08	0.31	0.24	0.81
Chla	0.83	0.90	0.92	0.36
logZAb	0.23	0.45	0.52	0.60

Exponentiated coefficients	Count model	Zero hurdle model
(Intercept)	0.17	0.11
Temp	1.31	**0.75**
Sal	1.21	1.08
Chla	1.11	2.29
logZAb	0.54	1.26

2.1.5. Discussion

2.1.5.1 Dynamics of the Aurelia coerulea benthic stage

Extensive patches of *Aurelia coerulea* scyphistomae cover a variety of anthropogenic submerged substrates in the Thau lagoon (Marques et al. 2015b), which allowed *in situ* evaluation of the intra-annual dynamics of its population at the benthic stage. Estimated densities in this study varied between 0.25 to 10.3 scyphistomae per cm^{-2}, in accordance with previous estimations for the same species in Japan, of 0.005 to 18 scyphistomae per cm^{-2} (Miyake et al. 2002; Ishii and Katsukoshi 2010), but also for other species of the *Aurelia* genus, for which mean densities of 7.3 ± 0.6 and 31.3 ± 1.3 scyphistomae cm^{-2} were registered in two sites in Tasmania (Willcox et al. 2008), and of 6 to 27 scyphistomae cm^{-2} in the Adriatic Sea (Malej et al. 2012; Hocevar et al. 2018). Nonetheless, comparisons among sites are to be considered with caution, because scyphistomae are usually distributed in patches, so the density value changes according to the total area assessed (Miyake et al. 2002) and the substrate type considered. In this study, for instance, scyphistoma density estimates from the photoquadrat survey were much lower than those in the samples used to assess asexual reproduction strategies (9.9 to 78.8 scyphistomae cm^{-2}). Still, these latter values are in accordance with those (88

scyphistomae cm^{-2}) reported by studies assessing the micro-distribution of scyphistomae on bivalve shells (Miyake et al. 2002).

The intra-annual pattern of demographic variation for *A. coerulea* scyphistomae in Thau is characterized by a peak in coverage in spring, followed by a decrease until minimum values are reached in the summer and autumn and a progressive recovery over the winter. This trend is not in agreement with previous observations made for *A. coerulea* (Ishii and Katsukoshi 2010; Makabe et al. 2014) and other *Aurelia* spp. (*e.g.* Gröndahl 1988; Willcox et al. 2008; Malej et al. 2012; Hocevar et al. 2018): scyphistomae densities in the *Aurelia* genus usually peak from spring to summer and are at their lowest in both the autumn and winter months. These differences are surprising because temperature appeared to positively affect the population size of scyphistoma in the wild (Willcox et al. 2008; Hocevar et al. 2018) and this study was conducted in an enclosed coastal habitat with a temperature range (7.6 to 25.8ºC) similar to those where investigations were made for *A. coerulea* in Japan (9ºC to 29ºC, Ishii and Katsukoshi 2010; Makabe et al. 2014) or, for example, for *A. aurita* in the Adriatic (6.3 ºC to 27.4 ºC, Hocevar et al. 2018). Although scyphistoma coverage was positively correlated with temperature in Thau, the interaction of high temperatures with high salinities appeared to be detrimental to *A. coerulea* scyphistoma. Indeed, the salinity range observed in our study site (35.0 to 39.6) was above that reported for the studies conducted in Japan (up to 33, Ishii and Katsukoshi 2010; Makabe et al. 2014), but similar to that reported in the Adriatic (32.8 to ca. 38, Hocevar et al. 2018), where the negative influence of salinity on scyphistoma density was also pointed out. So far, no clear negative effect of salinity was ever found on *Aurelia* spp. scyphistoma survival (Willcox et al. 2007; Holst and Jarms 2010; Widmer et al. 2016) nor somatic growth (Willcox et al. 2007; Hubot et al. 2017), except when reaching freshwater conditions (Holst and Jarms 2010). However, most laboratory studies so far, focused on the influence of freshwater inputs (*e.g.* Holst and Jarms 2010; Amorim et al. 2018) and were therefore performed at low salinities (<37) *i.e.* lower than the values registered in our study, especially in the summer (ca. 39). Still, Hubot et al. (2017) assessed the influence of relatively high salinities on the asexual reproduction and somatic growth of *Aurelia coerulea* from the Adriatic Sea and reported a decrease in physiological performances between 24 and 37 in salinity. To our knowledge, laboratory experiments on the effect of salinities > 37 have never been performed with *A. coerulea* but our results suggest that high summer salinity associated with high temperature conditions might be detrimental to its scyphistomae, contributing to the benthic population dynamics observed in the Thau lagoon.

Food availability is often pointed as one of the most important drivers of jellyfish population growth, boosting the production of new scyphistomae (Han et al. 2010; Schiariti et al. 2014; Ikeda et al. 2017). During this study, however, mesozooplankton abundance did not statistically influence scyphistoma coverage nor NMB. The few existing studies so far on the diet of *Aurelia* spp. scyphistomae suggested that they feed on microzooplankton (Kamiyama 2011, 2013) and small mesozooplankton species (*e.g.* copepods, cladocerans, gelatinous zooplankton; Östman 1997). Therefore, only a portion of the potential prey of *A. coerulea* scyphistomae was surveyed in the present work. To improve our understanding of the influence of food availability on the *in situ* dynamics of the benthic stage of this species, further investigations on scyphistoma diet associated with micro-, mesozooplankton and epibenthic prey abundance *in situ* are still required.

Apart from the already discussed impact of temperature and salinity on scyphistoma coverage, other interspecific interactions, such as predation and room for expansion, can also play an important role in reducing the density of jellyfish benthic populations (*e.g.* Willcox et al. 2008; Takao et al. 2014; Feng et al. 2017). Different species of benthic organisms are able to feed on *Aurelia* spp. scyphistomae. Some of these predators might even consume more than 600 scyphistomae per day (*e.g.* the crab *Hyastenus diacanthus*) (Takao et al. 2014). In Thau, several potential predators were identified in the photoquadrats (sea stars of the genus *Asterina,* gastropods: *Ocenebra erinaceus* and *Hexaplex trunculus*, nudibranchs: *Felimare villafranca* and sea urchins: *Paracentrotus lividus*), but the consumption of scyphistomae by these organisms has never been reported so far. Fishes feeding on benthic prey might also consume *A. coerulea* scyphistomae, through direct or indirect predation (*i.e.* targeting their fixation substrate, like bivalves). Their predation pressure might be high enough to significantly affect scyphistomae coverage, as shown in predation experiments involving the sparid *Sparus aurata* (Marques et al. 2016). The exact importance of predation in controlling the population of *A. coerulea* scyphistomae in the Thau lagoon, however, remains to be assessed.

Biofouling organisms compete for space with jellyfish scyphistomae, so their densities frequently have negative effects on scyphistoma population growth (Watanabe and Ishii 2001; Willcox et al. 2008; Makabe et al. 2014; Feng et al. 2017). Nevertheless, *Aurelia* spp. appear to be more resilient than other scyphozoans, mainly due to their asexual reproduction modes (Feng et al. 2017, 2018): their scyphistomae can adhere to the surface of different organisms by producing different types of budding, stolons, and can even detach themselves from the substrate and drift to another one (Schiariti et al. 2015). Colonization of other benthic organisms by jellyfish scyphistomae is frequent (Miyake et al. 2002; Willcox et al. 2008; Toyokawa et al.

2011) and even suggested as a promoter of settlement and proliferation for *A. coerulea* scyphistomae in China (Dong et al. 2018a). In Thau, scyphistomae of *A. coerulea* were recurrently found attached to red algae (*Peyssonnelia* sp.): in three out of the four photoquadrats surveyed in the present work but also in surrounding areas where scyphistomae were particularly abundant (R. Marques, personal observation). The decline of these algae observed in the study site in the summer might have contributed to the concomitant reduction of the benthic population of *A. coerulea*. These results corroborate the importance of interspecific interactions and settling substrates availability in the population dynamics of *Aurelia* spp.. Future studies on the *in situ* demography of the benthic stage of jellyfish should, therefore, be designed to embrace the variability of their settling substrates and the potential role on the population dynamics of certain biofouling organisms that provide adequate fixation substrate for their scyphistomae.

2.1.5.2 Contribution of the asexual reproduction

The growth of jellyfish benthic population results from both the production of new scyphistomae by asexual reproduction (*e.g. via* the production of non-motile buds or the excystment of podocysts) and the recruitment of pelagic planulae to the seafloor (Schiariti et al. 2015).

In the Thau lagoon, *A. coerulea* planulae are usually produced between May and June (Bonnet et al. 2012), when they swim to the bottom and settle on the substrate. Pelagic life duration before settlement is usually short (typically less than 4 days, Lucas et al. 2012), probably to decrease planulae vulnerability to predation in the pelagic environment (Lucas et al. 2012). Thus, we expected an increase of scyphistoma coverage after planulae release in 2017, which was not detected. Instead, scyphistoma coverage started to decrease in May 2017, when the first medusae with planulae about to be released were spotted in the lagoon (R. Marques, personal observation). Therefore, the recruitment of new scyphistomae by planulae fixation does not contribute most to the observed benthic population dynamics, at least at our study site. In *Aurelia* spp., planulae are thought to play an important role in the expansion of populations to new habitats through pelagic dispersion (Holst and Jarms 2007; Lucas et al. 2012). This is probably the case in Thau, where the presence of *A. coerulea* scyphistomae over the entire lagoon area might result from the dissemination of planulae, together with the widespread availability of suitable settling substrates and favorable hydrographic characteristics in the lagoon (Marques et al. 2015b).

Although podocysts excystment was suggested to play an important role in bloom formation for some jellyfish species (*e.g. Nemopilema nomurai*; Kawahara et al. 2013), its impact on scyphistoma density was very limited in the population of *A. coerulea* investigated so far (*e.g.* Thein et al. 2012). In this species, podocysts appear to lie in ensuring the survival of the benthic population under unfavorable conditions and providing protection from predators (Arai 2009; Thein et al. 2012; Hubot et al. 2017). In our study, the number of podocysts per scyphistoma was significantly correlated with scyphistoma coverage and it appears to follow the same environmental forcing, which may suggest a significant contribution of podocysts for the increasing of the benthic stage. Nevertheless, until the exact production, excystment and residency time are assessed for the species in the wild, it is impossible to tell whether there were more scyphistomae at our study site because more podocysts were produced or *vice-versa*. For this reason, the significance of the contribution of podocysts excystment to the increase of scyphistoma coverage of *A. coerulea* in Thau remains elusive.

The production of NMB, on the contrary, could be the main responsible for local increases of scyphistoma coverage. Although the temporal trend of NMB and scyphistoma coverage were not significantly correlated (with a mismatch during the summer), a high percentage of scyphistomae produced buds in March and April. Estimates for bud production intensity on the study site matched the peak of scyphistoma coverage, supporting the hypothesis that the bud production is the main asexual mode responsible for benthic population increases in Thau. During the end of spring and the beginning of summer, both NMB and scyphistoma coverage decrease, but more than 10% of the scyphistomae produced continuously at least one bud per scyphistoma, and it even peaked in September, when scyphistoma coverage was very low. Although in laboratory experiments, the production of buds is boosted by high temperatures and food availability (Han et al. 2010; Schiariti et al. 2014; Hubot et al. 2017; Ikeda et al. 2017), none of the environmental variables tested were significantly correlated with NMB at our study site. Still, we suspect that high salinities in Thau lagoon during the summer might be unfavorable to the production of buds, as demonstrated by Purcell (2007) and Hubot et al. (2017). However, additional information on the intra-annual availability of scyphistoma prey in the lagoon, together with a long-term survey, is needed to reach a more complete understanding of the drivers of this asexual reproduction mode followed by *A. coerulea* in the Thau lagoon.

2.1.5.3 Strobilation

In Thau, the strobilation period for *A. coerulea* appears to span from the end of the autumn (November) and the beginning of the spring (April), with a peak in November (33% of the population strobilated in November 2017). This result is in accordance with the previously reported period for ephyrae presence in the lagoon, from early winter to early spring (Marques et al. 2015a), and with the strobilation periods described so far in other areas for *A. coerulea* (Toyokawa et al. 2000; Watanabe and Ishii 2001; Miyake et al. 2002; Uye and Shimauchi 2005) and for *A. aurita* (Hocevar et al. 2018). As previously suggested by Holst (2012), the strobilation onset in our study seems to have been triggered by a sharp drop (of 8.3ºC) in water temperature, as temperatures in Thau fell to 10ºC over a few days in November 2017. Water temperatures below 15ºC have been shown to induce physiological changes in the scyphistomae of *A. coerulea*, probably to prepare them for metamorphosis (Han et al. 2010; Feng et al. 2018). This is possibly what happened in the *A. coerulea* scyphistomae of Thau in November 2017.

The magnitude of most jellyfish blooms is tightly reliant on the density of scyphistomae, but also on their strobilation strategy as this later directly determines the magnitude of the initial production of the pelagic individuals responsible for the blooms. The number of ephyrae released depends on the number of disks produced per strobila combined with the number of strobilating scyphistomae. In Thau, an average of 3.7 ± 1.4 disks per scyphistoma were produced by *A. coerulea* over the strobilation period, which is in accordance with previous observations (3.2 – 7.7 disks per scyphistoma) made for *Aurelia* spp. (Holst 2012; Makabe et al. 2014; Feng et al. 2018). Despite the low percentage of scyphistomae strobilating in February (< 5.5%) the estimated production of disks was relatively high (11 800 disks per m^2), due to the high density of scyphistomae at this time of the year (> 30 000 ind per m^2). However, the main period of *A. coerulea* strobilation was observed in November with a production of circa 19 100 disks per m^2. If our study was representative of a complete strobilation season (*i.e.* from November to April in the same year), the number of ephyrae released (of 82 301 ephyrae per m^2), at our study site would be much higher than previous estimations for *A. coerulea* in Japan (131 ephyrae per m^2) by Ishii and Katsukoshi (2010), but close to that (86 806 ephyrae m^{-2}) from Makabe et al. (2014). This production, though, was limited by the low densities of scyphistomae in this season, especially in November. Therefore, the magnitude of *A. coerulea* blooms in Thau is limited, not only by the mortality of ephyrae during the winter (Fu et al. 2014), but also by the important mortality of scyphistomae over the summer.

2.1.6. Conclusion

While climate change and the consequent ocean warming are currently expected to cause larger and more frequent jellyfish blooms, our results prompt the question if all populations of one of the most blooming genus, the *Aurelia*, will respond likewise. In this temperate lagoon, the seasonal dynamics of the benthic stage of *A. coerulea* in 2017 contrasted those previously described for *Aurelia* genus, mainly because of a combination of high temperatures and salinities in the summer that appear to be detrimental to scyphistomae of *A. coerulea*. The resulting decrease in scyphistomae density undoubtedly reduced the outcome of the late-autumn strobilation peak in Thau, thereby limiting the intensity of the subsequent pelagic bloom of *A. coerulea*. Because warm and dry summers are expected to be more frequent in the coming decades in the Mediterranean area (IPCC 2014), we may assist to a decrease in the benthic population size and in the intensity of the blooms of this jellyfish, at least in Thau. However, the short-term of this study hampers substantiated conclusions and further investigations, based on long-term studies, are still required to corroborate such suspicion.

Consequently, there is an urgent need for widespread *in situ* studies on the benthic population dynamics of scyphozoans and their local environmental drivers. In jellyfish, benthic population dynamics is an outcome of complex biotic and abiotic interactions which apparently act differently in each ecosystem. Our results show that predicting it needs a comprehensive understanding of the interspecific relationships that might regulate scyphistoma abundance. Long-term *in situ* studies, involving different species of jellyfish and encompassing diverse localities and habitats, are crucial if we want to understand the formation of jellyfish blooms and their fate in the face of the predicted climate change.

2.2 TROPHIC ECOLOGY OF BOTH *A. COERULEA STAGES* (PAPER II)

Understanding the trophic ecology of jellyfish is critical to understand the development of their blooms. Therefore, this section of the PhD aimed to describe the intra-annual trophic ecology of both the benthic and the pelagic life-stages of *A. coerulea* in Thau and to assess its potential influence on critical periods of the jellyfish population dynamics (*e.g.* peak of buds production, strobilation and medusae growth). For that, medusae gut content assessments, *in situ* food availability and stable isotopes analysis (SIA) of both stages of its life-cycle were determined over a year and combined, to (1) precise changes in their isotopic signatures during an annual cycle, (2) evaluate the contribution of different primary and secondary food sources to the diet of *A. coerulea* and (3) assess potential intra- and inter-specific trophic competition between the two *A. coerulea* life stages and with the oysters cultivated in Thau. This allowed understanding the bottom-up processes responsible for the regulation of jellyfish blooms in the lagoon and discussing their potential impacts on the local shellfish farming activity.

Paper II

This section will be submitted at the end of October and presented at the 6th Internation Jellyfish Bloom Symposium, 4-6 November 2019

Trophic ecology of the jellyfish *Aurelia coerulea* in a Mediterranean coastal lagoon

Marques R, Bonnet D, Roques C, Carré C, Darnaude AM (*In prep*)

2.2.1. Abstract

The trophic ecology of jellyfish is still poorly known, particularly at the benthic life stage. With this regard, the Thau lagoon is one of the rare habitats to harbour a resident population of the scyphozoan *Aurelia coerulea*, where the annual population dynamics of both benthic and pelagic stages have been described. This offers an exceptional framework to understand the possible trophic processes regulating jellyfish populations over time. For this, we assessed monthly variations in the carbon and nitrogen stable isotope signatures of *A. coerulea* scyphistomae and medusae for one year and compared them to those of their main potential food sources. Temporal changes in isotopic signature were observed for both life stages, revealing shifts in the trophic niche of *A. coerulea* during the year. Phytoplankton, microzooplankton, mesozooplankton and sedimentary organic matter were all important sources during critical periods of the *A. coerulea* life-cycle, but microzooplankton appeared to be of high importance as a promoter of buds production. Intra-specific trophic niche overlap was observed between scyphistomae and medusae. However, when compared with the oysters cultivated in the lagoon, interspecific food competition seems to be limited and therefore jellyfish blooms appear to have little direct impact on the local shellfish production.

2.2.2. Introduction

Due to the impact of their conspicuous blooms on coastal ecosystems functioning and economical activities, jellyfish have received increasing attention during the last decades (*e.g.* Richardson et al. 2009; Graham et al. 2014). The drivers of jellyfish blooms have been investigated, revealing a complex interaction of natural (*e.g.* Condon et al. 2012) and anthropogenic (*e.g.* Purcell 2012) causes. However, uncovering the drivers of blooms is particularly challenging for most scyphozoan blooming species because their life-cycle is complex, comprising a benthic (scyphistomae) and a pelagic (ephyrae and medusae) phase (*e.g.* Lucas 2001; Fuentes et al. 2011). Therefore, the formation of their blooms is a joint consequence of the production of pelagic medusae by the scyphistomae and of the survival and growth of the medusae in the water column.

Bottom-up processes within food webs control the structure and functioning of ecological systems and are amongst the most important drivers of jellyfish blooms (Boero et al. 2008). Food quality and availability are known to control the production of ephyrae by the scyphistomae (Han et al. 2010; Schiariti et al. 2014; Ikeda et al. 2017) and to modulate the growth rate of medusae (Lucas 1996; Lucas et al. 1997; Ishii and Båmstedt 1998). This supports the need for comprehensive studies on the trophic ecology of both life stages in the field. Yet, although an increasing amount of publications provide information on the trophic interactions of medusae (*e.g.* Hansson 2006; Javidpour et al. 2016; Milisenda et al. 2018), the diet of jellyfish scyphistomae is still poorly known.

Jellyfish from the *Aurelia* genus are among the most common scyphozoans that form blooms (Dawson and Martin 2001; Mills 2001). They are widely distributed in the Mediterranean, where they occur mainly in coastal areas and semi-enclosed seas (Mills 2001). The medusae of these species are described as zooplanktivorous, with a repeatedly reported contribution of mesozooplankton, especially copepods, in their diet (*e.g.* Ishii and Tanaka 2001; Hansson 2006; Lo and Chen 2008). So far, microzooplankton and benthic food sources have received little attention in trophic studies on jellyfish. They are, therefore, typically considered as less important although, based on new techniques (such as stable isotope analysis) some recent reports suggest the opposite (Javidpour et al. 2016).

The few existing studies regarding the diet of *Aurelia* sp. scyphistomae suggested that they feed on phytoplankton (Huang et al. 2015), microzooplankton (Kamiyama 2011, 2013) and small mesozooplankton species (*e.g.* copepods, cladocerans, gelatinous zooplankton; Östman 1997). In laboratory studies, newly hatched *Artemia* sp. are usually provided as food (*e.g.* Han et al. 2010; Purcell et al. 2012; Hubot et al. 2017). However, information about the

trophic ecology of this life stage is still very limited. Considering the critical role of scyphistomae in the formation of jellyfish blooms, it is urgent to fill in this gap of knowledge. It is also important to better understand intra-specific trophic interactions among the benthic and pelagic stages of the species and their potential impacts on local communities.

For this, the Thau lagoon presents the rare particularity to harbour a complete resident population of *Aurelia coerulea* (Bonnet et al. 2012; Marques et al. 2015b). This offers an exceptional framework to understand the possible trophic processes regulating jellyfish populations over time. *A. coerulea* scyphistomae are widespread in the lagoon, fixed mainly on biofouling organisms that grow on anthropogenic structures (predominantly on oysters and mussels; Marques et al. 2015b). They are present all year round, with a peak of coverage in the Spring (April) and lower densities in the Summer and Autumn (Marques et al. 2019b). Ephyrae appear in the early winter (November – December) and give rise to adult medusae at the beginning of the Spring (April – May), generating the annual jellyfish bloom, which persists until June - July (Bonnet et al. 2012; Marques et al. 2015a). Mesozooplankton abundance did not appear to impact the population dynamics of *A. coerulea* scyphistomae in the lagoon and it was, therefore, suggested that other food sources might sustain the species local production (Marques et al. 2019b). Nevertheless, further confirmation is still required in this regard.

Coastal lagoons are very productive environments with generally great contributions of continental inputs in nutrients and particulate organic matter (Nixon et al. 1995). This sustains high primary and secondary productions, benefiting the whole food web that enhances, for instance, the growth of juvenile fish (Escalas et al. 2015). In Thau, the high local productivity also supports a massive shellfish production: ~10% of the Pacific oyster *Crassostrea gigas* produced in France comes from the Thau lagoon, with a yearly shellfish production of 15 000 tons (Pernet et al. 2012a; Mongruel et al. 2013). Due to the high local economical importance of shellfish farming, it is important to assess whether *A. coerulea* medusae and scyphistomae might compete for food with the oysters or benefit them through indirect top-down control effects.

In this context, the present work aimed to describe the trophic ecology of both the benthic and the pelagic life-stages of *A. coerulea* in Thau and to assess its potential influence on critical periods of the jellyfish population dynamics (*e.g.* peak of buds production, strobilation and medusae growth) and on the local stocks of cultivated oysters. For that, we combined medusae gut content assessments with stable isotopes analysis (SIA). SIA has been increasingly used during the last decades to study the structure and transfer of organic matter within coastal food webs (Layman et al. 2012). It was also recently used to uncover the diet,

trophic levels and trophic interactions of different jellyfish species (Nagata et al. 2015; Fleming et al. 2015; Javidpour et al. 2016; Milisenda et al. 2018). Using it to evaluate the contribution of different primary and secondary food sources to the diet of *A. coerulea* and precise changes in their diet and trophic positions during an annual cycle should allow assessing whether *A. coerulea* scyphistomae and medusae occupy the same trophic niche than the oysters cultivated in the lagoon. This has strong implications for both the regulation of the jellyfish blooms and the sustainable development of shellfish farming in the lagoon.

2.2.3. Material and Methods

2.2.3.1 Study site

The Thau lagoon is a semi-enclosed, marine coastal lagoon that covers an area of 75 km^2 and is connected to the Mediterranean Sea by three narrow channels (Fig. 1). It is relatively shallow, with mean and maximum depths of 4 and 10 m, respectively (with the exception of a localized depression of 24 m). The Thau lagoon environment is characteristic of temperate regions with strong seasonality of all environmental parameters. Temperatures and salinity are lower in the winter (minimum of 7.6 and 35.0, respectively) and very high in the summer (maximum of 25.8 ºC and 39.6, respectively; Marques et al. 2019b). This lagoon has a weak tidal range (< 1m), which promotes a high residence time of water masses (1-4 months), and is highly influenced by seasonal strong wind events (Millet and Cecchi 1992; Fiandrino et al. 2012). The lagoon is supplied in N from two main sources: the marine waters from the Mediterranean Sea, entering the lagoon mainly by the Sète canal and the coastal runoff from its catchment area (290 km^2, Plus et al. 2006). This later is drained by small intermittent rivers that dry out between May and September and show occasional flush floods during the wet season (Tournoud et al. 2006). As a result, marine conditions prevail in the lagoon. The annual influence of the freshwater coming from the watershed is highly influenced by rainfall events during the winter season (Plus et al. 2006; Collos et al. 2009). Thau lagoon is under heavy human pressure, due to the vicinity of the touristic city of Sète, of many sparse villages and agriculture fields that surround it.

Shellfish farming is the most important economic activity on the lagoon (Mongruel et al. 2013). This activity covers around 20% of the lagoon surface, concentrated mainly in the northern and north-western part of the lagoon (Fig. 1).

The monitoring areas (benthic: 43°25'31.1"N; 03°42'0.9"E and pelagic: 43º23’59.1’’N; 03º36’37.2’’E; Fig 1) chosen for this study are situated in the eastern part of the lagoon, where

both the pelagic and the benthic population dynamics of *A. coerulea* have been described (Bonnet et al. 2012; Marques et al. 2015a, 2019b). Both monitoring stations are located nearby the most important channel connecting the lagoon to the Mediterranean Sea and, therefore, are mainly influenced by seawater influxes. Both stations are characterized by sandy or muddy bottoms, with sparse seagrass meadows of *Zostera noltii* and *Zostera marina*.

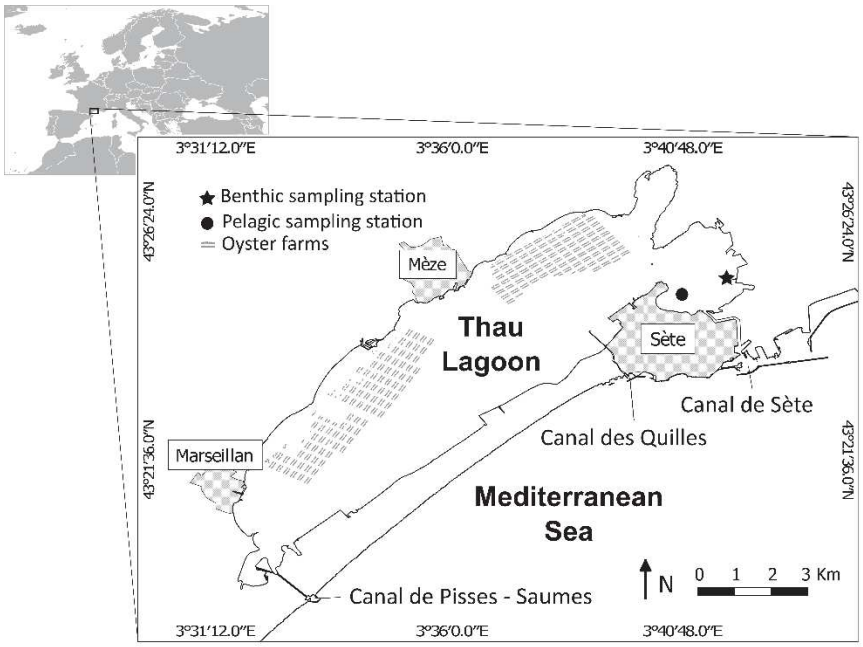


Fig. **1**: Map of the Thau lagoon showing the location of the benthic (star) and pelagic (circle) sampling stations for this study. Shaded areas represent urban areas and grey points represent oyster farms.

2.2.3.2 Jellyfish sampling

Pelagic medusae of *Aurelia coerulea* were collected every two weeks, from March to June 2017, when they were present in the lagoon. Benthic scyphistomae were collected monthly from January 2017 to January 2018, but extra samples were analysed (every two weeks) in May. Ephyrae are usually present in the lagoon from November to April (Bonnet et al. 2012; Marques et al. 2015a). However, ephyrae were collected in only one sampling date (January 2018), because it was not possible to collect enough individuals in 2017 for stable isotopes analysis.

Medusae were collected by hand net and transported to the laboratory in *in situ* seawater. Once in the laboratory, three individuals (except at the first sampling time, when eight small medusae were pooled per replicate) were kept for about 2h in 0.2 µm filtered seawater (ca. 20ºC). Each medusa was then placed on a paper towel for about 30 s (each side) in order to remove excess of water and then weighted (total wet weight in g) and measured (bell diameter in cm). Bell tissue was previously demonstrated as the most suitable body part for jellyfish SIA

(D'Ambra et al. 2014). Therefore, gonads, oral arms and gastric pouches were removed and bell tissue was rinsed with MilliQ water, before preservation at -30ºC.

Each month, three samples of scyphistomae, attached to the underside surface of mussel shells, were collected by SCUBA diving at the benthic monitoring site. Sampling was done on the same half-submerged fiberglass boat where the *A. coerulea* benthic population dynamics was previously described and at the same sampling dates (Marques et al. 2019b). Scyphistomae were brought alive to the laboratory in *in situ* seawater and placed in 0.2 µm filtered seawater (ca. 20ºC) for about 2h, to ensure complete gut evacuation. Fifty individual scyphistomae per sample were counted and collected under a dissecting microscope (Olympus SZ40; Olympus KL 1500 LCD), using needles and tweezers to carefully detach them, and they were placed in cryotubes before preservation at -30ºC. Ephyrae were collected near the water surface, by horizontal towing, using a modified WP2 plankton net (1.2 m long, 50 cm opening area and 200-µm mesh). Back to the laboratory, they were kept for ca. 2h in filtered seawater to ensure complete gut evacuation. Then, 50 individuals were pooled per sample, before preservation at -30ºC.

2.2.3.3 Medusae sampling for gut content analysis

Among the medusae collected at each sampling date (see above), 5 individuals were individually preserved in 4% buffered formaldehyde. Their gastric pouches, oral arms and the preserving solution were then scrutinized under dissecting microscope (Olympus SZX7 – ILLT). Prey were identified to the lowest possible taxonomic level, but the presence of many degraded exoskeletons often impeded the identification to species level. Only complete exoskeletons were considered in the analysis. This methodology is only suitable for medusae since scyphistomae are very small and their gastrovascular cavity was recurrently empty (R. Marques, personal observation).

2.2.3.4 Sampling of oysters

Fifteen oysters (*Crassostrea gigas*) were obtained from the shellfish producer *Huitres-Bouzigues.com* (mean size of 11.9 ± 1.0 cm) and from the benthic monitoring site (mean size of 11.5 ± 2.0 cm) at five sampling times (October 2017 and January, April, June, August 2018), representing different environmental conditions in the Thau lagoon. The oysters were transported to the laboratory in *in situ* seawater and then carefully dissected to collect the

adductor muscle. The tissues were rinsed with distilled water and preserved at -30ºC until further laboratory analysis.

2.2.3.5 Sampling organic matter (OM) sources for SIA

Plankton and sedimentary organic matter (SOM) were analysed as potential sources for *A. coerulea*. For this, they were collected at the pelagic and benthic sampling stations, respectively, at the same sampling days as scyphistomae and medusae. Three different size classes of plankton organisms were collected as potential sources, hereafter designated as mesozooplankton (>200 µm), microzooplankton (60 - 200µm) and phytoplankton (20 - 60µm). Mesozooplankton samples were collected near the surface, by horizontal towing, using a modified WP2 plankton net (1.2 m long, 50 cm opening area and 200-µm mesh). Each sample was filtered through a 60 µm mesh sieve to eliminate the excess of water and preserved at -30ºC. Microzooplankton and phytoplankton were collected near the surface, by horizontal towing, with a phytoplankton net (1 m long, 30 cm opening area and 20-µm mesh). Once in the laboratory, each sample was passed through a 200 µm sieve. The size fraction > 200 µm was discarded. The remaining sample was separated into two size fractions using a 60 µm sieve, each fraction being equally divided in 5 subsamples. Each subsample was collected on a pre-combusted (500ºC for 24h) Whatman GF/F filter. Two filters of each size fraction were acidified with 1% HCl and triple rinsed with distilled water, to remove inorganic C, which can bias C stable isotope results (Sarakinos et al. 2002; Yokoyama et al. 2005). The remaining non-acidified filters were used for N stable isotope analysis, since the acidification may affect this stable isotope signature (Pinnegar and Polunin 1999). All samples were preserved at -30ºC until further analysis. For SOM, the first 2 cm of the sediment were collected by SCUBA divers at the benthic monitoring site. Samples (2 replicates) were carefully scrutinized to eliminate any large organisms, sediment inorganic particles or vegetal debris, before preservation at -30ºC.

2.2.3.6 In situ abundance of plankton in the Thau lagoon

Phytoplankton, microzooplankton and mesozooplankton were collected at the pelagic monitoring site every two weeks from January to June 2017 and monthly onwards, until December 2017. Phytoplankton was collected from 10 to 20L of surface water filtered with 15 µm mesh net and preserved with 2% buffered formaldehyde. Microzooplankton were collected from a subsample of 30 ml of surface water preserved with 2% buffered formaldehyde (for ciliates) and from a subsample of 110 ml of surface water preserved with lugol (for

heterotrophic flagellates). Phytoplankton and microzooplankton species were identified and counted using sedimentation chambers and an inverted microscope (Olympus IX70), following the Utermöhl method (Utermöhl 1958). Mesozooplankton samples were collected near the surface, by horizontal towing, using a modified WP2 plankton net (1.2 m long, 50 cm opening area and 200-µm mesh). Samples were immediately preserved in 4% buffered formaldehyde until further analysis in the laboratory. Mesozooplankton abundance was determined by visual counting of organisms under dissecting microscope (Olympus SZX7 – ILLT). The species composition of mesozooplankton was not assessed.

2.2.3.7 Stable isotope analysis

All tissue samples (from medusae, scyphistomae and oysters) and SOM samples were freeze-dried for at least 48h and ground to a fine powder with mortar and pestle. Samples for the other potential OM sources were oven-dried at 60ºC for 48h and the biological material was scraped off the filters. The SOM samples were divided into two subsamples. One half was used directly for $\delta^{15}N$ analysis. The remaining subsample was acidified with 1% HCl for decalcification, rinsed several times with distilled water and oven-drying for at 70ºC.

Measurements of $\delta^{13}C$ and $\delta^{15}N$ were performed on 1.5 to 4 mg of biological samples, except for medusae (ca. 10 mg, after salt content correction, based on dry weight and ash-free dry weight relationships, Lucas et al. 1994; Pitt et al. 2009). The analysis was performed using a PDZ Europa ANCA-GSL elemental analyser interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). SOM samples (ca. 55 mg) were analysed using an Elementar Vario EL Cube or Micro Cube elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Calibration was performed against NIST Standard Reference Materials (IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64, and USGS-65). Isotope ratios were expressed as part per thousand (‰) differences from the internal references standards (glutamic acid, alfalfa flour, nylon 6, bovine liver and enriched alanine) using the following equation:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

where X is the ^{13}C or ^{15}N and R is the corresponding ratio, $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

As the lipid content of organisms affects their $\delta^{13}C$ signatures, $\delta^{13}C$ correction is required when C:N are higher than 3.5 (Post et al. 2007; Logan et al. 2008). Therefore, the $\delta^{13}C$

values obtained for *A. coerulea* scyphistomae and medusae (mean C:N 3.7 ± 0.1 and 3.9 ± 0.6, respectively) and those of the mesozooplankton (mean C:N of 6.9 ± 3.0) were corrected ($\delta^{13}C_{corr}$) according to the equation proposed by D'Ambra et al. (2014) for jellyfish:

$$\delta^{13}C_{corr} = \delta^{13}C_{initial} - 9.43 + 2.69 \times C{:}N$$

and Syväranta and Rautio (2010) for zooplankton:

$$\delta^{13}C_{corr} = \delta^{13}C_{initial} + 7.95 \times \left(\frac{C{:}N - 3.8}{C{:}N}\right)$$

2.2.3.8 Gut content data analysis

Although *A. coerulea* medusae (*i.e.* > 1 cm bell diameter) were present in the lagoon from March, gut contents analysis was only performed on individuals collected between April and June. The importance of each prey in the diet of *A. coeruela* medusae, was expressed by the following indices: (i) the index of frequency of occurrence of a prey (FO, %), which represents the percentage of medusae (with food content in their guts) with a given prey taxon; (ii) the index of relative importance of a prey (IRI, %), representing the percentage of the prey *i* in relation to the total prey in the guts; (iii) the mean abundance of each prey item in the guts (ind.medusae^{-1}).

2.2.3.9 Relationship between benthic population dynamics and plankton abundance

Data regarding the benthic population dynamics was obtained from Marques et al. (2019b). Generalized linear models (GLM, using linear and logistic regressions, without interactions), were employed to assess the contribution of non-averaged phytoplankton, microzooplankton and mesozooplankton abundance (after logarithmic transformation ln (x+1)) to the observed temporal trend of the mean scyphistomae coverage (%) and the proportion of population producing non motile buds (NMB). The models were validated by examination of plots of residuals versus fitted values (Zuur et al. 2009).

2.2.3.10 Determination of Isotopic Niche Periods (INP)

To reveal potential shifts in the trophic niches of *A. coerulea* scyphistomae and medusae over time, a cluster analysis was performed on the monthly mean isotopic values of both jellyfish life stages. This allowed identifying periods of the year when *A. coerulea* scyphistomae and medusae present stable isotopic signatures (i.e. stable Isotopic Niche Periods, INPs), providing the basis for understanding what are their main sources of OM at different times of

the year. INPs were defined according to Partitioning algorithms. Partitioning algorithms are clustering techniques that subdivide the data sets into a set of k groups, based on K-means clustering, in which each cluster is represented by the center of the data points belonging to the cluster. The number of k groups was defined after k-means method, which aims to partition the points into k groups such that the sum of squares from points to the assigned cluster centers is minimized. The clustering analysis was performed using the package "factoextra" (Kassambara and Mundt 2017).

2.2.3.11 Assessment of intra- and interspecific trophic competitions

While intraspecific competition between *A. coerulea* scyphistoma and medusae was assessed within each INP, interspecific competition between *A. coerulea* (scyphistoma and medusae) and oysters (cultivated and wild) was only assessed globally, using data from the whole study period, assuming that its potential inter-annual variability is negligible. In both cases, the competition was assessed using the Bayesian framework proposed by Jackson et al. (2011). First, Bayesian multivariate normal distributions were fitted to the signatures of each organism. Then, the overlap between their trophic niches was calculated based on maximum likelihood fitted ellipses, using the function "maxLikOverlap" from the R package "SIBER" (Jackson et al. 2011).

2.2.3.12 Determination of the contribution of OM sources for the diet of jellyfish

The relative contribution of the OM sources to the diet of *A. coerulea* life stages was assessed within each INP by Bayesian mixing models developed specifically for stable isotope studies, using the package "MixSIAR" (Stock and Semmens 2016). By generating the probability distributions of all potential mixing solutions with the associated confidence intervals (based on 300 000 chain length), this method allows the identification of the most likely contributions for all OM sources. The MixSIAR provides a graphical user interface (GUI) which allows investigation of the contributions of multiple sources of organic matter to the diet of our target predator (*i.e.* scyphistomae and medusae), taking into account not only the isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of the sources and the predators, but also the uncertainties and variability around these estimates. The method also allows the use of different fractionation factors and to include standard deviation values for each individual source.

Differences in isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) among the OM sources (phytoplankton, microzooplankton, mesozooplankton and SOM) were tested by

PERMANOVA analysis (Anderson 2017), based on a log10 transformed Bray-Curtis distance matrix (- $\delta^{13}C$ and $\delta^{15}N$), using the package "vegan" (Oksanen et al. 2019), followed by pairwise comparisons using "pairwiseAdonis" package in R (Martinez Arbizu 2019). Sources with no significant differences were grouped for MixSIAR models.

As previously performed in other jellyfish studies (*e.g.* Morais et al. 2017), the fractionation values estimated by Zanden and Rasmussen (2001) were applied, for both *A. coerulea* life stages and according to the type of OM source consumed (plant vs. animal): for $\delta^{13}C$ we used 0.47 ± 1.23 ‰ for all trophic levels and for $\delta^{15}N$ we used 2.52 ± 2.5 ‰ and 3.23 ± 0.41 ‰ for the first and the following trophic levels, respectively. Like Fleming et al. (2015) and Milisenda et al. (2018), we did not use the fractionation values reported by D'Ambra et al. (2014), since they are very distinct from those mostly used in the literature (Zanden and Rasmussen 2001; Post 2002; McCutchan et al. 2003) and still require further laboratory corroboration (D'Ambra et al. 2014).

The basal tissue turnover rate for *Aurelia* sp. is ca. 1 ‰ day^{-1} for $\delta^{13}C$ and ca. 2‰ day^{-1} for $\delta^{15}N$, taking 18 to 20 days to reach the stable isotopic steady state of its tissues (D'Ambra et al. 2014). Therefore, to account for such turnover rates, the MixSIAR models were run by INP, including a time lag of one month for the OM sources considered. The model for the medusae included only the signatures of the OM sources around the period when they were present in the lagoon (*i.e.* according to the time lag, from February to May).

2.2.4. Results

2.2.4.1 Medusae gut contents in link with plankton availability

Among the 25 medusae gut contents analysed during the study period, four were empty. The bell diameter of the medusae collected for gut content analysis did not vary over time (ANOVA, F (2) = 1.4, *p-value* = 0.2), remaining at ca. 8.5 cm from April to June. Overall, more than 88% of the prey items identified were mesozooplankton, while microzooplankton and phytoplankton represented only 8 and 4%, respectively. The phytoplankton organisms identified were diatoms and dinoflagellates, while microzooplankton organisms were mainly represented by tintinnids. Masses of unidentifiable organic matter were recurrently observed. Phytoplankton and microzooplankton were only found in the guts in April and May (Fig.2, Table 1, Supplementary Table 1). During these months, phytoplankton occurred in 20 and 33% of the gut contents analysed, while microzooplankton was observed in 60 and 56% of them (FO in April and May, respectively). Despite of their increasing trend from April to May (Fig. 2),

the IRI and abundances for phytoplankton and microzooplankton were still relatively low (IRI < 13% and a maximum of 2.2 ± 3.8 ind.medusa^{-1} for microzooplankton, Table 1). Yet, in May, microzooplankton was more important in the medusae gut (IRI 12.5%) than the prey gathered in the group of "other crustaceans", composed by cladocerans, ostracods, among others (IRI 10.0%, Table 1, Supplementary Table 1).

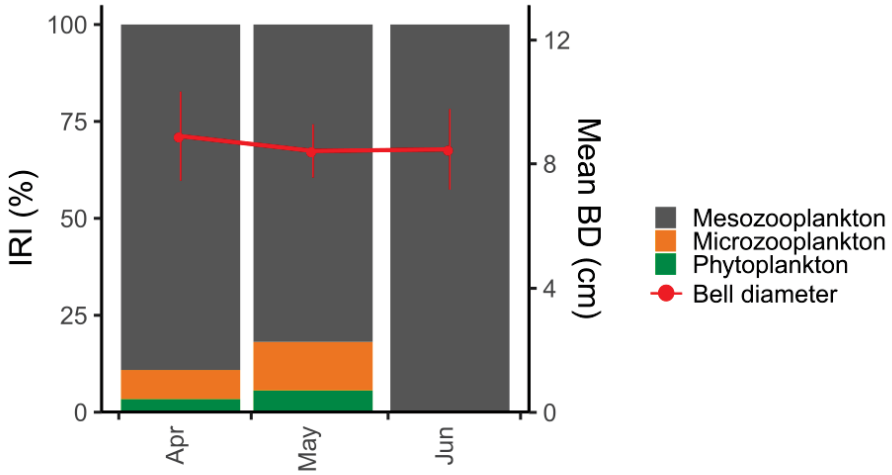


Fig. 2: Index of relative importance (IRI) of the three main prey groups assessed by gut content analysis and bell diameter of all medusae collected for gut content analysis.

Twenty-four different taxa of mesozooplankton were identified in the guts of the medusae. Among them, copepods and nauplii (from cirripeds and copepods) were the most important prey items: they occurred in 40 to 88.9% of the gut contents analysed and represented up to 46.3% of the prey items identified (in June, Table 1). The maximum abundance of mesozooplankton in the guts was recorded in April (26.2 ± 35.4 ind.medusae^{-1}), when copepods and non-crustacean taxa (mainly gastropod veliger) represented more than 80% (IRI) of the prey items found. In the next month, the importance of each taxa group was more homogeneous, with higher importance of nauplii (IRI 31.3%). In June, nauplii and copepods were the most important taxa groups, contributing to 85% (IRI) of the observed prey.

Table 1: Frequency of occurrence (FO), index of relative importance (IRI) and mean abundance of prey items found in *Aurelia coerulea* medusae gut contents during the period of its presence in Thau lagoon. Bold numbers in parenthesis are the numbers of medusae with prey items analysed.

	FO (%)			IRI (%)			Abundance (± SD) (ind.medusae^{-1})		
Prey	**Apr (5)**	**May (9)**	**Jun (8)**	**Apr (5)**	**May (9)**	**Jun (8)**	**Apr (5)**	**May (9)**	**Jun (8)**
Phytoplankton	20.0	33.3	0.0	3.4	5.6	0.0	1.0 (2.2)	1.0 (1.8)	0.0 (0.0)
Microzooplankton	60.0	55.6	0.0	7.5	12.5	0.0	2.2 (3.8)	2.2 (3.4)	0.0 (0.0)
Total Mesozooplankton	80.0	88.9	100	89.1	81.9	100	26.2 (35.4)	14.6 (13.4)	10.3 (18.3)
- Copepods	40.0	66.7	87.5	34.7	21.9	46.3	10.2 (20.1)	3.9 (5.7)	4.8 (9.9)
- Nauplii (copepods and cirripeds)	60.0	88.9	62.5	4.8	31.3	41.5	1.4 (2.1)	5.6 (8.5)	4.3 (7.8)
- Other crustaceans	20.0	55.6	50.0	0.7	10.0	8.5	0.2 (0.4)	1.8 (3.5)	0.9 (1.1)
- Non-crustaceans	60.0	66.7	25.0	49.0	18.8	3.7	14.4 (20.9)	3.3 (4.5)	0.4 (0.7)

All three components of the plankton (phytoplankton, microzooplankton and mesozooplankton), showed high intra-annual variability in abundance in the lagoon (Fig. 3). Peaks in abundance for phytoplankton were observed in January (25 138 ± 34 047 cell.L^{-1}) and May (35 794 ± 18 374 and cell.L^{-1}), for microzooplankton in February, April and September (> 6 200 cell.L^{-1}) while for mesozooplankton peaks were observed in June (90 895 ± 107 072 ind.m^{-3}). The taxa that most contributed to the phytoplankton and microzooplankton abundance during the study period were *Chaetoceros* sp. and *Strombidium* sp., respectively (Supplementary Table 2). Although mesozooplankton diversity was not assessed, *Acartia* sp. are recurrently the most abundant taxa in Thau (Boyer et al. 2013).

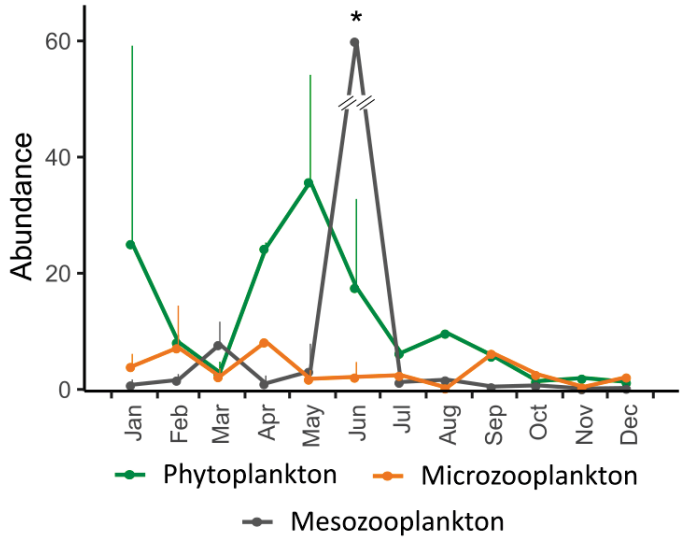


Fig. 3 : Temporal variability of the abundance of phytoplankton (x10^3 cell-L^{-1}), microzooplankton (x10^3 cell.L^{-1}) and mesozooplankton (x10^3 ind.m^{-3}) collected in the Thau lagoon during the study period. All values represent monthly means ± SD. In June 2017 (*), the mean and SD of the abundance of mesozooplankton were 90 895 ± 107 072 ind.m^{-3}.

2.2.4.2 Contribution of the plankton to the benthic population dynamics

The scyphistomae coverage peaked in April (11.6 ± 3.7 %) and was minimum in October (1.4 ± 1.3 %, Fig. 4). Scyphistomae coverage was not significantly correlated with the abundance of any of the seston components tested (*p-value* > 0.05, Table 2).

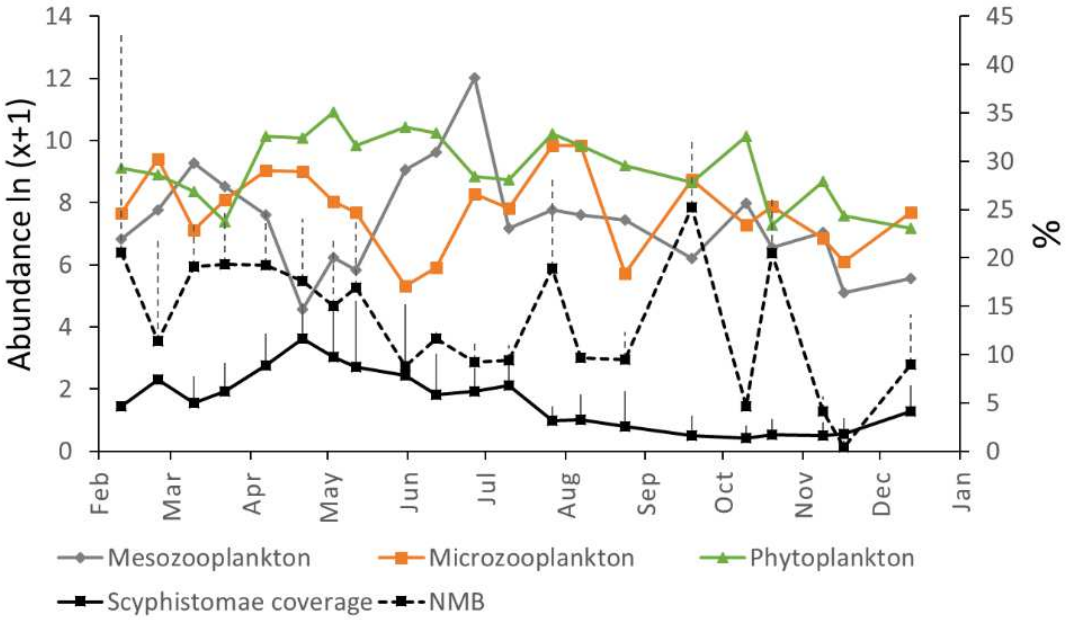


Fig. 4 : Temporal variability of the benthic population dynamics parameters and abundance of planktonic seston in the Thau lagoon during the study period (adapted from Marques et al. 2019b). Black lines represent the percentage of scyphistomae coverage (solid line) and the percentage of the scyphistomae producing buds (NMB, dashed line), collected every two weeks. Each point represents replicate means and vertical bars are SD (see Marques et al. 2019b for further information). Coloured lines represent the non-averaged abundance (after logarithmic transformation) of phytoplankton (cell-L^{-1}), microzooplankton (cell.L^{-1}) and mesozooplankton (ind.m^{-3}).

The mean percentage of scyphistomae producing buds (NMB) was highly variable during the study period, ranging from 0.4 ± 0.7 % in November to 25.2 ± 7.3 % in September (Fig. 4). The percentage of scyphistomae producing buds was positively correlated with the abundance of microzooplankton (GLM, *t*-value = 9.56, *p-value* < 0.01, Table 2).

Table 2 : Parameters of the generalized linear models (GLM) used to assess correlations between the benthic population dynamics variables [scyphistomae coverage and percentage of scyphistomae producing non-motile buds (NMB)] with the abundance [ln (x+1)] of phytoplankton (Phyto., cell-L-1), microzooplankton (Micro., cell-L-1) and mesozooplankton (Meso., ind.m-3).

	Estimate	**Std. Error**	***t* value**	***p-value***
Scyphistomae coverage (%)				
(Intercept)	-0.08	0.07	-1.11	0.28
Phyto.	0.01	0.01	2.06	0.06
Micro.	0.00	0.01	0.66	0.52
Meso.	0.00	0.00	-0.24	0.81
NMB (%)				
(Intercept)	-3.21	0.30	-10.59	**< 0.01**
Phyto.	-0.03	0.02	-1.31	0.19
Micro.	0.21	0.02	9.56	**< 0.01**
Meso.	-0.01	0.02	-0.57	0.57

2.2.4.3 Temporal variation of A. coerulea stable isotope

The $\delta^{13}C$ and $\delta^{15}N$ signatures showed significant temporal variation for both life stages (one-way PERMANOVA, *Pseudo-F* (11) = 22.7, *p-value* < 0.01 and *Pseudo-F* (3) = 38.6, *p-value* = 0.001, for scyphistomae and medusae, respectively), but differences between stages were never significant during the period of medusae presence, from March to June (one-way PERMANOVA, *Pseudo-F* (1) = 1, *p-value* = 0.4). The mean bell diameter of the medusae used for SIA, showed a sharp increase between March (1.0 ± 0.3 cm) and June (8.9 ± 1.1 cm), with an estimated overall growth of 0.8 mm.day^{-1}. The $\delta^{13}C$ signature of the medusae increased from -23.4 ± 0.1‰ in March to -19.4 ± 0.5‰ in June (Fig. 5), while their $\delta^{15}N$ remained stable for the first three months (at 8.1‰), increasing afterwards to a maximum at 8.9 ± 0.3‰ in June. For the scyphistomae, the minimum $\delta^{13}C$ value was registered at the beginning of the study period (in January 2017, -23.4 ± 0.1‰). $\delta^{13}C$ signature then increased to reach maximum values in June, July and August (> -19.4) and decreased again afterwards until January 2018 (-22.3 ± 0.4‰). The $\delta^{15}N$ signature of scyphistomae showed a similar temporal trend as that of $\delta^{13}C$, with minimum values at the beginning and the end of the study period (8.3 ± 0.1‰ and 8.0 ± 0.4‰ in January 2017 and 2018, respectively), and maximum values in July and August (9.1 ± 0.1‰). However, a sharp decline in $\delta^{15}N$ was observed in February (7.1 ± 0.5‰). Ephyrae (bell diameter of 0.21 ± 0.1 cm) were only collected in January 2018 showing $\delta^{13}C$ and $\delta^{15}N$ values of -22.8 ± 0.1‰ and 8.5 ± 0.3‰, respectively, with no significant differences from those of the scyphistomae collected at the same sampling time (T-tests, *p-value* > 0.05).

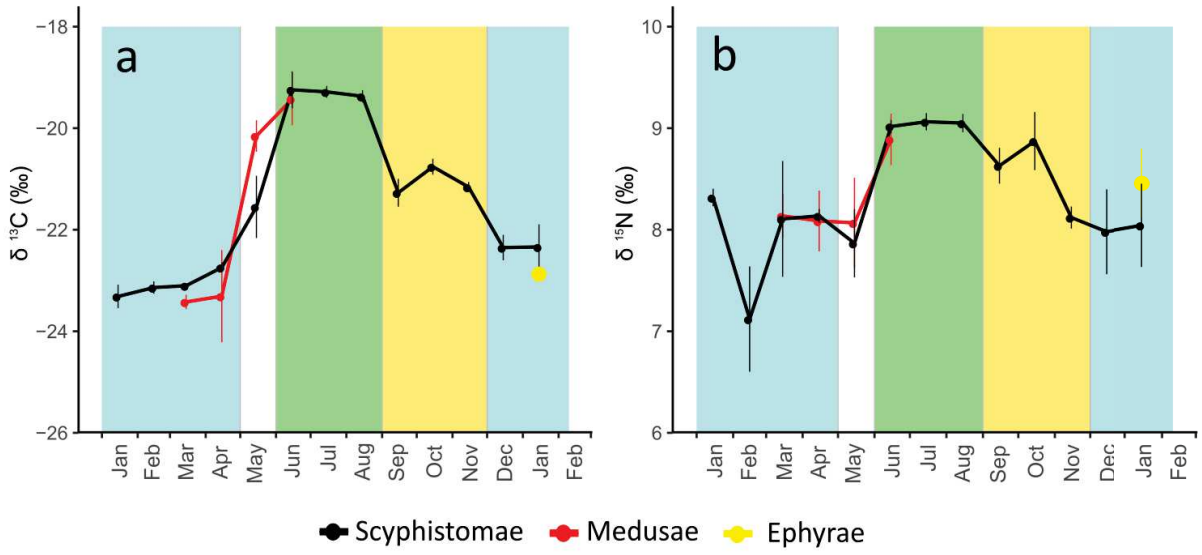


Fig. 5: Temporal variability of $\delta^{13}C$ (a) and $\delta^{15}N$ (b) of scyphistomae, medusae and ephyrae. All values represent monthly means ± SD. Background colours represent the different isotopic niche periods (blue: INP 1, green: INP 2, yellow: INP 3; see Fig.6). May represents a transitional period and not included in any INP.

The clustering analysis revealed 3 distinct groups among the monthly isotopic signatures obtained for both the medusae and the scyphistomae of *A. coerulea* (Fig. 6), which allowed to identify three periods of stable isotopic signatures during the year (Isotopic Niche Periods, INP). INP 1 comprised the $\delta^{13}C$ and $\delta^{15}N$ signatures of both stages from December to April, irrespective of the year (2017 or 2018). INP 2 grouped the signatures of both stages from June to August and INP 3 grouped the signatures from September to November, together with May. However, May was a particular month, with sharp changes in $\delta^{13}C$ and $\delta^{15}N$ reflecting a rapid transition from the isotopic signature of INP 1 to that of INP 2. Therefore, it was not included in any INP.

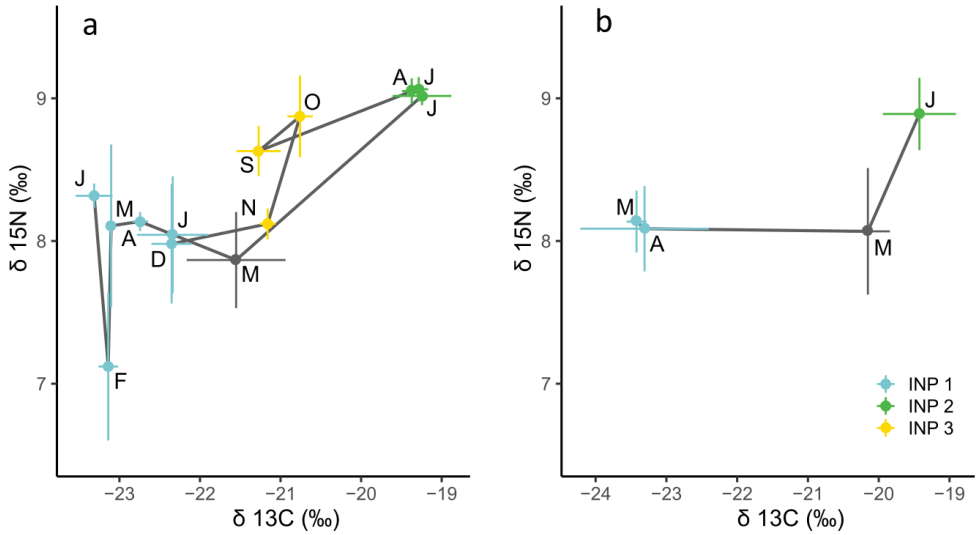


Fig. 6 : Time trajectory of the evolution of the isotope signature, averaged by month, from scyphistomae (a) and medusae (b). Letters represent months (from January 2017 to January 2018). Coloured points represent isotopic niche periods defined after cluster analysis: INP 1 is from January to April 2017, December 2017 and January 2018; INP 2 is from June to August 2017 and INP 3 is from September to November 2017. May represent a transitional period between the INP1 and INP2 and was therefore not included in any INP.

2.2.4.4 Monthly variability of OM sources signatures

$\delta^{13}C$ and $\delta^{15}N$ signatures varied among OM sources and over time over the study period (significant interaction, PERMANOVA, *Pseudo-F* (17) = 23.1, *p-value* < 0.01; Fig. 7). Minimum values of $\delta^{13}C$ for phytoplankton, microzooplankton and mesozooplankton were observed in March (-24.7 ± 0.3, -23.3 ± 0.1 and -23.7 ± 0.0 ‰, respectively) with a sharp increase in the following months, reaching maximum values in November for phytoplankton and microzooplankton (-19.0 ± 0.0 and -19.9 ± 0.1 ‰, respectively) and in May for mesozooplankton (-18.8 ± 0.2 ‰). Mesozooplankton was the OM source with the highest values of $\delta^{15}N$ (range from 7.3 ± 0.3‰ to 8.4 ± 0.0‰, in May and March, respectively). Phytoplankton and microzooplankton followed similar temporal variability with minimum

values in May (5.8 ± 0.5 ‰ and 6.0 ± 0.3 ‰, respectively) and maximum values in July (6.7 ± 0.3 ‰ and 7.4 ± 0.2 ‰, respectively) and in February for phytoplankton (6.7 ± 0.0 ‰). Both the $\delta^{13}C$ and $\delta^{15}N$ signatures of SOM decreased from March to April, but they remained constant afterwards, at around -20.4‰ and 5.4‰, respectively.

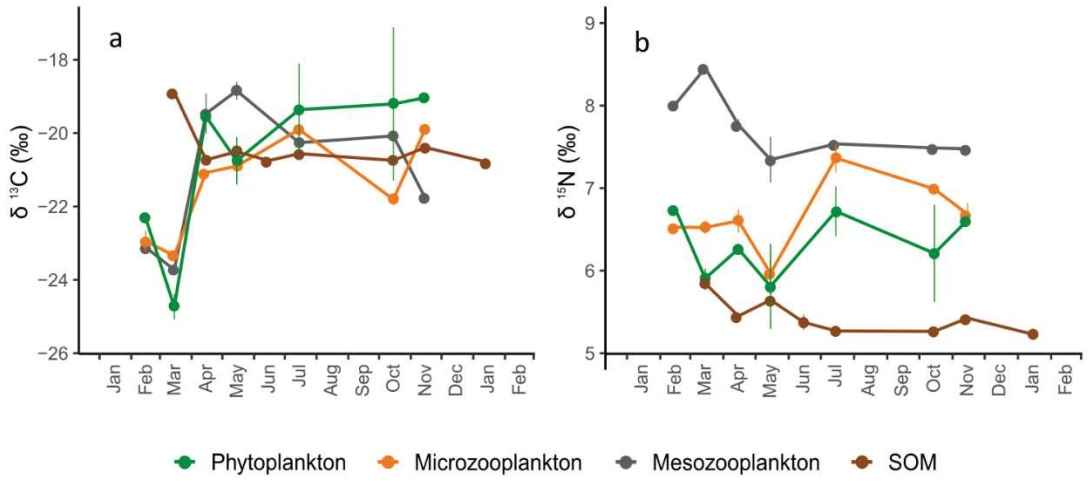


Fig. 7: Monthly variability of the $\delta^{13}C$ (a) and $\delta^{15}N$ (b) of the sources of OM collected in this study.

2.2.4.5 Contribution of OM sources to jellyfish isotopic signatures

Since the $\delta^{13}C$ and $\delta^{15}N$ signatures of phytoplankton and microzooplankton were not significantly different (PERMANOVA post-hoc test, *Pseudo-F* (1) = 5.7, *adjusted p-value* = 0.17) these two OM sources were pooled as Pelagic Organic Matter (POM) when assessing the contribution of each OM source to the isotopic signature of scyphistomae and medusae. The remaining sources were included individually in the model (Table 3).

Table 3: Stable C and N isotope values (mean ± SD) of *A. coerulea* and OM sources used in MixSIAR model. Source A are the values of OM sources used for *A. coerulea* scyphistomae, including all data, while Source B are the values of OM sources collected from February to May, used for *A. coerulea* medusae models. n is the number of samples used to calculate the mean. SOM: sedimentary organic matter, POM: pelagic organic matter, Mesoz.: mesozooplankton.

	INP 1			INP 2			INP 3		
Predator	**δ 13C (± SD) ‰**	**δ 15N (± SD) ‰**	**n**	**δ 13C (± SD) ‰**	**δ 15N (± SD) ‰**	**n**	**δ 13C (± SD) ‰**	**δ 15N (± SD) ‰**	**n**
Scyphistomae	-22.8 (0.4)	8.0 (0.5)	18	-19.3 (0.2)	9.0 (0.1)	9	-21.1 (0.3)	8.5 (0.4)	9
Medusae	-23.4 (0.7)	8.1 (0.3)	13	-19.4 (0.5)	8.9 (0.3)	7			
Source A									
POM	-22.1 (2.0)	6.5 (0.3)	18	-20.6 (0.8)	6.2 (0.7)	22	-21.0 (0.9)	6.7 (0.3)	6
Mesoz.	-22.9 (0.9)	8.0 (0.4)	9	-19.2 (0.7)	7.4 (0.3)	12	-20.1 (0.1)	7.5 (0.0)	3
SOM	-20.2 (0.9)	5.5 (0.3)	6	-20.6 (0.1)	5.4 (0.2)	6	-20.7 (0.0)	5.3 (0.0)	2
Source B									
POM	-23.3 (0.9)	6.4 (0.3)	12	-20.9 (0.5)	5.8 (0.3)	15			
Mesoz.	-23.4 (0.3)	8.2 (0.2)	6	-18.8 (0.2)	7.3 (0.3)	9			
SOM	-18.9 (0.0)	5.8 (0.1)	2	-20.5 (0.0)	5.6 (0.0)	2			

The contribution of each OM source to the isotopic signature of both the benthic and the pelagic stages of *A. coerulea* varied according to the INP (Fig. 8). For the scyphistomae, the model suggested a dietary shift from POM consumption in INP 1 (93.3%) to a diet based on benthic and pelagic sources in INP 2 (SOM: 36.6%, POM: 24.4% and Meso.: 39.3%). In INP 3, although POM was identified as the main source of OM (69.2%), the model revealed that SOM was still an important OM source (27.0%). For medusae, POM was the only food source (100%) in INP 1, but the diet changed in INP 2, including mainly SOM (64.3%) and Mesozooplankton (32.3%).

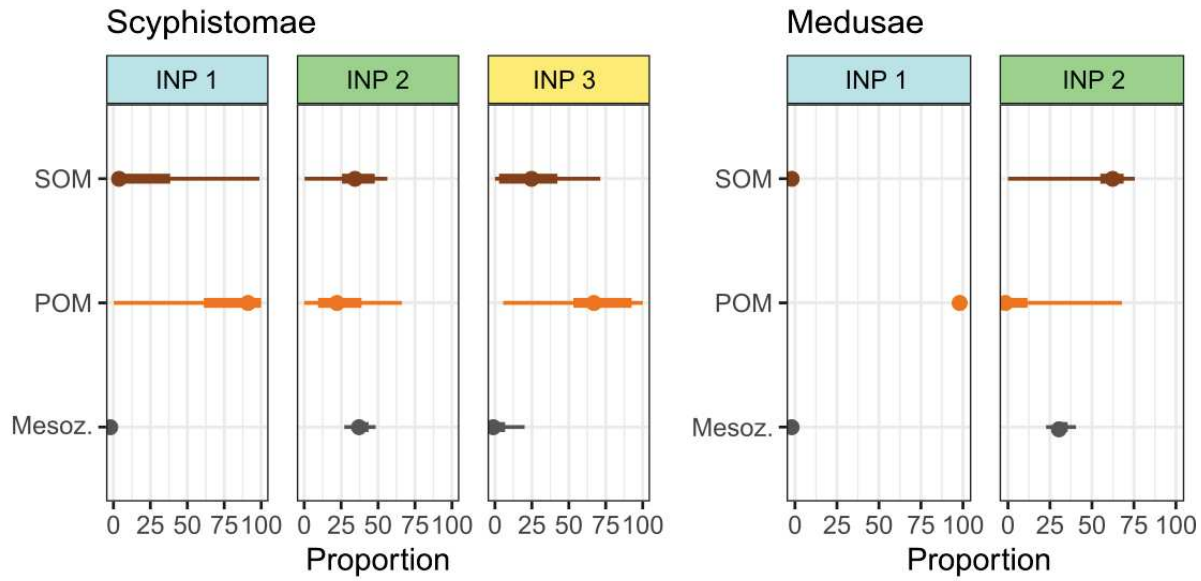


Fig. 8: Proportion of the contribution of each OM source to the diet of *A. coerulea* scyphistomae and medusae in the different trophic periods (TNP 1, TNP 2 and TNP 3). The proportion was calculated using MixSIAR mixing models. The circles indicate the median and the lines represent 75% and 95% Bayesian credibility intervals. SOM: Sedimentary organic matter, POM: Pelagic organic matter, Meso.: Mesozooplankton.

2.2.4.6 Intra and interspecific competition

Intraspecific isotopic niche overlap was observed during the period of co-occurrence of the benthic and pelagic stages of *A. coerulea* in the lagoon (March to June; Fig 9). However, it was found to be higher in INP 1 (41.5% of niche overlap) than in INP 2 (only 9.9%). Still, despite of the low overlap percentage in INP 2, the isotopic niche of medusae covers that one of scyphistomae. Only one ephyrae sample was collected in this study, which is positioned within the trophic niche of scyphistomae, suggesting high (although not quantifiable) trophic niche overlap.

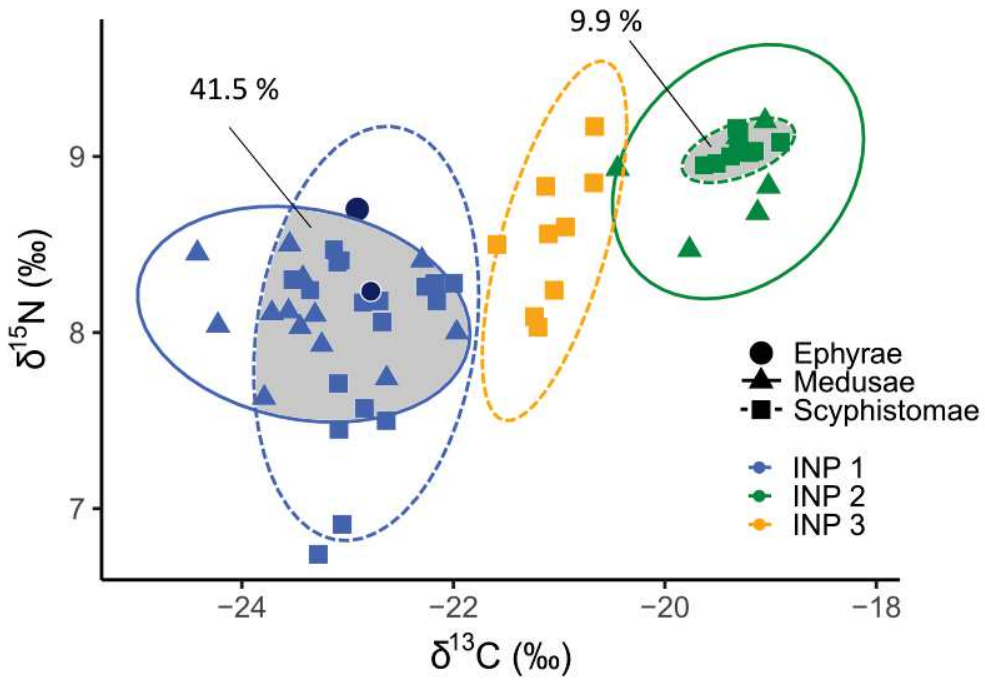


Fig. 9: Biplot of isotope values of *A. coerulea* ephyrae, medusae and scyphistomae. Ellipses indicate their isotopic niche in Thau lagoon, during the different isotopic niche periods (as 95% confidence ellipse of the bivariate means). Grey areas and associated values on the graph indicate the percentage of overlap, when observed.

Significant differences in the $\delta^{13}C$ and $\delta^{15}N$ signatures were observed between cultivated and wild oysters (PERMANOVA, *Pseudo-F* (11) = 12.4, *p-value* < 0.01; Fig. 10). For cultivated oysters the varied from -20.6 to -18.5 ‰ and from 8.4 to 9.1 ‰, respectively, while for wild oysters $\delta^{13}C$ and $\delta^{15}N$ signatures ranged from -25.6 to -19.6 ‰ and 8.7 to 9.4‰, respectively (Fig. 10). Interspecific isotopic niche overlap between both stages of *A. coerulea* and oysters appeared to be generally limited (< 30% of overlap), while it was higher between cultivated and wild oysters (35.4%). The isotopic niche overalp of both *A. coerulea* life stages was more important with cultivated oysters, but especially for medusae (29.1% of overlap). However, if we assume a negligible inter-annual variability of the oyster's isotopic signatures, overlapping niches were only observed in one particular period of the year (INP 2), with only the one from medusae overlapping those of oysters (21.8 and 21.1% with cultivated and wild oysters, respectively). During INP 1, the isotopic niche of both stages of *A. coerulea* and oysters did not overlap, while during INP 3, when scyphistomae and oysters were collected in the same year (2017), their isotopic niches were clearly different, indicating a lack of interspecific competition.

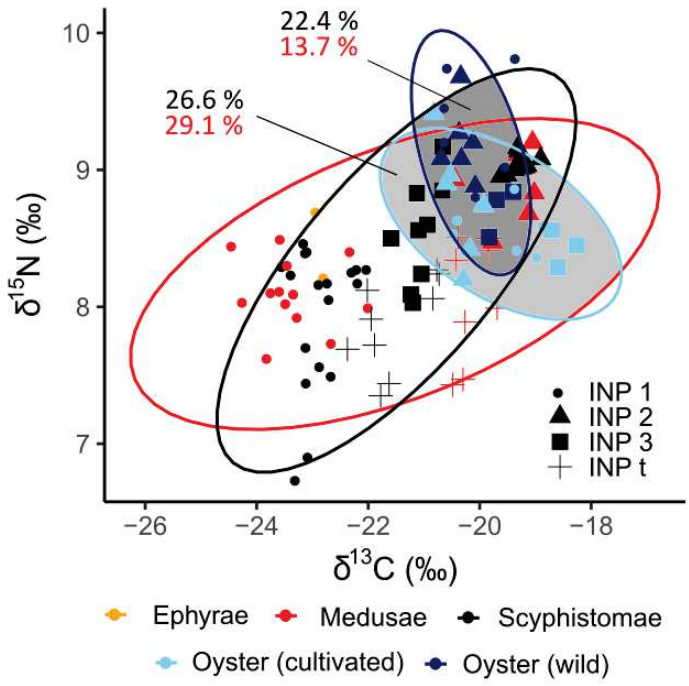


Fig. 10 : Biplot of isotope values of *A. coerulea* ephyrae, medusae, scyphistomae and oysters (cultivated and wild). Ellipses indicate their isotopic niche in Thau lagoon, considering the whole study period (as 95% confidence ellipse of the bivariate means). Dark and light grey areas indicate overlap between oysters (wild and cultivated, respectively) and *A. coerulea*. Associated values on the graph indicate the percentage of overlap with medusae (in red) and scyphistomae (in black). The shape of points represents isotopic niche periods (INP t: transitional period, i.e. samples collected in May).

2.2.5. Discussion

To our knowledge, this is the first study to investigate the trophic ecology of both the benthic and the pelagic stages of a jellyfish species (*A. coerulea*) in association with its *in situ* population dynamics. The Thau lagoon offered the rare opportunity to identify potential bottom-up processes regulating *A. coerulea* population, contributing to our understanding of its blooms formation. Furthermore, assessing *A. coerulea* potential trophic competition with the oysters found in the lagoon, is of high relevance due to the central role of shellfish farming on the local economy.

2.2.5.1 Limitation of the study

Although SIA is a powerful tool to assess the trophic ecology of jellyfish, our results from the MixSIAR models should be considered with caution. First, because the isotopic signatures of phytoplankton and microzooplankton were not significantly different in our study and, therefore, we were not able to precisely identify the importance of each of these two plankton components to the diet of both stages of *A. coerulea* in the model. In addition, the possible bias associated to the gut content analysis (*i.e.* rapid digestion of small and soft prey),

might conceal the importance of some prey such as phytoplankton and microzooplankton. Medusae and scyphistomae might have some level of prey selectivity, even within the same spectrum of prey size, and feed simultaneously on different prey sizes (*e.g.* Sullivan et al. 1994; Huang et al. 2015). Therefore, the contribution of phytoplankton *vs.* microzooplankton to the diet of scyphistomae and medusae might be different and further quantitative and qualitative studies on their diet should be performed to complement our findings. Secondly, despite of the extensive frequency of sampling of OM sources during our study, some periods of the year (*e.g.* July – September) were less represented in the database, which might bias the MixSIAR mixing model results. We should always keep in mind that the mathematical results of mixing models might not be biologically relevant, since they always provide a solution, and their accuracy decrease with increasing number of introduced OM sources (Dubois et al. 2007). Finally, the use of different fractionation values in the mixing models, drastically modify their final results. In our study, the use of the fractionation values proposed by D'Ambra et al. (2014) would result in a higher contribution of mesozooplankton to the diet in both stages of *A. coerulea*, which is in accordance with previous studies (*e.g.* Hansson 2006; Ishii and Tanaka 2006; Malej et al. 2007; Lo and Chen 2008). However, the values from D'Ambra et al. (2014) are very different from those typically reported in the literature (*e.g.* Zanden and Rasmussen 2001; Post 2002), leading to unrealistic trophic levels (Fleming et al. 2015; Milisenda et al. 2018). Therefore, we decided to use the traditional values, until further confirmation of the values proposed by D'Ambra et al. (2014) is available. Furthermore, temperature (which is highly variable in Thau lagoon), feeding condition, sexual maturity (*e.g.* Barnes et al. 2007) and, probably, life stage might also affect fractionation and turnover values. In our study, due to the monthly frequency of data analysis and following the results reported for *Aurelia* sp. (18-20 days, based on half-life, D'Ambra et al. 2014), long turnover values (one month) were used for both life stages. All and each of these parameters might lead to a potential bias in the MixSIAR results.

2.2.5.2 Trophic ecology of A. coerulea pelagic stages in the Thau lagoon

Although ephyrae were only collected once during the study period, their signature was similar to that of schyphitomae at the same sampling time. In Thau, ephyrae are mainly released in November, but strobilation continues until April (Marques et al. 2019b). Therefore, ephyrae could have been released few days or weeks before our sampling and their isotopic signatures still reflected the signature of the diet at the scyphistomae stage. This is very likely because ephyrae have a very low growth rate during the winter months (< 0.1 $mm.day^{-1}$, Marques et al. 2015a). Therefore, the ephyrae caught in January have probably not yet incorporated the

signature of the prey consumed after release (Fry and Arnold 1982; Frazer et al. 1997). Nevertheless, phytoplankton, microzooplankton (such as rotifers) and suspended particulate OM have been previously identified as important food sources for ephyrae (Sullivan et al. 1997; Bamstedt et al. 2001; Zheng et al. 2015), which is also in agreement with the OM source (*i.e.* POM) identified as the most important for the diet of scyphistomae at this time of the year.

Our results based on gut contents analysis are in agreement with previous reports, describing the *Aurelia* sp. medusae as zooplanktivorous organisms, feeding mainly on copepods (*e.g.* Hansson 2006; Ishii and Tanaka 2006; Malej et al. 2007; Lo and Chen 2008). Indeed, in Thau 88% of the prey of *A. coerulea* medusae belonged to the mesozooplankton, while only 12% were from microzooplankton and phytoplankton. *Aurelia* sp. medusae appear to have some level of prey selectivity and higher clearance rates over crustacean prey, such as copepods, cirriped larvae and cladocerans, and less preference for prey like echinoderm larvae and bivalve veliger (Purcell and Sturdevant 2001; Hansson et al. 2005; Hansson 2006; Lo and Chen 2008). In Thau, copepods and nauplii (mainly from cirripeds) were the most important prey items consumed by *A. coerulea* medusae over the study period, which is in agreement with the previous studies. Phytoplankton and microzooplankton also contributed to the diet of medusae in this study, but only in the first two months. As expected from the absence of difference in medusae bell diameter collected for gut content analysis over time, the diet found here likely reflected the available plankton community in the environment at the moment of sampling (*e.g.* Ishii and Tanaka 2001b). Indeed, abundances for microzooplankton and phytoplankton in the lagoon peaked in April and May, respectively (Fig. 3), which might explain the higher contribution of these prey to the diet of *A. coerulea* medusae during these months. Yet, despite of its lower *in situ* abundance, mesozooplankton represented consistently more than 80% (IRI) of the prey identified in the medusae gut content (Fig. 2, Table 1).

Although gut content analyses provided important qualitative information on the diet of jellyfish medusae, conclusions regarding the importance of each prey type for their growth, at longer time scales, should be drawn with caution. The digestion time of mesozooplankton in the gut of medusae might vary between 1 and 5h, depending on medusae size, temperature and prey type (Båmstedt and Martinussen 2000; Ishii and Tanaka 2001; Martinussen and BÅmstedt 2001), with smaller prey being digested faster (Martinussen and BÅmstedt 2001). Therefore, gut content analysis often leads to an overestimation of the importance of hard and big prey in the diet, such as crustaceans. This might have contributed to a general oversight of the potential relevance of the lower trophic levels to the diet of jellyfish (Javidpour et al. 2016).

The use of the complementary SIA approach, underlined the importance of phytoplankton and microzooplankton (pooled as POM) as well as that of the SOM for *A. coerulea* medusae in the Thau lagoon. The $\delta^{13}C$ (-23.4 to -19.4‰) and $\delta^{15}N$ (8.1 to 8.9‰) values of this life stage were in the range of the values published by Fleming et al. (2015) (-20.3 to -18.1 for $\delta^{13}C$ and 8.5 to 11.8 for $\delta^{15}N$) and D'Ambra et al. (2013) (mean of -20.5 ± 0.3‰ and 7.2 ± 0.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively), but $\delta^{15}N$ signature were lower than those reported by Javidpour et al. (2016) (-22.8 to -20.6 for $\delta^{13}C$ and 11.0 to 15.1 for $\delta^{15}N$). In the latter study though, the high local $\delta^{15}N$ values were highlighted and discussed (Javidpour et al. 2016), which suggest that our results are in the common range of $\delta^{13}C$ and $\delta^{15}N$ reported so far. In Thau, a significant temporal shift in the $\delta^{13}C$ and $\delta^{15}N$ signatures was observed, revealing two periods of different isotopic niche: INP 1 from March to April, when $\delta^{13}C$ and $\delta^{15}N$ values were low, and INP 2 (June) when enrichments of ca. 3.5 and 1‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, were recorded.

This change in isotopic signature, might be a reflection of rapid ontogenic changes in the diet of the medusae, as well as temporal variability of the OM sources signatures. Variations in the signature at the base of the food webs are reflected by the higher trophic levels (Post 2002). The values reported for the OM sources assessed in this study are in agreement with those previously reported in Thau lagoon (Pernet et al. 2012b) and in other north-western Mediterranean coastal lagoons (Vizzini et al. 2005; Carlier et al. 2007, 2009; Dierking et al. 2012; Escalas et al. 2015; Isnard et al. 2015). Between February and May (*i.e.* the period considered for the source of OM included in the medusae MixSIAR model), the signatures of most OM sources were highly variable. In Thau, ^{13}C-depleted terrestrial inputs come mainly from coastal drainage and are, therefore dependent on the rain, which was high in March and low in April (Meteo France). These climatic conditions likely contributed to the increase of $\delta^{13}C$ signatures of phytoplankton and microzooplankton during these months, which is likely reflected in the medusae isotopic signatures. However, the shift of the medusae isotopic niche observed during the study period was likely the additional reflection of the ontogenic changes in the medusae diet, from POM (*i.e.* phytoplankton and microzooplankton) in February - April to mesozooplankton and SOM in May. These results are in agreement with those from the gut content analysis which revealed higher contributions of phytoplankton and microzooplankton during the first months of medusae presence in the lagoon. Indeed, size-based and temporal shifts of the trophic niche of *Aurelia aurita* were also shown in Northern Ireland, where medusae feed on higher trophic levels by the end of their growing period (Fleming et al. 2015). Opposite results though, were shown for *A. aurita* in the Kiel Fjord, where the medusae shifted

from a mesozooplankton-based diet to a seston-based (< 20 µm size) diet over time (Javidpour et al. 2016). Despite these contrasting results and in line with our study, the latter reports uncover the likely underestimated importance of the lower trophic levels as sources of OM for *Aurelia* sp. medusae. Finally, our results underline the importance of SOM (64.3%) in the *A. coerulea* medusae diet in May, contributing to their isotopic signature in June. Indeed, non-identifiable organic masses were recurrently observed in medusae guts, which could have been aggregates of SOM. This is in agreement with the results of Javidpour et al. (2016), that also suggested a dietary shift from strictly pelagic to benthic food sources over time for *A. aurita* in Kiel Fjord. The Thau lagoon, like most shallow marine ecosystems, is subjected to sediment resuspension, triggered by river floods (high precipitation was recorded in May, Meteo France), strong wind activity and potential local dredging activities (Fouilland et al. 2012; Roberts 2012; Othman et al. 2017), which increases the availability of SOM in the water column.

2.2.5.3 Trophic ecology of A. coerulea benthic stage in the Thau lagoon

The few existing reports on the diet of jellyfish scyphistomae suggested that they feed on small mesozooplankton species such as copepods, cladocerans and cirripeda nauplii (Gröndahl 1988; Östman 1997; Ikeda et al. 2017), but microzooplankton and phytoplankton, such as dinoflagellates, ciliates, rotifers and diatoms, have also been identified as potentially important food types for scyphistomae (Kamiyama 2011, 2013; Wang et al. 2015; Huang et al. 2015). Gut content analysis of scyphistomae was not possible in our study, but the SIA results indicate a temporal variability of their $\delta^{13}C$ and $\delta^{15}N$ signatures, with two significant shifts in their trophic niche during the year.

As previously discussed, the origin of the carbon and nitrogen inputs in the lagoon might be also reflected on the scyphistomae signatures (Post 2002). In INP 1, their lower $\delta^{13}C$ observed likely reflect the stronger contribution of terrestrial inputs to the basis of the food web, after rainy periods (Vizzini et al. 2005; Pernet et al. 2012b). Likewise, the following increase in the scyphistomae $\delta^{13}C$ values, was likely the reflection of the exceptionally low terrestrial inputs from June onwards, due to a very dry summer and autumn in 2017 (> 80% loss of rain fall when compared with the mean between 1981 – 2010 in October, Meteo France). The parallel enrichment of $\delta^{15}N$ might be associated to the higher influence of wastewater effluent in the lagoon during dry periods (Perrin and Tournoud 2009), as previously suggested in other coastal lagoons (Vizzini et al. 2005; Dierking et al. 2012; Escalas et al. 2015). Despite of the intra-annual variability of the isotopic signatures at the base of the food web, the skewed pattern

of the scyphistomae isotopic signatures over the year likely reflect an additional trophic shift. In INP1, phytoplankton and/or microzooplankton (POM) represented the main food source of scyphistomae. This corresponded to their periods of highest availability in the lagoon, in January for phytoplankton and in February for microzooplankton. In INP2, the mesozooplankton and SOM gained importance in the composition of the scyphistomae diet. This is not surprising, since this co-occurred with the highest peak of mesozooplankton abundance in the lagoon. The ability of *A. coerulea* scyphistomae to prey on larger, highly motile, planktonic organisms is recognized and better performances (*i.e.* growth, asexual reproduction and strobilation) have been recurrently reported at higher abundances of mesozooplankton (mainly newly hatched *Artemia* sp.) in laboratory experiments (*e.g.* Han and Uye 2010; Schiariti et al. 2014; Hubot et al. 2017; Ikeda et al. 2017). Finally, in INP 3, POM and SOM became again the main OM sources in the diet of *A. coerulea* scyphistomae, possibly as an outcome of the food availability, after the peak of microzooplankton in September (Fig. 3).

Here we hypothesize that microzooplankton is more important as a source of OM for scyphistomae than phytoplankton. First, although phytoplankton may be a suitable alternative source of energy for survival and asexual reproduction of scyphistomae at low temperatures, this type of prey does not have enough nutritional value to support scyphistomae basic metabolic rates at high temperatures (20ºC) and during long time periods (Wang et al. 2015; Huang et al. 2015). Second, bigger and higher motility prey appear to be important features contributing to the positive feeding reaction of *Aurelia* sp. scyphistomae (Kamiyama 2011; Huang et al. 2015). Finally, the significant positive correlation between the abundance of microzooplankton and NMB (*i.e.* the percentage of scyphistomae producing buds) provide strong evidences that this type of prey promotes the production of buds, ultimately endorsing the benthic population density. Indeed, these results are in agreement with a previous laboratory experiment, which showed a promotion of buds production by the scyphistomae of *Aurelia aurita* reared on a ciliates based diet, when compared with the larger *Artemia* prey (Kamiyama 2013). Interestingly, although more buds were produced in April in the lagoon (due to high scyphistomae density) the peak of the percentage of the scyphistomae actually producing buds, as well as the maximum number of buds per scyphistoma, were registered in September (Marques et al. 2019b), co-occurring with high abundances of microzooplankton. Therefore, we do not exclude the contribution of phytoplankton to the diet of *A. coerulea* scyphistomae, especially during INP 1, but we believe that microzooplankton is more important food source than phytoplankton.

Like for the medusae, our results highlight the likely underestimated role of SOM sources in the diet of *A. coerulea* scyphistomae in the lagoon. The consumption of SOM by *A. coerulea* scyphistomae in the lagoon is less surprising than for medusae. Sedimentary organic matter was often observed on the scyphistomae samples collected *in situ* and previously suggested as a potential source of food for jellyfish benthic stages (Östman 1997). SOM is usually composed by a mixture of microphytobenthos, heterotrophic microorganisms (bacteria, ciliates, protozoans, nematodes) and detritus, classically associated and resuspended with mud (Shimeta et al. 1995; Dubois et al. 2007), which might provide a suitable source of prey for scyphistomae.

2.2.5.4 Intra and interspecific competition

Although inhabiting different habitats, the benthic scyphistomae and the pelagic medusae of *A. coerulea* appear to share, at least partially, the same OM sources available in the lagoon. During INP 1, their higher isotopic niche overlap and the results of the mixing models, indicate that both stages feed on phytoplankton and/or microzooplankton. In INP 2, despite of the lower percentage of overlap, the trophic niche from medusae covers entirely the one from scyphistomae. This suggests that during large medusae blooms and under food limitation conditions, intraspecific trophic competition might occur in the lagoon, with possible detrimental impacts for the scyphistomae population.

One of the main concerns regarding the *A. coerulea* blooms in Thau, is the potential food competition with the oysters produced in the lagoon, due to the high local economic value of shellfish production. In addition, the overspread distribution of scyphistomae in the lagoon, especially fixed on wild oysters (Marques et al. 2015b), might promote non-negligible levels of interspecific trophic competition. However, here we show limited trophic niche overlap between both stages of *A. coerulea* and the oysters collected at different places in the lagoon. Although oysters and *A. coerulea* medusae and scyphistomae were not collected in the same year (except in INP 3) we assumed that the isotopic signature of the oysters mostly varies intra-annually, which is in agreement with previous studies (Pernet et al. 2012b). If this is true, interspecific competition for food only potentially occurs between *A. coerulea* medusae and oysters (cultivated and wild) in INP 2. During this period, SOM was the most important OM source in the diet of *A. coerulea* medusae, and previously reported as part of the diet of oysters (Riera and Richard 1996; Dubois and Colombo 2014). This might explain the existence, although restricted, of interspecific trophic niche overlap between these two organisms. Nevertheless, in the literature, phytoplankton (especially diatoms) are often pointed as the main

source of food for oysters (Dupuy et al. 2000; Pernet et al. 2012b). Since in our study, phytoplankton and microzooplankton were pooled for the MixSIAR analysis, it is possible that both the medusae and scyphistomae consume higher proportions of microzooplankton, while oysters prey preferentially on phytoplankton organisms, explaining the general restricted interspecific trophic niche overlap observed in our study. Since scyphistomae were collected at the same sampling site and they are recurrently settled on the oyster's shells (Marques et al. 2015b), higher levels of trophic niche overlap between scyphistomae and wild oysters were expected to be observed, supporting the hypothesis that both organisms prey on different components of the POM. Low interspecific competition was also shown between oysters and their associated co-occurring suspension-feeding species (Dubois and Colombo 2014), which was linked to their different filtration and particle retention mechanisms. The *A. coerulea* medusae is considered as a cruising predator, capturing its prey using locally generated flow currents (Sullivan et al. 1994; Dabiri et al. 2005), while scyphistomae use a passive ambush strategy (Huang et al. 2015), contrasting with the true filter feeding strategy of the oysters (Riera and Richard 1996; Dubois et al. 2007; Dubois and Colombo 2014). Therefore, the different mechanisms to capture prey used by each organism, likely promoted the selection and ingestion of different OM sources, reducing the trophic competition for the same type of prey. On the light of these results we hypothesize that the blooms of *A. coerulea* medusae might indeed be advantageous for the production of oysters in the lagoon by a top-down cascade effect on the microbial community. *In situ* feeding experiments showed that *Aurelia* sp. feed on micro- and meso-zooplankton organisms, which released the predation pressure from these secondary producers on the lower trophic levels, boosting phytoplankton biomass and bacterial production (Turk et al. 2008).

2.2.5.5 Bottom-up control of the A. coerulea population dynamics

During the winter and early spring, *i.e.* before the *A. coerulea* bloom, phytoplankton and microzooplankton (pooled as POM) are the main food sources of the benthic and young pelagic stages of *A. coerulea.* This is particularly important since this is a critical period for the formation of the bloom in the current year, but also for the magnitude of the bloom in the following year. Ephyrae are produced in the lagoon from November to April with high levels of ephyrae liberation in early spring due to high density of scyphistomae at this time of the year (Marques et al. 2019b). As they grow to become medusae, the magnitude of the bloom is thus, tightly dependent on their accumulated production, survival and growth rate. Moreover, since the peak of scyphistomae coverage and the maximum production of buds also occurs between

February and April (Fig.11; Marques et al. 2019b), the bloom of the following year will be also affected by the density of scyphistomae at this period and their survival during the summer (Marques et al. 2019b). High microzooplankton abundance appears to be the main driver of buds production, which is, therefore, boosted in early spring when high abundances of microzooplankton are available in the lagoon (Fig. 3). Despite of the non-negligible overlap of scyphistomae and medusae isotopic niches, we hypothesize that intraspecific competition is probably low due to high food availability. It is not surprising thus, that both the benthic and the pelagic stages of *A. coerulea* take advantage from the high availability of these prey, to maximize their growth, survival and asexual reproduction in the lagoon.

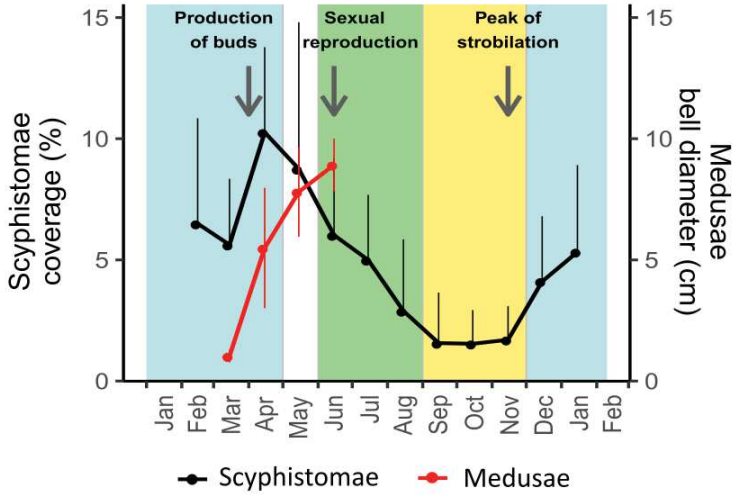


Fig. 11 : Scyphistomae coverage (from Marques et al. 2019b) and medusae bell diameter collected for SIA in this study (in red). The arrows indicate the main periods of sexual and asexual reproduction of *A. coerulea*. The background colours represent the isotopic niche periods identified in this study.

A rapid isotopic niche shift was observed for both *A. coerulea* life stages in May, associated to a switch from a strictly POM diet in winter and the beginning of spring, to a mix diet of all OM sources in late spring and summer. Here, we highlight the importance of the SOM (likely resuspended after rain episodes in May) and of the high abundance of mesozooplankton (peaking in June, Fig.3) supporting high medusae growth rates, boosting the bloom formation and upholding the sexual reproduction. The planulae production and liberation occurs in June (Fig. 11; Bonnet et al. 2012; Marques et al. 2015a), which might have implications on the subsequent scyphistomae population in Thau. Although planulae appeared to have a limited impact on the scyphistomae coverage, they appear to be important in the dispersion of scyphistomae within the lagoon (Marques et al. 2019b). This could increase the probability to expand their distribution to areas with lower variations in temperature and salinity, potentially increasing scyphistomae survival. Finally, it is during this period that

scyphistomae showed a decline in their coverage in the lagoon (Fig. 11, Marques et al. 2019b). Here, we have shown that the most important prey for scyphistomae, appears to be the microzooplankton. If we consider an exclusive scyphistomae diet on this type of prey, the concurrent decrease of its abundances might explain the declining trend of scyphistomae population. However, the *Aurelia* sp. scyphistomae are able to feed on mesozooplankton (Ostman et al 1997, Grongahal 1988b, Ikeda et al 2017), which peaked in June. So it is more likely that the decrease in microzooplankton results to a shift in diet than to a massive mortality. Therefore, we suspect that microzooplankton are critical to the asexual reproduction (*i.e.* the production of buds), but not for their survival. However, since the isotopic niche of medusae totally overlap the one from scyphistomae, the high abundance and potential high predation pressure of the medusae might lead to the reduction of food availability and increase intraspecific competition, which might have contributed to the observed decrease of the scyphistomae coverage.

During the following dry season (from September to November), POM become again the main OM source for scyphistomae. During this dry season, it prevails a bacteria-based food web in the lagoon, with internal regeneration of nitrogen, due to the absence of terrestrial fresh water inputs in the lagoon (Chapelle et al. 2000). Microzooplankton are recognized as important bacterivorous (Rassoulzadegan and Sheldon 1986), which probably explains the peak of these organisms in September (Fig. 3). Microzooplankton is likely the main source of OM for scyphistomae during this period, which supports the peak of asexual reproduction observed in September and the strobilation in November (Marques et al. 2019b), *i.e.* the foundation of the subsequent jellyfish bloom in the Thau lagoon.

2.2.6. Conclusion

Knowledge on the trophic ecology of jellyfish and their population dynamics is imperative to understand the main environmental drivers of jellyfish blooms. With this regards, the Thau lagoon offered an exceptional framework to study both benthic and pelagic trophic interactions and uncover the main OM sources supporting critical periods of *A. coerulea* life cycle. Here we provide evidence of the importance of bottom-up controls on the formation of the annual bloom of *A. coerulea* in the Thau lagoon, in particular the role of microzooplankton supporting high levels of asexual reproduction, mesozooplankton for the growth of medusae and also the contribution of SOM for both life stages.

Moreover, we demonstrate that the interspecific competition between jellyfish and the economically important oysters is limited in the Thau lagoon. Indeed, we hypothesize a positive

indirect effect of *A. coerulea* on the cultivation of oysters. The predation impact of this jellyfish, especially the medusae stage, on mesozooplankton and microzooplankton might have a cascading effect, promoting the increase of autotrophic and heterotrophic small microbial plankton, which ultimately might increase food availability for oysters in the lagoon. This hypothesis tough, requires confirmation.

2.2.7. Annex

Supplementary Table 1: Index of relative importance (IRI), Frequency of occurrence (FO) and mean abundance of prey items found in *Aurelia coerulea* medusae gut contents during the period of its presence in Thau lagoon. Bold numbers in parenthesis are the numbers of medusae with prey items analysed.

	IRI (%)			FO (%)			Abundance (± SD) (ind.medusae^{-1})		
Prey	**Apr (5)**	**May (9)**	**Jun (8)**	**Apr (5)**	**May (9)**	**Jun (8)**	**Apr (5)**	**May (9)**	**Jun (8)**
Phytoplankton									
Diatomacea	3.4	5.0	0.0	20.0	33.3	0.0	1.0 (2.2)	0.9 (1.7)	0.0 (0.0)
Dinoflagellata	0.0	0.6	0.0	0.0	11.1	0.0	0.0 (0.0)	0.1 (0.3)	0.0 (0.0)
Microzooplankton									
Tintinnidae	6.1	11.3	0.0	20.0	44.4	0.0	1.8 (4.0)	2.0 (3.2)	0.0 (0.0)
Foraminifera	1.4	0.6	0.0	40.0	11.1	0.0	0.4 (0.5)	0.1 (0.3)	0.0 (0.0)
Radiolaria	0.0	0.6	0.0	0.0	11.1	0.0	0.0 (0.0)	0.1 (0.3)	0.0 (0.0)
Mesozooplankton									
Copepoda									
Acartia clausi	0.0	0.6	1.2	0.0	11.1	12.5	0.0 (0.0)	0.1 (0.3)	0.1 (0.4)
Calanoida	7.5	7.5	14.6	40.0	44.4	37.5	2.2 (3.2)	1.3 (1.8)	1.5 (3.1)
Euterpina acutifrons	1.4	3.1	3.7	40.0	22.2	37.5	0.4 (0.5)	0.6 (1.3)	0.4 (0.5)
Microsetella sp.	0.0	2.5	0.0	0.0	22.2	0.0	0.0 (0.0)	0.4 (0.9)	0.0 (0.0)
Oithona	0.0	0.6	0.0	0.0	11.1	0.0	0.0 (0.0)	0.1 (0.3)	0.0 (0.0)
Pseudocalanus	0.7	0.0	0.0	20.0	0.0	0.0	0.2 (0.4)	0.0 (0.0)	0.0 (0.0)
Tisbe sp.	0.0	0.6	1.2	0.0	11.1	12.5	0.0 (0.0)	0.1 (0.3)	0.1 (0.4)
Copepods (NI)	25.2	6.9	25.6	20.0	22.2	25.0	7.4 (16.5)	1.2 (3.3)	2.6 (7.0)
Nauplii (copepoda and cirripeda)									
Cirripeda nauplii	4.8	14.4	17.1	60.0	88.9	62.5	1.4 (2.1)	2.6 (2.8)	1.8 (1.8)
Copepoda nauplii	0.0	4.4	0.0	0.0	33.3	0.0	0.0 (0.0)	0.8 (1.2)	0.0 (0.0)
Nauplii (NI)	0.0	12.5	24.4	0.0	11.1	12.5	0.0 (0.0)	2.2 (6.7)	2.5 (7.1)
Other crustacea									
Ostracoda	0.7	0.6	0.0	20.0	11.1	0.0	0.2 (0.4)	0.1 (0.3)	0.0 (0.0)
Caprellidae	0.0	0.0	1.2	0.0	0.0	12.5	0.0 (0.0)	0.0 (0.0)	0.1 (0.4)
Decapoda	0.0	3.1	0.0	0.0	55.6	0.0	0.0 (0.0)	0.6 (0.5)	0.0 (0.0)
Evadne	0.0	0.0	3.7	0.0	0.0	12.5	0.0 (0.0)	0.0 (0.0)	0.4 (1.1)
Podon	0.0	0.0	1.2	0.0	0.0	12.5	0.0 (0.0)	0.0 (0.0)	0.1 (0.4)
Crustacea (NI)	0.0	6.3	2.4	0.0	11.1	25.0	0.0 (0.0)	1.1 (3.3)	0.3 (0.5)
Non-crustacea									
Bivalve veliger	4.8	10.6	1.2	40.0	44.4	12.5	1.4 (2.2)	1.9 (3.1)	0.1 (0.4)
Gastropod veliger	42.2	5.6	0.0	40.0	33.3	0.0	12.4 (19.3)	1.0 (1.8)	0.0 (0.0)
Hydrachnidia	0.0	0.0	1.2	0.0	0.0	12.5	0.0 (0.0)	0.0 (0.0)	0.1 (0.4)
Insecta: Diptera	0.7	0.0	0.0	20.0	0.0	0.0	0.2 (0.4)	0.0 (0.0)	0.0 (0.0)
Polychaeta	0.7	0.6	0.0	20.0	11.1	0.0	0.2 (0.4)	0.1 (0.3)	0.0 (0.0)
Copepod eggs	0.7	0.6	1.2	20.0	11.1	12.5	0.2 (0.4)	0.1 (0.3)	0.1 (0.4)
Fish egg	0.0	1.3	0.0	0.0	22.2	0.0	0.0 (0.0)	0.2 (0.4)	0.0 (0.0)

Supplementary table 2 : Abundance (in. L^{-3}) and diversity of phytoplankton and microzooplankton taxa collected in the Thau lagoon in 2017. Columns represent sampling time (day/month). In parenthesis is the contribution of each taxa to the total abundance of the sample. Colors represent the values of contribution.

	10/01	24/01	09/02	21/02	09/03	20/03	06/04	18/04	04/05	15/05	30/05	13/06	28/06	13/07	23/08	18/09	17/10	15/11	14/12	Mean
Phytoplankton																				
Chaetoceros sp.	37 (3.5)	45150 (91.7)	6970 (77.0)	1703 (23.3)	55 (1.3)	123 (7.7)	14597 (58.4)	11802 (49.9)	42590 (77.3)	6024 (32.5)	301 (0.9)	16606 (58.6)	1519 (22.2)	361 (5.7)	6789 (69.7)	1732 (29.9)	67 (4.6)	0 (0.0)	496 (38.5)	9050 (57.1)
Pseudo-nitzschia sp.	9 (0.8)	0 (0.0)	15 (0.2)	0 (0.0)	0 (0.0)	11 (0.7)	4472 (17.9)	4920 (20.8)	2670 (4.8)	6313 (34.1)	31220 (92.4)	0 (0.0)	135 (2.0)	530 (8.4)	351 (3.6)	254 (4.4)	39 (2.7)	8 (0.4)	67 (5.2)	2398 (15.1)
Ollicola sp.	3 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	30 (1.9)	920 (3.7)	652 (2.8)	401 (0.7)	3340 (18.0)	100 (0.3)	4560 (16.1)	1370 (20.0)	927 (14.7)	351 (3.6)	127 (2.2)	11 (0.8)	11 (0.6)	0 (0.0)	558 (3.5)
Bicosoeca sp.	8 (0.7)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (0.2)	0 (0.0)	3160 (13.4)	7490 (13.6)	1280 (6.9)	351 (1.0)	0 (0.0)	15 (0.2)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	513 (3.2)
Microflagellate	23 (2.1)	50 (0.1)	29 (0.3)	2660 (36.4)	58 (1.4)	22 (1.4)	125 (0.5)	100 (0.4)	0 (0.0)	125 (0.7)	250 (0.7)	1354 (4.8)	842 (12.3)	241 (3.8)	445 (4.6)	159 (2.7)	6 (0.4)	0 (0.0)	0 (0.0)	325 (2.0)
Alexandrium sp.	4 (0.4)	0 (0.0)	44 (0.5)	66 (0.9)	195 (4.6)	82 (5.1)	0 (0.0)	50 (0.2)	0 (0.0)	50 (0.3)	50 (0.1)	135 (0.5)	150 (2.2)	144 (2.3)	0 (0.0)	0 (0.0)	61 (4.2)	1458 (73.8)	27 (2.1)	239 (1.5)
Prorocentrum sp.	52 (4.9)	50 (0.1)	15 (0.2)	226 (3.1)	466 (11.0)	911 (57.0)	42 (0.2)	350 (1.5)	201 (0.4)	100 (0.5)	50 (0.1)	632 (2.2)	150 (2.2)	698 (11.1)	140 (1.4)	287 (5.0)	340 (23.6)	61 (3.1)	27 (2.1)	233 (1.5)
Heterocapsa sp.	15 (1.4)	25 (0.1)	0 (0.0)	0 (0.0)	16 (0.4)	4 (0.2)	0 (0.0)	100 (0.4)	0 (0.0)	301 (1.6)	50 (0.1)	2751 (9.7)	1038 (15.1)	735 (11.7)	0 (0.0)	127 (2.2)	22 (1.5)	0 (0.0)	0 (0.0)	228 (1.4)
Scrippsiella sp.	126 (11.8)	225 (0.5)	15 (0.2)	74 (1.0)	969 (22.9)	119 (7.4)	209 (0.8)	351 (1.5)	335 (0.6)	75 (0.4)	100 (0.3)	135 (0.5)	120 (1.7)	325 (5.2)	234 (2.4)	445 (7.7)	145 (10.1)	42 (2.1)	3 (0.2)	209 (1.3)
Acanthoica sp.	50 (4.7)	376 (0.8)	15 (0.2)	975 (13.3)	1090 (25.7)	104 (6.5)	0 (0.0)	1000 (4.2)	134 (0.2)	50 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	48 (0.8)	84 (5.8)	0 (0.0)	0 (0.0)	172 (1.1)
Dinobryon sp.	457 (43.0)	201 (0.4)	117 (1.3)	0 (0.0)	0 (0.0)	0 (0.0)	961 (3.8)	251 (1.1)	201 (0.4)	276 (1.5)	150 (0.4)	0 (0.0)	0 (0.0)	48 (0.8)	94 (1.0)	32 (0.5)	6 (0.4)	0 (0.0)	0 (0.0)	154 (1.0)
Microzooplankton																				
Strombidium sp.	896 (36.1)	1568 (28.5)	489 (23.1)	7738 (62.8)	367 (29.5)	1324 (40.6)	4663 (55.9)	7351 (90.7)	2545 (82.2)	367 (16.7)	204 (100.0)	305 (83.3)	3156 (79.5)	1812 (73.6)	122 (40.0)	3136 (50.2)	1364 (52.3)	224 (50.0)	1446 (66.4)	1936 (57.0)
Mesodinium sp.	1018 (41.0)	326 (5.9)	305 (14.4)	692 (5.6)	163 (13.1)	224 (6.9)	916 (11.0)	265 (3.3)	143 (4.6)	1466 (66.7)	0 (0.0)	20 (5.6)	244 (6.2)	122 (5.0)	41 (13.3)	794 (12.7)	407 (15.6)	0 (0.0)	387 (17.8)	388 (11.4)
Leegardiella sp.	183 (7.4)	3217 (58.5)	20 (1.0)	591 (4.8)	20 (1.6)	305 (9.4)	41 (0.5)	0 (0.0)	20 (0.7)	0 (0.0)	0 (0.0)	0 (0.0)	489 (12.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	233 (6.8)
Tintinnopsis sp.	61 (2.5)	0 (0.0)	81 (3.8)	244 (2.0)	122 (9.8)	774 (23.7)	1751 (21.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	20 (0.5)	20 (0.8)	0 (0.0)	591 (9.4)	143 (5.5)	81 (18.2)	20 (0.9)	188 (5.5)
Uronema sp.	122 (4.9)	0 (0.0)	20 (1.0)	713 (5.8)	204 (16.4)	102 (3.1)	81 (1.0)	122 (1.5)	0 (0.0)	102 (4.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	102 (1.6)	0 (0.0)	0 (0.0)	122 (5.6)	106 (3.1)
Balanion sp.	41 (1.6)	81 (1.5)	448 (21.2)	448 (3.6)	0 (0.0)	0 (0.0)	183 (2.2)	122 (1.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	20 (0.3)	0 (0.0)	20 (4.5)	102 (4.7)	77 (2.3)
Strobilidium sp.	0 (0.0)	0 (0.0)	0 (0.0)	41 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	20 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	713 (11.4)	20 (0.8)	61 (13.6)	0 (0.0)	63 (1.9)
Holotriches sp.	0 (0.0)	0 (0.0)	387 (18.3)	183 (1.5)	20 (1.6)	81 (2.5)	163 (2.0)	41 (0.5)	20 (0.7)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	20 (4.5)	61 (2.8)	51 (1.5)
Urotricha sp.	0 (0.0)	183 (3.3)	122 (5.8)	265 (2.1)	102 (8.2)	81 (2.5)	81 (1.0)	61 (0.8)	0 (0.0)	20 (0.9)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	41 (0.7)	0 (0.0)	0 (0.0)	0 (0.0)	51 (1.5)
Tontonia sp.	0 (0.0)	0 (0.0)	41 (1.9)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	204 (8.3)	143 (46.7)	244 (3.9)	346 (13.3)	0 (0.0)	0 (0.0)	48 (1.4)
Lohmaniella sp.	20 (0.8)	0 (0.0)	61 (2.9)	61 (0.5)	20 (1.6)	41 (1.3)	61 (0.7)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	143 (5.8)	0 (0.0)	448 (7.2)	20 (0.8)	0 (0.0)	0 (0.0)	46 (1.3)
Pelagostrobilidium sp.	0 (0.0)	20 (0.4)	0 (0.0)	407 (3.3)	0 (0.0)	0 (0.0)	41 (0.5)	61 (0.8)	0 (0.0)	122 (5.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	41 (0.7)	0 (0.0)	41 (9.1)	0 (0.0)	43 (1.3)
Rhabdoaskenasia sp.	0 (0.0)	0 (0.0)	41 (1.9)	489 (4.0)	20 (1.6)	122 (3.7)	0 (0.0)	0 (0.0)	183 (5.9)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	42 (1.2)
Cyrtostrombidium sp.	41 (1.6)	41 (0.7)	0 (0.0)	224 (1.8)	0 (0.0)	0 (0.0)	326 (3.9)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	81 (3.3)	0 (0.0)	20 (0.3)	0 (0.0)	0 (0.0)	20 (0.9)	36 (1.1)

2.3 IN A NUTSHELL

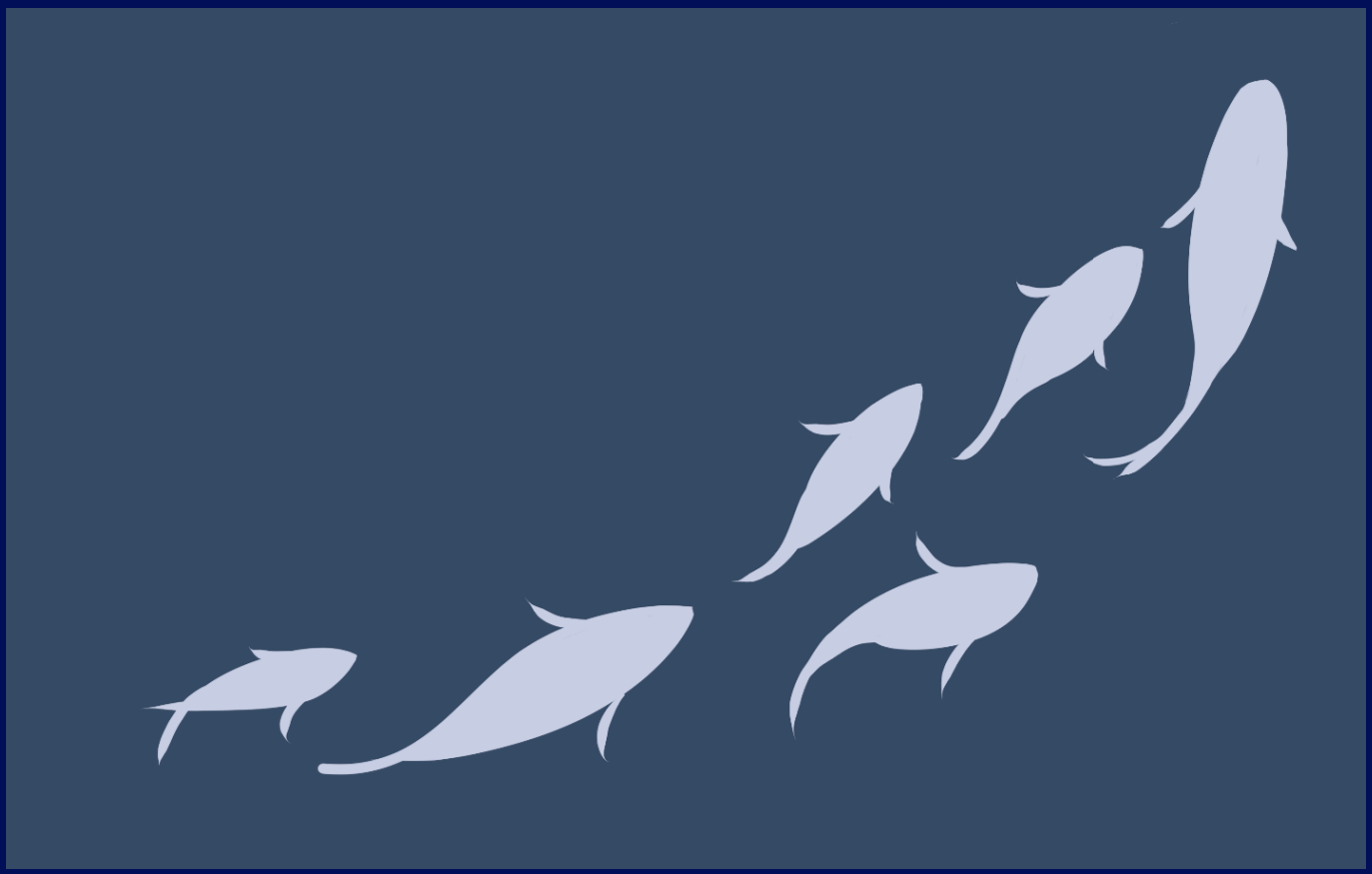
- The intra-annual pattern of demographic variation of *A. coerulea* scyphistomae in Thau is characterized by a peak in coverage in spring, followed by a decline until minimum values are reached in the summer and autumn.
- The growth of the benthic population was promoted by the production of buds, concomitant with increasing temperatures and food availability.
- Microzooplankton is the most important type of prey for scyphistomae, promoting the production of buds
- Scyphistomae appear to be negatively affected by the joint effect of high temperatures and high salinities during the summer and the autumn, but other drivers are not excluded, such as direct or indirect predation by top predators or intra-specific trophic competition.
- Strobilation is triggered by a drop of temperatures (~ 8ºC) in November, when the peak of ephyrae production occurs, but strobilation continues until April.
- The elevated production of ephyrae in November is a result of the high percentage of the population strobilating but highly limited by the low density of scyphistomae at this time of the year
- High levels of ephyrae production occur also in February-April due to the high density of scyphistomae during these months, despite the low percentage of the benthic population actually strobilating
- Both stages rely on phytoplankton and/or microzooplankton during most of the year, except during the warmer months, when they switch to a mix of all sources of organic matter (plankton and sedimentary organic matter).
- For medusae, although mesozooplankton is the most important prey, especially for the adult stage, phytoplankton and microzooplankton appear to be important contributions for young stages.
- Since both stages feed on the same sources of organic matter and their trophic niche overlap during the whole period of co-occurrence, intra-specific trophic competition might develop during the medusae blooms. This might be particularly important during the warmer months, which can contribute to the reduction of scyphistomae density at this time of the year.

- The trophic competition between both stages of *A. coerulea* and the oysters produced in the Thau lagoon is likely limited.
- Overall, temperature, salinity and food availability appears to be the main drivers of the blooms

CHAPTER 3. FATES OF A.COERULEA BIOMASS

Paper III: Fish predation on *A. coerulea*

Paper IV: Degradation of dead medusae



3.1 FISH PREDATION ON *A. COERULEA* (PAPER III)

Until recently, jellyfish have been ignored as an important source of food and therefore, the role of fish predation in the control of their populations has been largely overlooked. Although this paradigm is currently shifting, identifications of jellyfish fish predators are still rare. This section aimed to assess these trophic interactions using molecular techniques in order to identify potential predators of both the medusae and scyphistomae stages of *A. coerulea* in the Thau Lagoon. This allowed understanding the potential impact of fish predation in the regulation of *A. coerulea* populations in the lagoon, as well as the potential role of these organisms as a source of food for commercially important fish species.

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Molecular approach indicates consumption of jellyfish by commercially important fish species in a coastal Mediterranean lagoon

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3.1.1. Abstract

Until recently, jellyfish have been ignored as an important source of food, due to their low nutritional value. Here, quantitative PCR was used to detect and quantify the DNA of the jellyfish *Aurelia coerulea* in the gut contents of commercially important fish species from the Thau Lagoon. Individuals from five fish species were collected during two different periods: the bloom period, when the pelagic stages of *A. coerulea* are abundant, and the post-bloom period, when only the benthic stage – polyps – is present in the lagoon. The DNA of *A. coerulea* was detected in the guts of 41.9% of the fish analysed, belonging to four different species. The eel *Anguilla anguilla* and the sea bream *Sparus aurata* were important jellyfish consumers during the bloom and post-bloom periods, respectively. These results provide new insights on the potential control of jellyfish populations and on jellyfish importance as a food source for exploited fishes.

3.1.2. Introduction

Gelatinous organisms (scyphozoan, ctenophores, siphonophores, salps, pyrosomes and appendicularians, hereafter called jellyfish) are ubiquitous components of marine food webs and their noticeable outbreaks have been promoting recent research on their ecology. However, these studies have long focused on the drivers of jellyfish blooms (*e.g.* Purcell 2012) while little is known still on the causes of jellyfish mortality (Purcell and Arai 2001), although this information is fundamental though to understand their population dynamics.

So far, jellyfish were consistently considered as "dead ends" in marine food webs, due to their high water content and low nutritional value (e.g. 2.3-3.6 KJ.g.dry mass^{-1} for *A. aurita vs.* 15.6 – 27.9 for various fishes, Doyle et al. 2007). They were largely believed to be ignored by most predators, with the exception of a few specialists, feeding exclusively on gelatinous organisms, such as the ocean sunfish (*Mola mola*), the butterfish (*Peprilus triacanthus*) and the leatherback turtle (*Dermochelys coriacea*) (Mianzan et al. 1996; Purcell and Arai 2001; Arai 2005). Recent research though has led to a shift in this paradigm (Hays et al. 2018).

Historically, diet assessments were performed by gut content analysis, which may provide biased information regarding jellyfish consumption as it gives excessive importance to hard prey that are more resistant to digestion (Hyslop 1980). Gelatinous organisms are digested rapidly and often destroyed or shrunk by preservative methods (Arai 2005). Although gut contents still provide new evidences of the importance of jellyfish as prey (Díaz Briz et al. 2018), contemporary studies have been using new techniques to identify jellyfish predators, such as stable isotope analysis, animal-borne cameras, remotely operated vehicles and molecular analysis (Hays et al. 2018). Due to these modern techniques, the list of jellyfish predators has been growing and now includes commercially important fishes such as herring (*Clupea harengus*), whiting (*Merlangius merlangus*), bluefin tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*) (Cardona et al. 2012; Lamb et al. 2017). Jellyfish were also shown to be of high importance in the diet of the larvae of a critically endangered fish, the European eel, *Anguilla anguilla* (Ayala et al. 2018) and to be ingested even by herbivorous fishes (Bos et al. 2016). Likewise, cephalopods, anemones, crabs, echinoderms and several species of birds have been reported to feed on jellyfish (Ates 2017; Hoving and Haddock 2017; McInnes et al. 2017; Phillips et al. 2017; Thiebot et al. 2017). Jellyfish consumption apparently even occurs in deep benthic habitats of the Norwegian fjords, where mass falls of jellyfish carcasses can provide food for several scavengers, including the commercially exploited lobster *Nephrops norvegicus* (Sweetman et al. 2014; Dunlop et al. 2017).

The life cycle of many blooming jellyfish species (i.e. scyphozoans) is complex, though, comprising two pelagic stages (the young immature ephyrae and the sexually mature medusae) and an asexual reproductive benthic stage (the scyphistomae, hereafter called polyps). The magnitude of most jellyfish blooms is therefore dependent on the density of polyps and ephyrae survival. Therefore, the mortality during these two early life stages may have a major effect on jellyfish population dynamics (Lucas et al. 2012; Fu et al. 2014). Insights on the predation on polyps and ephyrae and its potential impact on jellyfish outbreaks are still limited though (*e.g.* Ishii et al. 2004; Takao et al. 2014). In a recent laboratory experiment (Marques et al. 2016), the jellyfish *Aurelia coerulea* was found to be a potentially non-negligible source of food for an opportunistic fish, the gilthead sea bream *Sparus aurata*. This fish was able to feed on all life stages of this jellyfish (including polyps) with potentially high ingestion rates. However, the predation of jellyfish by this fish has never been shown in the field, so far.

Jellyfish from the *Aurelia* Genus, are among the most common scyphozoans that form blooms (Dawson and Martin 2001; Mills 2001). They are widely distributed in coastal areas and semi-enclosed seas (Mills 2001). The Thau lagoon (NW Mediterranean, south coast of France) presents the rare particularity to harbour a completely resident population of *A. coerulea*, seemingly isolated from the Mediterranean Sea (Bonnet et al. 2012; Marques et al. 2015b). In this lagoon, *A. coerulea* ephyrae first appear in the early winter (in November - December) and grow during winter to give rise, at the beginning of spring (in March –April), to the adult medusae that form the annual bloom (Marques et al. 2015a). The medusae remain in the water column until the late spring (June) but disappear from the system afterwards. Polyps of *A. coerulea*, on the contrary, are found all year round in the lagoon (Marques et al. 2019b), mainly settled on biofouling organisms, such as oysters and mussels (Marques et al. 2015b). Therefore, the Thau lagoon offers an ideal framework to investigate whether marine predators benefit from the jellyfish annual blooms and identify which life stages of *A. coerulea* are consumed in the field. This is imperative to address the role of predation in controlling jellyfish population dynamics and the potential importance of jellyfish as food for exploited fish species.

To this end, commercial fish species were sampled at different periods of the year and molecular analyses of their gut content were used to study their consumption of *A. coerulea,* during and after its local pelagic bloom.

3.1.3. Material and Methods

3.1.3.1 Sampling and samples preparation

Fishing is the oldest economic activity in the Thau lagoon, which is mainly performed by small enterprises (50 to 65 fishing boats operating in the lagoon), who target different species of fish using different fishing gears (CÉPRALMAR 2006). Different fish species were collected in the Thau lagoon by a professional fisherman. Fishes were collected during the annual bloom of *A. coerulea* (hereafter called bloom period, between April and June; Bonnet et al. 2012; Marques et al. 2015a) in 2012, 2013 and 2018, and during a period (from September to November) in 2018, when the pelagic stages of *A. coerulea* are not present in the lagoon (hereafter called post-bloom period, Bonnet et al. 2012; Marques et al. 2015a). During the bloom period, fishes were collected by trammel nets, with an active fishing effort of maximum 3h. During the post-bloom period, the traditional 'capéchade', which is the most used fishing technique in Thau (Crespi 2002), was used to collect fish for this study. The 'capéchade' is a fishing trap gear, placed at the same location for several days. Fishes are collected when the sun rises, after 24h of fishing effort. The number of species and individuals collected were therefore dependent on their occurrence in the nets. Immediately after collection, the fish were placed in separate plastic bags by the fisherman in order to avoid possible loss (or mixing) gut contents during sampling. Bags were then filled with absolute ethanol and stored in individual containers. Once in the laboratory, the fish were weighted (Total weight in g), dissected and their entire gut contents were removed and preserved at -30°C until DNA extraction. For positive DNA templates, samples of both the pelagic (medusae) and benthic (polyps) stages of *A. coerula* were collected in the lagoon. Medusae were collected by a hand net and immediately preserved in absolute ethanol. Polyps attached to mussel shells were collected by SCUBA divers and transported in sea water to the laboratory. The samples were examined under a dissecting microscope (Olympus SZ40; Olympus KL 1500 LCD) and individual polyps were collected using needles. Fifty polyps were pooled per sample, frozen in liquid nitrogen and maintained at -30ºC until DNA extraction.

3.1.3.2 DNA extraction

After thawing, the fish gut contents were mechanically ground in a mixer mill (MM400, Retsch). Three subsamples of 25 mg were collected from each gut content (when possible) and DNA was extracted using DNeasy blood and tissue kit (QIAGEN) (Stopar et al. 2010). The extraction was performed according to the instructions of the manufacturer, with an extra lysis

step, performed overnight at 56ºC. The same protocol was used for *A. coerulea* medusae samples, which were previously washed with pure molecular MilliQ water for ethanol removal. This protocol was, however, inefficient for the extraction of the polyp's DNA, and therefore, their DNA was extracted by nucleic acid purification automated Maxwell ® instrument (Promega) and 16 LEV Blood DNA kit (Promega), with a modification of the lysis procedure, which was performed overnight at 56ºC, using 30 µl of Proteinase K (Promega). In all cases, the extracted DNA was quantified in Nanodrop (NanoDrop One, Thermo Scientific).

3.1.3.3 Detection of A. coerulea DNA

Detection and quantification of *A. coerulea* DNA in the fish gut contents was performed by quantitative PCR (qPCR). This technique has been employed to detect and quantify the DNA of a specific prey in gut contents and faecal pellets, when traditional visual methods fail to do so (Matejusová et al. 2008; Nejstgaard et al. 2008; Töbe et al. 2010). This sensitive approach allows the detection and quantification of very small amounts of DNA so even highly digested jellyfish can still be detected. All amplifications reactions were analysed using a Roche LightCycler 480 Real-Time thermocycler (qPHD-Montpellier GenomiX platform, Montpellier University, France). The total qPCR reaction volume was 1.5 µl and consisted of 0.5 µl DNA and 1 µl LightCycler 480 SYBR Green I Master mix (Roche) with 0.6 µM PCR primer (Eurofins Genomics). A 245 base pair gene fragment (partial sequences of mt-16S rDNA) was amplified by the species-specific (*A. coerulea*) primers AS3-F (5'-ATTGGTGACTGGAATGAATG - 3') and AS3-R (5'- TATGACAGCCCTTAGAGTTC - 3') designed by Wang et al. (2013). The best-suited primer concentration (0.4, 0.6 or 0.8 µM) was determined in preliminary tests on three samples of *A. coerulea* polyps and medusae. A Labcyte Acoustic Automated Liquid Handling Platform (ECHO) was used for pipetting each component of the reaction mixture into a 384-well plate (Roche). The qPCR program consisted in an enzyme activation step at 95ºC for 2 min, followed by 45 cycles of denaturation at 95ºC for 10 s, hybridization at 60ºC for 10s and elongation at 72ºC for 10 s. A final melting temperature curve (Tm) of the amplicon was performed (95ºC for 5 s and 65ºC for 1 min), in order to ensure the specificity of the primers. The same amplification conditions and reaction concentrations were used in all assays performed in this study.

The efficiency and specificity of target gene detection by the primer was tested on a 2-fold dilution series of *A. coerulea* medusae and polyps positive templates. Triplicate reactions were performed at each dilution in order to generate the standard curves for each template. An ANCOVA analysis was performed, in order to assess if the efficiency (*i.e.* the slopes) of the

two standard curves were significantly different. Absolute quantification of *A. coerulea* DNA in the fish gut contents was estimated using the regression equation of the standard curve obtained for the polyps positive template. The observed Cp values of each dilution of the positive template were plotted against its known DNA concentration to obtain the regression equation. The Cp value is defined as the cycle when the sample fluorescence exceeds the threshold above the background fluorescence. The Cp value is therefore related to the amount of DNA present in the sample (Dorak 2006).

The quantification of DNA in fish gut contents was only performed in the samples showing Cp values below 31, which was found to be the Cp correspondent to the minimum quantifiable concentration (1.37 x 10-4 ng μL^{-1}). Samples with the same Tm values as the positive templates (Tm peak at 81.5) and Cp values between 31 and 32.62 (maximum Cp observed for the positive templates) were considered as positive detection but non-quantifiable. Samples showing Cp values above 32.62 were considered as negative detection. For each gut content sample, a minimum of 9 replicates (3 experimental replicates, *i.e.* for DNA extraction, of the same gut content and 3 technical replicates for each experimental replicate), were performed, except for some samples with very low material, from which only one experimental replicate was collected. Only gut contents samples that showed positive detection in at least two technical replicates were considered to contain *A. coerulea* DNA.

The specificity of the primers and the detection of *A. coerulea* DNA was further confirmed by sequencing the positive templates and the qPCR product of 16 samples with positive amplifications. For that, 10 µL of molecular MilliQ water was added to the qPCR products. The DNA was purified using a commercial kit (QIAquick PCR Purification kit, QIAGEN), following the manufacturer protocol. The purified DNA was amplified by traditional PCR using PCR kit illustra puretaq ready to go (GE Healthcare), with 5 µL of purified DNA sample, 0.6 µM of each forward and reverse primers (primer pair AS3) and 27.5µl of molecular MilliQ water. The thermal profile for the PCR reaction was composed by 3 min at 95°C, 35 cycles of 1 min at 95°C, 1 min at 60°C and 90 s at 72°C, followed by 1min at 72°C (Stopar et al. 2010; Ramšak et al. 2012). The products of PCR reactions were analysed through electrophoresis (Mupid-One; Advance) at 100V for 30min in 0.5 X TAE buffer (Euromedex). An aliquot of 3 µL of samples was load on Agarose gel 1.5%, using loading buffer (AppliChem, Panreac) and 1Kb DNA ladder (Euromedex). Gels were stained with GelRed ® Nucleic Acid Gel Stain (Biotium), visualized and photographed on UV table using Molecular Imager Gel Doc ^{TM} XR System (Bio-Rad) for quality control of DNA amplification. Sequencing was performed at the genotyping and sequencing facilities in Montpellier University. The

purification of PCR products was performed by magnetic beads, using the CleanPCR kit (GCBiotech), performed by an automated liquid handler (Biomek 4000, Beckman Coulter). Sequencing was then performed with 55-60 ng of DNA using the BigDye Terminator Cycle sequencing v3.1 kit (Life Technologies), with the following PCR program: 3 min at 96ºC, 25 cycles of 10 sec at 96ºC, 5 sec at 50ºC and 4min at 60ºC. The products of the sequencing reaction were purified using magnetic beads, following the same protocol as previously described. The purified products were then analysed on an ABI 3500 xL capillary sequencer (Applied Biosystems, Darmstadt, Germany). A BLAST analysis of the resulting sequences against the GenBank nucleotide database was performed.

3.1.4. Results

3.1.4.1 Standard curve and DNA quantification

Both positive templates (polyps and medusae) were identified as *A. coerulea*, after the BLAST analysis. The standard curves of the qPCR assay (Fig. 1), determined with polyps and medusae positive templates, showed high assay efficiencies (86.64 and 93.80 %, respectively) and high correlation coefficient, R^2 (both 99%). The slope of both positive templates did not differ significantly (ANCOVA; $F = 0.03$, $P = 0.85$). However, the initial template concentration of polyps was higher (55.79 ng μL^{-1}) than that of medusae (11.89 ng μL^{-1}) and therefore, more dilution steps showed Cp values below 31. In consequence, the standard curve of polyps comprises more dilution steps and a wider range of quantifiable template concentration, increasing the accuracy of the regression fit. For this reason, its correspondent equation ($y = -3.69\ x + 16.74$) was selected to estimate the concentration of *A. coerulea* DNA in the fish gut content.

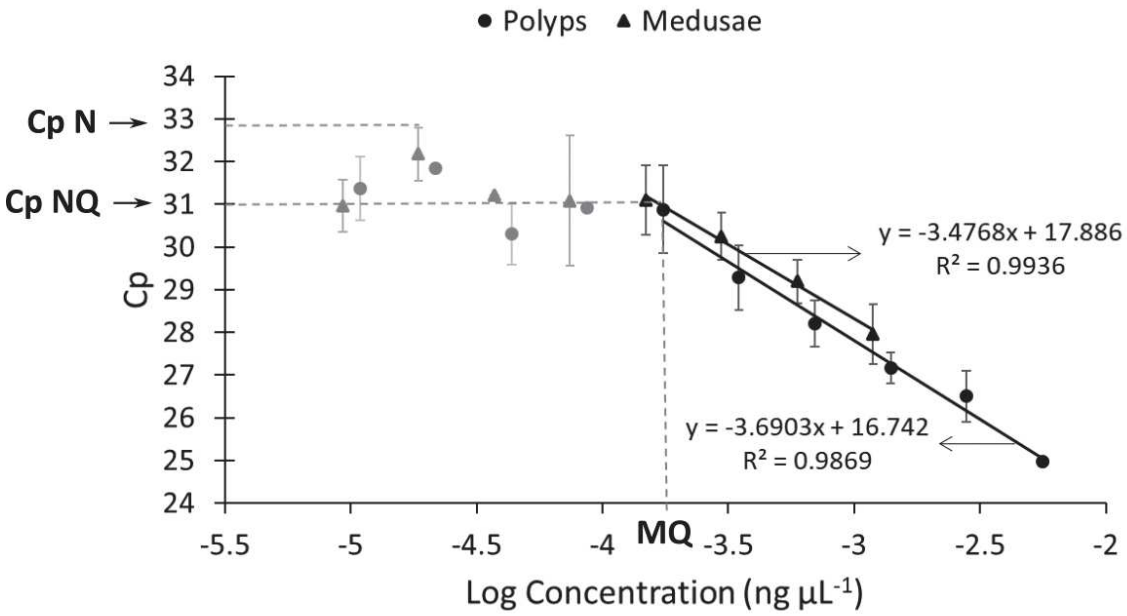


Fig. 1: Standard curves determined from 2-fold dilutions of polyps (circles) and medusae (triangles) positive templates. The dilutions included in the standard curve of each template are represented in black, while the dilutions excluded from the standard curve are in grey. In each case, the standard curve equation is shown, but only that of the polyp's template was used to estimate DNA concentration in fish gut contents (efficiency of 86.63%). The minimum quantifiable concentration (MQ = 1.37 x 10^{-4} ng μL^{-1}) corresponded to a Cp of 31 (*i.e.* the threshold for quantification; Cp NQ). Samples with Cp values between 31 (Cp NQ) and 32.62 (*i.e.* the threshold for detectability; Cp N) were considered positive but Non-quantifiable. Samples with Cp values above Cp N were considered negative (see methods section for further information). Error bars are standard deviations.

Although the more diluted samples of the positive template for *A. coerulea* polyps and medusae were positive (*i.e.* with proper melting curves), they showed low Cp values, indicating that their DNA concentrations were too low to be accurately quantified. Therefore, those dilutions were excluded from the standard curve. Among the three technical replicates analysed for each dilution sample, six false negatives (*i.e.* deviated Tm peak values) were observed. Although non-quantifiable, *A. coerulea* DNA was still detected at a maximum Cp of 32.62, which was therefore considered as the threshold of detectability.

The BLAST analysis revealed that all sequenced qPCR products of gut contents samples matched the previously designated *Aurelia* sp.1 (> 96.7% similarity), recently accepted as *A. coerulea* (Scorrano et al. 2016).

3.1.4.2 Fish ingestion of A. coerulea

During the period of *A. coerulea* bloom (from April to June) 50 fish individuals were provided by the fisherman. They belonged to five different species: the European eel (*Anguilla anguilla*, Linnaeus, 1758), the sand smelt (*Atherina boyeri*, Risso, 1810), the golden mullet (*Liza aurata*, Risso, 1810), the salema (*Sarpa salpa,* Linnaeus, 1758) and the gilthead sea bream

(*Sparus aurata,* Linnaeus, 1758) (Table 1). During the post-bloom period, when only polyps are present in the lagoon (September to November), only 12 individuals could be collected for this work. They belonged to three different species: the golden mullet (*L. aurata*), the salema (*S. salpa*) and the gilthead sea bream (*S. aurata*).

Table 1: Numbers of fish gut contents analysed (N) and of fish guts with positive detection of *A. coerulea* DNA (N Positives). In each case, the species, the range of weight and length of the sampled fish are indicated with the sampling period, from April to June (bloom) and from July to November (Post-bloom).

Period	Common name	Fish Species	Weight (g)	Length (mm)	N	N Positives (%)
Bloom	European eel	*Anguilla anguilla*	4.8 [a]	150 [b]	10	10 (100 %)
Bloom	Sand smelt	*Atherina boyeri*	0.41 - 8.1 [c]	40 - 99 [c]	5	0 (0 %)
Bloom	Golden mullet	*Liza aurata*	251.2 - 900	306.0 - 488.4 [a]	12	4 (33.3 %)
Bloom	Salema	*Sarpa salpa*	260.6 - 650	263.7 - 360.2 [a]	11	1 (9.1 %)
Bloom	Gilthead sea bream	*Sparus aurata*	133.6 - 300	95.5 - 126.7 [a]	12	4 (33.3 %)
Post-bloom	Golden mullet	*Liza aurata*	219 - 660.7	291.0 - 436.1 [a]	3	1 (33.3 %)
Post-bloom	Salema	*Sarpa salpa*	219.5 - 324.1	248.7 - 284.1 [a]	2	1 (50 %)
Post-bloom	Gilthead sea bream	*Sparus aurata*	159.9 - 234.6	101.7 - 116.3 [a]	7	5 (71.4 %)

[a] Calculated from length-weight relationships (Melià et al. 2006; Crec'hriou et al. 2012)
[b] Data not collected during the study, an approximate length of the individuals is provided.
[c] Data not collected during the study, but data from individuals collected in the Thau lagoon during the same period of the year is provided.

In total, DNA from *A. coerulea* was detected in the gut content of 26 fish (41.9 % of the 62 individuals analysed), among which 73% had been collected during the bloom period and 27% during the post-bloom period (Table 1). With the exception of the sand smelt, all species were shown to have consumed *A. coerulea*, irrespective of the period of sampling. During the bloom period, medusae DNA was detected in the gut contents of all the eels collected (10 individuals). One third of the golden mullets and gilthead sea breams analysed were also shown to have consumed *A. coerulea*, while positive detection was only observed in one individual of salema (9.1%). During the post-bloom period, *A. coerulea* was detected in only one golden mullet, one salema, and in 5 (71.4 %) gilthead sea bream.

The concentration of DNA in the fish gut contents was higher during the bloom than in the post-bloom period (Fig. 2). At this time of the year 63.2 % of the jellyfish consumers had a sufficient amount of DNA to be quantified (*i.e.* > 1.37 x 10^{-4} ng μL^{-1}). The maximum concentration (11.1 x 10^{-4} ng μL^{-1}) was detected in a golden mullet, but four other fish (two eels and two gilthead sea breams) showed DNA concentrations above 4 x 10^{-4} ng μL^{-1} in their gut contents. During the post-bloom period, the concentration of DNA in the guts was very low and, in most cases, non-quantifiable (Fig. 2).

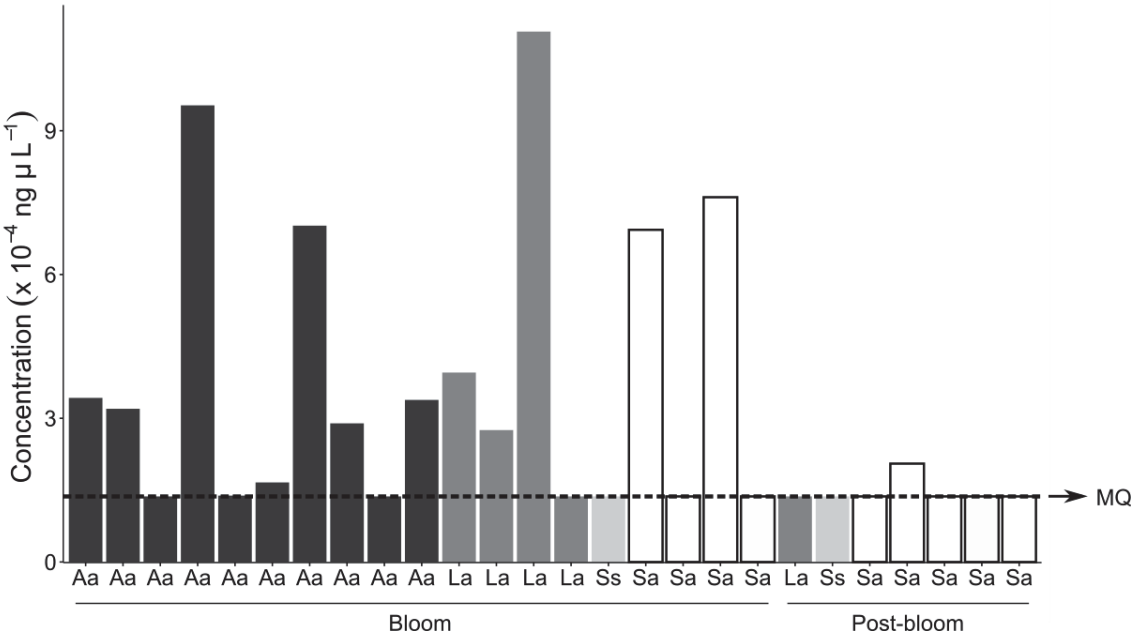


Fig. 2: Estimated concentration of *A. coerulea* DNA in the gut contents of the fish with positive detection: (Aa) European eel (*Anguilla anguilla*), (La) Golden mullet (*Liza aurata*), (Ss) Salema (*Sarpa salpa*), (Sa) Gilthead sea bream (*Sparus aurata*). The horizontal dashed line (MQ) indicates the minimum quantifiable DNA concentration (1.37×10^{-4} ng μL^{-1}, *i.e.* Cp = 31; see methods section for further information), below which the detection was positive but non-quantifiable.

3.1.5. Discussion

The present work brings new insights on the prey-predator relationships between fish and jellyfish in the Thau lagoon. Indeed, four of the five fish species analysed in this study were found to feed on *A. coerulea*. For some species, all the individuals tested had *A. coerulea* DNA in their gut, suggesting that this jellyfish might be a non-negligible source of food for commercial fish in the Thau lagoon.

The concentration of the target DNA in the gut contents was frequently low, with many individuals showing non-quantifiable DNA concentrations. This is not very surprising because jellyfish are rapidly digested in fish guts, compared to other prey (*e.g.* > 93% of the jellyfish biomass can be digested within 1h in controlled laboratory studies, Arai et al. 2003). In particular, due to the fishing method used, most of the fish captured during the post-bloom period probably had largely digested their prey during their prolonged captivity in the net. Therefore, we consider our results to be conservative and likely to underestimate *A. coerulea* consumption by commercial fish in the Thau lagoon. However, since only a few individuals of each species were analysed, especially during the post-bloom period, additional studies are needed to confirm the actual importance of *A. coerulea* as a source of food for fishes in the Thau lagoon.

During *A. coerulea* bloom periods, the only fish species which did not seem to consume jellyfish was the sand smelt. The diet of this species is opportunistic but mainly based on pelagic organisms such as zooplankton, phytoplankton, arachnids, insects and fish larvae (Vizzini and Mazzola 2005, Dias et al 2014, Yagci et al 2018). However, due to the small size of the specimens examined (< 7cm), they might have avoided jellyfish blooms, since they may become prey for large jellyfish medusae.

In contrast, the European eel was shown to be a potentially important consumer of jellyfish in the Thau lagoon. All the individuals tested showed positive detection of *A. coerulea* in their gut contents, with relatively high DNA concentrations. The consumption of gelatinous organisms by eels was also previously reported for their larvae (leptocephali) in the Sargasso Sea (Riemann et al. 2010; Ayala et al. 2018). Although there is a progressive ontogenic change in the diet of the eels (Costa et al. 1992; Proman and Reynolds 2000), it is not surprising that they retain the ability to feed on gelatinous organisms. After their migration from their spawning areas in Sargasso Sea (Ginneken and Maes 2005), European eels reach the Mediterranean lagoons as glass eels, with an average length of ca. 60–65 mm (Melià et al. 2006). At this stage, eels are considered to be non-feeding, starting to feed only when reaching the elver eel stage (Tesch et al. 2003). The individuals collected in this study were all at the elver stage (*i.e.* pigmented with a length of ca. 150 mm). The diet at this stage is mostly based on small-sized prey like amphipods, isopods, mysids and insects (Costa et al. 1992; Proman and Reynolds 2000) but it depends highly on prey availability (Costa et al. 1992; Bouchereau et al. 2006). Therefore, it is likely that the high abundances of jellyfish during the bloom might result in their ingestion by this opportunistic species.

The rate of standard metabolism of a European eel at 25ºC (*in situ* temperature in June 2013 was 20 ± 0.7 ºC) is 83.3 J g^{-1} day^{-1} (Owen et al. 1998). Assuming a similar energy requirement for the individuals collected in Thau, an eel with 4.72 g (estimated for a 15 cm eel, from length-mass relationships; Carss et al. 1999), would require 0.4 KJ d^{-1} of energy. One gram (wet weight) of *Aurelia* sp. provides 0.1 KJ of energy (Arai 1997 in Doyle et al. 2007, after wet weight estimation according to Lucas 1994). Therefore, one eel would require 3.8 g of medusae wet weight per day to meet its energy requirements. The eels analysed in this study were collected in June 2013, when the abundance of medusae was at its highest (75.5 ind 100 m^{-3}; Marques et al. 2015a). Because medusae are big in this time of the year (16.4 ± 2.8 cm; Marques et al. 2015a), which corresponds to 195.1 g of wet weight, estimated after Hirst and Lucas 1998, at the same salinity conditions), it is possible that the eels had bitten their umbrellas, taking advantage of the soft consistency of jellyfish body. Indeed, many jellyfish

predators do not ingest the whole medusae, but instead, they bite the umbrella margins and/or select particular parts of the medusae with higher nutritional values, such as gonadal tissue (Milisenda et al. 2014; Marques et al. 2016; Dunlop et al. 2017; Hoving and Haddock 2017). Therefore, in theory, one medusa could provide enough energy to sustain the standard metabolism of one eel for 51 days. Even though a large amount of jellyfish consumption is needed to meet such energy requirements (*i.e.* 80.5 % of the eel weight per day), the rapid digestion and gut clearance rates (Arai et al. 2003) allow the fish to increase its ingestion rates. Similar results were also reported for the leptocephali stage of the European eel (Ayala et al. 2018) and for other commercially important organisms (*e.g.* fish top predators, eel larvae, lobsters, deep water octopus), which, during blooms, jellyfish are able to meet and maybe overcome the entire energy requirements of these predators (Cardona et al. 2012; Dunlop et al. 2017; Hoving and Haddock 2017). Here we confirm the potentially important role of jellyfish as food for young stages of the European eel. These results are of great importance since the European eel is listed as a critically endangered species by IUCN (Freyhof and Kottelat 2010) and information regarding its diet is still limited.

The consumption of *A. coerulea* during its bloom period was also recorded for the gilthead sea bream and the golden mullet, both species showing, in some cases, high *A. coerulea* DNA concentration in their gut contents. This result is not surprising for sea bream as this species has been shown to prey on all life stages of *A. coerulea* in laboratory experiments, with high ingestion rates of polyps and small medusae (Marques et al. 2016). The sea breams with the highest concentrations of the target DNA in their guts were collected in April 2013, when the medusae bell diameter is < 3 cm (Marques et al. 2015a). In the laboratory, small medusae (1 cm bell diameter) were preferred by this fish, but larger ones (up to 8 cm bell diameter) were also preyed upon, by taking several bites on the edge of their umbrella (Marques et al. 2016). Therefore, our results provide evidence of possible active predation of sea bream individuals on pelagic jellyfish in the field. Jellyfish, though, was not selected in the laboratory when prey with higher nutritional value was equally available (Marques et al. 2016). In the field, gilthead sea breams prey mainly on polychaetes, small fishes, crustaceans, gastropods and bivalves but adapt their diet to local prey availability (Pita et al. 2002; Escalas et al. 2015). Therefore, we suspect that the high abundance and accessibility of *A. coerulea* medusae during the bloom periods, benefit this opportunistic predator by providing a suitable source of food when its preferred prey are less accessible (Marques et al. 2016; Díaz Briz et al. 2018).

More surprisingly, one third of the golden mullet specimens analysed had the target DNA in their gut contents. Mullets are detritivores, eating a mixture of sand, detritus,

microphytobenthos, macroalgae, zooplankton and benthic macrofauna (Laffaille et al. 2002; Almeida 2003). To our knowledge, the consumption of jellyfish by this species has never been described so far. It is possible that *A. coerulea* was consumed unintentionally since dead medusae are occasionally found decomposing on soft bottoms (R. Marques, personal observation) and the resulting organic matter may be incorporated in the surface sediment layer. One individual of this species, though, showed a high concentration of the target DNA in its gut content (the maximum concentration recorded in this study). Although the active predation of jellyfish by the golden mullet cannot be excluded, this particular individual was collected during the peak of *A. coerulea* abundance (in May 2018), when high biomass of jellyfish was also caught in the fishing nets (J. Fabrice, personal communication). Therefore, the high concentration of *A. coerulea* DNA in its gut contents might have been the consequence of its unintentional ingestion of medusae in the fishing net during sampling.

The ingestion of *A. coerulea* by salema might also be unintentional. Indeed, this species has been described so far as a true herbivore, with a diet largely based on seagrass leaves (Havelange et al. 1997). Because decaying medusae are also occasionally observed entangled among the seagrass leaves in the Thau lagoon (R. Marques, personal observation), they might have been ingested together with the target seagrass leaves. However, recent observations have shown that even herbivorous fish may actively prey on jellyfish (Bos et al. 2016), which cannot be excluded here. Still, additional individuals of this species should be analysed to test this hypothesis.

The consumption of *A. coerulea* was also observed when its pelagic stages were absent, which suggests that polyps might also be ingested by commercial fish species in Thau. The most important consumer of polyps in our study was the gilthead sea bream (71.4% of the individuals showed positive detection of *A. coerulea* DNA in their gut contents). In previous laboratory experiments (Marques et al. 2016), the sea bream was shown to consume polyps, likely in an indirect way. In this recent study, it was suggested that the actual target of the fish during the predation experiments, could have been the settling substrate of polyps (*i.e.* living mussels), rather on the polyps themselves. In Thau, most of the polyps of *A. coerulea* are found fixed on oysters or mussel shells (Marques et al. 2015b). Because bivalves are highly important in the diet of adult sea bream (Pita et al. 2002; Tancioni et al. 2003; Russo et al. 2007) and very abundant in Thau lagoon, we hypothesize that the consumption of *A. coerulea* polyps in the field results from an indirect ingestion, when fishes are preying on their settling substrates. In addition, pieces of mussel shells were recurrently observed in the sea bream gut contents. These findings highlight the likely underestimated impact of sea bream predation on the regulation of

the benthic population of *A. coerulea* in the lagoon, potentially contributing to the reduction of medusae abundances and to the magnitude of jellyfish blooms in this lagoon.

A. coerulea polyps consumption was also detected for both the salema and the golden mullet. This is surprising since polyps generally settle on the underside surface of hard substrates and have never been found on soft sediments or fixed to seagrass leaves (Marques et al. 2015b). Even though unintentional consumption can not be excluded, very few individuals of these two species were analysed in this study. Therefore, the importance of the consumption of *A. coerulea* polyps by their individuals in the lagoon still needs further investigation.

3.1.6. Conclusion

Our results demonstrate that the jellyfish *A. coerulea* is ingested by several commercially important fishes in Thau lagoon during its bloom period, when the abundance and biomass of its pelagic stages are high, but also in post-bloom periods when only *A. coerulea* polyps are present in this semi-enclosed ecosystem. This provides evidence that the vulnerability of jellyfish to fish predation has been underestimated in the lagoon but also, potentially, elsewhere. Indeed, predation pressure by a large number of fish species with broad diets is more ecologically important than that by a few specialized ones (Purcell and Arai 2001; Arai 2005). Here we highlight potential ecological implications for both fish and jellyfish ecology. On the one hand, direct predation on jellyfish pelagic stages or indirect predation on polyps might contribute to control jellyfish blooms, through top-down regulation. In this sense, the overexploitation of fish stocks might contribute to the increase of jellyfish outbreaks, by releasing the predation pressure over jellyfish populations (Roux et al. 2013). On the other hand, the availability and accessibility of jellyfish during their blooms provide an alternative food source for fish populations, that might actively consume jellyfish when their primary prey are less available (Diaz Briz et al. 2018; Mianzan et al 2001).

3.2 DEGRADATION OF DEAD MEDUSAE (PAPER IV)

Blooms of *A. coerulea* are produced annually in the Thau lagoon, which prompted the question regarding the fate of this organic matter. If not consumed by pelagic predators, it is expected that this large abundance of medusae will die and sink to the bottom. Therefore, the aim of this section was to investigate the degradation of dead *A. coerulea* medusae on the seabed of Thau and the potential importance of its consumption by the local macrobenthic communities. For this, *in situ* experiments were performed in the most common habitats in the lagoon (seagrass meadows and bare sediment) by adding jellyfish carcasses on the seabed. This allowed understanding the main trophic pathways responsible for the flow of the dead organic matter within the local food webs and shed light on the potential impacts of the *A. coerulea* blooms in the ecosystem functioning.

Paper IV

This section will be submitted in December 2019

Jellyfish degradation in a shallow coastal Mediterranean lagoon

Marques R, Rufino M, Darnaude AM, Carcaillet F, Meffre M, Bonnet D (*in prep*)

3.2.1. Abstract

Blooms of the jellyfish *Aurelia coerulea* are produced annually in a warm and shallow coastal Mediterranean lagoon (the Thau lagoon), which prompted the question regarding the fate of this organic matter. The aim of the current work was to investigate the degradation of the dead medusae, by estimating its decay rates and the potential impact of the macrobenthic communities on the jellyfish degradation. For this, we carried out two *in situ* experiments in the two most common habitats of the Thau lagoon (in seagrass meadows and on bare sediment), by adding jellyfish carcasses on the seabed. The *in situ* degradation of jellyfish in the Thau lagoon was very fast (remineralisation of 99% of the medusae biomass in about 19h on the sediment and in 32 to 78h on seagrass meadows). This rapid decomposition was likely a consequence of the fast microbial degradation since limited modifications were observed on the macrobenthic community structure. Indeed, only the gastropods from Nassaridae family revealed a significant response to the presence of dead medusae. Here we discuss the potential importance of the jellyfish blooms degradation on the biogeochemical cycle and on the food webs of the Thau lagoon, underlining the need to include this process in ecosystem based models.

3.2.2. Introduction

Jellyfish are particularly known for their conspicuous blooms, which may locally generate biomasses exceeding 10 t wet weight 100 m^{-3} (Lilley et al. 2011). The population dynamics of jellyfish (especially scyphozoans) at the pelagic stage is usually described as 'bloom and bust', since jellyfish blooms collapse rapidly, usually within a few weeks or months (Pitt et al. 2014). This causes a large accumulation of sinking dead jellyfish (referred to as *jelly-falls*) on the seafloor (Lebrato et al. 2012). Impressive accumulations of jelly-falls have been reported, especially in deep sea habitats (Billett et al. 2006; Yamamoto et al. 2008; Lebrato and Jones 2009; Sweetman and Chapman 2011, 2015) where they can form localized layers of up to 70 mm thickness (78 g C m^{-2}) on the seabed (Billett et al. 2006). The projected increase of jellyfish blooms, at least in some parts of the world (Brotz et al. 2012; Condon et al. 2012), calls for understanding the impacts of jelly-falls on functioning and productivity of benthic communities. In particular, such studies are imperative for coastal habitats, where anthropogenic impacts are intense and pointed as likely promoters of jellyfish blooms (reviewed in Purcell 2012). However, the scientific research so far has largely focused on the drivers of jellyfish blooms, whereas the fate of the alien organic matter brought by jelly-falls on the seabed and its impacts on benthic macrofaunal communities are still overlooked.

Jelly-falls start when gelatinous organisms die in the water column and begin to sink (Lebrato et al. 2012). Their organic matter then has several possible fates. First, it can be consumed directly by pelagic scavengers. Otherwise, the microbial degradation takes over and they sink to the seabed. The amount of jellyfish biomass that reaches the seafloor depends on the decay rate of each species, the sinking speed of the carcasses, the depth at which the jellyfish die and the depth of the water column itself (Lebrato et al. 2011). The decay rate of jellyfish depends on the temperature and the lability of jellyfish tissues, *i.e.* on the species (Pitt et al. 2009b), while their sinking rate is a function of their size, diameter, biovolume, geometry, density and drag coefficients (Yamamoto et al. 2008; Lebrato et al. 2011, 2012). If not degraded in the water column, jelly-falls accumulate on the seabed, with potentially important impacts on both the biogeochemical cycling and the functioning of benthic ecosystems (*e.g.* Sweetman et al. 2016). On the positive side, dead jellyfish can provide suitable additional food for benthic scavengers, thereby boosting benthic productivity, especially in deep water habitats (Sweetman et al. 2014). Hence, varied benthic species, including fishes, echinoderms, anthozoans, polychaetes and crustaceans, have been reported to feed on jellyfish carcasses (Lebrato et al. 2012; Sweetman et al. 2014; Ates 2017). This scavenging behaviour plays a key role in benthic ecosystem functioning as it determines the fate of the organic matter that reaches the seafloor,

i.e. whether the organic material from jelly-falls contributes to the microbial loop or enters macrofauna food webs (Sweetman et al. 2014). On the negative side, unconsumed jellyfish carcasses on the seabed both smoother its surface and act as a barrier to oxygen diffusion at the water-sediment interface (Billett et al. 2006; Pitt et al. 2009b; Chelsky et al. 2016). Jellyfish carcasses are usually rapidly degraded by the benthic microbial community, mainly due to their high water content and the high lability of their tissues (Pitt et al. 2009b). Indeed, the elemental composition (C:N:P) of jellyfish is similar to that of bacteria (Jane et al. 2009; Sweetman et al. 2016) which, together with their high proportion of proteins, supports high degradation rates (Jane et al. 2009; Pitt et al. 2009b; Tinta et al. 2010, 2012). The outcome is a release of large amounts of dissolved organic matter and inorganic nutrients that further boosts microbial activity (Jane et al. 2009; Pitt et al. 2009b). Therefore, dissolved oxygen concentrations on the seabed may drastically decrease in the vicinity of jellyfish carcasses (Jane et al. 2009; Pitt et al. 2009b). This induces inhospitable conditions for benthic organisms, decreasing its activity, causing local emigrations or even massive mortalities (Chelsky et al. 2016; Sweetman et al. 2016).

The microbial degradation of *jelly-falls* has been relatively well described (Titelman et al. 2006; Jane et al. 2009; Tinta et al. 2010, 2012; Condon et al. 2011; Frost et al. 2012; Blanchet et al. 2015; Sweetman et al. 2016). However, studies investigating the impact of *jelly-falls* on benthic macrofaunal communities (*e.g.* Sweetman et al. 2014; Chelsky et al. 2016) are still scarce. In particular, although coastal lagoons support important ecological processes and provide numerous ecosystem services (Newton et al. 2014; De Wit et al. 2017), very little information is available regarding jelly-falls fate within these ecosystems. Coastal lagoons are very productive enclosed systems, in which jellyfish blooms occur regularly (*e.g.* Fuentes et al. 2011; Marques et al. 2015a), with abundances that can exceed 530 tonnes km^{-2} (Pitt and Kingsford 2003). Despite the large biomasses of jellyfish blooms reported in some lagoons, to our knowledge, massive accumulations of jelly-falls on lagoon seabed's were never reported. This is surprising because medusae degradation rates in the water column are expected to be minimal since many lagoons are relatively shallow and therefore, many jellyfish are likely to reach the seabed even before they die (Lebrato et al. 2012). Therefore, their disappearance from the system implies that they are rapidly eaten by benthic scavengers and/or decomposed by benthic bacterial communities.

The aim of the current work is to investigate the degradation of the jellyfish carcasses and its impacts on the macrobenthic communities. For this, we carried out different *in situ* experiments in two habitats of the Thau lagoon (NW Mediterranean) by adding jellyfish

carcasses on the seabed. In particular, we tested if the addition of the dead jellyfish on the seabed alters the benthic community of macroorganisms by, for instance, attracting scavengers (Chelsky et al. 2016). We further tested if the loss in jellyfish biomass was faster in the presence of marine benthic scavengers since these are able to consume considerable amounts of *jelly-falls* biomass within a few hours (Sweetman et al. 2014). In addition, we hypothesize that the different macrobenthic community composition associated with each habitat would have a different impacts on the decay rate of the jelly-falls.

3.2.3. Material and Methods

3.2.3.1 Study site and jellyfish collection

The Thau lagoon (43°25'31.1"N; 03°42'0.9"E) is a semi-enclosed coastal lagoon of 75 km^2, connected to the Mediterranean Sea by three narrow channels. It is shallow, with mean and maximum depths of 4 m and 10 m, respectively (with the exception of a localized depression of 24 m) and is highly influenced by strong wind events (Fiandrino et al. 2012). The local tidal range is weak (< 1 m), which promotes a high water residence time (1 - 4 months, Fiandrino et al. 2012). With regards jellyfish, the Thau lagoon has the particularity to harbour a resident population of *Aurelia coerulea*, which is isolated from the Mediterranean Sea (Bonnet et al. 2012; Marques et al. 2015b). This offers a rare occasion to study the fate of the local blooms of this species. In the lagoon, ephyrae first appear in the early winter (November – December), to give rise to adult individuals at the beginning of spring (April – May), when temperature increases (Marques et al. 2015a). High abundances of medusae, associated with high growth rates generate the annual jellyfish bloom (Marques et al. 2015a), which collapses only in the late spring (June-July). Although sparse decaying medusae are often seen in the lagoon, either entangled on seagrass leaves or on bare sediment habitats (R. Marques, personal observation), large accumulations of *A. coerulea* carcasses were never observed in Thau.

This study was conducted in June 2018, during the collapse of the *A. coerulea* bloom. Two different *in situ* experiments were performed in order to (i) assess the decay rates of jellyfish under different scenarios of medusae accessibility for benthic scavengers, and (ii) study the impact of jellyfish degradation on the macrobenthic community composition. Both experiments were performed in a shallow area (< 1m depth) and repeated in the two most common habitats found in the lagoon (Plus et al. 2003): bare sandy sediment and seagrass meadows (*Zostera noltii*) habitats.

For both experiments, live medusae were collected on the 28th May 2018 by hand nets and transported to the laboratory in *in situ* seawater. They were kept alive for a few days, in 1 m^3 tanks (ca. 100 ind m^{-3}) with seawater open circulation system. Newly hatched *Artemia* was provided as food once per day. Before each experiment, medusae were equally distributed in 30 L cold boxes, filled with *in situ* seawater and killed by sparging the water with nitrogen gas for 3 to 6h (Chelsky et al. 2016).

3.2.3.2 Jellyfish decay rates

Experimental set-up

Jellyfish decay rates were assessed both on the seagrass meadows and sediment habitats, under two scenarios of accessibility to marine benthos: restricted to microorganisms (Micro) and accessible to macroorganisms (Macro). For the Micro scenario, individual medusae were placed in 20 x 15 cm net bags with a mesh size of 200 µm so they were accessible only to microorganisms < 200 µm (*e.g.* bacteria, microzooplankton and small mesozooplankton species). For the Macro scenario, medusae were placed in 20 x 15 cm net bags with a mesh size of 1 cm, which allowed additional scavenging by small macroorganisms (*e.g.* gastropods, amphipods, small crustaceans). In both Micro and Macro treatments, bags were protected with 1.5 x 2 x 0.15 m net cage with a coarse mesh size of 2.5 cm, to prevent medusae consumption by large organisms (*e.g.* large fish, echinoderms, crustaceans). The scenario Macro was replicated without the cage to assess if the medusae consumption by large scavengers was significant. Since the effect of the cage was not significant (GLNS, *p-value* = 0.17 and 0.62 for sediment and seagrass habitats, respectively), data from Macro scenarios with and without cage were pooled.

Before the experiment, individual dead medusae were wiped with paper to absorb the excess of water and mucus from their surface, weighted (wet weight in g, to the nearest 0.1 g) and measured (bell diameter in cm). Each medusa was then placed individually in a bag. In each scenario, 30 bags were fixed on the sediment using tent pegs, with a minimum distance of 1.5m between them. During the experiment (24h and 30h for the seagrass and sediment habitats, respectively), 3 replicates of individual medusae were collected per scenario (micro and macro) every 1 to 3h. The bags were collected carefully and placed immediately inside a hermetic plastic bag to avoid the loss of biological material. The remaining medusae biomass was wiped with paper to absorb the excess of water from the surface (when possible) and weighted to the nearest 0.1 g (wet weight). The temperature was measured (EC 300 VWR international/ WTW

model 350i) both before the start of the experiment and right before each medusae collection for weighing.

Data analysis

For each habitat (sediment and seagrass meadow) and accessibility scenarios (Micro and Macro), jellyfish decay rates were determined by fitting exponential decay models to the non-averaged wet weights of medusae (in percentage of the initial wet weight) as a function of time:

$$M_t = M_0 e^{-\lambda t}$$

where M_t is the percentage of medusae wet weight at time t (in hours), M_0 and λ are the model coefficients representing the initial (t = 0) medusae wet weight (in percentage) and the decay rate, respectively. The decay (λ) rates were then used to calculate the remineralisation time (R_t in hours), *i.e*. the time required to decompose 50% (t = 0.5) and 99% (t = 0.01) of the initial biomass of medusae, according to the following equation (Lebrato et al. 2011):

$$R_t = \frac{-\ln(t)}{\lambda}$$

Differences according to the accessibility scenarios and the habitat were tested by fitting NLS models using "nlme" package (Pinheiro et al. 2019), which allows fitting the model to zero values, using 100 and 0.01 as starting parameters (for M_0 and λ, respectively).

3.2.3.3 Benthic community changes

Experimental set-up

To test the impact of the jellyfish degradation on the benthic community composition, a second experimental set up was developed. The experiment was run in two habitats, on the seagrass bed and on the sediment, with a duration of 15h and a macrobenthos sampling frequency of 3h, taking into account the results of the jellyfish decay rates experiments. The experiments started (t_0) at 16h30 and 15h40 on the seagrass meadows and sediment, respectively. In each habitat, three different treatments were used: the *medusa* (M), the *procedure control* (PC), and the *control* (C). For the M treatment, individual medusae were placed in 20 x 15 cm net bags with a mesh size of 1 cm, which allowed scavenging by small macroorganisms (*e.g*. gastropods, amphipods, small crustaceans). The bags were protected with 1.5 x 2 x 0.15 m net cage with a coarse mesh size of 2.5 cm, to prevent medusae consumption by large macrobenthic organisms (*e.g.* large fish, echinoderms or crustaceans). The PC treatment aimed to test the effect of the experimental setup and therefore the M treatment was

reproduced but without medusae. For the C treatment, the sampling was performed on undisturbed areas of each habitat. To analyse the macrobenthic community structure, the sediment and the seagrass (when present) below each treatment were collected, including sediment surface organisms. Sampling was performed immediately after medusae (M) or empty bag (PC) collection. Three replicates were performed per combination of habitat, treatment and sampling time. In each case, the sediment was sampled using a shovel (0.03 m^2, 4 cm deep) and placed inside a hermetic plastic bag, ensuring a minimum sample loss. Samples were stored in cold boxes and frozen within 6h, until later laboratory analysis. The temperature was measured (EC 300 VWR international/ WTW model 350i) both before the start of the experiment and right before each medusae collection for weighing.

Once in the laboratory, the volume of sediment in each sample was measured using graduated beakers to standardize the abundance of organisms, but the results are presented by a unit of area (m^2). Sediment was sieved (1 mm mesh size) and macrofauna was sorted, counted and identified under dissecting microscope (Fauvel 1923, 1927; D'Angelo and Gargiullo 1978). The organisms were identified to the lowest taxonomic level, however, since the identification to the species level was not possible for all organisms, species of the same genus were grouped together. Annelids and Decapods were identified to the family level.

Data analysis

Only taxa that represented more than 1% of the total community biomass in each habitat were considered in the data analysis, in order to eliminate the influence of rare taxa. Diversity indices (Shannon and Pielou's evenness index) were calculated using the "BiodiversityR" package (Kindt and Coe 2005), based on "vegan" package in R (Oksanen et al. 2019). The changes in total abundance (after natural logarithmic transformation) and diversity indices, between habitat type (seagrass and sediment), scenarios (M, PC and C) and sampling times (3, 6, 9, 12, and 15h) were tested using linear models. For each variable (*i.e.* Total abundance, Shannon and Pielou's evenness indices) a full model was produced, with all main terms, *i.e.* habitats (seagrass meadows and sediment), treatment (M, PC and C), sampling times (3, 6, 9, 12, and 15h) and respective interactions (index ~ habitat * treatment * sampling time). Model selection procedure was then carried out using the Akaike information criterion (AIC), following Zuur et al. (2009). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. Differences between each combination of treatment and sampling time within each habitat were tested using post hoc Tukey HSD tests for multiple comparisons.

Changes in community composition among groups (*i.e.* habitat type, treatment and sampling time) were analysed using three different complementary approaches (Fig. 1)

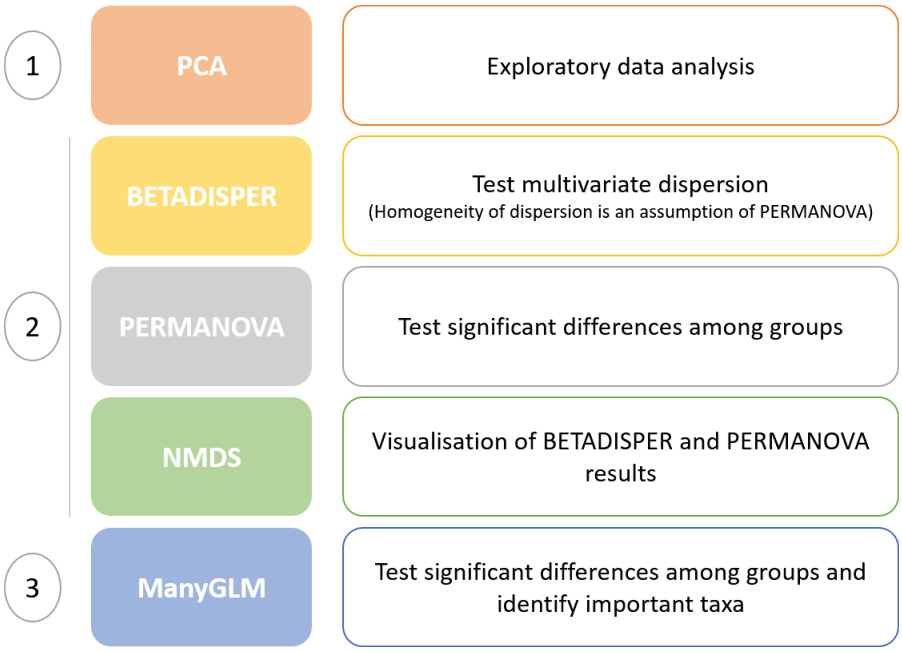


Fig. 1 Schematic representation of the analysis used to assess changes in the community composition and their specific objectives.

First, the community composition was represented through a principal component analysis (PCA) of the logarithmic transformed abundances (log(x+1)). Then, differences between community composition between habitat type, treatments and sampling times were assessed through a permutational multivariate analysis of variance (PERMANOVA, with 9999 permutations), using Bray-Curtis distance. Since homogeneity of dispersion between factors is an assumption of the PERMANOVA analysis, multivariate dispersion was first tested using BETADISPER. When significant differences were observed, a pairwise comparison was performed (PERMUTEST, with 9999 permutations). Nonmetric Multidimensional Scaling (NMDS) plots were used to visualize the results of BETADISPER and PERMANOVA, as recommended (Anderson 2017). These analyses were performed using the package "vegan" (Oksanen et al. 2019). Lastly, to cope with the potential limitations reported for PERMANOVA (Warton et al. 2012), we also ran a model based approach using generalized linear models for multivariate abundance data (ManyGLM, from package "mvabund"; Wang et al. 2012). A two fixed factor model structure (sampling time and treatment) was used, separately for each habitat, with a negative binomial distribution and a log-link function. The examination of residual plots of the model showed the absence of a clear pattern, validating the model. This analysis was also used to determine which taxa contributed most to the differences observed.

3.2.4. Results

3.2.4.1 Jellyfish decay rates

The initial medusae wet weights (Table 1) were similar among scenarios within each habitat (Kruskal-Wallis, $\chi^2 = 0.32$, df = 1, *p-value* = 0.57 and $\chi^2 = 0.61$, df = 1, *p-value* = 0.44 for sediment and seagrass, respectively), but differed between habitat type (Kruskal-Wallis, $\chi^2 = 81.33$, df = 1, *p-value* < 0.001). Temperatures were similar in the seagrass (23.5 ± 0.7 ºC) and the bare sediment (23.4 ± 0.5 ºC) habitats (T-test, *p-value* = 0.8). The degradation of *A. coerulea* biomass was fast irrespective of the scenario (Fig. 2), with decay rates ranging from -0.24 to -0.06 (Table 1).

Table 1: Initial wet weight (W) and bell diameter (BD) of the medusae used in each experiment and the resulting decay rate (λ in hours) and remineralisation time estimation (*Rt* in hours).

Scenario	**Initial W (g ± SD)**	**Initial BD (cm ± SD)**	**λ (h)**	***Rt* (h)**
		Sediment		
Macro	34.8 ± 12.4	8.0 ± 1.3	-0.24	19.51
Micro	32.8 ± 14.9	8.1 ± 1.5	-0.24	19.05
		Seagrass		
Macro	107.5 ± 20.0	12.8 ± 0.9	-0.06	78.04
Micro	111.8 ± 19.0	13.2 ± 1.0	-0.15	31.56

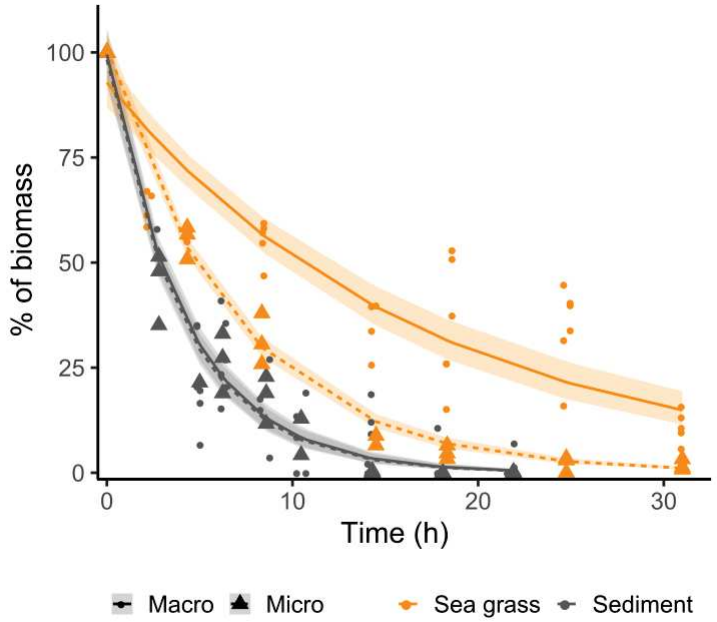


Fig. 2: Degradation of *A. coerulea* in both habitats for each accessibility scenario. Exponential decay models were fitted (lines) to the non-averaged data of biomass (in % of the initial wet weight), with 95% confidence intervals (shadow areas).

All model fits and correspondent coefficients were statistically significant (NLS, *p-value* < 0.001, Table 2). On the bare sediment habitat, the jellyfish decay rate was not affected

by the accessibility scenarios (NLS, *p-value* = 0.798), while on the seagrass meadow the decay rate was significantly higher (NLS, *p-value* < 0.001) in the Micro scenario than in the Macro one. Regardless of the scenario, medusae degradation was significantly faster on the sediment (NLS, *p-value* < 0.001), where 99% of the initial medusae biomass was remineralised in about 19 h in both accessibility scenarios (Table 1). The remineralisation was slower on the seagrass meadows: under the Macro scenario, *Rt* was estimated at 78 h, while microorganisms alone remineralised 99% of the biomass in 32 h. However, jellyfish degradation was consistently faster during the first few hours, with 50% of the biomass remineralised in 3h on the sediment (both scenarios), against 5 and 12h on the seagrass meadows, for Micro and Macro scenarios, respectively.

Table 2: Estimation of the parameters (M0 and λ) by the GNLS models used to assess differences between scenarios within each habitat. Significant differences (*p-value* < 0.05) are indicated in bold.

	Value	**Std.Error**	**t-value**	***p-value***
		Sediment		
M_0				
Macro (Intercept)	99.514	2.944	33.805	**< 0.01**
Micro	-1.228	5.025	-0.244	0.807
λ				
Macro (Intercept)	0.236	0.013	18.509	**< 0.01**
Micro	0.006	0.023	0.257	0.798
		Seagrass		
M_0				
Macro (Intercept)	92.834	2.511	36.974	**< 0.01**
Micro	8.045	6.095	1.320	0.192
λ				
Macro (Intercept)	0.059	0.004	14.525	**< 0.01**
Micro	0.087	0.017	5.142	**< 0.01**

3.2.4.2 Benthic community changes

General composition of macrobenthic communities

A total of 9478 benthic macrofauna organisms, belonging to 34 different taxa, were identified during the study period. The two habitats presented different taxa richness with a higher number of taxa identified on the seagrass meadows (29) than on the sediment (20). However, on the seagrass meadows, only nine taxa represented more than 1% of the total biomass, so the community was dominated by fewer taxa thus, less even (Fig. 3). In particular, the gastropod *Bittium* sp. (Br) and the bivalve *Ruditapes* spp. (Td) represented together more than 80% of the total abundance of potential scavengers in all treatments: Medusae (M, 67.8 and 17.4%, respectively), Control (C, 41.6 and 41.3%, respectively) and Procedure Control (PC, 58.5 and 25.4%, respectively). On the bare sediment, the total abundance was more equally

distributed among taxa: in the C treatment, 81.7% was represented by Glyceridae (28.2%), *Bittium* sp. (23.6%), *Tricolia* sp. (17.9%) and *Rissoa* spp. (12.1%); in the M treatment, the contribution of Gliceridae dropped to 12.5%, while taxa like *Ruditapes* spp. and *Tritia* spp. increased their importance representing 15.8% and 8.9% of total abundance, respectively; and in the PC treatment, the most abundant taxa were *Bittium* sp. (24.4%), *Tricolia* sp. (16.5%), *Rissoa* spp. (15.4%) and Glyceridae (12.2%).

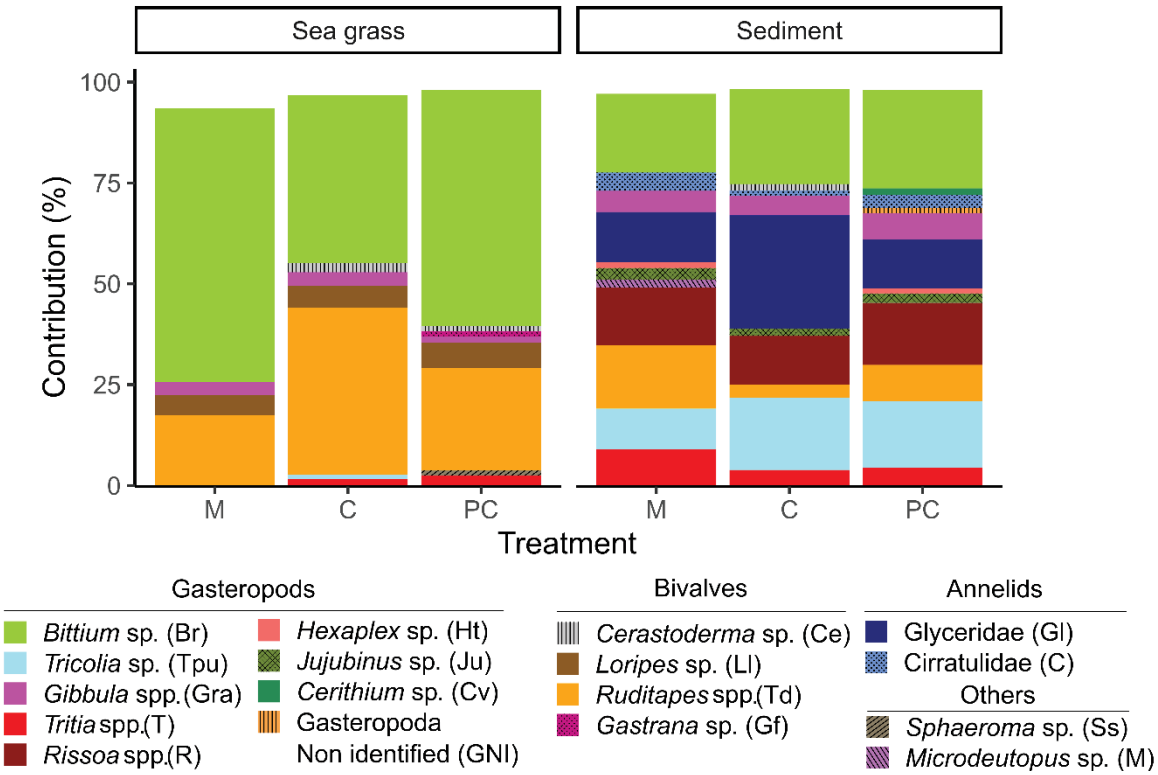


Fig. 3 : Contribution of the most important taxa to the total abundance of the community on the seagrass meadows and on bare sediment, in each treatment (M: Medusae, C: Control, PC: Procedure control). Only taxa that contributed to more than 1% of the total biomass are presented.

Abundance and diversity of the community

In both habitats, the total abundance of the organisms in the control treatment (C) did not vary significantly over time (Tukey HSD, *p-value* > 0.05), except at 12h in the seagrass habitat, where it was significantly lower than at t_0 (Tukey HSD, *p-value* = 0.02) (Fig. 4 A and B). Overall, the abundances were 10 times higher in the seagrass meadows (mean: 6 800 ± 8830 ind.m^{-2}) than on the sediment (mean: 637 ± 717 ind.m^{-2}). A peak of abundance was observed in both habitats at 3h for M and PC (> 1500 ind.m^{-2} and > 190 ind.m^{-2}, in seagrass meadows and sediment, respectively), decreasing afterwards.

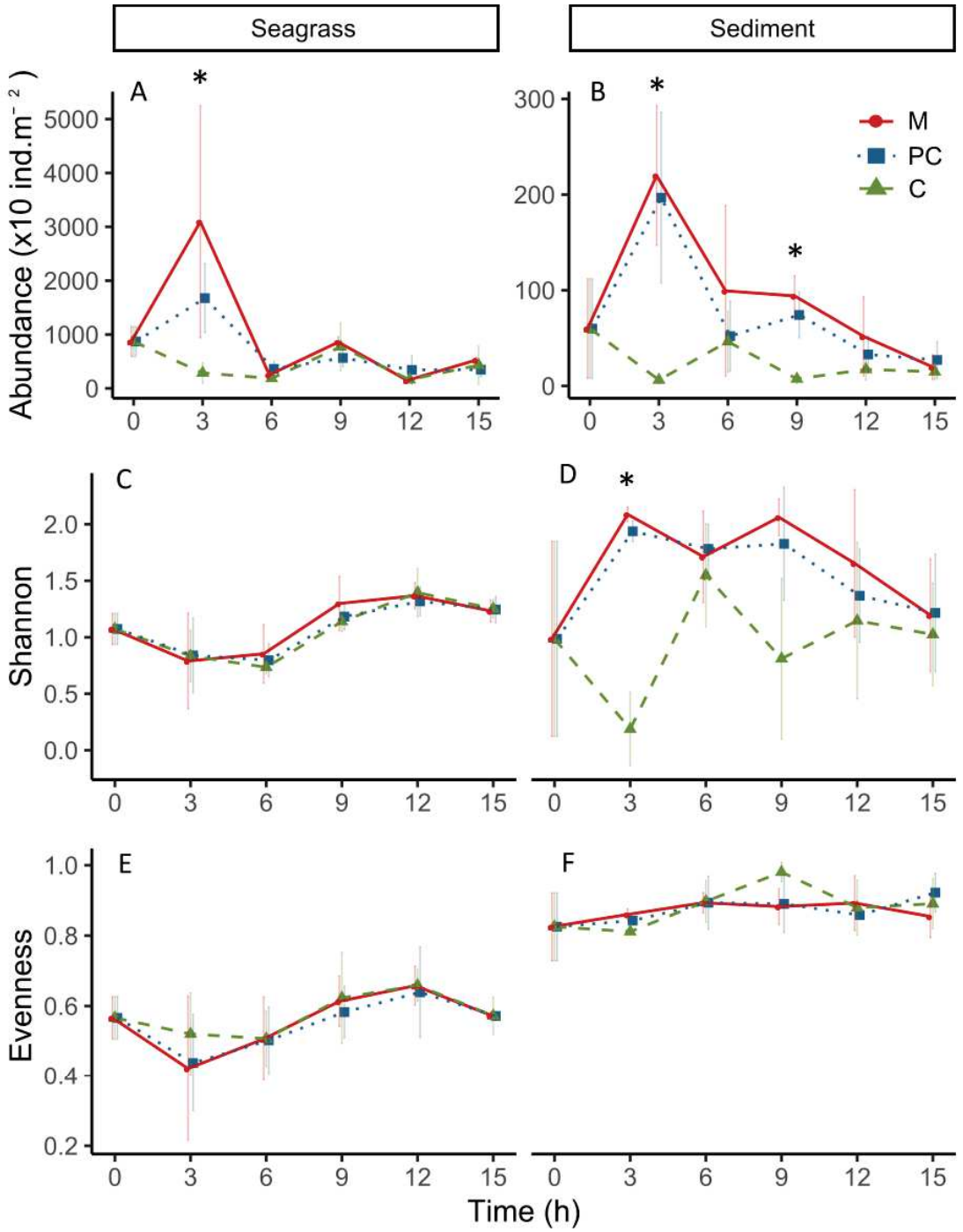


Fig. 4: Total abundance (A and B, note the different scales for the two habitats), Shannon diversity index (C and D) and Pielou's equitability index (Evenness) in the seagrass meadow (A, C and E) and sediment (B, D and F) habitats. Dots represent the average, whereas the vertical bars are standard deviations, for each treatment (M, PC and C). Asterisks indicate significant differences between treatments at $\alpha = 0.05$.

The total abundance of organisms differed significantly irrespective of the factor considered (habitat, sampling time and treatment, Table 3), but their overall interaction was not significant, indicating that the factors treatment and sampling time affected the abundance of organisms within each habitat. The total abundance significantly varied over time in both habitats (Tukey HSD, *p-value* < 0.05), but differences in total abundance between treatments

were only observed at 3h on the seagrass, and at 3 and 9h on sediment (Tukey HSD, *p-value* < 0.05; Fig.4 A and B). At these sampling times, the abundances of organisms were higher in M and PC treatments than in C (Tukey HSD, *p-value* < 0.05), but no differences were observed between M and PC (Tukey HSD, *p-value* > 0.05).

Table 3: Results of the linear models and the effect of each factor (Habitat, Sampling Time and Treatment), on each variable (Total abundance, Shannon and Evenness diversity indices). Bold values indicate significant differences between at least two groups, at α = 0.05.

Total abundance	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
S.Time	5	18.294	3.659	8.687	**<0.001**
Treatment	2	24.407	12.204	28.974	**<0.001**
Habitat	1	156.490	156.490	371.541	**<0.001**
S.Time:Treatment	8	19.163	2.395	5.687	**<0.001**
S.Time:Habitat	5	8.792	1.758	4.175	**0.002**
Treatment:Habitat	2	4.745	2.372	5.633	**0.006**
S.Time:Treatment:Habitat	8	6.233	0.779	1.850	0.084
Shannon					
S.Time	5	1.304	0.261	1.853	0.115
Treatment	2	2.986	1.493	10.610	**<0.001**
Habitat	1	2.528	2.528	17.962	**<0.001**
S.Time:Treatment	8	2.195	0.274	1.949	0.068
S.Time:Habitat	5	3.180	0.636	4.519	**0.001**
Treatment:Habitat	2	2.612	1.306	9.281	**<0.001**
S.Time:Treatment:Habitat	8	2.176	0.272	1.933	0.070
Evenness					
S.Time	5	0.201	0.040	6.956	**<0.001**
Habitat	1	2.332	2.332	403.462	**<0.001**
S.Time:Habitat	5	0.085	0.017	2.936	**0.017**

The Shannon diversity index was affected by the interaction of habitat with sampling time and with treatment (Table 3), indicating that within each habitat the diversity of the community was affected by only one factor. Indeed, in seagrass meadows, the diversity significantly increased over time, ranging from 0.73 ± 0.06 to 1.14 ± 0.09, at 3 and 12h respectively (Tukey HSD, *p-value* < 0.05; Fig. 4 C), but it did not vary between treatments. On sediment, differences were only observed between treatments, where the diversity was higher in M (2.09 ± 0.06) and PC (1.94 ± 0.09) than in C (0.19 ± 0.32) at 3h (Tukey HSD, *p-value* = 0.01; Fig. 4 D).

For Pielou's evenness index, only the sampling time and habitat factors were retained in the model (Table 3), showing that the treatment did not affect the community evenness irrespective of the habitat. On sediment, the community remained even over time (~ 0.87), while on the seagrass meadows it varied among sampling time (Tukey HSD, *p-value* < 0.05; Fig. 4 E

and F) with an imbalanced community at 3h (0.42) and the highest evenness at 12h (0.66 ± 0.05).

Exploratory analysis (1)

The PCA mainly separated the samples from the two habitats (Fig.5 A), showing that this factor is the main driver of community composition. In seagrass meadows, the community was characterized by high abundances of *Bittium* sp. (Br), *Ruditapes* spp. (Td) and *Loripes* sp. (Ll), whereas on the sediment Gliceridae and *Rissoa* spp. highly contributed to differentiate these groups. The effect of the treatment or time on the community composition was not evident in the PCA (Fig.5 B and C). However, some samples appeared to have a different community composition from the remaining ones (samples with higher Euclidean distance from the center, indicated by grey lines, Fig.5 A, B and C). This suggests that these samples were composed of higher abundances of some particular taxa, such as *Bittium* sp and *Ruditapes* spp. for samples collected in seagrass meadows and *Rissoa* spp. and *Tricolia* sp. for samples collected on the sediment (Fig.5 D). Most of these samples (10 out of 16) were collected at 3h (Fig. 5 C), implying a different community composition at this sampling time.

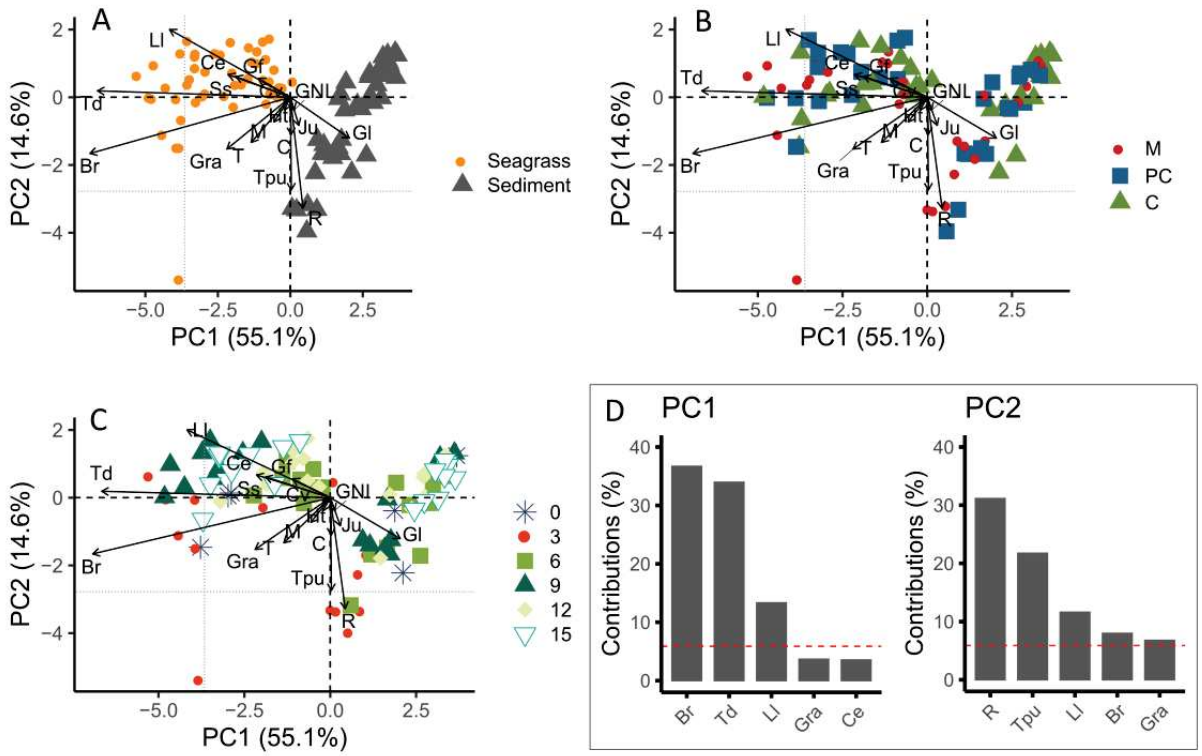


Fig. 5: Results of Principal Component Analysis (PCA). In A, B and C biplots of samples (points) and taxa (arrows) are presented. In A samples are identified according to the habitat (seagrass meadows and sediment), in B the samples are identified according to their treatment (M, PC or C) and in C the samples are identified according to sampling time (in h). Only the first two axes (PC1 and PC2) were retained since they represent the majority of the variability of the data (69.7%). Grey dotted lines are indicative thresholds to identify the samples with higher

Euclidean distance from the center. D represents the top 5 of the taxa that most contribute to each principal component (PC1 and PC2). The horizontal dashed line indicates the expected averaged contribution if all taxa would contribute equally to each PC. Contributions above this line are considered important. For the sake of simplicity, taxa names are abbreviated (see Fig. 3 with taxa codes).

Assessing differences among groups (2)

The multivariate dispersion of the community differed between habitats (F= 13.2, *p-value* < 0.001), but no changes in community dispersion were observed between sampling time (F= 0.7, *p-value* =0.6) or treatment (F=2.5, *p-value*=0.08). Considering these results, BETADISPER was re-run to determine the differences between treatment and sampling time for each habitat separately. On the seagrass meadows, homogeneity of dispersions was observed between treatments (F = 0.5, *p-value* = 0.6), but significant differences in the dispersions were observed across sampling time (F = 2.5, *p-value* = 0.045). Pairwise comparisons identified the samples collected at 3h as significantly dispersed from those collected at 6h, 9h (*p-value* < 0.05), 12h and 15h (*p-value* < 0.1) at this sampling site. After eliminating this sampling time from the BETADISPER analysis, homogeneity of community dispersion was observed among the remaining samples (F = 0.3, *p-value* = 0.9). This suggests that the samples collected at 3h in seagrass meadows were composed by different community composition. Accordingly, the PERMANOVA results indicate that the community composition did not vary between treatments (F = 0.6, *p-value* = 0.8), but showed significant differences over time (F= 9.3, *p-value* < 0.01) at this habitat type (Fig. 6 A and B).

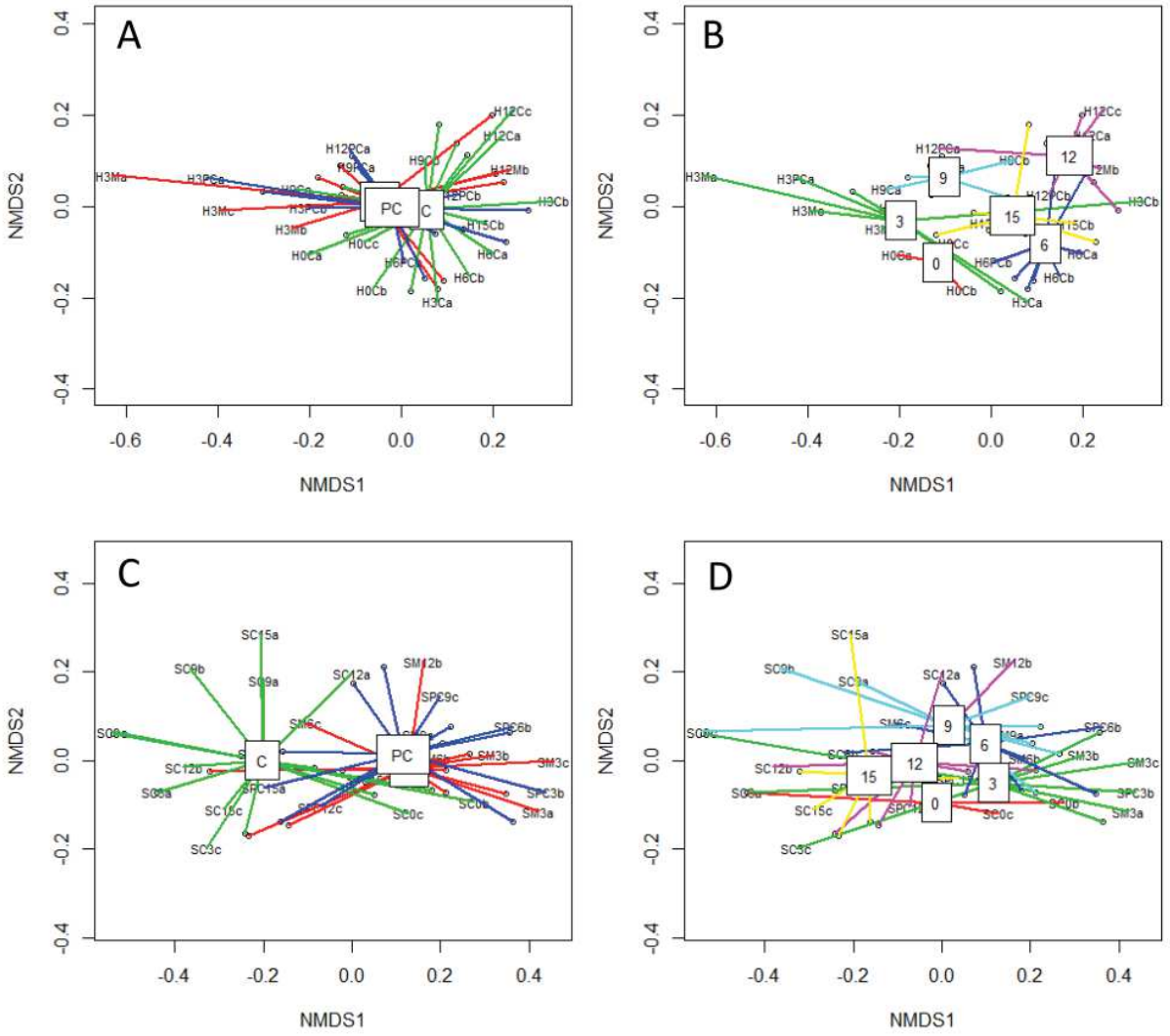


Fig. 6 : Results from the Nonmetric Multidimensional Scaling (NMDS) analysis showing the dispersion of the samples (points) in relation to the centroid of each group, by treatment (A and C) and by sampling time (B and D), on the seagrass meadows (A and B) and on the sediment (C and D).

In the sediment habitat, homogeneity of dispersions was observed between both factors ($F = 0.6$, *p-value* $= 0.7$ and $F = 0.4$, *p-value* $= 0.7$, for sampling time and treatment, respectively). Both the time (PERMANOVA, $F = 2.8$, *p-value* < 0.01) and treatment (PERMANOVA, $F = 4.8$ and *p-value* < 0.01) significantly affected the community composition. However, the interaction between both factors was not significant indicating that the changes in community across time were not affected by the treatment. PC and M presenting similar mean community composition, whereas the treatment C was significantly different (NMDS, Fig. 6 C and D).

Identifying important taxa

The results of the two-factor generalised linear model (ManyGLM), for each habitat, were consistent with the results of the PERMANOVA (reported above). In the seagrass meadows, the treatment alone did not affect the community composition, but the effect was significant when combined with sampling time (significant interaction, Dev = 175.6, *p-value* = 0.007). On the sediment, both the treatment and sampling time affected the community composition (*p-value* < 0.05). In the seagrass meadows, the different community composition observed in samples collected at 3h was promoted by the high abundance of the *Bittium* sp. (significant interaction, P_{adj} = 0.001, Table 4).

Table 4: Results of the 'species-by-species' two-factor multivariate linear model, with the terms and the significance of each term (adjusted *p-values*) in the model (Treatment, Sampling Time and interaction). Bold values indicate significant differences at α = 0.05.

	Treatment		**S. Time**		**Treatment:S. Time**	
Seagrass	**Dev**	**P_{adj}**	**Dev**	**P_{adj}**	**Dev**	**P_{adj}**
Cerastoderma sp.	0.433	0.982	26.982	**0.008**	5.557	0.945
Gastrana sp.	0.676	0.982	18.624	0.055	5.012	0.945
Loripes sp.	1.876	0.958	60.183	**0.001**	19.451	0.359
Ruditapes spp.	0.249	0.982	41.143	**0.001**	9.649	0.918
Bittium sp.	7.987	0.449	41.265	**0.001**	40.549	**0.001**
Cerithium sp.	2.013	0.958	7.663	0.768	4.902	0.945
Gibbula spp.	6.677	0.548	20.578	**0.030**	25.757	0.100
Hexaplex sp.	3.726	0.936	7.681	0.768	7.366	0.935
Jujubinus sp.	0.000	1.000	0.000	1.000	0.000	1.000
Rissoa spp.	3.409	0.941	9.682	0.555	8.813	0.918
Tricolia sp.	7.972	0.449	6.472	0.768	7.810	0.935
Gastropoda NI	0.000	1.000	0.000	1.000	0.000	1.000
Sphaeroma sp.	2.843	0.941	11.816	0.381	15.583	0.582
Microdeutopus sp.	3.262	0.941	4.412	0.850	8.919	0.918
Cirratulidae	2.402	0.941	3.750	0.850	0.001	0.945
Glyceridae	0.000	1.000	0.000	1.000	0.000	1.000
Tritia spp.	1.452	0.958	14.332	0.214	16.203	0.582
Sediment						
Cerastoderma sp.	0.391	0.843	7.686	0.661	9.641	0.794
Gastrana sp.	0.000	1.000	0.000	1.000	0.000	1.000
Loripes sp.	1.764	0.713	3.137	0.948	6.730	0.794
Ruditapes spp.	24.699	**0.001**	18.268	**0.036**	8.739	0.794
Bittium sp.	9.271	0.109	32.619	**0.001**	20.626	0.140
Cerithium sp.	6.039	0.395	2.509	0.948	4.872	0.794
Gibbula spp.	7.441	0.251	15.723	0.067	8.634	0.794
Hexaplex sp.	12.639	**0.024**	3.401	0.948	1.955	0.794
Jujubinus sp.	6.794	0.313	17.327	**0.048**	10.152	0.794
Rissoa spp.	8.154	0.177	22.319	**0.014**	19.967	0.145

Tricolia sp.	4.182	0.576	16.865	0.051	25.929	**0.046**
Gastropoda NI	4.280	0.576	15.542	0.067	2.883	0.794
Sphaeroma sp.	0.000	1.000	0.000	1.000	0.000	1.000
Microdeutopus sp.	4.852	0.567	5.147	0.892	0.000	0.830
Cirratulidae	4.720	0.567	24.968	**0.003**	8.259	0.794
Glyceridae	3.377	0.596	5.275	0.892	10.271	0.794
Tritia spp.	21.770	**0.001**	12.924	0.136	12.333	0.638

This taxon stands out for its significantly higher abundances for M (2572 ± 2179 ind.m^{-2}) and PC (1317 ± 706 x 10 ind.m^{-2}), when compared with C (31 ± 2 ind.m^{-2}) at 3h, but no differences of abundances between M and PC treatments were observed (P_{adj} = 1, Fig. 7). At the sediment sampling site, the differences of the samples collected at 3h were mainly driven by *Tricolia* sp. (significant interaction, P_{adj} = 0.046), which showed significantly higher abundances for PC (44.9 ± 23.1 x 10 ind.m^{-2}) and M (19.6 ± 10.2 ind.m^{-2}) than for C (absent, P_{adj} = 0.01). However, in this habitat, other taxa further contributed to the observed differences between treatments over the whole study period, such as the *Hexaplex* sp. (P_{adj} = 0.024), the *Tritia* spp. (P_{adj} = 0.001) and the *Ruditapes* spp. (P_{adj} = 0.001, Table 4). Over the whole study period, the abundances of these taxa were consistently higher for M and PC than for C (P_{adj} < 0.05), but differences between M and PC were only observed for *Tritia* spp. (P_{adj} = 0.04). This particular taxon showed high abundances for the treatment M during the first 9h of the study period (up to 14.9 ± 3.6 x 10 ind.m^{-2}, Fig. 7), while their abundance at the C and PC remained below 2.5 ± 4.3 ind.m^{-2} and 7.1 ± 2.4 ind.m^{-2}, respectively. Therefore, although *Bittium* sp. (in seagrass meadows), *Hexaplex* sp. and *Ruditapes* spp. (on bare sediment) appeared to have positively responded to the presence of jelly-falls, especially after 3h, only the *Tritia* spp. (on bare sediment) revealed statistical evidence of a positive response due to the presence of dead medusae on the bottom.

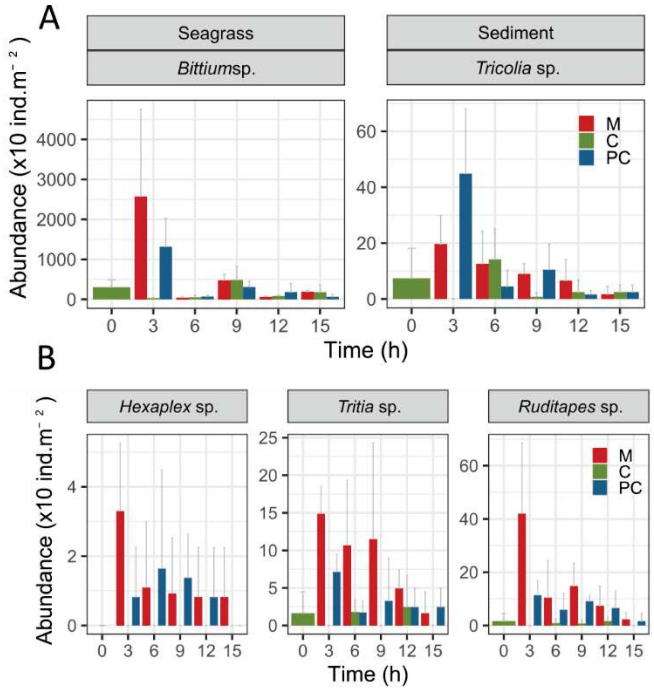


Fig. 7: Abundance of the taxa that showed significant differences (after ManyGLM) between treatments at 3h in both habitats (A) and between treatments over the whole study period on the sediment habitat (B). Note the different scales.

3.2.5. Discussion

3.2.5.1 Degradation of jellyfish in the Thau lagoon

The *in situ* degradation of jellyfish in the Thau lagoon was very fast, with values of decay rates ranging from 1.42 to 5.80 d^{-1} and a remineralisation of 99% of the medusae biomass in less than 1 day (ca. 19h) on the sediment and about 1 to 3 days (32 and 78h, respectively) on seagrass meadows. Although fast jellyfish degradation rates in the first 24 - 48h have been already shown (*e.g.* West et al. 2009; Tinta et al. 2010), our values are higher (*i.e.* more negative) than those generally reported in the literature (Table 5). Decay rates are known to vary with jellyfish species, size, ambient temperature, as well as the type and composition of the local scavenger and decomposers assemblages (Titelman et al. 2006; Lebrato et al. 2011, 2012), which contributes to the variability of the results in the literature.

Temperature is one of the most important factors driving differences in jellyfish degradation rates (Lebrato et al. 2011). Our decay rates are in the range of those estimated by the latter authors for tropical surface environments, where less than one day is required to decompose 99% of jellyfish organic matter. In the Thau lagoon, the collapse of the *A. coerulea* bloom coincides with the peak of summer temperatures (>23 ºC), which might promote the fast degradation in the water column and, therefore low export rates of jellyfish organic matter to

the seabed. However, since Thau is very shallow (< 10m) jellyfish biomass sinking and accumulation on the seabed is still to be expected, which has not been observed so far.

Degradation rate is also dependent on the jelly-falls biomass, with smaller jellyfish decaying faster than larger ones (Titelman et al. 2006). The jellyfish decay rates observed in our study are comparable to the ones reported by Titelman et al. (2006), when considering similar initial jellyfish biomass and similar types of scavengers (*i.e.* macroorganisms), despite different temperatures (10 vs 23ºC, Table 5). In this study, we assessed the decay rate of individual *A. coerulea* medusae, which are usually smaller in Thau lagoon than other *Aurelia* spp. found elsewhere (see Marques et al. 2015a) and other jellyfish species (*e.g.* Pitt 2000; Fuentes et al. 2011; Prieto et al. 2013), further explaining the rapid degradation of medusae in this lagoon.

Different decay rates are also dependent on the species and habitat considered. The elemental biochemical composition of jellyfish tissues determines its lability, which might vary between species (Pitt et al. 2009; West et al. 2009, *A. coerulea* C:N values in Thau: 3.9 ± 0.6, data not shown). Furthermore, the bacterial community and therefore, the associated degradation efficiency might be particular to each jellyfish biochemical composition and habitat (Titelman et al. 2006; Tinta et al. 2010, 2012), stimulating or inhibiting some particular bacteria (Titelman et al. 2006; Tinta et al. 2012). Indeed, Tinta et al. (2012), showed that one particular bacteria family (*Vibrionacea*) was dominant during *A. aurita* degradation but much less abundant for other jellyfish species, suggesting species-specific bacterial associations. Contrasting results were, however, reported by Blanchet et al. (2015) in a neighbouring Mediterranean lagoon, indicating the potential importance of the habitat and local indigenous bacterial community. Yet, in Thau *Vibrionacea* species were shown to be permanently present as free-living or plankton-attached (especially with the jellyfish *Obelia* sp.), with higher abundances in the summer (Cantet et al. 2013; Lopez-Joven et al. 2018). Although confirmation is still required, this hypothesis might also explain the rapid jellyfish degradation observed in the Thau lagoon in contrast with other places.

Finally, scavengers appear to have a significant impact on the consumption of jellyfish biomass that sinks to the seafloor, especially in habitats with low food availability (Sweetman et al. 2014). Likewise, the positive response of some taxa to the addition of dead medusae organic matter to the seafloor during our study, which was more evident on the habitat with less organic matter (*i.e.* on the bare sediment, Plus et al. 2003), might also contribute to the fast degradation rate observed in Thau.

Table 5 : Reported values of decay rates λ (d) in the literature. *Rt* (d) is the remineralisation time in days calculated using the formula of Lebrato et al (2011) or provided in the study as the time required for complete jellyfish degradation.

Species	Habitat	Weight (g)	Depth (m)	Temperature (°C)	Condition	Scavengers/ decomposers	Mesh/ Filtration	Experiment	λ (d)	*Rt* (d)	Reference
Thalia democratica	Laboratory containers	-	1	16.5	Fresh	Microbial	0.2 µm	Laboratory	-1.60	2.88	Sempéré et al. 2000
Chrysaora quinquecirrha	Laboratory containers	9.6 - 19.6	-	22	Fresh	Microbial	*In situ* seawater	Laboratory	-0.23	20.11	Frost et al. 2012
Cyanea nozakii	Laboratory containers	800	<1	-	Fresh	Microorganisms	200 µm	Laboratory	-	14.00	Qu et al. 2015
Nemopilema nomurai	Laboratory containers	955	2.5	8	Fresh	Microbial	-	Laboratory	-0.51	8.98	Iguchi et al. 2006
Nemopilema nomurai	Laboratory containers	884	10	2.7	Fresh	Microbial	-	Laboratory	-0.22	21.42	Iguchi et al. 2006
Aurelia aurita	Laboratory containers	12.5 $g.L^{-1}$	5	-	Homogenised	Microbial	0.8 µm	*In situ*	-0.13*	35.42	Tinta et al. 2012
Pelagia noctiluca	Laboratory containers	12.5 $g.L^{-1}$	5	-	Homogenised	Microbial	0.8 µm	*In situ*	-0.28*	16.45	Tinta et al. 2012
Rhizostoma pulmo	Laboratory containers	12.5 $g.L^{-1}$	5	-	Homogenised	Microbial	0.8 µm	*In situ*	-0.38*	12.12	Tinta et al. 2012
Periphylla periphylla	Pelagic	42.6	1	10.1	Fresh	Macroorganisms	5-10 mm	*In situ*	-1.12	4.11	Titelman et al. 2006
Periphylla periphylla	Pelagic	121	1	10.1	Fresh	Macroorganisms	5-10 mm	*In situ*	-0.72	6.43	Titelman et al. 2006
Periphylla periphylla	Pelagic	223	1	10.1	Fresh	Macroorganisms	5-10 mm	*In situ*	-0.67	6.91	Titelman et al. 2006
Periphylla periphylla	Pelagic	300	8	12.5	Fresh	Macroorganisms	5-10 mm	*In situ*	-0.84	5.46	Titelman et al. 2006
Catostylus mosaicus	Sandy sediment	1200 ± 50	1	23	Fresh	Macroorganisms	30 mm	*In situ*	-0.35‡	13.16	Chelsky et al. 2016
Catostylus mosaicus	Sandy sediment	1600	1.5	30	Frozen	Microorganisms	*In situ* seawater	*In situ*	-	9.00	West et al. 2009
Aurelia coerulea	Seagrass	111.8 ± 19.0	1	23.5 ± 0.7	Fresh	Microorganisms	200 µm	*In situ*	-3.50	1.32	Ts
Aurelia coerulea	Seagrass	107.5 ± 20.0	1	23.5 ± 0.7	Fresh	Macroorganisms	10 mm	*In situ*	-1.42	3.25	Ts
Aurelia coerulea	Sandy sediment	32.8 ± 14.9	1	23.4 ± 0.5	Fresh	Microorganisms	200 µm	*In situ*	-5.80	0.79	Ts
Aurelia coerulea	Sandy sediment	34.8 ± 12.4	1	23.4 ± 0.5	Fresh	Macroorganisms	10 mm	*In situ*	-5.66	0.81	Ts

* Decay rate expressed as decrease of dissolved proteins concentration (µg protein mL^{-1})
‡ Estimated from loss of biomass over time (in % of initial wet weight)
Ts: This study (see Table 1)

3.2.5.2 The impact of scavenger's accessibility and habitat

The lack of significant differences in jellyfish decay rates between the Micro and Macro scenarios on the sediment habitat suggests a limited impact of macrobenthic scavengers on jellyfish degradation. On seagrass meadows though, the degradation of medusae was significantly higher for the Micro scenario than for the Macro one. The unexpected faster degradation for the Micro scenario in the seagrass meadows might partially result from the experimental setup. Indeed, the utilization of a small mesh net bag (200 μm) prevents the accessibility of the macrobenthic organisms to the jellyfish biomass but it also reduced their predation on the microorganisms thriving in the vicinity of the medusae, which are now protected and able to proliferate. In addition, due to physical protection against local currents, the microorganisms might have benefited from the high concentration of organic matter without being advected and diluted in the surrounding water. Therefore, it is possible that the decay rates obtained in the Micro scenario are overestimated. On the light of these results the rapid degradation of jellyfish in the Thau lagoon is likely a result of heterotrophic consumption by small zooplankton species, microzooplankton (Iguchi et al. 2006; Titelman et al. 2006) and bacterial community (Hansson and Norrman 1995; Titelman et al. 2006; Tinta et al. 2010, 2012; Blanchet et al. 2015). This is in agreement with previous experiments on jellyfish decomposition that suggested a rapid shift of carbon uptake from the macroorganisms to bacterial degradation in the presence of dead medusae (Sweetman et al. 2016). Nevertheless, the impact of benthic scavengers cannot be excluded at least on the sediment habitats.

The habitat significantly affected the degradation rates of dead medusae, with higher decay rates on the sediment than on the seagrass meadows. The effect of the habitat, though, was not independent of the initial biomass of *A. coerulea* used in each experiment. The initial biomasses on the seagrass meadow were significantly higher than those on the sediment, which likely contributed to the observed contrasting results (Titelman et al. 2006). Even though individual organisms were randomly selected, the experiments were performed on different days which induced a biased effect on the weight of the medusae, due to the loss of biomass while in captivity. Under the scenario of the exclusive impact of the microorganisms, jellyfish degradation rates might also be influenced by the specific local bacterial communities (Iguchi et al. 2006; Titelman and Hansson 2006; Tinta et al. 2010, 2012). A location with frequent jelly-falls, likely have a native bacterial community with higher levels of predisposition for jellyfish degradation and thus, faster response to the addition of jellyfish substrate (Tinta et al. 2010). It is possible that aggregation processes in Thau, due to its hydrodynamics (Fiandrino et al. 2012), drive higher accumulations of jelly-falls in the central part of the lagoon, characterized by bare

sediment habitats (Plus et al. 2003). Therefore, we hypothesize that contrasting small-scale local bacterial communities could contribute to the different decay rates observed between habitat type. Furthermore, the levels of mineralization might be hampered in habitats with high organic matter, when the sediment metabolic capacity is exceeded (Valdemarsen et al. 2009; Sweetman et al. 2016). Since seagrass meadows have higher organic matter content than bare sediment (Plus et al. 2003; Holmer et al. 2004), it is possible that the addition of dead medusae locally exceeded the metabolic capacity of the sediment, reducing the microbial decay rates at this habitat type. Lastly, although not evident during our jellyfish decay rate experiments, the different macrobenthic communities and the presence of particular taxa in each habitat might also influence the rate of jellyfish degradation.

3.2.5.3 The potential impact of the macrobenthic community on jellyfish degradation

Irrespective of the habitat, in our study the macrobenthic organisms showed a weak response to the addition of jellyfish carcasses on the bottom, with the exception of one particular taxon (*Tritia* spp.). Our results indicate that both the habitat, the sampling time and the treatments significantly affected the local abundance of the macrobenthic fauna, their diversity and composition. Nevertheless, with the exception of *Tritia* spp., modifications of the macrobenthic community were unlikely driven by the presence of jelly-falls. The habitat was the most important factor affecting community composition. As expected, significant different communities inhabit seagrass meadows and sediment habitats (*e.g.* Thouzeau et al. 2007; Rueda et al. 2009), with higher abundances of some particular taxa, such as *Bittium* sp and *Ruditapes* spp. in seagrass meadows and Gliceridae and *Rissoa* spp. on bare sediment. Within each habitat, other causes might explain the observed differences in the community over time and between treatment. First, since our experiments covered day and night time, the differences observed over time, promoted by different taxa, likely reflect the dial activity rhythms of these benthic macroorganisms (Morgan 2004). Second, although divergences between treatments were observed in both habitats (at least at 3h), our results showed no differences between the treatments with and without medusae (M and PC, respectively), which hampers drawing statistically sustained conclusions on the effect of jelly-falls on the community structure. However, some taxa appeared to positively respond to the presence of decaying jellyfish organic matter, such as *Bittium* sp. in the seagrass meadows and *Tritia* spp., *Hexaplex* sp., and *Ruditapes* spp. on the bare sediment. In most cases they presented higher abundances for the M treatment, although not significantly different from the PC, with the exception of *Tritia* spp..

Bittium sp. is usually reported as a dominant species in the epifaunal of seagrass meadows (Rueda et al. 2009), which explains its general dominance observed in our study at this habitat sampling site. This gastropod is described as a microalgae herbivore feeding mainly on diatoms or directly on macroalgae (Van Montfrans et al. 1982; Rueda et al. 2009; Sureda et al. 2009). To our knowledge, scavenging behaviour was never reported for this species, but the opportunistic consumption of jellyfish may not be completely excluded. However, we believe that the observed high abundances of *Bittium* sp. are unlikely to be an outcome of scavenging behaviour. Studies of grazing by *Bittium* sp., showed that the periphyton crust on the seagrass leaves, which are the main food source for these gastropods, is composed by a mix of microorganisms, like microalgae and bacteria (Van Montfrans et al. 1982). We therefore hypothesize that *Bittium* sp. could be taking advantage of the high abundance of bacteria, likely thriving on the surface of the jellyfish carcasses during its decomposition. Moreover, in the first few hours, the jellyfish were rapidly decomposed, suggesting high bacterial productivity and availability which might explain the peak of *Bittium* sp. abundance at 3h.

In the sediment, *Tritia* spp., which belong to the Nassariidae family (Galindo et al. 2016), showed higher abundances in the M treatment than in C and PC ones, suggesting that the medusae carcasses were the target of these organisms, as previously reported elsewhere (Chelsky et al. 2016). The Nassariidae species are common on soft sediment habitats and reported as herbivorous, carnivorous, but mainly recognized as scavengers, feeding opportunistically on the available dead organic matter (Morton 2011). The behaviour of these organisms might explain why only this taxon revealed a significant positive response to dead medusae and only on the sediment habitat. These organisms rapidly detect carrion from long distances and move fast towards the carcass, but they leave it once they are satiated to avoid potential predators (Morton 2011). They appear to eat large amounts of organic matter (20 to 60% of their weight) in as fast as 8 min (Morton 2011; Lucena et al. 2012 and references therein). Therefore, the presence of these organisms during the first 9 hours of the experiment suggest a replacement of individuals over time. Furthermore, the amount and time spending on feeding appears to be a function of their level of hunger, with individuals living in habitats with lower food supply, eating larger amounts of food and spending more time on feeding (Morton and Chan 1999). Since bare sediments have lower amounts of organic matter when compared with seagrass meadows in Thau (Plus et al. 2003), this might explain the differences of their response to the presence of dead medusae observed between habitat type in our study. Therefore, the impact of its scavenging activity might, at least, contribute to the fastest degradation of jellyfish biomass on the bare sediment habitat, when compared with that

observed in the seagrass meadows. However, their importance relatively to that of the microorganisms on jelly-falls degradation remains elusive.

In addition to *Tritia* spp., the gastropods *Haxaplex* sp., as well as the bivalve *Ruditapes* spp. also showed a positive response to the addition of dead medusae to the seabed (although not significantly different from the procedure control). These taxa are common in soft sediment habitats in the Mediterranean Sea and associated lagoons, like Thau (Borsa and Millet 1992; Peharda and Morton 2006; Rueda et al. 2009). However, they are not scavengers: the *Hexaplex* sp is a carnivore (Peharda and Morton 2006; Rueda et al. 2009), while *Ruditapes* spp. is a suspension and deposit filter feeder (Sobral and Widdows 2000; Caro et al. 2015). Therefore, we believe that they might have opportunistically benefited from the availability of direct (by the medusae) or indirect (by the microorganisms feeding on medusae) food sources, but their impact on the medusae degradation remained probably low.

Whether feeding directly on the soft dead jellyfish biomass, or on the bacterial community responsible for the jellyfish degradation, we believe that the response of these (and maybe other) organisms could have been conspicuous if greater biomass was available or if the jellyfish decay rates were lower in the Thau lagoon. Indeed, the hypothesis of a greater impact of the jellyfish degradation on the macrobenthic community cannot be completely excluded in Thau, at least in some areas of the lagoon or in years of large jellyfish blooms. Dead medusae tend to accumulate in particular locations, due to physical hydrodynamic aggregation processes (R. Marques, personal observation, Graham et al. 2001). This biomass accumulation and organic matter availability might promote further noticeable small-scale local changes on the macrofaunal responses.

3.2.5.4 Potential ecological impacts of jellyfish degradation in Thau

Our results suggest that the rapid decomposition of *A. coerulea* blooms in the lagoon is likely a consequence of the fast microbial degradation, with a possible contribution of some particular scavenger species on the sediment habitat. These enhance periodic important release of organic and inorganic nutrients, with potentially positive and negative impacts on the biogeochemical cycle and microbial food webs in the lagoon. During the summer season, episodically anoxic crisis, known as ‘malaigues’, can occur in the Thau lagoon (Harzallah and Chapelle 2002). These anoxic episodes are related to the degradation of high concentrations of organic matter, favoured by the high residence of water masses, high water temperatures and weak winds, which promotes stratification of the water column and decrease oxygen exchange with the sea surface or with the Mediterranean Sea (Harzallah and Chapelle 2002). One of the

most important triggers of the 'malaigues' episodes in the lagoon is the nutrients input (Harzallah and Chapelle 2002). During jellyfish decomposition, large amounts of organic and inorganic nutrients are released, which stimulates microbial community production and oxygen depletion as a consequence of aerobic respiration of micro-organisms (Jane et al. 2009; Pitt et al. 2009b). Therefore, considering that the *A. coerulea* blooms collapse occurs in the summer, the addition of nutrients during their degradation might contribute to the magnitude of the anoxic impacts, potentially leading to massive benthic community mortalities. Moreover, it is possible that certain bacterial species are stimulated during the degradation process of *A. coerulea*, such as species of *Vibrionacea* family (Tinta et al. 2012). This is of particular importance since some of these species might cause mass mortalities of the cultivated Pacific oysters (Pernet et al. 2012a). It is unknown though, if and which *Vibrionacea* species are stimulated by the degradation of *A. coerulea* in the lagoon and therefore, further research should be carried on to confirm this potential association.

On the positive side, the increase of dissolved inorganic nutrients in the surroundings of decaying jellyfish might enhance the local phytoplankton and algal production by their direct assimilation of dissolved inorganic compounds (Pitt et al. 2009b; Blanchet et al. 2015). Therefore, the high level of mineralization of jelly-falls supports high nutrient regeneration (Chapelle et al. 2000; Plus et al. 2003), potentially contributing to the development of the phytoplankton blooms in the lagoon. In addition, bacterial production is recognized as an important food source for microzooplankton, increasing the energy transfer to higher trophic levels (Rassoulzadegan and Sheldon 1986). Likewise, even if dead jellyfish are not directly consumed by macrobenthic organisms, they may provide an environment for microbial communities to proliferate and, in turn, be preyed upon by other taxa (Sweetman and Chapman 2011). Dead jellyfish though, appear to contribute as a food source for, at least, some particular taxa of macrobenthic organisms, especially under low food availability conditions. These support the hypothesis that the available energy of jellyfish organic matter can be directly used by larger predators enhancing the energy transfer directly to higher trophic levels (Sweetman et al. 2014), helping to reduce the potential negative impacts of microbial degradation in shallow, warm coastal lagoons such as Thau.

3.2.6. Concluding remarks

Annual blooms of *A. coerulea* occur in the Thau lagoon with abundances that might overcome 300 ind.100 m^{-3} (Marques et al. 2015a). The blooms collapse in June – July but the fate of this decaying organic matter was still to be identified. Predation by pelagic predators,

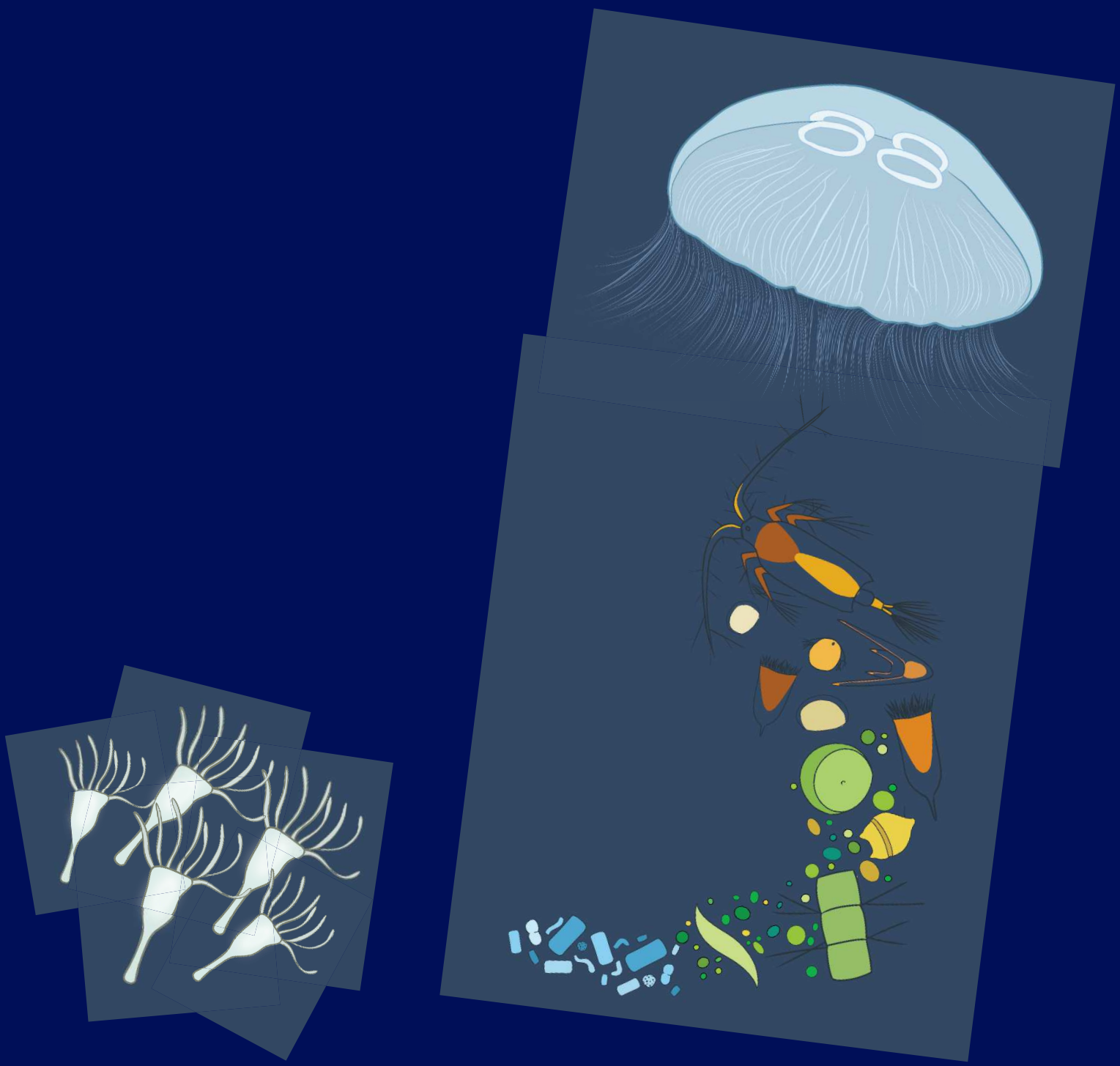
which have been identified as an underestimated source of jellyfish mortality in Thau and elsewhere (Hays et al. 2018; Marques et al. 2019a), might be one of the main fates of the jellyfish biomass. However, the high production of jellyfish biomass in the lagoon suggests that this organic matter likely enters other trophic pathways. Our initial hypothesis was high benthic consumption of jelly-falls by macrobenthic scavengers, but although our results reveal a rapid degradation of the medusae, the impact on the macrobenthic community seems to be limited, with only one taxon (the Nassariid *Tritia* spp.) showing a significant response to the presence of dead medusae. Therefore, we believe that the organic matter produced during the blooms of *A. coerulea* in Thau, when not consumed by pelagic predators, mainly contributes to the microbial food web and to particular scavengers under specific conditions.

The high decay rates of *A. coerulea* in the Thau lagoon, when compared with other places in the world, is likely a combined effect of high temperatures, the small size of the individuals, high lability of its tissues and a possible effect of the associated microbial community in the lagoon. Here we provide evidence of the potential importance of the jellyfish blooms degradation on the biogeochemical cycle, as well as on the trophic webs of the lagoon. Finally, we stress the need to include these processes (*i.e.* jellyfish consumption and degradation) in ecosystem based trophic and biogeochemical models in Thau and elsewhere.

3.3 IN A NUTSHELL

- Several fish species consume *A. coerulea* in the Thau lagoon, especially during their blooms. This indicates that the diversity of *A. coerulea* fish predators is likely underestimated as well as their role in the control of jellyfish blooms.
- The European eel and the gilthead sea bream appear to be important jellyfish predators during *A. coerulea* blooms, with potential high contributions to the control of their biomass.
- The gilthead sea bream also consumed *A. coerulea* scyphistomae, most likely by preying on their settling substrates (*i.e.* bivalves). This indirect predation on scyphistomae might contribute to the regulation of the benthic population size.
- Jellyfish might be a non-negligible important food source for commercially exploited fish species
- If not consumed in the water column, the medusae die and likely sink to the bottom where they are mainly degraded by the microbial community. However, although seemingly limited, the consumption by benthic scavengers might also contribute to the rapid decay rates observed in the lagoon.
- Overall, the energy produced during the *A. coerulea* blooms enters the food web in three ways: through predation by top predators like fish while in the water column or, when dead, *via* degradation by the microbial community and the consumption by benthic scavengers

CHAPTER 4. GENERAL DISCUSSION, CONCLUSION AND PERSPECTIVES



4.1 GENERAL DISCUSSION

The incredible diversity and complexity of jellyfish biology is an exceptional "playground" for scientists. Jellyfish are responsible for remarkable scientific discoveries and much more is still to come. However, in an ecosystem functioning perspective, the role of jellyfish has been ignored for long, mainly due to the lack of knowledge regarding their ecology. However, their ecological importance is increasingly recognized (e.g. Doyle et al. 2014; Graham et al. 2014), so they should be considered in ecosystem-based investigations, models and experiments. In addition, recurrent jellyfish blooms and the potential increase in their intensity in the future call for developing accurate predictive models of their blooms and impacts in the ecosystems. Doing so requires understanding the environmental factors that drive the abundances of jellyfish benthic and pelagic populations and evaluating their impacts on ecosystem functioning. This thesis provided fundamental information to do so.

4.1.1. Drivers of the blooms

The blooms of the scyphozoan *Aurelia coerulea* are the outcome of a complex life cycle and the environmental factors that control each life stage at different times of the year. Overall, this study allowed to identify two *boosting periods* of the population size, ultimately increasing the magnitude of the bloom, and two *bottleneck periods*, when mortality likely reduces the intensity of *A. coerulea* blooms (Fig. 1).

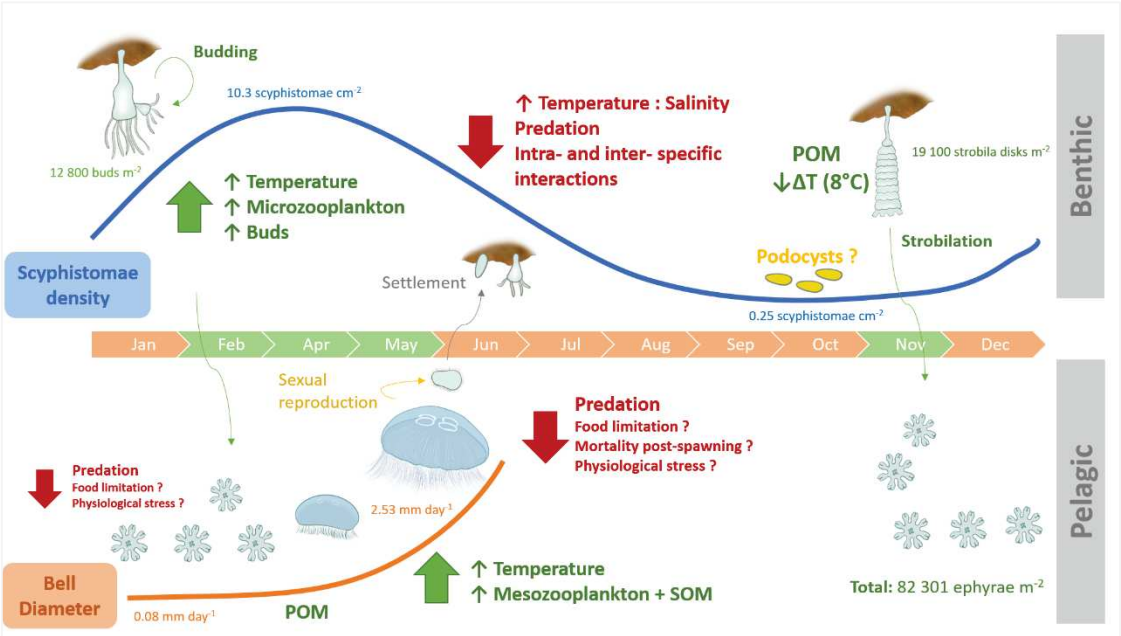


Fig. 1: Schematic representation of the *A. coerulea* population dynamics and the main environmental drivers of the demographic variations of each life stage. The *boosting* and *bottleneck* periods are indicated in green and orange, respectively, in the timeline of the figure. POM: phytoplankton and/on microzooplankton; SOM: sedimentary organic matter. Drawings by Justine Courboulès.

In Thau, the first boosting period occurs in early spring and is mainly due to the production of buds. The second occurs in late autumn and is mainly linked to strobilation. The two bottleneck periods occur in the summer and in the winter, associated with the mortality of scyphistomae and ephyrae, respectively. Both biotic and abiotic factors involved in each of these periods are discussed below.

4.1.1.1 Drivers regulating the benthic population

The scyphistomae of *A. coerulea* are widely distributed in the Thau lagoon, but mostly on man-made structures (Marques et al. 2015b). Therefore, the first key driver of the *A. coerulea* blooms of in Thau is the presence of anthropogenic structures, allowing the establishment and development of the scyphistomae population. In contrast with the ephemeral pelagic population, the scyphistomae are present in the lagoon all year round, with higher densities in the spring (April), followed by a decrease in the summer and autumn and a progressive recovery over the winter (Paper I).

The first *boosting period* of the population of *A. coerulea* takes place when the density of scyphistomae increases in the lagoon, peaking in April. This is an outcome of the elevated production of buds, which is likely driven by the increase in temperature and the high food availability that co-occur at this time of the year in the lagoon (Paper I and II). The positive effect of temperature and food availability on the asexual reproduction of scyphistomae has already been extensively demonstrated in laboratory experiments (e.g. (Han et al. 2010; Schiariti et al. 2014; Hubot et al. 2017; Ikeda et al. 2017). This thesis provided evidence that microzooplankton the most critical food source for *A. coerulea* scyphistomae in Thau (Paper II). We do not exclude a significant contribution of phytoplankton to the diet of *A. coerulea* scyphistomae, especially during the cold months, since it can be a suitable source of energy for scyphistomae survival at low temperatures (Huang et al. 2015; Wang et al. 2015). Likewise, it is likely that scyphistomae consumption of mesozooplankton and resuspended sedimentary organic matter also support their survival and growth. However, microzooplankton ingestion was found to be the most likely promoter of the asexual reproduction (*i.e.* the production of buds) in *A. coerulea* scyphistomae. This is of paramount importance since the increase in scyphistomae density in early spring controls the blooms in two ways. First, it supports the production of large amounts of ephyrae during the late strobilation period, when the ephyrae have a higher probability of survival due to more favourable environmental conditions. Second, it increases the probability of scyphistomae survival over the warm and dry season, which determines their density in the late autumn, *i.e.* during the strobilation season.

The recruitment of planulae would also be expected to contribute to the density increase of the *A. coerulea* benthic population during the early spring. However, this was not evident in the present study. Although the effect of planulae recruitment on *A. coerulea* benthic population densities might be significant in other parts of the lagoon (not surveyed here), planulae appear to mainly have a role in the expansion of the benthic population distribution and, possibly, in promoting its genetic diversity in Thau (Lucas et al. 2012). This might increase the survival of scyphistomae if planulae settle on substrates where variations in temperature and salinity are less severe during the year (*e.g*. deeper waters, locations under greater influence of the Mediterranean Sea).

The reduction of the scyphistomae population during the summer and autumn (decrease of nearly 90% of the scyphistomae density) is an important *bottleneck period* for the development of *A. coerulea* blooms in Thau. Many factors (*e.g.* temperature, salinity, hypoxia, pH, pollution, light, siltation, predation, inter- and intra-specific competition for food and space, Lucas et al. 2012) have been pointed out as potential inducers of scyphistoma mortality. In Thau, the most important environmental drivers affecting scyphistomae survival seem to be temperature and salinity, with high summer and autumn values of these two parameters co-occurring with the reduction of the benthic population densities (Paper I). The population size for *A. coerulea* scyphistomae started to decrease in May, when temperatures ranged between 15 and 23ºC. The *Aurelia* sp. scyphistomae, and especially those of *A. coerulea* (Hubot et al. 2017), are generally described as tolerant to a wide range of temperatures with maximum physiological tolerances to values approaching 27ºC (Chi et al. 2019). Therefore, one of the main drivers of *A. coerulea* scyphistomae mortality in the lagoon is probably the joint effect of increasing temperatures and high salinities. Although the negative effect of high salinities on *Aurelia* sp. scyphistomae has been previously suggested (Hubot et al. 2017; Hocevar et al. 2018), to our knowledge, the effect of the joint effect of high temperatures and salinities > 37 were never tested (Holst and Jarms 2010; Widmer et al. 2016; Hubot et al. 2017). Because this study was performed during a year with particularly hot and dry conditions (*e.g*. > 80% loss of precipitation when compared with the mean between 1981 – 2010 in October, Meteo France) we might have expected exceptionally high scyphistomae mortalities. This calls for further *in situ* monitoring studies to assess the relevance of hot and dry summer conditions in the control of *A. coerulea* blooms in Thau. Besides the negative effect of temperature and salinity, we should not exclude the influence of other abiotic variables that might affect the physiological condition of scyphistomae, such as hypoxia, pH, pollution and light. Although none of these parameters were assessed in this study, a potential negative impact of low oxygen

concentrations on scyphistomae survival cannot be excluded. Indeed, during the summer, anoxic crises, known as 'malaigues', can occur in the Thau lagoon (Harzallah and Chapelle 2002). Although anoxic events are occasional in the lagoon, low levels of oxygen concentration can decrease the survival of the scyphistomae (Ishii et al. 2008; Gambill and Peck 2014), which might have occurred in the lagoon. Therefore, understanding the causes of of summer and autumn mortalities requires further investigations.

The mortality of scyphistomae during the summer was also likely driven by predation. Several potential benthic predators of *Aurelia* sp. scyphistomae have been identified in Japan (Takao et al. 2014) so the potential top-down impact of some benthic organisms cannot be excluded in Thau. Indeed, during this study, some potential predators were identified in the photoquadrats (Paper I), but the confirmation of scyphistomae consumption by these organisms is still lacking. However, it is possible that these predators indirectly consumed scyphistomae while preying on their settling substrates (such as the red algae *Peyssonnelia* sp.). Furthermore, predators such as fish might have a great impact on the scyphistomae population. Indeed, scyphistomae were consumed by different fish species in Thau, such as the mullet, the salema and the gilthead sea bream (Paper III). This latter, in particular, might have an important top-down regulation of the *A. coerulea* benthic population, since it is possible that the gilthead sea bream feed indirectly on scyphistomae while preying on their substrates (mussels). Mussels are one of the main prey of this fish in the field, they are highly abundant in Thau and commonly used as a settling substrate for scyphistomae in the lagoon (Marques et al. 2015b). Indeed, indirect consumption of scyphistomae by the gilthead sea bream has been previously observed in laboratory experiments and suggested to be a potential contribution to the regulation of jellyfish populations (Marques et al. 2016). The decline of the population of *A. coerulea* scyphistomae in the Thau lagoon coincides with the migration of the gilthead sea bream to the lagoon, where the juveniles of this fish species seek to find food and shelter from bigger predators (Kara and Quignard 2018a). The potentially limited food resources for these fish in the lagoon due to high temperatures and low oxygen levels (see Isnard et al. 2015), might enhance their predation impact on the benthic population, by direct predation on scyphistomae or indirect ingestion while they feed on their settling substrates.

Lastly, bottom-up processes might also be responsible for the observed decline of the *A. coerulea* benthic population in Thau after its peak in April. The *A. coerulea* scyphistomae seem to have shifted from a diet of microzooplankton in late spring to a diet of mesozooplankton and sedimentary organic matter likely to cope with the decreasing abundance of microzooplankton in the field (Paper II). However, the co-occurring medusae appear to share

the same diet than its scyphistomae. Thus, the high abundance of medusae (Marques et al. 2015a) associated with their high predation pressure on a wide range of planktonic organisms (*e.g.* Ishii and Tanaka 2001), might lead to intraspecific trophic competition at this time of the year. The joint effect of higher energetic requirements of scyphistomae at higher temperatures (Gambill and Peck 2014), might contribute to physiological stress due to food limitation and ultimately, the demographic decline of scyphistomae density from April to August.

According to the demographic variation of the scyphistomae population observed in Thau, the longterm persistence of the benthic population in the lagoon is dependent on their survival during the summer (Paper I). The podocysts might play a meaningful role in this sense. Although their contribution to the *A. coerulea* scyphistomae population dynamics was not possible to assess in this study, this is a plausible hypothesis. Indeed, the production of podocysts by the *Aurelia* spp. appear to be triggered by temperatures close to their maximum physiological tolerance (Chi et al. 2019), which might explain the numerous podocysts observed in the end of the spring. The role of *Aurelia* spp. podocysts appear to lie in ensuring the survival of the benthic population under unfavourable conditions and providing protection from predators (Arai 2009; Thein et al. 2012; Hubot et al. 2017; Chi et al. 2019). Therefore, it is possible that, in the Thau lagoon, podocysts play a critical role in the survival of the benthic population during the warm and dry summers, ensuring the later recovery of the benthic population when temperatures decrease and precipitation increase.

4.1.1.2 Drivers of strobilation

The second *boosting period* of the *A. coerulea* population in the Thau lagoon takes place during the peak of strobilation, *i.e.* in November. Strobilation is the key life-cycle process for the development of the blooms since it is responsible for the bentho-pelagic coupling and it determines the abundance of ephyrae and medusae in the water column. In Thau, the strobilation was likely triggered by a drop in temperature (of ~8ºC, Paper I), as also previously demonstrated (e.g. Han and Uye 2010; Holst 2012; Feng et al. 2018). This peak of strobilation in November is not surprising since it seems to be common in different parts of the world, such as far as in Japan or within the Mediterranean area (Toyokawa et al. 2000; Watanabe and Ishii 2001; Miyake et al. 2002; Uye and Shimauchi 2005; Hocevar et al. 2018). In Thau, the production and release of *A. coerulea* ephyrae continue until April, which matches the season of ephyrae presence in the water column (*i.e.* from November to April, Marques et al. 2015a). Indeed, two main periods of ephyrae production were observed in Thau: that in November and in February-March (*i.e.* during the first *boosting period*). The production of ephyrae is a product

of the density of scyphistomae, the percentage of the population strobilating and the number of strobila disks produced per scyphistomae. Therefore, large numbers of ephyrae might be produced by different combinations of these three factors. Since the number of disks per scyphistomae observed during this study did not vary over time, the production of ephyrae is, therefore, a combination of density and the percentage of the scyphistomae actually strobilating. In November, the high levels of strobila disks production (19 100 disks.m^{-2}) are a consequence of the high percentage of the population actually strobilating, since the density of scyphistomae in the lagoon was at its lowest. In February-March, only a small percentage of the population was strobilating, but the high density of scyphistomae at this time of the year ensured the production of large amounts of strobila disks in the lagoon (> 10 000 disks.m^{-2} in February). This implies that the subsequent *A. coerulea* bloom in the lagoon is the result of the accumulation of the ephyrae produced during these two periods. If this study represented a complete strobilation season (*i.e.* uninterrupted monitoring survey from November to April), the estimated ephyrae release would be 82 301 ephyrae.m^{-2}. Therefore, two main factors may regulate the abundance of the pelagic stages. First, since November is the main period of strobilation, the low density of scyphistomae at this time of the year likely constrain the final number of ephyrae produced. Thus, the survival of scyphistomae during the summer and autumn (see the previous section) is a critical factor determining the final abundance of ephyrae released in November. Therefore, under the predicted climate change scenario, we may expect a further limitation of the magnitude of the *A. coerulea* blooms in Thau. Second, the bloom is also boosted by the ephyrae produced in February-March. Then, the increasing density of scyphistomae at this time of the year (see the previous section) is pivotal in the determination of the final magnitude of the blooms.

4.1.1.3 Drivers regulating the pelagic population

The *A. coerulea* bloom is also regulated by ephyrae mortality, *i.e.* the second *bottleneck period*. Ephyrae are present in the lagoon from November to April, growing fast between after April, when they become medusae (Marques et al. 2015a). The mortality at the ephyrae stage thus regulates the magnitude of the blooms in the lagoon. At least in some locations, 99% of the newly liberated ephyrae die before reaching the medusae stage (Ishii et al. 2004). Food limitation, physiological stress under extreme temperature conditions and predation are likely the main sources of ephyrae mortality (Ishii et al. 2004; Fu et al. 2014; Wang and Li 2015). High food availability has been shown to increase ephyrae survival and growth in laboratory experiments (e.g. Fu et al. 2014; Wang and Li 2015), but the type of food consumed appears to

be also important. Phytoplankton and/or microzooplankton are probably the main source of organic matter responsible for the survival of ephyrae in Thau. Considering that the abundance of these two components of the seston is low between November and December, we might expect higher mortalities due to starvation right after the peak of strobilation. If this is the case, the *A. coerulea* blooms in the Thau lagoon might be more dependent on the ephyrae produced in February-March, than from those produced in November. This was suggested to be the main driver of *A. coerulea* blooms in China (Wang and Li 2015). However, laboratory studies also revealed that *Aurelia* sp. ephyrae are very resistant to starvation, especially at lower temperatures (Fu et al. 2014). Indeed, the ephyrae appear to survive for about 60 days under starvation conditions and low temperatures, which is likely an adaptive strategy of this species, allowing them to cope with the concomitant seasonal food scarcity during the winter (Fu et al. 2014). This is a plausible scenario in the Thau lagoon, increasing the probability of survival of ephyrae after strobilation until the next winter phytoplankton bloom (Trombetta et al. 2019). In addition to food limitation, ephyrae mortality might be induced by physiological stress due to the low winter temperatures. Minimum temperatures (down to 5ºC) in Thau are typically registered between December and January (Marques et al. 2015a), which, therefore, raises the vulnerability of the ephyrae produced in November. Still, *Aurelia* spp. ephyrae are able to survive at low temperatures (Fu et al. 2014; Wang and Li 2015), but with very low growth rates or even shrinkage (Widmer 2005). To our knowledge, the effect of temperatures below 8ºC was never tested for *Aurelia* sp. ephyrae. Therefore, it is possible that exceptional cold winters in Thau result in high levels of ephyrae mortality. Nevertheless, if ephyrae survival is raised at higher temperatures, under the predictions of warmer winters in the Mediterranean area (Dubrovský et al. 2014), we may expect a higher contribution of the ephyrae produced in November to the final magnitude of the *A. coerulea* blooms in the Thau lagoon. Finally, predation might be an important source of ephyrae mortality, regulating their abundance in Thau as suggested in Japan (Ishii et al. 2004). The vulnerability of the young *A. coerulea* stages to fish predation was confirmed in laboratory investigations, where one sea ream individual of 200g is likely able to ingest 14 small medusae per hour (Marques et al. 2016). The impact of such predation in the wild remains to be quantified, but this PhD work (Paper III) further confirms the *in situ* ingestion of different stages of *A. coerulea* by this and other fish species. Considering that the presence of young medusae (April – May) in the Thau lagoon co-occurs with the presence of these migratory fish, it is likely that top-down trophic processes might be key in controlling the size of the blooms.

The final control on the magnitude of the blooms is the survival and growth rate of medusae, which overlaps with the first *boosting period* in the spring. Although highly variable between years, the growth rate of *A. coerulea* medusae in Thau (Marques et al. 2015a) appears to be within the range of the values reported elsewhere for *Aurelia* spp. (*e.g.* Van der Veer and Oorthuysen 1985; Lucas and Williams 1994) and to be mainly driven by higher temperatures and food availability (*i.e.* mesozooplankton abundance; Bonnet et al. 2012; Marques et al. 2015a). Indeed, the role of mesozooplankton abundance on the growth of jellyfish is largely recognized (*e.g.* Olesen et al. 1994; Lucas 1996; Ishii and Båmstedt 1998), but the quality of the prey was also pointed out as important (Bamstedt et al. 2001), which was not fully explored in the previous studies performed in Thau (Bonnet et al. 2012; Marques et al. 2015a). In this study, mesozooplankton was the main prey in medusae gut contents and appeared to be an important source of organic matter, especially for large medusae (Paper II). However, the importance of phytoplankton and/or microzooplankton during the early medusae stages, as well as that of the sedimentary organic matters during the later ones, is likely as a reflection of the availability of food in the water column. This highlights the great capability of *A. coerulea* medusae to adapt and benefit from all the available food sources, which might give them an ecological advantage against their potential trophic competitors and support high growth rates, ultimately explaining the magnitude of the blooms.

4.1.2. Fates of the blooms

To understand the ecological role of jellyfish and the potential impacts of their population dynamics on ecosystem functioning, it is essential to uncover the fate of the biomass accumulated during jellyfish blooms. Many studies have focused on the factors driving the blooms (reviewed in Purcell 2012) but few have investigated the trophic pathways responsible for their incorporation within food webs (*e.g.* Chelsky et al. 2016; Sweetman et al. 2016). In Thau, the biomass produced during *A. coerulea* blooms appears to enter the food web in three ways: *via* predation by top predators like fish while the medusae are in the water column, *via* degradation by the microbial community and *via* the consumption by benthic scavengers (Paper III and IV, Fig. 2).

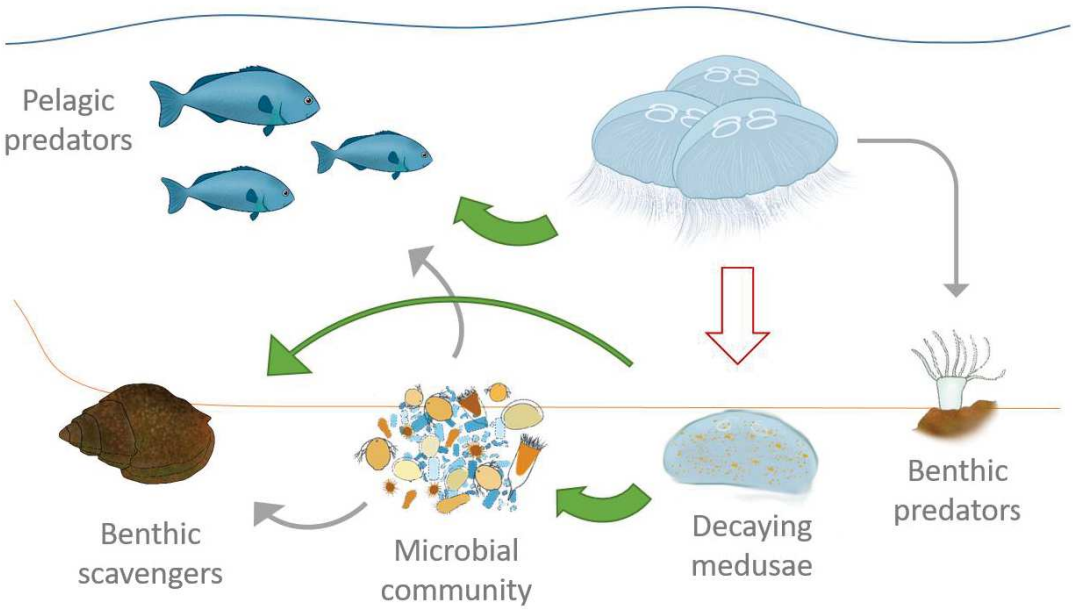


Fig. 2: Schematic representation of the fates of the *A. coerulea* blooms in the Thau lagoon. Green arrows indicate the main fates identified in this study. Thicker arrows represent the likely more important energy transfer. Grey arrows indicate possible fates but not assessed in this study. Drawings by Justine Courboulès.

The *A. coerulea* medusae vanish from the lagoon in June-July (Bonnet et al. 2012; Marques et al. 2015a). There are still many doubts regarding the causes of the jellyfish blooms collapse, but some have been proposed (reviewed by Pitt et al. 2014). Post-spawning mortality was suggested as a likely one for *A. coerulea* in Thau (Bonnet et al. 2012) as proposed for other *Aurelia* spp. in different places (*e.g.* Hamner and Jenssen 1974; Moller 1980; Lucas and Williams 1994; Lucas 1996). Nevertheless, other causes might lead to the collapse of the bloom, such as physiological stress due to elevated temperatures and salinities (the collapse coincides with the peak of temperature and high salinities in the lagoon), food limitation due to possible intra-specific trophic competition (see Paper II) and predation by several organisms. In this study, the likely critical role of fish predation on *A. coerulea* medusae is highlighted (Paper III).

Most of the fish species analyzed in this study were found to feed on *A. coerulea* during its bloom (Paper III). This suggests that the diversity of jellyfish predators in the Thau lagoon has been underestimated so far and, consequently, the importance of top-down control by fish on jellyfish populations is is probably important. The Thau lagoon is one of the Mediterranean lagoons with the highest species richness of fish (> 70 species), among which most are migratory remaining in the lagoon only during a certain period of the year. This is the case of the species considered in this study (except for the sand smelt which is resident, Table 1).

Table 1: Periods of the presence of the five fish species considered in this study (Paper III) in Mediterranean coastal lagoons. Light and dark grey indicate occasional and frequent presence, respectively. Data from (Kara and Quignard 2018b) (*) indicates the sampling period of each species in Thau lagoon.

Common Name	Species	J	F	M	A	M	J	J	A	S	O	N	D
European eel	*Anguilla anguilla*						*						
Sand smelt	*Atherina boyeri*						*						
Golden mullet	*Liza aurata*				*	*	*			*	*		
Salema	*Sarpa salpa*					*	*			*	*	*	
Gilthead sea bream	*Sparus aurata*				*	*	*			*	*		

Specimens of the fish species considered in this study are present in the lagoon during the blooms of medusae, but it also coincides with a period of high energy requirements for fish (due to mounting temperatures) and with a period of low food availability in the lagoon (when the levels of dissolved oxygen are low, Isnard et al. 2015). Because the migrations of juvenile fish to coastal lagoons are usually motivated by trophic requirements (Kara and Quignard 2018a), it is possible that these and likely other fish profit from the availability of the medusae biomass in the lagoon. Moreover, three of the five species considered in this study (the European eel, the mullet and the gilthead sea bream) are on the top five of the most common and widespread fish species in the Mediterranean lagoons (Kara and Quignard 2018a). This might suggest that the consumption of jellyfish by these species is likely not restricted to Thau and occurs in other Mediterranean areas, where jellyfish blooms are frequently observed (*e.g.* Fuentes et al. 2011; Brotz and Pauly 2012; Prieto et al. 2013; Scorrano et al. 2016). Therefore, not only the fish predation might represent an underestimated source of *A. coerulea* mortality, but jellyfish might also be a non-negligible source of food for commercially important fish species in the lagoon, as demonstrated for the critically endangered European eel (Paper III). This could have important economic implications because the high availability of medusae during the blooms, associated with their rapid digestion and gut clearance rates (Arai et al. 2003), allow them to consume large biomasses of jellyfish. Like so, fish might benefit from this source of organic matter, without wasting energy in foraging activity (Cardona et al. 2012).

Fish are not the only potential predators of *A. coerulea* in the Thau lagoon. In addition to the studied species, active predation was also observed by the bogue (*Boops boops*) and by benthic predators such as anemones (*Anemonia* sp.) (R. Marques, personal observation, Fig. 3). Indeed, many different organisms have been shown to feed on jellyfish, including cephalopods, anemones, crabs, echinoderms and several species of birds (Ates 2017; Hoving and Haddock 2017; McInnes et al. 2017; Phillips et al. 2017; Thiebot et al. 2017). Since many of these predators or scavengers (see Ates 2017) are common in the Thau lagoon, it is very likely that their role in the regulation of the *A. coerulea* medusae blooms is also underestimated.

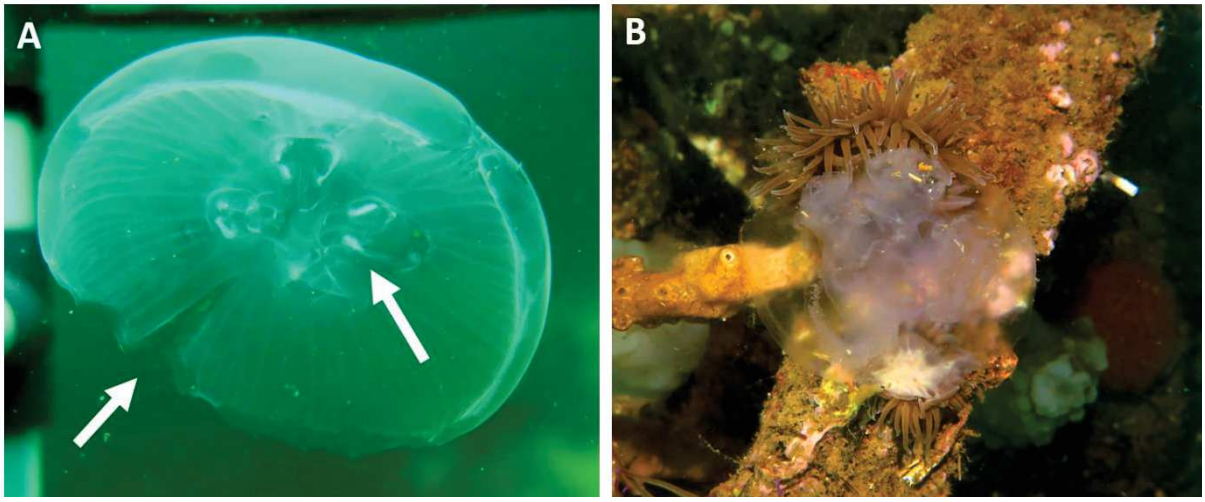


Fig. 3: *A. coerulea* medusae consumed by pelagic and benthic predators in the Thau lagoon. A) Medusae after being bitten by bogues. The arrows show the bites of the fish on the umbrella margins and gonads. B) Medusae consumed by anemones.

If not consumed while in the water column, the *A. coerulea* medusa die and sink to the bottom. Here, they might be consumed by scavengers but the remineralisation by microbial community appears to be the predominant fate. Indeed, the diversity of benthic scavengers that consume decaying medusa in Thau is seemingly very low, since only one taxon (the gastropods *Tritia* spp. from the Nassaridae family) revealed to be significantly attracted by the presence of dead medusa in the bottom (Paper IV). This suggests that the role of benthic scavenging in the lagoon is likely limited. However, the consumption of decaying organic matter by these particular organisms might be important, at least in habitats with less food availability, such as bare sediments (Morton 2011). Therefore, this trophic link can not be completely excluded. The degradation of medusa in the lagoon is very fast, being completely decomposed in 1 to 6 days. This is likely an outcome of high summer temperatures, small individual size and high tissue lability of *A. coerulea* medusa, as well as a native bacterial community well adapted to organic matter reminarisation (Titelman et al. 2006; Tinta et al. 2010; Lebrato et al. 2011; Sweetman et al. 2016). This rapid microbial degradation, combined with high fish predation pressure might explain why large jelly-falls are not frequently observed in Thau, in spite of the large blooms of *A. coerulea* medusae and the low depth of the lagoon. This might have important impacts on the biogeochemical cycle and trophic webs, possibly affecting the ecosystem services inThau.

4.1.3. Will jellyfish blooms increase?

The findings of this thesis grant basic knowledge on the ecology of *A. coerulea* and provide some clues on the potential future scenarios on the evolution of jellyfish blooms in the Thau lagoon and maybe elsewhere. Because the jellyfish life cycle is complex and a network of different ecological processes act at each and every one of its stages, predicting whether jellyfish blooms will increase is difficult. In addition, the knowledge acquired here might be species- and/or site-specific so extrapolations to other jellyfish populations should be performed with caution. Therefore, although not exclusive, this section is mainly focused on the *Aurelia* genus, to avoid potential misguided conclusions. Even within this particular genus, different species might be locally adapted to different ecosystems and show different responses to the same environmental drivers (Dawson and Jacobs 2001). Still, for these and likely other species of jellyfish, the findings of this thesis underline the critical role of the benthic population in the development of jellyfish blooms. Therefore, forecasting the evolution of jellyfish blooms under climate change and human ecosystems modifications clearly requires knowledge on species' benthic population dynamics. For the *A. coerulea* population of the Thau lagoon, the first control on jellyfish blooms is the presence of suitable substrates for the development of the scyphistomae population. Then, temperature, salinity, food availability and predation appear to be the main ecological processes regulating the final magnitude of the blooms.

In Thau, the presence of the *A. coerulea* benthic population is dependent on the wide distribution of anthropogenic constructions in the lagoon. The scyphistomae are settled only on these structures (Marques et al. 2015b) which stresses the critical role of human mediated changes of the marine physical habitat in the development of jellyfish blooms (Duarte et al. 2012). In order to cope with the increasing human population and global changes, urban infrastructures on coastal areas are expected to increase (Bulleri and Chapman 2010). Therefore, one can expect a rise of jellyfish blooms intensity and spatial distribution after the provision of novel habitats for scyphistomae development. However, this study further confirms the urgent need to assess the local population dynamics of the benthic stage and the impacts of the role of different ecosystem processes if we want to understand the future scenario of jellyfish blooms.

The temperature and salinity interaction appeared to be one of the main drivers of *A. coerulea* blooms in the Thau lagoon, and possibly that of the blooms of other *Aurelia* species and other scyphozoans. This raises the question of the impact of climate change on jellyfish development. In the Mediterranean coastal area, an increase in temperature in all seasons is predicted concomitant with a decrease in precipitation which will likely be more drastic during

the summer (Dubrovský et al. 2014). For *A. coerulea* in the Thau lagoon, the direct effect of higher temperatures and salinities might, on one hand, promote higher mortality of the scyphistomae during the summer, decreasing their density during the strobilation season and therefore, limiting the final abundance of the ephyrae. On the other hand, warmer winters might promote survival of the ephyrae produced in late autumn, which might counteract the negative effect of the lower scyphistomae densities during the strobilation peak in November. Although confirmation is still required, under the scenario of warmer and dry summers, it is possible that massive mortalities of scyphistomae in the lagoon may lead to the reduction of the abundance of the pelagic stages and therefore, the magnitude of the blooms, but probably not their disappearance. In this case, we may expect an increasing role of the podocysts in the development of the *A. coerulea* blooms. If this is true for other jellyfish species, we may witness a shift in the distribution of temperate species poleward, a decrease in population size for species inhabiting temperate and tropical areas and/or changes in time and duration of their pelagic stages (Dawson and Martin 2001; Purcell et al. 2007). However, this negative impact of climate change on jellyfish blooms is still speculative and might be restricted to particular environments, such as the Thau lagoon. Indeed, the *A. coerulea* is widely distributed around the world and can live under different climate regimes (Dawson and Martin 2001). Within the Mediterranean even though *Aurelia* spp. inhabit semi-enclosed basins such as the Thau lagoon (Scorrano et al. 2016), these habitats have often contrast environmental conditions and ecosystem functioning (Kara and Quignard 2018a) which should be taken into consideration. For instance, an opposite intra-annual benthic demographic variation than that found in Thau was reported for *Aurelia* spp. as close as in the Northern Adriatic Sea (Malej et al. 2012; Hocevar et al. 2018), which are under similar climate regimes, but also in other places around the world, such as in Japan, Tasmania and Sweden (Gröndahl 1988; Willcox et al. 2008; Ishii and Katsukoshi 2010; Makabe et al. 2014). This clearly underlines that the population dynamics of the benthic stages of *Aurelia* spp. and the subsequent development of their blooms is not exclusively dependent on temperature and salinity (despite their recognized critical role) and that in *in situ* local conditions other than these drivers are equally or even more important in the regulation of jellyfish populations.

This study also showed the critical role of food availability in the development of *A. coerulea* blooms in the Thau lagoon and highlighted the particular importance of the abundance of microzooplankton as a promoter of the production of buds. Because this is a vital biological process regulating the benthic population size and ultimately the abundance of the pelagic stages, an increase in the abundance of microzooplankton in the ecosystems might lead to

greater jellyfish blooms. Although the response of the plankton community to climate change is highly complex to predict, under the aforesaid climate predictions, planktonic communities are expected to change toward a dominance of small species (reviewed in Guinder and Molinero 2013), and potential increases of microzooplankton abundance (*e.g.* Rose and Caron 2007; Rose et al. 2009). Likewise, plankton community changes are also expected to occur in eutrophic areas (Sommer et al. 2002), which are suggested to favour the development of jellyfish blooms (Arai 2001). This seems to be particularly important for *Aurelia* spp. that inhabit highly human-impacted areas, where the medusa are able to feed on the modified plankton community and cope with the frequently associated low levels of dissolved oxygen, impairing their zooplanktivorous competitors (Arai 2001; Purcell et al. 2007; Purcell 2012). Indeed, large blooms of *Aurelia* spp. have been reported in coastal areas under strong levels of eutrophication like in Japan, China, Denmark, in the Baltic and Black Seas and in the Gulf of Mexico (*e.g.* Arai 2001; Daskalov et al. 2007; Dong et al. 2010). Therefore, the impact of climate change and eutrophication of coastal ecosystems might not only stimulate medusae growth but also boost the benthic population densities, by promoting the asexual reproduction of scyphistomae, and ultimately increasing the magnitude of the blooms.

Finally, this study revealed the potential importance of top-down control of all stages of *A. coerulea* in Thau, controlling the magnitude of the blooms directly by feeding on medusae, but also indirectly by preying on the benthic stages. Indeed, the diversity of fish and benthic predators feeding on *A. coerulea* is likely underestimated in Thau, but most likely in other ecosystems and for many other jellyfish species. Although direct predation on scyphistomae by some particular benthic predators has been previously demonstrated (Takao et al. 2014), the potential impact of indirect consumption, while predators prey on scyphistomae settling surfaces (*e.g.* mussels and red algae) has never been shown. We suspect that this source of mortality might be critical in the control of jellyfish blooms. Increasing knowledge supports the importance of predation in jellyfish blooms regulation (Hays et al. 2018), but most of the reports so far focused on the consumption of medusa (*e.g.* Ates 2017; Hoving and Haddock 2017; Thiebot et al. 2017) ignoring the impact of predators on jellyfish benthic population. In this sense, the overexploitation of fish stocks, does not only eliminate potential competitors of jellyfish, but it also releases the predation pressure on the pelagic and benthic stages. Therefore, larger blooms might be expected in coastal overfished areas. In contrast, in areas where fish and benthic communities are diverse and abundant, such as marine protected areas and low human impacted coastal areas, top predators might represent a natural regulator of jellyfish blooms.

Forecasting the evolution of jellyfish blooms requires comprehensive knowledge of each and every one of these ecological processes, but the final real response of jellyfish populations will likely rely on the interaction of many factors acting in synergy. Therefore, at this point, this task remains hypothetical. Nevertheless, this thesis provided ground information that emphasizes the extraordinary evolution of these organisms that, although anatomically simple, have complex life cycles that provide them a variety of adaptation strategies, promoting their survival, wide distribution and the formation blooms in many different environments (Hamner and Dawson 2009).

4.1.4. What are the potential impacts of jellyfish blooms?

Irrespective of the actual response of jellyfish populations to future environmental conditions, the persistence increase or decrease of their blooms will have important impacts on ecosystem functioning and ecosystem services (see general introduction section). The fundamental knowledge gathered here allows to infer the impacts of *A. coerulea* blooms within the Thau lagoon, but are also relevant for at least some other locations facing recurrent jellyfish blooms. Here, several negative and positive potential ecological impacts can be forecasted.

One of the main negative impacts expected from *A. coerulea* blooms in Thau is the reduction of food availability for zooplanktivorous fish. Medusae of *Aurelia* sp. have a very high impact on the abundance and structure of the zooplankton community (*e.g.* Behrends and Schneider 1995; Kinoshita et al. 2006; Han et al. 2009; Ramirez-Romero et al. 2018), and therefore, trophic competition between jellyfish and zooplanktivorous fish has been frequently suggested (*e.g.* Purcell and Arai 2001; Purcell and Sturdevant 2001; Robinson et al. 2014). It is possible that this might occur in Thau during *A. coerulea* blooms. This is of particular importance since the lagoon is recurrently colonized each spring by a variety of zooplanktivorous juvenile fish, many of which have a high economic value (Kara and Quignard 2018a). The potential reduction of zooplankton availability during the *A. coerulea* blooms might decrease juvenile fish survival during this period of their naturally high vulnerability.

The degradation of the biomass generated by *A. coerulea* blooms also has the potential to strongly affect the functioning of this semi-enclosed ecosystem. Acknowledging the importance of the microbial remineralisation of dead medusae in the Thau lagoon, an increase of bacterial abundance might be expected after the collapse of the blooms together with a reduction of the dissolved oxygen in the vicinity of the dead organic matter (Jane et al. 2009; Pitt et al. 2009b). The collapse of *A. coerulea* blooms coincides with the highest period of anoxic episodes occurrence (Harzallah and Chapelle 2002). Therefore, they can intensify these

lethal events. Moreover, jellyfish are hosts of a diverse bacterial community with a potential role as vectors of pathogens (Basso et al. 2019). Indeed, *Vibrionacea* bacteria appeared to thrive during the degradation of *A. coerulea* (Tinta et al. 2012) and it was also reported associated with other jellyfish organisms in the Mediterranean Sea (Basso et al. 2019). Considering that some *Vibrionacea* species might have drastic impacts on the local production of oysters (see Pernet et al. 2012a), further investigations of the microbial association with the *A. coerulea* during and after their blooms in the Thau lagoon should be further explored.

This having been said, the blooms of *A. coerulea* might also have positive impacts on ecosystem functioning and ultimately profit to some human activities in Thau. For instance, the predation by *A. coerulea* medusae on meso- and microzooplankton might release the predation pressure on phytoplankton which can increase its production (Turk et al. 2008) and ultimately periodically benefit filter feeders like bivalves. Likewise, the process of jellyfish degradation releases large amounts of inorganic nutrients (Pitt et al. 2009b) that potentially contribute to the development of phytoplankton blooms. This is of particular significance for the important economic activity of shellfish farming in the lagoon. Indeed, with the recent recovery of the ecological quality of Thau and the consequent reduction of phytoplankton biomass in the water column (Derolez et al. 2019), there is a concern regarding the carrying capacity of the lagoon to provide enough food to support high levels of oyster's production (Bec et al. 2019). The blooms of *A. coerulea* medusae coincide with one of the periods of the high growth rate of the oysters in Thau (from March to early July, Pernet et al. 2012a) and might, therefore, ultimately contribute to the production of oysters in the lagoon. Likewise, the fishing activity in Thau might benefit from the presence of *A. coerulea* blooms. This study showed that this jellyfish is consumed by several commercially important local fish. It might, for instance, represent a non-negligible source of food for the critically endangered European eel and the highly exploited gilthead sea bream. The *A. coerulea* biomass might therefore potentially contribute to the survival and recruitment of these fish in the area. It is possible that these positive impacts extend to other pelagic and benthic predators with low commercial value, but ecologically important since they transfer the energy to higher trophic levels. Likewise, during the degradation of the medusae, some scavengers might profit from the decaying organic matter, which might then be preyed upon by top-predators. Finally, the growth of microorganisms in the vicinity of the jellyfish carcasses might boost the abundance of microzooplankton organisms which are known as important bacterial predators (Rassoulzadegan 1986). This likely promotes the transfer of energy and biomass through various pathways in the food web, enriching the overall productivity of the ecosystem

4.2 CONCLUSION AND PERSPECTIVES

This PhD work highlighted the complex interaction of biotic and abiotic environmental parameters which, by jointly influencing both its benthic and pelagic populations, ultimately determine the timing and magnitude of the *A. coerulea* blooms in the Thau lagoon. Overall, temperature, salinity, food availability and predation appear to be the main ecological factors controlling the intensity of the blooms. The exceptional production of biomass associated to the blooms have three main fates, all with different impacts on the functioning of this semi-enclosed ecosystem. First, the medusae can be consumed alive by several pelagic predators like fish. Otherwise, they die and sink to the seabed, where they can be consumed by benthic scavengers like some gastropods, but most are rapidly remineralised by the local microbial community.

This is also the first time that such a comprehensive study is made on a jellyfish species. The high level of confinement that characterizes the Thau presented an exceptional framework to perform simultaneously *in situ* investigations of the multiple potential drivers of both the benthic and pelagic population dynamics of *Aurelia coerulea* in the lagoon, as well as to identify the fates of its blooms. This critical information broadens our understanding of jellyfish blooms development and its impacts on the marine environment. However, like most studies, during this thesis enough has been learned to make suggestions for improvement.

Despite the new insights obtained here on the potential future evolution of jellyfish blooms and on their potential impacts on coastal ecosystems, these processes remain speculative until quantifications and ecosystem modelling is performed. Therefore, the first step forward will be the development of local ecosystem-based models, including population dynamics, trophic and biogeochemical processes. This study provides information to do so in Thau, but their direct extrapolation at the global scale is not advised, due to the specificity of the ecosystem functioning of lagoons. Therefore, complementary investigations should first be made on the benthic and pelagic ecology of other jellyfish species and in varied places around the world. For instance, comparisons with other jellyfish populations, inhabiting other coastal Mediterranean lagoons (under the same climatic regime) or distant locations under very different environmental climate conditions (*e.g.* coastal areas of the Pacific Ocean), would provide evidence of the varied life strategies used by jellyfish to survive and thrive in such different ecosystems. This would help to predict the formation of jellyfish blooms at large spatial and temporal scales. Furthermore, more information is still required to reach a full understanding of the ecology of jellyfish species. For instance, even for *A. coerulea* in the Thau lagoon, the timing of podocysts production and excystment should be assessed, as well as the

mortality rate of the ephyrae during the winter, since these two stages might play preponderant roles in the development of the blooms. Finally, the quantification of *in situ* mortality rates due to pelagic and benthic predation on both life stages of *A. coerulea* is required to forecast the magnitude of their bloom. This is also important for understanding the production of fish stocks since the importance of jellyfish in their diets is currently ignored in marine food web modelling. Our knowledge on the fates of the jellyfish biomass is still at a basic level and the quantification of the proportion of the energy transferred through the different trophic pathways (pelagic or benthic predators and microbial community) is essential to forecast the ecological impacts of the blooms. This information should be improved and included in ecosystem-based models to forecast the evolution of local ecosystem services under the current global change scenarios.

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Abstract: Jellyfish are important components of marine ecosystems. Their spectacular blooms have severe ecological and socioeconomic impacts and are seemingly boosted by anthropogenic pressures on the marine environment. Concerns regarding increases in jellyfish blooms, at least in some areas of the world, call for a deeper understanding of their drivers. However, many jellyfish have complex life cycles, comprising both benthic and pelagic stages, which complicates the understanding of their blooms and predictions on their future evolution. Furthermore, the lack of knowledge regarding the fates of these large accumulations of biomass hampers the assessment of their impacts. With this regards, the semi-enclosed ecosystem of the Thau lagoon presents the rare particularity to harbour a complete resident population of the jellyfish *Aurelia coerulea*. Therefore, it offers the ideal background to study the multiple ecological processes affecting the dynamics of both its benthic and pelagic populations. This PhD built on this rare opportunity to precise the drivers and fates of the blooms of *A. coerulea*. This was accomplished in two steps. First, the benthic population dynamics in the lagoon was investigated and complemented with studies on its drivers and on the trophic ecology of both life stages over one year. To do so, *in situ* monitoring surveys and both stomach content and stable isotope analyses were employed. Second, the fate of *A. coerulea* biomass in the lagoon was assessed by investigating fish predation on its pelagic and benthic life stages and by studying the degradation of its medusae once dead on the seabed. This was performed by molecular analysis of fish gut contents and *in situ* experiments evaluating the decay rates of medusae and the potential role of the benthic fauna in their disappearance. The results obtained highlight a complex interaction of biotic and abiotic environmental parameters, which modulate bloom intensity by jointly influencing both the benthic and pelagic populations of *A. coerulea*. Temperature, salinity, food availability and predation appear to be the main drivers of the blooms of *A. coerulea* in Thau, with four critical periods, either boosting or lessening local bloom formation each year. Finally, the biomass produced by *A. coerulea* blooms has three main fates within the lagoon. The medusae can first be consumed alive by several pelagic predators like fish. Otherwise, when they die and sink to the seabed, some can be consumed by benthic scavengers like gastropods, but most are rapidly remineralised by the local microbial community. These findings shed light on the potential evolution of jellyfish blooms in the face of the ongoing anthropogenic forces on the marine environment, and on their impacts on coastal ecosystems functioning. However, they also highlight how intricate jellyfish blooms forecasting is and stress the need for similar comprehensive studies, not only for other jellyfish species but also in many other parts of the world.

Keywords : Population dynamics, Asexual reproduction, Trophic ecology, Predation, Degradation

Résumé : Les méduses sont des composants importants des écosystèmes marins. Leurs proliférations spectaculaires ont de graves impacts écologiques et socio-économiques et sont apparemment renforcées par les pressions anthropiques en milieu marin. Les inquiétudes suscitées par l'accroissement de la fréquence et de l'intensité de ces proliférations, du moins dans certaines régions du globe, appellent à une compréhension plus approfondie de leurs causes. Cependant, la plupart des méduses ont un cycle de vie complexe, comprenant à la fois des stades benthiques et pélagiques, ce qui complique la compréhension des épisodes de proliférations et empêche toute prévision fiable de leur évolution. De plus, le manque de connaissances sur l'avenir de la biomasse générée par les proliférations entrave l'évaluation de leurs impacts. Pour cela, l'écosystème semi-fermé d'étang de Thau présente la particularité rare d'abriter une population complète et résidente de la méduse *Aurelia coerulea*. Il offre donc le cadre idéal pour étudier les multiples processus écologiques qui affectent la dynamique de ses populations benthiques et pélagiques. Ce travail de thèse tire parti de cette opportunité rare afin de préciser l'origine et le devenir des proliférations d'*A. coerulea*. Cela a été accompli en deux étapes. Premièrement, la dynamique de la population benthique de l'espèce a été étudiée dans l'étang et complétée par une étude de l'écologie trophique des deux stades de vie sur une année. Pour ce faire, des suivis *in situ* ont été réalisés et complétés par l'analyse de contenus stomacaux et des comparaisons de signatures en isotopes stables. Deuxièmement, le devenir de la biomasse d'*A. coerulea* dans la lagune a été étudié en évaluant la prédation des poissons sur ses stades benthiques et pélagiques et en suivant la disparition de ses méduses mortes, une fois posées sur le fond. Ceci a été réalisé par analyse moléculaire du contenu des intestins de poisson et par des expériences *in situ* évaluant les taux de décomposition des méduses et le rôle potentiel de la faune benthique dans leur disparition. Les résultats obtenus mettent en évidence l'interaction complexe de paramètres environnementaux biotiques et abiotiques qui modulent l'intensité des proliférations en influençant conjointement les populations benthiques et pélagiques d'*A. coerulea*. La température, la salinité, la disponibilité en nourriture et la prédation semblent être les principaux facteurs écologiques contrôlant les proliférations de *A. coerulea* dans l'étang de Thau, avec quatre périodes critiques dans l'année, où la formation des proliférations est soit facilitée soit minimisée. Enfin, les blooms ont trois principaux devenirs dans la lagune. Les méduses sont avant tout consommées vivantes dans la colonne d'eau par les prédateurs pélagiques (notamment les poissons). Sinon, lorsqu'elles meurent et coulent sur le fond, elles peuvent être consommés par certains organismes benthiques (notamment des gastéropodes) mais sont surtout rapidement reminéralisés par la communauté microbienne locale. Ces résultats apportent des informations précieuses pour prédire l'évolution des proliférations de méduses en réponse aux effets anthropogéniques sur le milieu marin en cours, et anticiper leurs impacts sur le fonctionnement des écosystèmes. Cependant, ils soulignent également la difficulté d'obtenir de telles prévisions et soulignent la nécessité de mener des études approfondies similaires, non seulement pour d'autres méduses mais aussi dans d'autres régions du monde.

Mots-clés : Dynamique des populations, Reproduction asexuée, Ecologie trophique, Prédation, Dégradation