THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Biologie des populations et écologie

École doctorale GAIA

Unité de recherche UMR MARBEC

ANALYSE DE LA VARIABILITE SPATIO-TEMPORELLE DU ZOOPLANCTON DANS LE GOLFE DU LION ET CONSEQUENCES SUR LES POPULATIONS DE PETITS PELAGIQUES

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Le 07 décembre 2020

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Abstract

In the mid-2000s, the Gulf of Lion was faced with a real crisis in pelagic fisheries, mainly for anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*). The drop in landings of these two species was not caused by a drop in abundance but by a decrease in their size and body condition, as fish that are too small are less economically interesting for fishermen. Various hypotheses have been put forward to explain these changes in fish populations (epizootic disease, natural predation, overfishing), but only the hypothesis of bottom-up control seems likely. The fish seem to have changed their diet, now consuming smaller prey, supposedly with less energy. The aim of this thesis was therefore to determine whether changes may have taken place in the planktonic community over the last two decades, in terms of density, size or taxonomic composition, which could explain the changes in the diet of sardines and anchovies and their declining condition. As plankton data are limited in the Gulf of Lion, we first focused on the variability of different environmental key factors for the planktonic community dynamics. Our results indicate that environmental conditions have broadly changed in the Gulf of Lion, with a major change in the mid-2000s, affecting Chlorophyll concentration (with a regime shift in 2007), but also SST, upwelling, thermal fronts, Rhone flow (and in particular N and P nutrient inputs) and winter deep convection. These environmental changes may have affected plankton production and, consequently, the small pelagic fish community, which showed similar patterns of variation. Based on data from PELMED's summer oceanographic campaigns (in 2007-2008 and since 2014), several types of phyto-plankton community have been identified, some dominated by dinoflagellates, notably *Gymnodinium* sp and others by diatoms, mainly *Chaetoceros* sp, *Leptocylindrus* sp and *Proboscia* sp. Concerning zooplankton, the main communities identified were dominated by cladocerans such as *Penilia* sp or *Evadne* sp and others by copepods such as *Claucocalanus* sp, *Oithona* sp or *Centropages* sp. However, no strong links were observed either with the environment or with the condition of the fish and these different summer communities. Finally, the long-term variability of zooplankton was studied in the Ligurian Sea, revealing a high stability of the community in terms of density, size and taxonomic composition. Marked changes were observed in 2015 with a decrease in density of the smallest crustaceans as well as a decrease in density of gelatinous filter feeders or carnivorous, possibly related to the increase in temperature and changes in winter conditions. Thus, although no causal relationship could clearly be established between planktonic dynamics and small pelagics, environmental changes have indeed occurred in the Gulf of Lion, and the planktonic production of the shelf seems to have been impacted. Strong and punctual processes, as in 2015, seem to have a strong and rather durable impact on the planktonic communities. Although no clear conclusion can be drawn as to a possible bottom-up control of small pelagic populations, this hypothesis cannot be discarded. The main obstacle appears to be the lack of monitoring of the planktonic community in the Gulf of Lion, which it seems necessary to put in place in order to understand its dynamics in the face of climate change and the possible impact on small pelagics.

Key words : bottom-up control, time series, zooplankton, small pelagics, climate change

Résumé

Au milieu des années 2000, le Golfe du Lion a été confronté à une véritable crise des pêcheries pélagiques, principalement pour l'anchois (*Engraulis encrasicolus*) et la sardine (*Sardina pilchardus*). La chute des débarquements de ces deux espèces n'a pas été causée par une baisse de l'abondance mais par la diminution de leur taille et condition corporelle, les poissons trop petits étant moins intéressants économiquement pour les pécheurs. Différentes hypothèses ont été avancées pour expliquer ces changements dans les populations de poissons (épizootie, prédation naturelle, surpêche), mais seule l'hypothèse d'un contrôle bottom-up semble probable. Les poissons auraient changé leur régime alimentaire, consommant maintenant des proies plus petites, supposées moins énergétiques. L'objectif de cette thèse était donc de déterminer si des changements ont pu avoir lieu dans la communauté planctonique au cours des deux dernières décennies, aussi bien en terme de densité que de taille ou de composition taxonomique, qui pourraient expliquer les changements de régime alimentaire de la sardine et de l'anchois et leur baisse de condition. Les données de plancton étant limitées dans le golfe du Lion, nous nous sommes en premier lieu focalisés sur la variabilité de différents facteurs environnementaux clefs pour la dynamique de la communauté planctonique. Nos résultats indiquent que les conditions environnementales ont largement changé dans le Golfe du Lion, avec un changement majeur au milieu des années 2000, affectant la concentration de Chlorophylle (avec un changement de régime en 2007), mais aussi la SST, les upwelling, les fronts thermiques, le débit du Rhône (et en particulier les apports de nutriments N et P) ainsi que la convection profonde hivernale. Ces changements environnementaux ont pu affecter la production de plancton et, par conséquent, la communauté des petits poissons pélagiques, qui a montré des patterns de variation similaires. A partir des données issues des campagnes océanographiques d'été de PELMED (en 2007-2008 et depuis 2014), plusieurs types de communauté phyto-planctoniques ont été identifiées, certaines dominées par des dinoflagellés, notamment *Gymnodinium sp* et d'autres par des diatomées, principalement *Chaetoceros sp, Leptocylindrus sp* et *Proboscia sp.* Concernant le zooplancton, les principales communautés identifiées étaient dominées par des cladocères comme *Penilia sp ou Evadne sp* et d'autres par des copépodes tels que les *Claucocalanus sp, Oithona sp ou Centropages sp.* Cependant, aucun lien fort n'a été observé ni avec l'environnement ni avec la condition des poissons et ces différentes communautés d'été. Finalement, la variabilité à long terme du zooplancton a pu être étudiée en mer Ligure révélant une forte stabilité de la communauté aussi bien en terme de densité que de taille ou de composition taxonomique. Des changements marqués ont été observés en 2015 avec une baisse de densité des plus petits crustacés ainsi qu'une baisse de densité chez des gélatineux filtreurs ou carnivores, possiblement en lien avec l'augmentation de température et des modifications des conditions hivernales. Ainsi, si aucune relation de cause à effet n'a clairement pu être établie entre la dynamique planctonique et les petits pélagiques, des changements environnementaux ont bien eu lieu dans le Golfe du Lion, et la production planctonique du plateau semble avoir été impactée. Des processus forts et ponctuels comme en 2015 semblent par ailleurs avoir un impact fort et assez durable sur les communautés planctoniques. Bien qu'on ne puisse clairement conclure quant à un éventuel contrôle bottom-up sur les populations de petits pélagiques, cette hypothèse ne peut être écartée. Le principal obstacle apparait être le manque de suivi de la communauté planctonique dans le Golfe du Lion qu'il semble nécessaire de mettre en place afin de comprendre ses dynamiques face au changement climatique et l'impact possible sur les petits pélagiques.

Mots clefs : contrôle bottom-up, séries temporelles, zooplancton, petits pélagiques, changement climatique

Remerciements

Je tiens en premier lieu à remercier France Filière Pêche et l'IFREMER pour le financement de ces 3 années de thèse.

Je remercie également les membres du jury, tout d'abord Sakina et Jean-Louis pour avoir accepté de consacrer une partie de votre temps afin de rapporter ce travail de thèse ainsi que Catherine et Martin pour avoir accepté d'examiner ce travail.

Au cours de mon stage de master au MIO à Marseille, Jean-Christophe et David m'aviez conseillé de postuler à cette offre de thèse en m'assurant que l'encadrement serait top. Bien m'en a pris de vous écouter et un grand merci à vous deux de m'avoir mis sur la voie de ce projet.

Un énorme MERCI à mes 3 encadrants de thèse, Claire, Jean-Marc et Lars pour avoir toujours été présents, bienveillants, à l'écoute et disponibles malgré la distance pour certains et vos emplois du temps bien chargés. Il parait que l'encadrement joue pour beaucoup dans le bon déroulé d'une thèse… et c'est vrai ! Vous avez toujours suivi de près mes diverses avancées et c'est grâce à vous que j'ai pu mener à bien ces travaux. Claire, merci pour ta gentillesse, ta réactivité et tous tes bons conseils. Tu as su me conseiller quand j'en avais besoin et toujours avec pédagogie. Jean-Marc, grâce à toi j'ai vraiment pris gout à l'analyse de données et tous tes conseils m'ont permis d'apprendre énormément. C'est très certainement une des compétences acquises au cours de ces 3 ans qui me servira le plus à l'avenir alors pour ça je t'en remercie. Lars, grâce à toi je connais mieux ce monde intriguant qu'est celui du plancton. Nos diverses discussions m'ont permis d'acquérir de nombreuses connaissances qui m'auront été très précieuses au cours de ces 3 années. Je garderai de ces trois ans un excellent souvenir que ce soit d'un point de vue professionnel et humain et c'est en grande partie grâce à vous !

Merci également à Hervé et Tarek qui avez chacun suivi de près et participé à une partie de mes travaux. Hervé, quelle que soit la donnée de satellite que je cherchais, je savais que tu l'aurais quelque part sur un disque dur, il suffisait juste de trouver le bon disque ! Tu as toujours su me conseiller sur les différentes données existantes en fonction de ce que je voulais faire et m'a été d'une grande aide. Tarek, à chaque problème ou questionnement, tu avais l'analyse ou méthode nécessaire pour pouvoir y répondre. J'ai appris énormément de choses grâce à toi et cela aura été très agréable de travailler ensemble.

Merci aux équipages présents sur l'Europe lors des campagnes PELMED ainsi qu'à Jean-Hervé, Luisa, Blandine, Tarek, Claire et tous les autres pour la bonne ambiance dans l'équipe scientifique à bord. J'ai pris à chaque fois beaucoup de plaisir à participer à cette campagne et n'aurait pas hésité une seule seconde à en faire une de plus si cela avait été possible.

Je remercie également l'équipe du LOV à Villefranche de m'avoir accueilli une semaine ainsi que Laetitia, Amanda, Corine, Jean-Olivier et la PIQv pour tout votre travail sur les données du zooscan et ecotaxa.

Merci également aux sportifs du labo, Jonathan (je n'aurai jamais pensé t'inclure dans cette catégorie mais comme quoi tout arrive !) pour les parties de tennis endiablées ainsi que Philippe, Fabien, Taha, Nicolas et les autres pour les parties de futsal.

Enfin, merci à toi Morgane pour ton soutien sans faille, ces 3 années n'auront pas toujours été simples mais tu auras toujours su faire en sorte que tout se passe pour le mieux.

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Chapitre I. *Introduction*

I-1 Le plancton dans les océans

Les océans recouvrent plus de 70% de la surface de la Terre et rassemblent une très grande diversité d'espèces, pour une grande partie encore non découverte (Bron et al., 2011). L'ensemble des organismes marins est rassemblé en deux grands groupes : le benthos et le pelagos (Pérès & Devèze, 1963). Le benthos regroupe les organismes vivant sur les fonds marins tandis que le pelagos est composé de ceux vivant dans la colonne d'eau. Selon leur puissance de nage les individus du pelagos vont être classifiés en deux grands ensembles : le necton et le plancton. Les individus du necton ont la capacité de nager contre les courants marins et de se mouvoir librement, on y retrouve notamment les mammifères marins et les poissons pélagiques. A l'inverse, les individus du plancton sont incapables de s'opposer aux courants et se laissent porter par les mouvements des masses d'eau (Pérès & Devèze, 1963). Ils ont toutefois, pour une partie d'entre eux, la capacité de se déplacer de façon verticale dans la colonne d'eau (Lampert, 1993). Les organismes du plancton qui vont avoir un cycle de vie totalement pélagique sont désignés par le terme holoplancton. Le méroplancton, quant à lui, caractérise les individus planctoniques présents dans la colonne d'eau de façon temporaire. C'est notamment le cas de certaines larves d'organismes benthiques, présentes une partie du temps dans la colonne d'eau avant de se fixer au substrat pour continuer leur développement. Plus communément, dans le cadre de l'étude du fonctionnement des écosystèmes et des réseaux trophiques, on fera simplement la distinction entre le plancton végétal, le phytoplancton, et le plancton animal : le zooplancton.

I-1.1 Les classes de tailles du plancton

Le plancton représente une très grande diversité au niveau de la taille des individus et se répartit sur plusieurs ordres de grandeur. La classification en taille du plancton classiquement utilisée est celle établie par Sieburth et al., (1978) (Figure I-1). Les plus petits organismes, les virus, sont présents uniquement dans le Femto-plancton (0.02 – 0.2 µm) tandis que les bactéries se trouvent majoritairement dans le pico-plancton (0.2-2µm). Le phytoplancton, qui rassemble les organismes autotrophes, se répartissen essentiellement sur trois classes de taille : le pico-phytoplancton (0.2 – 2.0 µm), le nano-phytoplancton (2.0 - 20 µm) et le micro-phytoplancton (20 - 200 µm). La première classe représente généralement les cyanobactéries des genres *Synechococcus* et *Prochlorococcus*. Les deux autres classes regroupent majoritairement les Coccolithophores, les Dinoflagellés, les Cryptophytes ainsi que les Diatomées, également présentes dans le meso-phytoplancton et beaucoup étudiées pour leur importance dans le fonctionnement de la pompe biologique (Armbrust, 2009; Assmy et al., 2013; Rembauville et al., 2015). Concernant le zooplancton, on le retrouve essentiellement du nano-plancton avec quelques groupes du proto-zooplancton (organismes unicellulaires du zooplancton) jusqu'au mega-plancton. Toutefois, les classes les plus étudiées sont celles du micro et meso-zooplancton pouvant être pêchées par les filets à plancton. Bien que le nano- et micro-zooplancton jouent un rôle important dans les transferts d'énergie comme nous le verrons par la suite, uniquement le meso-zooplancton sera étudié au cours de ce manuscrit. De même pour le phytoplancton, seulement la composition du micro-phytoplancton sera abordée.

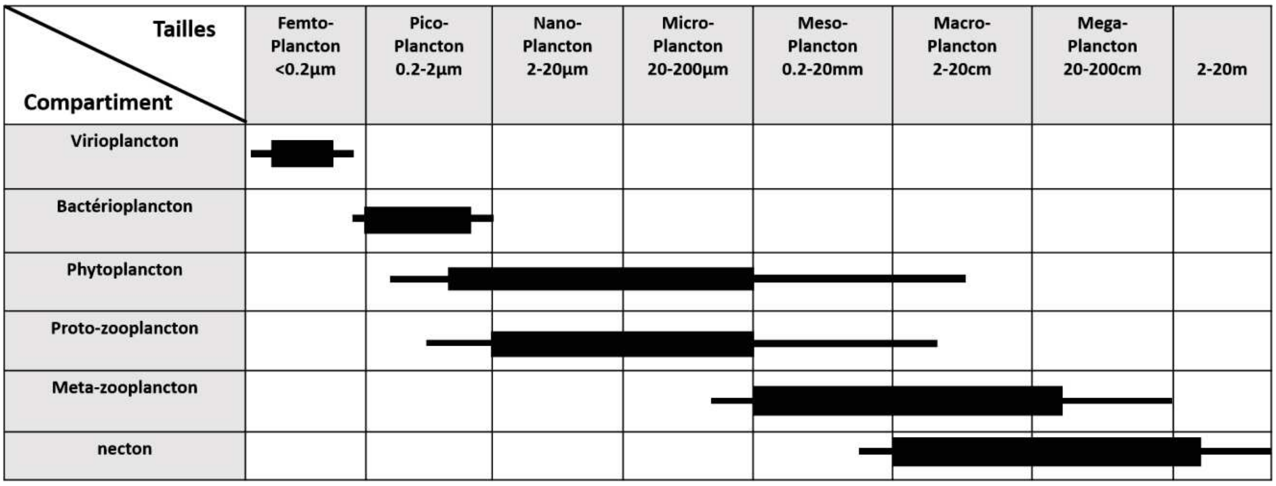

Figure I-1 ***Répartition des différents groupes planctoniques dans les différentes classes de tailles. Figure issue de (Sieburth et al., 1978).***

I-1.2 Le phytoplancton : diversité et rôle

Le phytoplancton est constitué d'organismes unicellulaires procaryotes (cyanobactéries) et eucaryotes vivant principalement dans la partie supérieure de la colonne d'eau, la zone euphotique, où la lumière est suffisante pour réaliser la photosynthèse (Falkowski et al., 2004). Bien qu'une grande partie des eucaryotes unicellulaires planctoniques soient autotrophes, de nombreuses espèces peuvent également assimiler des nutriments organiques. On les considère alors comme mixotrophes (Mitra et al., 2014). Les organismes phyto-planctoniques les plus souvent échantillonnés et/ou étudiés appartiennent généralement aux Cyanobactéries, aux Haptophytes, parfois appelés primnesiophycées (comprenant les Coccolithophores), les Dinoflagellés et les Diatomées (Simon et al., 2009). Le phytoplancton constitue la base des réseaux trophiques marins, assurant plus de 45% de la production primaire nette annuelle de la planète (Field et al., 1998) . Il joue ainsi un rôle important dans la production d'énergie pour l'ensemble du réseau trophique et dans l'assimilation du CO2 et sa séquestration sous forme de matière carbonée dans les océans, permettant ainsi de réguler le climat à l'échelle mondiale (Raven & Falkowski, 1999). Les diatomées assurent environ 45% de la production primaire à travers le monde aussi bien en zones côtières que dans l'océan ouvert (Carstensen et al., 2015; Field et al., 1998; Tréguer et al., 2018) bien que le nano-phytoplancton soit très dominant dans les couches superficielles à travers le monde (Alvain et al., 2008).

I-1.3 Initiation des efflorescences printanières du phytoplancton

Dans une grande partie des écosystèmes marins tempérés, on observe entre la fin de l'hiver et le printemps une augmentation de la biomasse phytoplanctonique appelée «efflorescence» (« bloom » en anglais) (Cloern, 1991; d'Ortenzio & Ribera d'Alcalà, 2009; Mayot et al., 2017; Platt et al., 1991). Cette grande quantité de phytoplancton est la principale source d'énergie des écosystèmes, entraînant par effet de cascade une augmentation de la biomasse des organismes brouteurs s'en nourrissant et supportant ainsi l'ensemble du réseau trophique.

I-1.3.1 Contrôle par l'environnement

Sverdrup fût le premier, en 1953, à émettre une hypothèse sur les facteurs contrôlant ces efflorescences (Sverdrup, 1953). Sa théorie, appelée "Critical depth hypothesis", stipule que l'initiation d'une efflorescence ne peut se faire seulement que lorsque la croissance phytoplanctonique excède les pertes, dues principalement à la respiration et la mortalité (Figure I-2a). Le taux de mortalité est supposé constant dans la colonne d'eau, contrairement à la capacité de photosynthèse du phytoplancton qui diminue avec la profondeur, la lumière disponible étant de plus en plus faible. La profondeur à partir de laquelle la croissance photosynthétique est égale aux pertes est appelée la "profondeur critique". Pendant l'hiver, la plongée de la couche de mélange entraine le phytoplancton en profondeur, en dessous de la profondeur critique, diminuant ses capacités photosynthétiques et rendant la croissance plus faible que la mortalité. A la fin de l'hiver ou début du printemps, quand la limite inférieure de la couche de mélange passe au-dessus de cette "profondeur critique", la production devient supérieure aux pertes et la biomasse phytoplanctonique augmente. C'est alors l'initiation de l'efflorescence printanière.

I-1.3.2 Contrôle par les interactions trophiques

Cette théorie ne fait cependant pas l'unanimité et différentes observations n'ont pu être expliquées par ce seul processus de profondeur critique (Behrenfeld, 2010; Townsend et al., 1994), des efflorescences phytoplanctoniques ayant été observées avant la remontée de la profondeur limite de la couche de mélange. Une autre hypothèse couplant les processus physiques et interactions trophiques a été proposée pour expliquer l'initiation des efflorescences (Banse, 1994; Behrenfeld, 2010; Behrenfeld et al., 2013) : c'est l'hypothèse de perturbation-rétablissement (Disturbance-recovery hypothesis) (Figure I-2b). Celle-ci suggère que l'efflorescence phytoplanctonique est due à une perturbation venant rompre temporairement la relation proie-prédateur entre le phytoplancton et les brouteurs. En hiver, lors de la plongée de la couche de mélange, les interactions proies-prédateurs sont rendues moins fréquentes par le fait de la dilution des individus dans un volume d'eau plus grand, diminuant la mortalité par le broutage. La croissance photosynthétique devient supérieure aux pertes ce qui permet l’accumulation de biomasse phytoplanctonique. Au printemps, la remontée de la limite inférieure de la couche de mélange engendre une concentration des organismes planctoniques et des nutriments dans la couche euphotique entraînant une forte concentration phytoplanctonique et activité photosynthétique. Le développement des brouteurs va alors s’initier et la pression de broutage va augmenter jusqu’à dépasser la croissance phytoplanctonique. Cela va caractériser la fin de l’efflorescence et une décroissance de la biomasse phytoplanctonique.

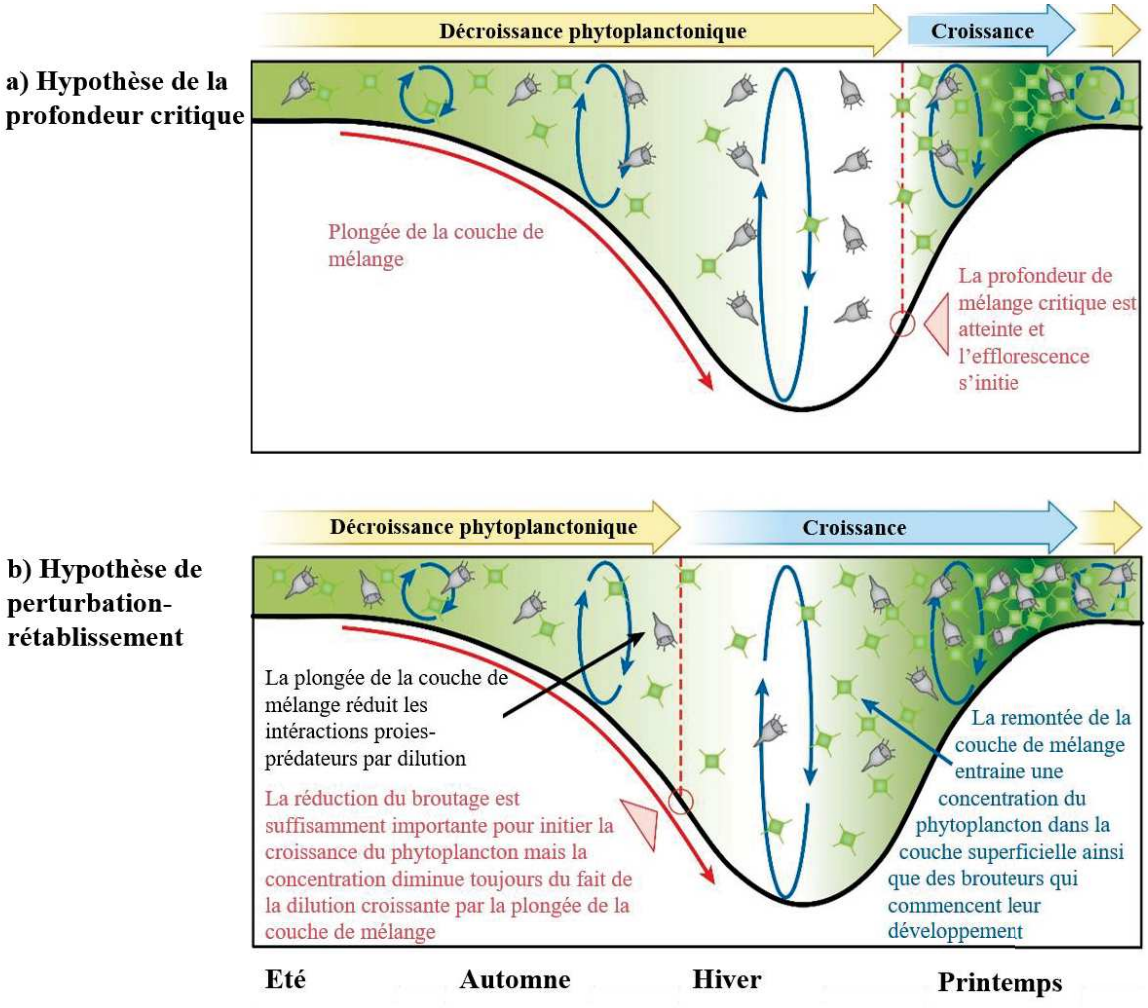

Figure I-2 *Schéma de l'hypothèse de profondeur critique et de perturbation-rétablissement modifiée à partir de (Behrenfeld & Boss, 2014).*

I-1.4 Le zooplancton : diversité et rôle

Le zooplancton est un groupe d’une grande diversité taxonomique rassemblant des organismes à différents niveaux du réseau trophique. Le proto-zooplancton rassemble les organismes unicellulaires du zooplancton et est composé majoritairement de flagellés hétérotrophes, de ciliés et de certains dinoflagellés hétérotrophes qui vont se nourrir principalement de pico et nano-phytoplancton ainsi que de bactéries. Dans le meso-zooplancton échantillonné par les filets à plancton, on va retrouver différents grands groupes tels que les gélatineux filtreurs se nourrissant pour certains de pico et nano phytoplancton comme les Appendiculaires ou sur du micro-phytoplancton comme les dolioles et les salpes, les crustacés broutant majoritairement du micro-phytoplancton ou encore des individus carnivores comme les Chaetognathes et le grand groupe des hydrozoaires se nourrissant de zooplancton (Acuña, 2001; Dallot et al., 1988; Katechakis et al., 2004; Sommer et al., 2002). Les oeufs mais aussi les larves de poissons (dont le comportement de nage n'est pas encore assez fort pour nager contre le courant) sont également considérés comme faisant partie du zooplancton. Parmi tous ces groupes, les crustacés sont de loin le groupe majoritaire, essentiellement dominé par les Copépodes, et ce dans tous les océans du globe (Bron et al., 2011; Humes, 1994; Siokou-Frangou et al., 2010). Le zooplancton a une position clef dans le réseau trophique marin en réalisant la production secondaire. En broutant le phytoplancton et en étant ensuite consommé par les niveaux trophiques supérieurs, il permet de faire le lien entre les producteurs primaires et le reste du réseau trophique (Cushing, 1989; Fransz et al., 1991).

Le zooplancton est également un acteur clé de la pompe à carbone biologique. La pompe à carbone biologique est le processus par lequel la matière organique issue de la production photosynthétique est exportée dans les couches inférieures de l'océan selon une combinaison de différents facteurs tels que la sédimentation des particules, les mélanges verticaux de matière organique dissoute ou les migrations verticales effectuées par diverses espèces animales (Turner, 2015) (Figure I-3). Bien qu'une importante partie des flux verticaux de matière soit issue de la neige marine (agrégats de matière organique sédimentant de façon continue des couches supérieures vers les couches inférieures) et de la sédimentation d'une partie du phytoplancton, notamment les diatomées, au moment des efflorescences, le zooplancton joue un rôle important dans la pompe biologique. En effet, le zooplancton produit des pelotes fécales (Turner, 2002, 2015; Turner & Ferrante, 1979) qui vont s'agréger et sédimenter vers les couches inférieures. De plus, le zooplancton réalise d'importantes migrations verticales en allant en profondeur le jour pour échapper aux prédateurs et en remontant dans les couches supérieures la nuit pour se nourrir (Brierley, 2014; Lampert et al., 1986). On parle alors de migrations nycthémérales. Lors de ces migrations, de la matière organique est transportée vers le fond participant également au transfert de matière vers les profondeurs (Packard & Gómez, 2013). Ainsi, en plus d'avoir un rôle essentiel dans le transfert d'énergie vers les niveaux trophiques supérieurs, le zooplancton joue également un rôle important dans la pompe à carbone biologique et, de façon indirecte, dans la régulation du climat à l'échelle mondiale (Beaugrand & Kirby, 2010; Richardson, 2008).

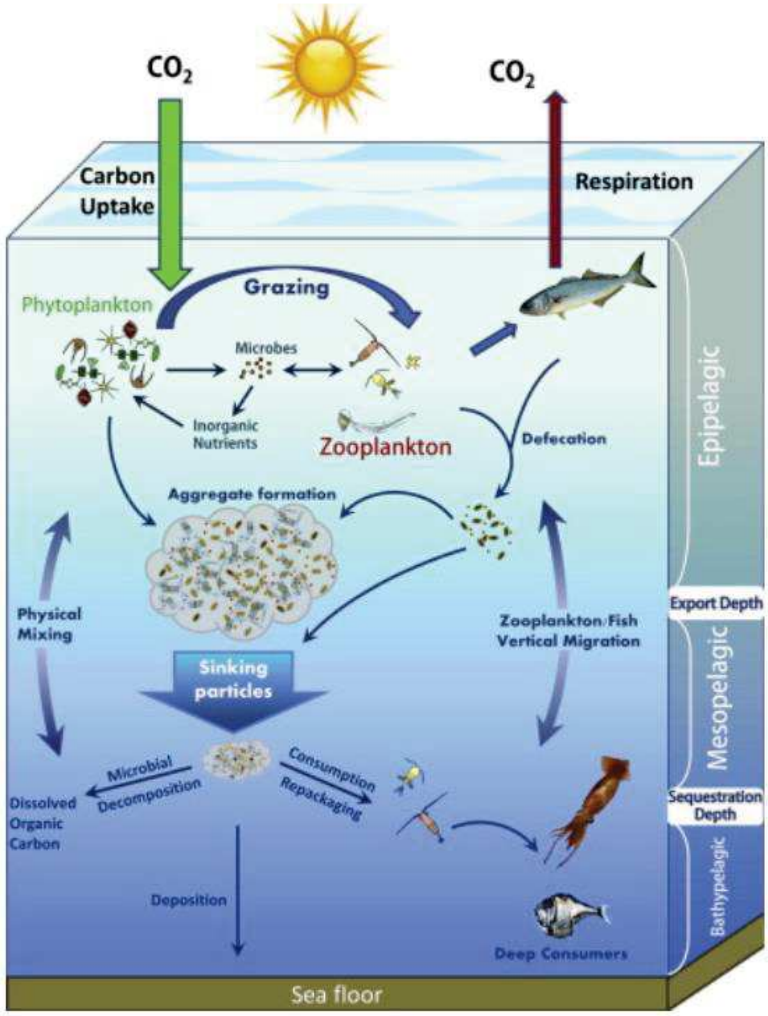

Figure I-3 ***Schéma conceptuel de la pompe à carbone dans les océans issu de Turner, (2015).***

I-1.5 Transfert de matière et d'énergie au sein du compartiment planctonique

Le transfert de l'énergie issu de la photosynthèse phytoplanctonique à l'ensemble de l'écosystème se fait majoritairement de deux façons. La première, principalement issue d'une production par le micro-phytoplancton se fait via le broutage direct du méta-zooplancton, consommé à son tour par les niveaux trophiques supérieurs. C'est ce que l'on appelle communément le réseau trophique classique, herbivore, ou encore la voie autotrophe (Cushing, 1989; Mostajir et al., 2015; Thingstad & Rassoulzadegan, 1999) (Figure I-4). Elle représente une voie de transfert relativement directe et linéaire entre les nutriments et les niveaux trophiques supérieurs. La deuxième, principalement issu d'une production pico et nano-phytoplanctonique, assure le transfert de l'énergie aux niveaux trophiques supérieurs via les protistes hétérotrophes, faisant essentiellement partie du proto-zooplancton : c'est la voie hétérotrophique (Figure I-4). En effet, une partie de la production primaire phytoplanctonique, produite par le nano – et pico - phytoplancton va être broutée par les protistes hétérotrophes, notamment les flagellés et ciliés hétérotrophes, à leur tour consommés par le méta-zooplancton puis les niveaux trophiques supérieurs (Sherr & Sherr, 2002). Une autre partie de la production phytoplanctonique est exsudée, prenant part à la matière organique dissoute et assimilable par les bactéries hétérotrophes, consommées ensuite par les protistes hétérotrophes (Sherr et al., 1988; Weisse, 2002) puis le mésta-zooplancton : c'est la boucle microbienne. Ces deux dernières voies composent le réseau trophique hétérotrophe (Azam et al., 1983; Mostajir et al., 2015). Cette voie de transfert est moins directe et ne suit pas le schéma linéaire classique phytoplancton -> zooplancton -> prédateurs carnivores. Longtemps sous-estimée, la boucle microbienne assurerait le transfert de 10% à 50% de la production primaire aux niveaux trophiques supérieurs (Mostajir et al., 2015), soulignant la très forte non linéarité du transfert de matière depuis le pool de nutriments jusqu'aux niveaux trophiques supérieurs. Il existe un continuum trophique entre ces différentes voies, la voie autotrophe se développant plutôt dans des conditions eutrophes tandis que les systèmes oligotrophiques vont présenter une activité microbienne plus importante (Mostajir et al., 2015).

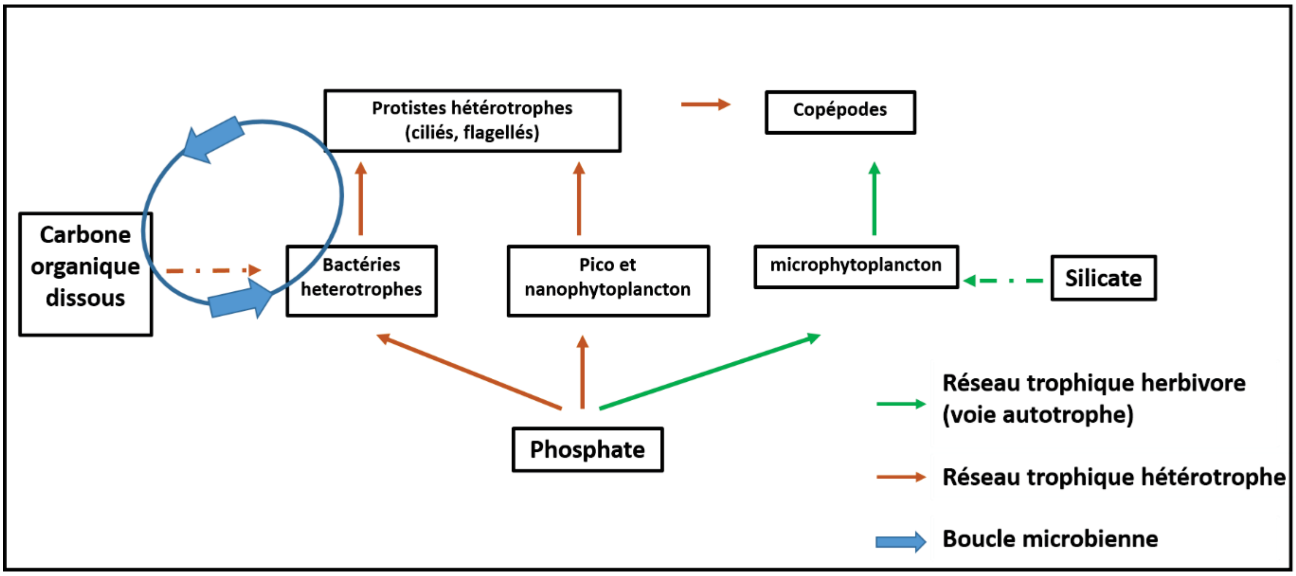

Figure I-4 ***Représentation schématique du réseau trophique autotrophe et hétérotrophe ainsi que la boucle microbienne. Figure modifiée de (Thingstad & Rassoulzadegan, 1999).***

I-1.6 Relation entre le plancton et l'environnement

Le zooplancton est un bon indicateur de changements environnementaux car contrairement à un grand nombre d'autres espèces marines, peu d'espèces de zooplancton sont exploitées commercialement et par conséquent, les changements à long terme sont généralement attribués au changement climatique (bien que d'autres facteurs puissent rentrer également en compte comme la pollution ou bien la relaxation de la prédation due à la pêche ou les prédateurs) (Hays et al., 2005). De plus, la plupart des espèces zooplanctoniques ont une durée de vie courte, la population est donc moins influencée par la persistance des individus des années précédentes ce qui conduit à un couplage étroit entre le changement environnemental et la dynamique du zooplancton. Certains processus comme la diapause peuvent toutefois avoir une importance dans la dynamique planctonique d'une année sur l'autre (Colebrook, 1985; Sommer et al., 2012). Enfin, les réponses non linéaires des communautés biologiques peuvent entrainer des modifications importantes suite à de subtiles changements environnementaux (Hays et al., 2005; Taylor et al., 2002). Ainsi, des variations à plus ou moins long terme ont pu être observées à partir de longues séries temporelles de zooplancton, forcées par différents paramètres environnementaux comme la température, la richesse en nutriments du milieu ou encore les courants marins (Alheit & Niquen, 2004; Atkinson et al., 2004; Skjoldal et al., 1992). On qualifiera de régime shift un changement abrupt dans une communauté (Hays et al., 2005; Scheffer & Carpenter, 2003). De tels changements peuvent avoir lieu en réponse à une modification rapide de l'environnement ou bien à un forçage lent et continu, amenant à un moment le système à un point de bascule (Scheffer & Carpenter, 2003). De plus des phénomènes d'hystérésis existent, pouvant rendre difficile le retour à l'état initial, les conditions forçantes devant être ramenées à des valeurs bien en amont du point de bascule afin de ramener le système dans son état d'origine (Figure I-5).

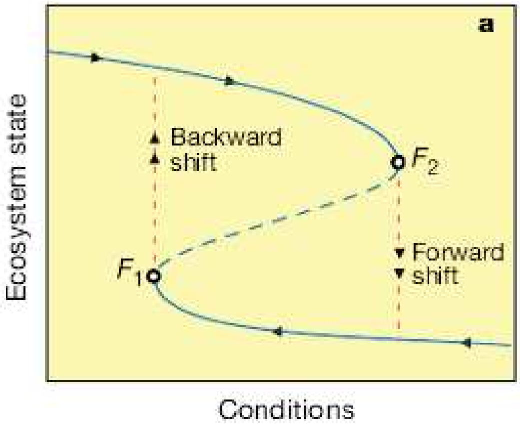

Figure I-5 ***Principe du phénomène d'hystérésis dans un écosystème. Figure issue de Scheffer & Carpenter, (2003). Les conditions forçantes augmentent petit à petit amenant le système à un point de basculement en F2. Pour ramener le système à son état initial, il ne suffit pas de diminuer le forçage pour revenir aux conditions de F2 mais il faut atteindre les conditions en F1.***

I-1.6.1 Les forçages hydrographiques et la production planctonique

Différents forçages hydrographiques peuvent être impliqués dans la dynamique de la production planctonique et en particulier les forçages ayant un impact sur la disponibilité des nutriments. Les processus de brassage de la colonne d'eau par exemple jouent un rôle majeur, aussi bien dans les systèmes côtiers qu'hauturiers. En hiver, la remise en suspension des nutriments des couches profondes vers la couche euphotique sous l'action du vent et du refroidissement des eaux superficielles permet le développement du phytoplancton au printemps (Lavigne et al., 2013; Mann & Lazier, 2013). A certains endroits, ce phénomène de mélange peut devenir très intense et initier des phénomènes de convection profonde jusqu'à plusieurs milliers de mètres de profondeur, remontant ainsi d'importantes quantités de nutriments soutenant une très forte production phyto et zoo-planctonique au printemps (Donoso et al., 2017; Herrmann et al., 2014; Macias et al., 2018a). Dans certains systèmes côtiers, des upwellings entrainent des remontées d'eaux profondes sont également observées sous l'action des vents soufflant parallèlement à la côte, déplaçant les masses d'eau vers le large par le biais du transport d'Ekman (Bakun, 1996; Millot, 1979). Ces upwellings côtiers sont dans certaines régions à la base de la production planctonique soutenant par la même occasion d'importantes pêcheries mondiales (Cury & Shannon, 2004; Van der Lingen et al., 2006). Enfin d'autres processus peuvent impacter la dynamique planctonique comme les fronts thermiques à méso-échelle qui vont pouvoir de par leur aspect convergeant agréger les nutriments et le plancton et créer des zones riches et productives (Bakun, 2006; Nieto et al., 2012; Woodson & Litvin, 2015).

I-1.6.2 Les effets du réchauffement global sur la production planctonique

La température est un paramètre clé dans de nombreux processus biologiques et de ce fait un facteur important de la répartition spatiale des différentes espèces. Ainsi, un des effets déjà observé du réchauffement global est la modification de l'aire de répartition de nombreuses espèces, se déplaçant de plus en plus vers les pôles afin de rester dans des températures favorables à leur développement (Lenoir et al., 2020; Pinsky et al., 2013; Poloczanska et al., 2013). Ce déplacement des individus vers les pôles s'observe aussi bien dans les systèmes terrestres qu'aquatiques et semble plus rapide dans les océans (Lenoir et al., 2020).

Une deuxième conséquence attendue du réchauffement des eaux est une augmentation de la stratification de la colonne d'eau, entrainant une réduction des échanges de nutriments entre les couches profondes et riches et la couche euphotique. Cela aurait pour conséquences une diminution de la production primaire de l'océan global, cet enrichissement par le fond étant nécessaire au développement du phytoplancton qui a besoin à la fois de la lumière et des nutriments pour effectuer la photosynthèse (Bopp et al., 2005; Herrmann et al., 2014). Le réchauffement favorise les plus petites classes de taille du phytoplancton (pico- et nano-phytoplancton) qui possèdent des cinétiques d'assimilation des nutriments plus adaptées à l'oligotrophie au détriment du micro phytoplancton (Falkowski & Oliver, 2007; Herrmann et al., 2014; Winder et al., 2009). Avec la baisse du micro-phytoplancton, le méso-zooplancton ne pouvant brouter le pico et nano-phytoplancton s'orienteraient alors vers les protistes hétérotrophes. Par répercussion top-down, les bactéries hétérotrophes devenant moins prédatées par les protistes hétérotrophes augmenteraient leur activité au sein de la boucle microbienne. Ainsi, comme attendu en cas d'oligotrophisation du milieu, les transferts d'énergie et de matière dans les écosystèmes planctoniques pourraient donc dépendre de plus en plus de la boucle microbienne (Azam et al., 1983; Mostajir et al., 2015).

Enfin, la phénologie du phyto- et zooplancton pourrait être modifiée. En effet, il a déjà été observé un impact de la température sur la dynamique de l'efflorescence printanière de phytoplancton et pic de zooplancton, s'initiant généralement plus tôt lorsque la température augmente (Edwards & Richardson, 2004; Lewandowska & Sommer, 2010). De même, l'amplitude de l'efflorescence de phytoplancton semble dépendre de la température et être moins importante lorsque la température est plus élevée (Henson et al., 2013). Ces différents changements pourraient s'accompagner de modifications dans la communauté phytoplanctonique avec des changements de taille comme expliqué précédemment mais également de composition spécifique (Calbet et al., 2014; Sommer & Lengfellner, 2008; Trombetta et al., 2019). Par répercussion, des changements pourraient s'opérer dans la communauté zoo-planctonique mais également dans l'ensemble du réseau trophique (Sommer & Lengfellner, 2008).

I-1.6.3 Changements stœchiométriques liés à l'acidification des océans

L'acidification des océans, associée à l'augmentation du CO2 dans la colonne d'eau, est soupçonnée de pouvoir modifier les ratios carbone-nutriments (par exemple, C:N, C:P) du phytoplancton (Burkhardt et al., 1999; Schoo et al., 2013; Verschoor et al., 2013). Les changements dans la stœchiométrie élémentaire des producteurs primaires pourraient se traduire par des proies de moins bonne qualité pour les consommateurs herbivores avec une efficacité de transfert trophique réduite (Rossoll et al., 2012; Schoo et al., 2013). Les modifications du contenu biochimique peuvent affecter la reproduction et le développement du zooplancton herbivore par un apport insuffisant de métabolites essentiels, et donc modifier l'efficacité du transfert d'énergie entre les producteurs primaires et les niveaux trophiques supérieurs (Cripps et al., 2016; Rossoll et al., 2012; Schoo et al., 2013).

I-1.6.4 Modification de la circulation marine et atmosphérique à large échelle

Différents forçages hydro-climatiques à large échelle jouent également un rôle important dans la dynamique phyto- et zoo-planctonique tels que la circulation océanique et atmosphérique. En mer du Nord par exemple, un régime shift a été observé dans les communautés pélagiques et notamment le phyto- et zooplancton, induits par une augmentation de température et des vents dominants impactant l'hydrographie au niveau local et les communautés biologiques (Beaugrand, 2004). Dans le courant Humbolt, le phénomène « El Niño Southern Oscillation » (ENSO) joue un rôle important dans la dynamique phyto- et zoo-planctonique, les phases d'eau chaude entraînant une réduction de la production de phyto- et zoo-plancton en raison d'une réduction des remontées de nutriments et, par conséquent, une diminution de la nourriture pour les niveaux trophiques supérieurs (Alheit & Niquen, 2004). Enfin en Méditerranée, différentes études ont montré des relations entre les oscillations Nord-Atlantique (NAO) et la dynamique zoo-planctonique (Fullgrabe et al., 2020; García-Comas et al., 2011;

Vandromme et al., 2011) ainsi que les oscillations méditerranéennes (WeMO) (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012). De manière générale, ces forçages climatiques et océanographiques à large échelle ont été identifiés comme des facteurs clé dans différents écosystèmes de l'hémisphère nord et mis en cause dans de nombreux changements dans les populations (Beaugrand et al., 2015).

I-1.7 La dynamique des poissons petits pélagiques : impact de l'environnement et du plancton

I-1.7.1 Les petits pélagiques dans l'océan mondial

Les poissons petits pélagiques présentent une distribution mondiale et une importance à la fois écologique et économique. Ces espèces sont un maillon central des réseaux trophiques, faisant le lien entre les compartiments phyto- et zoo-planctoniques et les niveaux trophiques supérieurs notamment certaines espèces d'intérêt commercial comme le thon et le merlu (Bănaru et al., 2013; Cury et al., 2000) ou les mammifères et oiseaux marins (Cury et al., 2011). Ils représentent le compartiment le plus pêché au monde, comptabilisant pour 30% des pêcheries mondiales, consommés directement par l'Homme ou utilisés en tant que farine animale pour l'élevage (Tacon & Metian, 2009).

Les populations de petits pélagiques présentent des dynamiques très variables, pouvant présenter des fluctuations de biomasses très importantes, dans des laps de temps courts (Lluch-Belda et al., 1989). Ces fortes variations peuvent avoir des conséquences majeures dans la structure du réseau trophique, impactant à la fois les niveaux trophiques supérieurs dont ils sont les proies et les niveaux trophiques inférieurs sur lesquels ils se nourrissent (Cury et al., 2000).

Trois types de contrôle trophique ont été observés dans les écosystèmes marins régissant la structure des réseaux trophiques (Cury et al., 2000; Fréon et al., 2005). Le premier, le contrôle bottom-up qualifie les systèmes contrôlés par la ressource. Ainsi, des changements s'opérant aux premiers niveaux trophiques (phytoplancton ou zooplancton) vont se répercuter dans le réseau vers les plus hauts niveaux trophiques (Figure I-6a). A l'inverse, les systèmes contrôlés par les prédateurs vont être qualifiés de top-down et des modifications dans les populations de prédateurs vont se répercuter sur les niveaux trophiques inférieurs (Figure I-6b). Finalement, un troisième type de contrôle a été décrit dans les systèmes à upwelling où des forçages externes peuvent impacter un groupe central dans le réseau tel que les poissons petits pélagiques avec des répercussions à la fois top-down vers les niveaux inférieurs et des contrôles bottom-up vers les niveaux supérieurs. On parle alors de contrôle wasp-waist (Figure I-6c).

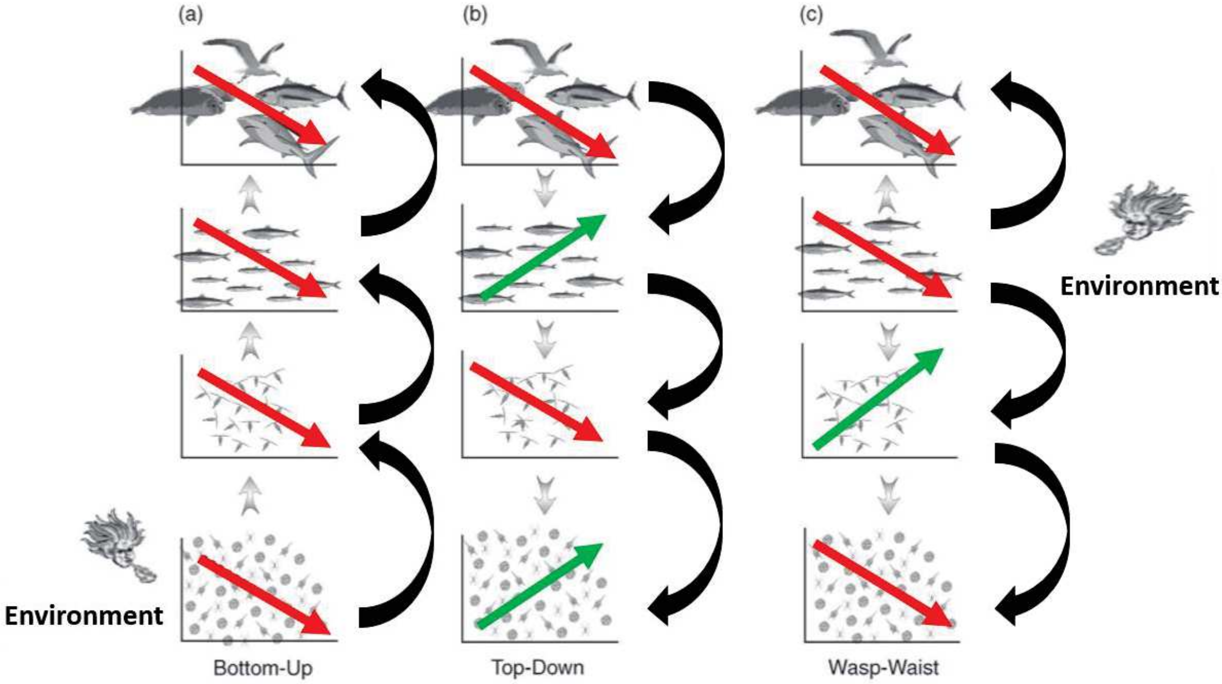

Figure I-6 ***Représentation des processus de contrôle bottom-up, top-down et wasp-waist dans les écosystèmes marins, modifiée de Fréon et al., (2005). Dans l'exemple bottom-up, l'environnement physique, induit une baisse de l'abondance du phytoplancton, qui à son tour a un impact négatif sur l'abondance du zooplancton. La diminution de l'abondance du zooplancton induit alors une baisse de l'abondance des poissons petits pélagiques planctonophages, ce qui entraîne une diminution de l'abondance des top-prédateurs. Pour le contrôle top-down, une baisse de l'abondance des top prédateurs induit une diminution de la prédation sur les petits pélagiques et une augmentation de leur abondance. Cette augmentation d'abondance entraine une augmentation de la pression de prédation sur le zooplancton qui diminue, entrainant une diminution du broutage et une augmentation de l'abondance de phytoplancton. Finalement, lors du contrôle wasp-waist, un forçage externe impacte le compartiment des petits pélagiques, en général par le biais du recrutement, sans impacter les autres compartiments du réseau. La baisse d'abondance des petits pélagiques entraine alors une baisse de l'abondance des prédateurs et dans le même temps une augmentation du zooplancton par diminution de la prédation. L'augmentation du zooplancton entraine alors une augmentation du broutage sur le phytoplancton et une baisse de l'abondance phytoplanctonique.***

I-1.7.2 Importance du recrutement

Les petits pélagiques présentent une stratégie « fast » (Sih, 1987), caractérisée par un cycle de vie court et la production d'un grand nombre d'œufs, tôt dans le cycle de vie. Le recrutement joue un rôle essentiel dans la dynamique des populations de petits pélagiques et entraine, selon son efficacité, de fortes fluctuations dans la population. Celui-ci est principalement déterminé par la survie des larves et juvéniles, dépendant fortement de la disponibilité et qualité des ressources. Hjort, (1914) a été un des premiers à montrer l'importance du plancton dans la dynamique des petits pélagiques, notamment dans les premiers stades de vie avec l'hypothèse de la « période critique » qui stipule que le recrutement est très dépendant des premiers stades de vie des individus. Cushing, (1990) s'inspirera plus tard de ses travaux pour proposer l'hypothèse du match-mismatch (Figure I-7). Cette hypothèse stipule qu'une synchronie est nécessaire entre la disponibilité du plancton dans le milieu et la production de larves, avec l'idée que la phénologie de la production planctonique est supposée plus variable (car très influencée par la variabilité environnementale) que celle de la reproduction des poissons. Sans cette synchronie, les larves ne peuvent se développer et un mauvais recrutement s'opère. Bakun, (1997) proposera un peu plus tard le principe de la « triade » reposant sur 3 points essentiels au bon recrutement des populations. Le premier est la nécessité d'avoir un processus d'enrichissement du milieu permettant une bonne production planctonique et la présence de nourriture pour les larves. Le deuxième point est la nécessité d'un processus de concentration afin de rassembler et maintenir cette production planctonique et enfin un processus de rétention des larves dans la zone de concentration, favorable à leur développement.

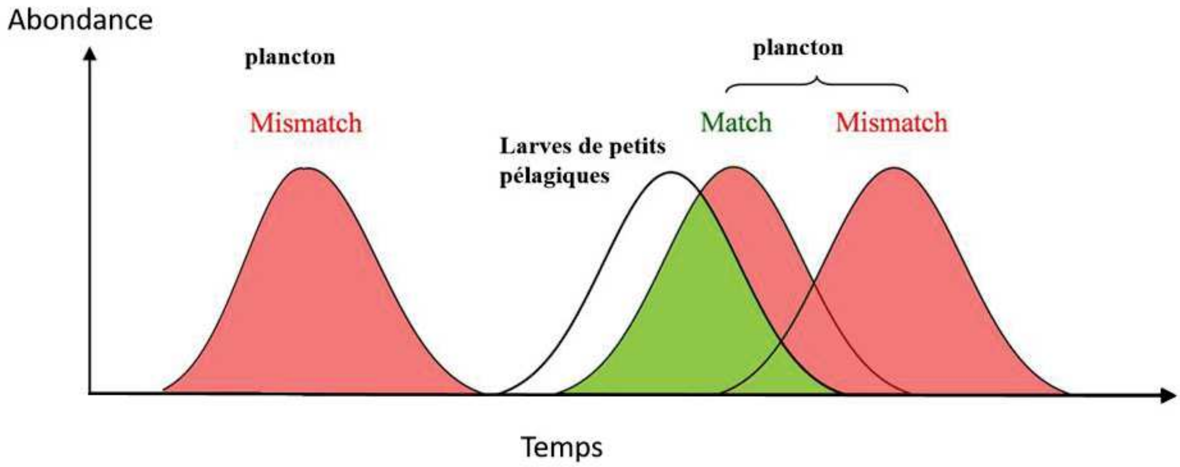

Figure I-7 ***Principe du phénomène de match-mismatch entre le plancton, et les larves de poissons, modifié de Cushing, (1990). Si le pic de plancton arrive trop en avance ou en retard par rapport à l'arrivée des larves, il n'y a pas assez de nourriture pour soutenir leur développement et un mauvais recrutement s'opère. A l'inverse, si la synchronie est bonne entre les larves et le plancton, les larves peuvent se développer correctement et le recrutement est bon.***

I-1.7.3 Régime shift dans les populations de petits pélagiques et poissons planctonophages en lien avec le plancton

Le recrutement étant un facteur clé de la dynamique des populations de petits pélagiques et directement lié à la communauté planctonique, des modifications dans la dynamique de la communauté planctonique peuvent avoir des effets considérables sur les populations de petits pélagiques. Beaugrand et al., (2003) ont montré en Mer du Nord que des changements environnementaux ont entrainés des modifications dans la composition planctonique d'été avec un impact fort sur le développement des larves de morue. En effet, la phénologie de différentes espèces planctoniques a été modifiée avec notamment le pic de petits copépodes printaniers retardé à l'été, entrainant une réduction de la taille des proies disponibles pour les poissons juvéniles et une baisse de la biomasse du stock. De tels changements en réponse aux changements climatiques s'observent dans la communauté planctonique mais également à d'autres niveaux trophiques avec des effets variables pouvant entrainer des phénomènes de mismatch. Toujours en mer du Nord, Edwards & Richardson, (2004) ont montré que l'augmentation de la température a entrainé une avancée de l'efflorescence printanière dans certains groupes de phytoplancton ainsi que du pic d'abondance de différents groupes de zooplancton mais de façons différentes. En effet, alors que les diatomées n'ont subi aucun changement, le pic de dinoflagellés a été avancé de 23 jours tandis que celui des copépodes de seulement 10 jours. Enfin, celui de certaines larves de poissons a quant à lui été avancé de 27 jours. Ces différences d'intensité dans la modification de la phénologie des différents niveaux trophiques a ainsi entrainé un phénomène de mis-match au sein du réseau trophique (Edwards & Richardson, 2004). Cependant, les changements de phénologie ne sont pas toujours négatifs et peuvent parfois être bénéfiques pour les populations de petits pélagiques. C'est par exemple le cas en mer du Japon où un retard de l'efflorescence printanière, due à un retard en hiver des températures minimales, a permis d'augmenter la période de co-présence des larves de sardines et de leurs proies, favorisant leur développement (Kodama et al., 2018).

Finalement, si le timing entre la production planctonique et la présence des larves de poisson est importante pour maintenir la population, la composition de la communauté planctonique est également importante et peut avoir un impact sur la dynamique des individus adultes. En effet, il a été montré dans différents systèmes à upwelling que sardines et anchois présentaient des différences dans leur alimentation et notamment au niveau de la taille de leurs proies, la sardine étant plus efficace pour filtrer de petits individus alors que l'anchois est plus efficace pour chasser les plus gros copépodes (Tam et al., 2008; Van der Lingen, 2002; Van der Lingen et al., 2006). Ainsi, dans l'upwelling du Benguela par exemple, Van der Lingen et al., (2006) ont montré que les périodes de forte activité d'upwelling étaient plutôt dominées par des diatomées, conduisant à des copépodes de plus grandes tailles et favorisant la population d'anchois. A l'inverse, les périodes de faible activité d'upwelling étaient dominées par des flagellés de plus petite taille, conduisant à de petits copépodes et favorisant la population de sardines (Figure I-8). Des chaines planctoniques similaires ont été observées dans le courant de Humbolt, amenant également à des dynamiques différentes entre anchois et sardines (Tam et al., 2008). Par le biais de ces différents exemples, on peut voir que les populations de petits pélagiques peuvent être très variables souvent en réponse à des changements dans la communauté planctonique induits par différents processus environnementaux.

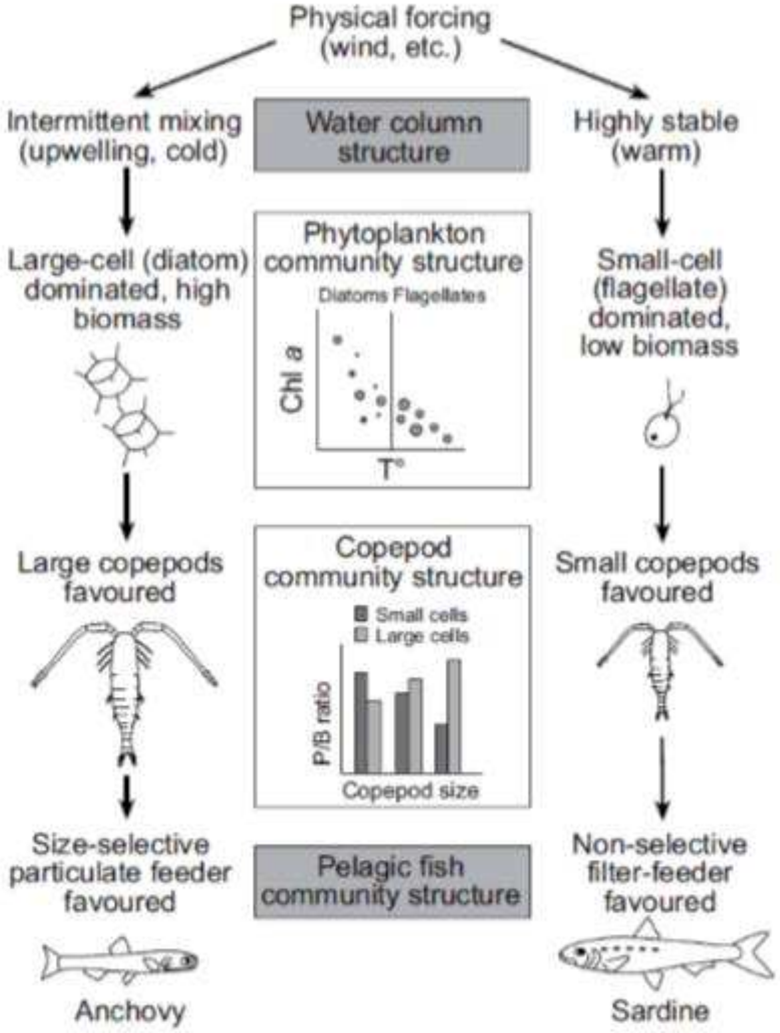

Figure I-8 ***Schéma conceptuel du principe d'alternance de chaines planctoniques dominées par des diatomées et gros copépodes en périodes de fort upwelling favorisant la population d'anchois (à gauche) et des chaines dominées par les flagellés et petits copépodes en période de faible mélange favorisant les sardines (à droite) issu de Van der Lingen et al., (2006).***

I-2 Les petits pélagiques dans le Golfe du Lion, une situation inédite

I-2.1 Le Golfe du Lion : Généralités

Le Golfe du Lion est situé en mer Méditerranée Nord Occidentale, délimité à l'Ouest par la frontière entre la France et l'Espagne et à l'Est par les canyons au large de Marseille. Il couvre une superficie d'environ 15000 km², s'étalant de la côte jusqu'à l'isobath 2500m (Mellon-Duval et al., 2017). Il est caractérisé par la présence d'un plateau continental se terminant aux alentours de l'isobath 200m. Comparé au reste de la Méditerranée, considérée comme oligotrophe, le Golfe du Lion est une région productive (Millot, 1990; Petrenko et al., 2005). La production du plateau est soutenue en premier lieu par d'importants apports nutritifs provenant du Rhône et diverses processus physiques comme les upwellings côtiers locaux (Lefevre et al., 1997; Millot, 1990,1999; Palomera et al., 2007). Au large, se trouve une importante cellule de convection hivernale pouvant, sous certaines conditions (forts vents associés à des conditions froides et sèches), induire un mélange de la colonne d'eau jusqu'à 2000m entrainant une remise en suspension de grandes quantités de nutriments dans la couche euphotique et favorisant le développement de fortes efflorescences printanières (Herrmann et al., 2017).

I-2.2 La crise des petits pélagiques

Au cours des deux dernières décennies, les débarquements des petits pélagiques ont drastiquement diminué, passant de 14 000t en 1993 à moins de 1000t ces dernières années pour la sardine (Figure I-9) (Saraux et al., 2019). De façon surprenante, cette diminution des débarquements n'était pas liée à une raréfaction des individus, les abondances étant restées à des niveaux similaires voire légèrement supérieurs (Figure I-9) (Saraux et al., 2019; Van Beveren et al., 2014). Il s'agit plutôt d'une conséquence de la diminution de la taille et condition corporelle relative (Krel) des poissons depuis 2008, les rendant moins intéressants économiquement car plus difficiles à vendre (Figure I-10). S'en est suivi un désintéressement des pêcheurs pour ces espèces pélagiques, préférant se tourner vers des espèces démersales économiquement plus intéressantes telles que le merlu (GFCM, 2016). Cette diminution de la taille moyenne des individus a essentiellement été induite par une combinaison de deux facteurs, une baisse de la croissance des individus et une disparition des plus vieux et plus gros individus (Saraux et al., 2019; Van Beveren et al., 2014). Cette situation dans le Golfe du Lion est inédite par le fait que ces différents changements dans la population ne sont pas liés à une diminution du recrutement comme c'est généralement le cas dans les grandes populations des systèmes à upwelling, ce dernier étant resté à des valeurs élevées depuis 2008 (Saraux et al., 2019).

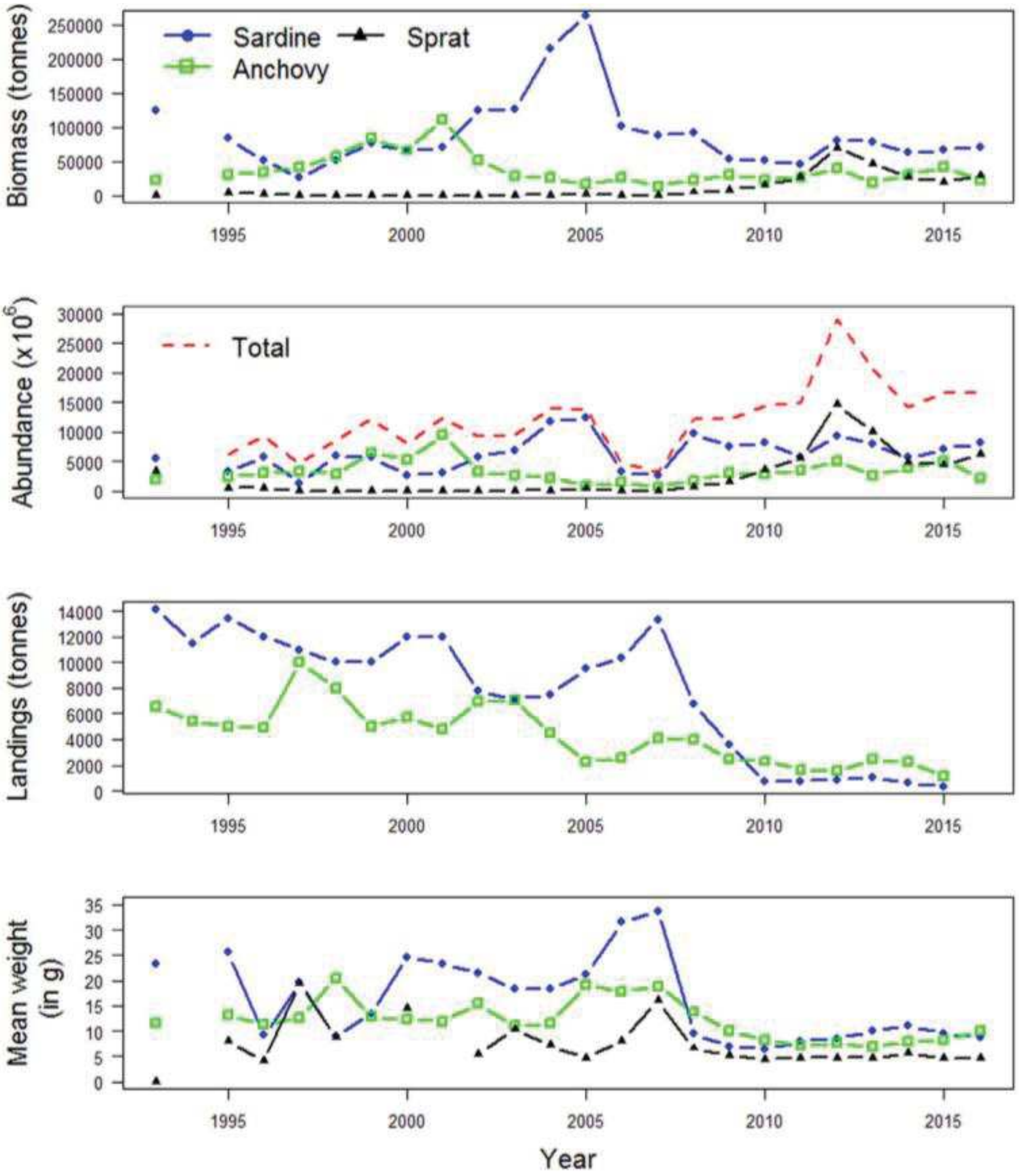

Figure I-9 *Variabilité de la biomasse, abondance, débarquement et poids moyen de l'anchois, sardine et sprat dans le golfe du Lion entre 1993 et 2016. Figure issue de Saraux et al., (2019).*

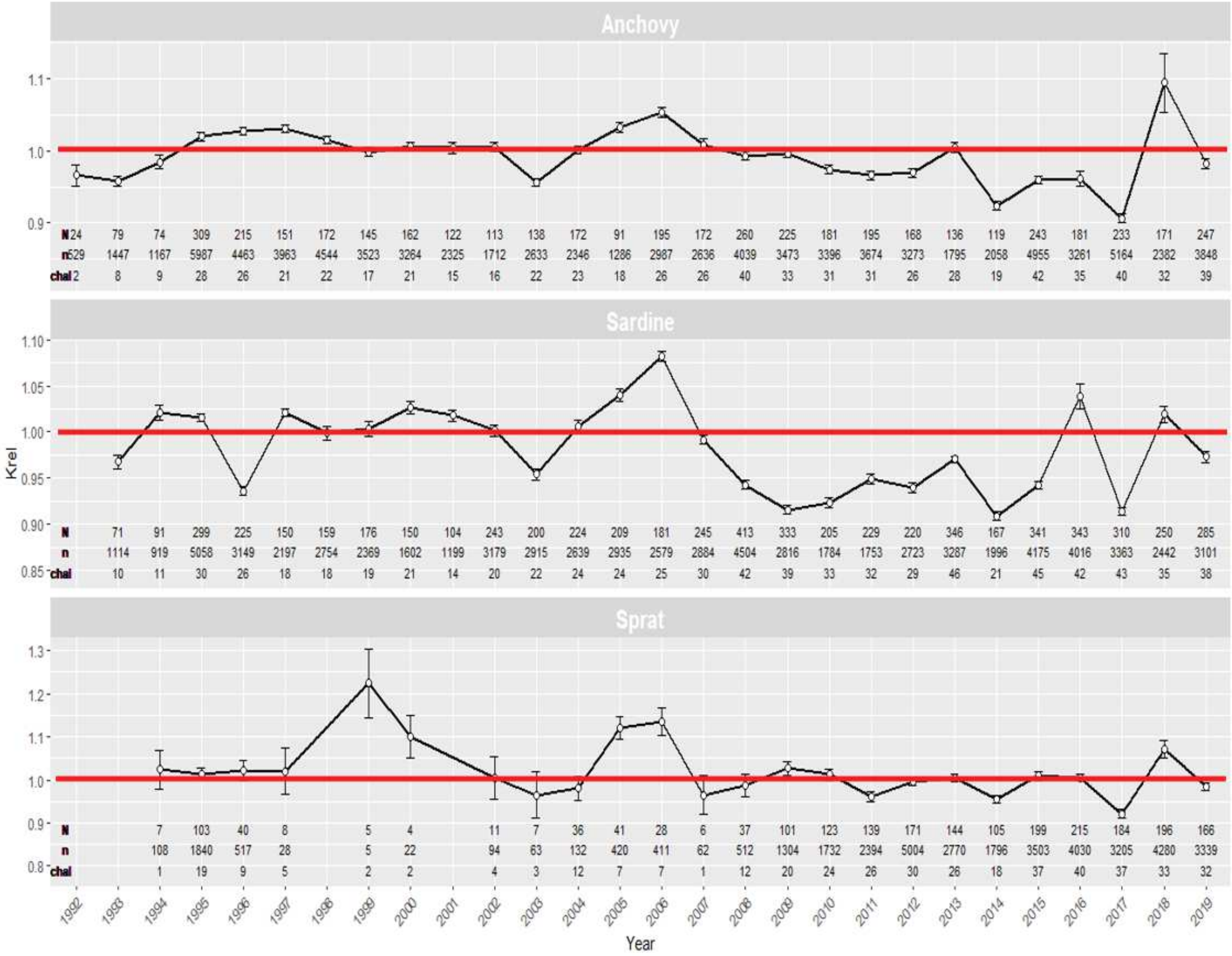

Figure I-10 ***Variation de l'indice de condition corporelle relative (Krel) entre 1992 et 2019 dans le Golfe du Lion en Juillet pour l'anchois, la sardine et le sprat. Figure issue de Van Beveren et al., (2014) actualisée. La barre horizontale rouge indique une condition corporelle relative de 1. N indique le nombre de classes de tailles considérées en considérant tous les chaluts et n le nombre total de poissons considérés. Chal indique le nombre total de chaluts utilisés.***

Différentes hypothèses ont alors été mises en avant et testées afin d'essayer d'expliquer le mauvais état des populations de petits pélagiques dans le Golfe du Lion. En premier lieu l'impact de la pêche a été évalué, la pêche pouvant impacter la structure de la communauté. En effet, les plus gros individus étant plus intéressants économiquement, les pêcheries vont avoir tendance à cibler les plus grandes classes de taille afin de maximiser leurs profits (Daan et al., 2005; Law, 2000). Le taux d'exploitation par la pêche s'est finalement révélé assez faible dans le Golfe du Lion, aussi bien pour la sardine que l'anchois, représentant en moyenne 1% de la population au cours de la dernière décennie et le niveau des captures se retrouvant inférieur à celui observé depuis le début des années 1900s (Saraux et al., 2019; Van

Beveren et al., 2016a). Pour autant, bien que la pêche ait été très faible ces dernières années, la population n'est pas revenue à son état d'avant 2008, écartant la surpêche des causes possibles du déclin des populations de petits pélagiques du Golfe du Lion. De la même façon, la population croissante de thons (*Thunnus thynnus*) dans le golfe, se nourrissant essentiellement de petits pélagiques (Van Beveren et al., 2017) a été considérée comme facteur potentiel de la disparition des adultes. Des travaux de modélisation basés sur les densités estimées de thons par survols aériens dans la zone et de leurs besoins énergétiques ont cependant estimé leur taux de prédation sur les populations de petits pélagiques à moins de 2% de la population totale, sans sélection sur la taille de leurs proies (Van Beveren et al., 2017). De façon similaire, Queiros et al., (2018) ont estimé la pression de prédation des deux principales espèces de dauphins dans le golfe, *Tursiops truncatus* et *Stenella coeruleoalba* à moins de 0.1% écartant également l'hypothèse de surmortalité des petits pélagiques par la prédation des prédateurs supérieurs.

Une autre hypothèse regardée a été la potentielle migration des gros individus vers une zone potentiellement plus propice. Au regard de la géographie de la zone et la présence du courant nord longeant le plateau continental d'Est en Ouest, il a été suggéré que la migration se serait faite vers l'Espagne, la zone Ligure à l'Est étant de surcroit plus oligotrophe et donc potentiellement moins favorable (d'Ortenzio & Ribera d'Alcalà, 2009). De façon surprenante, la distribution en taille des populations en Espagne s'est trouvée similaire à celle observée dans le Golfe du Lion avec également une disparition des plus grandes classes de taille (Saraux et al., 2019). L'hypothèse de migration a donc de ce fait également été écartée des causes possibles. Une dernière hypothèse écartée a été une éventuelle surmortalité des individus liés à des pathogènes comme cela a déjà été observé avec un herpes virus en Australie (Van Beveren et al., 2016b; Whittington et al., 1997). En effet, aucun virus ou bactérie n'a été détecté chez les petits pélagiques dans le golfe du Lion et aucunes traces de lésions des tissus ou de maladie n'a été observé (Van Beveren et al., 2016b).

Finalement, l'hypothèse du contrôle bottom-up semble être la plus probable, l'idée étant que des changements dans la communauté planctonique en terme d'abondance ou de composition seraient à la base des changements de taille et condition observés dans les communautés de petits pélagiques. En effet, des analyses préliminaires sur des contenus stomacaux d'anchois et de sardines avant et après la baisse de condition ont révélé un potentiel changement d'alimentation avec une importance plus forte de petites proies après la baisse de condition comparé à avant (Brosset et al., 2016a). Pour la sardine par exemple, les cladocères supérieurs à 1mm présentaient une part importante des proies et ont été remplacées après 2007 par de petits copépodes comme les *Microsetella* et *Oncaea*. De même pour l'anchois dont le régime était dominé par de gros copépodes avant 2007 comme les *Clausocalanidae* et remplacés après par les *Microsetella* et *Oncaea*, inférieurs à 1mm (Brosset et al., 2016a). Ce changement de taille dans les proies des poissons petits pélagiques pourrait être une des causes de la baisse de condition des poissons, les individus petits présentant une densité énergétique plus faible (Barroeta et al., 2017; Zarubin et al., 2014). De plus, des expérimentations menées en bassin ont montré l'importance de la taille de la nourriture indépendamment de la densité énergétique. En effet, des sardines nourries avec des granulés de petite taille présentaient une condition corporelle moins bonne que celles nourries avec la même masse de granulés de plus grosse taille et de densité énergétique identique (Queiros et al., 2019). Si un tel changement dans le régime alimentaire pourrait expliquer la baisse de condition des poissons, aucune étude n'a montré à ce jour de changements dans la communauté planctonique du Golfe du Lion pouvant supporter cette hypothèse. De façon générale, les données de plancton sont assez rares dans le Golfe du Lion comparé à d'autres zones de méditerranée Nord-Ouest où différentes séries à long terme sont disponibles (voir Figure I-11). Dans le Golfe du Lion, la seule source actuelle de données de plancton disponible sur plusieurs années est la campagne océanographique PELMED (PELagiques MEDiterranée) qui a lieu tous les ans en été depuis 1993. Le but de cette campagne est avant tout d'évaluer chaque année l'état des stocks de poissons petits pélagiques, cependant des prélèvements de plancton ont également été effectués certaines années (1995-1996, 2007-2008 et depuis 2013) afin d'avoir une vision plus globale du système du Golfe du Lion.

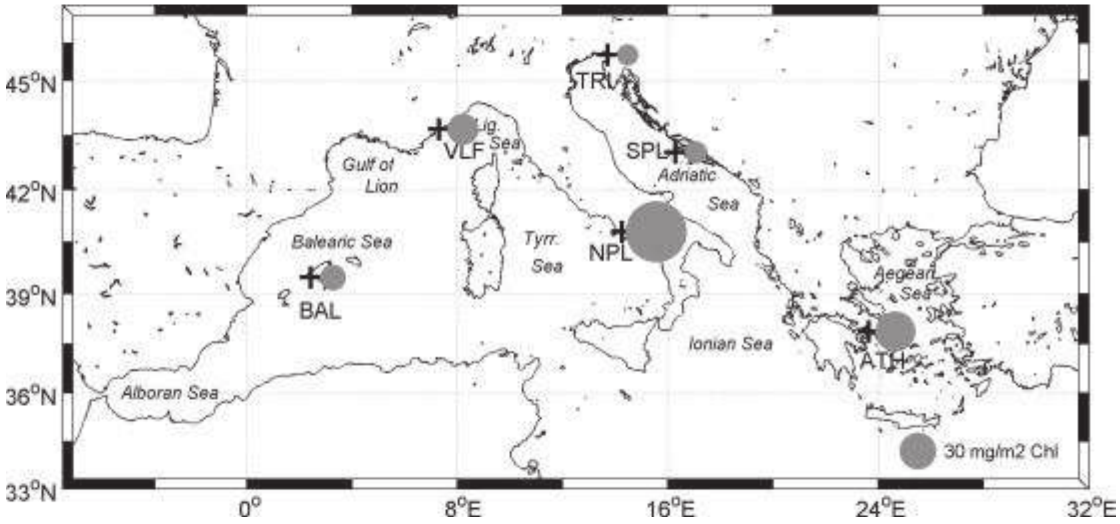

Figure I-11 ***Répartition des différentes séries à long terme de zooplancton en méditerranée issue de Berline et al., (2012). Les croix noires représentent la position des séries et les cercles la concentration moyenne en chlorophylle-a de la station prélevée.***

I-3 Etat de l'art sur la dynamique du plancton en Méditerranée Nord-Ouest

La mer Méditerranée est une mer relativement oligotrophe mais présente de grandes disparités géographiques en terme de production planctonique, aussi bien d'un point de vue quantitatif que de la dynamique saisonnière et des processus sous-jacents (d'Ortenzio & Ribera d'Alcalà, 2009; Siokou-Frangou et al., 2010). Ainsi, les zones côtières, fortement soumises à l'impact anthropique et aux apports terrigènes présentent des concentrations relativement élevées comparé aux autres zones (Berline et al., 2012; d'Ortenzio & Ribera d'Alcalà, 2009; Siokou-Frangou et al., 2010) (Figure I-12a). De même, la mer d'Alboran à l'Ouest présentant des échanges avec les eaux d'Atlantique par le Détroit de Gibraltar ainsi que des upwelling côtiers présente également des concentrations de chlorophylle plus importantes (d'Ortenzio & Ribera d'Alcalà, 2009; Mercado et al., 2007). Enfin, la mer Méditerranée est une des rares mers excepté aux pôles où une zone de convection hivernale profonde est présente, soutenant une production planctonique assez importante dans l'océan ouvert avec de fortes efflorescences printanières (Donoso et al., 2017; Herrmann et al., 2014; Macias et al., 2018a). En plus de ces niveaux de production très différents, la dynamique planctonique varie également assez fortement d'une zone à une autre ce qui a conduit à la distinction de différentes bio-régions, essentiellement basées sur les caractéristiques des efflorescences printanières (d'Ortenzio & Ribera d'Alcalà, 2009) (Figure I-12b).

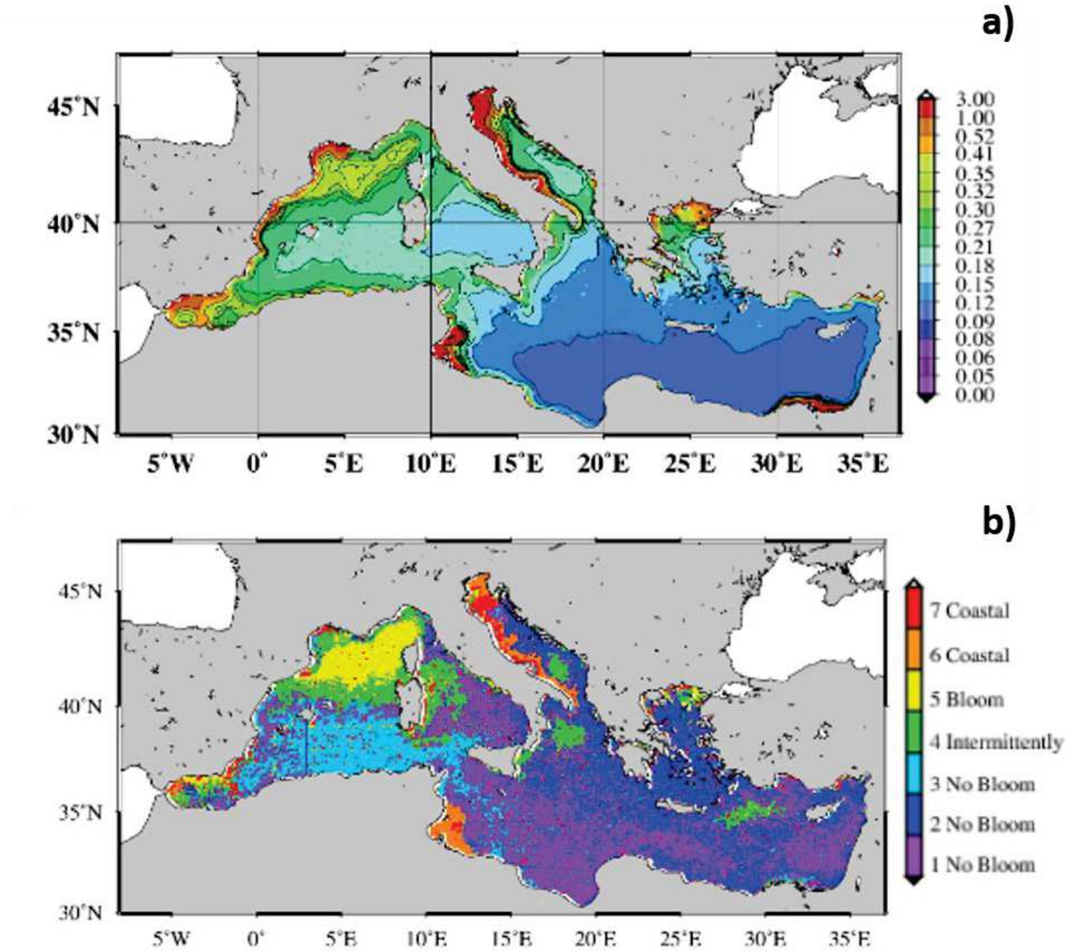

Figure I-12 ***Répartition de la concentration en chlorophylle satellitaire en méditerranée (a) et distribution des bio-régions méditerranéennes (b) issue de (d'Ortenzio & Ribera d'Alcalà, 2009).***

I-3.1 La dynamique à long terme du phytoplancton en Méditerranée nord-ouest

La dynamique à long terme du phytoplancton a été étudiée dans différentes zones de Méditerranée nord-ouest, par le biais de la chlorophylle satellitaire (Mayot et al., 2017; Salgado-Hernanz et al., 2019) ainsi que par prélèvements in situ (d'Alcalà et al., 2004; Fullgrabe et al., 2020; Zingone et al., 2019). La concentration en chlorophylle satellitaire en Méditerranée nord-ouest semble montrer une légère tendance positive à long terme entre les années 1998 et 2014, en particulier dans la partie nord de la mer d'Alboran et au niveau de la zone de convection du Golfe du Lion (Salgado-Hernanz et al., 2019). A l'inverse, le plateau du Golfe du Lion apparait comme une des rares régions de Méditerranée nord-ouest avec une tendance décroissante de concentration en chlorophylle sur cette période (Salgado-Hernanz et al., 2019). Des séries de prélèvements in situ présentent toutefois des variabilités différentes de celles observées par satellite, par exemple en mer d'Alboran où une décroissance du phytoplancton est observée in situ, probablement liée à des différences de dynamiques observées entre le phytoplancton de surface et en profondeur (García-Martínez et al., 2019). Différents processus vont être impliqués dans la dynamique phytoplanctonique notamment entre la côte et le large. Ainsi les zones côtières vont fortement dépendre des échanges avec le milieu terrestre, notamment par les apports des fleuves qui peuvent supporter une grande part de la production comme dans le Golfe du Lion où 50% de la production primaire est estimée être associée aux apports du Rhône (Lefevre et al., 1997; Macias et al., 2018). D'autres processus côtiers comme les upwellings vont également jouer un rôle important à certains endroits en remontant, parfois localement, des nutriments des couches inférieures sous l'action du vent (Mercado et al., 2007; Millot, 1979, 1990). Dans l'océan ouvert, les processus majeurs semblent être l'intensité des mélanges de la colonne d'eau en hiver, en particulier par le biais des processus de convection profonde (Donoso et al., 2017; Herrmann et al., 2014; Macias et al., 2018a). Concernant la variabilité de la taille du phytoplancton, quelques études à partir de séries de prélèvements in situ ont pu mettre en évidence une réduction de la taille des cellules au cours du temps (Ribera d'Alcalà et al., 2004) ou suggéré une diminution de la taille en lien avec une réduction de la densité de diatomées (García-Martínez et al., 2019). L'augmentation de la température induisant une stratification de la colonne d'eau est supposée être un facteur important régissant la taille du phytoplancton car limitant l'apport de nutriments à la surface et favorisant les petites cellules phyto-planctoniques plus compétitives dans un milieu oligotrophe (García-Martínez et al., 2019; Herrmann et al., 2014).

I-3.2 La dynamique à long terme du zooplancton en Méditerranée nord-ouest

La dynamique à long terme du zooplancton a été étudiée dans différentes zones de Méditerranée nord-ouest, essentiellement en mer d'Alboran, en mer Baléares, en mer Ligure, dans le Golfe de Naples, dans le Golfe de Trieste ainsi qu'en baie de Calvi (Berline et al., 2012; Fullgrabe et al., 2020). La majorité des prélèvements à long terme sont effectués avec des filets de 200 ou 300µm de vide de maille ciblant ainsi majoritairement le méso-zooplancton (Berline et al., 2012; Fullgrabe et al., 2020). La plus ancienne série de Méditerranée est celle prélevée à la station du point B située à l'entrée de la rade de Villefranche-sur-Mer, commencée en 1966 et toujours d'actualité. Sa longueur a permis d'étudier la variabilité à long terme de la communauté zoo-planctonique et de mettre en évidence différents forçages climatiques. Ainsi, Molinero et al., (2005) ont étudié l'abondance de plusieurs espèces cibles de zooplancton de 1967 à 1993 au point B et proposé une cascade de relations entre le schéma climatique à grande échelle qui se produit dans l'Atlantique Nord (associé à l'indice climatique NAO) et la variabilité climatique locale pour expliquer la variabilité de la communauté. D'autres recherches sur la même série zoo-planctonique à long terme, comparées avec d'autres séries à long terme, ont suggéré qu'un changement de régime avait eu lieu en 1987 dans la mer Ligure et de façon plus globale dans différents bassins de l'hémisphère nord (Beaugrand et al., 2015; Conversi et al., 2010; Molinero et al., 2008). Selon les auteurs, l'augmentation de la température ainsi que les régimes de circulation hydrographiques et atmosphériques à large échelle ont été désignés comme les principaux facteurs régissant la composition du zooplancton. En complétant la série temporelle du point B jusqu'en 2005, García-Comas et al., (2011) et Vandromme et al., (2011) ont mis en évidence une périodicité quasi décennale dans les fluctuations de la communauté zoo-planctonique et ont proposé le forçage physique hivernal sur la production primaire comme le facteur principal à l'origine des changements dans les densités de zooplancton. Pendant les années sèches et froides, la couche de mélange plus profonde apporterait une importante quantité de nutriments dans la couche de surface et, par conséquent, stimulerait la production primaire bénéfique pour le zooplancton. En revanche, pendant les années humides et chaudes, moins de nutriments seraient mélangés dans la couche de surface réduisant la production primaire et la dynamique zoo-planctonique (Auger et al., 2014). A partir d'une série plus courte en baie de Calvi entre 2004 et 2016, Fullgrabe et al., (2020) ont également suggéré l'importance des conditions climatiques hivernales sur la dynamique du pic printanier de zooplancton. La dynamique cyclique de la communauté est également suggérée avec des densités de copépodes plus faibles sur la période 2011-2016 comparée à la période 2004-2010 sans pouvoir l'affirmer du fait du faible nombre d'années considérées. Une relation avec l'indice NAO est également mise en évidence dans cette zone ainsi qu'en mer Baléares entre les années 1994 et 2003 (Fernández de Puelles & Molinero, 2007; Fernández de Puelles et al., 2004). Cette relation avec le NAO semble toutefois varier dans le temps comme suggéré par Berline et al., (2012) qui n'ont pas trouvé de relation avec le NAO pour 6 séries méditerranéennes de zooplancton dont le point B en mer Ligure et la série en mer Baléares. Concernant les années récentes, les analyses n'ont pas été encore prolongées pour toutes les séries disponibles, dont le point B, mais il a été observé à plusieurs endroits en Méditerranée nord-ouest une diminution des densités de copépodes, notamment en baie de Calvi et en mer d'Alboran (Fullgrabe et al., 2020; García-Martínez et al., 2019). De nombreuses connaissances sont ainsi disponibles concernant la dynamique à long terme de la densité de zooplancton en Méditerranée nord-ouest, en revanche, très peu d'études portent sur la variabilité de la taille du zooplancton dans le temps. Romagnan et al., (2016) ont ainsi regardé la variabilité saisonnière du spectre de taille des copépodes sur une année en mer Ligure et Zhou et al., (2010) ont regardé la variabilité du spectre de taille des copépodes sur 2 années dans le Golfe du Lion. Aucune information n'est cependant disponible sur la variabilité à long terme de la taille du zooplancton en Méditerranée nord-ouest.

I-4 Objectifs de la thèse

L'objectif principal de cette thèse est donc d'étudier plus en détail la variabilité spatio-temporelle de la communauté planctonique dans le Golfe du Lion, peu étudiée jusqu'à maintenant, afin d'identifier d'éventuels changements pouvant supporter l'hypothèse du contrôle bottom-up sur les populations de petits pélagiques. Le corps de ce manuscrit s'articule ainsi autour de 3 études. Ne disposant pas de données de plancton continues sur le long terme dans le Golfe du Lion, nous nous sommes intéressés dans un premier temps à la variabilité environnementale dans le Golfe du Lion au cours des 20 dernières années. Le premier objectif était de voir si des changements susceptibles d'impacter la production planctonique ont eu lieu au niveau environnemental dans le Golfe du Lion au cours des deux dernières décennies. Pour cela, différents processus physiques et environnementaux connus comme pouvant impacter la production planctonique ont été regardés, tels que les upwellings côtiers, le débit et apports en nutriments du Rhône, la température, la stratification ou encore les fronts thermiques ainsi que la chlorophylle satellitaire comme proxy de la biomasse phytoplanctonique. Un deuxième objectif était de quantifier l'importance de ces différentes variables dans la production planctonique du Golfe du Lion afin de définir celles pouvant avoir potentiellement un impact fort sur la dynamique planctonique. Finalement, le dernier objectif était d'identifier d'éventuelles co-variations entre ces différents processus environnementaux et les données de biomasse, taille, abondance et condition des petits pélagiques issues des campagnes océanographiques PELMED. Ces différentes analyses ont permis d'avoir une idée de la variabilité de la productivité du Golfe du Lion au cours des deux dernières décennies, en lien avec les différents paramètres environnementaux, et des effets potentiels sur la dynamique des populations de petits pélagiques.

Dans la deuxième étude nous nous sommes intéressés plus en détail sur la composition de la communauté phyto- et zoo-planctonique en été dans le Golfe du Lion à partir des données issues des campagnes PELMED. Le premier objectif était de caractériser la composition de la communauté phyto- et zoo-planctonique en été dans le Golfe du Lion en lien avec l'environnement. Ainsi, en se basant sur les données de 11 années pour le zooplancton et 8 pour le phytoplancton, échantillonnées au cours des 2 dernières décennies, différentes communautés zoo et phyto-planctoniques ont été caractérisées, et les relations avec différentes variables environnementales ont été regardées. Un deuxième objectif était de mettre en évidence de potentielles associations entre la communauté phyto- et zoo-planctonique. Les alternances de différents groupes de phytoplancton, notamment les diatomées et dinoflagellés, sont connues dans les systèmes à upwelling comme étant induites par des changements environnementaux et affectant la dynamique zoo-planctonique et par conséquent les populations de petits pélagiques (Tam et al., 2008; Van der Lingen et al., 2006). De potentielles associations entre phytoplancton et zooplancton, ont donc également été étudiées dans le Golfe du Lion afin de déterminer si de tels processus pouvaient avoir lieu. Enfin, un troisième objectif était de voir si une relation pouvait être établie entre la composition de la communauté zoo-planctonique et la condition des petits pélagiques. Pour cela, les principaux groupes zoo-planctoniques associés aux bonnes et mauvaises conditions des poissons ont été examinés afin de mieux comprendre si les changements de condition des petits pélagiques pouvaient être en lien avec la composition de la communauté planctonique dans le milieu.

Les analyses inter-annuelles étant difficiles avec les données issues de PELMED, la dernière étude est consacrée à l'analyse d'une des plus longues séries temporelles de zooplancton en Méditerranée nord-ouest, située au point B en mer Ligure. L'objectif était de caractériser la variabilité à long terme de la communauté zoo-planctonique au niveau mensuel en Méditerranée Nnord-ouest au cours des 2 dernières décennies, aussi bien en terme de densité que de taille des individus et composition taxonomique afin de voir s'il était possible d'identifier des changements synchrones à ceux observés sur les petits pélagiques du Golfe du Lion et qui auraient résulté d'un même forçage environnemental régional. Ainsi, les dynamiques de ces 3 variables de la communauté zoo-planctonique ont été étudiées par le biais de 2 filets (WP2 et Régent) afin de caractériser son évolution au cours du temps et détecter d'éventuels changements. Un deuxième objectif était de mettre en évidence d'éventuelles relations entre la communauté zoo-planctonique et l'environnement, aussi bien au niveau local que global, afin de comprendre les facteurs régissant la dynamique zoo-planctonique. Un focus a été fait sur la variabilité de la taille des individus zoo-planctoniques, paramètre au cœur de l'hypothèse du contrôle bottom-up des petits pélagiques mais pas disponible dans les échantillons prélevés dans le Golfe du Lion et de façon général peu étudié sur le long terme en Méditerranée.

Chapitre II. *Concomitant changes in the environment and small pelagic fish in the gulf of Lions*

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Keywords: Environmental change, Bottom-up control, Chlorophyll-*a*, Small pelagic fish, Northwestern Mediterranean Sea.

Published as : Feuilloley, G., Fromentin, J.-M., Stemmann, L., Demarcq, H., Estournel, C., & Saraux, C. (2020). Concomitant changes in the Environment and small pelagic fish community of the Gulf of Lions. *Progress in Oceanography*, 102375.

Abstract

An important decrease in small pelagic fish condition and size has been observed in the most productive ecosystem of the Mediterranean Sea, the Gulf of Lions, since 2008, leading to an important fishery crisis. Previous studies suggested bottom-up control to be the most probable cause for these changes. Here, we investigate whether an environmental change might have caused such a situation. In the absence of zooplankton time series, this study aims at describing temporal changes in key abiotic factors for the planktonic and fish production of the Gulf of Lions, such as SST, meso-scale fronts, wind-induced coastal upwelling, river discharge, water stratification and deep convection and then at understanding potential link on Chl-*a* concentration as well as small pelagic fish populations. Our results indicate that the environmental conditions have broadly changed in the Gulf of Lion, with a major change in the mid-2000s, affecting the Chla concentration (which showed a regime shift in 2007), but also the SST, the upwelling and frontal activities, the Rhone river discharge (and particularly the N and P nutrients inputs) as well as the deep winter convection. Those changes could have affected the plankton production and consequently the small pelagic fish community that displayed similar patterns of variations as the environmental conditions.

II-1 Introduction

Small pelagic fish play a key role in regulating ecosystems, by providing energy and nutrient transfer from low (plankton) to high trophic levels (top predators, Cury et al., 2000; Larkin, 1996). Nonetheless, small pelagic fish populations are known for their important fluctuations and therefore understanding how they might be controlled by lower trophic levels (phyto- and zoo-plankton) and the abiotic environment is of primary importance (Schwartzlose & Alheit, 1999). This is especially true in a context of both climate change and important socio-economic stakes, as small pelagics are the most commonly fished species (Lindegren et al., 2013).

As plankton is closely related to abiotic environment, environmental changes can modify plankton phenology, biomass or community composition and then impact plankton feeders, such as small pelagic fish (Alheit & Niquen, 2004; Rykaczewski, 2018). In the Northwest Pacific for instance, changes in temperature and upwelling strength can delay the phytoplankton bloom and impact zooplankton size (Kudela et al., 2006). Such changes are known to directly affect small pelagic fish recruitment and subsequently fish population size either positively (match) or negatively (mismatch) (Cushing, 1990). In the sea of Japan, delays in the spring bloom have increased the temporal overlap with sardine larvae, resulting in higher recruitment of the Japanese sardine (Kodama et al., 2018). Similarly in the Barents sea, variations in zooplankton biomass induced by changes in currents and winds regime, affected both the growth rate and recruitment of capelin (Skjoldal et al., 1992). These examples show how environmental parameters often affect plankton dynamics and in turn small pelagic fish populations.

Changes in the small pelagic community were recently described in the NW Mediterranean Sea, and in particular in the Gulf of Lions (Saraux et al., 2019; Van Beveren et al., 2014). There, three main small pelagic fish species are present. Two of them, the European pilchard *Sardina Pilchardus* and the European anchovy *Engraulis encrasicolus* are targeted by commercial fisheries, while the other, the sprat *Sprattus sprattus* is not. Since 2008, landings of small pelagics have sharply decreased reaching their lowest values in 150 years (Van Beveren et al., 2016a). Fishermen indeed stopped fishing these species because of the absence of market for fish being too small and too skinny (Van Beveren et al., 2014, Saraux et al., 2019). Crashes in small pelagic fish landings and abundance have often been observed worldwide, generally due to environmentally-driven recruitment (Toresen & Østvedt, 2000; Barange et al., 2009; Chambers & Trippel, 2012). However, the Gulf of Lions case is different. Indeed, the decrease in size resulted from the combination of a lower growth and the disappearance of the oldest and largest individuals, but the recruitment was maintained (or even increased), due to an earlier sexual maturity (Brosset et al., 2016b). Interestingly, sardine and anchovy abundance have slightly increased since 2008, but their biomass did not because of lower body condition, mean length and weight (Van Beveren et al., 2014). Different hypotheses have been formulated and investigated to understand this unusual phenomenon, but top-down controls (fishing or natural predators), emigration of largest individuals, or diseases have all been refuted (Queiros et al., 2018; Saraux et al., 2019; Van Beveren et al., 2016b; Van Beveren et al., 2017). Even if a cocktail effect of some of the above pressures cannot be excluded, the hypothesis of a bottom-up control has been suggested as the most probable underlying mechanism (Saraux et al., 2019). Brosset et al., (2016b) suggested that both sardine and anchovy maintained high reproductive investments after 2008 despite their decrease in body condition, so that their survival during reproduction or just after may be impaired and highly dependent on prey availability. Sardine, anchovy and sprat mostly feed on zooplankton (Brosset et al., 2016a; Costalago et al., 2012), so a decrease in abundance and/or in quality of zooplankton could explain the observed decrease in body condition and growth and increased mortality after the reproduction period (Saraux et al., 2019). Brosset, et al., (2016a) found changes in small pelagics diet before and after 2008, based on stomach content and stable isotope analyses, with smaller plankton species consumed after 2008. However, zooplankton data remain scarce in this area, so bottom-up control could not be directly validated through the analysis of zooplankton time series.

The aim of this study was therefore to investigate this hypothesis of bottom-up control, using Chl-*a* satellite data, as a proxy of phytoplanktonic biomass and various oceanographic variables of interest to detect potential co-variation pattern with small pelagic fish. In the Gulf of Lions, three main oceanographic processes are known to play a role in phyto- and zooplanktonic production over the continental shelf : the Rhone river inflows, wind-induced coastal upwellings and the Northern current (Millot, 1979, 1990; Salat, 1996). The Rhone River is indeed an important source of terrestrial nutrients such as N and P and suspended matter (Lefevre et al., 1997; Macias et al., 2018b), its plume flowing mainly south-westward, but also sometimes drifting to the West side and along the coast (Demarcq & Wald, 1984; Fraysse et al., 2013). The area is also governed by strong northerly winds, the Mistral and Tramontane, that induce coastal upwellings which upwell deeper waters towards the surface, contributing to local phytoplankton bloom (Millot, 1979). At the shelf border, the Northern Current, which flows from east to west can, under certain climate conditions, produce meanders which penetrate onto the shelf and impact the biogeochemistry (Millot, 1999; Petrenko, 2003; Ross et al., 2016). Indeed, the Northern current is an oligotrophic current which can negatively affect the phytoplanktonic biomass on the shelf during intrusions modifying concentration of nutrients (Petrenko, 2003; Ross et al., 2016). On top of these variables, we also investigated other phenomena potentially important for phytoplankton production such as thermal fronts, the stratification of the water column and deep winter convection. Finally, the WeMO index (Martin-Vide & Lopez-Bustins, 2006) was also studied to have a broader vision of the system. Indeed, large scale variables are more integrative and sometimes allow to better predict animal populations than local environmental variables (Stenseth et al., 2003; Stenseth & Mysterud, 2005). If those process are known and there role for primary production have already been demonstrated in the literature, no quantification of their importance is available. Indeed, the relative contribution of each have never been studied and particularly on long-term inter-annual variability. As the objective was to investigate whether recent changes in small pelagic fish population may result from bottom-up processes, we further examined the temporal changes in the body condition, abundance, biomass and mean size of sardine, anchovy and sprat over the same period and compared the main patterns of (co)variations of the environmental variables with those of the small pelagic fishes.

II-2 Material and Methods

II-2.1 Environmental data

All environmental variables were computed and averaged over the continental shelf, delimited by the 200m isobaths (blue area on Figure II-1) except the deep winter convection index which was calculated by Herrmann et al., (2017) in the open ocean, and the Chl-*a* concentation in the Northern current which was averaged in the beige area in the Ligurian sea (Figure II-1). Different size area were tested for the Ligurian Chl-*a* time series, avoiding the spring bloom area which is more productive but separated from the Northern Current, and identical results were obtained regardless of the area defined. From each environmental variable (except for the deep convection and stratification, see below), annual values were derived averaging from September (year t-1) to August (year t) monthly data in order to integrate processes which mostly spread throughout the winter period (i.e. November to March), such as the coastal upwellings or the Rhone river outflow.

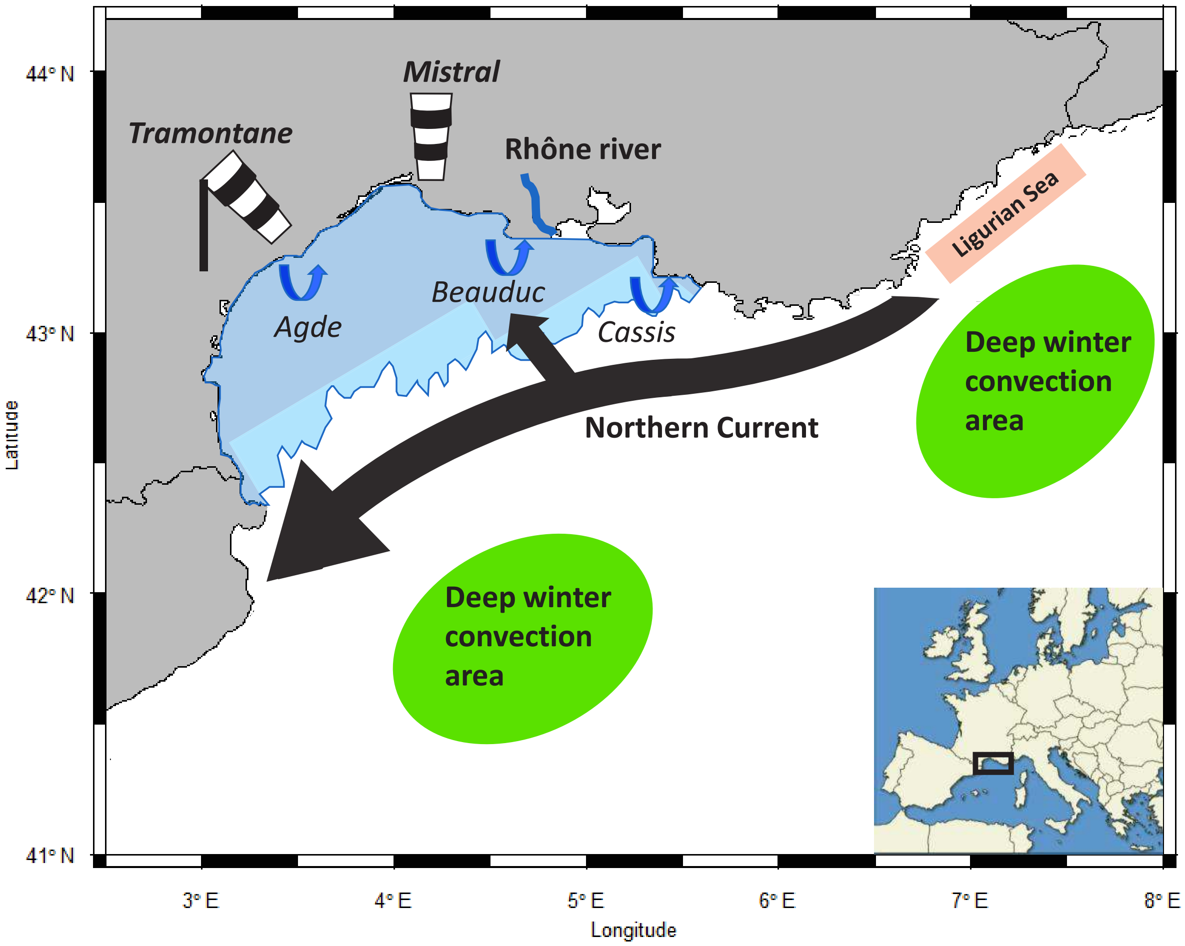

Figure II-1 *Map of the Gulf of Lions and its main oceanographic characteristics. The blue area represents the continental shelf until the 200m isobaths. Coastal curved arrows indicate the upwelling areas defined in (Millot, 1979) (Agde to the West, Beauduc in the middle and Cassis to the East). The black arrow is the Northern Current, with the thin arrow indicating possible intrusion onto the shelf. Mistral and Tramontane are the main northerly winds. The green areas indicate the deep winter convection cells and the beige area is the Ligurian sea surface used to calculate Chl-a concentration.*

II-2.1.1 Rhône river

N and P nutrient concentrations in the Rhone River were measured at the Arles station, either monthly from 1990 to 2004 and 2014-2017 or daily from 2005 to 2013. Monthly time series were constructed and the impact of the change of resolution in the samples was checked. A change in the variance was observed in 2004, but not in the mean value and no discontinuities were observed at this period in further analyses from both series. The river flow was measured at Beaucaire station and covered the period 1960-2017 at a daily resolution. Those data are available on (http://www.hydro.eaufrance.fr). N and P nutrient inputs were also studied, multiplying nutrient concentration by the river flow.

II-2.1.2 SST

Sea surface temperature (SST) was estimated using the Advanced Very High Resolution Radiometer (AVHRR) daily data from 1982 to 2017 at a 4km resolution, obtained on the NASA platform (https://data.nodc.noaa.gov/pathfinder/Version5.3/L3C/). For each pixel, the maximum value between day and night was kept. Because the original criteria available for the cloud masking were not satisfying for our study area, a specific mask has been generated for each daily data using the departure from a monthly climatology, considering a variable threshold according to temporal variability of the SST at each pixel. A monthly SST time series was then built over the continental shelf, until the 200m isobaths, averaging all the data available during each month.

II-2.1.3 Thermal fronts

Thermal fronts between two water masses of different temperatures can locally increase nutrient concentration and phytoplanktonic biomass when convergent (Bakun, 2006; Franks, 1992; Woodson & Litvin, 2015). Thermal fronts were detected with the Single Edge Detection algorithm based on a bimodal histogram in order to detect the presence of two water masses, initially developed by Cayula & Cornillon, (1992) and modified by Roa-Pascuali et al., (2015). This algorithm is not based on the direct measurement of a local gradient and is therefore particularly suitable for remote sensing data where the SST of numerous pixels is biased by various atmospheric artifacts that correspond to false local high gradients, which would be otherwise considered as fronts. For each daily frontal pixel previously computed, the local Sobel gradient is separately computed and a gradient threshold of 0.042°C.km^{-1} was used to select the strongest fronts, more likely associated to major physical processes (Roa-Pascuali et al., 2015). A monthly front index was constructed as the ratio between the sum of all gradient values where fronts were detected in the entire month and the total number of pixels of available SST in the month.

II-2.1.4 Chl-*a*

Chl-*a* concentrations were estimated using L3 daily data from SeaWiFS Aqua portal at 9km resolution from 1998 to 2002 and L3 daily data from MODIS Aqua portal at 4km resolution from 2003 to 2017 (https://oceancolor.gsfc.nasa.gov/l3/order/). Anomalous high values of concentration were detected at very coastal pixels and in the Rhone plume. These were thought to derive from turbidity i.e. water belonging to the “case 2” optical properties as defined by (Morel & Prieur, 1977), generally not compatible with the fluorescence to concentration algorithm (Gohin, 2002; Gohin et al., 2005). As such, concentration data were truncated to a maximum value of 5µg/L, allowing to keep high but reasonable values and so to avoid any potential overestimation of the Chl-*a* concentration on the shelf. No problem of compatibility was detected between the two satellites, as time series from MODIS and SeaWiFS were highly similar during their common period of use, i.e. 2003-2006 (slope = 0.95, intercept = -0.02, R^2=0.96).

II-2.1.5 Deep winter convection

Deep winter convection occurs when a dry and cold wind blows during several days and induces a decrease in SST and an increase in salinity due to evaporation, leading to an increase of the surface water density. This water dives and a convection phenomenon starts (Herrmann et al., 2017). In the deep winter convection area, outside the shelf, important spring blooms are observed (Herrmann, et al., 2013; Herrmann, et al., 2014). Whether these deep convections can influence the phyto- and zooplanktonic production on the shelf remains unknown, but worth to be investigated. To incorporate the convection in our analysis, we used the annual deep winter convection time series in NW Mediterranean Sea calculated by Herrmann et al. (2017). This series covered the period 1998-2016 and represented the maximum volume of mixed water, obtained from both altimetry and ocean colour satellite data. Indeed, volume of mixed water was estimated by numerical modelling and linear regression was performed between volume of mixed water, surface Chl-*a* concentration and sea level anomaly to establish relationships by means of regression parameters. The time series of volume of mixed water could then be extended after the end of the numerical runs (in 2013) with Chl-*a* satellite concentration, satellite sea level anomaly and the regression parameters estimated. Because this process occurs only in winter, no monthly time series was available.

II-2.1.6 Upwelling

The upwelling index was calculated from CCMP (Cross Calibrated Multi-Platform) L3 wind daily data with a resolution of 1/4°, provided by the Remote Sensing System (http://www.remss.com/measurements/ccmp/). This dataset combines satellite data, moored buoy wind data, and ERA-Interim model wind fields. The index was based on Ekman transport (T_{ek}) (Bakun, 1996; Caverivière & Demarcq, 2002). With the action of the Coriolis strength, the wind blowing parallel to the coast transports water on the right (in the Northern Hemisphere) perpendicularly to the coast. The Ekman index was computed by dividing the coastal trait into segments (sensitivity analyses showed similar results regardless of the resolution used for the pixels and results are presented for 1/16 degree resolution). Then, in each pixel, the wind component parallel to the coast was calculated and used to apply the Ekman equation to estimate the volume of water upwelled with:

$$T_{ek} = \frac{CP^2 * \rho_{air} * cd}{2 * \Omega * \sin(lat) * \rho_{eau}} * L_{coast} \qquad (1)$$

where CP is the wind component parallel to the coast, ρ_{air} =0.0012, ρ_{eau} =1.027, cd =0.013 the drag coefficient, Ω =7.14e^{-5} the angular velocity of Earth, lat the latitude and L_{coast} the length of coastal trait.

Upwelling indices were then built using the sum of water volume upwelled from all coastal pixels over the entire Gulf of Lions.

II-2.1.7 Stratification

The stratification index was estimated using temperature and salinity outputs from NEMO model provided by CMEMS (http://marine.copernicus.eu/services-portfolio/access-to-products/) from the MEDREA re-analysis (Simoncelli et al., 2014). Water density was then calculated at each depth layer of the model with the Equation of Sea water EOS-80 (UNESCO, 1981) and stratification estimated as follow:

$$\text{Stratification} = \int_{Z}^{0} \big(d(Z) - d(z)\big)dz \qquad (2)$$

With d(Z) the bottom density, d(z) and dz respectively the density and the thickness of layer z (Estournel et al., 2016). Regarding the stratification index, the annual maximum value rather than the mean was kept, because this series of maximum contained most of the variance. As maximal stratification usually occurred in August, i.e. at the end of our year period (the other annual time series were constructed by averaging monthly data from September year t-1 to August year t), the Stratification time series was lagged by one year, so that we could thus examine a potential effects of stratification on the other environmental variables or the biological variables (the latter being sampled in July of each year, see above).

II-2.1.8 Western Mediterranean Oscillation (WeMO)

The WeMO index was preferred to others such as the NAO because of its stronger capacity to represent NW Mediterranean Sea environmental conditions (Martin-Vide & Lopez-Bustins, 2006). This index represent differences in standardized surface atmospheric pressure between San Fernando (Spain) and Padua (Italy) and integrate fluctuations in rainfall, river flow, wind mixing and temperature. Positive values of the index are associated to lower temperature and higher river flow and wind mixing, though to be favourable for plankton productivity (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012). The annual index was preferred to the winter index as it has already been shown to have an importance for small pelagic variability in the NW Mediterranean Sea (Brosset et al., 2015; Martín et al., 2012). The WeMO monthly data were downloaded on the University of East Anglia website (https://crudata.uea.ac.uk/cru/data/moi/).

II-2.2 Biological data

Small pelagic fish data were obtained during the PELMED scientific survey (Bourdeix & Hattab, 1985), which has occurred every July since 1993. The aim of this survey is to assess the stock size of anchovy, sardine and sprat in terms of abundance and biomass, using acoustic detection and identification trawls in the Gulf of Lions. Acoustic detection is performed along 9 parallel transects, covering the shelf from the coast to the edge (20-200m isobaths). Acoustic data were recorded every 1 nm using multi-frequency echosounders (Simrad EK500 and ER60), while travelling at a constant speed of 8 nm.h^{-1}.Energies from the 38 kHz frequency were used to estimate fish energy. Species discrimination and echo-partitioning were performed based on trawl composition conducted along the transects. Species biomass and abundance were finally estimated from species energy using specific target strength (TS=20 log(L) - 71.2, where L is the length of the fish for all 3 species (Doray, 2012; Saraux et al., 2014). Depending on the year, between 20 to 50 trawls were conducted in July over all the shelf. Individuals were randomly sampled from the trawls to take measurements such as weight, length and gonad maturity. As the species exhibited an allometric growth pattern (Brosset et al., 2015; Van Beveren et al., 2014), body condition was estimated with the Le Cren index (Le Cren, 1951) which also avoid a potential length effect (Brosset et al., 2015). The index was expressed as :

$$\mathrm{Kn} = \frac{\mathrm{W}}{\mathrm{Wr}} \tag{3}$$

With W the observed weight and W_r the theoretical weight of an individual calculated with

$W_r = \alpha L^{\beta}$, where α and β are the regression parameters of the length–weight relationship with $\alpha = 3.86 \times 10^{-3}$, 5.90×10^{-3} and 3.21×10^{-3} and $\beta = 3.20$, 3.10 and 3.37 for anchovy, sardine and sprat respectively (Van Beveren et al., 2014). Finally, 4 variables were available for each species: abundance, biomass, mean size and mean body condition index. These variables were all estimated from the PELMED survey, thus representing the summer situation (July) and intra-annual variability could not be estimated.

II-2.3 Statistical analyses

All the analyses presented above were conducted with R v. 3.4.1 (R Core Team, 2018).

II-2.3.1 Univariate time series analyses

Analyses were conducted for both monthly and annual time series of each environmental variable. Because monthly time series presented both inter-annual and intra-annual variability, seasonal cycle and intra-annual variability were highlighted with contour plot of monthly time series, while trends were studied after a 5 year smooth with loess in order to remove seasonal variation (Figure II-2). To investigate inter-annual variability, breakpoints analyses were computed on annual time series, using the strucchange package and an algorithm testing structural changes in time series (Kleiber et al., 2002). Optimal number of segment partition was based on BIC criterion in order to compute only the most relevant changes.

II-2.3.2 Multivariate analyses

Climatological time series were also constructed, representing the mean value of each month, so as to investigate seasonality patterns. In order to investigate the seasonality of the whole environmental system of the Gulf of Lions, principal component analyses (PCA) were run on correlation matrices of climatological time series (i.e the mean value of each month during the entire period), for SST, Chl-*a*, stratification, thermal front, nutrient concentration and Rhone outflow time series.

II-2.3.3 Modelling the Chl-*a* concentration

To identify the environmental variables that would be related to the variability in interannual Chl-*a* concentration, a generalized linear model (GLM) was applied on the annual time series, using a Gaussian family and a log link. Explanatory variables represented processes known in the literature to modify nutrient availability and affect phytoplanktonic production, i.e., the upwelling index, the winter convection index, the thermal front index, concentration of N and P and the Rhone river flow. The concentration of Chl-*a* in the Ligurian Current as well as the WeMO index were also considered because of their potential impacts on plankton production (see above). Because, N and P nutrient inputs were strongly correlated with the Rhone outflow, it was not possible to consider them in a single model. Two similar GLMs were thus built with all previously mentioned variables, as well as (i) the Rhône river flow and the two time series of N and P nutrient concentrations (case 1) and (ii) N and P nutrient inputs instead of nutrient concentrations and Rhone river flow (case 2). In both GLMs, a stepwise forward and backward selection was run to select the most explanatory and significant variables based on AICc. Multicollinearity between variables was checked by computing Variance Inflation Factor (VIF). Finally, residuals and the goodness of fit of the model were checked to evaluate the quality of the model.

II-2.3.4 Dynamic Factor Analysis

Dynamic Factor Analysis (DFA) is a multivariate time-series technique used to identify *M* hidden common trends in a set of *N* time series and that could further estimate the effects of explanatory variables in a biological time-series data set (Zuur et al., 2003). The time series are modelled as a linear combination of different components with :

Data = Trend + Explanatory variables + constant + noise (4)

It can be mathematically expressed by : $y_t = Lx_t + Dd_t + c + e_t$ (5)

where y_t is a vector Nx1 containing the values of the N time series at time t, x_t is a vector Mx1 containing the values of the M common trends at time *t*, *L* is a matrix NxM containing the factor loadings on the M common trends, d_t is a vector Kx1 with the values of the K covariates at time *t*, *D* is a matrix NxK containing the unknown regression parameters between times series and covariates, *c* is a Nx1 constant level parameter which allow each linear combination of common trends to move up or down and e_t is the noise component distributed as a multivariate normal distribution with mean 0 and covariance matrix R.

In this study, different hypotheses on the covariance matrix (R) of the noise component were tested:

-Same variance and no covariance (diagonal-equal)

-Different variances and covariance (unconstrained)

-Same variance and covariance (equalvarcov).

DFA was first performed on standardized annual time series of environmental variables (i.e substracting the mean and dividing by the standard deviation) from 1993 to 2017 to investigate the main environmental patterns of the environmental system. Models were constructed with 1 to 4 hidden trends, and the performance of the models have been evaluated according to AICc (AIC corrected for small samples) following Zuur et al., (2003). DFA can handle missing values in Chl-a and Convection time series between 1993 and 1997, but these two time series did not contribute to the construction of the common trends over those 5 years. Technically, the L matrix containing the factor loadings was replaced by L x W_t matrices, where W_t is a design matrix N_t x N with N the number of variables and N_t the number of variables with non missing values at time t. W_t contains 1 on the diagonal and 0 elsewhere (See Zuur et al., 2003 for further details). Then to investigate the relationship between small pelagics and environment, DFA was performed on annual time series of small pelagic biological data with annual environmental variables as covariates. Because missing values are not allowed in covariates time series, DFA was performed on the 10 small pelagic biological data (the abundance of sardine and the condition, biomass and size of sardine, anchovy and sprat) from 1998 to 2016 (the period of convection time series), with10 environmental covariates (Upwelling, Thermal fronts, Chl-*a*, Rhone flow, WEMO, SST, deep winter convection, N and P concentration and stratification). Biomass and abundance variables were first log transformed and then all the biological variables were standardized. All the combination of environmental covariates were tested (from 0 to all covariates in the same model). Once more, the performance of the models have been evaluated according to AICc. Finally, DFA was performed on biological data from 1993 to 2017, without covariates. As previously, variables were prior standardized and biomass and abundance were log transformed. Because no environmental covariates were retained in the best model from 1998 to 2016, we presented the results of the two DFA from 1993 to 2017 to investigate the links between small pelagic fishes and environment.

II-3 Results

II-3.1 Analyses of the environmental times series

II-3.1.1 Seasonality

Except for P concentration and the WeMO index, time series were highly seasonal, but not synchronous (Figure II-2). SST (Figure II-2a) and stratification (Figure II-2b) were both highest in summer and their seasonal cycle was stable. In opposition, Chl-*a* (Figure II-2c), Rhone flow (Figure II-2d), N concentration (Figure II-2e) and upwelling (Figure II-2g) were highest during winter to early spring period. The timing of the Chl-*a* peak was variable and occurred between February and May. Similar variability in the timing of the peaks was also detected for the Rhône flow, N Concentration and Upwelling, but between November and May this time. Thermal front index presented a different pattern with two seasonal peaks, in winter and summer. These outcomes were summarized in the Principal Component Analysis (PCA) on monthly averages (climatological time series) of all variables during the period 1998-2017 (Figure II-8). The two first principal components (PC) of the PCA accounted for 86% of the variability. As expected, SST and stratification covaried, with maximum values generally in August (Figure II-8), and were opposed to the upwelling index, the N nutrient concentration, the Rhone flow and the Chl-*a* concentration, which peaked during winter and/or spring (Figure II-8). Thermal Front and P concentration were associated to the second axis because of the two seasonal peaks for the first one and the absence of seasonal cycle for the second.

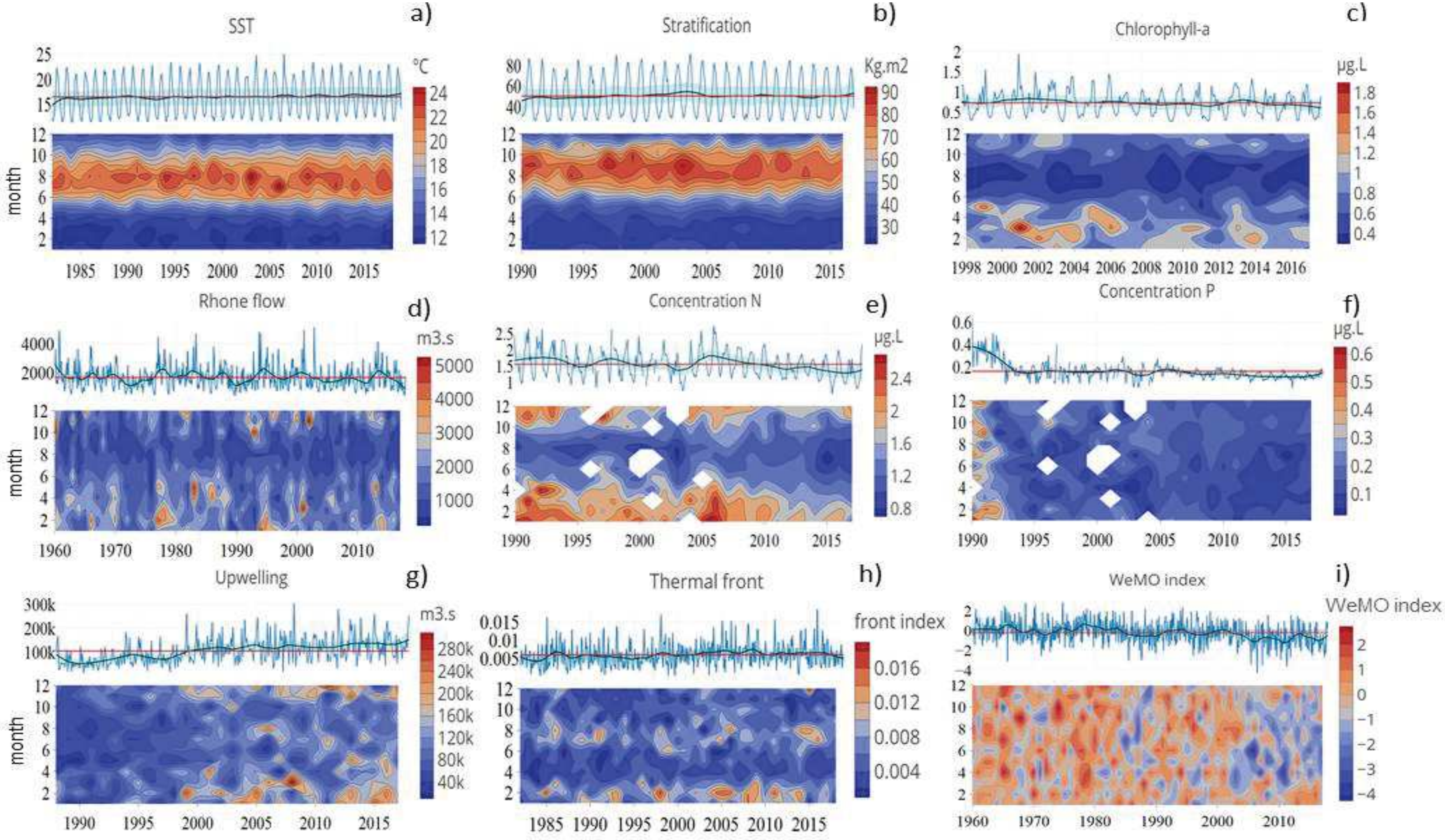

Figure II-2 *Contourplot of the monthly time series for the different environmental variables. The blue curve is the monthly mean time series and a loess smooth with a five years window size. The red line represent the mean of the time series for the entire period.*

II-3.1.2 Trends and discontinuities

Annual SST time series (Figure II-3a) displayed a clear linear increase over the entire period (slope= +0.019, $p<0.001$), ranging from 16.1°C in 1983 to 16.8°C in 2017, while the stratification index (Figure II-3b) was stable. No discontinuities were found in annual time series for both variables (Figure II-3). The Chl-*a* concentration monthly time series did not display any strong long term trend (Figure II-2c), but the concentration during the late winter to spring period decreased since 2007 (Figure II-2c). A breakpoint was detected in 2007 in the annual time series of Chl-*a* (Figure II-3c), which remains coherent with results on monthly time series, as spring and winter accounted for most of the annual phytoplanktonic biomass (32% and 31% respectively vs. 16% and 21% for summer and autumn respectively). Annual mean concentrations in Chl-*a* were around 0.76 ± 0.05 $\mu g.L^{-1}$ before 2007 and 0.71 ± 0.05 $\mu g.L^{-1}$ after (Figure II-3c) and the difference was significant (Wilcoxon test, $p=0.009$).

The Rhône's flow presented a strong variability, both intra-annual with a marked seasonal cycle and inter-annual (Figure II-2d). However, no breakpoint was detected and no long-term trend was observed. Concentration of N nutrient (Figure II-2e) remained stable until 2005 and started to decrease in 2006. A breakpoint was found in 2010 for the annual time series (Figure II-3e). Concentration of P nutrient (Figure II-2f) highly decreased between 1990 and 1995, as confirmed by the discontinuity in 1993 (Figure II-3f), and values ranging from 0.36 $mg.L^{-1}$ in 1990 to 0.15 $mg.L^{-1}$ in 1995. The series then slightly decrease (slope = -0.002, $p<0.001$), but no other breakpoint was detected. This decrease of nutrient concentrations induced a decrease of nutrient inputs, both for N and P nutrients (Figure II-3i and j). However, breakpoints detected were different from those of the concentrations because of the variability of the river flow which also influence the inputs. Indeed, a breakpoint for N nutrient input was observed in 2001 and it was in 1994 and 2002 for P input. In brief, the Rhone system displayed high variability at both seasonal and inter-annual levels together with a significant impoverishment in nutrient concentration over time.

The upwelling index (Figure II-3g) displayed a positive long-term trend (slope= +2806, $p<0.001$ for the annual time series). Two discontinuities were detected in 1993 and 1999 (Figure II-3g). For the thermal front index, a discontinuity was detected in 1997, with mean annual value of 0.0054 ± 0.00075 before 1997 and 0.0065 ± 0.00076 after (Wilcoxon test, p-value < 0.001). Finally, the WeMO which is the only large scale climatic variable of the dataset presented a significant decreasing trend (slope =-0.035, $p<0.001$) and a unique breakpoint was detected in 2002.

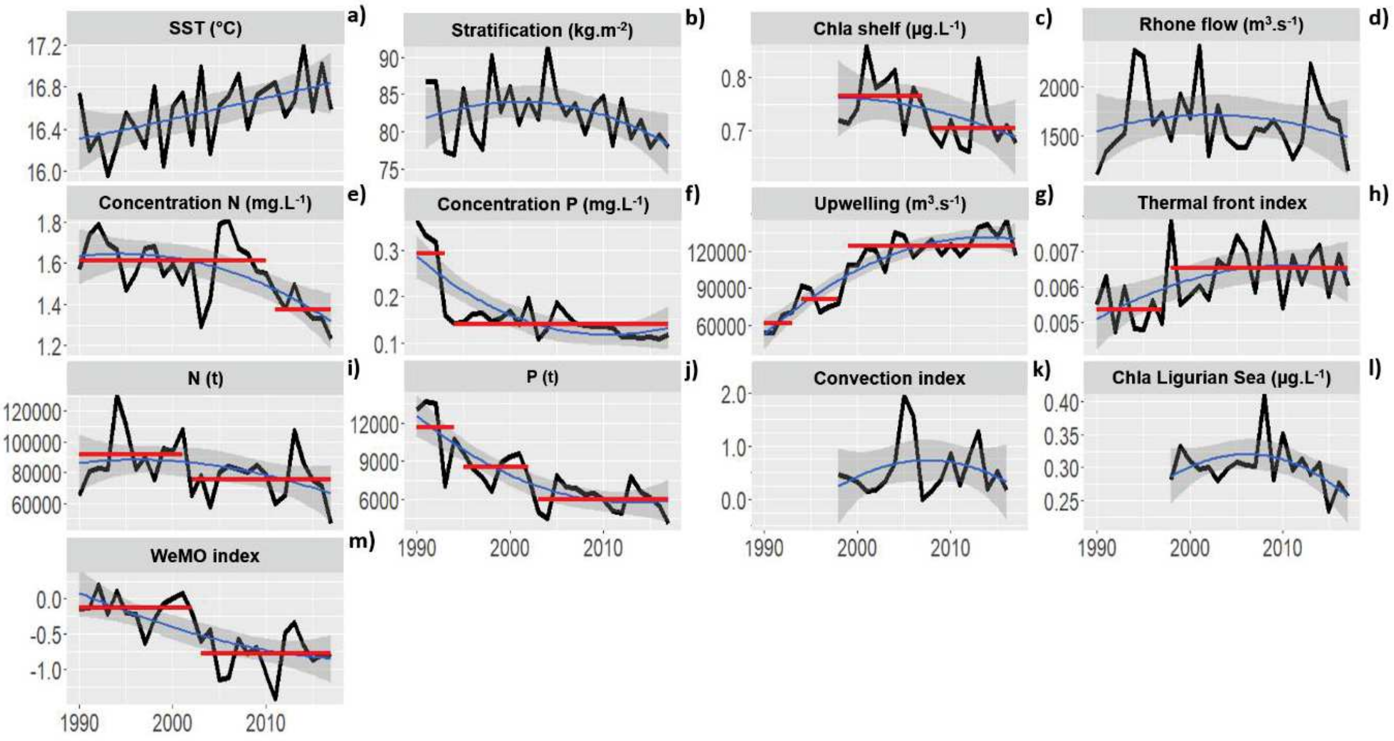

Figure II-3 ***Annual time series of environmental variables. The blue curve is the loess smoothed 5 years trend and red lines represent the mean values between breakpoints. N(t) and P(t) represent the annual N and P nutrients inputs (in tons), calculated as the product between N and P nutrient concentrations and the river flow.***

II-3.2 Modelling the Chl-*a* concentration

To determine the principal drivers of Chl-*a* variability on the Gulf of Lions shelf, a GLM analysis was run for the 2 cases described below (case 1 : with Rhone inflow and nutrient concentrations and case 2 : nutrient inputs). For the first case, only the Rhone's flow variable was retained in the best model ($p<0.01$), with both forward and backward stepwise selection. Residuals were normally distributed and the correlation between Chl-*a* observed and predicted was significant at the 5% level ($r=0.55$, p-value=0.015) (Figure II-4). The Rhone's flow alone explained about 30% of the variability of the Chl-*a*. For the second case, only the N nutrient inputs variable was kept, but it was only significant at the 10% level ($p=0.055$) with both forward and backward stepwise selection. Residuals were normally distributed but the correlation between Chl-*a* observed and predicted was however lower and only significant at the 10% level ($r=0.45$, p-value=0.055) (ESM Figure II-9).

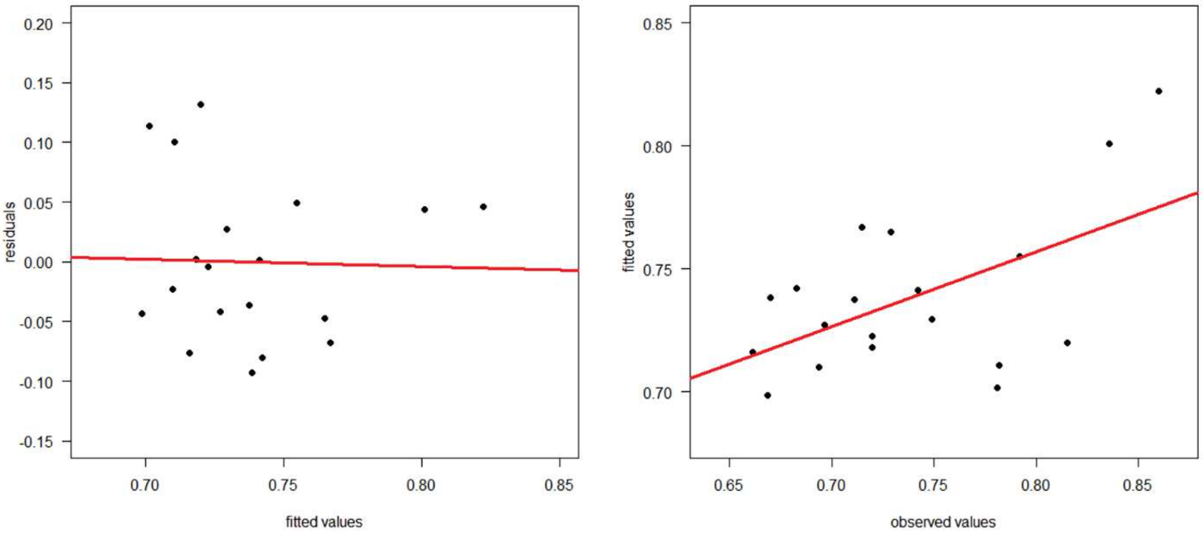

Figure II-4 ***Diagnostic plots of glm analysis with the Rhone's flow as the only explanatory variable of Chl-a concentration. The left plot is residuals versus predicted Chl-a values and the right plot is predicted Chl-a values versus observed Chl-a values.***

II-3.3 The Dynamic Factor Analyses

The first DFA was performed on the 10 environmental time series from 1993 to 2017 to investigate the underlying common trends of this dataset. To do so, we built 12 models with 1 to 4 common trends and tested 3 different hypothesis on the noise term matrix ("diagonal and equal", "equalvarcov" or "unconstrained"). The AICc values indicated that the model containing 2 common trends and a "diagonal and equal" noise matrix was the optimal one.

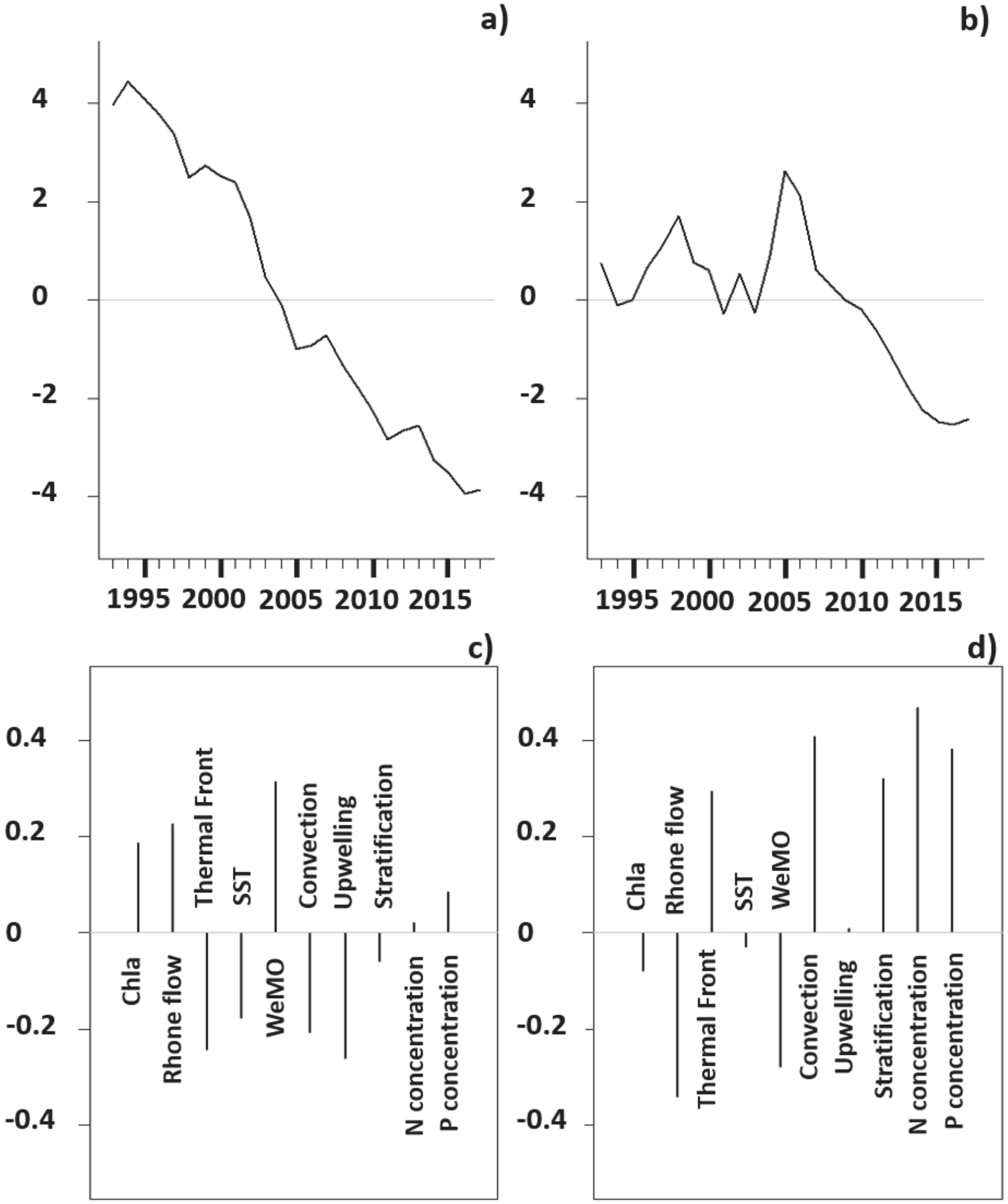

Figure II-5 ***First (a) and second (b) common trends identified by the best model (lower AICc) of the DFA performed on the 10 environmental time series and the factor loadings of the different environmental time series for first (c) and second (d) common trend.***

The first common trend (Figure II-5a) presented a strong linear and monotonous trend, which opposed Chl-*a*, Rhone flow and WEMO (displaying decreasing trends) to Thermal front, SST, winter convection and upwelling (displaying increasing trends). The second common trend (Figure II-5b) presented a different pattern with a quite stable period between 1993 and 2003, followed by a rapid increase during

2 years (peaking in 2005) and then by a sharp and continuous decrease until 2017. This common trend opposed mainly N and P concentrations, stratification, winter convection and thermal fronts (positively related to this trend) to Rhone flow and WEMO (negatively related to it). The fitted curves from the combination of these two common trends indicated that the environmental time series were reasonably fitted (ESM Figure II-10). As expected, the fit was better for variables displaying high factor loadings, e.g. N concentrations, WEMO, winter convection, Rhône river flow, than for variables displaying rather low factor loadings (< 0.3) on both trends, e.g. SST, Chl-*a* and upwelling.

II-3.4 Small pelagic variability and link with environment

Correlation test between biological variables reveled that abundance of sprat and abundance of anchovy were highly correlated to respectively biomass of sprat and biomass of anchovy. We then decided to remove the abundance of those two species from the analyses. For sprat condition and mean size, values estimated with less than 10 individuals were removed from the analyses. A second DFA was then performed on the 10 small pelagic biological time series (1998-2017) to identify the main patterns of variation of the population, using the environmental variables as exploratory variables, up to 4 common trends and 3 different matrices of noise component. After model selection based on AICc, the best model was the one with two common trends and a "diagonal and equal" R matrix, but did not retained any exploratory variables. Therefore, we could perform the DFA on longer biological time series (i.e., 1993-2017) without exploratory variables (some of them only starting in 1998). The best model identified by the AICc was also the one with two common trends and a "diagonal and equal" R matrix. The first common trend displayed an increase during the first three years, then a plateau at high values until 2000, followed by a sharp decrease until 2005, a rapid increase in 2006 followed by a new plateau at values close to zero until 2017 (Figure II-6a). This trend mainly opposed the biomass of anchovy and the mean size of sprat (positively related to this trend) to the biomass and abundance of sardine (negatively related to it). The second trend presented a stable (slightly increasing) period from 1993 to 2001, followed by a short decrease and then a rapid increase peaking in 2006 (Figure II-6b). The trend was then characterized by a strong and continuous decrease until 2012 at values 3 times lower than the beginning and stayed at these low levels until 2017. This trend opposed the biomass of sprat to the mean size of the three fish species, the condition of sardine and anchovy and the biomass of sardine (Figure II-6d). All the variables displayed rather high factors loading (> 0.3) on at least one common trend, so that the fitted curves from the combination of these two common trends were quite good for the 10 biological time series (and better than for the environmental variables, which could indicate that the biological time series dataset was more homogeneous than the environmental one (ESM Figure II-11).

If a continuous linear trend was only observed in the environmental variables, the second common trend of the DFA performed on the environmental variables was unexpectedly similar to the second trend of the DFA performed on the biological variables (Figure II-7). Both trends displayed a stable phase from

1993 to 2003, then 2 years of increase, followed by a sudden and sharp decrease (this decrease starting one year sooner in the DFA of the environmental variables than this on the biological variables, Figure II-7) and finally by a stabilisation at low values in the most recent years.

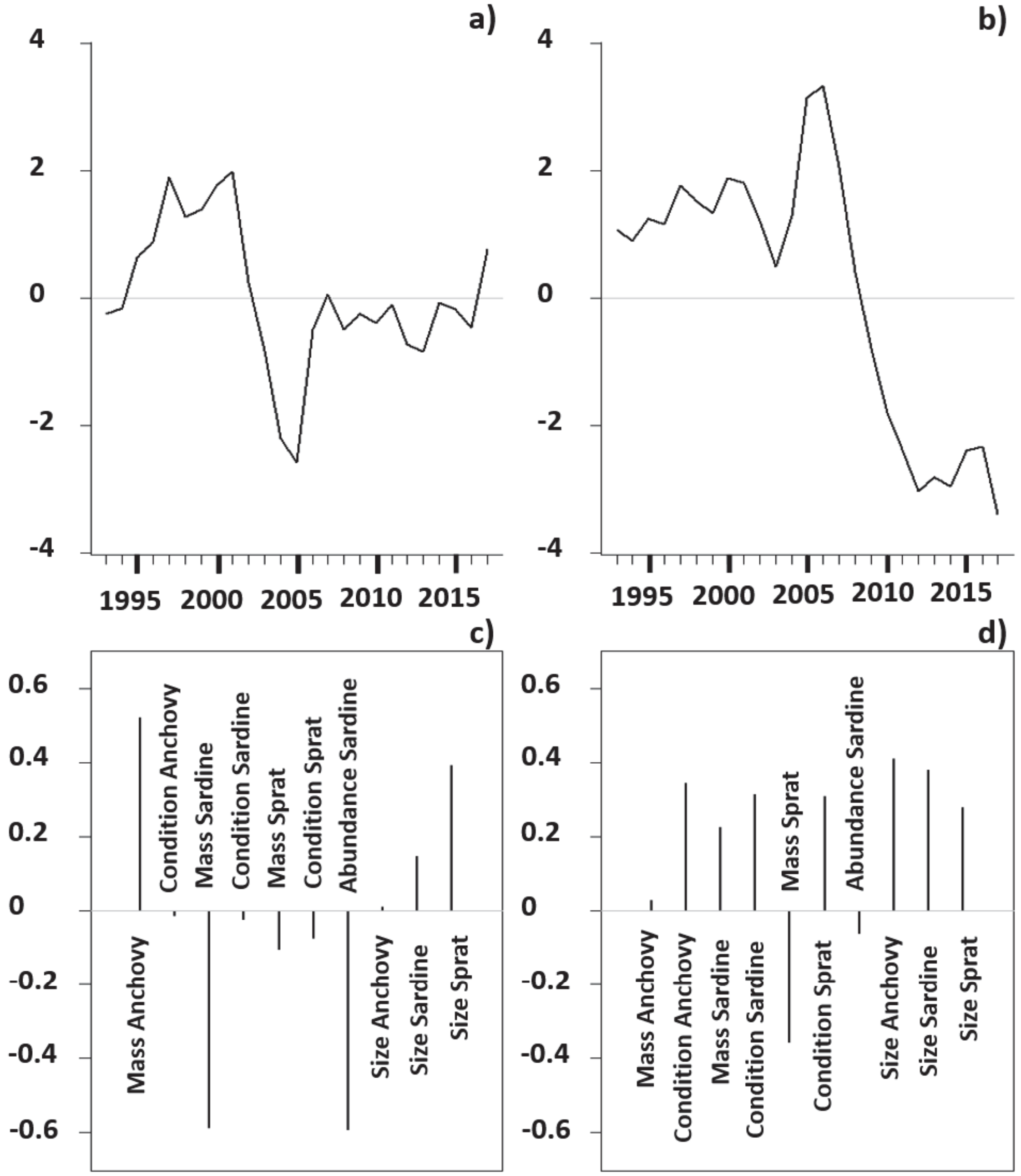

Figure II-6 *First (a) and second (b) common trends identified by the best model of the DFA performed on the 10 biological time series and the factor loadings of the different biological time series for first (c) and second (d) common trend.*

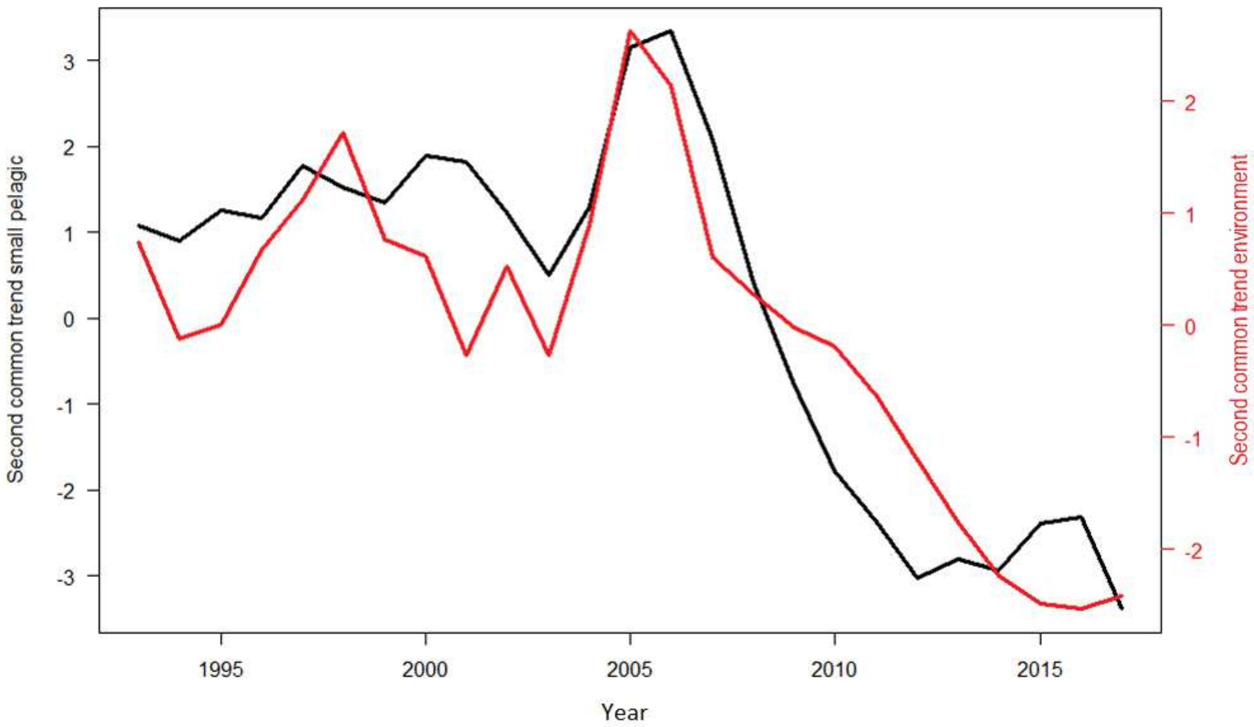

Figure II-7 ***Second common trends of the DFAs performed on the environmental variables (red) and on the biological variables (black).***

II-4 Discussion

Small pelagic fish feed mainly on zooplankton and could thus be impacted by changes in the plankton community (i.e in quality or quantity), induced by environmental variability (bottom-up control) (Csirke et al., 1996; Espinoza & Bertrand, 2008). Because zooplankton time series were scarce in the study area, we used various oceanographic variables that are known to affect the plankton production in the Gulf of Lions and Chl-*a* satellite data to depict and compare the main patterns of (co)variations of the environmental variables and of the small pelagic fish. If all the variables presented have already been studied, in relation with primary production in the area, it was the first time that the main forcing processes were pooled together, enabling us to partition the variance. However, the aim was not to have a detailed study of each process, but rather an overall understanding of the planktonic production and variability in this area. Such approach allowed us to investigate the hypothesis of a bottom-up control in the recent small pelagic fish crisis, albeit the absence of zooplankton time series. In this approach, time series were constructed considering the average over the entire shelf even if it is known that spatial heterogeneity is present within the shelf (Lefevre et al., 1997). Different points of the results will be discussed below as well as some potential implication for small pelagic fish.

II-4.1 Environmental variability in the Gulf of Lions

Seasonal variations are clearly marked on the shelf with a productive period in late winter and spring and an oligotrophic period in summer and early autumn. Chl-*a* concentration peaks, which occur between January and May, also vary quite substantially in amplitude among years, between 0.82µg.L^{-1} and 1.93µg.L^{-1} for the studied period. An important result is the decrease of the Chl-*a* concentration since 2007 with a breakpoint detected in the annual time series, indicating currently a lower phytoplanktonic biomass on the shelf. This decrease was mainly due to a decrease during the spring period, with weaker spring bloom on the shelf. This period is critical for the functioning of the system and changes of intensity could be linked to differences of community structure and then induce modification in the succession of plankton species and more generally in the food web (Mayot et al., 2017). Another significant decrease has been detected in the N and P nutrient concentration of the Rhone river. This could be explained by different regulation implemented during the past decades to improve water quality of French Rivers, such as change in fertilizer use, modifications in washing liquid composition, or an increase in water treatment on land, all viewed as improvement in terms of water quality, with a 3-fold decreases of N and P nutrient concentrations from 1990 to 1995 (Agence de l'eau, 2018). Nonetheless, these changes led to a diminution of the Rhone runoff inputs onto the continental shelf, as observed with the decreasing trends in the annual nutrient inputs time series and breakpoints detected in 2002 for N nutrient and in 1994 and 2002 for P nutrient.

Other environmental variables displayed increasing trend over the period, such as SST (that could be related to the global warming as already shown in this area, see (Vargas-Yáñez et al., 2010), upwelling, which result of an intensification of Northerly winds in term of occurrence and intensity over the last decades and thermal fronts, partly impacted by the increase of coastal upwelling. If SST presented no breakpoints in the time series, both upwelling and thermal fronts had, in 1997 for fronts and 1993 and 1999 for upwelling.

Finally, others presented decreasing trends such as the WeMO index with a breakpoint in 2002. This large scale variable integrate different process and for this reason, different pattern of variation were shared with other variables such as the decreasing trend of stratification and Chla, generally positively related to WeMO, and the increase of SST generally opposed to WeMO values. The convection time series presented no clear trend over the period except 2 strong values in the mid 2000s.

As a whole, the environmental conditions in the Gulf of Lions displayed 2 main common trends highlighted by the DFA. The first one was a continuous linear change, similar to this observed for SST, upwelling, fronts and WeMO while the second trend, characterized by an abrupt discontinuity in the mid of the 2000s, could not be entirely identified in any single environmental time series. Indeed, several series shared only parts of this trend and combining those different parts lead to the common trend identified. Those two common trends indicated that the environmental conditions in the Gulf of Lions have globally changed since the early 1990s, with more abrupt changes in the mid 2000s, which could have affected the planktonic and small pelagic fish communities of this area.

Results from the GLM analyses showed that the Rhone flow was the most important and only significant contributor of the annual Chl-*a* production, explaining up to 30% of the variability in Chl-*a* concentrations. The GLM outputs were also supported by the DFA performed on the environmental variables, both variables displaying factor loadings of the same sign on both common trends (and also of similar value on trend 1). Relationship between Chl-*a* concentration and Rhone river flow was further rather obvious when considering extreme values. River flood, as in 2001, was related to a peak in Chl-*a* concentration while low river flows, such as in 2011-2012, were related to low Chl-*a* concentrations. As the annual time series of the Rhone river runoff did not display any significant long term trend (or breakpoints), we put forward that the decrease in Chl-*a* concentration since 2007 could be mostly related to a decrease in nutrients inputs from the Rhone river (an hypothesis that nonetheless needs to be validated by further studies, possibly modeling studies). The GLM without the river flow, but including the nutrient inputs, indicated that variations in Chl-*a* concentrations were best explained by the N nutrients inputs. This relation between variations in phytoplanktonic biomass on the Gulf of Lions shelf and the Rhone river discharge is in agreement with past studies, which estimated that 50% of the phytoplanktonic biomass was supported by Rhone river terrestrial inputs (Coste, 1974; Lefevre et al., 1997; Morel et al., 1990). Similarly, Macias et al., (2018b) estimated, through modeling study, that the Rhone inputs would be now responsible for 20 to 40% of the Chl-*a* concentration on the shelf, with a decreasing gradient from East to West.

In opposition to this impoverishment linked to Rhone river inputs, coastal upwellings, known to support phytoplanktonic production and, thus, pelagic fish populations (Brochier et al., 2018; Lips & Lips, 2010; Schwartzlose & Alheit, 1999) continuously increased through time because of stronger northerly winds. However, a detailed analysis (see Table II-1 and ESM Figure II-12 and 13) showed that while upwelling activity had a positive impact on phytoplanktonic biomass at a local scale (i.e. focusing on upwelling cell), this impact seemed not sufficient to act at the scale of the entire shelf. Moreover, Cassis upwelling area, which is the strongest upwelling cell in the Gulf of Lions, could have only a moderate impact because upwelled waters could be potentially carried away by the northern current (Millot, 1990). In the same line, this strong increase of the upwelling intensity did not seem to be strong enough to counterbalance the warming of the entire shelf, as also observed in some major coastal upwelling systems (Schwing & Mendelssohn, 1997). While the correlation between upwelling and SST was negative at the daily and local scales (see Table II-1 and ESM Figure II-12 and 13), annual SST continued to increase over the entire shelf of the Gulf of Lions, confirming the rapid and strong warming of the Western Mediterranean waters due to climate change (Vargas-Yáñez et al., 2010). For those reasons, we observed an increase of annual SST due to the global warming despite the increase of upwelling. Similarly, the spatial influence of the upwelling remained probably too limited to compensate the diminution in nutrient inputs from the Rhone river, leading to an overall impoverishment of the entire shelf. As the increase of fronts is partly due to the increase of upwelling, this hypothesis would then explain why the upwelling index and thermal fronts displayed opposite factor loadings on the DFA, and so opposite trend, compared to Chl-*a* concentration. However, without the increasing trend of the upwelling, the decrease of Chl-*a* would have probably been stronger. Finally, the DFA performed on the 10 environmental time series between 1993 and 2017 showed that the factor loadings on the first trend (i.e. the monotonic trend) of the WeMO was of the same sign as those of Rhone river flow and Chl-*a*, but opposed to those of SST. On the second trend, the factor loading of the WEMO was also of the same sign as those of Rhone river flow and opposed to those of stratification. All these observations were in accordance with (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012), which showed that positive phase of the WeMO index values were correlated with low SST and high river runoff (and *vice versa*).

II-4.2 Comparison of variability in environmental conditions and small pelagic fishes

Small pelagic fish are key species of most pelagic ecosystems (including the Gulf of Lions) due to their central place in the food web, transferring energy from the lowest trophic levels (plankton) towards top-predators (Cury et al. 2000). Their short lifespan and high fecundity make them further strongly dependent on changes in environmental conditions (Bakun 1996).

In the Gulf of Lions, the biomass, condition and size of sardine, as well as the condition of anchovy have strongly declined over the last decade, causing an important fishery crisis (Saraux et al., 2014, 2019). In the meantime, abundance and biomass of sprat strongly increased. The present study investigated potential common trends in these three small pelagic fish, using several variables (abundance, biomass, condition and size) from 1993 to 2017. The first common trend opposed anchovy biomass to sardine abundance and biomass, indicating that the 2 species had quite different dynamics. This opposition between the two species is a well-known process in upwelling ecosystems (Alheit & Niquen, 2004; Csirke et al., 1996). Moreover, this opposition could suggest different responses of the both species to environmental changes, maybe linked to differences in their diet (Brosset et al., 2016a). This trend was associated to higher fluctuations of the population from the early 1990s to the mid of the 2000s and finally a third period with a low variability around intermediate levels until the end of the series. The second common trend, characterized by a strong and continuous decrease from the mid-2000s opposed the biomass of sprat to the mean size of the three fish species, the condition of sardine and anchovy and the biomass of sardine. This clearly confirms previous studies showing that the sprat might have profited from the decrease in size and condition of sardine and anchovy. Summarising the DFA results, it seems that the small pelagic fish community, represented by these three species, has significantly changed in the mid-2000s, with an increase in sprat biomass concurrent to a decrease in sardine and anchovy size and condition. Previous studies have suggested that such changes might be mediated by bottom-up control and a change in plankton (Brosset et al 2016a), we further investigated the link between environment and small pelagic fishes through a DFA on the 10 biological time series using the environmental time series as covariates. However, after model selection based on AICc, the best model did not retain any exploratory variable. Such a result may reflect that only indirect links were present between the small pelagic fish community and environment, e.g. through the plankton community, or that the small pelagic fish community was not affected by a single given environmental variable, but rather by a global environmental change that would combine several abiotic processes. This second hypothesis was supported by the comparison of the 2 DFA (the environmental one and the biological one). While both datasets were totally independent, we obtained two very similar trends, showing a co-variation of the environment and the small pelagic community. Indeed, both second common trends displayed a rather stable phase from 1993 to 2003, then 2 years of increase, followed by a sudden and sharp decrease and then a stabilisation in the most recent years. As all statistical analyses, the results from the DFA do not demonstrate for any causal link between environmental conditions in the Gulf of Lions and the small pelagic fish community, but the synchrony of the two common trends questions. Interestingly, Brosset et al., (2016a) found with isotopic analysis that the dietary of anchovy, sardine an sprat changed between 2005 and 2010 and remained the same since 2010. This suggests that the plankton community have possibly been also impacted by those environmental changes. Our results thus tend to indicate that the environmental conditions have broadly changed in the Gulf of Lions, with a major change in the mid-2000s, affecting the Chl-*a* concentration (which showed a breakpoint in 2007), but also the SST, the upwelling and frontal activities, the Rhone river discharge (and particularly the N and P nutrients inputs). Those changes could have affected plankton production and consequently the small pelagic fish community that displays similar patterns of variations as the environmental conditions. If changes in the food of small pelagic fish is our first hypothesis to explain changes observed in the small pelagic community, other ones could also be investigated. Indeed, the increase of sprat abundance could have led to an increase of competition with sardine and anchovy, inducing their decrease. Surprisingly, sprat seems to better accommodate than sardine and anchovy to environmental changes in the Gulf of Lions despite the global warming observed. An hypothesis is that with the increase of upwelling, cells of cold water are present near to the coast and favourable for sprat, allowing them to support increasing temperature. However, because sardine are strongly present at the coast (Saraux et al., 2014), we can assume that the competition between both species will increase with the increase of SST as the sprat could be more and more associated to those coastal areas of cold water. Moreover, this hypothesis could explain the differences observed between sardine and anchovy biomass, with the biomass of anchovy decreasing since early 2000s probably in response to environmental changes and the biomass of sardine decreasing abruptly in mid 2000s, possibly in response of the strong increase of the biomass of sprat. Those different results are then definitively in agreement with the hypothesis of a bottom-up control, but further analyses are needed to better understand the variability in the zooplankton community.

II-4.3 Large scale interactions

If environmental changes were observed at the scale of the Gulf of Lions with possible impact on small pelagic fish, changes at a larger scale are likely to have played a role on the Gulf of Lions. As already noted, global warming seems to strongly impact SST in the northwestern Mediterranean and possibly other key oceanic features that we did not investigate, such as the meso-scale circulation. In our study, we saw that the WeMO displayed high factor loadings on both common trends of the DFA performed on the environmental variables, indicating a link between the regional atmospheric circulation regime depicted by this index (see Martin-Vide and Lopez-Bustins 2006) and key oceanographic variables of the Gulf of Lions. Brosset et al., (2015) also found significant correlation between the WeMO index and sardine body condition, indicating that environmental variability at a larger scale could have indirect impact on the fish population dynamics. In the same way, (Martín et al., 2012) found a correlation between the annual WeMO index and the landings of sardine and anchovy of the Catalan coasts, with the hypothesis that positive WeMO phase were associated to a better recruitment and favorable condition for small pelagic fishes.

Moreover, around 2006, changes have been observed in North Western Mediterranean Sea at different places and for different compartments of the ecosystems. In the Gulf of Trieste in Adriatic sea, a decrease of Chl-*a* concentration was also observed in 2006, related to a decrease of river flow and nutrients inputs (Mozetič, et al. 2012). In the Ligurian sea, extrem convection event was observed in winter 2005-2006 and induced changes in the properties of the Ligurian Intermediate Water with a decrease of O_2 concentration and an increase of Temperature and density (Coppola et al., 2018). Then, if no clear links have been made yet between those different changes, the mid-2000s seems to be critical in the Western and Central Mediterranean Sea.

II-5 Acknowledgement

We thank the captain and the crew of the RV “l’Europe” as well as all the scientists on board for their assistance during the PELMED surveys. The authors express their thanks to the three anonymous reviewers who helped to greatly improve the manuscript. Part of this research was funded through the MONALISA project, which was co-funded by the European Union and the French Ministry of Agriculture in the framework of the European Maritime and Fisheries Fund (EMFF, grant number PFEA280017DM0910001) and by France Filière Pêche (France).

II-6 Supplementary materials

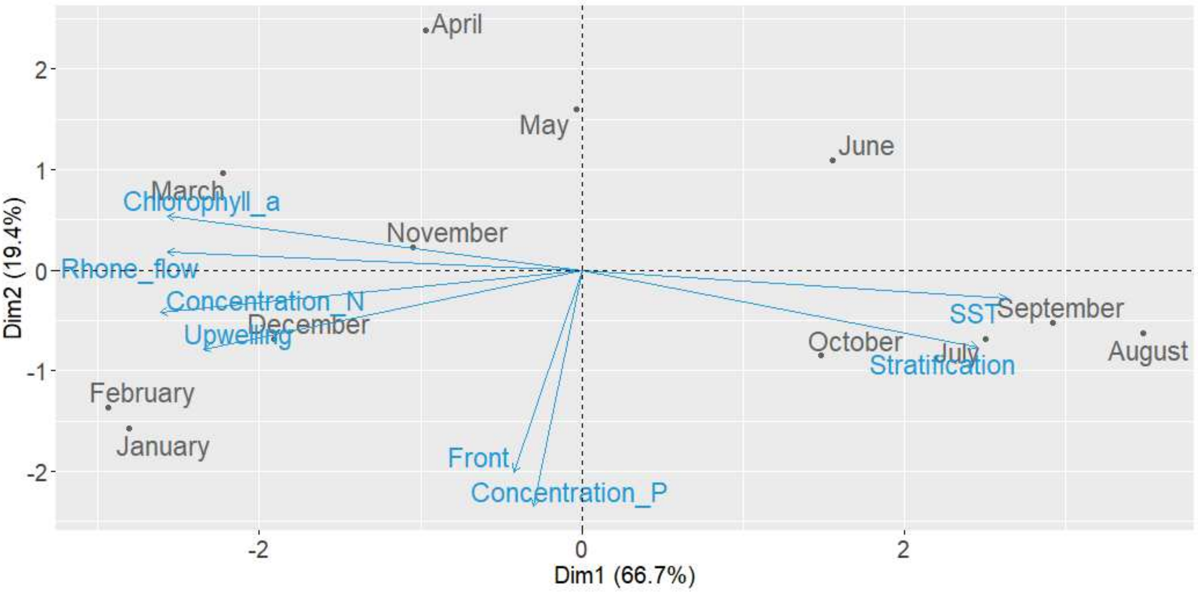

Figure II-8 ***PCA of the climatological time series (i.e. the mean value of each month during the period 1998-2017).***

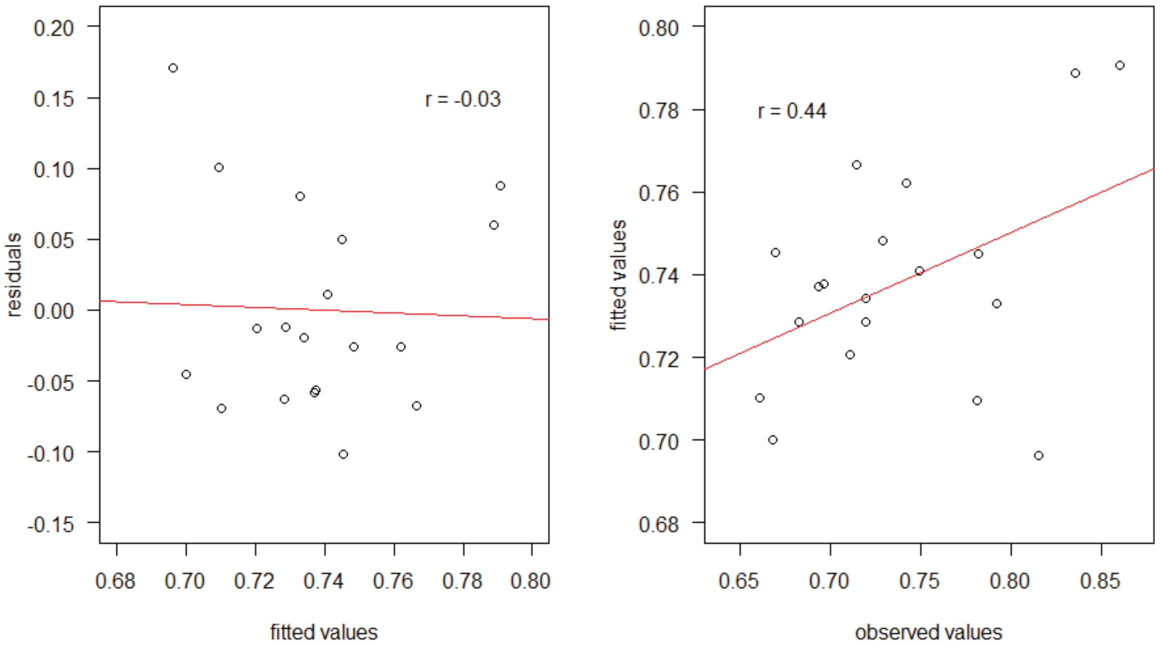

Figure II-9 ***Diagnostic plots of glm analysis with the N inputs as the only explanatory variable of Chl-a concentration. The left plot is residuals versus predicted Chl-a values and the right plot is predicted Chl-a values versus observed Chl-a values.***

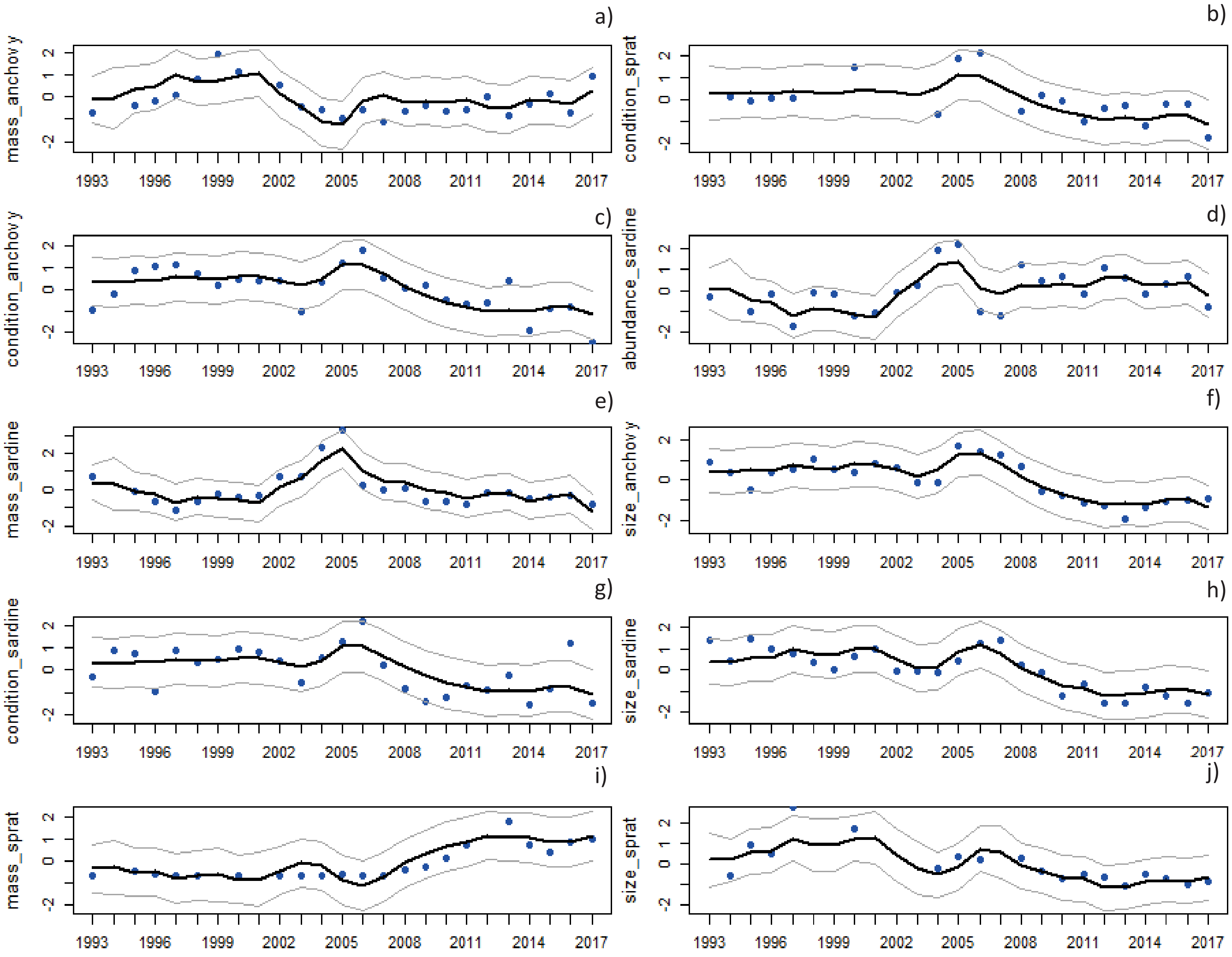

Figure II-10 *Standardized observed values (blue points) and fitted curves obtained from the best model of the DFA performed on the 10 biological time series from 1993 to 2017.*

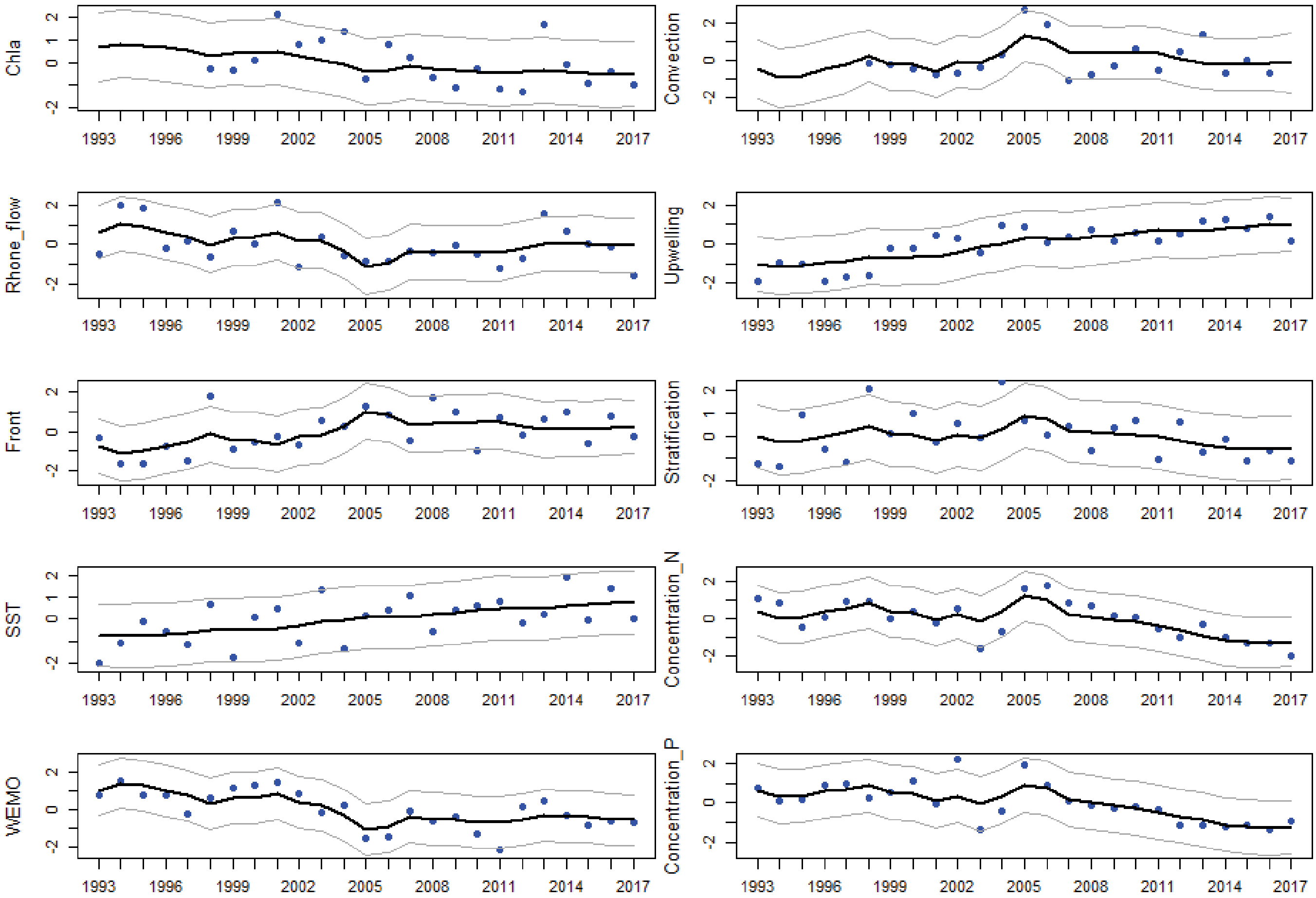

Figure II-11 *Standardized observed values (blue points) and fitted curves obtained from the best model of the DFA performed on the 10 environmental time series from 1993 to 2017.*

Detailed analysis of upwelling event

The impact of coastal upwelling on the primary production was further studied at a daily resolution, testing whether an upwelling event produced an increase of the Chl-*a* concentration. Only Agde and Cassis upwelling areas were studied because of the proximity of the Rhone River plume with Beauduc upwelling area. Because daily time series presented high level of autocorrelation, significance of the correlation test was corrected by the autocorrelation of the time series (Pyper & Peterman, 1998).

While upwelling indices had no effect on global annual Chl-*a* concentration, we investigated whether it could have more local impacts on Chl-*a* at a fine time scale using detailed analyses on the upwelling cells of Cassis and Agde. First, SST decreased when upwelling was stronger in spring, summer and autumn, for both Cassis and Agde areas. Correlation was the highest in summer at Cassis (r= -0.47, p < 0.001) and in spring and summer at Agde (r = -0.35, p < 0.001) (Table 1). Conversely, there was no effect in winter for both areas because of homogenous water column. Regarding the impact on Chl-*a*, the concentration increased when upwelling was stronger, in all four seasons at Cassis with the maximum correlation in autumn (r= 0.38, p < 0.001) (Table 1). At Agde, there was a positive and significant correlation only in spring and summer with the maximum in summer (r= 0.3, p < 0.001). Therefore, upwelling have the most positive impact on primary production in Summer and Autumn, when conditions are mostly oligotrophic (Summer and Autumn representing respectively 16% and 21% of the yearly primary production).

Table II-1 ***Spearman correlation between Chl-a, SST and upwelling index at Cassis and Agde upwelling area for different season.***

	Cassis		**Agde**	
	Chl-*a*	**SST**	**Chl-*a***	**SST**
Spring	r = 0.2 ; p < 0.01	r = -0.37 ; p < 0.001	r = 0.22 ; p < 0.01	r = -0.35 ; p < 0.001
Summer	r = 0.31 ; p < 0.001	r = -0.47 ; p < 0.001	r = 0.3 ; p < 0.001	r = -0.35 ; p < 0.001
Autumn	r = 0.38 ; p < 0.001	r = -0.23 ; p < 0.01	r = 0.04 ; p > 0.05	r = -0.2 ; p < 0.05
Winter	r = 0.14 ; p < 0.05	r = -0.1 ; p > 0.05	r = 0.06 ; p > 0.05	r = -0.02 ; p > 0.05

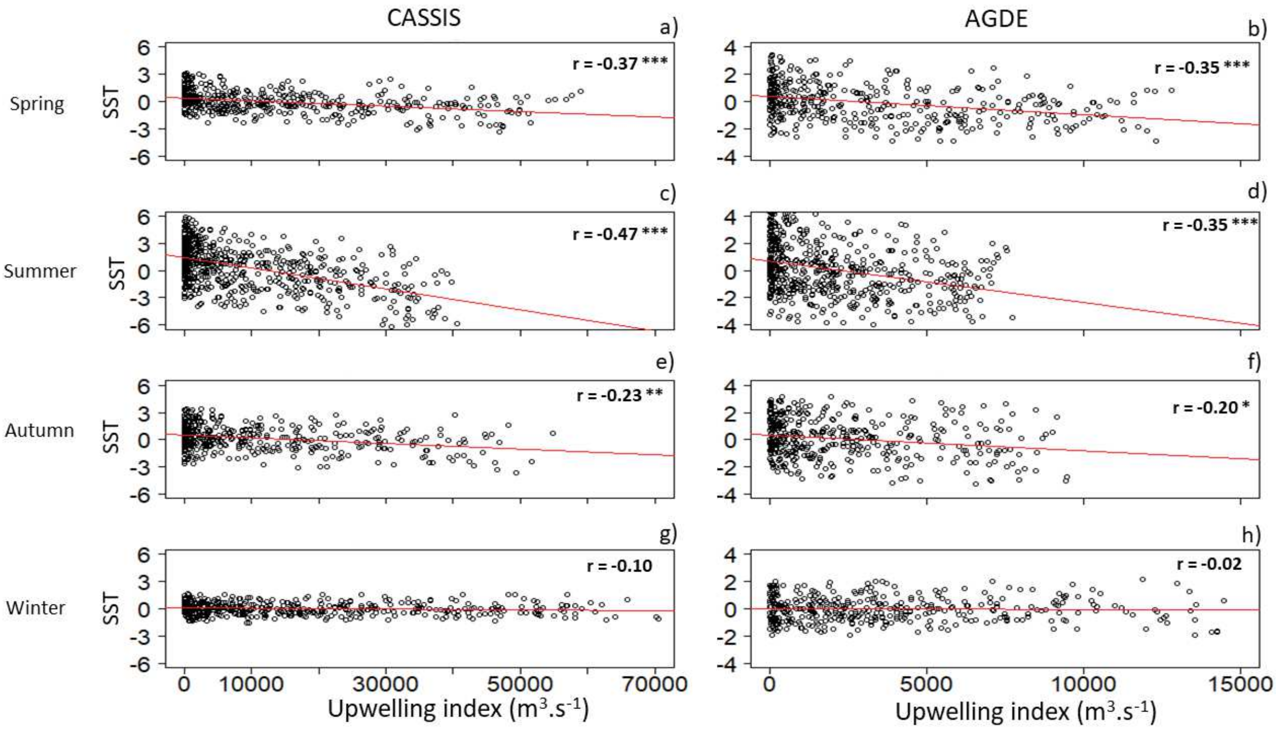

Figure II-12 *Spearman correlation between daily SST anomalies (i.e daily data corrected by the mean of each month) one day after the upwelling event and the upwelling index at Cassis and Agde for the different seasons* ***(oceanic season: winter is December, January, February).***

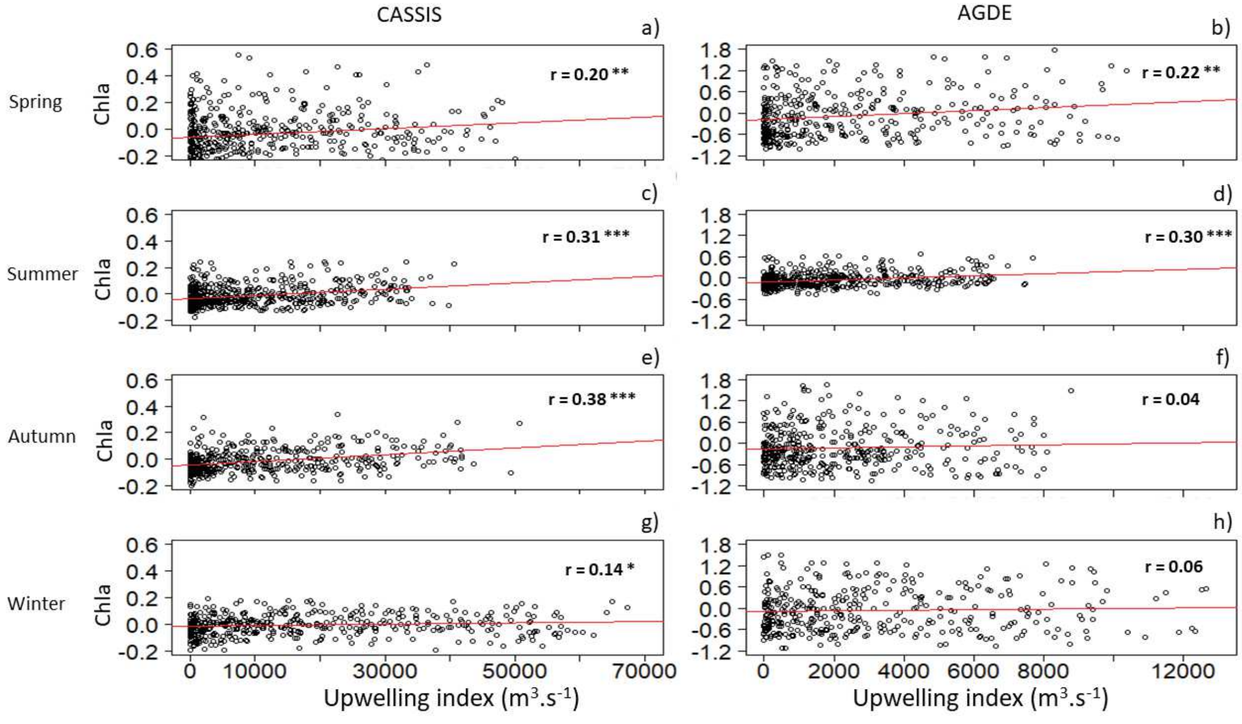

Figure II-13 *Spearman correlation between daily Chl-a anomalies (i.e daily data corrected by the mean of each month) one day after the upwelling event and the upwelling index at Cassis and Agde for the different seasons* ***(oceanic season : winter is December, January, February).***

Résumé du chapitre 2 et introduction au chapitre 3

Dans le deuxième chapitre, nous avons vu que la production planctonique du Golfe du Lion semblait diminuer comme l'atteste la baisse de concentration en chlorophylle observée en 2007. Nous avons trouvé que le Rhône apparaissait comme un acteur principal de la dynamique de la chlorophylle sur le plateau, suggérant son impact fort sur la communauté planctonique. Cette baisse de chlorophylle est en partie liée à une diminution des apports en nutriment du Rhône, ses concentrations en azote et phosphates ayant fortement diminuées au cours des 20 dernières années. Si cet appauvrissement a pu possiblement avoir un impact sur les populations de petits pélagiques, il semblerait néanmoins que ces derniers ne répondent pas à un unique processus mais plutôt au système environnemental dans son ensemble, considérant aussi bien l'environnement local comme les fronts thermiques, les upwellings ou les apports du Rhône que des forçages à large échelle, synthétisés par l'indice WeMO ou la température associée au réchauffement global des eaux méditerranéennes. Ainsi, si des changements semblent s'opérer au niveau de la dynamique planctonique (représentée par la concentration en chlorophylle) et des forçages environnementaux, synchrones avec la dynamique des poissons, aucune information n'est disponible concernant le compartiment zoo-planctonique, directement lié aux petits pélagiques. De plus, la question se pose du type de changement s'opérant dans la communauté phytoplanctonique conduisant à cette baisse de concentration en chlorophylle. Ainsi, le chapitre 3 aura pour objectif d'étudier plus en détail les communautés phyto- et zoo-planctoniques sur le plateau du Golfe du Lion en Juillet à partir des données issues des campagnes PELMED. Une étude passée ayant mis en évidence une certaine spatialité dans la distribution des biomasses des différentes espèces de petits pélagiques en Juillet sur le plateau, la variabilité spatiale du plancton sera regardée à partir de modèles linéaires. Afin de déterminer les différents types de communautés présents à cette période de l'année, un clustering sur les différentes stations de phyto- et zooplancton sera fait. D'éventuelles relations entre phyto- et zooplancton seront regardées afin de voir si certaines chaines planctoniques caractéristiques peuvent se mettre en place, notamment par le biais d'alternances de dominances entre dinoflagellés et diatomées. De même, d'éventuelles relations entre les différentes communautés planctoniques observées et l'environnement seront étudiées de façon qualitative par le biais de spider diagrammes. Enfin, la densité et proportion des différents groupes de zooplancton seront comparés entre les stations où les poissons présentaient les meilleures/moins bonnes conditions afin de cibler ceux pouvant potentiellement jouer un rôle dans la variabilité de la condition corporelle des petits pélagiques.

Chapitre III. *Variability in phyto- and zooplankton summer communities in the Gulf of Lions and relationship with small pelagic fish condition*

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Keywords: Environmental change, Bottom-up control, plankton community, Small pelagic fish, Northwestern Mediterranean Sea.

Abstract

An important decrease in small pelagic fish condition and size has been observed in one of the most productive ecosystem of the Mediterranean Sea, the Gulf of Lions, since 2008, leading to an important fishery crisis. Previous studies suggested bottom-up control to be the most probable cause for these changes supposing phytoplankton and zooplankton community changes. Here, we investigate the summer phytoplankton and zooplankton community based on samples from PELMED survey for several years between 1995 and 2019. Our objective was to determinate the summer phytoplankton and zooplankton community composition and identify potential characteristically links between both and with the environment. A second objective was to identify potential relationship between zooplankton groups and small pelagic fish condition in order to identify the ones that could potentially affect small pelagic fish condition. Our results showed a strong dominance of diatoms in phytoplankton community, mainly with *Chaetoceros*, *Leptocylindrus* and *Proboscia* but with some few samples dominated by dinoflagellates like in 2008 with *Gymnodinium*. The zooplankton was dominated by cladocerans, mainly *Penilia* and *Evadne* or Copepods like *Clausocalanus*, *Oithona* and *Centropages.* No clear relationship was identified between phytoplankton and zooplankton, neither with the environment. Concerning the links between zooplankton and fish condition, *Clausocalanus*, *Penilia* and *Doliolida* was identified to be more linked to fish in bad condition whereas *Oithona* and *Evadne* were more linked to fish on good condition. Those results suggest a potential importance of the zooplankton community for fish condition, however, more data should probably be necessary to further investigate those relationships and understand the mechanism driving the plankton community.

III-1 Introduction

Bottom-up control is one of the key processes structuring ecosystems, where the biomass of each trophic level is regulated by the resource availability (Cury & Shannon, 2004). It is opposed to the top-down control where the biomass of each trophic level is determined by the predators (Worm et al., 2002). In marine ecosystems, bottom-up control is generally believed to be the main control process, with phyto- and zoo-plankton at the basis of the food web controlling forage fish at the central position (often small pelagics), themselves transferring energy from plankton to higher trophic levels (Cury et al., 2000; Larkin, 1996). As a consequence, this cascading transfer of energy is closely linked to environment as phyto- and zoo-plankton could have rapid responses to environmental changes and impact first small pelagic fishes with possible modifications up to the highest trophic levels (Beaugrand & Kirby, 2010; Lynam et al., 2017).

Environmental changes can for example impact phytoplankton phenology, modifying the timing of bloom as observed in the Northwest Pacific for instance, with changes in temperature and upwelling strength delaying the phytoplankton bloom and impacting zooplankton size (Kudela et al., 2006). Such changes are known to directly affect small pelagic fish recruitment, and subsequently fish population size, either positively (match) or negatively (mismatch) (Cushing, 1990). In upwelling systems, intensity of cold water mixing have been found to favor diatom chains, large copepods and anchovy dominance whereas warmer and stratified waters leads to chains of small dinoflagellates, small copepods and sardine dominance (Tam et al., 2008; Van der Lingen et al., 2006). Those alternation in the plankton community are a well-known and studied phenomenon in upwelling systems, however, fewer information are available about such alternation in the plankton structure in other less productive areas like the Mediterranean sea. Such process started to be investigated in North-Western Mediterranean Sea (NWMS), based on fish stable isotope analyses but the question still remain (Cardona et al., 2015; Pethybridge et al., 2014). In the Gulf of Lions located in NWMS, the Rhone river flow was identified as one of the main factors influencing primary production on the shelf, according to Chla satellite concentration (Feuilloley et al., 2020; Lefevre et al., 1997; Macias et al., 2018). Small pelagic fish seemed however to respond not only to the river flow and chla concentrations but rather to the global environmental system as several factors seemed involved in addition to river flow and chla concentration such as the temperature and the WeMO index (Brosset et al., 2015; Feuilloley et al., 2020). Then, as for upwelling systems, the quantity of food available (estimated by Chla concentration) could be not the only driver but also to the quality of food, depending of the plankton community composition and driven by the environment. Understanding how the plankton community varies in North Western Mediterranean sea in terms of taxonomic composition appears then also of primary importance as it could be an important driver of several small pelagic fish commercial species.

In the Gulf of Lions, as well as in other areas of NWMS, a strong decrease in size and body condition have been observed in small pelagic fish population since the late 2000s, mainly for sardine and anchovy (Brosset et al., 2017; Saraux et al., 2019; Van Beveren et al., 2014), leading to a drop of the landings and a real crisis for the fishermen. Interestingly, if the abundances varied, they did not display any trend and recruitment of sardines and anchovy remained at average to good levels (Van Beveren et al., 2014). While top-down control hypotheses have already been refuted, whether by fisheries or top predators (Queiros et al., 2018; Saraux et al., 2019; Van Beveren et al., 2016a, 2017), a potential dietary shift for sardine and anchovy has been suggested by stomach content and stable isotope analyses (Brosset et al., 2016a; Costalago et al., 2012). Indeed, the diet of sardines seemed to have shifted from large size prey, with a high contribution of cladocerans over 1 mm before 2008 to smaller prey, with copepods less than 1 mm such as *Microsetella* and *Oncaea* in the most recent years (Brosset et al., 2016a). Similarly for anchovy, large copepods such as *Clauso-Paracalanidae* were replaced by smaller ones, mainly *Microsetella* and *Oncaea* after 2008. Moreover, the biomass of sprat started to increase, concomitantly with the decrease of sardine and anchovy suggesting a possible competition between species for resources as all started to feed on the same prey since 2007 (Brosset et al., 2016a). Small pelagic fish seemed then to feed on smaller prey than before, possibly due to modification of the phyto and zooplankton community, which could potentially lead to a decrease of energetic incomes and explain the body condition decrease and over-mortality (Saraux et al., 2019).

However, long-term phyto- and zoo-plankton time series are very scarce in the NWMS making the study of the interactions between phytoplankton, zooplankton and small pelagic fish difficult. Fisheries survey were initially only focused on fish sampling to estimate stock variability of commercial species but started to become in the last decade more ecosystemic, performing also phytoplankton and zooplankton samples in order to have a broader vision of the ecosystem (Doray et al., 2018; Petitgas et al., 2018). This is the case for the PELMED survey (Bourdeix & Hattab, 1985) which is the only one sampling small pelagic fish, phyto- and zooplankton in the whole Gulf of Lions every year in summer. However, as the main goal of this survey remain to estimate small pelagic fish stocks and not the plankton community, samples are performed in summer, the optimal period for fish but not for plankton for which maximum densities are found in late winter and spring (Chen et al., 2019; García-Martínez et al., 2019; Gaudy et al., 2003). Moreover, in case of bad weather for example, fish trawl are prioritized instead of plankton samples, possibly leading to unbalanced plankton sampling between years. Few studies about the phyto- and zooplankton community composition have been done in the Gulf of Lions, only based on punctual samples (Costalago et al., 2014; Gaudy et al., 2003) or spatially restricted (Chen et al., 2019). Based on PELMED data, the first objective of this work was then to characterize the phyto- and zooplankton community in summer over the whole shelf of the Gulf of Lions, considering up to 11 years sampled. Saraux et al., (2014) highlighted spatial structure in small pelagic fish biomass estimated during PELMED with sardine being more coastal compared to anchovy. However, the condition of fish had not been spatially studied yet. The second objective of this study was then to investigate the spatial distribution of the phyto- and zooplankton community and fish body condition in order to determine if the fish spatial distribution could be related to the phyto- and zooplankton distribution. The third objective was to characterize potential changes in the zooplankton community, in relation with environment. Then, potential characteristic chains between phytoplankton and zooplankton were investigate, with a focus on diatoms and dinoflagellates. Finally, the relationship between the zooplankton community composition and density and the condition of small pelagic fish was investigated to identify potential changes in the zooplankton possibly responsible of the small pelagic body condition decrease in the past 2 decades.

III-2 Material and methods

All samples were collected during the PELMED scientific survey (Bourdeix & Hattab, 1985), occurring in July, thus representing the summer situation (July) and intra-annual variability could not be estimated.

III-2.1 Fish condition sampling

Small pelagic fish have been sampled during the PELMED scientific survey (Bourdeix & Hattab, 1985), every July since 1993. The objective of this survey is to assess the stock of small pelagic fish (anchovy, sardine and sprat) in terms of abundance and biomass, using acoustic detection and identification trawls in the Gulf of Lions. Depending on the year, between 20 to 50 trawls were conducted in July over the entire shelf following 9 transect. Fish individuals were randomly sampled from the trawls to take measurements such as weight, length and gonad maturity. As the species exhibited an allometric growth pattern (Brosset et al., 2015; Van Beveren et al., 2014), body condition was estimated with the Le Cren index (Le Cren, 1951) which avoids a potential length effect (Brosset et al., 2015). The index was expressed as:

$$K_n = \frac{W}{W_r} \qquad (3)$$

With W the observed weight in g and W_r the theoretical weight of an individual calculated with

$W_r = \alpha L^{\beta}$, where α and β are the regression parameters of the length–weight relationship with $\alpha = 3.86 \times 10^{-3}$, 5.90×10^{-3} and 3.21×10^{-3} and $\beta = 3.20$, 3.10 and 3.37 for anchovy, sardine and sprat respectively (Van Beveren et al., 2014). Because some very small individuals presented extreme values of conditions, possibly due to errors in mass (difficulty to weigh at sea), a limit in size was considered for the 3 species in order to remove the smallest individuals and avoid bias in condition index. Based on the size distribution of the individuals of the 3 species, the limits were defined at 7.5cm for sardine, 9cm for anchovy and 7cm for sprat (see SM-Figure III-11).

III-2.2 Plankton sampling

Since 2014, phyto- and zoo-plankton samples have been performed at the beginning and end of each transect as well as after trawls in order to have a good coverage of the shelf. Phytoplankton was also sampled in 2007-2008 and zooplankton in 1995-1996-2007-2008-2013, albeit under a less strict spatial design (but for zooplankton in 2013). Further, due to bad weather conditions in 2014, the number of samples was lower that year. Zooplankton was sampled with a WP2 (200µm mesh size) towed vertically from bottom to surface and samples conserved in formaldehyde 5%. Back to the lab, individuals were identified with binocular, when possible at the species or genus level, by the same person for all samples except for the years 1995 and 1996. Phytoplankton samples were collected with niskin bottle at the surface and the maximum chlorophyll depth in 2007, 2008 and since 2016 and only at the surface in 2014 and 2015. The maximum chlorophyll depth was determined based on fluorimeter profile. Samples were then conserved at 4°C after addition of Lugol. Identification was performed with microscope, at the species or genus level, always by the same person for all the samples.

III-2.3 Fish trawl and plankton station associations

Because some plankton stations, especially at the beginning and end of each radial, were performed without trawl, we decided to associate each zoo- and phytoplankton stations to the nearest trawl, in a limit of 30km. This limit of 30km was determined based on the relative spatial homogeneity of fish condition in this geographical range, according to mantel correlogram. However, plankton stations and trawl were generally closer as the mean distance for the associations was 6.3km and the median distance was 2.3km. A delay of +/- 1 day was allowed for the association as some trawls were performed at the end of the day and plankton sampled the next day early in the morning. Zooplankton and phytoplankton were generally sampled together but in few cases one was missing because of the lost of the sample or differences in the number of samples funded for both. All the stations and possible associations are represented in the map Figure III-1. In a few cases, trawl, zoo and phytoplankton stations could not be associated (indicated as *alone* on the map).

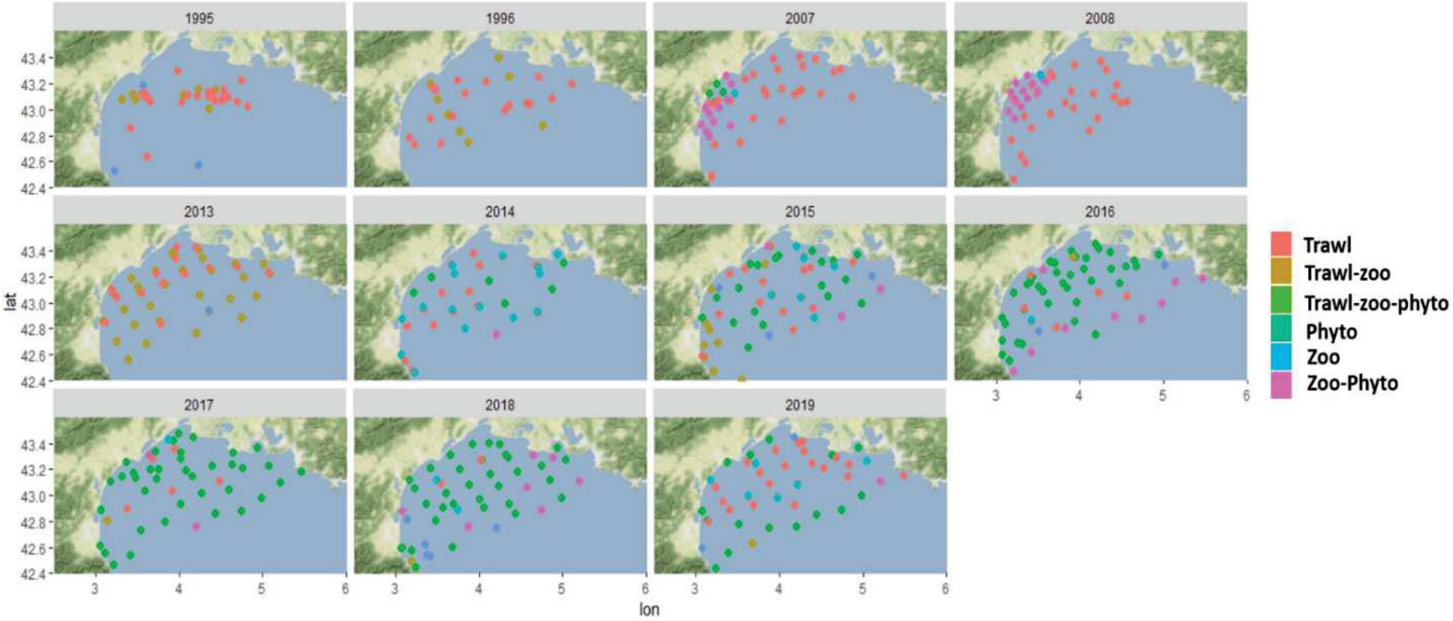


Figure III-1: *Map of the different stations and possible associations between fish Trawl, zooplankton and phytoplankton for each year from 1995 to 2019.*

III-2.4 Description of the phytoplankton and zooplankton community

Zoo- and phytoplankton were studied at the genus level and only groups representing at least 1% of the community over all stations and the whole period were conserved. The log density was considered, (log Ind.m^{-3} +1) for zooplankton and log biovolume (log µm^{-3}.L^{-1} +1) for phytoplankton. In order to characterize the global summer community of phytoplankton and zooplankton, 2 PCoA were performed based on Bray-Curtis dissimilarity matrix of log densities of zooplankton and log biovolumes of phytoplankton (as explained below in section 2.6 surface phytoplankton community was considered in this study).

III-2.4.1 Plankton and fish condition spatial variability

The spatial variability of phyto- and zooplankton was investigated through linear models between the 2 first axis of each PCoA and the longitude/bathymetry in order to investigate East-West or bathymetric gradient in both community composition. Both longitude and bathymetry were incorporated in the models and backward variable selection was performed to keep only significant relationship. Same models were performed between total log densities/biovolumes of zooplankton/phytoplankton and longitude/bathymetry. Similarly, the spatial variability of fish body condition was investigated testing linear relationship between anchovy, sardine and sprat condition and the longitude/bathymetry of each trawl. Only significant relationships are presented in the results.

III-2.4.2 Analyses of the different plankton communities

To differentiate between communities, a hierarchical clustering analysis was performed on the Bray-Curtis dissimilarity matrix based on log densities/biovolumes of each group at each station. The Ward's algorithm was preferred to others as it presented the highest value of agglomerative coefficients. The agglomerative coefficient has a dimensionless range between 0 and 1, with small values indicating no clustering pattern and large values indicating a distinct clustering structure (Kaufman & Rousseeuw, 2009) (SM Table III-1). The optimal number of cluster of each dendrogram was determined by applying the Kelley–Gardner–Sutcliffe penalty function (KGS). This function maximized the differences between the groups and the cohesiveness within the groups. Its minimum value corresponds to the optimal number of clusters (Kelley et al., 1996).

Then, to compare communities, dendrogram were compared, only considering the stations where both community were sampled. For that, a measure of entanglement was done with the dendextend R package between both dendrogram after rotating the branches using the "step_2side" permutation function for visual correspondence (Galili, 2015). To compare the correlation of the 2 dendrograms, the Baker's gamma index was also calculated (Baker, 1974). Baker's Gamma Index is a measure of similarity between the structure of two dendrograms. The value can range between -1 to 1 with near 0 values meaning that the two trees are not statistically similar (see ESM for further details about the index). This procedure was first applied to compare surface and maximum chlorophylle depth phytoplankton community. As consistent results were obtained between both depths, with a Baker's gamma index of 0.41 between both dendrogram, surface phytoplankton was considered as it allowed to consider the years 2014 and 2015 not sampled at the maximum chlorophyll depth (SM Figure III-12 and 13). The same analyses were performed to compare the zooplankton community to the surface phytoplankton community, based on the stations where both were sampled.

III-2.5 Environmental data in relation with plankton

In order to test for a potential link between phyto or zooplankton community and environment, annual time series of different environmental parameters were constructed.

III-2.5.1 Rhone river and WeMO index

The river flow was measured at Beaucaire station and covered the period 1993-2019 at a daily resolution. Those data are available on (http://www.hydro.eaufrance.fr).

The WeMO index was considered because of its capacity to represent NW Mediterranean Sea environmental conditions (Martin-Vide & Lopez-Bustins, 2006). This index represents differences in standardized surface atmospheric pressure between San Fernando (Spain) and Padua (Italy) and integrates fluctuations in rainfall, river flow, wind mixing and temperature. Positive values of the index are associated to favourable plankton conditions with lower temperature and higher river flow and wind mixing (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012). The annual index was preferred to the winter index as it has already been shown to have an importance for small pelagic variability in the NW Mediterranean Sea (Brosset et al., 2015; Martín et al., 2012). The WeMO monthly data were downloaded on the University of East Anglia website (https://crudata.uea.ac.uk/cru/data/moi/).

As plankton and fish were sampled in July, we considered the environmental conditions prior to this period by averaging for each year t from August the year t-1 to June the year t.

III-2.5.2 Sea surface temperature (SST)

Sea surface temperature (SST) was estimated using the Advanced Very High Resolution Radiometer (AVHRR) daily data from 1993 to 2019 at a 4km resolution, obtained on the NASA platform (https://data.nodc.noaa.gov/pathfinder/Version5.3/L3C/). For each pixel, the maximum value between day and night was kept and a specific cloud mask was applied as in (Feuilloley et al., 2020). This mask, applied on each daily data used the departure from a monthly climatology, considering a variable threshold according to temporal variability of the SST at each pixel. A monthly SST time series was then built over the continental shelf, until the 200m isobaths, averaging all available data during each month.

The annual SST was then separated in two time series, the winter SST averaged from January to March and the spring SST averaged from April to June as temperature in winter and spring are one of the main factors modulating phytoplankton spring bloom (Trombetta et al., 2019).

III-2.5.3 Chl-*a* concentration and bloom

Chl-*a* concentrations were estimated using L3 daily data MODIS Aqua portal at 4km resolution from 2003 to 2019 (https://oceancolor.gsfc.nasa.gov/l3/order/). Anomalous high values of concentration were detected at very coastal pixels and in the Rhone plume. These were thought to derive from turbidity i.e. water belonging to the "case 2" optical properties as defined by (Morel & Prieur, 1977), generally not compatible with the fluorescence to concentration algorithm (Gohin, 2002; Gohin et al., 2005). As such, concentration data were truncated to a maximum value of 5µg/L, allowing to keep high but reasonable values and so to avoid any potential overestimation of the Chl-*a* concentration on the shelf as in (Feuilloley et al., 2020). Daily data was then aggregated, averaging data in octad, 4 equal time periods per month without overlaps between months compared to classical calendar weeks. An annual time series was then built over the continental shelf, until the 200m isobaths, averaging octad mean values from August year t-1 to June year t. Because an annual mean could translate very different processes, such as a short but strong bloom *versus* a long more diffused bloom, we constructed other chlorophyll indices. To characterise the variability of the Chl-*a* in different years, the coefficient of Variation

(CV_chla) was computed based on octad data from August year t-1 to June year t. Finally, the bloom was characterised in terms of initiation date and duration. For that, the cumulative sum of octad concentration was computed and the date of initiation was considered to be the moment where 15% of the total cumulative sum was reached for each year. The end of the bloom was considered when 85% of the total cumulative sum was reached. The duration of the bloom was considered as the number of octad between the beginning of the bloom and the end of the bloom. The threshold values 15% and 85% were visually selected but different tests for the sensibility of the threshold were performed (SM Figure III-14) and similar results were obtained as correlation of 0.87 was obtained for the duration bloom comparing the threshold 15%-85% with the threshold 10%-90% and 0.9 when comparing with 20%-80%. Concerning the date of initiation, correlation of 0.85 was obtained for the duration of the bloom comparing 15%-85% with 10%-90% and 0.88 comparing with 20%-80%.

III-2.6 Relationship between zooplankton and fish condition

In order to investigate potential relationship between fish condition and zooplankton community, a PCoA based on Bray Curtis dissimilarity matrix of log zooplankton densities was performed based on all the stations where the association between zooplankton and trawl was possible. The stations in the PCoA were colored based on the condition of the fish. Only the Sardine and Anchovy condition were considered for the color gradient as Sprat was less sampled compared to the others. Zooplankton densities were fitted in the ordination plot with the envfit function from the “vegan” R package. Finally, linear models were performed between the condition of the 3 fish species and the PC1/PC2 of the PCoA and zooplankton total densities in order to consider the impact of food quality as well as the food quantity on fish condition. Because collinearity was observed between the PC1 of PCoA and total zooplankton (Variance inflation factors values over 5) the different plankton variable were investigated separately in relation with fish body conditions.

III-2.7 Comparison of « good condition stations » vs « bad condition stations »

To limit the importance of the noise in the data and because relationship between zooplankton and small pelagic fish could be non linear, a focus was made on the extreme stations presenting the highest and lowest conditions for anchovy, sardine and sprat to try to better discriminate zooplankton community related to fish in good and bad conditions. For this, a threshold of 15% was fixed and good condition stations were, for each species, the 15% highest ones and the bad condition stations were the 15% lowest ones. Then, t-tests were performed between the log densities and proportions of each zooplankton groups in stations of good and bad conditions. The 15% threshold represented a compromise between the number of stations considered, which has to be high enough to statistically test for differences between good and bad conditions, and the range of conditions covered by both groups which also needs to be sufficiently different. Nevertheless, analyses were tested with different threshold values in order to investigate the sensibility of the results to the threshold (SM Figure III-17 and 18).

III-3 Results

III-3.1 Zooplankton and phytoplankton summer community

In order to have a synthesis of the Zooplankton and Phytoplankton summer community, PCoA were performed on log densities Bray-Curtis dissimilarity matrix for zooplankton and log biovolumes Bray-Curtis dissimilarity matrix for phytoplankton. The 2 first axes explained 30.7% and 21.4% for the zooplankton and 43.9% and 15.4% for the Phytoplankton (Figure III-2). For the zooplankton, most groups were linked negatively to the first axis except for *Penilia*, Doliolida, *Pseudevadne*, which distributed along the second axis and *Oncaea* and other calanoida which were negatively linked to both. Similarly, the PCoA on Phytoplankton discriminated between a large number of groups positively linked to the first axis and *Gymnodinium* and *Heterocapsa*, that were positively associated to the second axis, *Tripos*, *Pleurosigma* and other phytoplankton that were negatively associated to the second axis, and *Protoperidinium* negatively associated to the first axis. Interestingly, the main groups associated to the second axis (*Gymnodinium*, *Tripos* and *Heterocapsa*) were dinoflagelates whereas the other groups associated to the first axis, except *Protoperidinium*, were mainly diatoms.

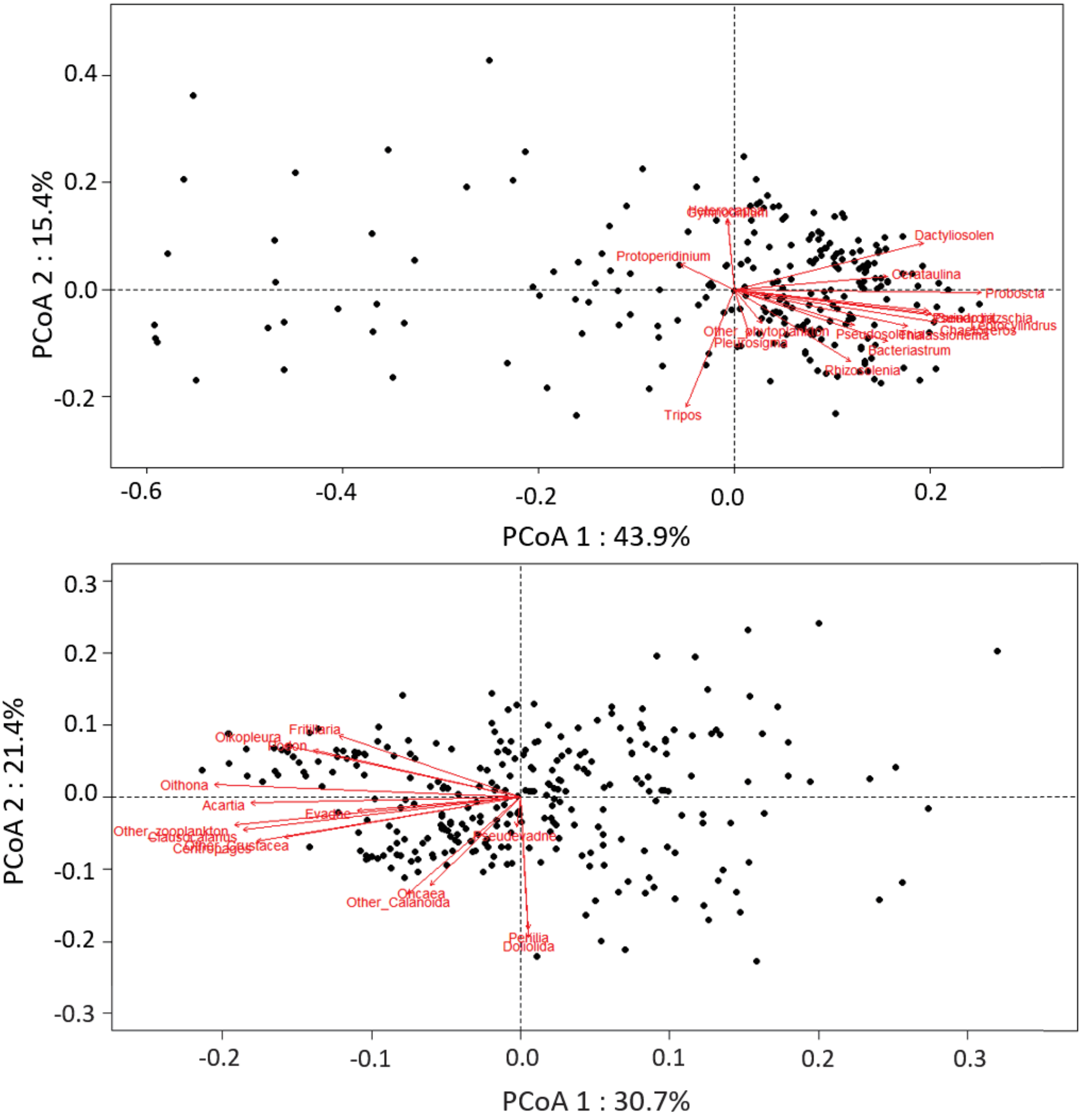


Figure III-2 *PCoA performed on Bray-Curtis dissimilarity matrix of log biovolume of surface phytoplankton based on all the stations sampled (top) and on Bray-Curtis dissimilarity matrix of log densities of zooplankton based on all the stations sampled (down). Black dots are all the stations sampled.*

III-3.2 Plankton community and fish condition spatial variability

The spatial variability of plankton community was investigated through linear models between the 2 first axis of zooplankton and phytoplankton PCoA or total log densities/biovolume and the longitude/bathymetry of the sampled stations. For the plankton, only the PC1 of phytoplankton presented a significant relationship with the longitude (slope=0.0682; p <0.001) but the very low R^2 value (0.0531) suggested that the East-West gradient effect was very low on the phytoplankton community. Moreover, outliers were found in the residuals of the model indicating that the relationship should be taken with caution (SM Figure III-15). No relationship was found between the zooplankton community or total density and the longitude. Concerning the bathymetric gradient, only the total phytoplankton and PC2 zooplankton presented significant (slope =0.0026; p<0.01 and slope=0.0003; p<0.05 respectively) but also very weak relationship (R^2=0.0320 and 0.0152 respectively), suggesting also only low effect of the bathymetry on the zooplankton and phytoplankton community. The dispersion of the data around the regression line highlighted a strong spatial heterogeneity, both for zooplankton and phytoplankton. As for the zooplankton and phytoplankton, the spatial variability of small pelagic fish condition was investigated. The sprat presented only significant negative relationship with the Longitude (slope=-0.0276; p<0.01) but very weak (R^2=0.0221) and outliers were found in the residuals of the model highlighting the poor quality of the model (SM Figure III-15). In the models of sardine and anchovy, both longitude and bathymetry were conserved and significant relationship were observed. Sardine presented a negative relationship with bathymetry (slope=-0.0006; p<0.001) and longitude (slope=-0.0257; p<0.001). For anchovy, negative relationship were also found with both bathymetry (slope=-0.0244; p<0.01) and longitude (slope=-0.0266; p<0.001). Both for sardine and anchovy, the spatial effect was very weak (R^2=0.0488 for sardine and 0.0482 for anchovy) and outliers were found in the residuals. As for the plankton, the dispersion of the data around the regression line highlighted a strong spatial heterogeneity. All those results seemed then to indicate the presence of strong variability over the shelf and no clear defined spatial pattern, both for the plankton community and fish condition.

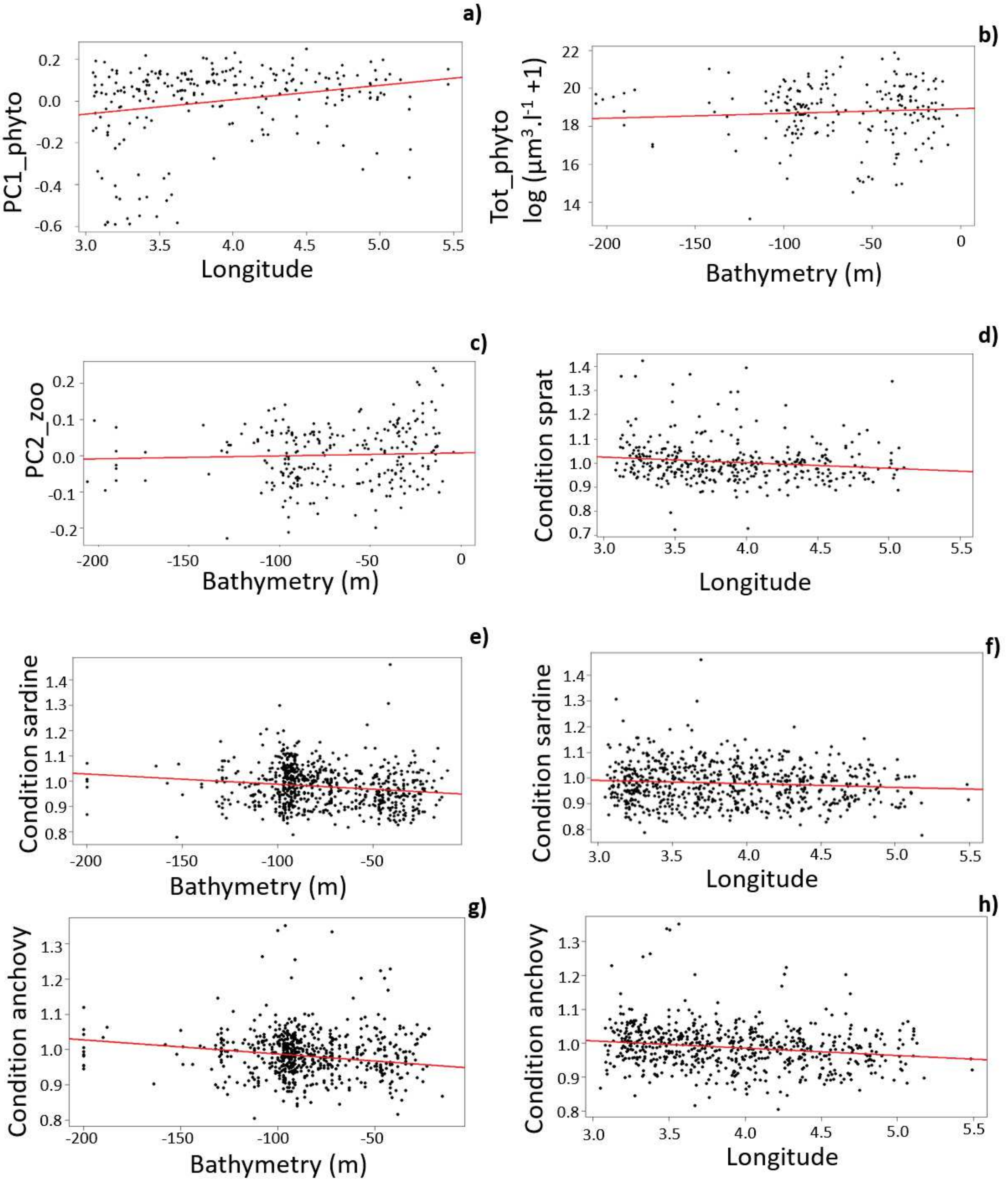


Figure III-3 *Linear models between first axis of PCoA performed on phytoplankton biovolumes and longitude (a), between total phytoplankton biovolume and bathymetry (b), between second axis of PCoA performed on zooplankton densities and bathymetry (c) and between sprat condition and Longitude in (d). For sardine and anchovy models, both longitude and bathymetry were considered. The lines in (e) and (g) represent the prediction of the model considering the bathymetry and a constant longitude, set to the mean longitude value. For (f) and (h), the longitude and the mean value of bathymetry are considered and prediction of the model represented by the red line.*

III-3.3 Zooplankton community and relationship with the environment

6 cluster were identified from the Hierarchical clustering of Bray-Curtis dissimilarity matrix calculated on zooplankton log densities at stations from 1995 to 2019 (Figure III-4).The cluster 1 was mainly composed of stations sampled in 2013 and characterized by strong proportions of *Clausocalanus*, *Oithona*, *Evadne* and *Acartia* representing respectively 25.6%, 17.7%, 12.5% and 11.9% of the total cluster (Figure III-4). Similar groups were present in top positions in the cluster 6 with *Clausocalanus* (19.9%), *Oithona* (10.9%) and *Evadne* (10.4%), however, *Acartia* (4.5%) was poorly represented. Compared to all the clusters, the proportion of Other zooplankton, was the highest in the cluster 6 (in second position with 13.6%). While this cluster was dominated by 2016, it was still the most diversified in terms of years with at least one sample of each year present except 1995 and 1996. Both cluster 1 and 6 presented a diversified community with no strong dominance (SM Figure III-16).

The stations of the years 1995 and 1996 were all grouped in the cluster 3, characterized by a strong dominance of Penilia (41.4%) but also Doliolida (13.9%) and *Clausocalanus* (13.3%). It was the only cluster with a strong proportion of Doliolida. The cluster 5 presented also a strong dominance of Penilia (43.4%) and then *Claucocalanus* (11.9%) and other zooplankton (7.6%).The years 2007 and 2008 were well represented in this cluster. The years 2016 and 2017 presented also a high proportion of the cluster, however it represented only a small part of the stations of those years (6/52 for 2016 and 5/42 for 2017). The cluster 4 was the one with the strongest proportion of Evadne (41.5%), then *Clausocalanus* (15.5%) and other zooplankton (6.5%). The year 2015 represented almost half of the cluster, however, only 21 stations composed this cluster separated in 6 different years. All those 3 cluster presented a strong dominated community, with the cluster 4 as the most dominated one (SM Figure III-16).). Finally, the cluster 2 seemed to present a more diverse zooplankton community, 10 groups presenting proportions higher than 5% (*Clausocalanus* (16.8%), Penilia (13.5%), Other *calanoida* (10.3%) and other zooplankton (9.3%) being the most abundant), although this could be due to the high number of stations (99). The rank frequency diagram showed however that the cluster was as well diversified as the cluster 6 (SM Figure III-16).). The years 2017 and 2018 were strongly present and represented more than 75% of the cluster.

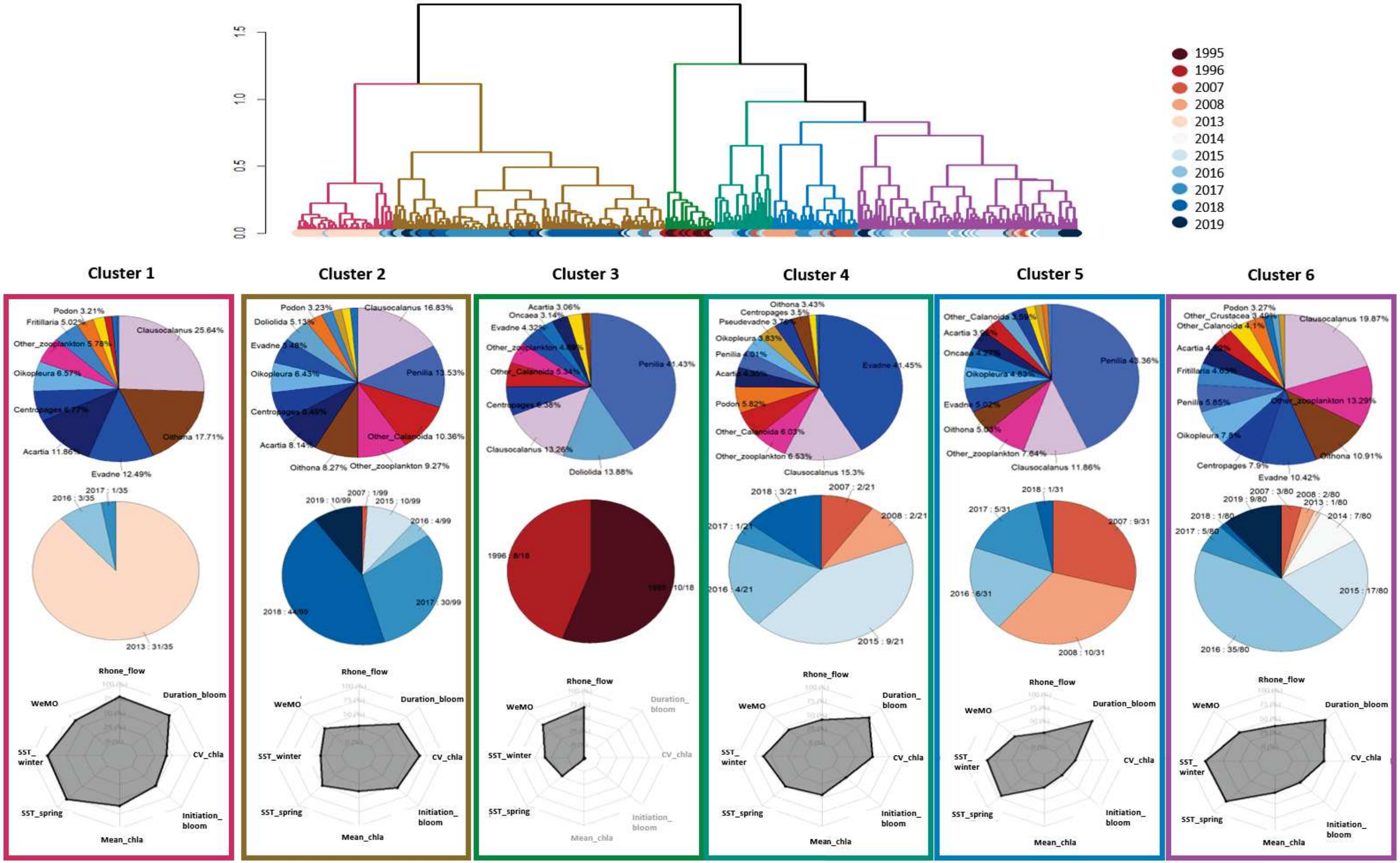


Figure III-4 *Dendrogram of hierarchical clustering performed on Bray-Curtis dissimilarity matrix based on zooplankton log densities at stations from 1995 to 2019. 6 clusters are identified with KGS criteria and colored on the dendrogram. Top Pie charts represent the mean community of each cluster, ordered as in the dendrogram and colored with the same color. In middle panels, the pie chart and number of stations of each years composing each cluster. In bottom panels, spider diagrams of the environment calculated as the mean of each years composing the cluster pondered by the proportion of each years. Each environmental variables are represented as a percentage, with 0% as the minimal annual value observed between 1993 and 2019 and 100% the maximum observed. Variable with no data available are set in grey.*

Concerning the relationship with environment, it is first important to note that chla satellite data were not available for the years 1995-1996 leading to a spider diagram shape different from the others. Strong variability was observed between clusters but no clear relationship with plankton community was observed. For example cluster 3 and 5 presented strong dominance of Penilia but opposed environmental variables. Indeed, cluster 3 presented strong river flow and WeMO but low SST in winter and spring whereas cluster 5 showed low river flow and WeMO but high SST in winter and spring. In another way, cluster 4, 5 and 6 presented this time similar environmental patterns with high bloom duration, low river flow and WeMO and high SST in winter and spring but zooplankton communities were different.

III-3.4 Relationship between phytoplankton, zooplankton and environment

The phytoplankton was studied based on surface samples as consistent results were obtained with maximum chlorophyll depth samples (see SM Figure III-12 and 13 for the comparison between community at the surface and deep chlorophyll maximum depth). A hierarchical clustering was performed on the Bray-Curtis dissimilarity matrix of phytoplankton biovolume for the stations where both phytoplankton and zooplankton were sampled and 5 clusters were identified (Figure III-5). A strong dominance of diatoms was observed, represented in green in the phytoplankton pie chart mainly with *Chaetoceros, Proboscia* and *Leptocylindrus* (Figure III-5). Clusters were strongly unbalanced as all contained between 4 and 24 stations except the cluster 2 containing 134 stations. Cluster 1 was dominated by Chaetoceros (28.8%), Leptocylindrus (27.4%), Proboscia (10.6%) and Pseudosolenia (9.7%). It was mainly composed of few stations sampled in 2016, 2017 and 2018. Similar community was observed in cluster 2, regrouping more than 65% of all the stations sampled. An inversion of the importance of Leptocylindrus (12.9%) and Proboscia (15.6%) was however observed. Chaetoceros was again the most important group (26.6%) and Pseudosolenia was, as for the cluster 1, in fourth position with 11.3%. The main difference was the presence of Cerataulina (8.6%), poorly represented in the other clusters (<3%). Those 2 cluster were the less dominated ones as observed in the rank frequency analysis (SM Figure III-17). Clusters 3 and 4 presented strong dominance of other phytoplankton (32.0%) and dinoflagellates. In particular, Tripos (16.8%), Protoperidinium (12.9%) and Gymnodinium (8.3%) were important in cluster 3. Diatoms were poorly represented and the most important was Pleurosigma (13.8%). This cluster was maily composed of stations sampled in 2007 and all the stations of 2008. The cluster 4 presented also a strong dominance of dinoflagellate with Gymnodinium (64.0%) but was only composed of 4 stations which is very few compared to the others. Finally, the cluster 5 was dominated by Chaetoceros (61.4%) and mainly composed by stations of 2007 and 2018. Those last 3 cluster presented a community highly dominated, the first group representing up to 60% of total biovolumes in general (SM Figure III-17). Concerning the importance of the environment, the Rhone river flow and the mean chla concentration presented variability between clusters but no clear interactions with the phytoplankton community was identified. The cluster 3 and 4, mainly dominated by dinoflagellates, presented lower SST in spring compared to the other clusters dominated by diatoms. Moreover, the chla bloom seemed to initiate earlier in those 2 clusters and last longer over time as the duration of the bloom was higher. In clusters 1 and 2, low values of both winter SST and WeMO were observed compared to other cluster where at least one of the two was higher. Those 2 clusters presented higher values of Leptocylindrus for the phytoplankton and Doliolida for the zooplankton which could represent a potential association between phyto- and zooplankton. Except the potential link between Leptocylindrus and Doliolida, no clear associations with the zooplankton community was detected as Penilia and Clausocalanus were always the 2 most important groups in all clusters, both with dominance of Diatoms or Dinoflagellates, except the cluster 4 only composed of 4 stations. This weak relationship between phytoplankton and zooplankton was highlighted by the tanglegram of the 2 dendrograms (Figure III-6). The appearance of beams in Figure III-6 highlighted the fact that some stations appeared grouped together such as in 2007 and 2008 considering phytoplankton or zooplankton. The entanglement measure between both was 0.31 indicating similarities but not a strong match. Indeed, the correlation of the structure of the whole dendrograms, measured by the Baker's gamma index, appeared finally weak (0.075) even if significant (SM Figure III-18).

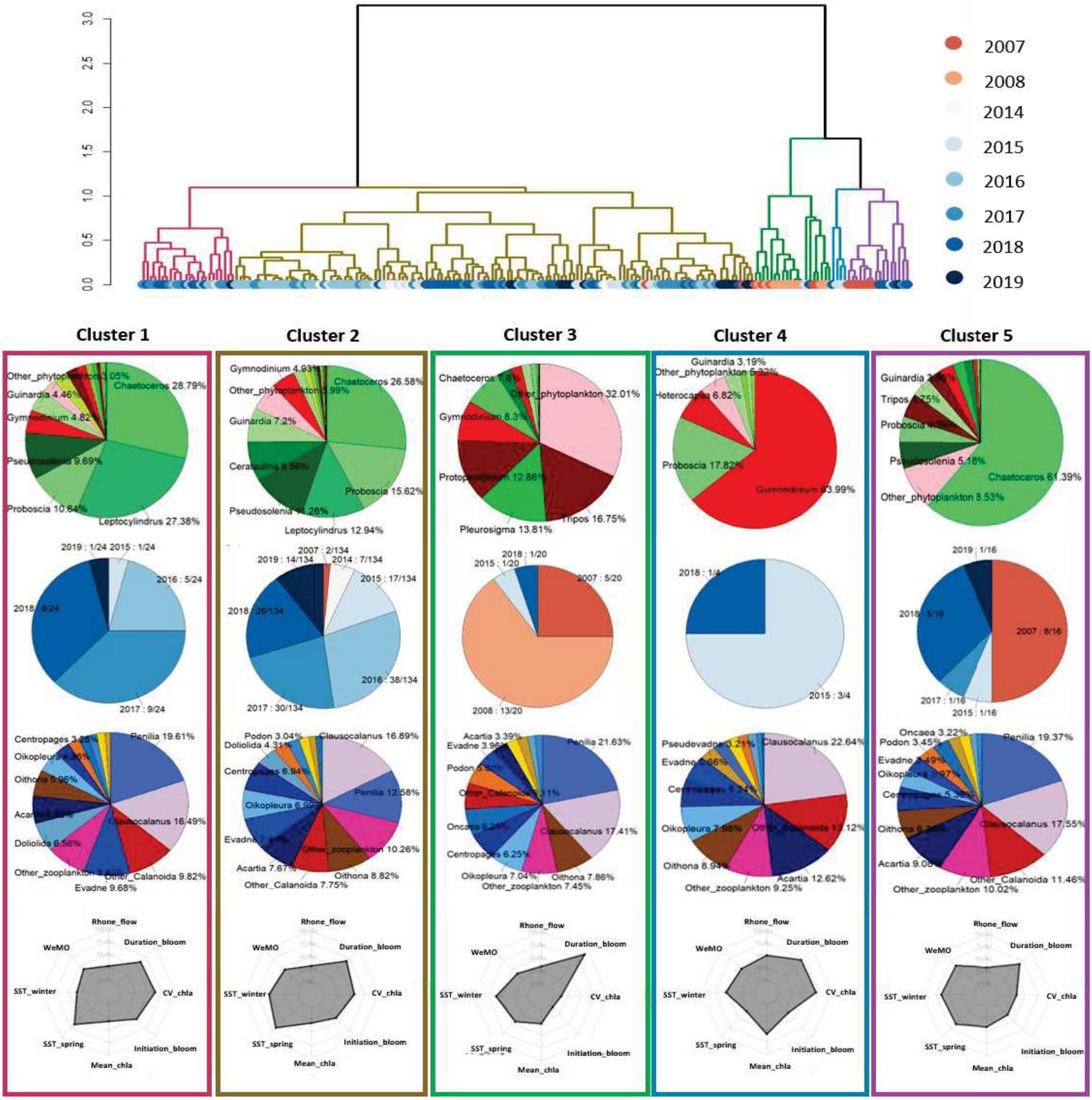


Figure III-5 *Dendrogram of Bray-Curtis dissimilarity matrix based on zooplankton log biovolumes at stations where phytoplankton and zooplankton were sampled. 5 clusters are identified with KGS criteria and colored on the dendrogram. Top Pie charts represent the mean phytoplankton community of each cluster, ordered as in the dendrogram and colored with the same color. Diatoms are represented in green in the pie chart and dinoflagellate in red. In the second line of panels, the pie chart and number of stations of each years composing each cluster. The third line of panels represent the mean zooplankton community in each phytoplankton cluster. Finally, the bottom line of panels*

represent spider diagrams of the environment calculated as the mean of each years composing the cluster pondered by the proportion of each years. Each environmental variables are represented as a percentage, with 0% as the minimal annual value observed between 1993 and 2019 and 100% the maximum observed.

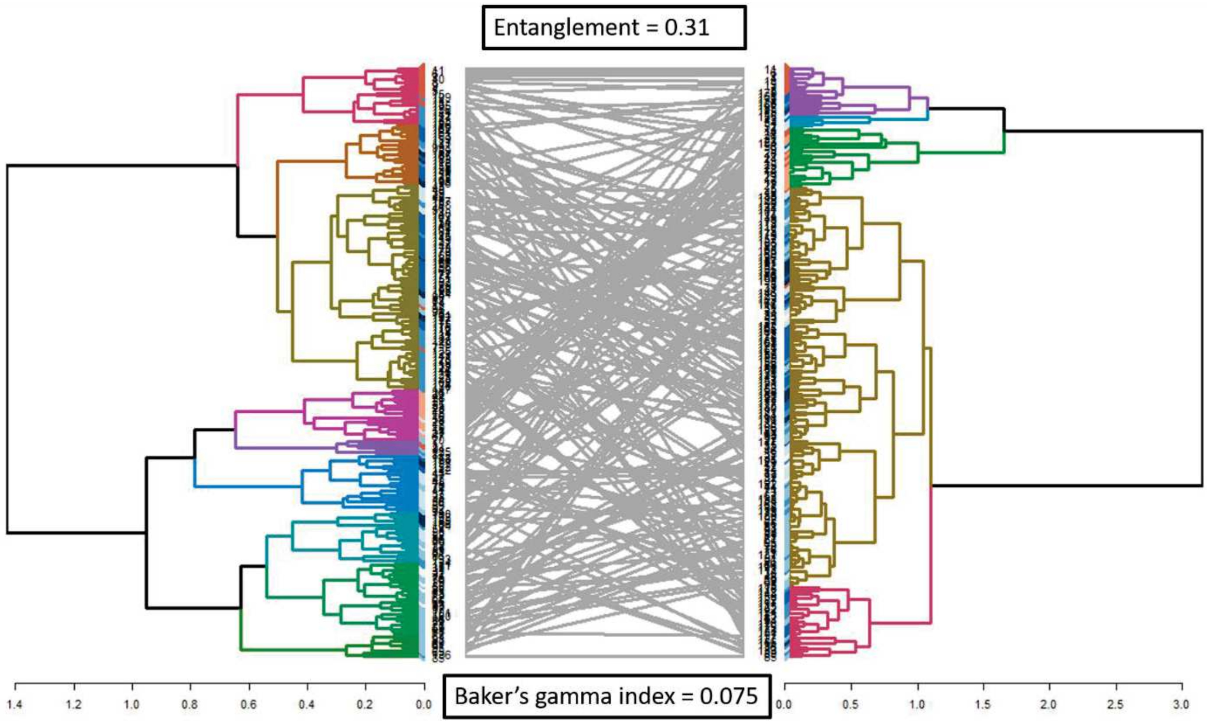
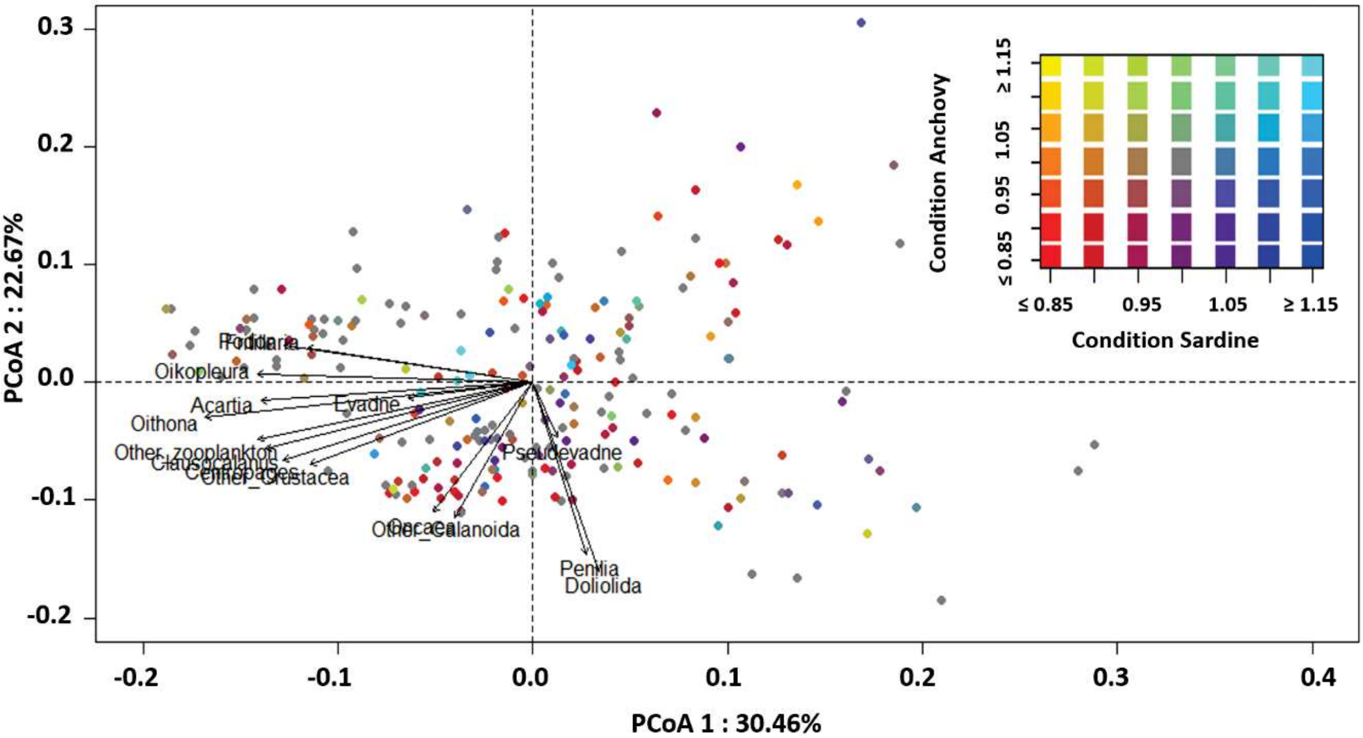


Figure III-6 ***Tanglegram between Dendrogram of hierarchical clustering performed on Bray-Curtis dissimilarity matrix based on zooplankton log densities at stations where phytoplankton was sampled (left) and Dendrogram of hierarchical clustering performed on Bray-Curtis dissimilarity matrix based on phytoplankton log biovolumes (right). Each grey line rely the same station in each dendrogram. Entanglement and Baker's gamma index are two measure of the similarity between the two dendrograms.***

III-3.5 Relationship between zooplankton and small pelagic fish conditions

To investigate the potential relationship between small pelagic fish condition and zooplankton, a PCoA based on Bray-Curtis dissimilarity of zooplankton densities was performed with stations where both zooplankton sample and fish trawl were conducted. Very similar results were obtained compared to the same analysis performed on all zooplankton stations previously described in section 3.1 as only few ones were not associated with a trawl. No clear pattern were observed in sardine and anchovy condition (represented by the gradient color) in the space of PCoA, highlighting the strong variability of the data and possibly weak relationship between fish condition and zooplankton community composition. As only visual inspection was possible with this analysis, linear models were performed between the PC1/PC2 of the PCoA and the conditions of sardine, anchovy and sprat. To investigate also the importance of total zooplankton instead of the community composition, models between the zooplankton total density and fish condition were also performed (Figure III-8). However, no significant relationship were found except between the PC2 of the PCoA and sprat condition, where a significant positive relationship was found (pvalue slope =0.04). Sprat seemed then to present higher conditions at the stations where Penilia, Doliolida, Oncaea, Other_clanoida and secondarily pseudevadne were less abundant. However, this result have to be taken with caution as R² was very low (0.026) and some outliers were detected in the residuals (SM Figure III-19).

Figure III-7 ***PCoA performed on Bray-Curtis dissimilarity matrix based on zooplankton log densities at stations were a trawl was also conducted. Stations are colored based on the condition of sardine and anchovy in the trawls. Red colors indicate bad conditions for both species and light blue colors when both presented good conditions. The different possible combinations of colors depending of the conditions are presented in the top right panel. When only one of the 2 species was sampled, the station was colored in grey.***



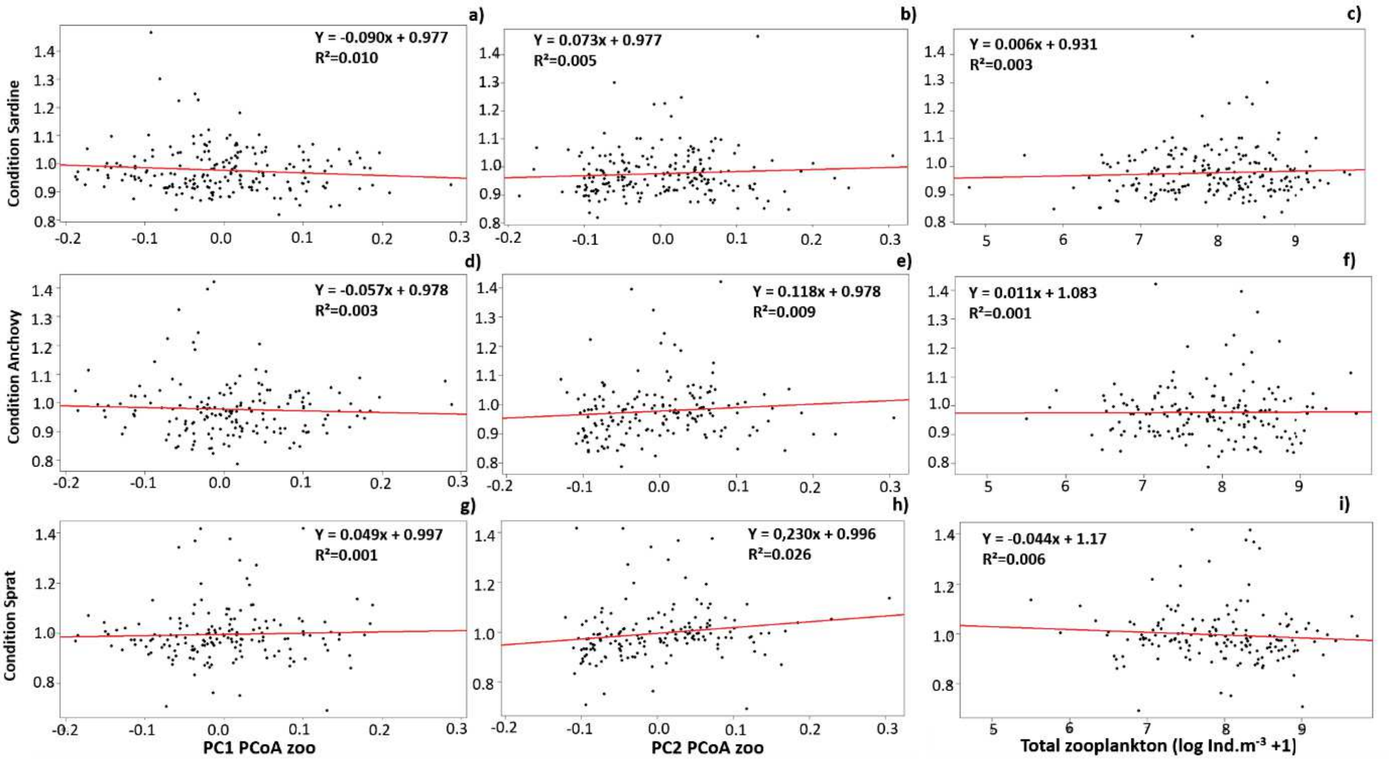


Figure III-8 ***Linear regression between fish condition and PC1 (left column) and PC2 (middle column) of PCoA performed on Bray-Curtis dissimilarity matrix based on zooplankton log densities at stations were a trawl was also conducted. In the right column. In the left column linear models between condition and total zooplankton log densities.***

In order to reduce the variability in the zooplankton and fish condition data, and because relationship between zooplankton and small pelagic could be not linear, a focus was made on the stations presenting extreme values of conditions determined as the 15% stations with highest conditions and 15% lowest for each fish species. Conditions ranged for sardine from 1.04 to 1.31 for good condition stations and from 0.77 to 0.91 for bad condition stations. For anchovy, bad conditions ranged from 0.81 to 0.89 and from 1.04 to 1.35 for good conditions. Finally, sprat bad conditions ranging from 0.81 to 0.91 and good conditions from 1.05 to 1.42. The comparison of zooplankton densities between stations of good and bad conditions highlighted several potential key species, with the higher presence of *Clausocalanus*, *Centropages*, *Penilia*, Doliolida, *Oncaea* and *Oikopleura* at stations where anchovy presented bad conditions (Figure III-9). For sardine, *Evadne*, *Oithona* and other zooplankton were higher at stations where conditions were good. Finally, for sprat, Evadne presented higher densities at stations with bad conditions whereas *Penilia* and Doliolida were higher at stations of bad conditions.

The same analyses were performed based on proportions of zooplankton instead of log densities in order to investigate differences in the composition of the community. *Clausocalanus* and *Penilia* presented a higher part of the community in stations of bad conditions for sardine and anchovy, as well as Doliolida for the 3 species (Figure III-10). On contrary, *Evadne* was proportionally more present in stations of good conditions for sardine and anchovy, as well as *Oithona* for the 3 species. Finally, Other calanoida and other zooplankton were proportionally more present at stations of good conditions for anchovy (Figure III-10). Tests of sensibility for the threshold value presented some variability but were generally consistent for the different threshold (SM Figure III-20 and 21).

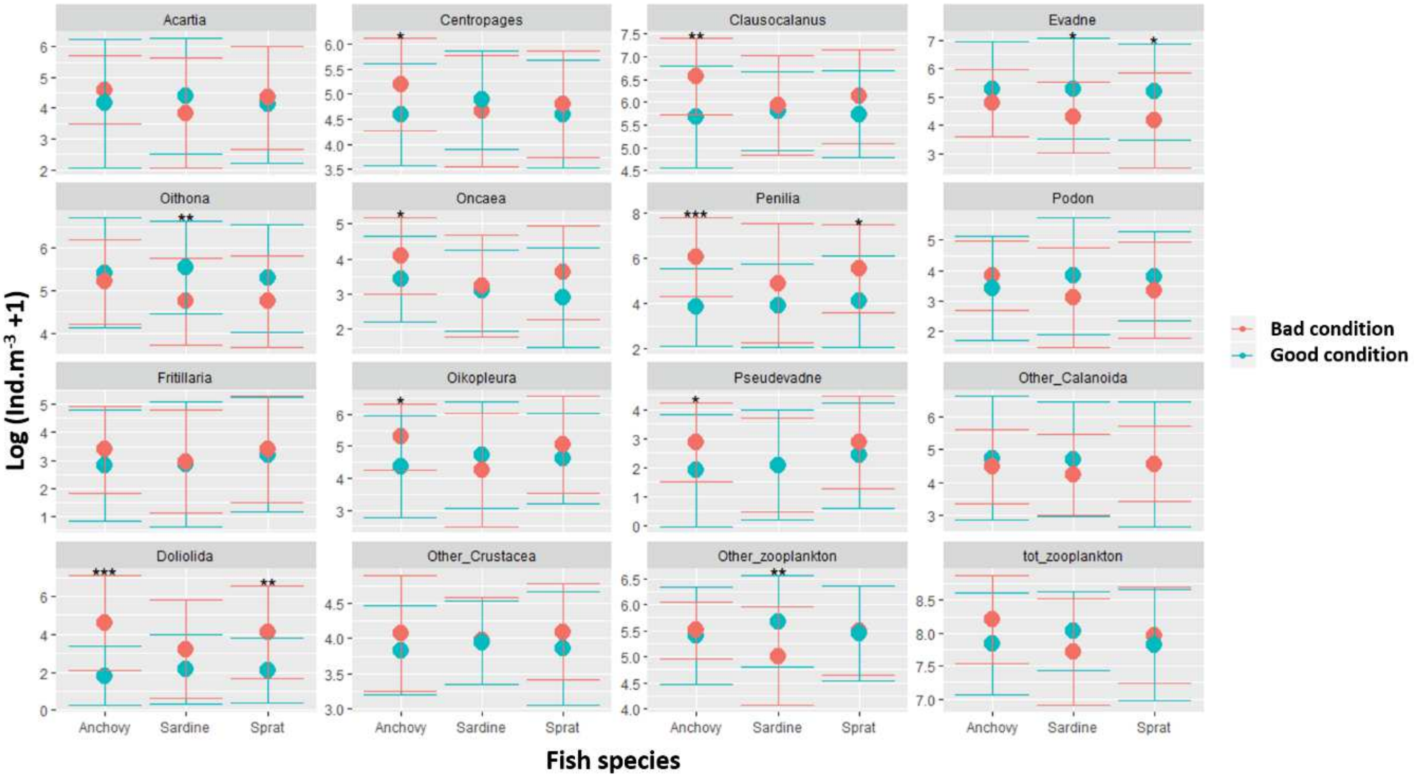


Figure III-9 *Mean log densities +/- sd of the different zooplankton groups at the stations of « good » and « bad » conditions of anchovy, sardine and sprat. The good and bad stations were considered as the 15% stations with the best and worst conditions for each fish considering all the trawls associated to zooplankton sample.* ***26 stations were considered for good and bad conditions of anchovies, 32 for sardine and 24 for sprat.*** *Stars represent the significance of T-test performed between the zooplankton densities of good and bad conditions stations.*

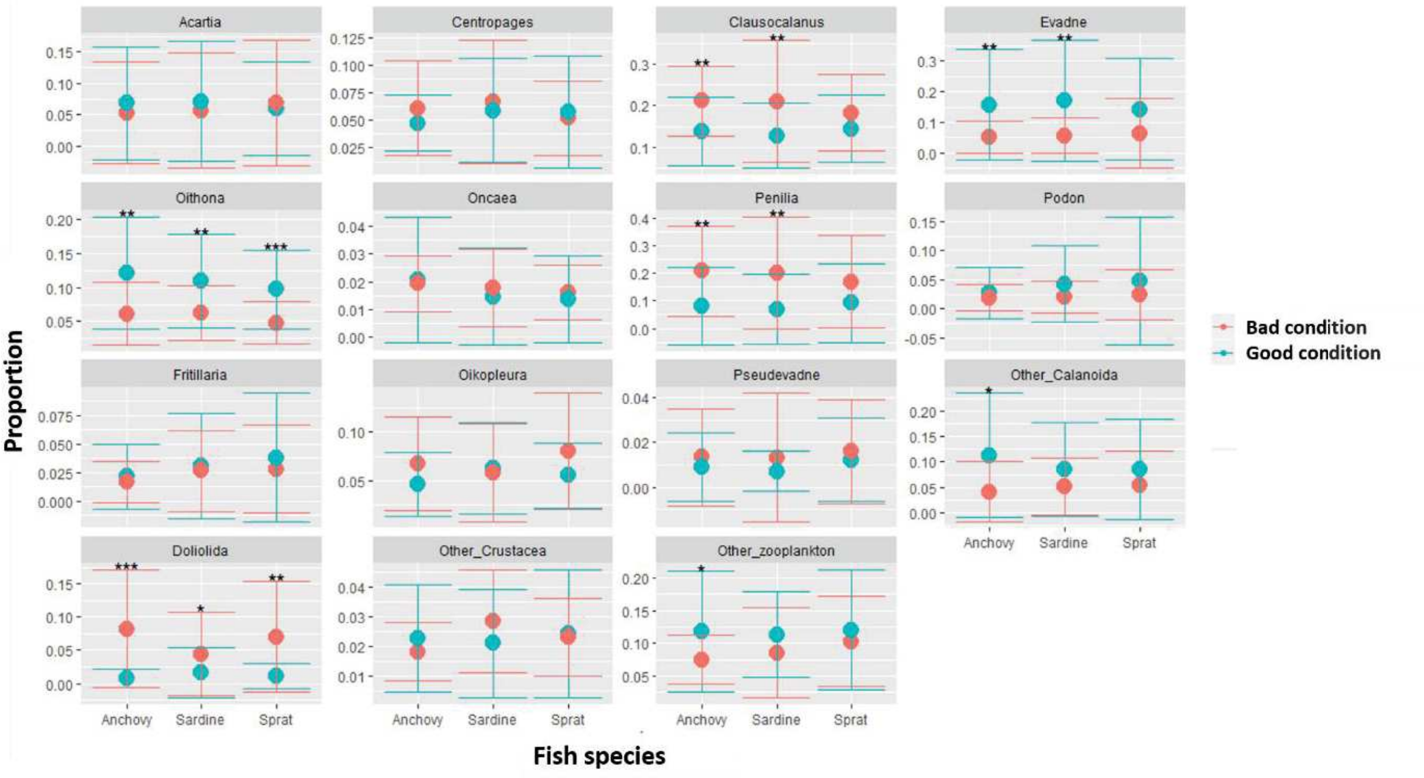


Figure III-10 ***Mean proportion +/- sd of the different zooplankton groups at the stations of « good » and « bad » conditions of anchovy, sardine and sprat. The good and bad stations were considered as the 15% stations with the best and worst conditions for each fish considering all the trawls associated to zooplankton sample. 26 stations were considered for good and bad conditions of anchovies, 32 for sardine and 24 for*** *sprat. Stars represent the significance of T-test performed between the zooplankton proportions of good and bad conditions stations.*

III-4 Discussion

Small pelagic fish crisis in the Gulf of Lions has been widely studied (Brosset et al., 2017; Saraux et al., 2019; Van Beveren et al., 2014) to investigate the reason of the sudden drop of biomass and fish size and conditions observed in the mid-2000s. The hypothesis of a bottom-up control with possible changes in small pelagic fish diet from large to smaller zooplankton has been suggested (Brosset et al 2017). This kind of trophic modifications have already been observed in upwelling systems with the alternation of diatoms chains favoring large zooplankton and anchovy population and dinoflagellate chains favoring small zooplankton and sardine population (Tam et al., 2008; Van der Lingen et al., 2006). Whether such a change in diet translated a change in the plankton community in the Gulf of Lions remains unknown due to the scarcity of zooplankton data in the area. This study thus aims at depicting the principal characteristics of the phytoplankton and zooplankton community in terms of density and taxonomic composition in the Gulf of Lions in summer. The potential environmental drivers of the phyto- and zooplankton community were investigated, as well as the potential presence of characteristics phytoplankton-zooplankton chains and the relationship with the small pelagic fish condition.

III-4.1 Limits of the study

This study presented different limits, mainly due to the fact that plankton samples were performed during the PELMED fisheries scientific survey for which the main goal was to asses small pelagic fish stock and not investigate the plankton community. This implies that the priority was given to fish sample in case of logistic problem or bad weather, leading to unbalanced number of sample between years, strong differences in sample spatial coverage and even years with no data. For all those reasons, even if many plankton samples were available from up to 11 different years, time series analysis and was not possible as well as inter-annual comparison. The second point was that only the early summer plankton community was sampled, known to be less productive than the spring community in temperate areas (d'Alcalà et al., 2004; Siokou-Frangou et al., 2010; Zingone et al., 2019)

III-4.2 Spatial variability in the gulf of Lions

The gulf of Lions in one of the most productive area in the north western Mediterranean sea (Palomera et al., 2007) and presents also spatial heterogeneity partly due to environmental factors. Indeed, the Rhone river, present in the eastern part of the gulf has been shown to be one of the most important drivers of primary production on the shelf (Coste, 1974; Feuilloley et al., 2020; Lefevre et al., 1997; Macias et al., 2018b). Under certain wind condition, the plume can however drift westward along the coast and also impact the western side of the shelf (Demarcq & Wald, 1984; Fraysse et al., 2013). At the coast, upwelling cells are present and under northern wind regime, can locally increase productivity (Feuilloley et al., 2020; Millot, 1979,1990). Finally, thermal fronts have been shown to be favorable areas, aggregating phyto- and zooplankton and locally enhancing productivity (Bakun, 2006). Concerning the biological compartment, heterogeneity has also been observed in small pelagic fish distribution with a higher presence of sardine at the coast whereas anchovies were more abundant offshore, in the 150-200m stratum (Saraux et al., 2014). Such spatial pattern in the fish distribution could be due to plankton distribution as sardine and anchovy are known to feed generally on different prey (Brosset, et al., 2016; Costalago et al., 2014; James, 1987; Van der Lingen, 2002; Van der Lingen et al., 2006) even if their diets became more similar in recent years (Brosset, et al., 2016a). In this study, the spatial variability of the phytoplankton and zooplankton community, as well as the small pelagic fish condition was investigated in order to see if similar pattern were found with the fish biomass spatial distribution. Generally, the spatial structuration of phytoplankton, zooplankton and fish condition was very weak over the shelf and presented a strong heterogeneity. This result could be expected for fish condition as small pelagic can move all over the shelf and that the condition integrate the life history of fish a few time ago, leading to a weak relationship between the fish condition and its instantaneous spatial position. It was however more surprising for the plankton community as East-West or bathymetric gradient could have been expected due for example to the presence of the Rhone river at east or upwelling at the coast. However, the impact of those process vary in time as the Rhone plume can flow off the shelf on the East side but also drift westward along the coast and can then impact opposite part of the shelf during the survey from a year to another. Similarly, coastal upwelling are very local and punctual process, not occurring during every survey and coastal sampling not always performed during upwelling process. Some years seemed to present spatial pattern in the plankton and fish condition but not recurrent from a year to another (SM

Figure III-22 to 26 for the different map of the composition of phytoplankton and zooplankton stations and the condition of the 3 fish species). The fact that all the years were pooled together is probably the reason why no spatial distribution was observed in the plankton community and fish condition. All those results seem to indicate that the Gulf of Lions is very heterogeneous at the biological scale, with no strong persistent spatial pattern in time both for the plankton community and fish condition, probably due to the spatial variability observed in the environmental process over the shelf.

III-4.3 Zooplankton and phytoplankton summer community

Strong differences were observed in the community composition between stations, some dominated by copepods with *Clausocalanus, Oithona* and *Centropages* and others dominated by cladocerans, mainly *Penilia* and *Evadne*. Cladocerans are classically found to be one of the most important group in zooplankton summer community in NWMS, especially *Penilia avirostris* and some *Evadne* species (Costalago et al., 2014; García-Martínez et al., 2019; Jamet, Jean et al., 2005). Concerning Copepods, they are generally strongly abundant in spring, just after the phytoplankton bloom, but some species such as *Oithona nana* are also found in high proportion in summer in NWMS due to their capacity to adapt to different types of prey such as phytoplankton, ciliates or detritus (Atienza et al., 2006; Calbet et al., 2001; Lampitt & Gamble, 1982). In our case, *Oithona* was not the main group of Copepods as found in other studies but rather *Clausocalanus*, possibly due to the differences of mesh size (200µm in our study and less than 100µm for others) (Calbet et al., 2001; Jamet et al., 2005). Concerning the phytoplankton, Diatoms were strongly dominant on the shelf, already observed before by Costalago et al., (2014). In the classical phytoplankton succession described by Margalef (1958), diatoms are found mainly in spring, the smaller one initiating the bloom and followed after by larger individuals. In summer, during the period with lower nutrients concentration due to stratification, small flagellates and Dinoflagellates are expected to be more abundant. Indeed, Dinoflagellate and small flagellates are generally found as dominant in other NWMS areas in summer such as in Alboran and Catalan Sea, but sometimes both diatoms and Dinoflagellates are present such as in the bay of Toulon (García-Martínez et al., 2019; Rossi & Jamet, 2009). The presence of diatoms in summer is supposed to be due to external factors such as terrestrial inputs of wind mixing at coast, increasing the nutrient concentrations. The presence of the Rhone river, the most important of NWMS, is possibly one of the reasons of the strong presence of diatoms in summer over the Gulf of Lions shelf.

III-4.4 Zooplankton and phytoplankton environmental relationship

Due to its short life span and short reproduction cycle, plankton is very sensible to environmental change and important changes can have repercussion to higher trophic levels such as small pelagic fish. Therefore, the relationship between zooplankton community and environment was investigated based on community clustering. No clear relationship was observed with the environment as similar conditions could lead to copepods or cladocerans dominance. However, plankton and environment were considered at different scales which could limit our capacity to detect interactions. Indeed, the environment was considered at the annual scale averaging the 11 months before the survey or only the winter/spring conditions depending of the variables. This allowed to cover the period of the phytoplankton bloom, starting generally in winter and supposed to initiate the plankton annual succession (Margalef, 1958). However, the summer plankton community is probably not only related to the past environment but rather to the plankton succession, modulated by the environment and also by biological interactions such as predation and grazing (Behrenfeld, 2010; Hairston et al., 1960; Lampert et al., 1986; Romagnan et al., 2015; Sherr & Sherr, 2007). A second point is that the environment was averaged annually over the entire shelf whereas zoo- and phytoplankton were punctual sampled points, presenting strong inter and intra-annual variability. As discussed before, the intra-annual variability could be induced by the environment at smaller scale, such as for example thermal fronts which have the capacity to aggregate plankton locally and increase heterogeneity or the river flow impacting different part of the shelf depending of the wind conditions (Bakun, 2006; Millot et al., 1990). Then, comparing an homogenous environment over the whole shelf with cluster of punctual stations of different years have possibly introduce some noise due to the scale differences. Considering the plankton at the same scale as the environment, averaging the stations for each year over the whole shelf could limit this effect but as discussed before, the number of years available was still too limited for such an investigation and differences in the sampling effort too important.

III-4.5 Zooplankton and phytoplankton relationship

The relationship between zooplankton and phytoplankton was also studied as it could have strong importance for the rest of the food web. For example, different chains of phyto- and zooplankton have been already found to favor different species of small pelagic fish, depending of their feeding capacity. Van der Lingen et al., (2006) identified 2 chains related to temperature and water mixing: the “diatoms chain” linked to cold and well water mixed periods, favoring large zooplankton and anchovy because of their ability to hunt large prey, and the “flagellate chain” linked to warmer and less mixed periods, favoring small zooplankton and sardine which have a better capacity to filtrate small prey (Garrido et al., 2007, 2008; Plounevez & Champalbert, 2000). The importance of such changes in the phytoplankton community already started to be investigated in NWMS, analyzing fish lipid content and highlighting better feeding condition in the case of diatoms-supported food web compared to dinoflagellate-supported food web (Pethybridge et al., 2014). Potential similar chains were investigated in this study, trying to identify links between phytoplankton and zooplankton. In our data, the year 2008 appeared as the one with the strongest proportion of Dinoflagellates and a phytoplankton bloom initiated earlier. However, only the west part of the shelf was sampled this year with stations spatially and temporally close avoiding any conclusion about the stronger presence of dinoflagellates this year. The other stations were mainly composed of diatoms and similar zooplankton community were found. A potential association between Leptocylindrus and Doliolida was observed but remains to be validated by further studies. Doliolida is a filter feeder, potentially in competition with copepods for resources and could then indirectly impact small pelagic fish (Molinero et al., 2005; Molinero et al., 2008). However, Doliolida was mainly observed in 1995-1996 and less in the more recent years when small pelagic fish populations suffered from smaller size and condition. Concerning the hypothesis of diatoms versus dinoflagellates chains such pattern was not observed as similar zooplankton community were observed when diatoms or dinoflagellates dominated the phytoplankton community. However, no data was available for phytoplankton before small pelagic fish decline and zooplankton was unequally sampled before and after 2007 limiting our conclusions. Nonetheless, such description of the plankton community is possibly too simplistic in systems less productive like the Mediterranean sea, where several external factors are involved in the plankton production, compared to upwelling systems where the strength of the upwelling is the main factor driving the system productivity. More generally, the weak relationship between phytoplankton and zooplankton could possibly be explained by the fact that zooplankton community observed in summer is probably the result of the succession of species since winter/spring period. Then, the zooplankton observed during the survey should be more linked to the phytoplankton and zooplankton community observed several weeks before than the community observed at the same moment as a delay is generally observed between phytoplankton and zooplankton development (Romagnan et al., 2015; Sommer et al., 1986). It appears then crucial to have information of the plankton functioning and succession since the phytoplankton bloom in winter/spring until the summer to try to depict the phytoplankton-zooplankton interactions leading to the summer community in the Gulf of Lions.

III-4.6 Small pelagic fish diet change and zooplankton community

Previous analyses on stomach gut content and isotope ratio showed possible changes in small pelagic fish diet. Indeed, Brosset et al., (2016a) found that isotopic niche of sardine and anchovy, different from sprat before 2007, shifted and overlapped after 2007-2008 suggesting changes in the diet of the 3 species starting to feed on the same prey. Stomach gut content of sardine and anchovy performed before and after 2007-2008, the period when drops in the small pelagic populations were observed, showed consistent differences. Indeed, different prey were found as dominant for anchovy and sardine diet before and around 2007: Acartia, other copepods and clausocalanidae for Anchovy in 1994 and Cladoceran, Euterpina and Temora for sardine in 2007. After 2007, the similar prey were found in stomach of both species with Oncaea, Microsetella and Corycaeidae (Brosset et al., 2016a). Those changes in the diet seemed to not reflect changes in the plankton community as Clausocalanidae and Cladocerans, mainly consumed by fish before 2007 and replaced after by smaller prey were found as dominant in the community in the recent years. In this study, the relationship between zooplankton and small pelagic fish condition was not evident. No links were found between fish body condition and zooplankton community composition or total density when studying all the stations sampled. This could potentially be explained by the fact that the condition is a time integrative process, depending of the life history of the fish and not responding instantaneously to environmental factors and food availability. Moreover, zooplankton was sampled with a WP2 (200µm mesh size) which is not effective to sample some zooplankton groups such as microsetella or Oncaea, strongly present in small pelagic gut content in recent years but not in our zooplankton samples (Brosset et al., 2016a; Siokou-Frangou et al., 2010). Indeed, a recent study in the Ligurian sea showed that the WP2 200µ mesh size would effectively capture crustaceans over 0.65mm which eliminate all the smallest prey captured by small pelagic fish, thought to feed in the size range 0.1-1.4mm approximately (Le Bourg et al., 2015, Feuilloley et al., in prep). Nevertheless, when focusing on particular stations with strongest and lowest conditions in order to better discriminate situations of fish good and bad conditions, some zooplankton groups appeared more related to stations with good and bad conditions. Indeed, Evadne and Oithona were always more abundant in terms of total density and proportions at stations with good conditions whereas Clausocalanus, Doliolida and Penilia were more abundant at stations with bad conditions. No details of Cladocerans in sardine gut content was available in 2007 when fish presented good conditions so the relationship with the stronger presence of Evadne or Penilia is difficult to investigate more. Concerning Oithona, this groups was never found in stomach content, neither for sardine or anchovy and seems then to be not closely linked to fish condition (Brosset et al., 2016a). Clausocalanidae, associated to bad conditions in this study, presented a small and constant part in sardine diet before and after 2007 and was less consumed by anchovy after 2007 compared to before indicating that the lower consumption of this group by anchovy is probably not the main explanation of the decreasing fish body condition. Finally, the main prey consumed after 2007 such as Microsetella and Oncaea appeared poorly present, possibly due to the net used, with a mesh size of 200µm probably too large to efficiently sample such small organism (Ioanna Siokou-Frangou et al., 2010). No direct link could then be made between the presence of the different zooplankton groups and the conditions of fish, however, it could be interesting to understand the plankton trophic interactions since the phytoplankton bloom and the environmental factors leading to the summer community to try to explain the fish conditions variability in the Gulf of Lions. Moreover, the use of a mesh with a smaller mesh size could possibly allow to sample smaller zooplankton strongly present in fish dietary and partly not considered for now in the analyses.

III-5 Acknowledgement

We thank the captain and the crew of the RV "l'Europe" as well as all the scientists on board for their assistance during the PELMED surveys. Part of this research was funded through the MONALISA project, which was co-funded by the European Union and the French Ministry of Agriculture in the framework of the European Maritime and Fisheries Fund (EMFF, grant number PFEA280017DM0910001) and by France Filière Pêche (France).

III-6 Supplementary materials

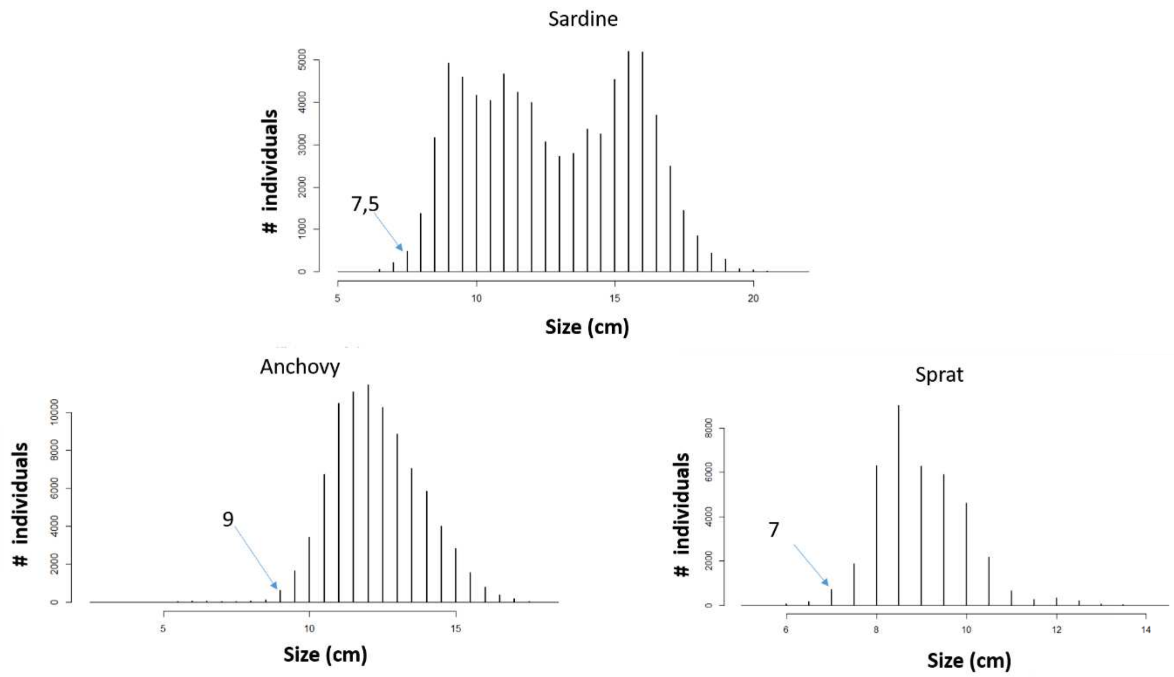


Figure III-11 ***Individual size distribution of all individuals sampled from 1993 to 2019 during PELMED survey for sardine (top), Anchovy (left) and sprat (right).***

Agglomerative coefficients of zooplankton and phytoplankton hierarchical clustering

Table III-1 ***Agglomerative coefficient calculated for average, single, complete and Ward algorithm based on dendrograms of surface and max chlorophyll depth phytoplankton biovolume and zooplankton log density.***

	Average	**Single**	**Complete**	**Ward**
Surface phytoplankton	0.84	0.79	0.88	0.96
Zooplankton all years	0.78	0.67	0.85	0.95
Zooplankton at phytoplankton surface stations	0.73	0.64	0.81	0.93

Baker’s gamma correlation index

Baker’s Gamma Index (Baker, 1974) is a measure of similarity between two dendrograms. It is defined as the rank correlation between pairs of objects in each of the two dendrograms. It is calculated by taking two object of the dendrogram, and see what is the highest possible level of k (number of cluster groups created when cutting the dendroram) for which the two objects still belongs to the same cluster. That k is returned, and the same is done for the same pair of objects in the second dendrogram. This operation is then repeated for all the possible combination of pairs. Then, a Spearman correlation is calculated between the 2 vectors containing the values of k for each pairs of objects in the 2 dendrograms. The value can range between -1 to 1. With near 0 values meaning that the two dendrograms are not statistically similar. To test the significance, permutation over the labels of one tree was performed 500 times, in order to calculate the distribution under the null hypothesis (distribution of the gamma index between the dendrogram and the same dendrogram permuted 500 times). This measure of correlation is not affected by the height of a branch but only of its relative position compared with other branches.

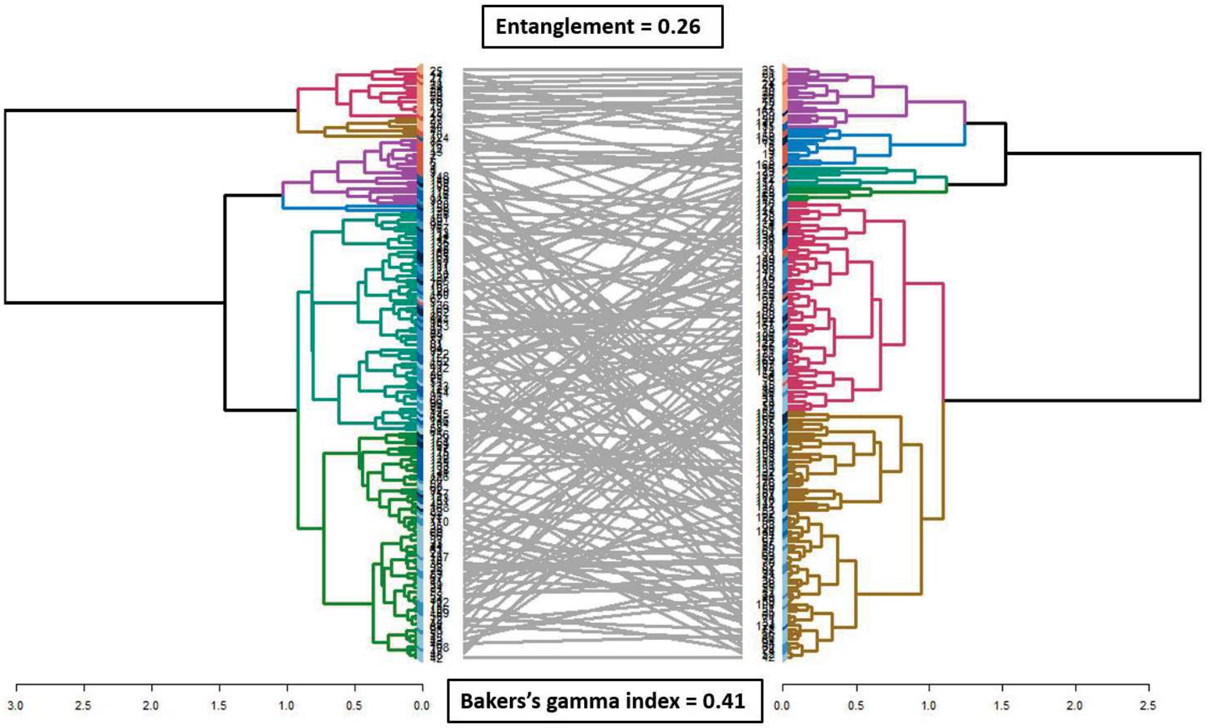


Figure III-12 ***Tanglegram between Dendrogram of hierarchical clustering performed on Bray-Curtis dissimilarity matrix of phytoplankton log biovolume at maximum chlorophyll depth (left) and surface (right) for stations where both were sampled. Each grey line rely the same station in each dendrogram. Entanglement and Baker’s gamma index are two measure of the similarity between the two dendrograms.***

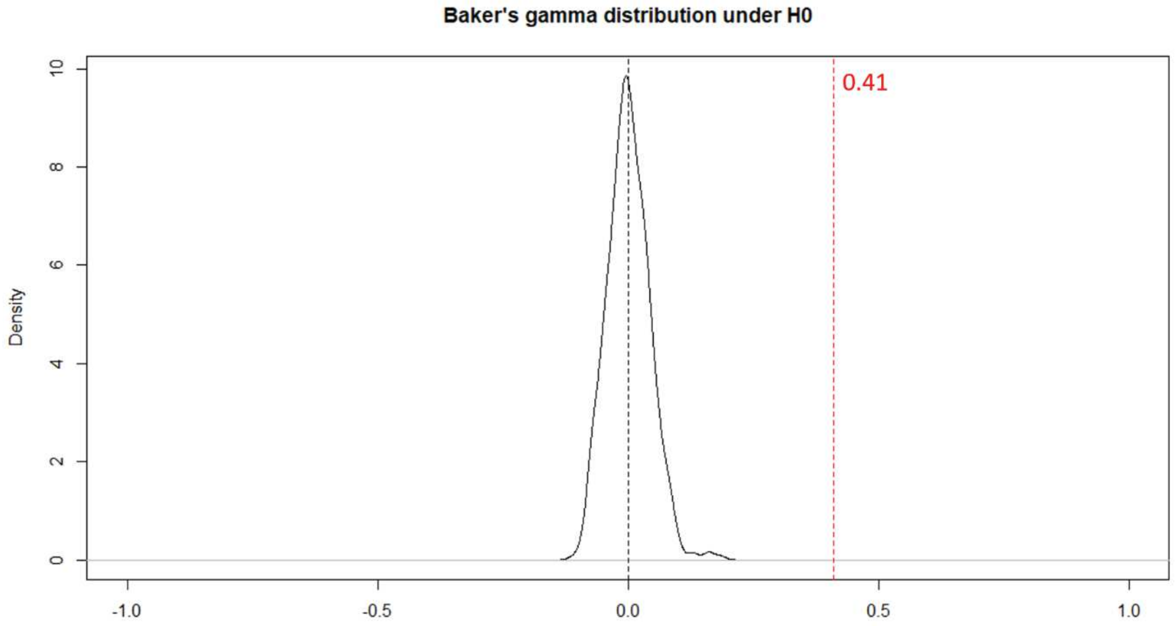


Figure III-13 ***Distribution of the Baker gamma index between the dendrogram of phytoplankton at maximum chlorophyll depth and itself after permutation, repeated 500 times. The vertical red line represent the Baker gamma index between the dendrogram of phytoplankton at maximum chlorophyll depth and the dendrogram of phytoplankton at the surface.***

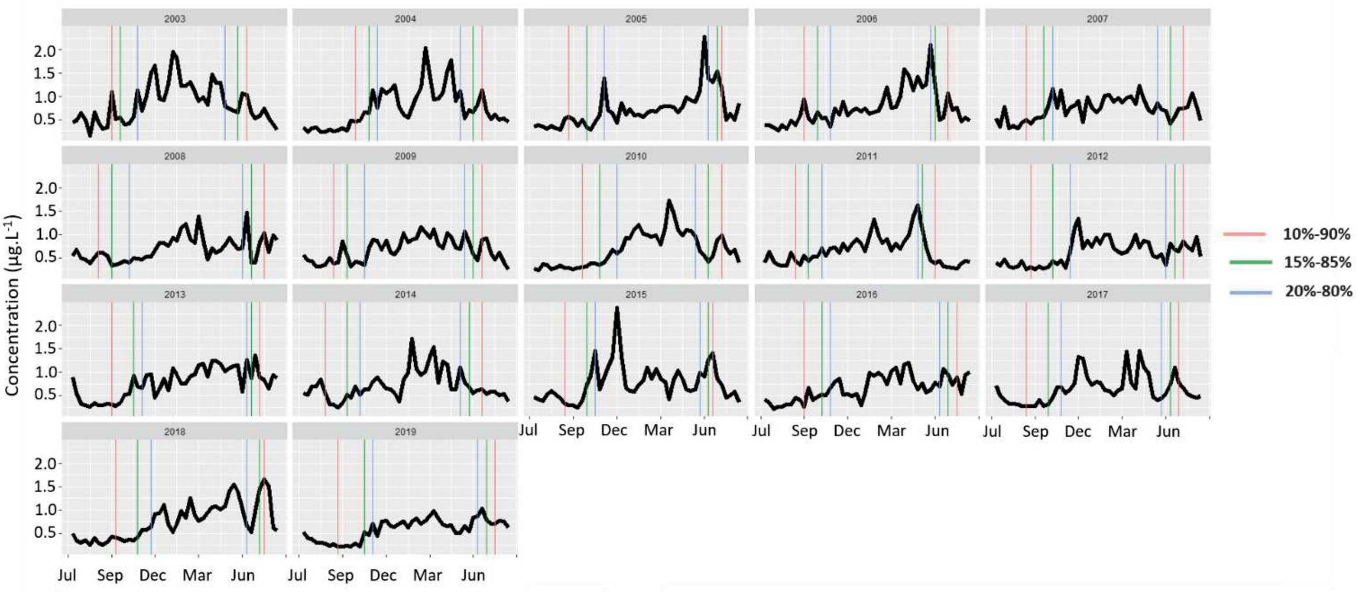


Figure III-14 *Octad time series of Chla concentrations averaged over the whole shelf each year from 2004 to 2019. Vertical lines represent the dates of initiation of bloom (left side of panels) and end of bloom (right side of panels) for different values of threshold. In the legend, the left number correspond to the threshold of the initiation of the bloom and the right number to the end of the bloom. The bloom initiation/end is considered at the moment when the threshold of initiation/end is reached based on cumulative Chla time series.*

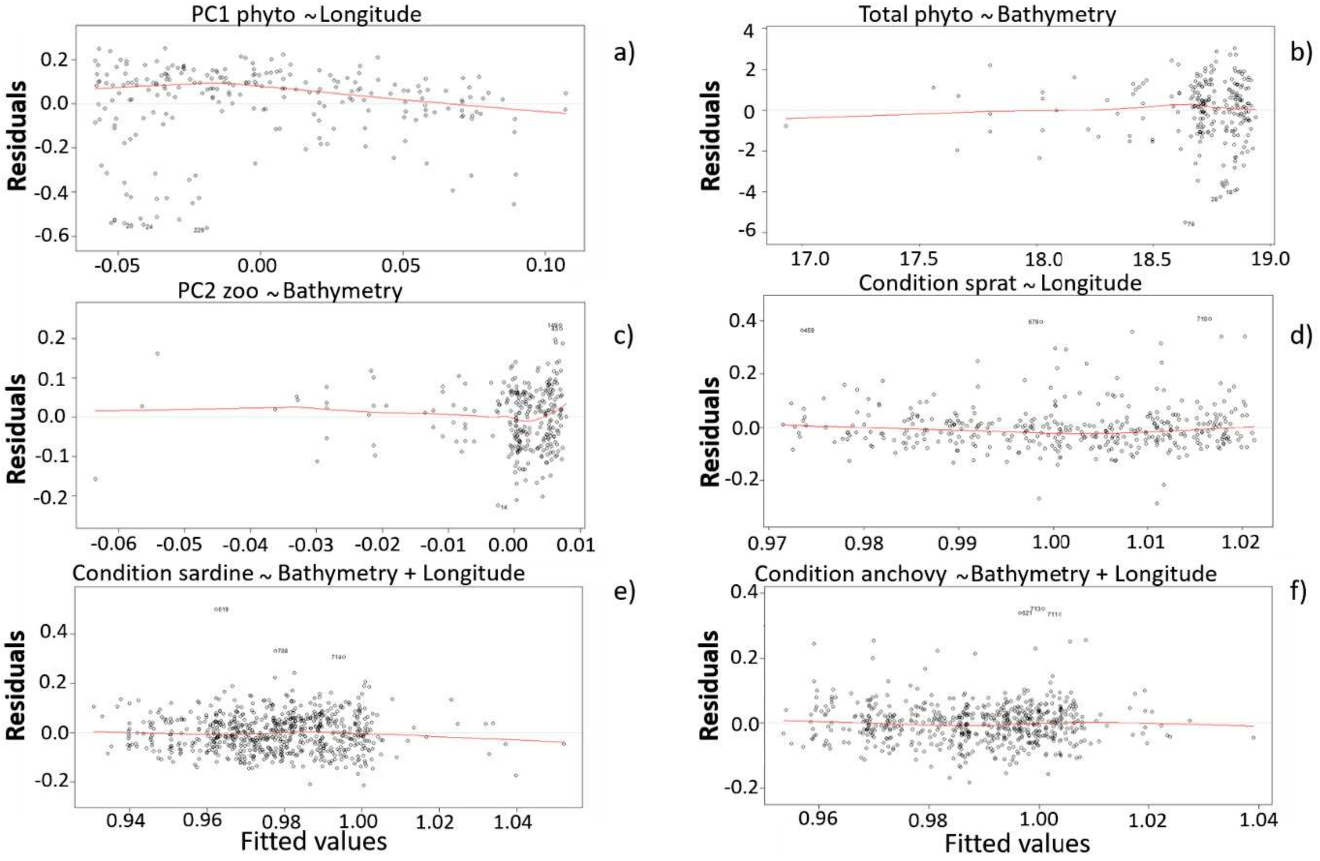


Figure III-15 ***Residuals of the models versus fitted values for the different spatial models for zooplanknton, phytoplankton and fish condition.***

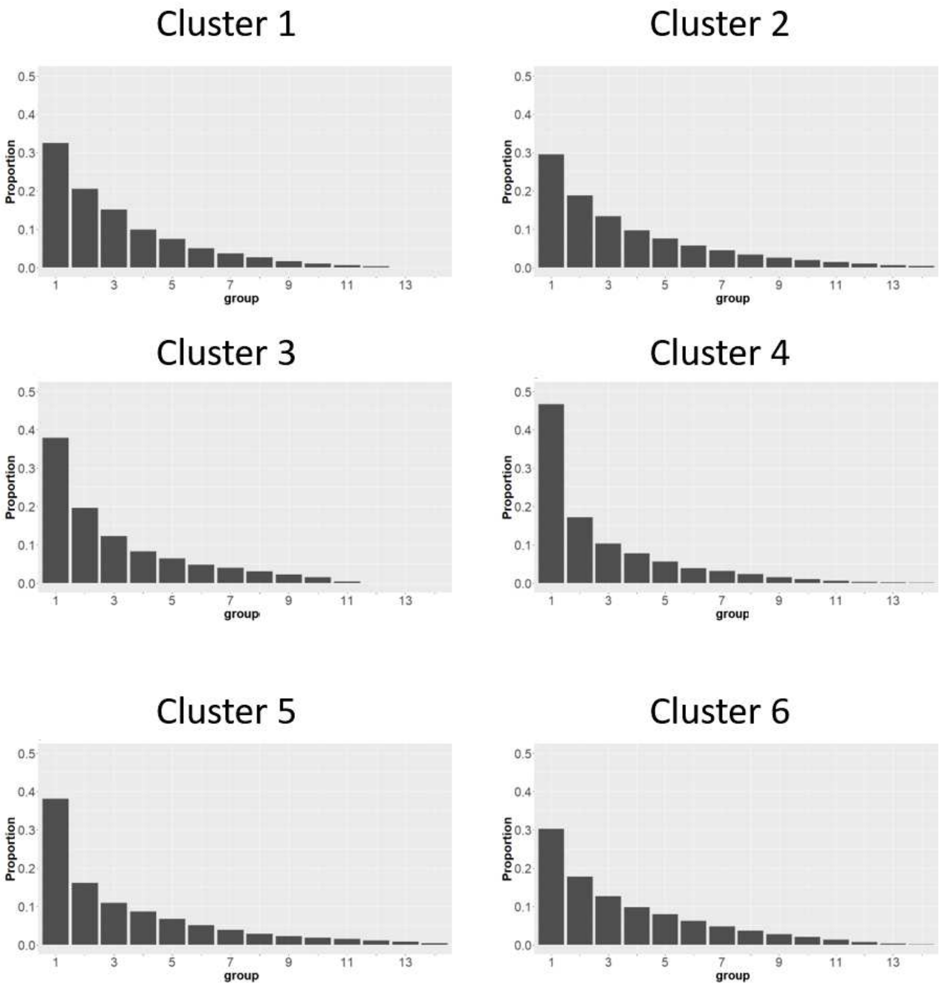


Figure III-16 ***Rank-frequency diagram for the 6 cluster identified in the zooplankton community from 1995 to 2019.***

The rank frequency diagrams represent the dominance of the community. To do this, for all the stations in each cluster, groups are ordered in a decreasing order depending of their proportion. Then, for each cluster, the mean proportion of each rank is calculated, independently of the groups, and represented in the diagram.

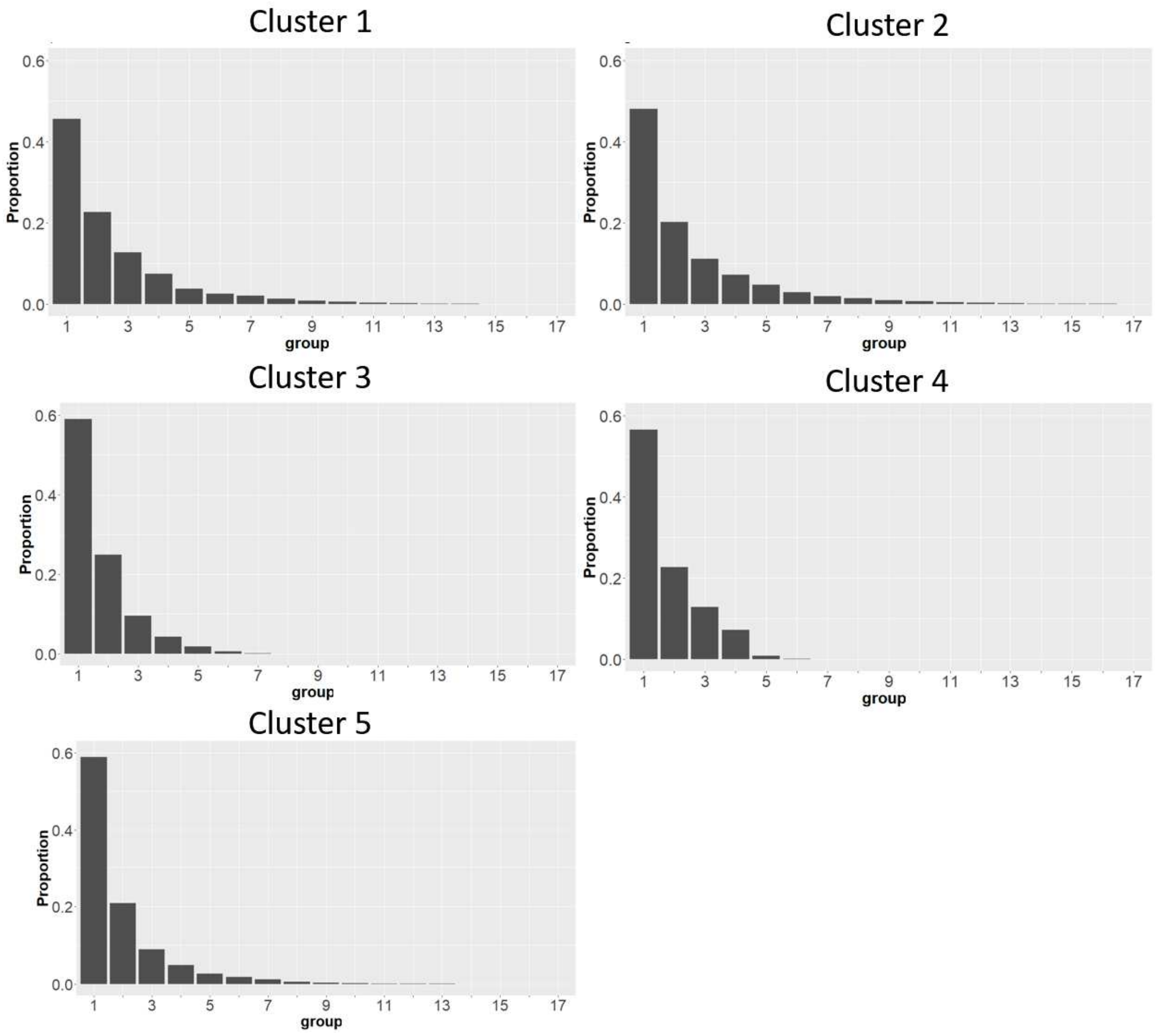


Figure III-17 ***Rank-frequency diagram for the 5 cluster identified in the surface phytoplankton community from 2007 to 2019 at the stations where both surface phytoplankton and zooplankton were sampled.***

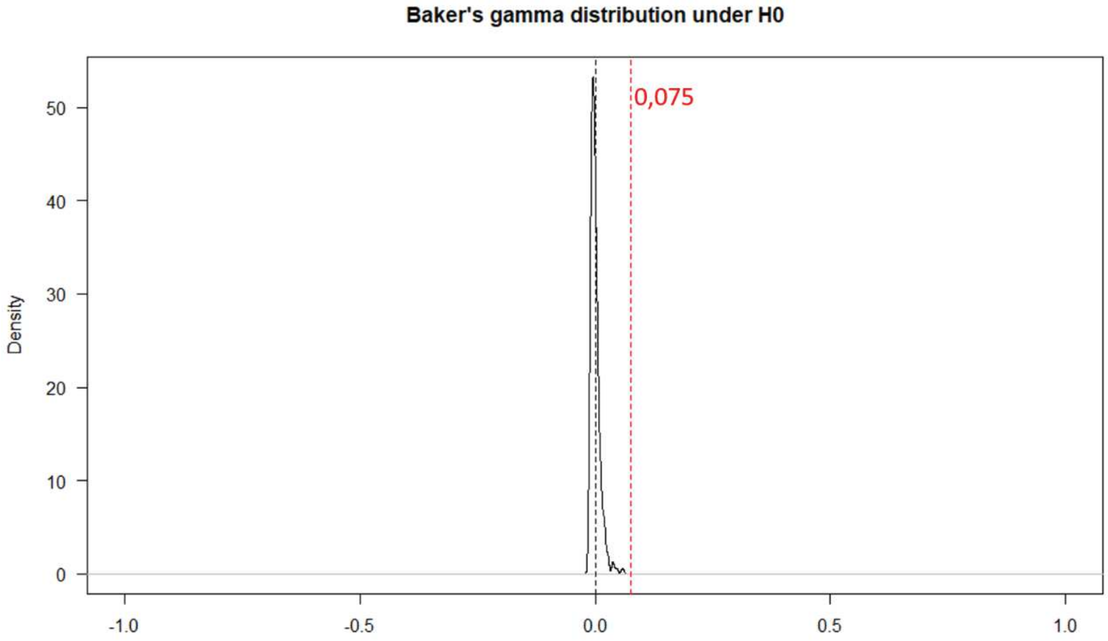


Figure III-18 *Distribution of the Baker gamma index between the dendrogram of zooplankton at stations where surface phytoplankton was sampled and itself after permutation, repeated 500 times. The vertical red line represent the Baker gamma index between the dendrogram of zooplaknton and the dendrogram of phytoplankton at the surface.*

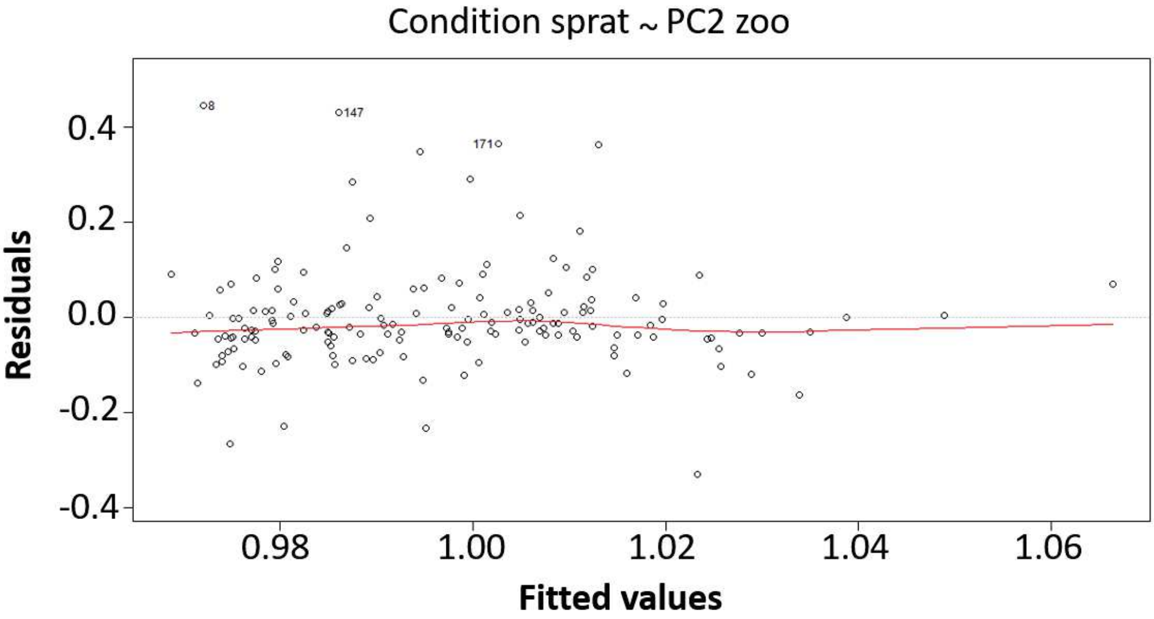


Figure III-19 ***Residuals vs fitted values of the linear model between the sprat condition and the PC2 of the PCoA performed on the bray-Curtis dissimilarity matrix of zooplankton log densities.***

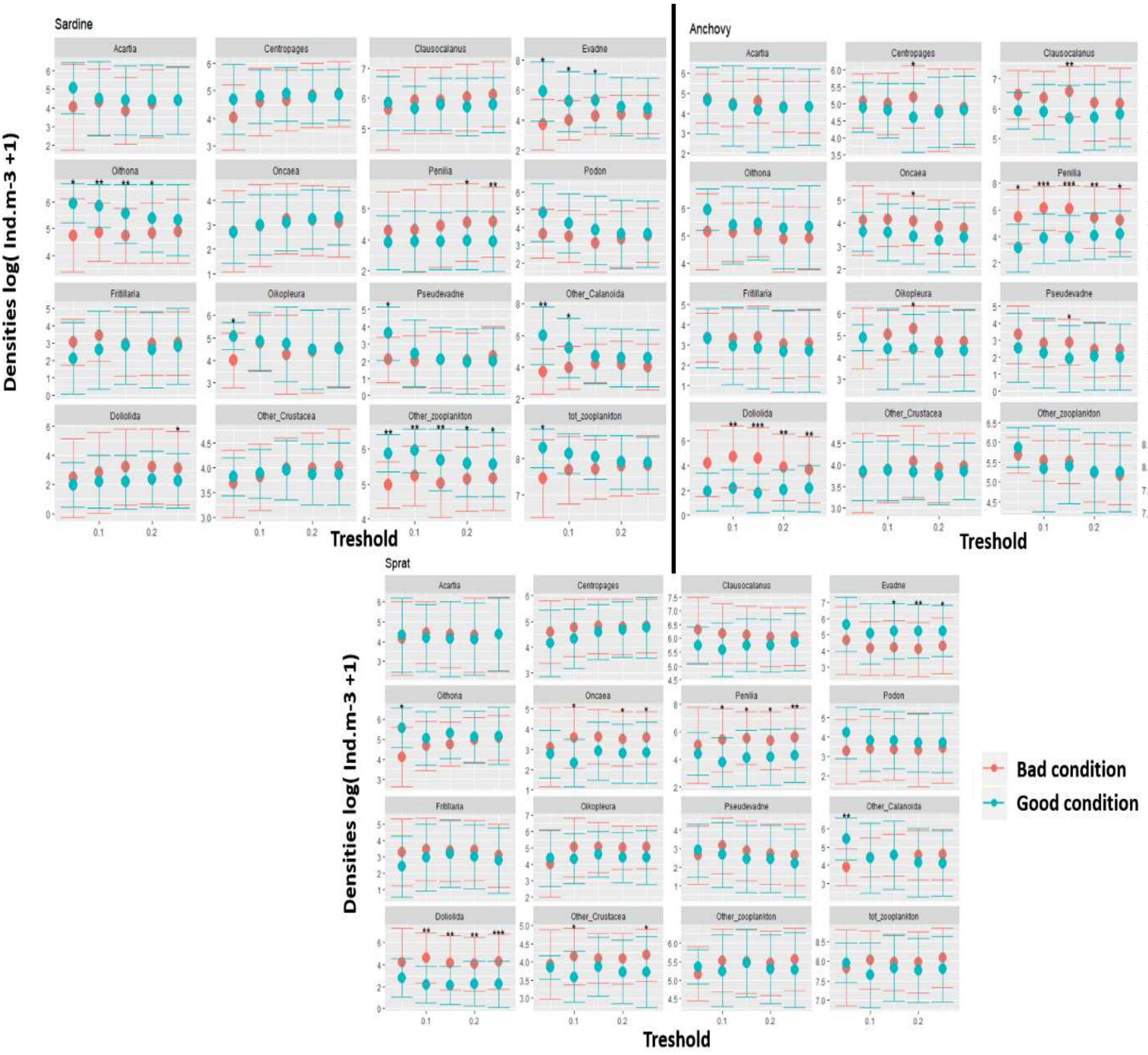


Figure III-20 *Mean log densities ± sd of the zooplankton at stations of good and bad conditions of sardine (top left), Anchovy (top right) and sprat (bottom). Different threshold for good and bad conditions are tested, from the 5% highest and lowest condition to the 25% highest and lowest condition. Stars indicate the significance of the T-test performed on the zooplankton densities between stations of good and bad conditions.*

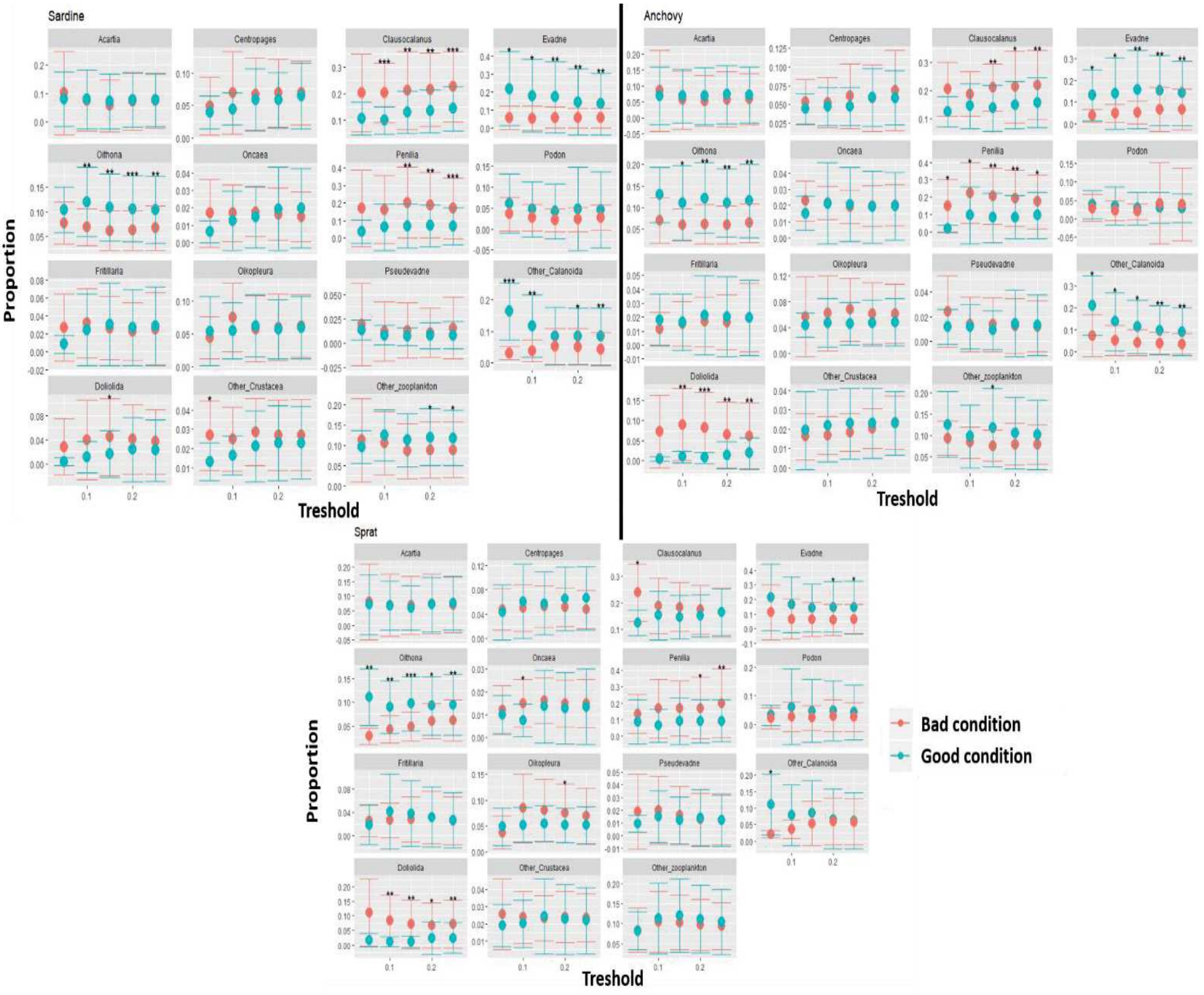


Figure III-21 *Mean proportion ± sd of the zooplankton at stations of good and bad conditions of sardine (top left), Anchovy (top right) and sprat (bottom). Different threshold for good and bad conditions are tested, from the 5% highest and lowest condition to the 25% highest and lowest condition. Stars indicate the significance of the T-test performed on the zooplankton proportions between stations of good and bad conditions.*

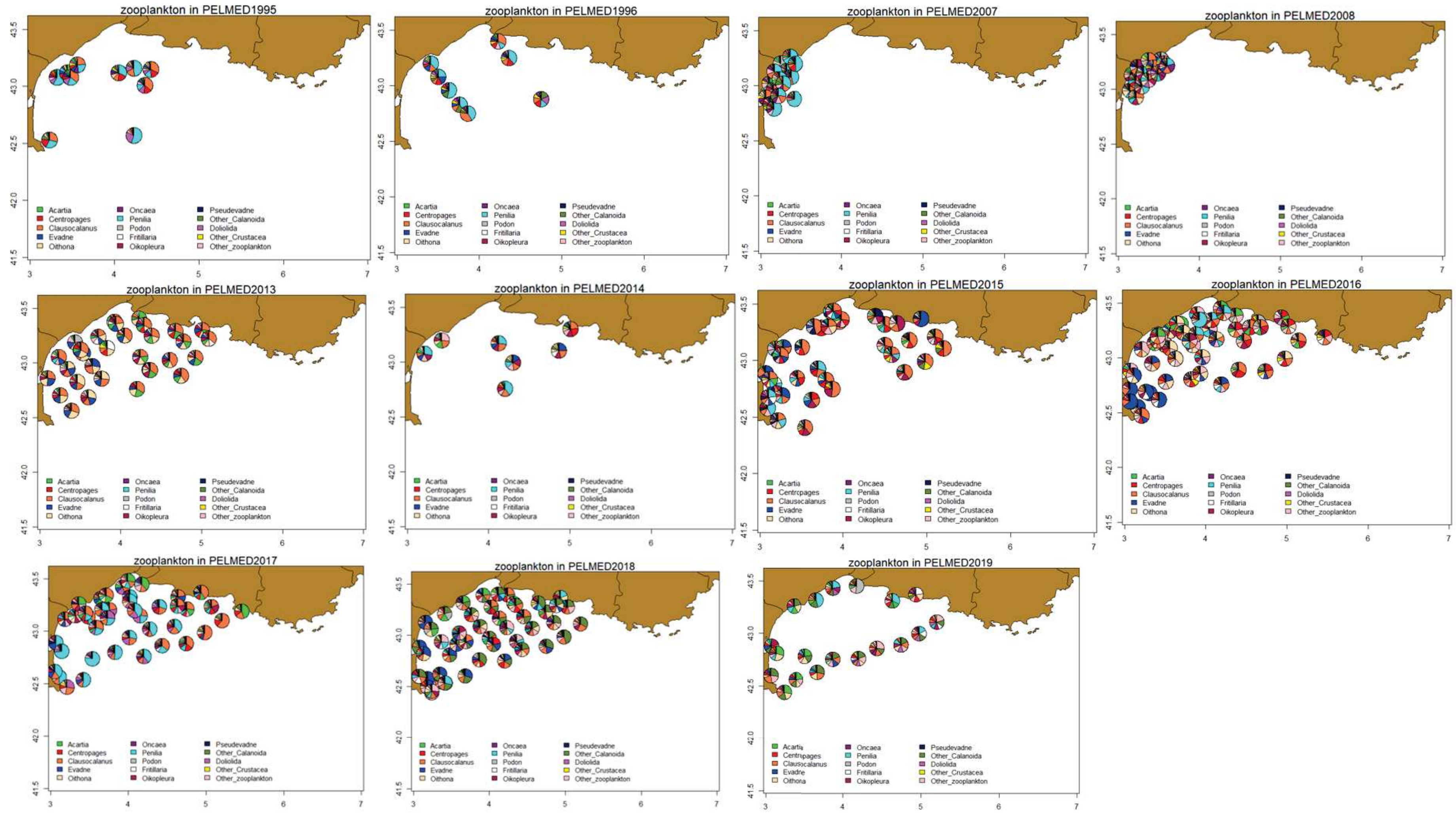


Figure III-22 *Map of the community composition of the different zooplankton stations sampled over the Gulf of Lions shelf from 1995 to 2019.*

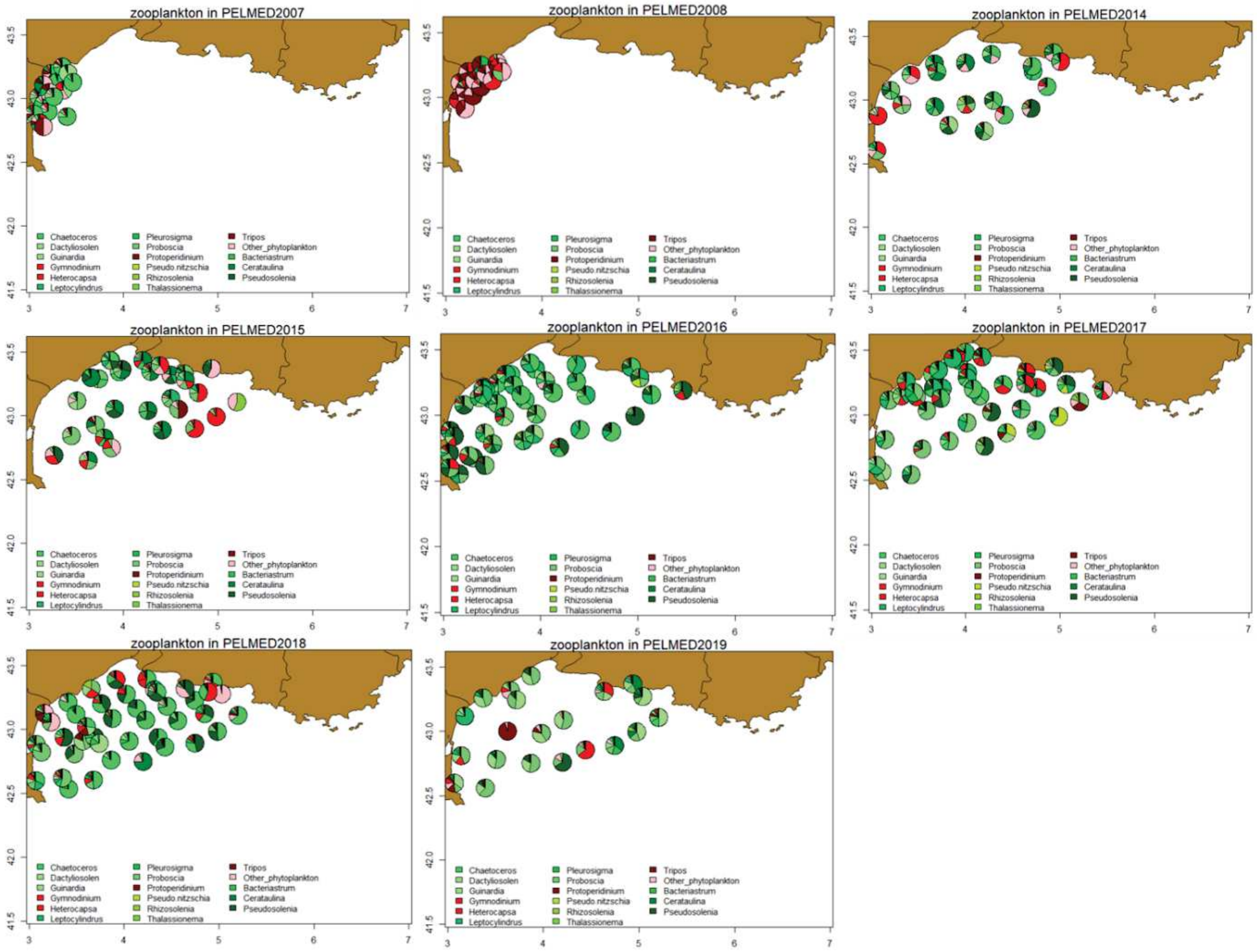


Figure III-23 *Map of the community composition of the different phytoplankton stations sampled at the surface over the Gulf of Lions shelf from 2007 to 2019.*

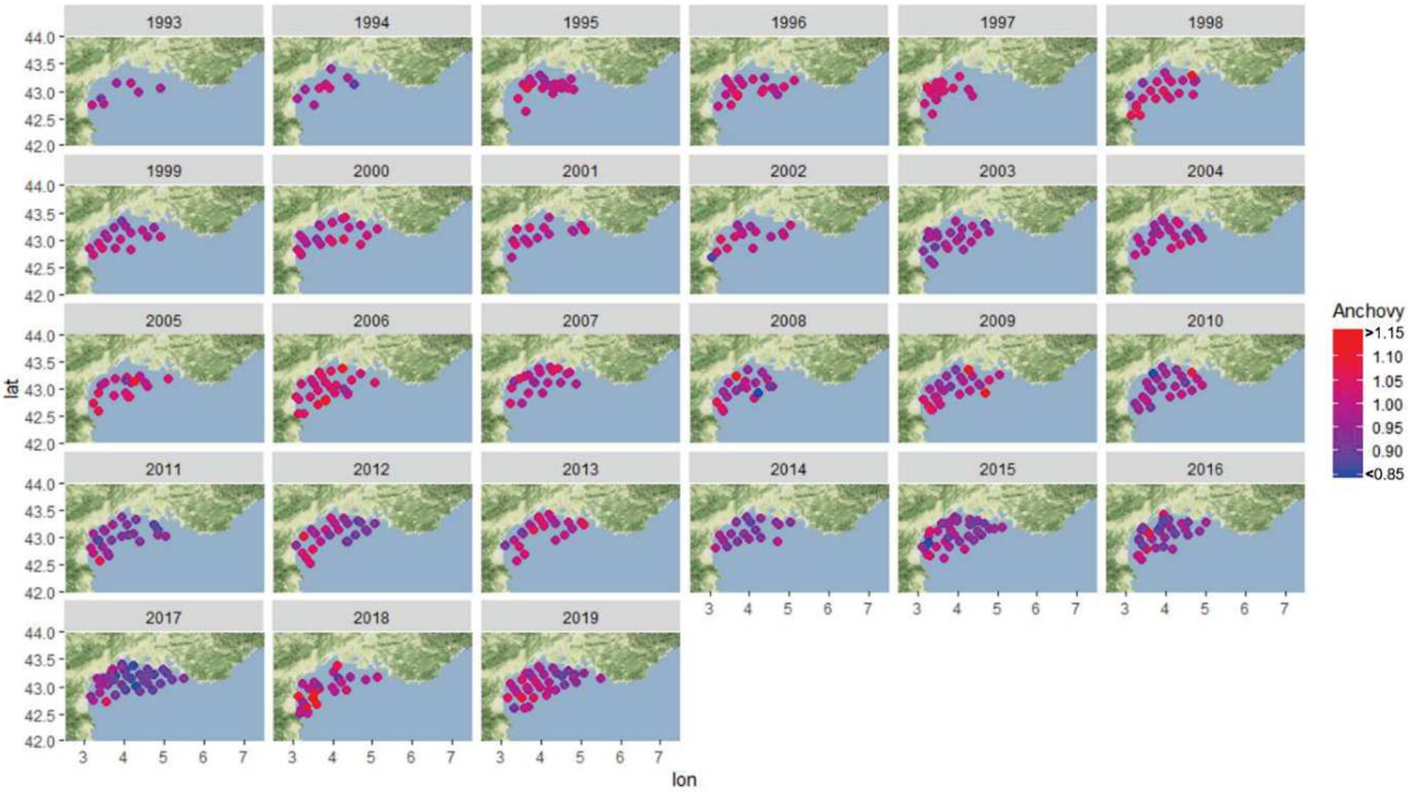


Figure III-24 *Map of the body condition of anchovy for the different trawl conducted from over the Gulf of Lions shelf from 1993 to 2019.*

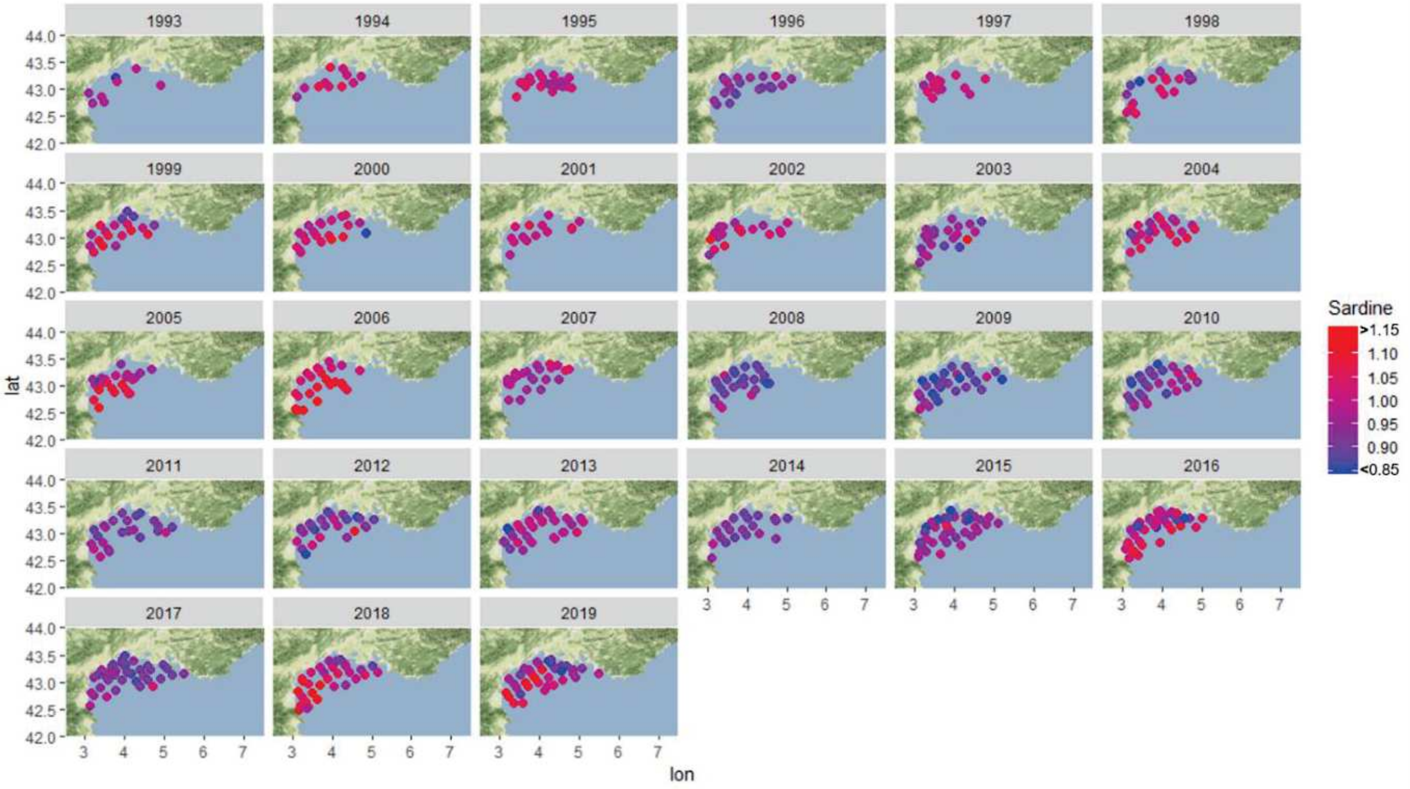


Figure III-25 *Map of the body condition of sardine for the different trawl conducted from over the Gulf of Lions shelf from 1993 to 2019.*

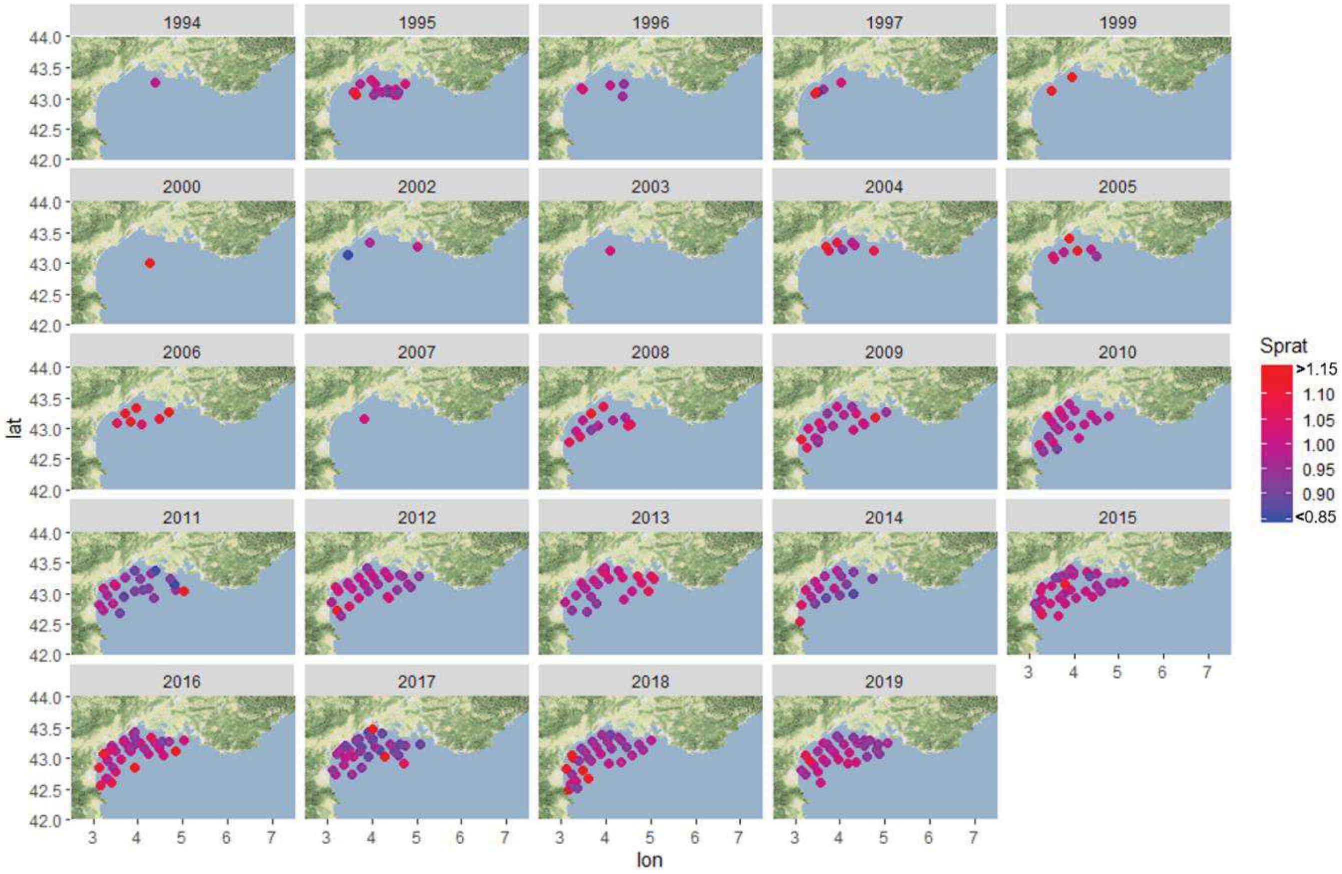


Figure III-26 *Map of the body condition of sprat for the different trawl conducted from over the Gulf of Lions shelf from 1994 to 2019.*

Résumé du chapitre 3 et introduction au chapitre 4

Dans le chapitre 3, une analyse fine de la communauté phyto- et zoo-planctonique estivale a été menée dans le Golfe du Lion à partir des données issues des campagnes successives de PELMED. Nous avons observé différents types de communautés phyto-planctoniques, certaines dominées par des dinoflagellés principalement du genre *Gymnodinium* et d'autres dominées par des diatomées des genres *Chaetoceros*, *Leptocylindrus* et *Proboscia*. Concernant le zooplancton, différentes communautés ont également été identifiées, certaines dominées par des cladocères du genre *Penilia* et *Evadne* et d'autres par des copépodes, essentiellement *Clausocalanus*, *Oithona* et *Centropages*. Malheureusement, les relations avec l'environnement se sont révélées assez faibles et n'ont pas permis de définir les conditions amenant à une communauté ou une autre, que ce soit pour le phytoplancton ou le zooplancton. Concernant les potentielles associations entre les communautés de phyto- et zooplancton, aucune association n'a pu être mise en évidence, les stations dominées par des diatomées ou dinoflagellés présentant des communautés zoo-planctoniques très similaires. Certains groupes de zooplancton tels que *Evadne* et *Oithona* ont été identifiés comme étant plus présents aux stations présentant des bonnes conditions des poissons alors que les groupes *Clausocalanus*, *Penilia* et *Doliolida* ont été identifiés comme étant plus présents aux stations présentant de mauvaises conditions des poissons, suggérant de possibles relations entre communauté planctonique et condition des poissons petits pélagiques. Néanmoins, les principales proies des petits pélagiques indiquées dans la littérature n'ont pas été retrouvées dans nos échantillons de plancton limitant nos interprétations dans la relation plancton-poisson. Enfin, aucune analyse à long terme n'a été possible, les données de plancton n'étant disponibles que l'été et seulement pour une dizaine d'années au cours des 20 dernières années, avec des différences d'échantillonnages assez importantes entre années.

Ainsi le chapitre 4, est consacré à l'analyse d'une des plus longues séries temporelles de zooplancton en Méditerranée nord-ouest, située au point B en mer Ligure. L'objectif était de caractériser la variabilité à long terme de la communauté zoo-planctonique au niveau mensuel en Méditerranée nord-ouest au cours des 2 dernières décennies, aussi bien en terme de densité que de taille des individus et composition taxonomique afin de voir s'il était possible d'identifier des changements synchrones à ceux observés sur les petits pélagiques du Golfe du Lion et qui auraient résulté d'un même forçage environnemental régional. Ainsi, les dynamiques de ces 3 variables de la communauté zoo-planctonique ont été étudiées par le biais de 2 filets (WP2 et Régent) afin de caractériser son évolution au cours du temps et détecter d'éventuels changements. Un deuxième objectif était de mettre en évidence d'éventuelles relations entre la communauté zoo-planctonique et l'environnement, aussi bien au niveau local que global, afin de comprendre les facteurs régissant la dynamique zoo-planctonique. Un focus a été fait sur la variabilité de la taille des individus zoo-planctoniques, paramètre au cœur de l'hypothèse du contrôle bottom-up des petits pélagiques mais pas disponible dans les échantillons prélevés dans le Golfe du Lion et de façon général peu étudié sur le long terme en Méditerranée.

Chapitre IV. *Short- to long-term changes in zooplankton size, abundance and taxonomic composition in the North Western Mediterranean Sea*

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Keywords : *zooplankton time series, zooplankton size spectra, long-term variability, environmental drivers, zooplankton community*

In preparation for submission in ICES special issue **“*Marine zooplankton time series: essential tools to understand variability in productivity-determining processes in the oceans*”**

Abstract

Zooplankton, and mainly crustaceans, are a key trophic compartment of marine food web, transferring energy of primary production to small pelagic fish. In this study, we investigated zooplankton density, size and taxonomic compositions at a coastal station in the North-Western Mediterranean Sea from 1995 to 2018. A focus was made on Crustaceans, one of the most important group of zooplankton and the main prey of several commercial fish species. Our objective was to evaluate the main patterns of temporal variations and to identify the main drivers of those changes. No long-term monotonous trend was observed in Crustaceans density, size and taxonomic compositions, as could have been expected in a context of climate change. Yet, our results showed a strong stability in the zooplankton and crustaceans community in terms of density, size and taxonomic composition. An intriguing change was however observed in 2015, with a decrease in density of small crustaceans as well as several gelatinous, both carnivorous and filter-feeders. After this drop, the crustacean community stayed at lower values, as well as carnivorous gelatinous but gelatinous filter feeders slightly recovered. No clear link was identified with environmental variables but changes in 2015 could be partly driven by temperature increase and changes in winter conditions affecting winter water mixing and nutrient availability, thought to be crucial for spring phyto- and zooplankton development.

IV-1 Introduction

Zooplankton is a key component of the ecosystem, providing the link between primary producers and upper trophic levels. They are very responsive to environmental changes and could consequently impact upper trophic levels with possible repercussions up to top-predators (Beaugrand & Kirby, 2010; Cury et al., 2000; Lynam et al., 2017). Different responses of zooplankton to environmental changes could have repercussion on trophic food web, such as phenological changes (Aberle et al., 2012; Thackeray et al., 2010; Winder et al., 2012) directly affecting planktivorous species recruitment, either positively (match) or negatively (mismatch) (Cushing, 1990). Further, changes in temperature can control zooplankton individual size and total biomass because of stratification and nutrient limitation, as observed in the Northwest Pacific (Kudela et al., 2006). Variations in zooplankton size could result in important modifications of the energy available to upper trophic levels, as small individuals are generally less energetic than large individuals (Barroeta et al., 2017), which may affect planktivorous species. Indeed, a recent experimental study on Mediterranean sardines showed that sardines feeding on bigger food size were in better condition and displayed higher growth rate than those feeding on smaller food size, despite food quantity (Queiros et al., 2019). Understanding how the plankton community varies in terms of taxonomic composition, body size and density appears then of primary importance to understand potential impacts on higher trophic levels, especially in a context of climate change.

This study, thus, aims at better understanding zooplankton dynamics in the North Western Mediterranean Sea (NWMS), using one of the longest zooplankton time series, the Point B station in the Ligurian Sea. Previous studies in the Ligurian sea have shown inter-annual variability in zooplankton taxonomic composition that was forced by large-scale climatic forcing, such as the NAO (García-Comas et al., 2011; Molinero et al., 2005; Vandromme et al., 2011; Fullgrabe et al., 2020). According to these studies, inter-annual variability in winter conditions leads to changes in the availability of nutrient resulting in different spring bloom intensities. During favorable years (in the 80's and early 2000's), increased primary production would then favor the development of zooplankton for the rest of the year. However, no information is available on the zooplankton size spectrum, when changes were observed in the NWMS both in the biogeochemical parameters, zooplankton community composition and in different planktivorous fish population, such as sardine and anchovy in the Gulf of Lions, supposed to be impacted by zooplankton changes (Brosset et al., 2016a; Coppola et al., 2018; Van Beveren et al., 2014; Fullgrabe et al., 2020).

In addition of bottom-up process linked to winter conditions, interactions with other gelatinous zooplankton was suggested to be another main factor impacting copepods variability (Molinero et al., 2005; 2008; Licandro et al., 2006). Indeed, gelatinous filter feeders, more efficient grazers of small phytoplankton than copepods have been proposed to successfully over compete copepods during warm years when pico and nanophytoplankton dominate (Licandro et al., 2006). Moreover, carnivorous gelatinous such as chaetognatha or siphonophorae could also have an impact increasing the top down pressure on copepods (Molinero et al., 2008).

Concerning the body size variability of zooplankton, only few information are available in the NW Mediterranean sea in short time series because of the difficulty to have long and consistent time series of zooplankton individuals size. Romagnan et al., (2016), investigated size spectra variability of Copepods across a year at Point B station and highlighted a seasonal variability, possibly linked to copepods reproduction. In the gulf of Lions, the variability of Biomass size spectra of copepods were investigated between 2002 and 2004 with no strong changes observed in the slope of the spectra (Zhou et al., 2010).

The main objective of this work was to study long-term, inter-annual and seasonal variations in zooplankton density, body size and taxonomic composition to identify potential changes since the late 1990s. A focus was made on crustaceans, which are the most abundant group of meso-zooplankton and also the principal prey of many small pelagic commercial species such as sardine and anchovy (Brosset et al., 2016; Espinoza & Bertrand, 2008), but also on gelatinous carnivorous and filter feeders which could impact crustaceans variability. We further investigated the potential causes of crustaceans variability among different ecological processes, such as density-dependence, community composition turnover and environmental changes.

IV-2 Material and Methods

IV-2.1 Sample collection

Zooplankton samples were collected weekly at “Point B” (43°41.10’N, 7°18.94’E; 85m water depth), a coastal monitoring station at the entrance of the bay of Villefranche-sur-Mer (NW Mediterranean Sea, France). Sampling was done by vertical tows (75m deep to surface) of a Regent net (mesh size of 680µm, mouth aperture of 0.785m^2) and WP2 net (mesh size of 200µm, mouth aperture of 0.25m^2). For the present study, 919 samples collected once to 4 times a month from 1995 to 2019 were used for Regent net and 666 for WP2, from 2004 to 2019. All samples were manually fractionated with a Motoda box and then analysed with the Zooscan/Zooprocess system (Gaby Gorsky et al., 2010). This process allows having a picture for each individual, from which the identification and size measurements are performed. Identification was performed using automatic recognition followed by the validation of each picture by an expert. All the zooplankton data are available on the EcoTaxa platform (https://ecotaxa.obs-vlfr.fr/).

IV-2.2 Taxonomy in both WP2 and Regent

Analyses based on monthly crustaceans size spectra, investigating the distribution of all size spectra mod from 1995 to 2019 for Regent and from 2004 to 2019 for WP2 showed that the nets accurately sampled individuals measuring at least 1.5mm and 0.65mm respectively (see supplementary materials (SM) for details). For that reason, individuals lower than 1.5mm for Regent and 0.65mm for WP2 were not considered in all the following analyses. Those limits were also applied for the other groups than crustaceans.

Because of the small size of individuals in the WP2 net, taxonomic identification at fine level was difficult and not homogenous for the whole period. The 15 groups that were homogenously identified for the whole time were finally retained, i.e., “Eumalacostraca”, “Cladocera”, “Ostracoda”, “Copepoda” and “Other_crustacea” for the crustaceans ; “Chaetognatha”, “Siphonophorae”, “Other Hydrozoa”, “Salpida”, “Doliolida” and “Appendicularia” for gelatinous species and finally “Harosa”, “Annelida”, “Mollusca” and “Other zooplankton”. The gelatinous were analysed regrouped in two groups, the “herbivorous” filter feeders (Doliolida, Salpida and Appendicularia) and the carnivorous (Chaetognatha, Siphonophorae and Other hydrozoa) (Acuña, 2001; Dallot et al., 1988)

IV-2.3 High resolution taxonomy in the Regent

In the Regent, a high resolution taxonomic identification was possible, especially for crustaceans, because of a greater size of the individuals allowing a better recognition compared to smaller one. The taxonomy was determined as a compromise between the resolution allowed by the image quality, avoiding high resolution taxonomy for small individuals, and the necessity to aggregate rare groups. Because the Calanoida order was dominant (around 60% of Crustaceans), analyses were performed at the family level for this order, while Decapoda, Amphipoda, Mysida and Euphausiacea were only identified at the order levels. Two groups “Other_Calanoida” and “Other_crustacea” were also kept and represented mainly individuals identified at a low resolution taxonomy. Regarding the “Other_crustacea” group, around 90% of the individuals were identified as Eumalacostraca, at the subclass level.

IV-2.4 Time series analyses of the zooplankton density

Because both changes in plankton phenology and density could affect upper trophic levels, we investigated crustacean and gelatinous (herbivorous and carnivorous) densities time series both at a monthly time scale. Data were expressed in individuals/m^3 and log-transformed to stabilize the variance (Curran-Everett, 2018). A wavelet analysis was performed to quantify the main patterns of variability (Carey et al., 2016; Chatfield, 2003) and the significance of the wavelet spectrum was performed against white noise, as the time series displayed variance at both high and low frequencies (Rouyer et al., 2008).

The long-term trend was extracted with the Eigen Vector Filtring (EVF), which allowed us to estimate the percentage of variance associated to this trend (Ibanez & Dauvin, 1988). To do this, a PCA was performed on a matrix of the time series lagged from 0 to n time lags (in this study, n being equal to 36 months, which allowed us to investigate inter-annual variations without considering seasonal variability). The analyses were peformed using the “pastecs” R package (Grosjean et al., 2014). To investigate potential regime shifts along the time series, breakpoints analyses were also performed, using the “strucchange” R package and an algorithm testing structural changes in time series (Kleiber et al., 2002). Optimal number of segment partitions was based on BIC criterion in order to compute only the most relevant changes.

IV-2.4.1 Time series analyses of the zooplanktonic community

To study the variations in the composition of the zooplanktonic community, monthly time series of densities of each group were constructed (see Sections 2.2 and 2.3). Monthly densities of each group were then plotted on stacked plots to depict both the inter-annual variations and the phenology of the zooplantonic community and the proportion of each group. The long-term trends of each groups were further extracted by means of EVF analysis. Note that the proportion of each group per year (or month) was calculated on the raw data (without log transformation) and represented in “stacked plot” as the log density of total zooplankton multiplied by the proportion of each groups.

IV-2.4.2 Time series analyses of crustaceans size spectra

Because crustaceans are mostly ellipsoid, size of each individual was defined as the primary axis of the best fitting ellipse calculated during the Zooprocess (Gorsky et al., 2010; Romagnan et al., 2016). A sensitivity analysis was run to determine the minimal number of individuals within a sample to perform a reliable size spectrum. The results led us to keep a minimum of 200 and 45 individuals/sample for the WP2 and the Regent, respectively (SM Figure IV-12). Monthly and annual size spectra were then computed, by means of Normalized Density Size Spectra (NDSS) similar to the well known Normalized biomass size spectra (Sheldon et al., 1977; Zhou et al., 2010) but based on density instead of biomass. To do so, the density of each size class was calculated and divided by the width of the size class in order to normalize the spectra. Size classes increased each time by a factor of 1.3 in order to have both details in smaller size and avoid empty size classes in higher body size. The slope of each size spectrum was estimated through a linear regression without intercept. The time series of the slopes of the monthly NDSS were finally constructed and analysed through EVF (to extract the trend) and breakpoint analysis (to identify potential regime shifts).

IV-2.5 Dealing with missing data

The minimal number of individuals by sample necessary to construct reliable a size spectrum (see above) led to some missing values, i.e., 14 of the 300 months in the slopes time series of Regent were missing, while 6 of the 192 months were missing for the WP2. Furthermore, 4 of 192 monthly densities of the WP2 were also missing. To fill missing values, an algorithm based on iterative PCA was used from the MissMDA package (Josse & Husson, 2012). First, the monthly time series was transformed in a year x month matrix and missing values were replaced by the mean of the variable (here the months). Then a PCA was performed and mean values inserted to fill missing data were replaced by the values estimated by the PCA. A second PCA was performed and values estimated by the first PCA were replaced by the one of the second PCA. Following this scheme, iterative PCA were performed until the values estimated stabilise.

IV-2.6 Environment data and analyses

IV-2.6.1 Environmental data

Because one of the objectives was to investigate whether the inter-annual variability observed in crustacean density and size spectra could be explained by environmental parameters, we gathered a set of environmental variables that are known to affect plankton dynamics at both local and regional scales. All the local environmental data have been sampled weekly since 1995 at the same location as the plankton tows (the "Point B") at 5 different depths (1m, 10m, 20m, 30m and 50m). Water for nutrients and chlorophyll-a analyses was sampled by Niskin bottles. Nitrate (NO3 $\mu mol.l^{-1}$) and Silicate (SiOH4 $\mu mol.l^{-1}$) nutrients were considered, but not Phosphorus because concentrations were at the limit of the detection threshold. Nutrients concentrations were analysed by Technicon. Data at the 1m and 50m layers were averaged, as those two depths were the only ones with complete data from 1995 to 2019. Chla concentration ($\mu g.l^{-1}$) was analysed with spectrophotometer until 2002 and then with Lorenzen fluorimetry until now (Lorenzen, 1966). Chla was considered as a proxy of phytoplankton biomass and was averaged at the 5 available depths from 1 to 50m. A Seabird SBE25 CTD was used to measure sea water temperature, which was also averaged at the 5 available depths from 1 to 50m. Finally, the stratification of the water column was calculated as the difference of water density between the 10m layer and the 50m layer, as in Vandromme et al., (2011). All these environmental data were provided by SOMLIT (http://somlit-db.epoc.u-bordeaux1.fr/bdd.php).

In addition, a winter water mixing index was constructed, reflecting the potential mixing of the water column during the winter period (from December to March). Indeed, higher winter water mixing has been shown to be related to higher planktonic production in this area (see García-Comas et al., 2011; Vandromme et al., 2011). To construct an winter mixing index, a Principal Component Analysis (PCA) was performed on the winter temperature, winter stratification(Vandromme et al., 2011), winter salinity and winter water density at the “Point B” (SM Figure IV-13). All Winter time series were constructed by averaging monthly values from December to March. The first axis of this PCA, which represented 56.6% of the total variance, was considered as the winter water mixing time series (see also Vandromme et al., 2011).

Finally, the large scale WeMO index (Martin-Vide & Lopez-Bustins, 2006) was also considered and preferred to the NAO index (as used in past studies, such as Molinero et al. 2005) because of its better representation of the North Western Mediterranean sea regional environmental conditions (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012). This index represents differences in standardized surface atmospheric pressure between San Fernando (Spain) and Padua (Italy) and reflects changes in regional weather conditions, especially in rainfall, river flow, wind strength and direction and temperature. Positive values of the index are associated to lower temperature and higher river flow and wind, thought to be favourable for plankton productivity (Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012).

IV-2.6.2 Environmental drivers of the variations in zooplanktonic densities and size spectra

To identify the potential relationships between environmental variables and the log-density or size spectra of crustaceans linear models (LM) were investigated, as these two biotic variables were normally distributed. Environmental time series of local Temperature, Chla, nitrate, silicate and the winter water mixing index as well as the WeMO index were used as explanatory variables. The linear models were based on annual time series for both the environmental and zooplanktonic variables to eliminate the strong autocorrelation in the monthly time series due to the seasonal cycle. A stepwise forward and backward selection was run to select the most explanatory and significant variables based on AICc. Variance Inflation Factor values (VIF) were checked in order to avoid multicollinearity between variables. Finally, residuals and the goodness of fit of each model were then investigated through standard tests.

All the analyses presented above were conducted with R v. 3.4.1 (R Core Team, 2018).

IV-3 Results

IV-3.1 Zooplankton densities variability

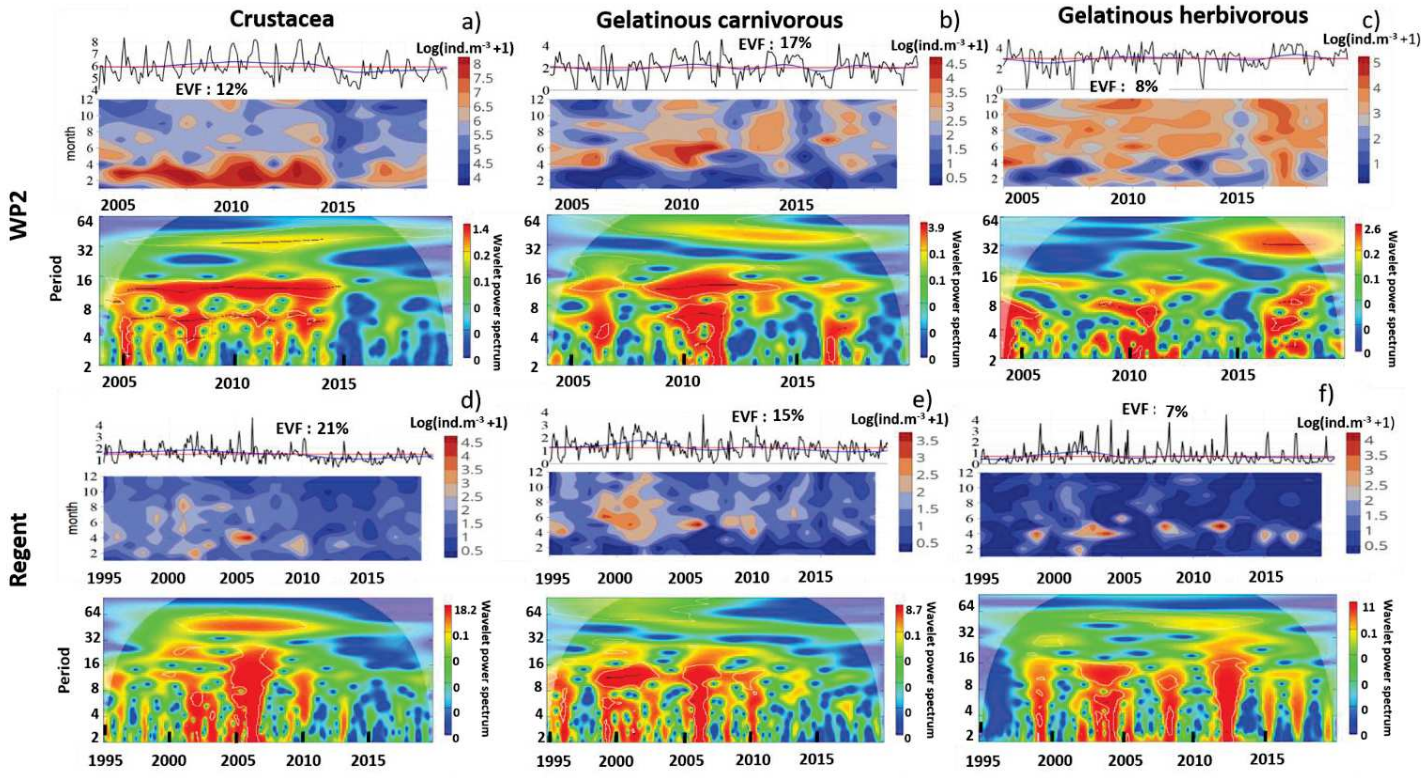


Figure IV-1 ***Monthly log densities (ln (ind.m^{-3} +1)) and wavelet analyses of Crustacea, gelatinous carnivorous and gelatinous herbivorous for WP2 (upper panels) from 2004 to 2019 and for the Regent (lower panels) from 1995 to 2019. For each block, the upper panel represent the monthly time series in black with the trend extracted with the EVF (in blue) and the mean over the whole period (in red). In the mid panel, the contourplot of the monthly densities. In the bottom panel, wavelet analysis performed on monthly densities with significant variance delimited by white lines.***

The long-term trend derived from the EVF explained a rather small proportion of the total variance of the WP2 time series, i.e., between 8% and 17%, indicating little inter-annual variability in crustaceans and gelatinous densities. However, the year 2015 appeared very particular, characterized by low densities for the 3 groups (Figure IV-1a, b and c). Gelatinous herbivorous and carnivorous seemed to recover after 2015 densities similar than before (respectively around 3 *log (ind.m^{-3} +1) and* 2 *log (ind.m^{-3} +1))*, but Crustaceans stayed after 2015 at lower values than before, around 5.5 *log (ind.m^{-3} +1).* The wavelet analyses showed that all 3 series showed higher variance at the seasonal scale, as well as high frequencies (2 to 8 months), indicating also the presence of short-term variations or noise (Figure IV-1). Intra-annual (or seasonal) variability was indeed strongly present in crustaceans time series of the WP, with higher densities between February and May, up to 8 *log (ind.m^{-3} +1)* (Figure IV-1a), which translates in high power values at around 12 months in the wavelet analysis. Note, however, that this seasonality is weaker and even absent since 2015 during the period of lower densities (Figure IV-1a). The seasonality of gelatinous carnivorous in the WP2 was less marked than crustacean, but also present (Figure IV-1b), with maximum densities around May and June, just after the Crustacean peak. Gelatinous herbivorous did not displayed seasonality, even if lower densities seemed to occur generally in winter. However, no signal was observed around the 12 month in the wavelet analysis (Figure IV-1c).

For the Regent, the long-term trend represented also a small part of the total variance (between 7 and 20%), but, the period between 2000 and 2005 was marked by higher densities for the gelatinous carnivorous and secondarily for the 2 other groups. Crustaceans in the Regent as well as gelatinous herbivorous did not present seasonal signal, but short-term variations, as observed in the wavelet analysis, even if highest densities seemed to occur generally in Spring. Finally, gelatinous carnivorous were the only one to present seasonality with highest densities generally between May and June (Figure IV-1e).

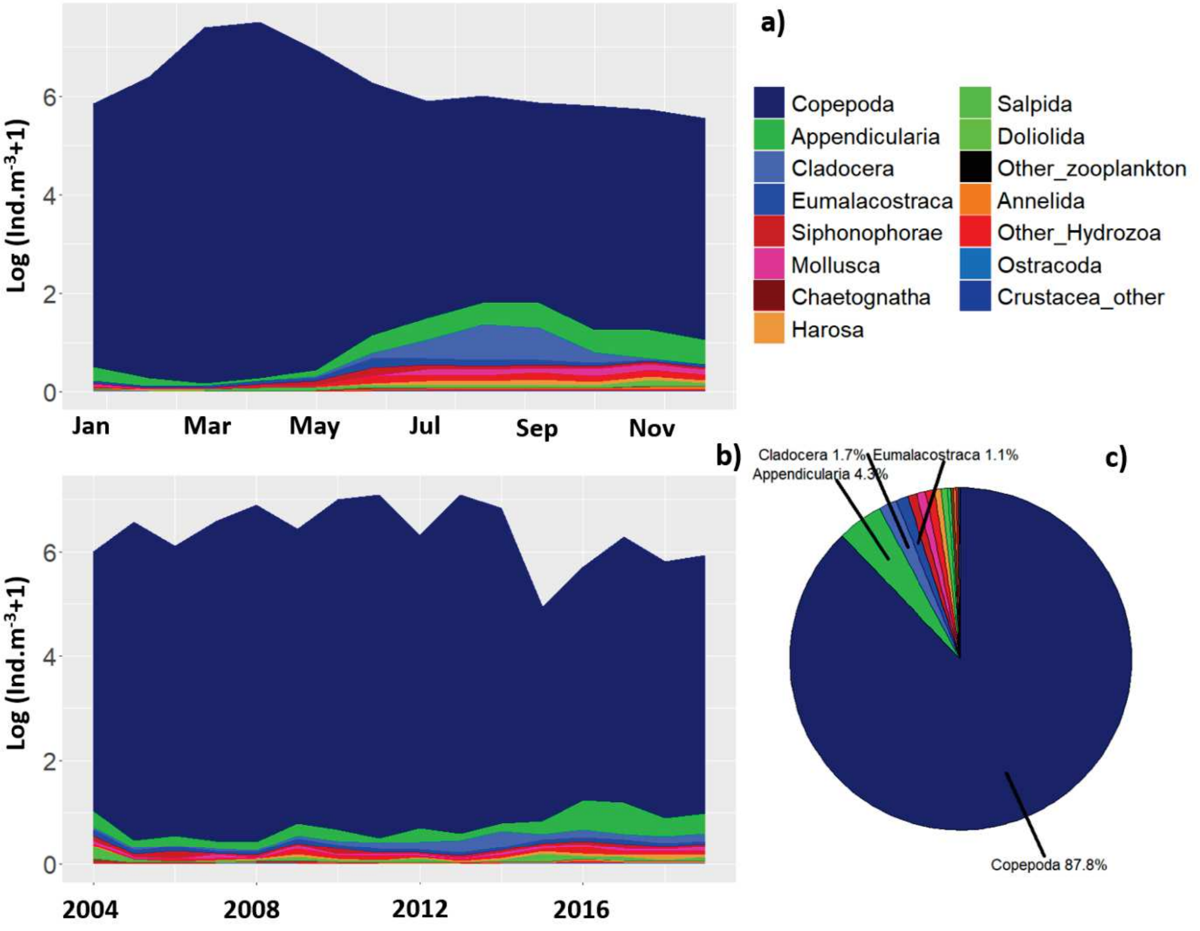


Figure IV-2 ***Stacked mean densities in the WP2 net (for individuals over 0.65mm body length) of each groups for each months from 2004 to 2019 (a), stacked yearly densities of each groups from 2004 to 2019 (b) and mean proportion of the different groups for the whole period (c). Blue colors represent the crustaceans, red colors the gelatinous carnivorous and green colors the gelatinous herbivorous. Groups are ordered in the plots following their proportion over the whole period.***

Copepoda was the most abundant group, highly dominant in the WP2 both at seasonal and inter-annual scales. This group represented 87.8% of total density of the zooplankton density collected by this net from 2004 to 2019 (Figure IV-2c). No long-term trend was observed in total zooplankton density, but a sudden diminution was observed in 2015, mainly due to Copepoda density decrease. In opposition, Appendicularia increased at the same moment, but not enough to counterbalance the copepod decrease. Phenological differences were observed between groups, with copepoda more abundant in spring (March and April) whereas Appendicularia and Cladocera were more abundant in summer (between July and October, Figure IV-2b). This was confirmed regarding more precisely the monthly time series of the different groups, classified mainly in 2 categories : (i) those displaying high densities in spring until early summer, such as Copepoda, Salpida, Siphonophorae or Eumalacostraca, and (ii) those having high densities in summer and early autumn, such as Cladocera, Doliolida or gelatinous carnivorous with Chaetognatha an other hydrozoa) (SM Figure IV-14). Interestingly, no phenological shift was observed over the two decades.

In the Regent, the copepods were also the most abundant group, but not so dominant (25.8%). The total of gelatinous groups (including herbivorous and carnivorous ones) were in a higher proportion than crustaceans (around 50% vs 40% respectively) (Figure IV-3c). Total zooplankton slightly increased from 1995 to 2001 and then decreased until 2019. There was however strong year-to-year variation, such as peaks of Copepoda in 2006, Mollusca in 2000 or Salpida in 2013 (Figure IV-3b). The peaks of zooplankton densities were observed in April, with Copepoda and Salpida, just followed by Hydrozoa in May and then Eumalacostraca from June to September and Chaetognatha from July to December (see also in SM Figure IV-15). No phenological shift were observed over the three decades. Due to the large mesh size of the net, some groups were poorly represented and even totally absent, such as Ostracoda or Cladocera (Figure IV-3 and SM Figure IV-15).

The crustacean community in the Regent that could also be investigated at the family level (see Material & Methods) was well diversified with no strong dominance. The most abundant group was Calanidae, representing around 25% of total densities and other crustacean (22%). A decrease in total densities was observed since 2002, but with strong year-to-year fluctuations. In 2001, all the groups increased while in 2006 Calanidae displayed a strong peak and represented more than 60% of the total Crustacean community this year (Figure IV-4b). Highest densities occurred between March and April, around 2.4 *log* $(ind.m^{-3} +1)$, mainly with Calanidae (Figure IV-4a). Eumalacostraca, mainly represented by “Other crustacea” (see section 2.3) and Decapoda, were more abundant in late spring and summer. Metridinidae and candacidae (each one representing around 10% of the community) were stable over time, with no seasonality and no inter-annual changes (Figure IV-4). Some groups were however poorly represented, such as Penilia, Oithonidae, Oncaeidae or Acartiidae, and could therefore hardly be analyzed (see SM Figure IV-16). As for the other groups, no phenological shift was observed over the three decades (see SM Figure IV-16).

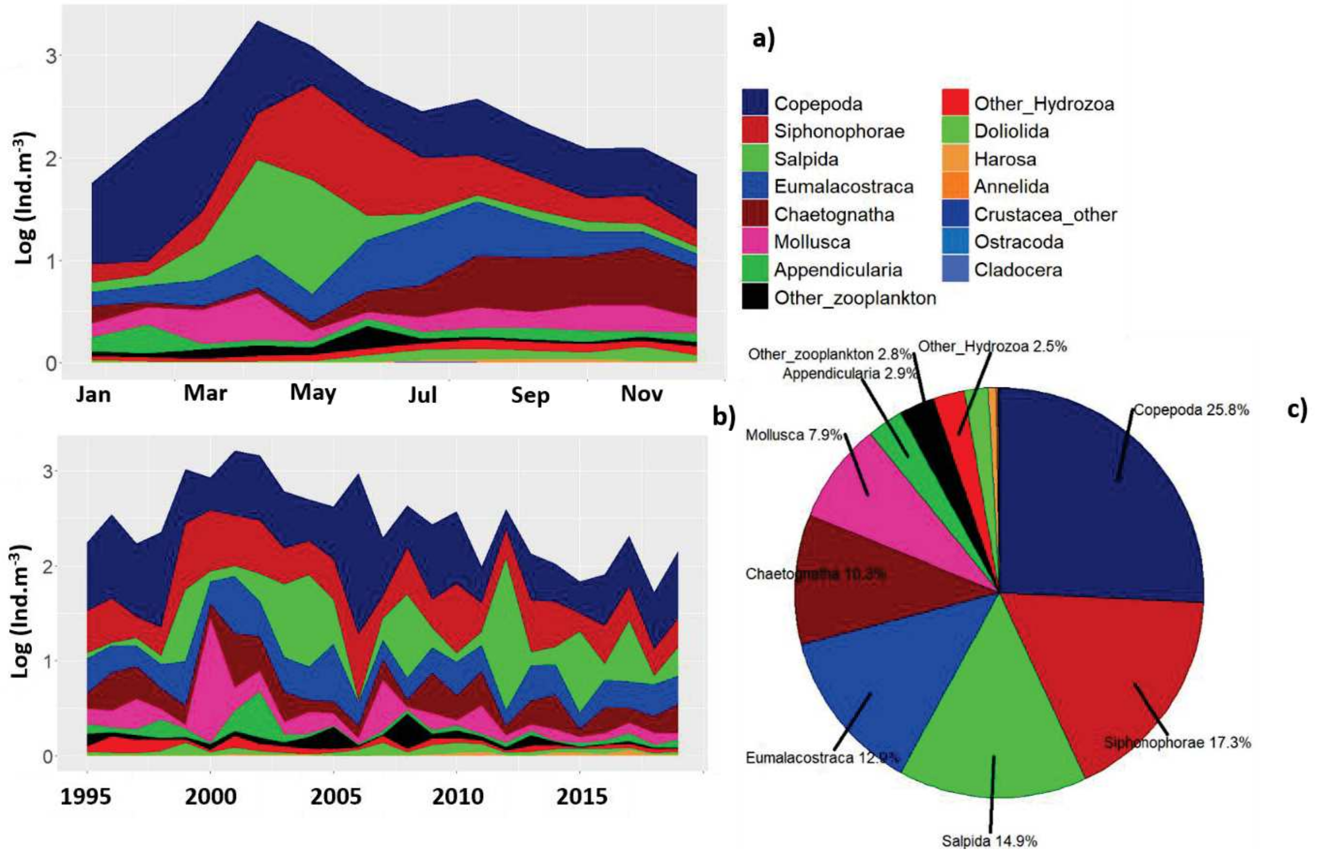


Figure IV-3 *Stacked mean densities in the Regent net (for individuals over 1.5mm body length) of each groups for each months from 1995 to 2019 (a), stacked yearly densities of each groups from 1995 to 2019 (b) and mean proportion of the different groups for the whole period (c). Blue colors represent the crustaceans, red colors the gelatinous carnivorous and green colors the gelatinous herbivorous. Groups are ordered in the plots following their proportion over the whole period.*

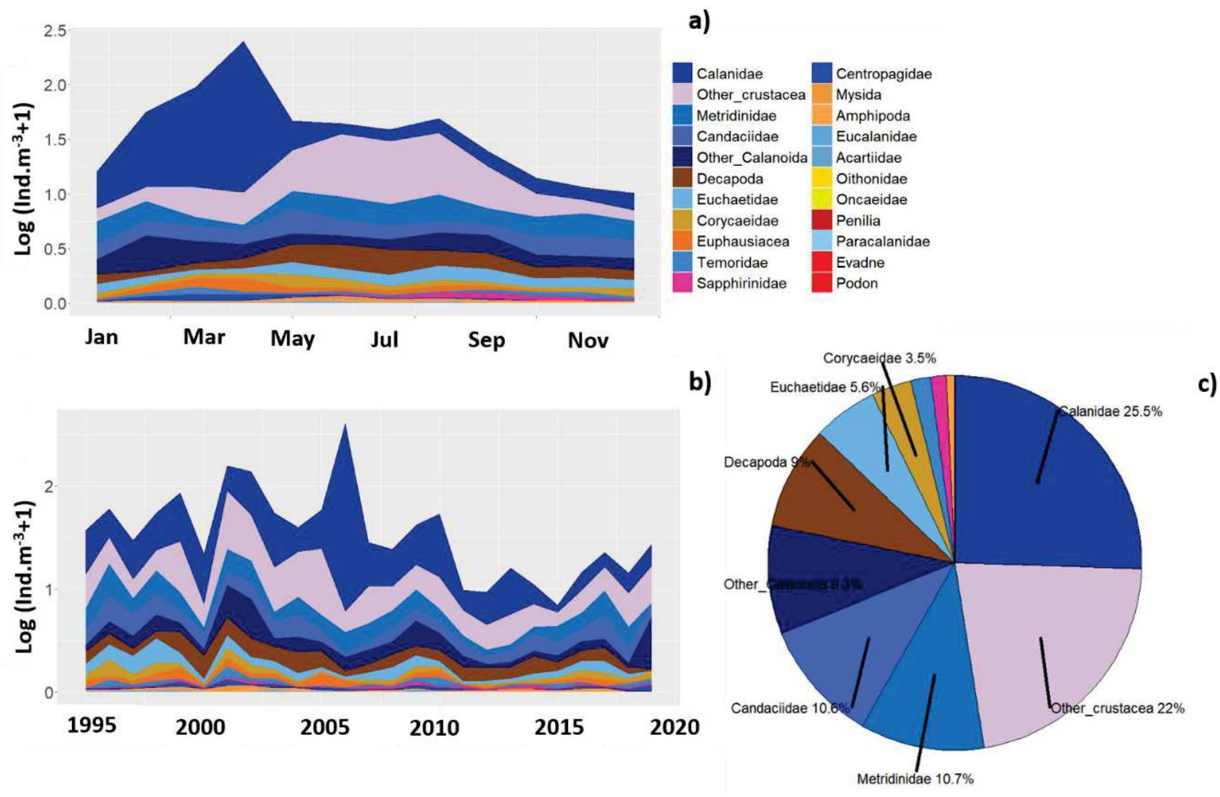


Figure IV-4 ***Stacked mean densities in the Regent net (for individuals over 1.5mm body length) of each Crustacean order or family for each months from 1995 to 2019 (a), stacked yearly densities of each groups from 1995 to 2019 (b) and mean proportion of the different groups for the whole period (c). Blue colors represent the Calanoida families, red colors the Cladocera and brown to orange colors the Eumalacostraca families. Groups are ordered in the plots following their proportion over the whole period.***

IV-3.2 Size spectra analysis

The long-term trend of Crustaceans NDSS slope presented only 7.2% of the variability of the series. The series was quite stable from 2004 to 2014 at values around -5.5 and increased rapidly in 2015 to stay after at higher values around -5.2. A breakpoint was detected in 2015, when spectra become flatter. Seasonal variations were present in the shape of the spectra, with steeper spectra in spring and flatter spectra in summer and autumn (Figure IV-5). This seasonality was confirmed by the wavelet analysis with high power values at around 12 months. However, this seasonality also disappeared in 2015, when spectra were flatter during all the year. After 2015, spectra in spring seemed flatter than before (Figure IV-5).

Concerning the Regent, the long-term trend of Crustaceans NDSS slope presented a higher percentage of the total variability of the series, at around 27%. The series was rather stable between 1995 and 2002 at values around -2.2 and then increased in 2003 with a breakpoint detected and spectra becoming flatter (mean slope of -1.8). The slopes of the spectra remained stable until 2010 and a second breakpoint was found in 2011 with spectra becoming even more flatter (slope around 0.9). Finally, a last breakpoint was observed in 2016, when spectra become steeper with mean slope at around -1.7 until 2019. No clear seasonal pattern was observed on the contourplot, but the wavelet showed high signal at around 12 months for some years, mainly between 2000 and 2005 period. Moreover, high frequencies (2 to 8 months) presented also strong signal indicating also the presence of short-term variations or noise (Figure IV-6). Additional analyses have been further performed and showed that the slopes of the NDSS carefully track changes in size spectra of the zooplanktonic community collected by the WP2 or by the Regent (see SM Figure IV-17 and 18 for further details).

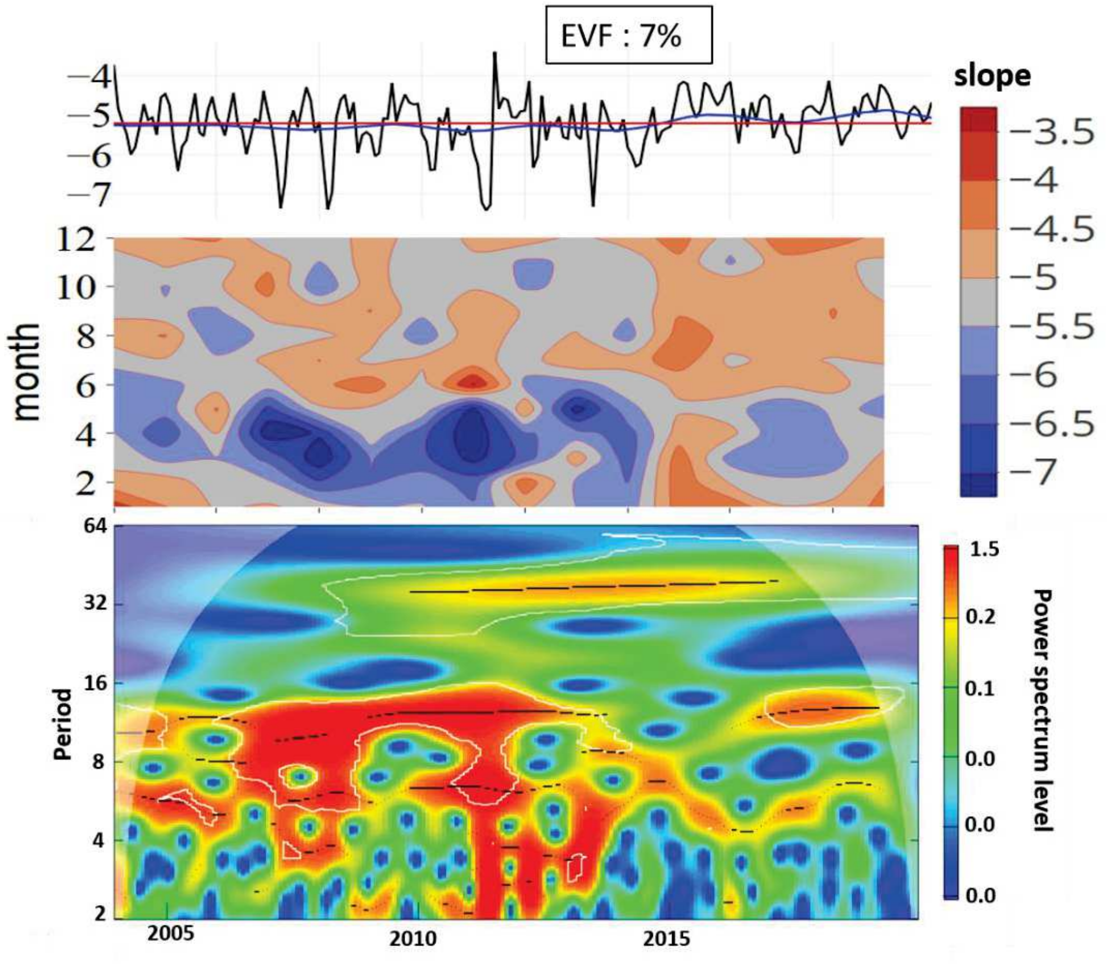


Figure IV-5 *Monthly time series of WP2 NDSS slopes from 2004 to 2019. The upper panel represent the monthly time series in black with a 3-year trend extracted with EVF (in blue) and the mean over the whole period (in red). In the mid panel, the contourplot of the time series and in the bottom panel, wavelet analysis with significant variance delimited by white lines.*

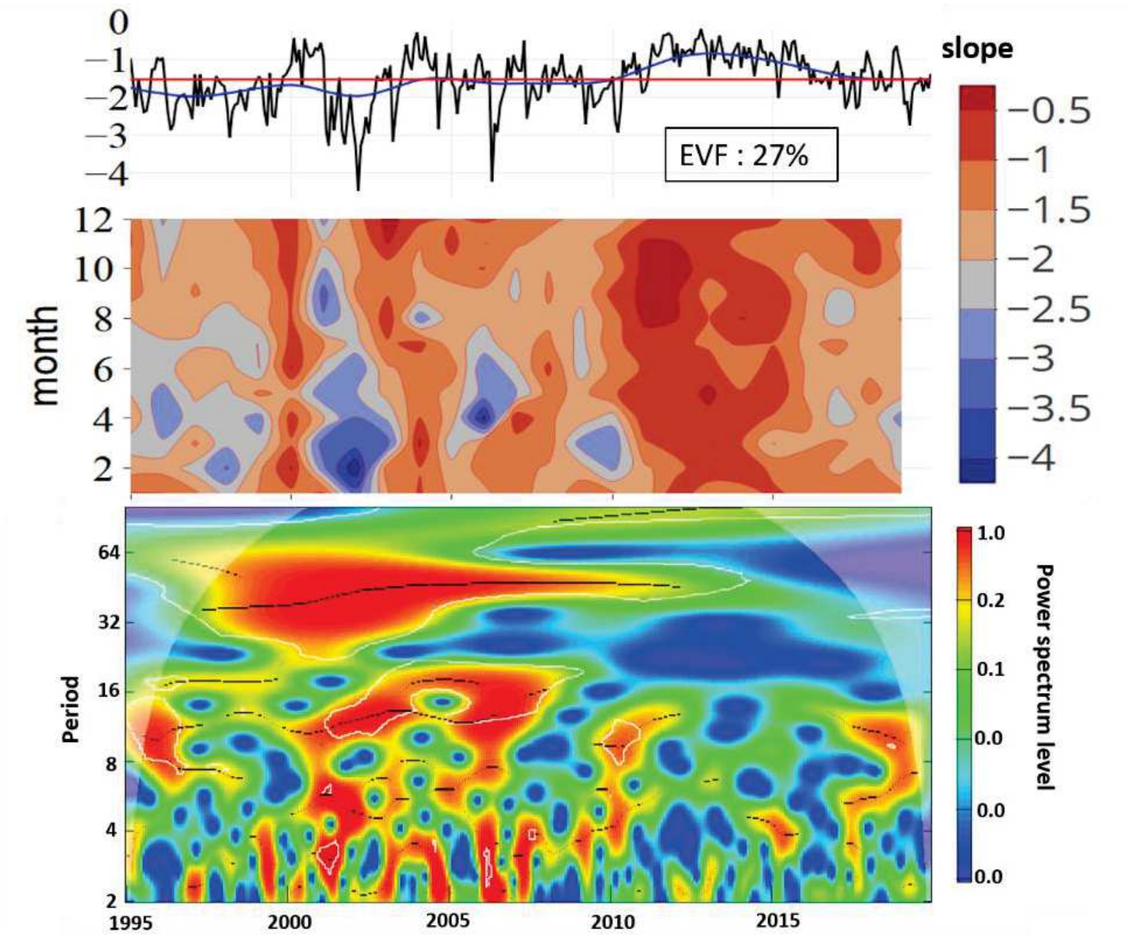


Figure IV-6 ***Monthly time series of Regent NDSS slopes from 1995 to 2019. The upper panel represent the monthly time series in black with a 3-year trend extracted with EVF (in blue) and the mean over the whole period (in red). In the mid panel, the contourplot of the time series and in the bottom panel, wavelet analysis with significant variance delimited by white lines.***

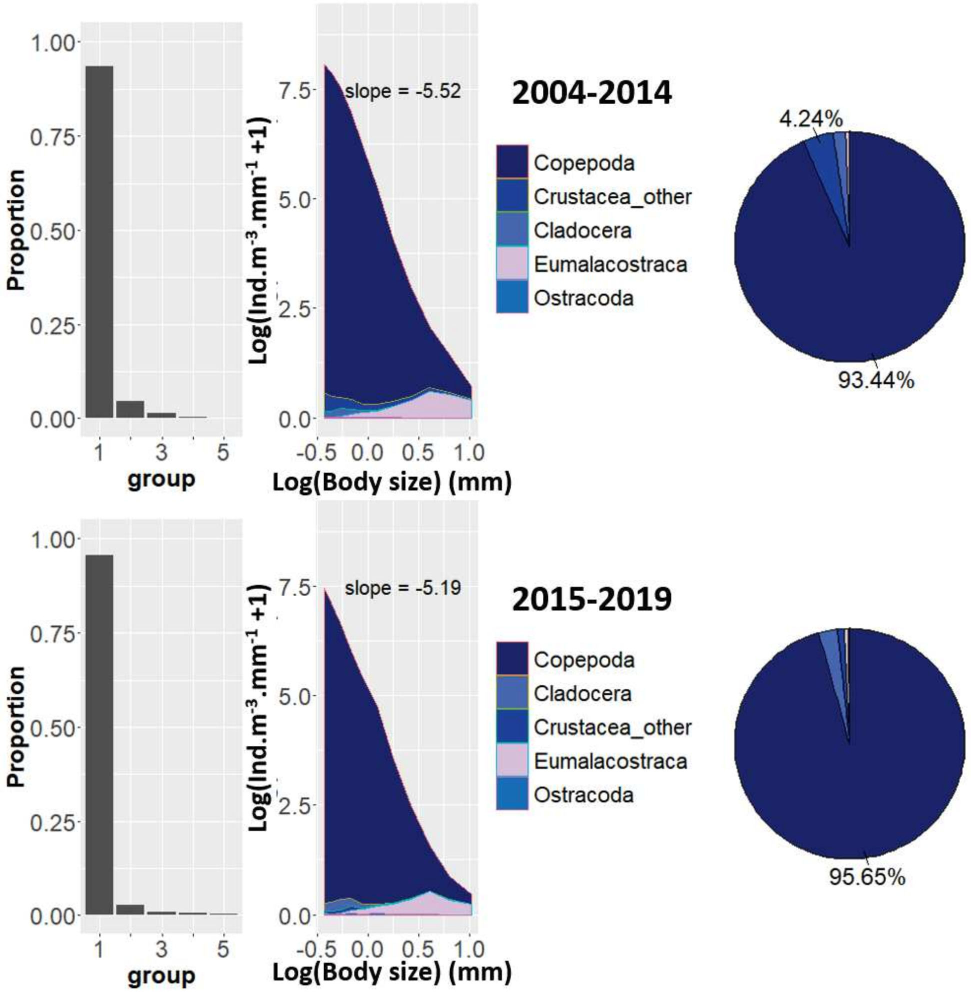


Figure IV-7 ***Rank-frequency diagram (left), mean NDSS size spectra (middle) and mean proportions of crustacean groups (right) for the 2 time periods identified with breakpoints performed on monthly time series of Crustaceans NDSS slopes in wp2. The slope of the mean spectra are indicated in each panel.***

As already seen above, Copepoda was the most abundant group dominating the zooplanktonic community in the WP2 and it represented up to 95% of total densities of the Crustaceans between 2015 and 2019 (Figure IV-7). The first period between 2004 and 2014 presented steeper size spectra with a mean slope of -5.52 compared to 2015-2019 period, for which mean slope of spectra was around -5.19. Note that the slope of the size spectra and the log-densities seemed to be positively related. The rank frequency analyses presented only poor variability between periods, the mean proportion of the first group ranging from 0.94 to 0.96 (Figure IV-7).

In the Regent, Copepoda was also the most abundant group, representing between 60% and 70% of total Crustaceans densities depending the periods while Eumalacostraca was the second group representing between 26% and 36% of total crustaceans densities (Figure IV-8). The first period between 1995 and 2002 was characterized by the steepest spectra, with a mean slope of -2.2 and also with the highest densities (up to 2.1 log(densities.mm^{-1})). In opposition, the third period between 2011 and 2015 displayed the flattest spectra, with mean slope of -0.91 and also the lowest densities (up to 0.9 log(densities.mm^{-1})). Rank-frequency analysis showed small variations, the first group representing between 60% and 70% of the community. Interestingly, the third period which was the less abundant was also the less dominated (Figure IV-8).

The same analysis at the family level for the Regent displayed in general little differences in the community composition between periods characterized by flat and steep size spectra, except the higher presence of Decapoda in the third period when spectra were flatter (Figure IV-9). The community was rather diversified, as indicated by the shape of the rank-frequency diagram and the rather low percentage of first group (<30% for all periods). A high stability was also observed in the composition of the community with the same dominant groups, i.e., other crustacean and Calanidae always the 2 first except in the last period where other calanoida was in second position. The following most important groups were Metridinidae, Candacidae Corycaeidae or Decapoda, which represented between 6% and 11% of the community. No disappearance of groups was observed, neither the replacement of one by another except Calanidae partly replaced by other Calanoida in the last period (Figure IV-9). Crustacean community appeared thus fairly stable and rather diversified, with no strong changes over times, despite changes in the size spectra slopes.

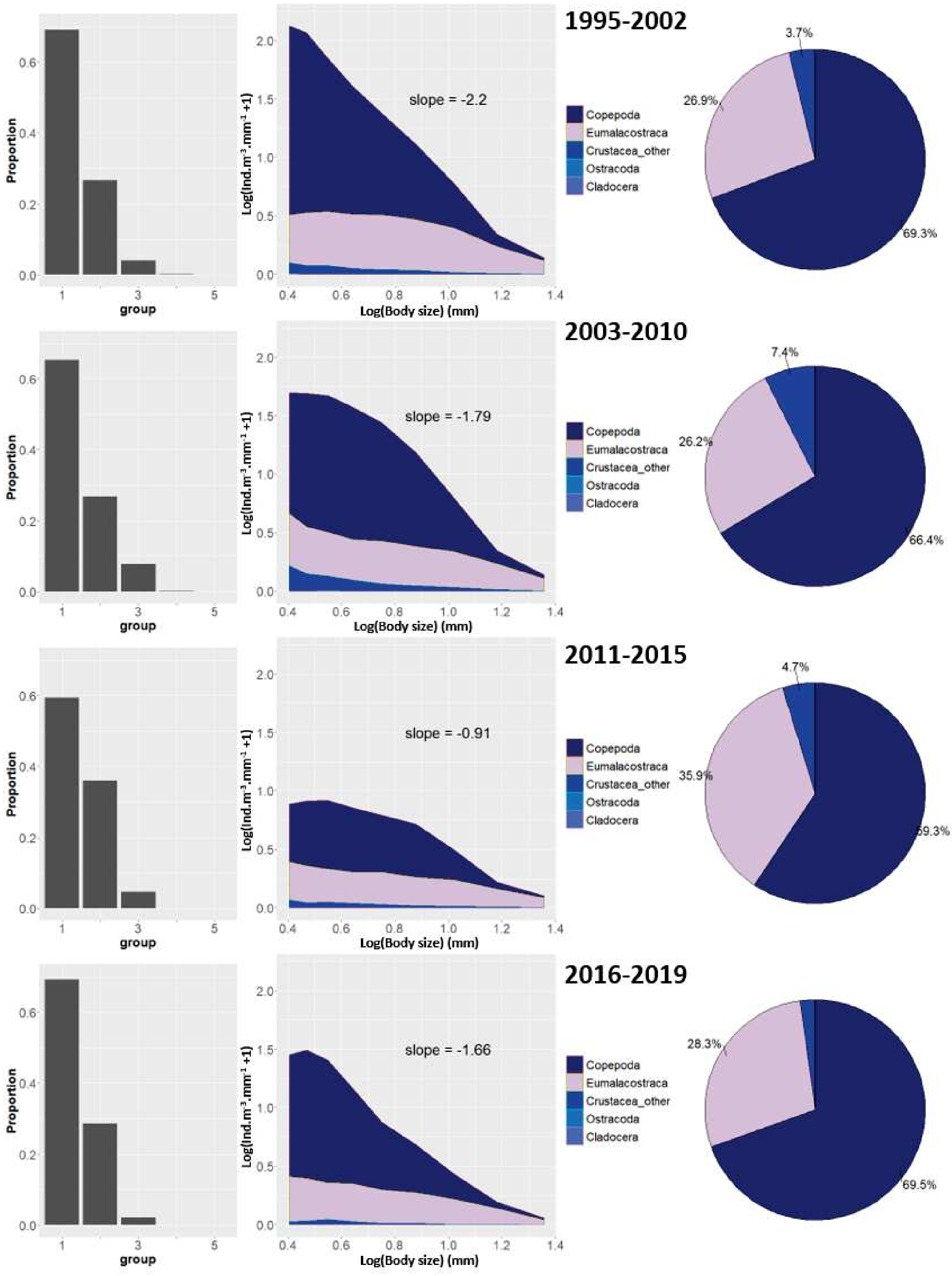
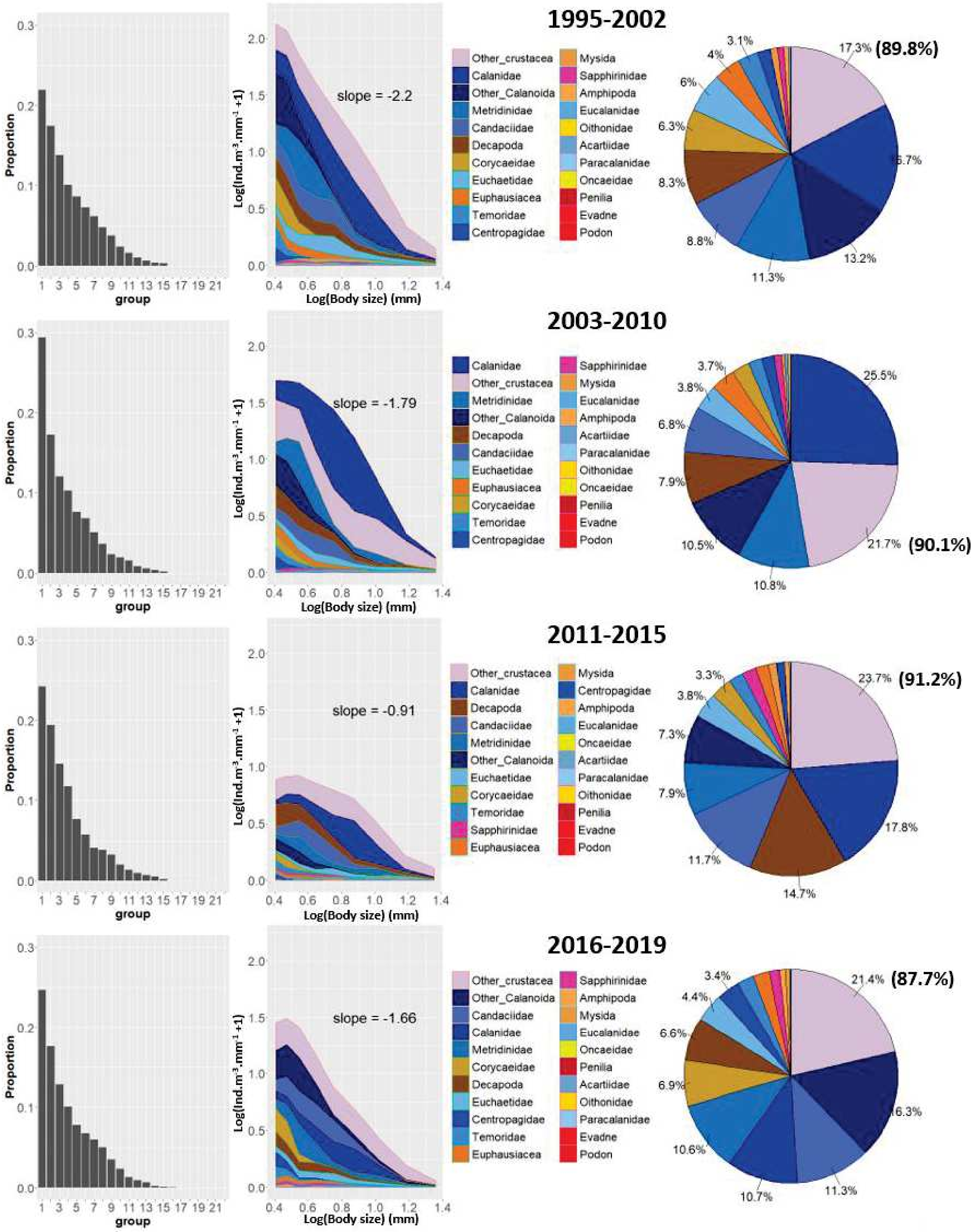


Figure IV-8 *Rank-frequency diagram (left), mean NDSS size spectra (middle) and mean proportions of crustacean groups (right) for the 4 time periods identified with breakpoints performed on monthly time series of Crustaceans NDSS slopes in Regent. The slope of the mean spectra are indicated in each panel.*



1995-2002
Proportion
group
0.0
0.1
0.2
0.3
1 3 5 7 9 11 13 15 17 19 21
Log(Ind.m-3.mm-1 +1)
Log(Body size) (mm)
0.4 0.6 0.8 1.0 1.2 1.4
0.0 0.5 1.0 1.5 2.0
slope = -2.2
Other_crustacea
Calanidae
Other_Calanoida
Metridinidae
Candaciidae
Decapoda
Corycaeidae
Euchaetidae
Euphausiacea
Temoridae
Centropagidae
Mysida
Sapphirinidae
Amphipoda
Eucalanidae
Oithonidae
Acartiidae
Paracalanidae
Oncaeidae
Penilia
Evadne
Podon
17.3%
(89.8%)
6.7%
13.2%
11.3%
8.8%
8.3%
6.3%
6%
4%
3.1%
2003-2010
slope = -1.79
Calanidae
Other_crustacea
Metridinidae
Other_Calanoida
Decapoda
Candaciidae
Euchaetidae
Euphausiacea
Corycaeidae
Temoridae
Centropagidae
Sapphirinidae
Mysida
Eucalanidae
Amphipoda
Acartiidae
Paracalanidae
Oithonidae
Oncaeidae
Penilia
Evadne
Podon
25.5%
21.7%
(90.1%)
10.8%
10.5%
7.9%
6.8%
3.8%
3.7%
2011-2015
slope = -0.91
Other_crustacea
Calanidae
Decapoda
Candaciidae
Metridinidae
Other_Calanoida
Euchaetidae
Corycaeidae
Temoridae
Sapphirinidae
Euphausiacea
Mysida
Centropagidae
Amphipoda
Eucalanidae
Oncaeidae
Acartiidae
Paracalanidae
Oithonidae
Penilia
Evadne
Podon
23.7%
(91.2%)
17.8%
14.7%
11.7%
7.9%
7.3%
3.8%
3.3%
2016-2019
slope = -1.66
Other_crustacea
Other_Calanoida
Candaciidae
Calanidae
Metridinidae
Corycaeidae
Decapoda
Euchaetidae
Centropagidae
Temoridae
Euphausiacea
Sapphirinidae
Amphipoda
Mysida
Eucalanidae
Oncaeidae
Penilia
Acartiidae
Oithonidae
Paracalanidae
Evadne
Podon
21.4%
(87.7%)
6.3%
11.3%
10.7%
10.6%
6.9%
6.6%
4.4%
3.4%

Figure IV-9 ***Rank-frequency diagram (left), mean NDSS size spectra (middle) and mean proportions of crustacean groups (right) for the 4 time periods identified with breakpoints performed on PC1_{size} in Regent net. Calanoida are represented with blue colors, Cladocera in red and Eumalacostraca in brown to orange colors. The slope of the mean spectra are indicated in each panel. In each pie chart, the percent of Eumalacostraca in "other crustacea" group is indicated in bold.***

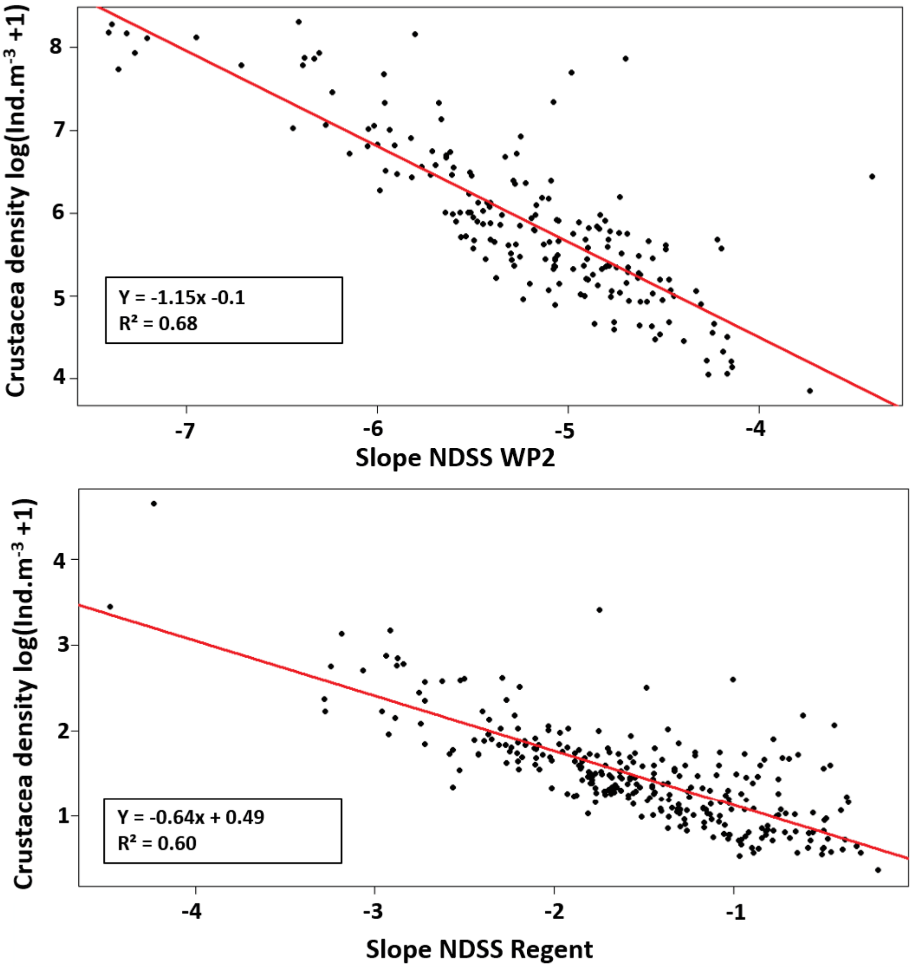


Figure IV-10 ***Linear regression between the monthly time series of crustacean density and the slopes of monthly crustaceans NDSS for WP2 (top) and Regent (down).***

As already suggested from Figure IV-7 and 8, there was a significant relationship between the crustacean total densities and the slopes of the size spectrafor both the WP2 and Regent ($p<0.001$,Figure IV-10). High densities of crustaceans seemed to be associated with steeper spectra and *vice versa*.

IV-3.3 Environmental and zooplankton variability

Breakpoint analyses on annual time series of environment and zooplankton (see SM Figure IV-19 for annual time series) revealed no clear synchrony between environmental variables as breakpoints were observed at different dates for the different variables. Concerning the biological variables, only few changes were observed except around 2015 where Crustaceans decreased in the WP2 concomitant with a flattering of the crustaceans size spectra (Figure IV-11). In the Regent, Gelatinous carnivorous decreased in 2015 and crustacean size spectra became steeper in 2016. No clear link was made with the environment but a sudden increase of temperature was observed in 2014. A similar pattern was observed for crustaceans in the Regent in 2011 with a decrease of density and size spectra flattering but not observed in the WP2 (Figure IV-11). A decrease of SiOH4 concentration was also observed in 2011 concomitant with crustaceans changes. Several other changes were observed with the environment before 2007 but not in the biological compartment.

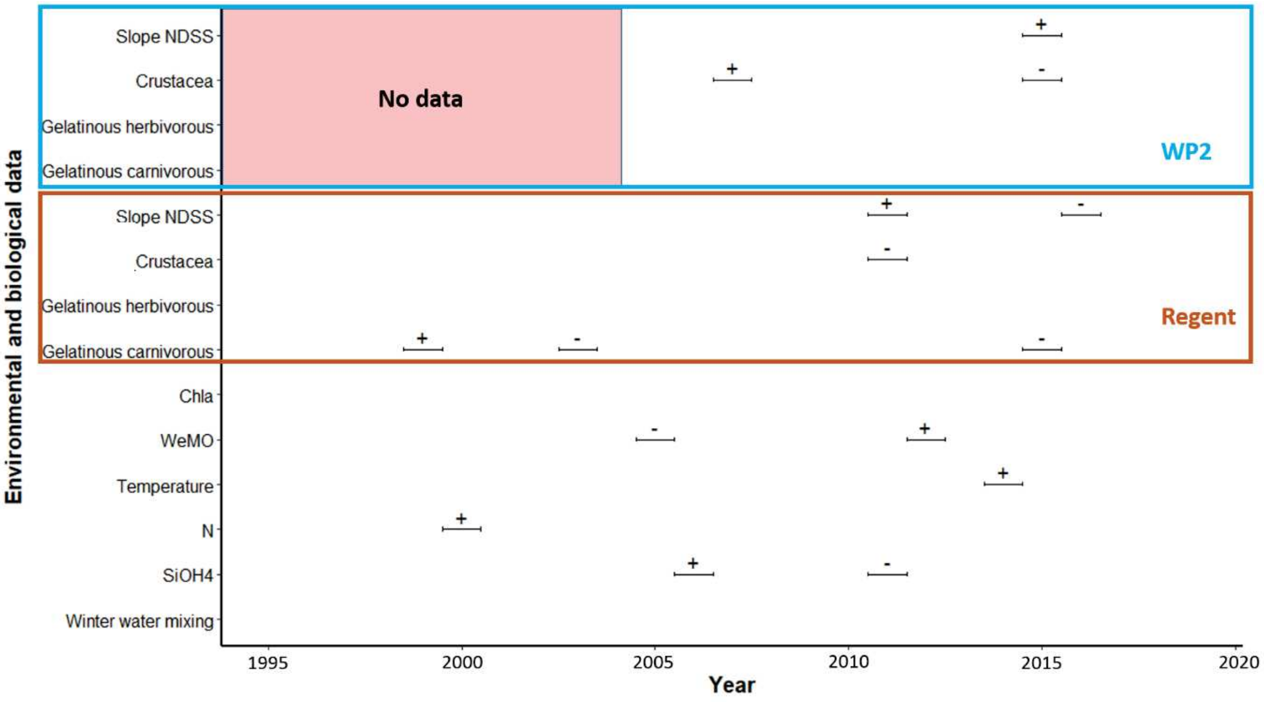


Figure IV-11 ***Synthesis of breakpoints detected in annual time series of Crustaceans NDSS slopes, densities of Crustaceans, gelatinous herbivorous and carnivorous and the environment. "+" indicate an increase of densities or environmental variables and spectra becoming flatter and inversely for "-", with a decrease of densities or environmental variables and spectra becoming steeper. Biological data in the WP2 are in the blue box and in the brown box for Regent.***

IV-3.4 Relationship between crustaceans and environment

To determine the potential environmental drivers of inter-annual variations in total crustacean log-density and size spectra, linear models were run considering 5 environmental explanatory variables: N and SiOH4 local concentration, mean annual sea temperature, mean annual WeMO and the winter water mixing index. Chla was not incorporated in the complete model because of high level of Variance Inflation Factor (VIF) (>4) with the winter water mixing index, revealing collinearity between both. After model selection based on AICc, the best model retained for WP2 Crustacean log-densities was the one with mean annual temperature (but a rather low level of probability, $p = 0.091$) (Table 1), which explained 19% of the variability. Residuals of the model were moderately satisfactory due to the presence of a few outliers, but the predicted versus observed values was reasonable (see SM Figure IV-21). Concerning the Crustacea density in the regent, only the winter water mixing was retained (at a higher probability value than the previous model, $p=0.018$) (Table 1), positively related to the crustacean log-densities, and explained 22% of the variability. Residuals of the model were relatively satisfactory as well as the plot of the predicted versus observed values but here also 3 outliers were detected (see SM Figure IV-21).

Regarding the size, no variable were conserved for the WP2 and only the WeMO index was kept after selection for the Regent ($p = 0.118$) (Table IV-1). It was negatively related to the time series of slopes, indicating that strong values of WeMO were related to steeper size spectra, but explained only 10.3% of the variability. The residuals of the model were rather normally distributed however the plot of the predicted versus observed values presented quite strong dispersion (see SM Figure IV-21).

Table IV-1 *Statistics of the explanatory variable retained in the best model of crustaceans densities and size in the WP2 and Regent nets. Variable with grey areas were not retained in the best GLM model after variable selection*

	Crustacea WP2				Crustacea Regent				NDSS slopes Regent			
PARAMETER	Estim.	SE	t	p	Estim.	SE	t	p	Estim.	SE	t	p
Intercept	19.251	7.142	2.696	0.017	1.643	0.074	22.263	<0.001	-1.744	0.163	-10.720	<0.001
Temperature	-0.747	0.411	-1.815	0.091								
WeMO									-0.393	0.242	-1.626	0.118
Winter water mixing					0.128	0.050	2.552	0.018				

IV-4 Discussion

The objective of this study was to investigate the main patterns of temporal variations of zooplankton with a focus on crustaceans, weekly sampled at a fixed station at the entrance of the bay of Villefranche-sur-Mer (NW Mediterranean Sea), to identify changes in density, size spectra and taxonomic composition. If the density variability had already been studied until early 2005 at this location (García-Comas et al., 2011; Molinero et al., 2008; Vandromme et al., 2011), it was the first time that total density, size and community composition were studied together. Those 3 variables are of primary importance to understand trophic interactions, as size and community composition could modulate predator-prey relationships and in the case of crustaceans also energy transfer to higher trophic levels (Barroeta et al, 2017; Chen et al., 2019; Scharf et al., 2000).

IV-4.1 Limits of the study

This study presented different limits, mainly related to zooplankton sample collection. The first one was due to the type of net used. The Regent net had a large mesh size (680µm), which implies that organisms <1500 µm were considered to be not correctly sampled while the WP2 has a smaller mesh size (200µm), which was considered to be effective for individuals over 650µm. Similar size threshold was identified by Vandromme et al., (2012) as optimal for WP2 based on NBSS, with a maximum of biomass spectra around 0.029mm3, corresponding to individuals of around 650µm. Then, individuals under 650µm were not considered in our study. In the literature, the threshold between small and large crustaceans is generally fixed at 1mm (Hassel et al., 1991; Svensen et al., 2011; Wahlström et al., 2000), so that WP2 analyses embraced both small and large crustaceans while the Regent solely mostly focused on large ones. Another important limit of the present study is that all the samples come from a fixed coastal station. This makes difficult to get an idea of the spatial footprint of both the plankton community and the environmental variables sampled at this station. The presence of the Ligurian current in the one hand and the dominance of large zooplankton with a life span of several weeks in the other hand led us to suppose that the spatial footprint of this study is not limited to a local area, but more possibly to a regional one. Molinero and Nival (2004) also postulated to the presence of a relative spatial homogeneity in the Ligurian sea due to strong currents. Moreover, the period 1999-2003 appeared as the one presenting the highest densities for many groups, such as Eumalacostraca, gelatinous carnivorous or Appendicularians in the Regent. This time period was found as abundant in other studies at the same place (García-Comas et al., 2011; Vandromme et al., 2011) and also elsewhere in the Mediterranean sea (García-Martínez et al., 2019). This suggests that the zooplankton community at the Point B is probably partly impacted by process acting at a regional scale, i.e. the North Western Mediterranean sea. To take into account the possible diversity of spatial scales, we have used both local data and basin scale indicators of climatic changes.

IV-4.2 Comparison of WP2 and Regent net

The WP2 has already been widely used to study crustaceans and mostly copepods variability as recommended by the UNESCO manual (Cook & Hays, 2001; Raybaud et al., 2008; Tranter, 1968; Vandromme et al., 2014) compared to Regent, which has been mostly used to sample gelatinous organisms (Buecher & Gibbons, 1999; Licandro et al., 2001). Their differences in mesh size allowed us to cover a wider size range of the zooplankton community, resulting in different community composition. The zooplanktonic community sampled by the WP2 was strongly dominated by the copepods (87% in average) while this sampled by the Regent was more diversified , with Gelatinous in general representing up to 50% of total zooplankton in the net. The comparison between the 2 nets (even considering only individuals in the wp2 over 1.5mm, see ESM) showed that the Regent underestimated the densities of all the groups (including gelatinous ones) compared to the wp2. This observation was quite surprising, especially for the gelatinous, as Regent net is supposed to be more adapted for those groups, providing for tissue damages (Buecher & Gibbons, 1999).

Concerning the size spectra analyses of crustaceans, differences were also observed between both nets. First, spectra presented differences in the slopes, around -5 for wp2 and between -0.5 and -3 for Regent. Secondly, the last period between 2016 and 2019 was the one with larger individuals and flattest size spectra for the WP2, whereas it was the period 2011-2014 for the Regent net. Those differences in the size structure of crustacean community in both nets could be possibly explained by the differences in the proportion of the different groups sampled by each net. For instance, Eumalacostraca for example represented one third of the community in the Regent, but less than 1% in the WP2. Such differences have already been observed in other studies, such as the one by Calbet et al., (2001) who observed strong differences in the community sampled by nets of 53µm and 200µm mesh size at the same time. Finally, seasonality was marked for crustacean in the WP2, both for size and density in opposition to the Regent net which presented a low seasonal signal. On the opposite, Regent net presented a stronger inter-annual variability, both for size and density compared to the WP2. Those 2 points will be further discussed below.

The detailed identification at the family level for crustaceans in the Regent, not available in the WP2 because of the difficulty to precisely identify small scanned individuals, was an interesting additional information to understand crustaceans community variability. However, as the Regent missed a consistent part of the crustacean community the detailed taxonomic information in the Regent appeared then difficult to extrapolate to the whole community. The WP2 appeared then as a better choice to study the zooplankton community, both for crustaceans and gelatinous individuals compared to the Regent and should probably be the one to consider for future studies. It seems then important to develop new process to automatically identify small crustaceans individuals at family or species level to better understand the links with the environment and interactions with upper trophic levels.

IV-4.3 Inter-annual and Seasonal variability of Crustaceans in the WP2 and Regent nets

Crustaceans size and density time series did not display any clear long-term trend, neither for the WP2 or the Regent, but rather some year-to-year fluctuations. The most striking one was detected around 2015, characterised in the WP2 by a sudden drop of crustaceans densities as well as those of the other groups, such as gelatinous ones (but to a lesser extent). This decrease in the proportions of crustaceans (mostly copepods of small size) led to change in the size spectra (being flatter). The year 2015 presented also low densities in other areas of the North western Mediterranean sea, such as in the Bay of Calvi and the Alboran sea (Fullgrabe et al., 2020; García-Martínez et al., 2019). No clear mechanism was identified to explain this common pattern however, higher temperature and lower winter mixing were suggested as potential factors to explain lower biomass and densities in all 3 areas; lower winter mixing inducing lower nutrients concentrations at the surface and thus a lower primary production (Fullgrabe et al., 2020; García-Martínez et al., 2019; Vandromme et al., 2011). Indeed, primarily analyses on chla pigment concentration suggested a decrease of diatoms proportion since 2013 and totally absent in 2015, replaced by dinoflagellates (pers.comm). Such changes in the phytoplankton community composition could have negatively impacted crustaceans and on contrary favoured Appendicularians, slightly increasing after 2015, known to feed on smaller prey in the micro- and nanophytoplankton (Katechakis et al, 2004; Sommer, et al., 2002a; Sommer et al, 2002b). Concerning the community composition, it appeared very stable both in the WP2 and Regent. Copepods were the most important group for both, strongly dominant in WP2 and less in the Regent for which gelatinous in general represented half of the individuals sampled. Punctual changes were observed some years but generally, the different groups increased and decreased similarly among years leading to as stable community composition. When focusing on crustaceans, copepods were even more dominant in WP2 and less in the Regent for which Eumalacostraca represented a third of the community. Similarly to the total zooplankton community, inter-annual changes were similar for the different groups leading to a stable community. The Crustaceans were also investigated at a higher taxonomic level but only in the Regent because of the poor taxonomic detail available in the WP2 and presented also at this level a strong stability and diversity. Such stability and resilience in zooplankton community was already observed in North western Mediterranean sea despite environmental variability such as in the Gulf of Naples (Mazzocchi et al., 2011), though to be supported by trophic interactions (McGowan & Walker, 1979). Finally, a strong stability was observed in the crustacean size spectra in the WP2, which is coherent with the community composition stability. As discussed above, the unique important change was observed in 2015 with the reduction of small individuals. Size spectra in the Regent presented stronger variability but not linked to changes in the community as similar community was observed in the spectra of different shape. A possible reason of this stronger variability compared to WP2 was the lower number of individuals considered to construct size spectra in the Regent probably leading to more variable size distribution.

As said above, seasonality was present in crustacean time series in the WP2, both for size and density. This seasonality is well documented in the literature, resulting from the phyto- and zooplankton production coupling (Romagnan et al., 2015,2016; Rossi & Jamet, 2009). The phytoplanktonic production is generally initiated by the stabilization of the water column after the input of nutrients at the surface driven by winter water mixing and by the reduction of the grazing pressure (Behrenfeld, 2010; Jamet et al., 2005; Margalef, 1958; Sommer et al, 1986). The development of zooplankton populations follows the spring phytoplankton bloom, with successive development of grazers and carnivorous predators (Sommer et al., 1986). This scheme was observed in our data with copepods peaks between February and May, followed by gelatinous carnivorous more abundant from late spring to autumn. For copepods, recruitment of copepodites occurs mainly in spring, but can be modulated by environmental conditions (Romagnan et al., 2016). This seasonality of recruitment was also detected in the variability of the crustacean size spectra from the WP2, with steeper size spectra in spring when densities are higher. However, no seasonality was observed in crustacean data of the Regent, neither for size or densities. It could be explained by the fact that this seasonal pattern seems strongly dependant of the small size class due to the reproduction cycle. Because of the large mesh size of the Regent, only individuals over 1.5mm body length were considered in the analysis, probably excluding most of the copepodites. We thus postulate that the lack of seasonal pattern in the Regent data is due to its selectivity that prevents from catching the sudden emergence of copepodites in spring.

IV-4.4 Crustaceans and environment

Previous studies in the Ligurian sea investigated the importance of winter conditions for the zooplankton community. Garcia-Comas et al., (2011) suggested the occurrence of a quasi decadal fluctuation driven by changes in winter mixing intensity and the input of nutrient at the surface. According to those authors, years presenting strong winter mixing, such as in the 80s and from 1999 to 2003 would lead to an increase of nutrient input and a subsequent higher primary and secondary production in Spring. Our study did not detect any strong relationship between the Crustaceans log-densities or size spectra and environmental variables. The dates of the breakpoints between the environmental and biological variables were in general not synchronous, except around 2015 and the percentages of variance explained by the GLM did not exceed 20% while the probabilities of the explanatory variables kept after the AICc selection were > 0.05, except for the winter mixing in the second model. Thus, relationship between Crustacean density in the Regent and winter water mixing is the main result supporting Garcia-Comas et al., (2011)'s hypothesis. It was however not the case for crustacean in the WP2, poorly linked to winter conditions and nutrient concentrations. A possible explanation could be that only 16 years were considered for the WP2 and Garcia-Comas et al., (2011) suggested quasi decadal variations (8-9 years) of copepods linked to winter conditions.

However, another potential explanation could be that interactions between zooplankton and environment are mostly non linear, due to trophic interactions with the phytoplankton. Small primary producers are usually part of a four steps chain with ciliates, herbivorous and carnivorous zooplankton and are generally negatively impacted by carnivorous zooplankton. On the contrary, large primary producers are mainly found in three steps chain without ciliates and positively impacted by carnivorous zooplankton (Stibor et al., 2004). Such processes highlight the complex non-linear link between nutrient concentration, phytoplankton and zooplankton. The absence of relationship between zooplankton and nutrient concentration could also suggest that the planktonic dynamics are also affected by the phytoplankton-zooplankton coupling, as suggested by Behrenfeld, (2010). Analyses of the phytoplankton community composition appear then of primary interest to understand interactions with the zooplankton community in this area, possibly driving the zooplankton variability in addition to environment.

Trophic interactions have also been found to be a potential driver shaping the size spectra of plankton community. A study about zooplankton size structure in a lake suggested that the predation by fish could be an important factor shaping the size distribution, reducing the mean size of the community (Brucet et al., 2010). We found in this study negative correlations between the slope of size spectra and carnivorous densities, which is in accordance with a possible modification of size distribution (steeper spectra) due to predation (see SM Figure IV-20). Finally, the dynamics of the zooplantonic community (in terms of density, taxonomic composition and size spectra) in North Western Mediterranean sea could then be more complex than previously thought and modulated by several biotic (e.g. trophic interactions) and abiotic factors (e.g. winter mixing) which could possibly explain the absence of direct and linear relationship with the environment.

IV-4.5 Zooplankton variability in a context of global warming

Global change and its impact on marine ecosystem functioning is a central question in recent ecological studies (Bopp et al., 2005; Henson et al., 2018; Herrmann et al., 2014; Richon et al., 2019). Global warming is likely to increase water stratification, deplete water from inorganic nutrients, enhance microbial activity, thus favouring small phyto- and zoo-plankton individuals and decreasing total plankton biomass (Bopp et al., 2005; Herrmann et al., 2014). As noted and explained above, this study did not display any clear relationships between environmental and planktonic variables, albeit a negative (but statistically fragile) relationship between crustacean density in the WP2 and annual temperature. Such a relationship between crustaceans densities and temperature has been also documented in other studies (see Fernández De Puelles & Molinero, 2008; Fernández de Puelles et al., 2004). However no link was observed between the crustacean size spectra and the temperature in this study as in other studies (Dziuba et al., 2017; García-Comas et al., 2014). As discussed previously, no long-term changes were observed in the zooplanktonic dynamics, but it is of interest to stress the sudden drop of different zooplankton groups densities in 2015. This drastic and sudden change in the whole phyto- and zooplanktonic communities could be due to an exceptional weak winter mixing and strong stratification of the water column (see above). However, it is likely that this singular and strong environmental event resulted from regional atmospheric and oceanographic changes that may themselves be related to global warming (Herrmann et al., 2014, 2008; Somot et al., 2006). Indeed, global warming is thought to increase water stratification and reduce winter convection process, leading to a diminution of nutrient concentration in upper layer, reducing the plankton production and favoring smaller phyto and zooplankton. Such an hypothesis needs however to be validated by further work, but it tends to confirm that global warming could indeed decrease the zooplanktonic production in this area and primarily this of Crustaceans, which would negatively impact the fish production in the region (Brosset et al., 2016a; Saraux et al., 2019).

Another supposed consequence of the global warming is the increase of gelatinous species, with potential impact on copepods by competition for resources or predation (Molinero et al., 2008). Warm temperatures are indeed thought to promote an increase of asexual reproduction of hydrozoans and, consecutively, an increase of gelatinous species (Purcell, 2005). However, our results do not fully support this hypothesis, as gelatinous groups did not display any clear trends or link with the temperature, except gelatinous herbivorous in the WP2 (a group, mainly composed of Appendicularians), which increased in the last years concomitantly with the abrupt raise of temperature). Nonetheless, the gelatinous herbivorous in the Regent did not show such an increase at the end of the series (on the contrary, the densities were below the average), so that no clear conclusion can be drawn regarding the temperature-gelatinous herbivorous relationship.

IV-4.6 Top-down versus bottom-up controls

Based on time series from the same site, Molinero et al. (2005, 2008) proposed a top down control of jellyfish on copepods, because the densities of the later dropped during the late 80s and early 90s when the former increased. However, with 10 additional years to the same time series, Garcia-Comas et al. (2011) found that total copepods recovered almost the densities of the 80s around 2003 while jellyfish remained abundant. In our study, gelatinous were separate in two groups based on their diet: the carnivorous and the herbivorous (filter-feeders). Both can have interactions with Crustaceans and copepods, the first one by predation and the second one by competition for resources (Molinero et al., 2008). Crustacean and gelatinous carnivorous densities were highly positively correlated in both in the WP2 and Regent (see SM Figure IV-20), which does not support the hypothesis of a top-down control of gelatinous on Crustaceans. No evidence of competition was either found in our study, as only a weak positive covariation was found between crustaceans and gelatinous herbivorous in both the WP2 and Regent. Furthermore, the gelatinous herbivory densities did not display any trend and remain rather stable, even during the Crustaceans drop around 2015. As stressed before, the Crustaceans dynamics can hardly be explained by a simple top-down control through the gelatinous groups, neither be explained by a single bottom-control through the primary production (albeit the 2015 event showed that exceptional environmental conditions could punctually lead to a clear bottom-up control), but rather by a mixture of environmental (bottom-up) and trophic (mostly top-down) factors.

IV-5 Acknowledgements

We thank the PIQv for their work on zooplankton ptB samples and the ecotaxa database. Part of this research was funded through the MONALISA project, which was co-funded by the European Union and the French Ministry of Agriculture in the framework of the European Maritime and Fisheries Fund (EMFF, grant number PFEA280017DM0910001) and by France Filière Pêche (France).

IV-6 Supplementary materials

Characteristics of monthly NDSS size spectra

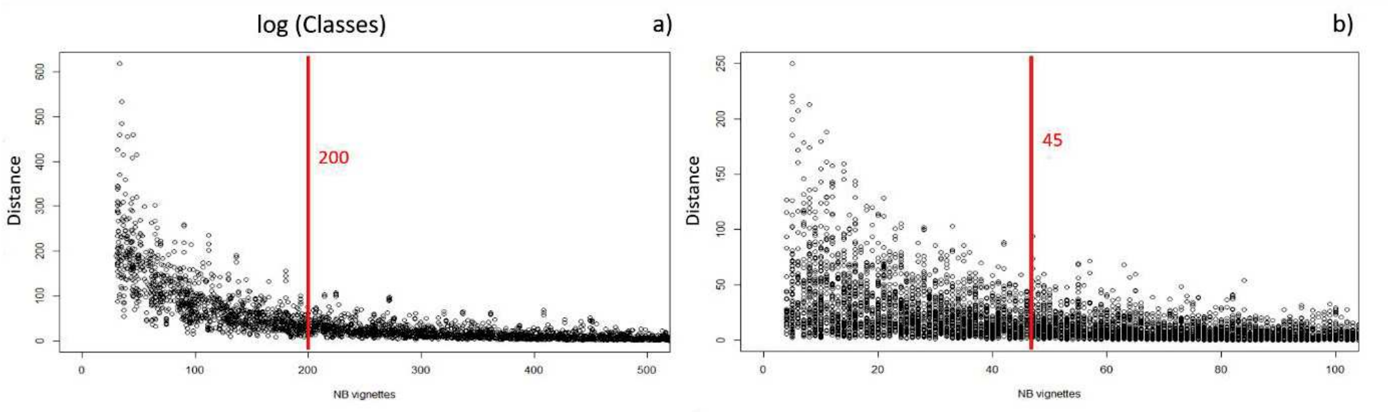


Figure IV-12 ***Plot of the sum of the squared difference between the subsample spectra and the full spectrum for the 20 repetitions and the number of vignettes in the subsample spectra for WP2 in (a) and Regent in (b). The minimum number of measured individuals (vignettes) to consider samples is indicated by the vertical red line.***

To determine the lower limit of NDSS, spectra were computed starting at 200µm for WP2 and 650µm for the Regent with a first size class of 50µm increasing by 1.3 from a class to another. Then, the position of the mod was identified for each spectra and the distribution of this position was investigated. The lower limit of the spectra for each net was considered as the mod of the mod distribution of all monthly spectra.

To determine the minimum size of samples to consider for analyses, tests of sensibility were performed. For that, analyses were performed on the half most abundant samples. For each sample, the full spectra was constructed with all crustaceans as well as a spectra based on a subsample randomly selected with first 5% of the total individuals. Then the sum of the squared difference between the subsample spectra and the full spectra was computed and represented the spectra variability. This operation was repeated 20 times. Subsample spectra represented from 5% to 95% of total individuals, by step of 5%. We then represented the sum of the squared difference between the full spectra and the subsample spectra in function of the number of individuals composing the subsample (Figure IV-12a for WP2 and IV-12b for Regent). The number of individuals to keep was 200 for WP2 and 45 for Regent, considered as the turning point of the curves represented by the vertical red lines.

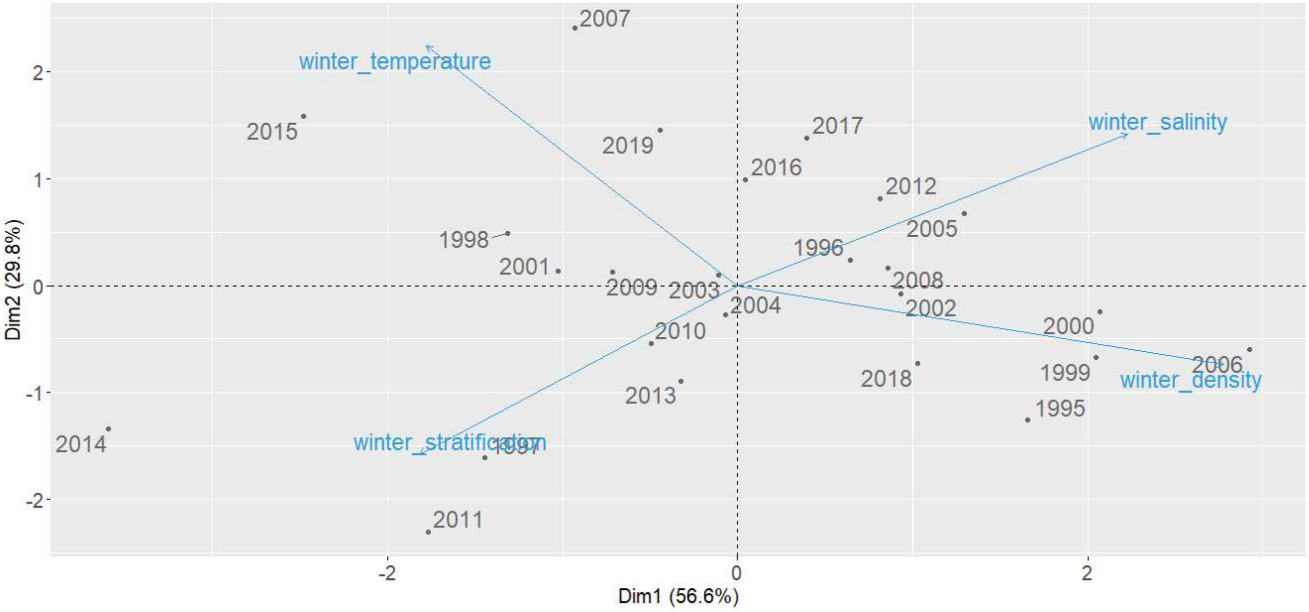


Figure IV-13 *Biplot of the PCA performed on winter environmental condition (stratification, temperature, salinity and density). The first principal component of the PCA was considered as the winter water mixing index as in Vandromme et al., (2011).*

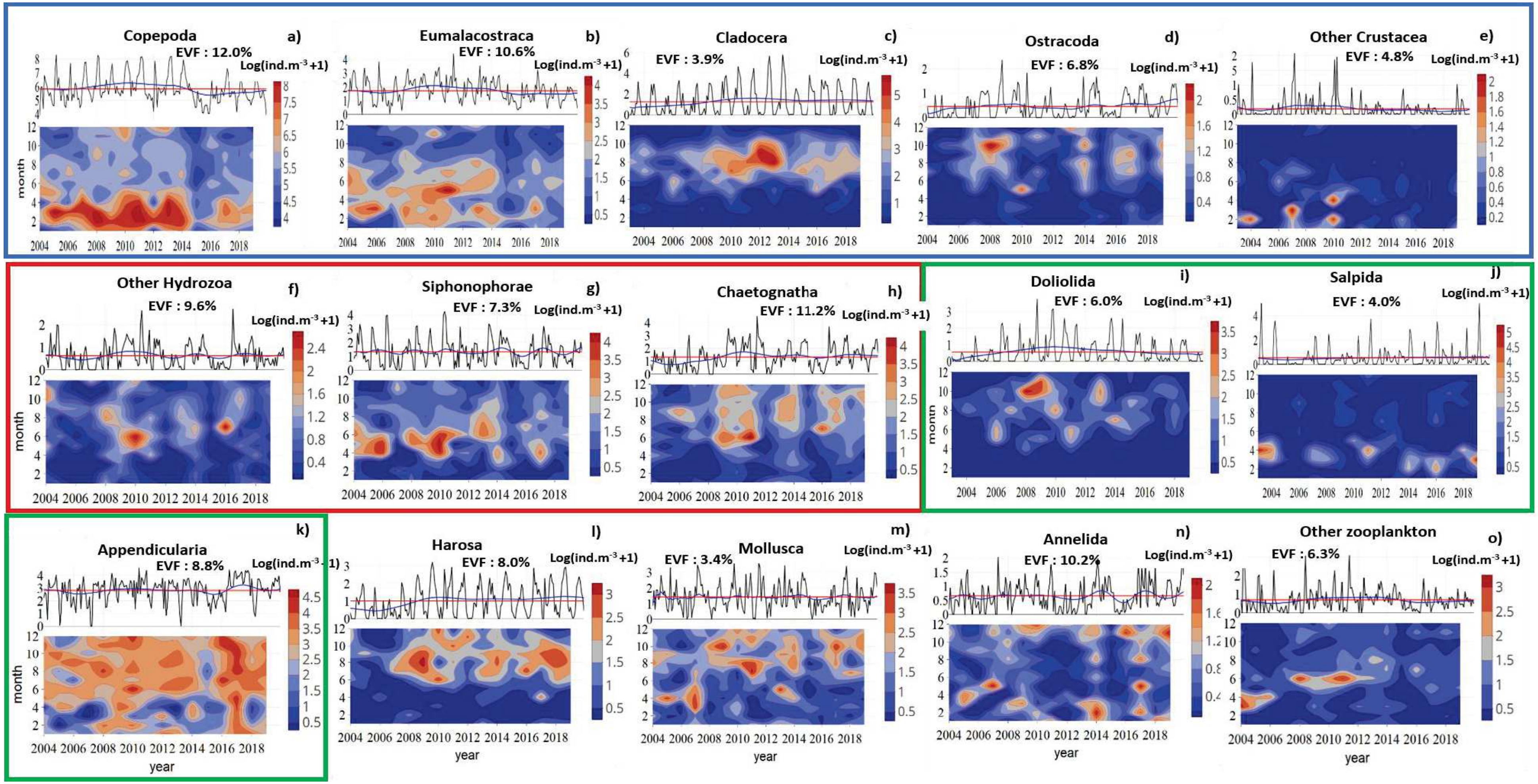


Figure IV-14 *Monthly log abundance (ind.m^{-3} +1) of zooplankton groups from 2004 to 2019 in the WP2 net. For each group in the upper panel the monthly time series in black with a 3 years trend extracted with EVF (in blue) and the mean over the whole period (in red). In the lower panel, the contourplot of the monthly abundances. Panels in blue box are the crustaceans, in red box the gelatinous carnivorous and in green box the gelatinous herbivorous.*

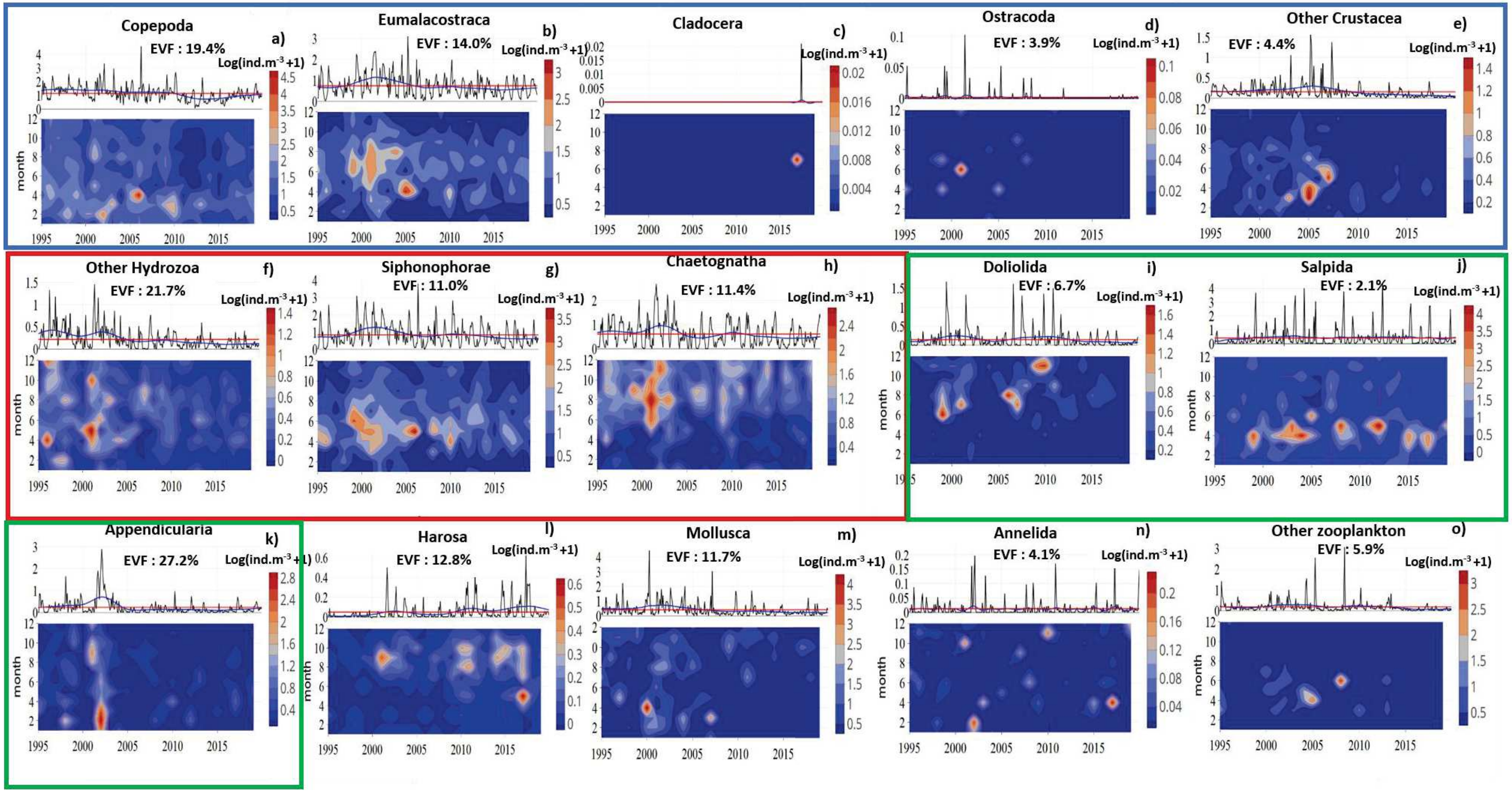


Figure IV-15 *Monthly log abundance (ind.m^{-3} +1) of zooplankton groups from 1995 to 2019 in the Regent net. For each group in the upper panel the monthly time series in black with a 3 years trend extracted with EVF (in blue) and the mean over the whole period (in red). In the lower panel, the contourplot of the monthly abundances. . Panels in blue box are the crustaceans, in red box the gelatinous carnivorous and in green box the gelatinous herbivorous.*

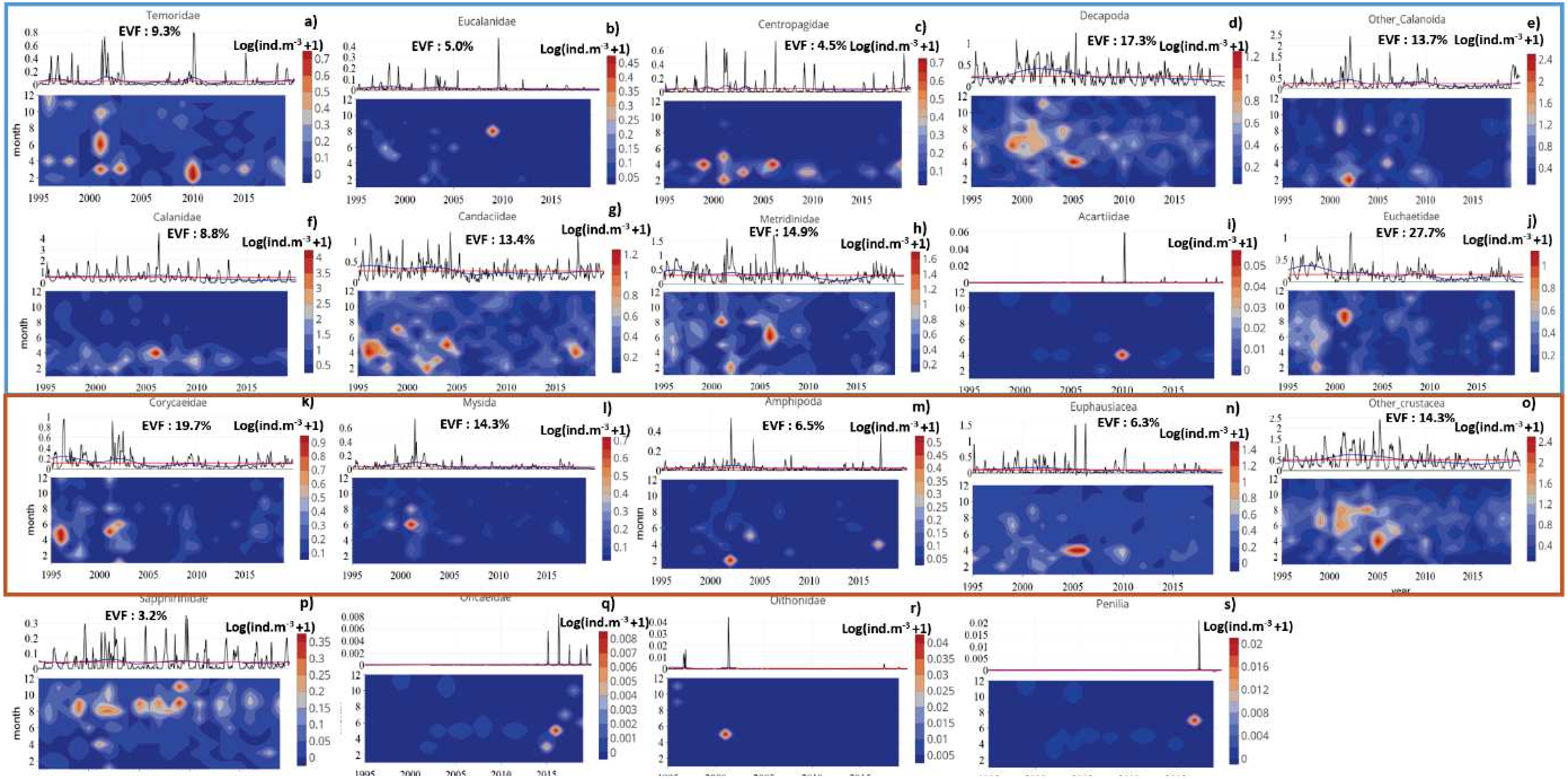


Figure IV-16 *Monthly log abundance (ind.m^{-3} +1) of crustaceans orders/families from 1995 to 2019 in the Regent net. For each family in the upper panel the monthly time series in black with a 3 years trend extracted with EVF (in blue) and the mean over the whole period (in red). In the lower panel, the contourplot of the monthly abundances. Panels in blue box are the calanoida, and in brown box Eumalacostraca which represent over 90% of "other crustacea" incorporated in the box.*

Size spectra analysis: functional principal component

Temporal changes in size spectra were analysed by the mean of the functional principal component analysis (FPCA) (Nerini & Ghattas, 2007; Ramsay & Silverman, 1997). FPCA is a statistical methodology that treats an entire sequence of measurements for an individual as a single functional entity rather than a set of discrete values and that investigates the dominant modes of variation of the functional data. Treating the data as functions preserves all of the information contained in the data. This method allowed comparing spectra based on the entire shape instead of defined characteristics such as the maximum value or the slope of the spectra. As we aimed at depicting temporal variations in size spectra independently of changes in abundance, all spectra were transformed, substracting to each size class the density of the first size class minus 1. This allowed to start all the spectra to a density of 1 and to compare them only by their differences in slope. Then, scaled spectra were fitted with a linear combination of 8 B-spline functions (B-splines constituting an orthonormal eigenvector basis). The number of B-splines was chosen so as to ensure the error between the empirical and reconstructed spectra to be lower than 0.1%. Coefficients of this linear combination of B-splines were stored in a matrix and a PCA analysis was performed on the variance-covariance matrix of these coefficients. The values of the first principal component were analysed (further called $PC1_{size}$) as well as the deformation of the spectra along this first axis. long-term variability in size distribution was estimated using the EVF decomposition with a 3-year window, and inter-annual variability by means of breakpoints analysis. To investigate discontinuities in the monthly PC1 time series, breakpoints analyses were performed. To do this, the “strucchange” R package and an algorithm testing structural changes in time series was used (Kleiber et al., 2002). Optimal number of segment partitions was based on BIC criterion in order to compute only the most relevant changes.

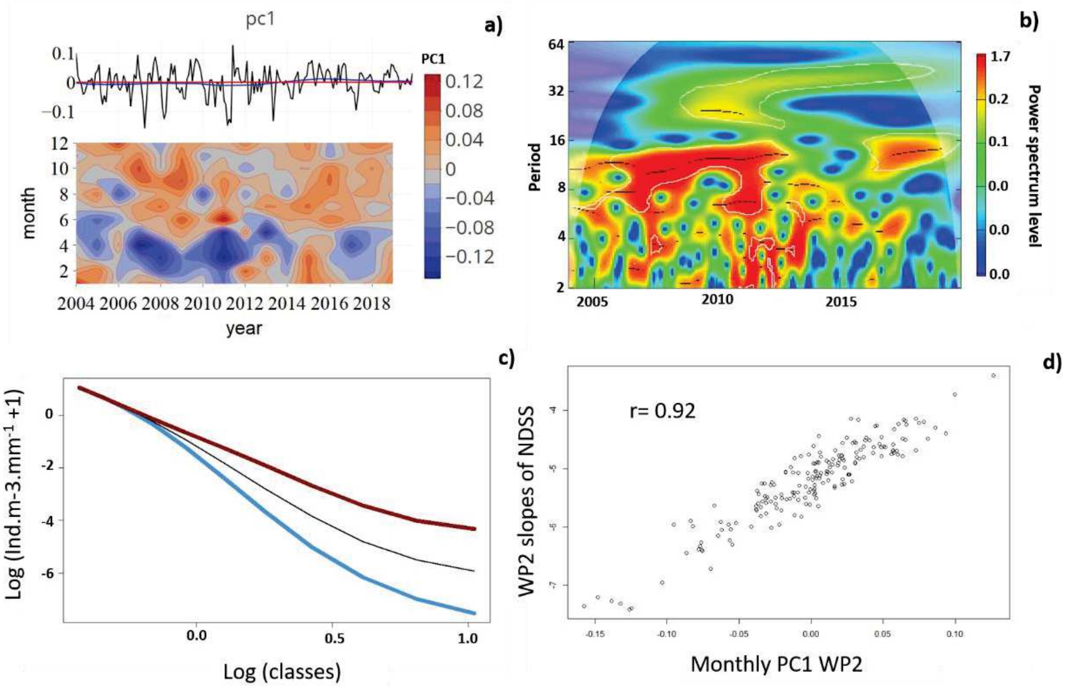


Figure IV-17 ***Functional PCA performed on monthly Crustaceans NDSS (scaled to 1 for the first class) for WP2 net from 2004 to 2019. Monthly time series of the first principal component with the contourplot above in a), Wavelet analysis in b), deformation of NDSS along the first principal component with in red the shape of the spectra in extreme positive values of the PC1 and in blue for extreme negative values of PC1 in c) and correlation between the time series of slopes and the PC1 of the PCA in d).***

The 2 first axis of the functional PCA performed on monthly NDSS of crustaceans in the wp2 accounted for 91,7% (75,2% and 16,5%). The first axis represented changes in the slope of the spectra as observed in Figure IV-17c and the correlation between the PC1 and the monthly time series of NDSS slope was strong (r=0.92, p<0.001 Figure IV-17d). Indeed, higher positive values of PC1 were associated to flatter NDSS (red spectrum in Figure IV-17c) while negative values of PC1 were associated to steeper NDSS (blue spectrum in Figure IV-17c). The same breakpoint as for the analyses of slopes was found in 2015 and the same seasonal pattern was identified in the shape of the spectra, with steeper spectra in spring and flatter spectra in summer and autumn (Figure IV-17a).

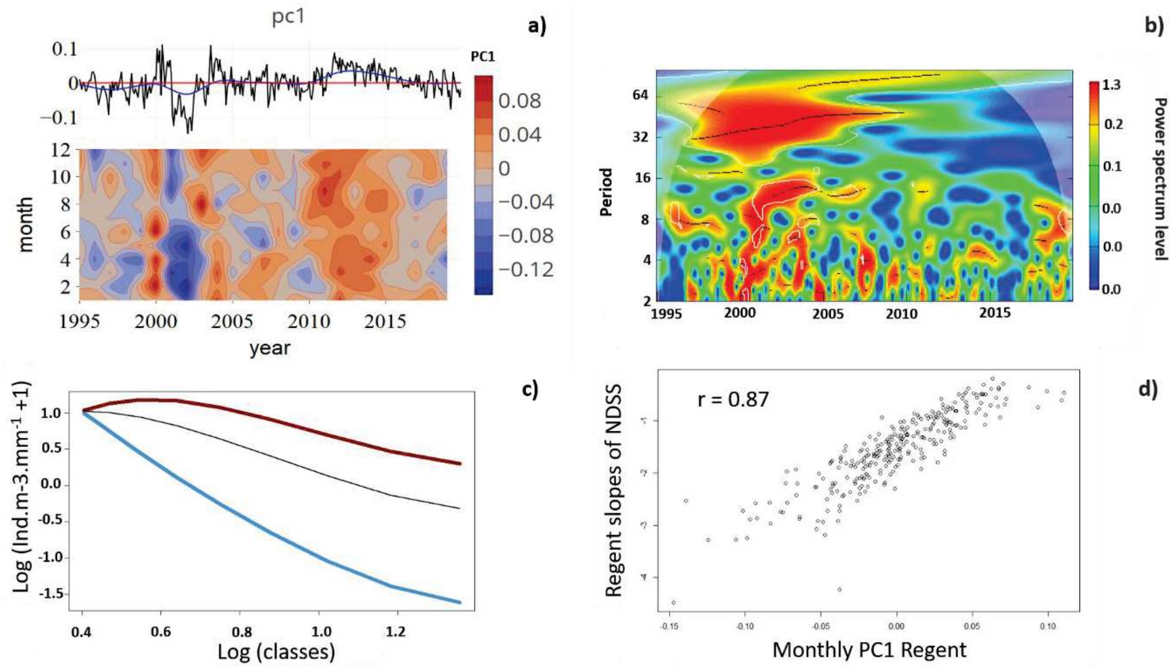


Figure IV-18 ***Functional PCA performed on monthly Crustaceans NDSS (scaled to 1 for the first class) for Regent net from 1995 to 2019. Monthly time series of the first principal component with the contourplot above in a), Wavelet analysis in b), deformation of NDSS along the first principal component with in red the shape of the spectra in extreme positive values of the PC1 and in blue for extreme negative values of PC1 in c) and correlation between the time series of slopes and the PC1 of the PCA in d).***

Concerning the size variability in the Regent net, the 2 first axis of the functional PCA performed on monthly NDSS of crustaceans accounted for 96,5% (87% and 9,5%). The first axis represented changes in the slope of the spectra as observed in Figure IV-18c. As for the WP2, the correlation with the monthly time series of NDSS slope was also strong (r=0.87, p<0.001 ESM-Fig IV-18d). Higher positive values of pc1 were associated to flatter NDSS (red spectrum in Figure IV-18c) while negative values of PC1 were associated to steeper NDSS (blue spectrum in Figure IV-18c). The breakpoint analysis showed the same results as for the slopes, with breaks in 2003, 2011 and 2016. Finally, as for the time series of slopes, no seasonality was observed but rather inter-annual changes (Figure IV-18a).

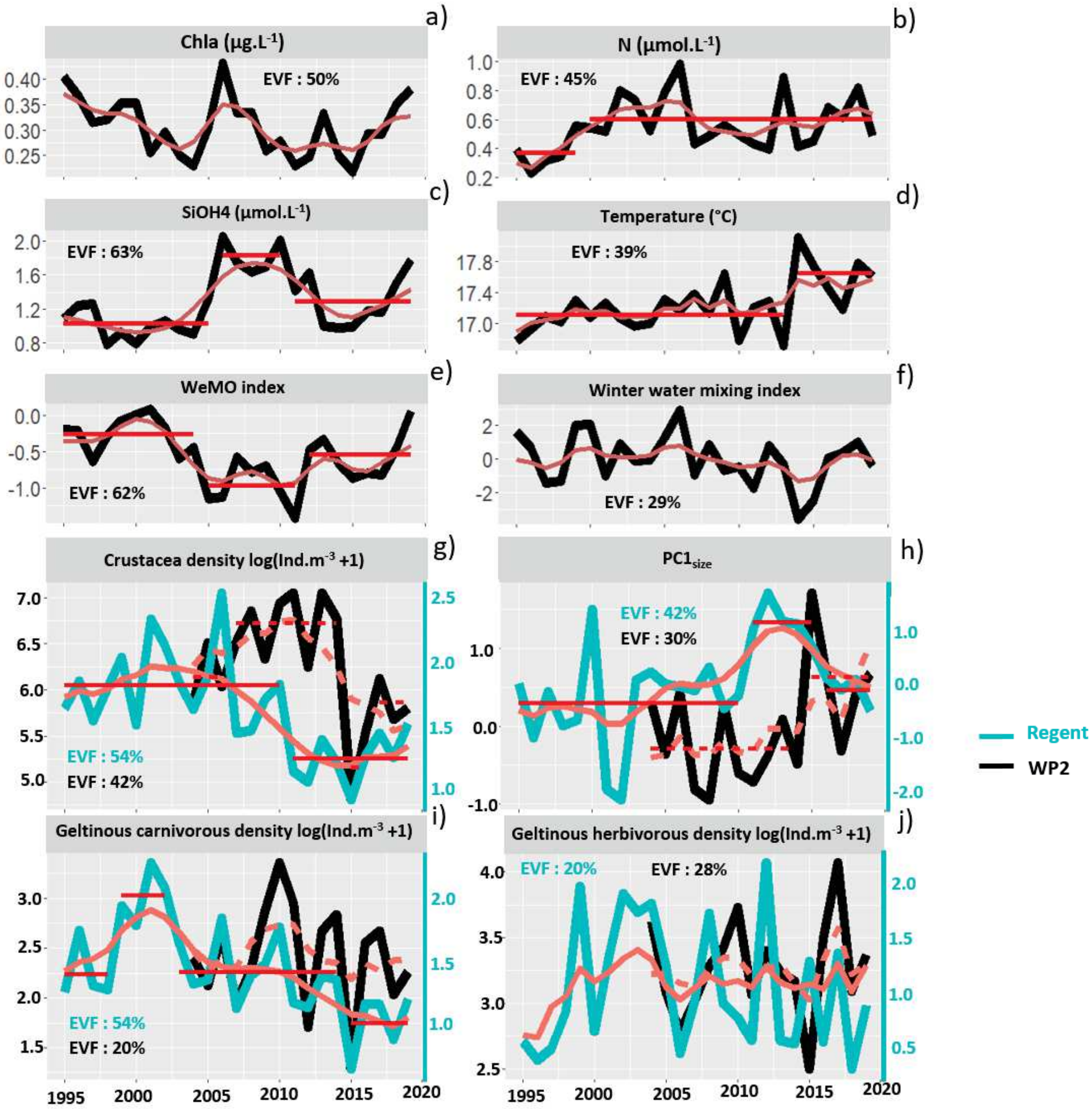


Figure IV-19 *Yearly time series of environmental variables and biological data in regent (blue lines in the 4 bottom panels) and WP2 (black lines in the 4 bottom panels). In Orange a 3-year trend extracted with EVF and red strait lines represent means over periods identified by breakpoints. For biological data in the 4 bottom panels, dotted lines either for trend and breakpoints are associated for WP2.*

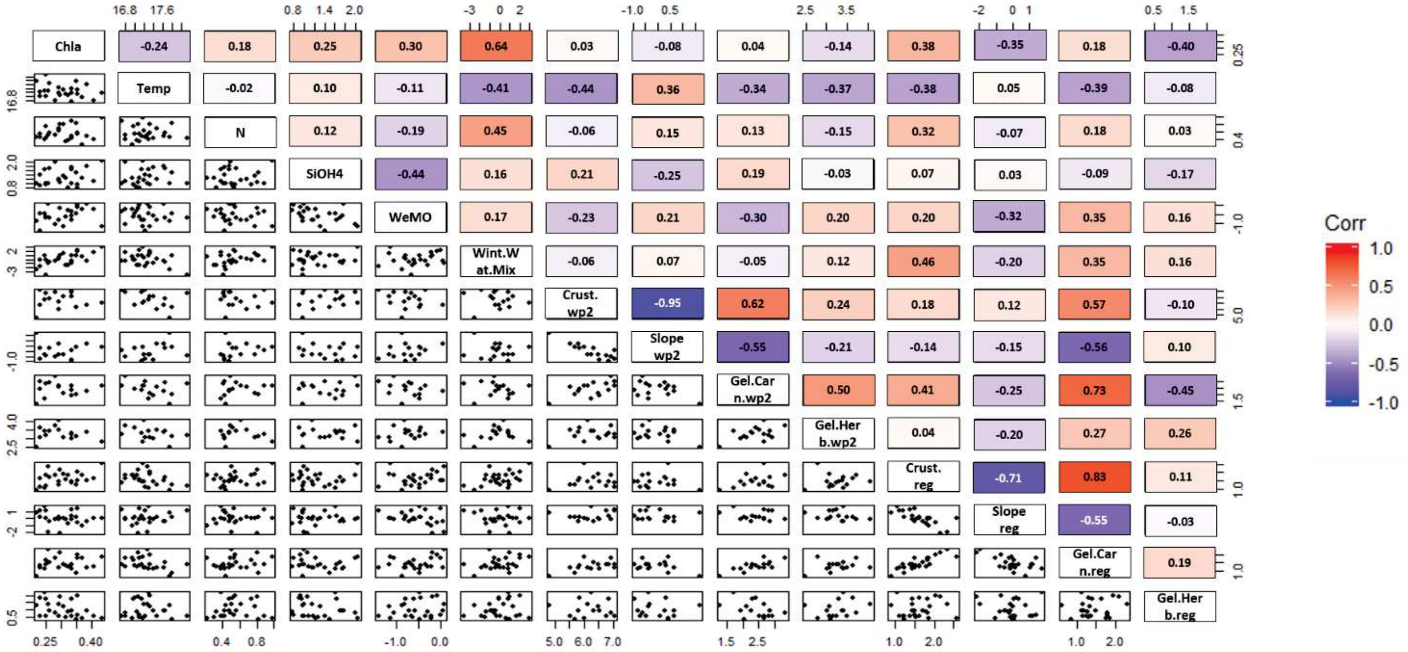


Figure IV-20 ***Correlations between yearly environmental variables and yearly biological variables.***

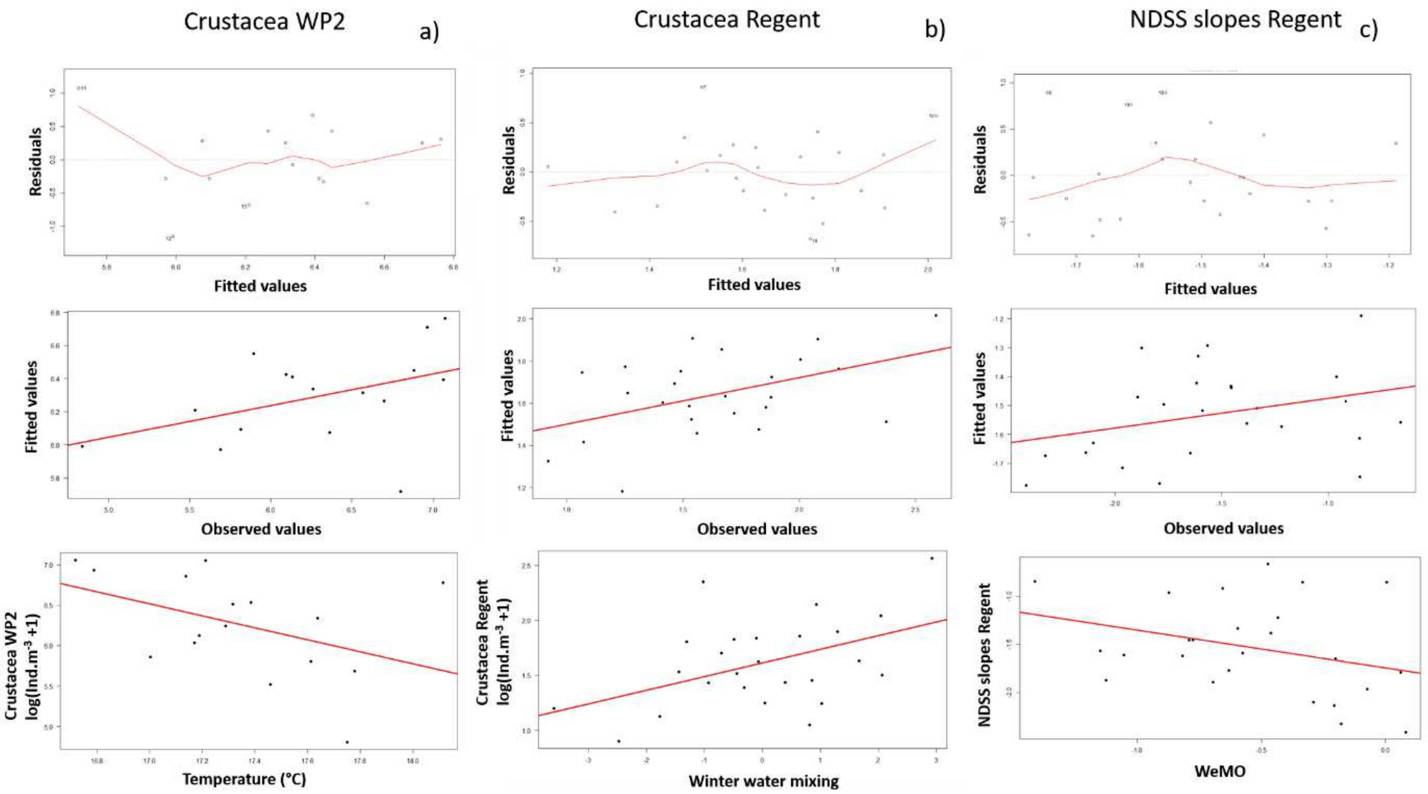


Figure IV-21 ***Diagnostic plots of the GLM performed on yearly abundances of crustaceans in WP2 (a), and Regent (b) and and yearly NDSS slopes of Regent (c). The first line of panels represent the residuals of the models versus fitted values and the second line is the fited values versus observed values. The third line represent the observed values versus the variable retained in each model after model selection.***

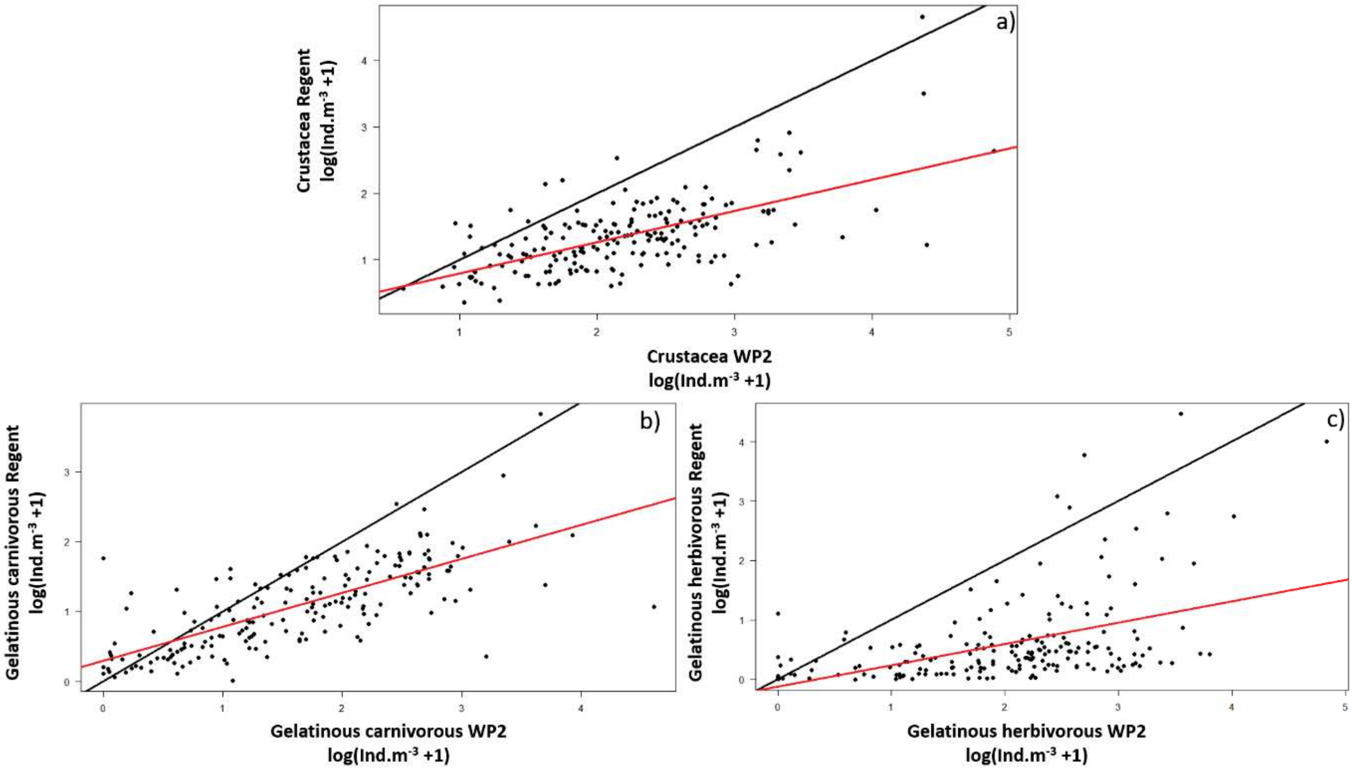


Figure IV-22 ***Densities in the Regent vs Wp2 of individuals measuring at least 1.5mm length for Crustacea (a), Gelatinous carnivorous (b) and Gelatinous herbivorous (c). The black line represent y=x and the red line is the linear regression.***

Chapitre V. *Discussion Générale*

L'objectif de cette thèse était d'étudier la variabilité de la communauté planctonique dans le Golfe du Lion et le bassin Ligure au cours des 20 dernières années afin de comprendre si des changements de communauté ou de structure en taille avaient eu lieu pouvant confirmer l'hypothèse d'un contrôle bottom-up sur les populations de petits pélagiques et expliquer leur baisse de condition (Saraux et al., 2019; Van Beveren et al., 2014). En effet, une des hypothèses envisagée est un changement de régime alimentaire des petits pélagiques se nourrissant sur des proies zoo-planctoniques plus petites et moins énergétiques (Brosset, et al., 2016a; Saraux et al., 2019). La faible quantité de données disponibles dans la zone nous a d'abord amené à étudier la communauté planctonique par le biais de proxy tel que la concentration en chlorophylle. La variabilité de différents processus environnementaux jouant un rôle majeur dans la dynamique planctonique, a été caractérisée sur le plateau du Golfe du Lion afin de comprendre si d'éventuelles modifications de l'environnement avaient pu impacter le plancton. Une analyse plus fine de la communauté phyto- et zoo-planctonique a ensuite été menée en été à partir des données issues des campagnes PELMED. Cela a permis de regarder l'impact de l'environnement sur la composition taxonomique de la communauté planctonique et de voir si certains groupes étaient majoritairement retrouvés en périodes de bonnes ou mauvaises conditions des poissons. Finalement, la dynamique à long terme de la communauté zoo-planctonique en réponse à des forçages environnementaux a été étudiée dans une zone adjacente, la Mer Ligure à partir d'une des plus longues séries de zooplancton eu Europe. Cela a permis d'étudier à la fois la variabilité à long terme de la densité de plancton mais également d'éventuels changements de taille et de composition taxonomique en lien avec l'environnement, potentiellement importants pour comprendre la dynamique des petits pélagiques dans le Golfe du Lion.

V-1 Synthèse des résultats principaux

Le Golfe du Lion est une des zones les plus productives de Méditerranée mais semble s'être appauvri au cours des deux dernières décennies comme l'atteste la diminution de la concentration en chlorophylle observée sur le plateau. Nous avons trouvé que le Rhône apparaissait comme un acteur principal de la dynamique de la chlorophylle sur le plateau, suggérant son impact fort sur la biomasse phytoplanctonique. Cette baisse de chlorophylle est en partie liée à une diminution des apports en nutriment du Rhône, ses concentrations en azote et phosphate ayant fortement diminué au cours des 20 dernières années. Si cet appauvrissement a pu possiblement avoir un impact sur les populations de petits pélagiques, il semblerait néanmoins que ces derniers ne répondent pas à un unique processus mais plutôt au système environnemental dans son ensemble, considérant aussi bien les forçages locaux comme les fronts thermiques, les upwellings ou les apports du Rhône que des forçages à large échelle, synthétisés par l'indice WeMO ou la température associée au réchauffement global des eaux méditerranéennes. Ainsi, il est possible que ces changements aient impactés la communauté planctonique et par conséquent les petits pélagiques qui présentent des dynamiques similaires avec l'environnement. Le compartiment zoo-planctonique, directement en lien avec les petits pélagiques n'a cependant pas pu être étudié au cours de cette étude par manque de données. De plus, cette première étude n'a pas permis de comprendre si la baisse de biomasse de phytoplancton s'accompagnait d'un changement dans la communauté des espèces de phytoplancton.

Dans le chapitre 3, une analyse plus fine de la communauté phyto- et zoo-planctonique estivale a été menée à partir des données issues des campagnes successives de PELMED. Nous avons observé différents types de communautés phyto-planctoniques, certaines dominées par des dinoflagellés principalement du genre *Gymnodinium* et d'autres dominées par des diatomées des genres *Chaetoceros*, *Leptocylindrus* et *Proboscia*. Concernant le zooplancton, différentes communautés ont également été identifiées, certaines dominées par des cladocères du genre *Penilia* et *Evadne* et d'autres par des copépodes, essentiellement *Clausocalanus*, *Oithona* et *Centropages*. Malheureusement, les relations avec l'environnement se sont révélées assez faibles et n'ont pas permis de définir les conditions amenant à une communauté ou une autre, que ce soit pour le phytoplancton ou le zooplancton. Concernant les potentielles associations entre les communautés de phyto- et zooplancton, aucune association n'a pu être mise en évidence, les stations dominées par des diatomées ou dinoflagellés présentant des communautés zoo-planctoniques très similaires. Certains groupes de zooplancton tels que *Evadne* et *Oithona* ont été identifiés comme étant plus présents aux stations présentant des bonnes conditions des poissons alors que les groupes *Clausocalanus*, *Penilia* et *Doliolida* ont été identifiés comme étant plus présents aux stations présentant de mauvaises conditions des poissons, suggérant de possibles relations entre communauté planctonique et condition des poissons petits pélagiques. Néanmoins, les principales proies des petits pélagiques indiquées dans la littérature n'ont pas été retrouvées dans nos échantillons de plancton limitant nos interprétations dans la relation plancton-poisson. Enfin, aucune analyse à long terme n'a été possible, les données de plancton n'étant disponibles que l'été et seulement pour une dizaine d'années au cours des 20 dernières années, avec des différences d'échantillonnages assez importantes entre années.

Enfin dans le chapitre 4, la longue série temporelle de zooplancton du point B en Mer Ligure a été étudiée afin d'avoir une vision à long terme de la communauté zoo-planctonique. Cela nous a permis d'avoir une idée de la variabilité de la densité de différents groupes de zooplancton dont les crustacés, principale proie des poissons petits pélagiques, mais également de la variabilité de leur taille, facteur potentiellement clé pour la condition des poissons, par le biais de spectres de taille. Une forte stabilité depuis 1995 de la communauté planctonique a été observée, aussi bien en termes de composition taxonomique qu'en densité totale ou en taille des individus. Une saisonnalité a été observée aussi bien dans les tailles que les densités mais pas de tendance à long terme. En revanche, l'année 2015 se démarque avec une forte diminution des petits crustacés, concomitante avec la baisse de densité d'autres groupes notamment chez les gélatineux filtreurs et carnivores. Pas de relation statistique n'a pu être établie avec l'environnement mais les années récentes semblent être caractérisées par des températures anormalement élevées et des conditions hivernales potentiellement moins propices au brassage de la colonne d'eau et la fertilisation par les nutriments.

V-2 Forçages locaux versus globaux

La dynamique des communautés biologiques (planctoniques et autres) peut être impactée par des processus locaux propres à chaque zone (apport d'un fleuve, upwelling local, présence d'un front permanent) (Gorsky et al., 1991; Lefevre et al., 1997; Claude Millot, 1990) ou bien commun et à plus large échelle (circulation climatique large échelle, réchauffement climatique global, modification des courants à large échelle) (Beaugrand et al., 2015; Beaugrand & Reid, 2003). Entre le milieu et la fin des années 1980, des régimes shifts dans les communautés biologiques marines ont été mis en évidence, du phytoplancton aux poissons planctonophages, dans différents bassins de l'hémisphère nord comme en Atlantique nord-Ouest (Frank et al., 2005; Greene et al., 2013), en Mer du Nord (Reid et al., 2001; Weijerman et al., 2005), en Mer Baltique (Moellmann et al., 2009) ainsi qu'en Méditerranée nord-ouest (Molinero, Ibanez, et al., 2008) et en Mer Noire (Daskalov et al., 2007) suggérant la présence de forçages climatiques à large échelle impactant les communautés. Dans une étude comparative de séries à long terme de zooplancton prélevé dans différents bassins de l'hémisphère nord, les principales causes avancées pour expliquer des changements synchrones observés dans les différentes communautés zoo-planctoniques étaient en premier lieu l'impact de la température (réchauffement global) ainsi que des phénomènes de circulation atmosphérique et océanique (Beaugrand et al., 2015) qui contribuent à modifier régionalement le climat et en particulier les températures. Beaugrand et al., (2019) ont par la suite montré en contraignant un modèle d'habitat basé sur la température par les observations de plancton que l'impact local des forçages peut s'inscrire dans une tendance plus globale d'évolution des écosystèmes pélagiques. En Méditerranée nord-ouest, l'augmentation de la température a également été identifiée comme jouant un rôle dans la dynamique des communautés planctoniques (Fernández de Puelles et al., 2004; Fernández de Puelles & Molinero, 2008), de même que la circulation atmosphérique large échelle représentée par différents indices tels que le NAO (Fullgrabe et al., 2020; Molinero et al., 2005) ou le WeMO, moins utilisé mais supposé plus représentatif des conditions atmosphériques méditerranéennes (Brosset et al., 2015; Martin-Vide & Lopez-Bustins, 2006; Martín et al., 2012). Ces indices climatiques à large échelle permettent d'intégrer différents phénomènes en même temps tels que le vent, la température ou encore la pluie qui vont ensuite impacter l'environnement local puis les communautés biologiques (Fernández de Puelles & Molinero, 2007; Hurrell, 1995; Pettorelli et al.,2005; Stenseth & Mysterud, 2002; Stenseth et al., 2003). On peut envisager par exemple un changement du régime des vents dominants à large échelle, qui peut impacter les processus du brassage de la colonne d'eau ou l'intensité d'upwelling locaux et modifier la disponibilité en nutriments ou bien un changement de régime de pluies modifiant le débit des fleuves et par la même occasion les apports en nutriments d'origine terrestre (Martin-Vide & Lopez-Bustins, 2006; Mercado et al., 2005, 2007). Certaines interactions entre espèces comme la compétition peuvent également être impactées par ces processus à large échelle comme observé avec le NAO en Atlantique nord (Fromentin & Planque, 1996). L'hypothèse centrale de cette thèse était la présence d'un contrôle bottom-up sur les populations de petits pélagiques avec une modification de la communauté zoo-planctonique induite par des modifications environnementales. Faute de données sur le plancton dans Golfe du Lion, nous avons regardé si les variables environnementales connues pour impacter le plancton avaient varié et il semblerait que ce soit bien le cas. Ainsi, différents changements ont été observés au cours de cette thèse au niveau environnemental, aussi bien à large échelle avec une diminution du WeMO ou l'augmentation de température (possiblement liée au réchauffement global), qu'au niveau local avec une augmentation des upwellings et des fronts thermiques ou bien la diminution des apports du Rhône. Le fait que les communautés de petits pélagiques semblent répondre aussi bien à l'environnement local que global laisse à penser que certaines modifications observées localement pourraient découler de changements à large échelle (Stenseth & Mysterud, 2002; Stenseth et al., 2003). Un deuxième point soutenant cette hypothèse est le fait que les changements dans les populations de petits pélagiques n'aient pas seulement lieu dans le Golfe du Lion mais de façon synchrone dans différentes zones de Méditerranée nord-ouest comme en mer Catalane ainsi que sur la façade Atlantique dans le Golfe de Gascogne (Brosset et al., 2017; Saraux et al., 2019; Véron et al., 2020). Que ce soit en Méditerranée ou en Atlantique, une augmentation de la température a été observée et des changements dans la qualité du plancton sont supposés être le facteur principal impactant la condition des poissons (Brosset et al., 2016a; Véron et al., 2020). Ces différentes zones d'Europe centrale, du sud et Méditerranée sont connues pour être reliées d'un point de vue climatique et impactées par les changements de circulation atmosphérique (Hurrell, 1995). Ainsi, il est possible que des changements à large échelle comme l'augmentation de température ou la circulation atmosphérique impactent la dynamique planctonique simultanément à différents endroits comme cela a déjà été observé par le passé (Beaugrand et al., 2015) avec des répercussions sur les petits pélagiques.

V-3 L'impact des forçages anthropiques en méditerranée nord-ouest

La Méditerranée est une mer fortement soumise aux pressions anthropiques avec une forte densité de population sur ses côtes et étant une importante destination touristique (Mermex Group., 2011). Toutes les régions ne sont pas impactées de la même façon mais les zones sous influence des fleuves ou proches de grandes agglomérations semblent être les plus soumises aux pressions anthropiques, notamment en terme de concentration en polluants (Mermex Group., 2011; Thébault et al., 2008). Certaines différences dans les communautés de zoo-planctoniques ont ainsi été observées localement entre différentes régions méditerranéennes côtières soumises à des pressions anthropiques. Par exemple, Calbet et al., (2001) ont trouvé que le groupe *Clausocalanus* était dominant en hiver dans la baie de Blanes alors que dans la baie de Marseille, ce groupe semble autant présent en hiver que le reste de l'année (Chen et al., 2019). Bien que toute deux soumises aux pressions anthropiques, la baie de Marseille semble particulièrement impactée par les contaminations et les rejets. En effet au large de Marseille, l'émissaire de Cortiou semble jouer un rôle dans la dynamique zoo-planctonique, une réduction de la biomasse de poissons planctonophages et une modification de la structure trophique du réseau ayant été observée suite à la réduction des rejets (Ourgaud et al., 2015). Au cours de nos analyses, nous avons trouvé que les *Clausocalanus* étaient le groupe majoritaire des copépodes dans le Golfe du Lion en été, indiquant toutefois sa forte présence ailleurs qu'en hiver également dans la zone du plateau du Golfe du Lion beaucoup plus vaste que la baie de Marseille. De même pour le groupe *Oithona*, alors que plusieurs études rapportent des abondances maximales en hiver en Méditerranée (Mazzocchi & d'Alcalà, 1995; Siokou-Frangou, 1996), il semble être à nouveau présent toute l'année dans le Golfe du Lion (Chen et al., 2019) ainsi que dans la baie de Toulon, une autre zone fortement anthropisée (Jamet et al., 2005). Concernant le Golfe du Lion, nous avons ainsi vu que les apports du Rhône semblaient jouer un rôle essentiel dans la concentration en chlorophylle satellitaire, un proxy de la biomasse phyto-planctonique, sur le plateau du Golfe du Lion et suggéré que ces apports pouvaient varier en partie par l'action de l'Homme (Feuilloley et al., 2020). Le panache du Rhône pouvant se déplacer assez loin sur le plateau, aussi bien vers le large que longeant la côte vers l'ouest, il est possible qu'une partie de la dynamique planctonique du plateau soit liée aux activités humaines notamment via des rejets de nutriments mais peut-être également par d'éventuelles pollutions. Un exemple concret est celui de la baie de Toulon, où la petite baie, beaucoup plus soumise aux pressions anthropiques et plus polluée présente une dynamique phyto- et zoo-planctonique différente de la grande baie présentant plus d'échanges avec l'océan ouvert (Jamet et al., 2005). Ainsi, en plus de l'action combinée de forçages environnementaux globaux et locaux comme vu précédemment, la pression anthropique joue également possiblement un rôle important et ajoute une nouvelle source de variabilité dans les communautés planctoniques à prendre en compte pour comprendre leur dynamique. La démographie humaine étant en constante augmentation, les pressions anthropiques seront probablement de plus en plus fortes à l'avenir et auront un rôle important dans la dynamique des communautés planctoniques et marines.

V-4 Changement de régime alimentaire chez les poissons petits pélagiques

Une question centrale de cette thèse était de savoir si les petits pélagiques dans le golfe du Lion avaient pu changer de régime alimentaire, en réponse à des changements dans la communauté planctonique, expliquant leur baisse de condition. De tels changements ont déjà pu être observés dans d'autres zones avec des répercussions fortes sur les populations de petits pélagiques, notamment en terme d'abondance (Ayón et al., 2011; Tam et al., 2008; Van der Lingen et al., 2006). Cela a été regardé dans le chapitre 3 en comparant les communautés planctoniques observées avec les données de contenus stomacaux des sardines et anchois dans le Golfe du Lion disponibles dans la littérature, issues de Brosset et al., (2016a). Cependant, aucune réponse claire n'a pu être donnée car de grandes différences ont été observées entre les groupes zoo-planctoniques présents dans les contenus stomacaux et ceux présents dans les échantillons issus des campagnes PELMED des années récentes. Plusieurs hypothèses peuvent être avancées quant aux différences observées entre les contenus stomacaux et les échantillons de zooplancton dans le milieu comme par exemple la préférence des poissons pour certaines proies, qui ne vont donc pas prélever l'ensemble de la communauté planctonique de façon homogène mais cibler les proies avec par exemple le meilleur apport énergétique. Ces préférences sont mises en évidence par le biais d'indices de sélectivité en comparant les contenus stomacaux des poissons avec les concentrations de plancton dans le milieu au même moment (Borme et al., 2009; Costalago et al., 2012; Plounevez & Champalbert, 2000). Les petits pélagiques vont présenter deux modes d'alimentation, la chasse active plutôt sur des grandes proies et la filtration passive, plutôt sur les petites proies (Garrido et al., 2007, 2008). Ainsi, la sélection sera plutôt faite sur les grandes proies lors de la chasse et moins sur les petites proies filtrées passivement (Plounevez & Champalbert, 2000). En comparant les contenus stomacaux de la sardine en 2007 avec les données in situ analysées dans le chapitre 2 pour la même année, il semblerait toutefois que ce facteur ne soit pas la cause principale des différences, les plus gros zooplanctons comme

Acartia, *Centropages* ou *Clausocalanus* représentant une faible part des apports des poissons bien qu'étant présents dans le milieu.

Une deuxième explication potentielle aux différences observées est le fait de comparer la communauté de certaines années avec les contenus stomacaux d'autres années. En effet, les analyses du chapitre 3 ont révélé des différences à la fois intra- et interannuelles au niveau de la composition zoo-planctonique dans le Golfe du Lion. De telles différences sont également observées dans les contenus stomacaux des petits pélagiques ainsi que dans les indices de sélection des proies. Brosset et al., (2016a) par exemple ont trouvé que les Appendiculaires étaient peu consommés que ce soit par l'anchois ou la sardine au cours des 4 années intégrées à leur étude (1994, 2007, 2011 et 2012) alors que Costalago et al., (2012) ont trouvé, pour le même mois en 2008, les Appendiculaires (ainsi que les cladocères) comme proie majoritaire des deux espèces, avec un indice de sélectivité élevé. Il est cependant important de noter ici que les méthodes d'estimation diffèrent entre les deux études (comptage dans l'estomac et analyse isotopique) ce qui peut, peut-être entrainer quelques différences dans les estimations. Cependant, des différences sont observées Table V-1 en comparant les contenus stomacaux et les échantillons d'une même année, indiquant que d'autres facteurs rentrent en compte. Il apparait toutefois important d'avoir sur quelques années successives les contenus stomacaux des poissons prélevés en même temps que les échantillons de plancton afin de pouvoir déterminer d'éventuels liens entre la composition de la communauté planctonique et les contenus stomacaux des poissons et de quantifier la variabilité interannuelle de ces relations.

Finalement, un dernier aspect plus méthodologique et peut être le plus important pouvant limiter nos interprétations sur la relation plancton-poisson est le type de filet utilisé pour prélever les échantillons de zooplancton. En effet, bien que le WP2 200µm de vide de maille soit le filet recommandé pour étudier la communauté zoo-planctonique (UNESCO, 1968), ce dernier n'est peut-être pas optimal pour étudier la dynamique de l'ensemble des proies consommées par les poissons petits pélagiques. A partir des analyses de la série de zooplancton à long terme issue du point B, nous avons observé que ce filet n'était efficace pour les crustacés qu'à partir 650µm et sous-estimait les individus de plus petite taille. Les petits pélagiques se nourrissant dans la gamme 0.1-1.4mm (Le Bourg et al., 2015), une partie de leurs proies n'est donc de ce fait pas considérée ou tout du moins mal estimée. Cela pourrait expliquer l'absence de certains individus de nos échantillons comme *Microsetella* ou *Euterpina,* mesurant pour la majeure partie moins de 700µm (Razouls et al., 2020) et faisant partie des proies principales en 2007 Table V-1. Cette observation avait déjà été faite par Plounevez & Champalbert, (2000), qui avaient observé des densités largement sous estimées de certaines proies principales des petits pélagiques, notamment *Microsetella*, avec un filet de 200µm comparé au filet de 80µm. Après 2007, *Microsetella* ainsi que *Oncaea* (faisant également partie des petites proies) représentant la majorité des proies des petits pélagiques (Brosset et al., (2016a) mais sont peu voir pas présents dans nos échantillons. Ainsi, il pourrait être interessant à l'avenir de conserver les prélèvement au filet 200µm afin de garder la continuité temporelle de la série planctonique mais d'ajouter également des prélèvements avec un filet 53µm ou 80µm afin de mieux échantillonner les individus des gammes de taille inférieures consommées par les petits pélagiques et ainsi avoir une meilleure estimation de leurs proies disponibles dans le milieu.

Table V-1 ***Comparaison des contenus stomacaux de la sardine en 2007 dans le Golfe du Lion issus de (Brosset et al., 2016a) avec la proportion de chacun des groupes zoo-planctoniques dans la communauté in situ issus des données de campagne PELMED ainsi que de leur taille moyenne.***

Taxons	% IRI (Sardine)	% communauté	Taille (mm)
Acartia	0	10.35	1.0 - 1.8
Clauso-Paracalanidae	4.36	16.35	0.6 – 1.5
Centropages	0	4.28	0.79 – 1.9
Corycaeus	4.28	<1	0.74 – 1.5
Clytemnestra	0	<1	0.4-1.6
Candacia	1.60	<1	1.7 - 3.1
Oithona	0	3.18	0.5 – 1.3
Oncaea	8.48	7.00	0.5-1.1
Microsetella	10.60	<1	0.5 – 0.8
Euterpina	10.03	<1	0.6
Temora	11.46	<1	1.5
Autres_copepodes	9.50	6.7	
Cladocères	31.48	39.90	0.4-1.5
Autres zooplancton	6.15	12.1	

V-5 Eastern Boundary Upwelling System (EBUS) vs. zones méditerranéennes moins productives

Les plus grandes populations de petits pélagiques se trouvent essentiellement dans les grandes zones d’upwelling ce qui implique que de nombreuses études s’intéressant à la dynamique des petits pélagiques ont été menées dans ces zones très productives (Alheit & Niquen, 2004; Ayón et al., 2011; Schwartzlose & Alheit, 1999). Il est néanmoins possible que le fonctionnement de ces populations diffère entre ces zones très productives et d’autres zones moins riches comme la Méditerranée de par les différences de productivité et de dynamique de l’environnement. Une première différence majeure entre le Golfe du Lion et ces zones d’upwelling est le rôle du recrutement dans la dynamique des populations. Dans les zones d’upwelling, les régimes shifts observés dans les populations de petits pélagiques sont souvent liés à des changements dans le recrutement, principalement déterminé par la survie des larves et des juvéniles en fonction de la disponibilité des ressources. Ainsi, une baisse de production planctonique ou des changements phénologiques du plancton entrainant des phénomènes de mis-match peuvent induire une baisse du recrutement et impacter la dynamique de la population toute entière aussi bien en abondance que biomasse du fait du cycle de vie court des individus (Bakun, 1996; Cushing, 1990). De même, la rétention des larves dans les zones de production favorables est un paramètre important du recrutement dans les EBUS. Dans le cas du Golfe du Lion, le recrutement ne semble cependant pas être la cause des changements dans les populations, ce dernier étant resté plutôt stable et les changements étant observés plutôt chez les plus vieux individus (Brosset et al., 2016b; Saraux et al., 2019, Van Beveren et al., 2014). De plus, l'abondance des individus n'a pas été impacté Un deuxième point est le fait qu'il est suspecté dans le Golfe du Lion une baisse de la taille des proies des poissons ayant entrainé une baisse de leurs conditions. Plusieurs études ont montré que la sardine possédait une meilleure capacité de filtration que l'anchois et était avantagée lorsque les proies étaient plus petites (Ayón et al., 2011; Garrido et al., 2007, 2008). Pourtant, la sardine semble beaucoup plus impactée que l'anchois dans le Golfe du Lion (Van Beveren et al., 2014). Bien que cette hypothèse de diminution de la taille des proies dans le Golfe du Lion n'ait pas pu être clairement confirmée par le biais des analyses des campagnes PELMED, cela suggérerait cependant des réponses différentes des petits pélagiques aux modifications de la communauté planctonique entre zone à upwelling et zones moins productives comme le Golfe du Lion. Un processus amenant à des proies plus petites dans les systèmes à upwelling est l'alternance de dominance dans le phytoplancton entre dinoflagellés et diatomées (Tam et al., 2008; Van der Lingen et al., 2006). Ce type d'alternance a été spécifiquement recherché lors de nos analyses mais n'a pu être observé, les diatomées étant largement dominantes dans une grande partie de nos échantillons et ce pour la majorité des années. De même en mer Ligure, les analyses ont révélé une forte stabilité de la communauté zoo-planctonique et aucun changement résultant d'une potentielle alternance entre diatomées et dinoflagellés n'as été observé sauf peut-être à partir de 2015 mais des analyses complémentaires sont nécessaires. Cependant, certaines études en Méditerranée ont montré que de tels changements étaient possibles, notamment en mer d'Alboran, une des zones les plus productives de Méditerranée nord-ouest, où un upwelling quasi permanent a été observé (d'Ortenzio & Ribera d'Alcalà, 2009; Mercado et al., 2007; Siokou-Frangou et al., 2010). Ainsi, Mercado et al., (2005,2007) ont montré que la communauté phytoplanctonique était dominée par les diatomées entre 1994 et 1997 puis par les dinoflagellés entre 1998 et 2002 suite à une baisse de l'intensité de l'upwelling. Ce processus est très similaire à celui observé dans les grandes zones d'upwelling avec une dominance de dinoflagellés lorsque l'intensité de l'upwelling diminue (Van der Lingen et al., 2006). Ce type d'alternance dans la communauté planctonique semble ainsi se mettre en place dans des systèmes très productifs, soutenus par un processus fort et continu comme les upwellings et dont les variations d'intensité induisent des changements forts dans la communauté. L'absence d'un tel processus fort et continu dans le Golfe du Lion est peut-être la raison de l'absence d'alternance dans la communauté planctonique entre les années. Cependant, Pethybridge et al., (2014) ont mis en évidence une variabilité intra-annuelle dans la composition des acides gras de la sardine et de l'anchois expliquant cela par les différentes communautés zoo-planctoniques prédatées, soutenues à la base par une production de diatomées ou dinoflagellés. Ainsi, l'anchois et la sardine présentaient une meilleure condition alimentaire lorsque la communauté phytoplanctonique était dominée par les diatomées comparé aux périodes où la communauté était dominée par des dinoflagellés (Pethybridge et al., 2014). Il semblerait donc que de tels changements dans le phytoplancton puissent également avoir lieu dans le Golfe du Lion au moins au niveau intra-annuel avec un impact sur les apports énergétiques des petits pélagiques mais n'entrainant cependant pas une alternance entre l'anchois et la sardine comme dans les systèmes à upwelling mais plutôt une co-variation. Une des hypothèses serait que dans des zones moins productives comme le Golfe du Lion, comparé à la mer d'Alboran ou les systèmes à upwelling, filtrer pourrait ne jamais être vraiment efficace. Ainsi, les alternances entre sardines et anchois observées dans les zones productives liées notamment aux différences de capacités de filtrations n'auraient pas lieu, des petites proies devenant moins favorable aussi bien pour la sardine qui adopterait une stratégie de filtration peu efficace en zone moins productive que pour l'anchois se nourrissant moins efficacement sur les petites proies (Van der Lingen et al., 2006). Il est donc possible que la dynamique des petits pélagiques dans le Golfe du Lion diffère de celle des grandes zones à upwelling plus productives et que certains processus ne soient pas transposables d'une zone à une autre, ayant des effets possiblement différents sur les populations. Aucune étude n'a cependant montré de tels changements au niveau interannuel dans le Golfe du Lion comme cela est observé dans les zones d'upwelling et nos analyses n'ont pas non plus permis de le mettre en évidence, possiblement par manque de données.

V-6 Limites dans les interprétations de relations zooplancton-petits pélagiques

V-6.1 Problèmes d'échelle temporelle et de disponibilité des données de plancton

L'absence ou la faible disponibilité des données de plancton dans le Golfe du Lion a été un obstacle important pour comprendre sa dynamique planctonique et le lien potentiel avec les petits pélagiques qui n'a jamais vraiment pu être clairement mis en évidence au cours de nos diverses analyses. Dans le chapitre 2, nous avons observé d'une part une réduction de la concentration en chlorophylle satellitaire au milieu des années 2000s traduisant possiblement une baisse de la production planctonique dans le Golfe du Lion et d'autre part que les petits pélagiques semblaient répondre à un changement global de l'environnement, probablement de façon indirecte via une réponse du plancton. Ainsi, l'hypothèse d'une réponse bottom-up des poissons suite à des changements dans le plancton semble se renforcer, mais l'absence de données zoo-planctoniques, compartiment trophique directement lié aux petits pélagiques, a empêché d'établir une réponse claire. Ce manque d'information de la communauté zoo-planctonique aurait pu être comblé par les analyses du chapitre 3 pour lesquelles un détail taxonomique était disponible et pouvait être mis directement en relation avec la condition des poissons. Cependant, les relations entre condition des poissons et communauté zoo-planctonique se sont avérées faibles. Une des principales causes supposée est la couverture temporelle des données (uniquement le mois de Juillet de chaque année), et ce pour deux raisons. La première est que les données de zooplancton utilisées rendent compte de l'état instantané de la communauté alors que la condition des poissons intègre les conditions rencontrées pendant plusieurs semaines avant. Cette différence au niveau de l'échelle temporelle pourrait avoir une importance forte, d'autant plus que la condition des poissons en juillet pourrait encore être fortement influencée par les conditions printanières, le bloom de phytoplancton pouvant s'étendre jusqu'à mai comme vu dans le chapitre 2. De plus dans de nombreuses zones de Méditerranée, les communautés de printemps, aussi bien pour le phytoplancton que le zooplancton sont bien différentes des communautés d'été ce qui impliquerait que la condition de juillet reposerait plus sur la variabilité des espèces printanières qu'estivales (Ribera d'Alcalà et al., 2004; García-Martínez et al., 2019;

Zingone et al., 2019). Enfin, un aspect intéressant de nos résultats renforçant l'idée de l'importance de la communauté printanière est la diminution de l'intensité des efflorescences printanières dans le Golfe du Lion à partir de 2007 entrainant la baisse de concentration annuelle observée. En revanche, aucun changement dans la phénologie du bloom n'a été observé, ni dans l'initiation ni dans la durée du bloom comme cela pourrait être attendu dans un contexte de réchauffement global (Trombetta et al., 2019). Des changements ont également été observés au printemps dans nos analyses en mer Ligure avec une diminution des pics printaniers de zooplancton depuis 2015 et une modification du spectre de taille. Bien qu'il n'y ait pas de correspondance temporelle de ces changements entre les deux zones, cela indique néanmoins que les modifications de la communauté planctonique au printemps ont un impact important pour le reste de l'année, rendant cette période particulièrement cruciale et à étudier de façon plus précise. La mise en place d'un suivi de la communauté planctonique avec des prélèvements dès l'hiver semble donc une nécessité afin de combler les manques de données actuels et pouvoir mieux comprendre la dynamique planctonique dans le Golfe du Lion ainsi que les interactions plancton-poisson.

V-6.2 Représentativité du point B pour le Golfe du Lion

La variabilité de la taille du zooplancton n'a pu être étudiée qu'au point B en mer Ligure car l'information n'était pas disponible dans les échantillons de PELMED dans le Golfe du Lion. Nous avons observé une variabilité saisonnière du spectre de taille ainsi qu'une forte stabilité interannuelle ce qui n'a pas permis de valider l'hypothèse d'un éventuel changement de taille dans la communauté zoo-planctonique, en réponse à des changements environnementaux interannuels, qui auraient pu affecter les petits pélagiques. Afin de comparer les communautés présentes dans le Golfe du Lion et au point B, les données du WP2 au point B ont été spécifiquement triées aux mois de Juillet afin d'avoir un détail taxonomique plus fin que pour la série complète, notamment pour les copépodes, permettant ainsi une comparaison plus fine des deux communautés. Cette comparaison des communautés zoo-planctoniques en Juillet a révélé des différences assez fortes et sous estimées en début de travail. Sur le plateau du Golfe du Lion, les cladocères ont été retrouvés en proportion beaucoup plus importante qu'au point B, principalement les genres *Evadne* et *Penilia (*Figure V-1*).* En revanche, les *Calanoides* représentaient au point B une fraction beaucoup plus importante de la communauté que dans le Golfe du Lion (Figure V-1). Des différences de communautés zoo-planctoniques entre les deux zones étaient en partie attendues, du fait des différences dans les forçages propres aux deux endroits, mais à des niveaux plus faibles.

En effet, des différences existent entre le Golfe du Lion (et en particulier le plateau continental) et la mer Ligure, qui sont classées selon d'Ortenzio & Ribera d'Alcalà, (2009) dans deux bio régions différentes sur la base de leur dynamique saisonnière de concentration en chlorophylle satellitaire. Le plateau du Golfe du Lion est très fortement lié aux apports terrigènes, notamment via les apports du Rhône, un des principaux fleuves de Méditerranée nord occidentale (Feuilloley et al., 2020; Lefevre et al., 1997; Macias et al., 2018b). A l'inverse, la communauté zoo-planctonique au point B semble liée aux processus de convection et mélange hivernal (García-Comas et al., 2011; Vandromme et al., 2011). Enfin, Donoso et al., (2017) ont observé des différences dans la communauté zoo-planctonique pendant et après un évènement de convection hivernale entre des stations sur le plateau du Golfe du Lion et en dehors, les stations du plateau semblant moins impactées par ce processus. Ainsi, les deux régions présentent des forçages hydrodynamiques différents pouvant expliquer les différences de communautés. Dans l'océan ouvert, les copépodes dominent en général la communauté zoo-planctonique alors que d'autres groupes peuvent être retrouvés en proportion importante à la côte comme les cladocères par exemple (Ramfos et al., 2006). Cela correspond à nos résultats avec une importance plus forte des *cladocères* sur le plateau du Golfe du Lion et des *calanoides* au point B. La communauté zooplanctonique semble ainsi plutôt côtière pour le plateau du Golfe du Lion et hauturière pour le point B. Du fait de ces différences assez fortes dans les communautés, des différences dans la variabilité à long terme de la taille des crustacés pourraient également être présentes entre les deux zones. Il semble donc difficile de faire un rapprochement direct entre le point B et le Golfe du Lion concernant la dynamique à long terme de la communauté zoo-planctonique et une analyse de la taille du zooplancton dans le Golfe du Lion apparait donc nécessaire pour faire le lien avec les populations de petits pélagiques.

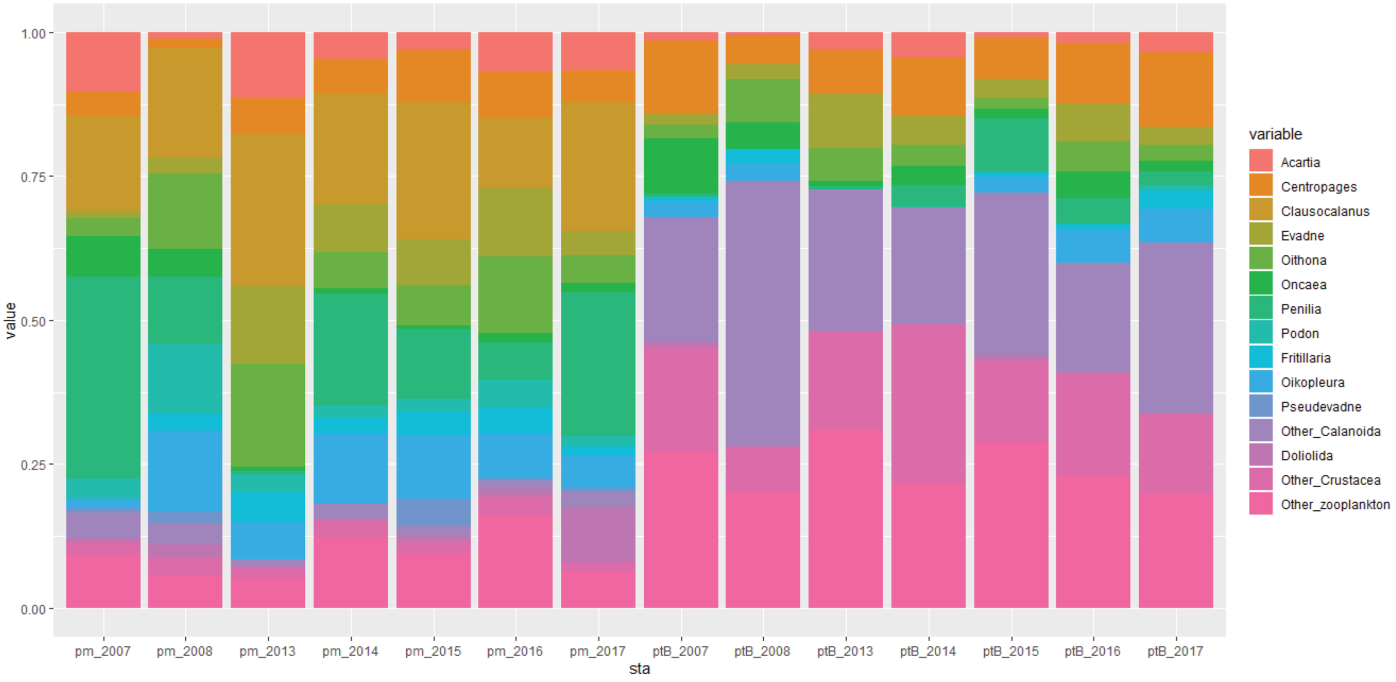


Figure V-1 ***Comparaison de la composition de la communauté zoo-planctonique prélevée par WP2 entre le plateau du Golfe du Lion et le point B en Juillet basée sur les groupes principaux identifiés dans le Golfe du Lion pour les années 2007-2008 et de 2013 à 2017. « pm » représente les données du Golfe du Lion issues de la campagne PELMED et « ptB » les données au point B en mer Ligure.***

V-7 L'impact de la pollution sur la dynamique planctonique

La piste d'une éventuelle pollution n'a été que peu traitée pour l'instant dans le Golfe du Lion et devrait probablement être plus approfondie du fait de ses concentrations fortes en polluants (Harmelin et al., 2012) le rendant une des zones les plus polluées de Méditerranée en terme de PCB (Bodiguel et al., 2008; Gómez-Gutiérre et al., 2007). Nous avons essayé au cours de cette thèse de reconstruire des séries de polluants dans le Rhône, notamment divers pesticides pouvant impacter la production phytoplanctonique, à partir des données de l'Agence de l'eau mais ces suivis ayant été menés par différentes entreprises, les protocoles de mesures ont varié au fil du temps avec des niveaux de seuils différents et les données n'ont finalement pu être utilisées (Figure V-2). L'impact des pesticides dans le Golfe du Lion pourrait toutefois être important car plusieurs études ont montré que les seuils établis par la législation Européenne pour certains herbicides, notamment le diurion ou le terbulazine seraient au-dessus du seuil de réponse du plancton suggérant un potentiel risque pour la communauté phytoplanctonique (Booij et al., 2015; Sjollema et al., 2014). Les espèces planctoniques pourraient donc être impactées par la pollution (Tiano et al., 2014), ce qui pourrait entraîner un changement de communauté et/ou d'abondance, chaque espèce présentant des réponses différentes aux niveaux de concentration (Buma et al., 2009; Magnusson et al., 2010; Uriarte & Villate, 2005). Concernant l'effet sur les poissons, pour les quelques polluants (PCB, PBDE, Hg et 137Cs) examinés jusqu'à présent dans l'anchois et la sardine du Golfe du Lion (voir Harmelin et al., 2012), les niveaux ce sont avérés semblables à ceux dans d'autres régions européennes (Bocio et al., 2007; Martí-Cid et al., 2007). Il n'est toutefois pas à exclure un possible effet cocktail de polluants qui pourrait avoir un impact supérieur à l'effet de chaque polluant seul. Une approche par la modélisation DEB pourrait être envisagée pour étudier l'impact des contaminants sur les poissons, notamment par le biais d'un module DEB-tox afin d'inclure l’impact des contaminants d’un point de vue énergétique et observer les effets sur différents paramètres tels que la maintenance la croissance ou encore la reproduction (Accolla et al., 2020; Jager & Zimmer, 2012).

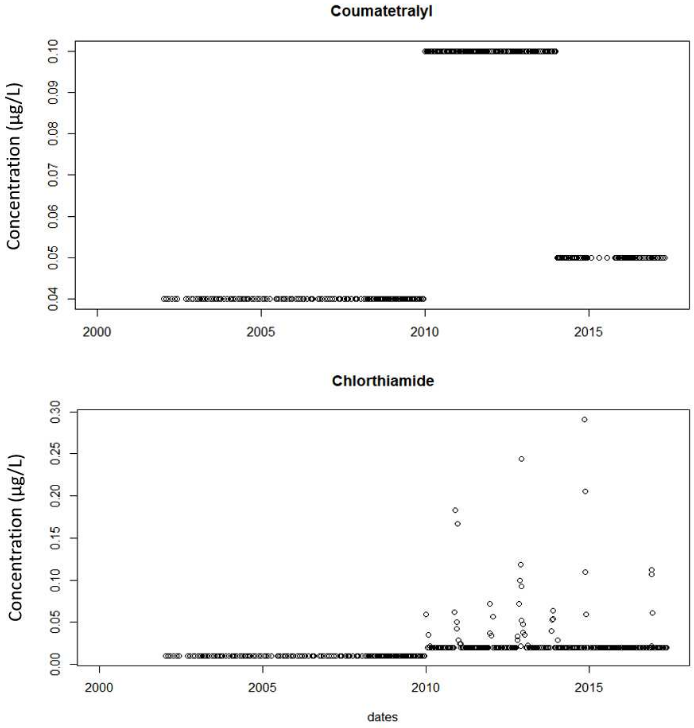


Figure V-2 ***Exemple de séries temporelles de concentration de polluants dans le Rhône à la station de prélèvements à Arles. Les changements d’entreprises effectuant le suivi des concentrations en 2010 et 2014 sont visibles avec des changements au niveau des seuils de détections.***

V-8 Dynamique future du plancton et des petits pélagiques dans le contexte du changement climatique

Bien qu’il existe de grandes différences entre les différents modèles de projections du climat futur, une grande partie s’accorde à dire que la température globale va continuer d’augmenter durablement (Bopp et al., 2013; Kwiatkowski et al., 2020). Il a déjà été observé expérimentalement (Peter & Sommer, 2012) et in situ (Morán et al., 2010) qu’une augmentation de température peut entrainer une réduction de la taille du phytoplancton. Cela s’explique par le fait que les petites cellules vont être favorisées à plus haute température par une plus forte cinétique d’assimilation des nutriments, et une meilleure croissance due à leur plus grand ratio taille-volume (Falkowski & Oliver, 2007; Sommer et al., 2017). Ainsi, le développement des espèces plus petites se fait au détriment d’espèces plus grosses telles que les diatomées de par leur compétitivité réduite en conditions plus chaudes. Une réduction de la taille de la communauté phytoplanctonique modifierait fondamentalement le transfert d’énergie vers les niveaux trophiques supérieurs par amplification de la voie hétérotrophe. Les bactéries ainsi que le pico et nanophytoplancton sont majoritairement broutés par les protistes hétérotrophes (Mostajir et al., 2015; Moustaka-Gouni et al., 2016; Thingstad & Rassoulzadegan, 1999). Ces micro-organismes sont eux même prédatés par le meso-zooplancton carnivore, assurant le transfert d'énergie vers les niveaux trophiques supérieurs. Cependant, la voie hétérotrophe est moins efficace en terme de transfert d'énergie du fait du plus grand nombre d'intermédiaires comparé à la voie autotrophe, supportée essentiellement par les diatomées et brouté directement par le gros zooplancton tels les copépodes (Berglund et al., 2007; Dahlgren et al., 2011; Fenchel, 1988). Une augmentation du transfert hétérotrophe au détriment de la voie autotrophe dite classique dans un environnement plus chaud entrainerait alors une réduction de l'énergie entre la production primaire et les niveaux supérieurs, impactant la productivité des écosystèmes et les niveaux supérieurs comme par exemple les petits pélagiques (Berglund et al., 2007; Dahlgren et al., 2011; Fenchel, 1988; Mostajir et al., 2015).

Ajouté à cela, les processus de mélange verticaux et en particulier la convection profonde en hiver, considérés comme un support majeur de la production planctonique en Méditerranée nord-ouest, pourrait être amenés à diminuer (Herrmann et al., 2014). En effet, l'augmentation de la température provoquerait également une augmentation de la stratification rendant les mélanges plus difficiles. Cette réduction des mélanges aurait alors pour conséquence une baisse de la concentration en nutriments dans la couche euphotique moins alimentée par les eaux profondes et induirait une diminution de la taille du phytoplancton et de la production primaire (Bopp et al., 2005; Herrmann et al., 2014). Certaines études de modélisation prédisent un phénomène inverse à horizon 10-15 ans avec une intensification de ces processus de mélange, principalement dûs à une augmentation des régimes de vents refroidissant les couches supérieures et activant le brassage par le biais des frottements, induisant une augmentation de la production phytoplanctonique (Macias et al., 2018a). Cependant, le même modèle utilisé sur un intervalle de temps plus long prédit pour la fin du 21^{e} siècle une réduction de la production phytoplanctonique et une réduction des mélanges dans la colonne d'eau (Macias et al., 2015). Bien que la dynamique future des convections profondes hivernales semble encore incertaine, peu de fortes convections ont été observées au cours des dernières années. La dernière forte convection observée en méditerranée semble être celle de 2013 (N.Mayot, pers.comm) et nous avons observé dès 2014 une augmentation assez marquée de la température de l'eau rendant probablement plus difficile les mélanges depuis. Ces modifications précèdent la baisse de concentrations de certains groupes de zooplancton en mer Ligure dont les crustacés et les gélatineux filtreurs et carnivores observés en 2015. De plus, des analyses préliminaires sur des séries de pigments prélevés depuis 2009 au point B semblent montrer une réduction des diatomées depuis 2014, remplacées plutôt par du pico-phytoplancton et notamment des prochloroccocus. Ainsi, il est possible que l'on commence déjà à observer l'effet de l'augmentation de température et de la diminution du mélange avec une réduction de l'importance des diatomées et une augmentation des individus de plus petites tailles. Cela pourrait être les prémices d'une oligotrophisation du milieu, avec de possibles répercussions dans l'ensemble du réseau trophique. On pourrait donc s'attendre à l'avenir à une réduction de la production primaire et une diminution de la taille du phytoplancton, stimulant la voie trophique hétérotrophe moins efficace en terme de transfert d'énergie vers les niveaux supérieurs. Bien que le Golfe du Lion semble moins impacté par ces phénomènes du fait des apports du Rhône qui soutiennent une production planctonique assez forte, il est attendu à l'avenir une réduction des débits des fleuves induit par un climat plus chaud et sec (Adloff et al., 2015). Tous ces éléments combinés pourraient ainsi avoir des conséquences négatives et très fortes sur les populations de petits pélagiques mais également dans l'ensemble du réseau trophique.

V-9 Perspectives de poursuite du travail

V-9.1 Un meilleur suivi de la communauté planctonique

Différents résultats obtenus au cours de cette thèse ont amené à différentes suggestions dans l'étude future de la communauté planctonique en lien avec les petits pélagiques. Tout d'abord, nous avons vu que l'utilisation du filet WP2 200µm, bien qu'étant le filet standard et recommandé pour étudier la communauté zoo-planctonique, ne semble pas être optimal pour étudier la dynamique des proies des petits pélagiques, notamment les petits copépodes certainement sous-échantillonnés et mal représentés. L'ajout de prélèvement avec un filet à mailles plus petites, par exemple de 53µm plus efficace pour prélever les petits individus apparait nécessaire afin de comparer le plancton dans le milieu et dans les contenus stomacaux des petits pélagiques et caractériser les proies préférentielles des poissons. Concernant le lien entre la condition des poissons et la communauté planctonique, nous avons fait l'hypothèse que la communauté planctonique observée au moment de la pêche des poissons n'avait possiblement qu'un faible impact sur la condition instantanée des poissons et que les conditions printanières étaient sans doute plus informatives pour expliquer la condition des poissons en été. De plus, les changements observés au pic printemps dans le plancton en Méditerranée nord-ouest semblent avoir une importance pour le reste de l'année. Sur le plateau du Golfe du Lion, nous avons vu dans le chapitre 2 que l'initiation du pic printanier pouvait même avoir lieu dès la fin de l'hiver entre fin novembre et début décembre. De ce fait, la mise en place d'un suivi du plancton dès l'hiver semble important à la fois pour mettre en relation avec la condition des poissons au moment de PELMED en juillet mais également pour mieux comprendre la dynamique planctonique dans le Golfe du Lion. Enfin, il sera peut-être intéressant d'analyser la communauté phyto- et zoo-planctonique à des niveaux plus fins, peut-être à l'espèce ou alors considérer des groupes fonctionnels. En effet, regarder à des niveaux trop grossiers peut empêcher de voir la dynamique de certaines espèces en particulier et passer à côté de changements potentiellement importants (Berline et al., 2012). Toutefois, si un tel détail pourrait permettre de mieux comprendre la dynamique de la communauté zoo-planctonique, il est possible que les caractéristiques telles que la taille ou la densité énergétique des proies soient plus importantes pour les petits pélagiques que l'aspect taxonomique (Queiros et al., 2019; Saraux et al., 2019). Essentiellement la voie de transfert d'énergie autotrophe a été considérée dans nos diverses études, en considérant majoritairement les individus du micro-phytoplancton et le meso-zooplancton. Cependant, il semblerait qu'à l'avenir avec le réchauffement global la voie de transfert hétérotrophe prenne de plus en plus d'importance (Calbet et al., 2014; Mostajir et al., 2015). Il semble donc intéressant d'inclure dans les futurs prélèvements et analyses une quantification du pico et nano-phytoplancton ainsi que des protistes hétérotrophes afin d'avoir une meilleure vision du transfert d'énergie jusqu'aux petits pélagiques.

V-9.2 Densité énergétique du zooplancton et modélisation DEB

Une des hypothèses liée à un plancton plus petit serait une diminution de la disponibilité énergétique pour les petits pélagiques, le petit zooplancton ayant une densité énergétique plus faible (Barroeta et al., 2017). Des analyses préliminaires de mesure de densité énergétique par bombe calorimétrique pour plusieurs classes de taille de zooplancton, toutes espèces confondues, prélevé au cours d'une campagne PELMED ont montré une grande variabilité au sein d'une même classe de taille. Cela est probablement dû au fait que différents groupes taxonomiques très différents étaient mélangés, aussi bien crustacés que gélatineux. Ainsi, une nouvelle approche par bombe calorimétrique serait à envisager pour mesurer la densité énergétique de quelques grands groupes de copépodes et autres zooplanctons pour différentes gammes de tailles. Combinées aux données de densité, ces mesures de densité énergétique pour différents groupes permettraient ensuite de construire des séries d'énergie disponibles pour les petits pélagiques. Cela permettrait d'avoir directement une idée de la variabilité de l'énergie représentée par le zooplancton et disponible pour les poissons fourrages et de tester l'hypothèse que la mauvaise condition des petits pélagiques résulte d'un appauvrissement en terme énergétique de la communauté planctonique. Ce type de série pourrait ensuite être utilisée par exemple en entrée de modèle DEB (Kooijman, 2000) qui est en cours de développement pour la sardine en Méditerranée et ainsi tester différents paramètres tels que la survie, croissance, reproduction, etc… en fonction de l'énergie disponible en entrée (Queiros phd thesis). Différents scénarios futurs pourraient être testés comme l'augmentation de la température couplée à des réductions d'énergie en entrée de modèle pour simuler aussi bien une diminution de la production planctonique qu'une réduction du transfert d'énergie vers les poissons, induite par exemple par une importance plus grande de la voie hétérotrophe considérée moins efficace. De plus, avec des données de densités énergétiques pour différentes classes de tailles de plancton, l'énergie d'entrée du modèle pourrait être modulée pour tenir compte par exemple d'une importance plus grande des petites classes de tailles attendues à l'avenir, supposées moins énergétiques. Ce type d'étude pourrait permettre de mieux appréhender les dynamiques futures de ces espèces qui présentent actuellement un intérêt économique fort.

V-9.3 La dynamique du phytoplancton par le biais de l'algorithme PHYSAT

Une de nos hypothèses pour expliquer la baisse de condition des petits pélagiques était une possible baisse de qualité de la communauté planctonique. Cela a déjà été observé dans certaines zones à upwelling par la mise en place de différentes chaines phyto et zoo-planctoniques, souvent supportées par des alternances de dominance entre dinoflagellés et diatomées (Tam et al., 2008; Van der Lingen et al., 2006). Ce genre d'alternance n'a pas été observé dans nos échantillons mais différentes études ont montré en méditerranée que cela pouvait se produire (Mercado et al., 2005, 2007) et induire des modifications dans la composition des acides gras des petits pélagiques comme observé au niveau saisonnier dans le Golfe du Lion (Pethybridge et al., 2014). Il n'est donc pas exclu que ce genre de phénomène ait eu lieu dans le Golfe du Lion, peut-être à un autre moment de l'année que le mois de Juillet étudié au cours de cette thèse. Une façon de creuser cette piste serait d'utiliser l'algorithme PHYSAT (analyse de la couleur de l'eau à partir d'images satellites) pour le Golfe du Lion (Alvain et al., 2005, 2008). Cet algorithme permet de décomposer le signal de chlorophylle satellitaire en différentes concentrations de pigments caractéristiques des grands groupes de phytoplancton (nanoeukaryotes, diatomées, *Synechococcus*, *Prochlorococcus*, *Phaeosystis* et coccolitophoridés). Cela permettrait d'avoir une information sur l'évolution de ces différents grands groupes phytoplanctoniques à l'échelle mensuelle depuis 1998 jusqu'à aujourd'hui dans le Golfe du Lion et de voir si des changements ont pu avoir lieu au moment des changements dans les populations de petits pélagiques. Cet algorithme a déjà été utilisé dans différentes zones ainsi qu'à large échelle (Alvain et al., 2005; Demarcq et al., 2012; Navarro et al., 2014) mais doit être calibré pour la zone du Golfe du Lion. Ainsi, des mesures des concentrations de pigments de surface sont effectuées en continu au cours des différentes campagnes océanographiques dans le Golfe du Lion à l'aide d'une pocket ferry box afin de pouvoir avoir un ensemble de données suffisamment conséquent pour pouvoir réaliser le calibrage de l'algorithme.

V-10 Conclusion

Ce travail de thèse a permis d'étudier un peu plus l'hypothèse d'un contrôle bottom-up, via le bon fonctionnement du réseau alimentaire planctonique, sur les populations de petits pélagiques dans le Golfe du Lion en étudiant plus en détail la variabilité environnementale et la dynamique planctonique, ces 20 dernières années, dans le Golfe du Lion ainsi qu'en Méditerranée nord-ouest de façon plus générale. Nous avons ainsi pu mettre en évidence des changements environnementaux dans le Golfe du Lion, aussi bien au niveau local avec une augmentation continue des upwellings depuis la fin des année 1990s en lien avec une intensification des vents de nord et nord-ouest ainsi que des fronts thermiques ou encore une baisse des apports en nutriments du Rhône depuis le début des années 1990s. Au niveau plus régional des changements dans la circulation atmosphérique du bassin caractérisés par une diminution de l'indice climatique WeMO ainsi que l'augmentation continue de la température de surface, observée dans la grande majorité du bassin méditerranéen. Ces changements dans leur ensemble apparaissent synchrones avec les modifications observées dans les populations de petits pélagiques au milieu des années 2000s, notamment leur baisse de taille et condition, et supportent donc l'hypothèse d'un contrôle bottom-up. Cette dernière n'a cependant pu être clairement confirmée par manque de données zoo-planctoniques sur le long terme et les faibles relations observées entre la communauté zoo-planctonique et la condition des poissons pour les données disponibles en été. La réponse du zooplancton (communauté décrite en grands groupes et taille) à des changements environnementaux sur le long terme a pu être étudiée en mer Ligure à la station du point B de 1995 à 2018. L'étude a montré une très grande stabilité interannuelle, aussi bien au niveau de la densité totale que de la composition taxonomique ou de la structuration en taille des individus malgré la variabilité dans les forçages. Un changement abrupt dans la densité et la taille du zooplancton en 2015 a toutefois été observé possiblement en relation avec une augmentation des températures et des changements dans les conditions hivernales impactant le mélange des masses d'eau. Ces résultats suggèrent donc une forte résilience du zooplancton aux perturbations environnementales sur la période étudiée. Cependant, l'analyse préliminaire du zooplancton entre le Golfe du Lion et le point B a révélé des différences dans la composition de la communauté zoo-planctonique des deux zones qui ont de ce fait pu présenter des dynamiques différentes au cours des deux dernières décennies. Plusieurs questions restent donc pour l'instant sans réponse quant à la variabilité du phyto- et zooplancton sur le plateau du Golfe du Lion, notamment sur les changements à long terme de la quantité et qualité du plancton. Plusieurs pistes ont été suggérées afin de combler certains manques dans les données et avoir une meilleure compréhension dans les relations entre plancton et poisson, notamment la mise en place d'un suivi de la communauté planctonique dès l'hiver, l'utilisation d'un filet à vide de maille plus petit afin de mieux couvrir les gammes de tailles de proies des poissons ou encore l'utilisation de l'algorithme PHYSAT afin d'avoir une meilleure idée de la composition et dynamique phytoplanctonique, bien que grossière, des années passées. Toutes ces propositions et analyses à venir devraient pouvoir apporter de nouvelles connaissances quant à la dynamique zoo-planctonique à long terme sur le plateau du Golfe du Lion que nous n'avons pas pu vraiment étudier jusqu'à maintenant et peut être enfin permettre de résoudre le mystère de la crise des petits pélagiques dans le Golfe du Lion.

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