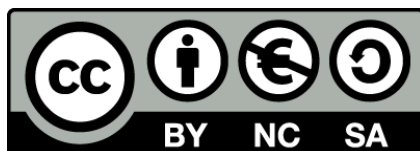




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Unravelling causes and consequences of marine biodiversity changes in East Atlantic and Mediterranean ecosystems

Carlos Veloy Dominguez



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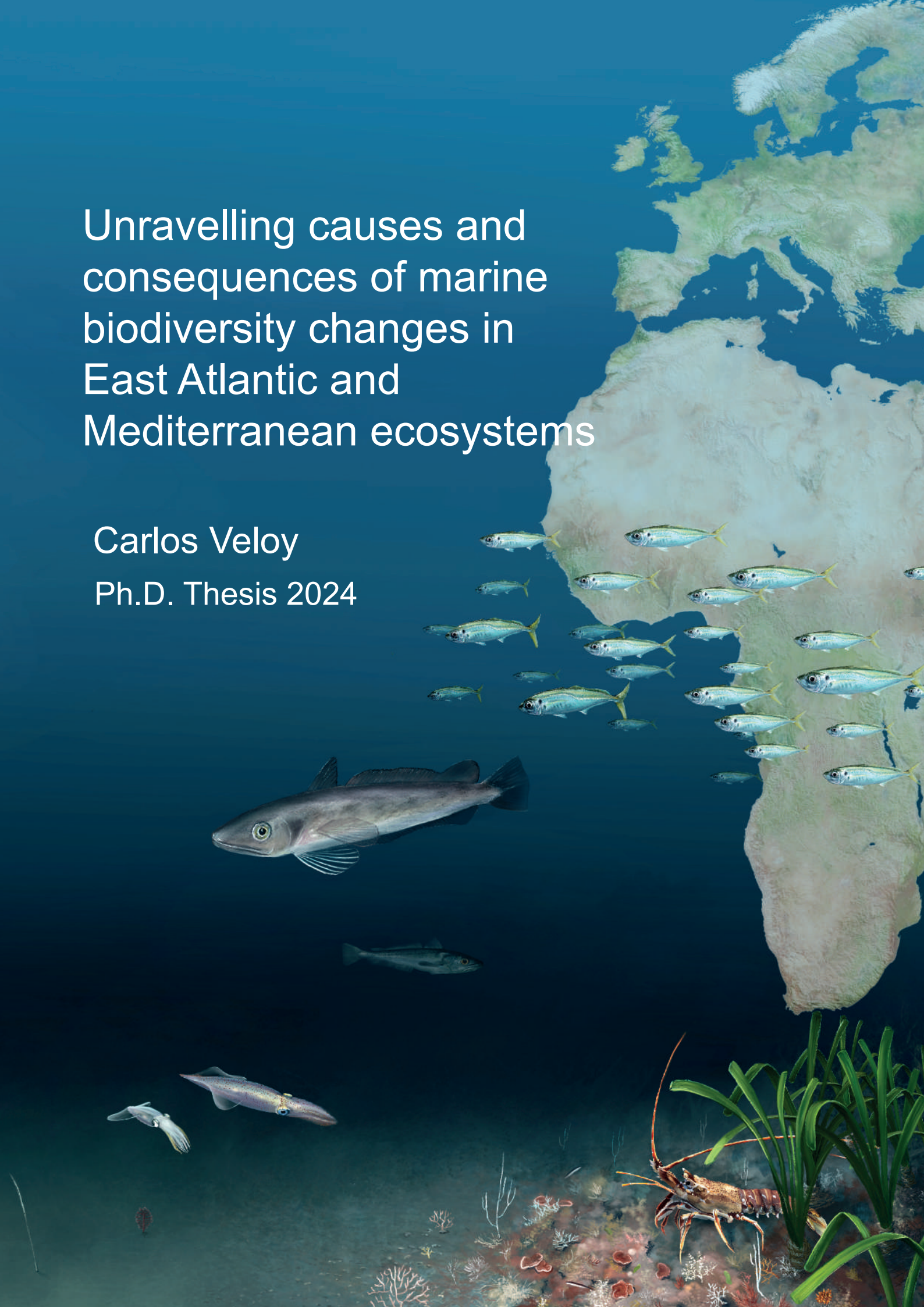
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Unravelling causes and consequences of marine biodiversity changes in East Atlantic and Mediterranean ecosystems

Carlos Veloy

Ph.D. Thesis 2024



Unravelling causes and consequences of marine biodiversity changes in East Atlantic and Mediterranean ecosystems

Carlos Veloy Domínguez

Thesis presented to obtain the Doctoral Degree by the University of
Barcelona (UB), Ph.D. Program in Marine Sciences

Ph.D. Advisors:

Dr. Marta Coll Montón
(Institut de Ciències del Mar, CSIC)

Dr. Jose Manuel Hidalgo Roldán
(IEO Palma de Mallorca)

Academic tutor:

Dr. Luis Cardona Pascual
(University of Barcelona, UB)

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*The whole of life is coming to terms with yourself and
the natural world. Why are you here? How do you fit in?
What's it all about?*

– Sir David Attenborough

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Abstract

Marine communities have been affected by multiple stressors increasing over the last decades, such as overfishing and climate change, resulting in negative effects throughout ecosystems. However, these impacts do not have homogeneous effects globally. Instead, systems across regions experience different impacts and rates of change shaped both by regional and global drivers. Furthermore, organisms within the same community can suffer from different impacts or respond to the same impact in distinct ways due to different ecological traits or life history strategies. These responses can include reductions or increments in the abundance of the populations of affected species, with the term "winners" often used to refer to organisms that may benefit from global change. Another common response, especially to warming, is a shift in distribution ranges. Distributional shifts can be latitudinal, migrating northwards, or vertical, moving towards deeper waters. Previous studies have addressed these processes mainly focusing on abundance and biomass displacements, but a holistic approach that considers several aspects of the ecosystem, such as production, biodiversity and trophic characteristics across different taxonomic groups, is still missing.

The main goal of this PhD was to analyse biodiversity changes in Atlantic and Mediterranean marine ecosystems using an integrative analysis of indicators, calculated from scientific bottom trawl surveys; in order to achieve a better understanding of ongoing spatiotemporal changes and the influence of environmental processes and anthropogenic pressures. Several types of indicators were used to analyse different aspects of ecosystem functioning and dynamics. To reflect the variety of responses, three taxonomic groups were analysed (fishes, cephalopods, and crustaceans) when calculating the indicators, in which several traits were included. Spatial variability was accounted both at the regional scale by comparing different subregions of the Western Mediterranean and at the oceanic scale with a study comparing the Barents Sea, North Sea, Western Mediterranean, and South African coast.

Complementary methods were applied for addressing several specific questions regarding the distribution and ecosystem dynamic. Analyses of subregional differences and temporal trends in the Western Mediterranean were performed using analysis of variance and linear regressions, respectively. Then, the relationship between ecological indicators

and environmental variables and fishing were studied using Generalised Additive Models (GAMs) to assess the status of alleged winner taxa in the Western Mediterranean and test the bathymetric changes of the indicators in the East Atlantic areas and the Mediterranean Sea.

Several regional patterns were detected in the Western Mediterranean, often following the latitudinal gradient of temperature within the area. However, interrupted or even discontinuous gradients were reported as well, due to localised influence in the environment and/or human impacts, especially on the North Catalan coast. In terms of taxa, fishes showed negative trends in most indicators, while cephalopods and crustaceans experienced more favourable results. Despite this, a detailed examination of cephalopods signalled the possibility of negative effects of increasing temperatures beyond certain thresholds. In the East Atlantic and Mediterranean Sea comparison, temporal changes in depth range were found in accordance with the Depth refuge hypothesis, although they did not follow large scale gradients but were rather influenced by the conditions and characteristics of individual regions.

Overall, this PhD reveals the existence of numerous spatial patterns and temporal trends regarding marine biodiversity and emphasises the unequal responses to both environmental drivers and anthropogenic pressures among the considered ecological groups and regions. These differences were further signalled by the variation and interrelationship of several indicators, often related to shifts in the community, such as the functional changes in the North Sea and Barents Sea, the eastward migrations occurring in South Africa, or the complex sub-regional combination of fishing and environmental impacts observed over the Western Mediterranean such as changes in relative contribution of fishes and invertebrate taxa. Overall, these results highlight that environmental change and fishing impacts can have notable consequences for ecosystem composition and changes in functioning at several scales. Results also show that the use of complementary ecological indicators and taxonomic groups can be a useful tool to further increase our understanding of the ongoing marine changes as well as their extent and implications.

Resumen

Las comunidades marinas se han visto afectadas por el incremento de múltiples presiones durante las últimas décadas, como la sobrepesca y el cambio climático, las cuales han generado numerosos efectos negativos en los ecosistemas. Sin embargo, dichos impactos no tienen efectos homogéneos a escala global, de hecho, los sistemas experimentan diferentes impactos y tasas de cambio por la influencia de distintas presiones regionales y globales a lo largo de las distintas regiones. Además, organismos dentro de la misma comunidad pueden sufrir diferentes impactos o responder al mismo impacto de distinta forma debido a diferencias en rasgos ecológicos o estrategias vitales. Estas respuestas pueden incluir reducciones o incrementos en la abundancia de las poblaciones de especies afectadas, siendo frecuentemente usado el término “ganadores” para referirse a aquellos organismos que puedan beneficiarse por el cambio global. Otra respuesta común, especialmente al calentamiento, son los cambios en los rangos de distribución. Estos cambios pueden ser latitudinales, migrando hacia el norte, o verticales moviéndose a aguas más profundas. Estudios previos han abordado dichos procesos enfocándose principalmente en desplazamientos de la abundancia y biomasa, pero aún hace falta una estrategia holística que considere varios aspectos del ecosistema tales como producción, biodiversidad y características tróficas en varios grupos taxonómicos.

El objetivo principal de este P.hD ha sido analizar los cambios de biodiversidad en áreas del Atlántico y Mediterráneo utilizando un análisis integrador de indicadores calculados con datos de campañas de arrastre científico; para conseguir un mejor entendimiento de los cambios espacio-temporales en estas zonas, considerando el impacto de las variabilidad ambiental y las presiones antrópicas. Se han usado varios tipos de indicadores para analizar diferentes aspectos del funcionamiento y dinámica de los ecosistemas. Para reflejar la variedad de respuestas y calcular dichos indicadores, se han considerado tres grupos taxonómicos (peces, cefalópodos y crustáceos), de los que se han analizado varios rasgos. La variabilidad espacial fue tomada en cuenta tanto a escala regional comparando diferentes regiones del Mediterráneo Occidental como a escala oceánica con un estudio comparando el Mar de Barents, el Mar del Norte, el Mediterráneo Occidental y la costa de Sudáfrica.

Para ello, se han aplicado métodos complementarios para abordar varias cuestiones específicas sobre la distribución y dinámica de los ecosistemas. Se realizaron análisis de diferencias subregionales y tendencias temporales en el Mediterráneo Occidental usando análisis de la varianza y regresiones lineales, respectivamente. Luego la relación entre diferentes indicadores ecológicos y variables ambientales y pesca se ha estudiado usando Modelos Aditivos Generalizados (GAMs) para determinar el estado de supuestos taxones ganadores en el Mediterráneo Occidental y testar los cambios batimétricos en áreas del Atlántico Este y el Mar Mediterráneo.

Se han detectado varios patrones regionales en el Mediterráneo Occidental, siguiendo el gradiente latitudinal de temperatura presente en el área. Sin embargo, en muchos casos se han descrito gradientes interrumpidos e incluso discontinuos, debido a la variabilidad local de impactos ambientales y/o humanos, especialmente en el norte de la costa catalana. En términos de taxones, los peces han mostrado tendencias negativas en la mayoría de indicadores, mientras que cefalópodos y crustáceos han experimentado resultados más positivos. A pesar de esto, un examen detallado de los cefalópodos ha señalado la posibilidad de efectos negativos del incremento de temperaturas una vez superados ciertos límites térmicos. En la comparación del Atlántico Este y el Mar Mediterráneo se han descrito cambios temporales en el rango batimétrico para varios indicadores de acuerdo con la Hipótesis de Refugio Profundo, aunque los resultados han mostrado que en lugar de seguir gradientes a gran escala los gradientes están influenciados por condiciones y características de las regiones individuales.

En resumen, este Ph.D. ha revelado la existencia de numerosos patrones espaciales y tendencias temporales sobre la biodiversidad marina enfatizando las respuestas desiguales a drivers ambientales y presiones antropogénicas en los distintos grupos ecológicos. Dichas diferencias han sido también señaladas por la variación e interrelación entre varios indicadores, muchas veces relacionados con cambios en la comunidad, como los cambios funcionales en el Mar de Barents y el Mar del Norte, las migraciones hacia el este ocurridas en Sudáfrica o la compleja combinación subregional de impactos pesqueros y ambientales observada en el Mediterráneo Oeste como los cambios en las proporciones de peces e invertebrados. Estos resultados subrayan que el impacto del cambio ambiental puede tener consecuencias notables para la composición ecosistémica a varias escalas. Los resultados han mostrado también que el uso de indicadores

ecológicos y grupos taxonómicos puede ser una herramienta útil para un mayor entendimiento sobre los cambios que ocurren actualmente en el medio marino, así como su extensión e implicaciones.

Resum

Les comunitats marines s'han vist afectades per l'increment de múltiples pressions durant les darreres dècades, com la sobrepesca i el canvi climàtic, les quals han generat nombrosos efectes negatius en els ecosistemes. Tanmateix, aquests impactes no tenen efectes homogenis a escala global; de fet, els sistemes experimenten diferents impactes i taxes de canvi per la influència de diferents pressions regionals i globals al llarg de les diferents regions. A més, organismes dins de la mateixa comunitat poden patir diferents impactes o respondre al mateix impacte de manera diferent a causa de diferències en trets ecològics o estratègies vitals. Aquestes respostes poden incloure reduccions o increments en l'abundància de les poblacions d'espècies afectades, utilitzant-se freqüentment el terme "guanyadors" per referir-se a aquells organismes que poden beneficiar-se del canvi global. Una altra resposta comuna, especialment a l'escalfament, són els canvis en els rangs de distribució. Aquests canvis poden ser latitudinals, migrant cap al nord, o verticals movent-se a aigües més profundes. Estudis anteriors han abordat aquests processos enfocant-se principalment en desplaçaments de l'abundància i biomassa, però encara manca una estratègia holística que consideri diversos aspectes de l'ecosistema com ara producció, biodiversitat i característiques tròfiques en diversos grups taxonòmics.

L'objectiu principal d'aquest doctorat ha estat analitzar els canvis de biodiversitat en àrees de l'Atlàntic i el Mediterrani utilitzant una anàlisi integradora d'indicadors, calculats amb dades de campanyes d'arrossegament científic, per aconseguir una millor comprensió dels canvis espaciotemporals en aquestes zones, considerant l'impacte de la variabilitat ambiental i les pressions antròpiques. S'han utilitzat diversos tipus d'indicadors per analitzar diferents aspectes del funcionament i dinàmica dels ecosistemes. Per reflectir la varietat de respostes i calcular aquests indicadors, s'han considerat tres grups taxonòmics (peixos, cefalòpodes i crustacis), dels quals s'han analitzat diversos trets. La variabilitat espacial s'ha tingut en compte tant a escala regional comparant diferents regions del Mediterrani Occidental com a escala oceànica amb un estudi comparant el Mar de Barents, el Mar del Nord, el Mediterrani Occidental i la costa de Sud-àfrica.

Per a això, s'han aplicat mètodes complementaris per abordar diverses qüestions específiques sobre la distribució i dinàmica dels ecosistemes. S'han realitzat anàlisis de diferències subregionals i tendències temporals en el Mediterrani Occidental utilitzant

anàlisis de la variància i regressions lineals, respectivament. Després, la relació entre diferents indicadors ecològics i variables ambientals i pesca s'han estudiat utilitzant Models Additius Generalitzats (GAMs) per determinar l'estat de suposats taxons guanyadors en el Mediterrani Occidental i testar els canvis batimètrics en àrees de l'Atlàntic Est i el Mar Mediterrani.

S'han detectat diversos patrons regionals en el Mediterrani Occidental, seguint el gradient latitudinal de temperatura present a l'àrea. Tanmateix, en molts casos s'han descrit gradients interromputs i fins i tot discontinus, a causa de la variabilitat local d'impactes ambientals i/o humans, especialment a la costa catalana. En termes de taxons, els peixos han mostrat tendències negatives en la majoria d'indicadors, mentre que cefalòpodes i crustacis han experimentat resultats més positius. Malgrat això, un examen detallat dels cefalòpodes ha assenyalat la possibilitat d'efectes negatius de l'increment de temperatures una vegada superats certs límits tèrmics. En la comparació de l'Atlàntic Est i el Mar Mediterrani s'han descrit canvis temporals en el rang batimètric per a diversos indicadors d'acord amb la Hipòtesi de Refugi Profund, encara que els resultats han mostrat que en lloc de seguir gradients a gran escala, els gradients estan influenciats per condicions i característiques de les regions individuals.

En resum, aquest doctorat ha revelat l'existència de nombrosos patrons espacials i tendències temporals sobre la biodiversitat marina, destacant les respostes desiguals a drivers ambientals i pressions antròpiques en els diferents grups ecològics. Aquestes diferències també han estat assenyalades per la variació i interrelació entre diversos indicadors, moltes vegades relacionades amb canvis en la comunitat, com els canvis funcionals en el Mar de Barents i el Mar del Nord, les migracions cap a l'est ocorregudes a Sud-àfrica o la complexa combinació subregional d'impactes pesquers i ambientals observada al Mediterrani Occidental com els canvis en les proporcions de peixos i invertebrats. Aquests resultats subratllen que l'impacte del canvi ambiental pot tenir conseqüències notables per a la composició ecosistèmica a diverses escales. Els resultats han mostrat també que l'ús d'indicadors ecològics i grups taxonòmics pot ser una eina útil per a una major comprensió sobre els canvis que esdevenen actualment en el medi marí, així com la seva extensió i implicacions.

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Chapter 1. General Introduction

1.1. Global change and marine communities

1.1.1 Global change effects on marine communities

Change has been a constant throughout the history of life. Variations of climate, geology and even the evolution of species, always had profound consequences on the species life history, the species composition as well as the interactions and functions taking place in the ecosystems (Mittelbach et al., 2007). However, during the last decades, the planet has experienced numerous rapid changes of anthropogenic origin that have been affecting the Earth and ocean biodiversity and ecosystems at several levels of organisation (Mantyka-Pringle et al., 2015; Díaz et al., 2019b; ONU, 2021; Jaureguiberry et al., 2022; Isbell et al., 2023). These changes include populations of species becoming extinct at several scales (Hooper et al., 2005), or species shifts that span several kilometres, to changes at the ecosystem level (Walther et al., 2002).

These impacts have contributed to a global biodiversity crisis as showcased by both trends and state of several biodiversity metrics (Jackson et al., 2001; Butchart et al., 2010; Tittensor et al., 2014; Díaz et al., 2019b, 2019a). For example, 30% of taxa are either endangered or extinct since the XVIth century according to global estimates (Isbell et al., 2023). Rates of terrestrial biodiversity loss are, on average, higher than rates of marine biodiversity loss, although one of the highest percentages of loss was estimated to be on the Pacific coast of Central America (where it is estimated to be between 48% up to 55%) (Isbell et al., 2023).

Over the planetary scale, climate change is becoming the main driving force of these changes, which can influence and even radically change the functioning and structure of ecosystems (Poloczanska et al., 2016; Jaureguiberry et al., 2022). Ocean warming, for example, can lead up to displacements of fauna towards cooler environments, with prominent examples at high latitudes of the northern hemisphere (Frainer et al., 2017; Pecuchet et al., 2017; Gordó-Vilaseca et al., 2023a).

Other factors to consider are human impacts related to the use and exploitation of the natural resources, often acting at regional and local scales. In the marine environment, fishing and its increasing impact has been a very influential factor to consider since ancient times (Jackson et al., 2001; Lotze et al., 2006), not only due to the extraction of individuals of targeted species but also because of other effects such as by-catch of non-target species and discards, or benthic habitat loss due to high-impact fishing activity such as the impact of the bottom trawling on the habitat structure (ONU, 2021; FAO, 2022). Fishing has also been historically associated to depletion of demersal and pelagic populations due to overfishing, having notable consequences at local and regional scales (Rosenberg et al., 2004; Juan-Jordá et al., 2011; Roux et al., 2013; Ellingsen et al., 2015). This is especially relevant for species with high trophic levels or long lived species due to their low population growth (Shackell et al., 2010; McKeon et al., 2024).

These factors are even more prevalent on semi-closed systems, which are hotspots of cumulative impacts such as the Mediterranean Sea (Coll et al., 2012; Cooley et al. 2022) and, alongside high latitude seas nearing the Arctic, are some of the most vulnerable systems to environmental and climate change (Rantanen et al., 2022; EEA, 2023). Because these processes can alter the ecosystem dynamics at several scales, untangling these ongoing changes and their effects is needed to develop better strategies for the management of marine sources and ecosystems through an integrative and holistic approach.

1.1.2 Gradients and regional effects

The understanding of species distributions and hierarchical organisation has been the main focus of biogeography. One of the conclusions of this field is that biodiversity organisation follows gradients based on several environmental variables at different scales both in land and at sea (Worm and Tittensor, 2018). These organisational patterns are usually related to the physiology of organisms and are influenced by global gradients, such as altitude, depth and temperature, or the availability of resources, like light and primary production (Costello and Chaudhary, 2017; Sharifian et al., 2020). For instance, species richness in the tropics tends to be higher than in northern areas due to warmer temperatures (Figures 1.1 and 1.2a) that allow the development of more diverse communities (Hillebrand, 2004; Mittelbach et al., 2007).

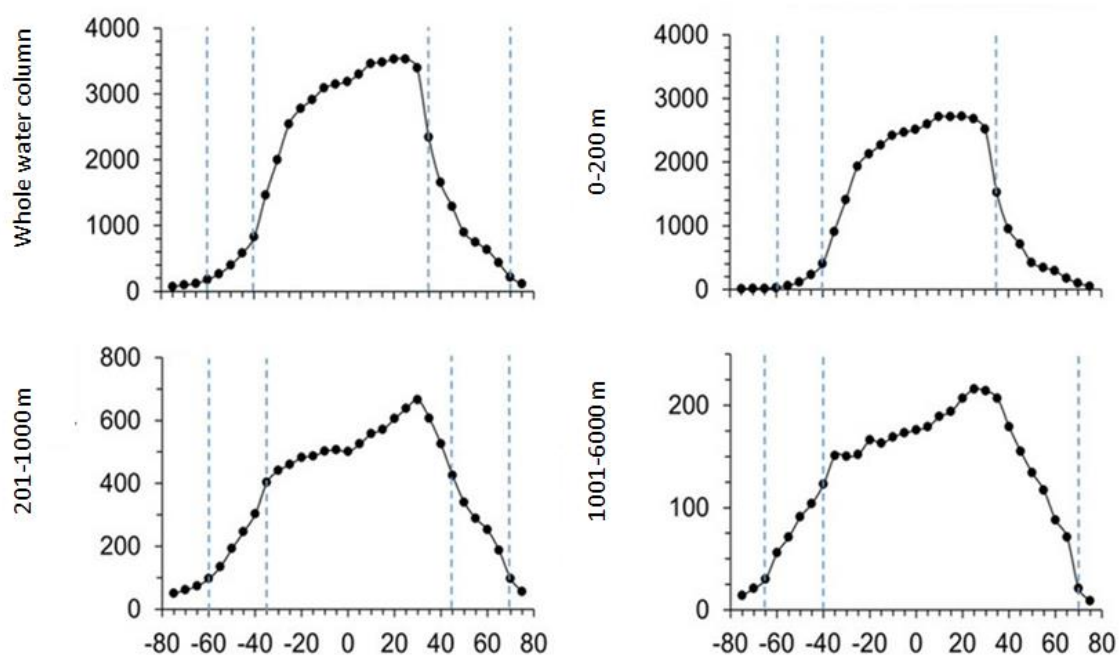


Figure 1.1: Latitudinal gradient of species richness of marine fishes through different depth ranges. Source: Adapted from Lin et al. (2023)

In terrestrial ecosystems, species also distribute at different heights within their respective realms, high altitude ecosystems are less rich in species than lowland ones due to harsher conditions and less availability of food. In the ocean, the distribution of the community through the bathymetric gradient is analogous to altitude on land (Cure et al., 2021; Lin and Costello, 2023). Ecosystems found in the deep waters are normally less rich in species than those at shallow depths (Costello et al., 2010; Costello and Chaudhary, 2017) (Figure 1) as temperature decreases, pressure increases, and primary production becomes negligible below the photic zone.

At smaller scales, however, diversity gradients can show heterogeneous gradients due to regional differences in the environment (Costello et al., 2010; Narayanaswamy et al., 2013). One example of this can be found in the Mediterranean Sea, where the Eastern Basin is characterised by higher temperatures and lower primary production while the Western Basin features colder, and more productive waters (Estrada, 1996; Coll et al., 2010; Danovaro et al., 2010) (Figure 1.2b). As a result, the general trend is that the Eastern Mediterranean waters show less biodiversity than those more adjacent to the Atlantic Ocean following an east-west longitudinal gradient (Gaertner et al., 2007; Coll et al., 2010; Keller et al., 2016). However, given strong environmental complexity at sub-regional level, one could expect small-scale differences in the biodiversity patterns (Ayata et al., 2018).

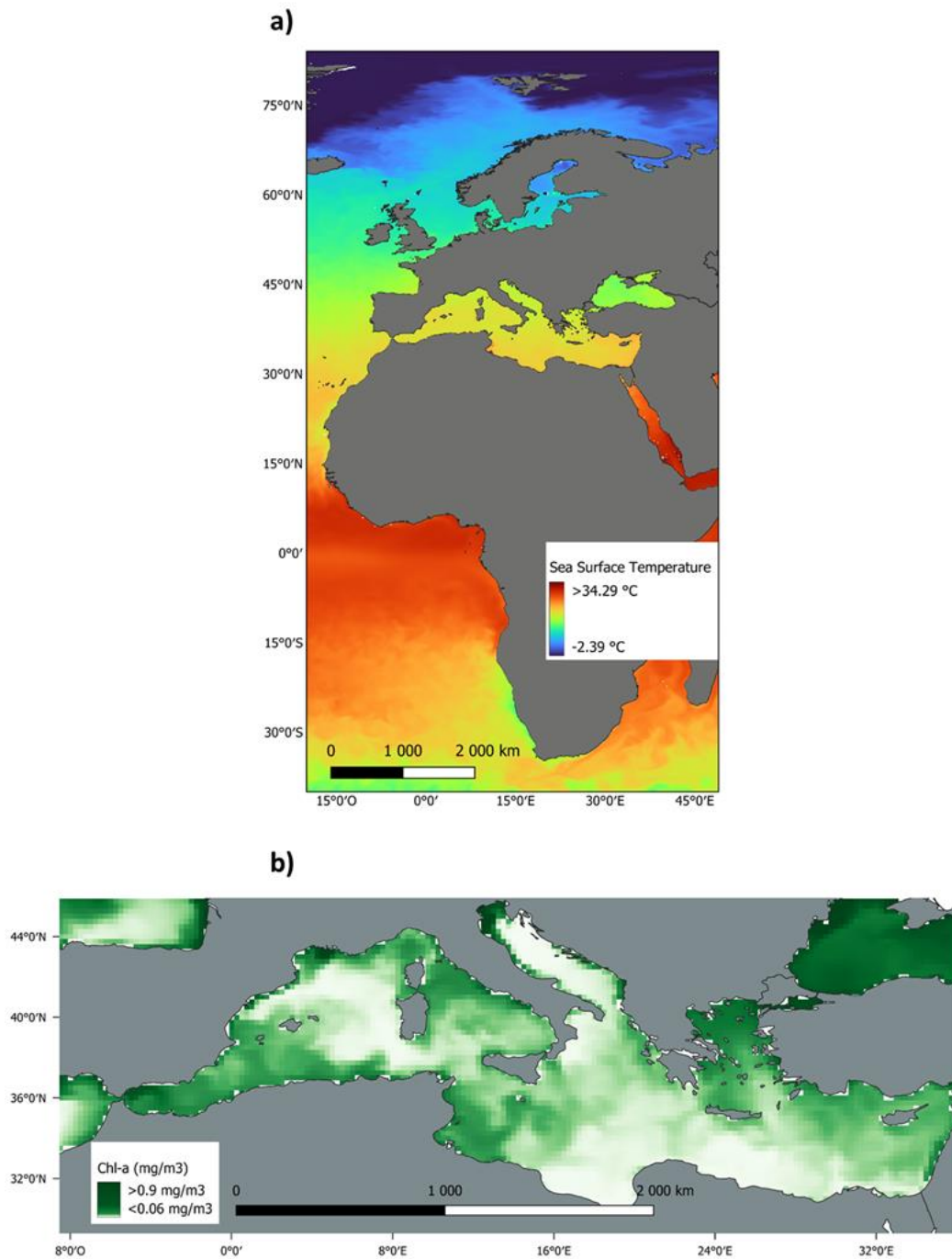


Figure 1.2: Examples of the spatial distribution of environmental variables affecting biodiversity gradients at large and small scales. a) Latitudinal gradient of Sea Surface Temperature in May 2020, and b) the regional variation of primary production in the Mediterranean Basin during May 2020. Both maps have been done using data from the following COPERNICUS products GLOBAL_MULTIYEAR_PHY_001_030 and GLOBAL_MULTIYEAR_BGC_001_029 (COPERNICUS, 2021). Source: Own production.

In the context of global change, it is important to acknowledge these regional differences, as current baseline status plays a role in the response of the communities to certain impacts and their sensitivity and vulnerability to cross-scale stressors. Arctic areas, for instance, have been shown to warm four times faster than other areas due to polar amplification (Rantanen et al., 2022), and at the same time their overall richness has increased due to northward migrations of boreal species (Fossheim et al., 2015; Gordó-Vilaseca et al., 2023b, 2023a). In the case of more direct human impacts, the distribution of human populations as well as their activities play a role in species distribution and thus the regional variations of the communities (Farriols et al., 2020).

Overall, the scientific knowledge gained through decades of biodiversity studies evidence that it is important to take into account regional disparities as well as large scale gradients of both environmental factors and human activities to know the distribution of current fauna, the impacts it may face as well as the responses of the community to the incoming and increasing changes.

1.1.3 Winners and losers of change

Even within the same ecosystem, communities, assemblages and species can experience the same changes differently. Biological traits as well as the differences in human pressures can result in differential modifications of assemblages, communities and ecosystems (Pecuchet et al., 2017; Beukhof et al., 2019a).

Some taxa may be negatively affected by certain factors because their life history traits and physiology make them more vulnerable. For instance, short lived species tend to be more sensitive to unpredictable seasonal fluctuations than species with longer life cycles (Winnemiller and Rose, 1992; Arvanitidis et al., 2002; Forsythe, 2004; Otero et al., 2009; Pecuchet et al., 2017), but also more prone to faster recoveries. When it comes to human impacts, both the susceptibility of being targeted by certain activities (such as fishing) as well as their ability to cope with an impact can hinder species recovery. For example, those with slower life cycles such as most elasmobranchs often suffer higher impacts as their changes trigger longer and more persistent impacts that are more difficult to reverse (e.g. trophic cascades; Jackson et al., 2001; McKeon et al., 2024). Therefore, traits such as larger maximum size with higher age at maturity, often corresponding to predators, have been shown to be related to declines in response to fishing effort (Jennings et al., 1998). The degree of this effect is also dependent on factors such as scale, as fishing is highly variable in space and some species within the community display different behavioural movement traits (McKeon et al., 2024).

Relevant differences in the recovery potential occur between fish versus cephalopods. Compared to fishes, cephalopods are fast growing species and tend to have shorter lifespans with smaller ages at maturity, allowing them to experience higher turnover rates (Pech and Jackson, 2008; Guerra et al., 2010). Fishing has disproportionately affected the trends of both taxa, both directly by population reduction of fishes and indirectly due to

the effects of this mortality within the community. For example, the decrease of cephalopods' main fish competitors and predators allow these mollusks to thrive (Hastie et al., 2009; Staudinger et al., 2013; Doubleday et al., 2016; Quetglas et al., 2016) (Figure 1.3). However, this initial advantage might not persist, as it has been shown that warming can negatively affect certain aspects of cephalopod physiology and ecology (Pecl and Jackson, 2008; Pierce et al., 2008; Schickele et al., 2021). Also, the high demand and exploitation of these species by certain fisheries could pose a bigger problem when coupled with the effect of temperature increase on their dynamics (Hunsicker et al., 2010; Ospina-Alvarez et al., 2022). Therefore, the general understanding of cephalopods as global winners of climate change must be challenged and investigated under a more complete and broad ecosystem perspective.

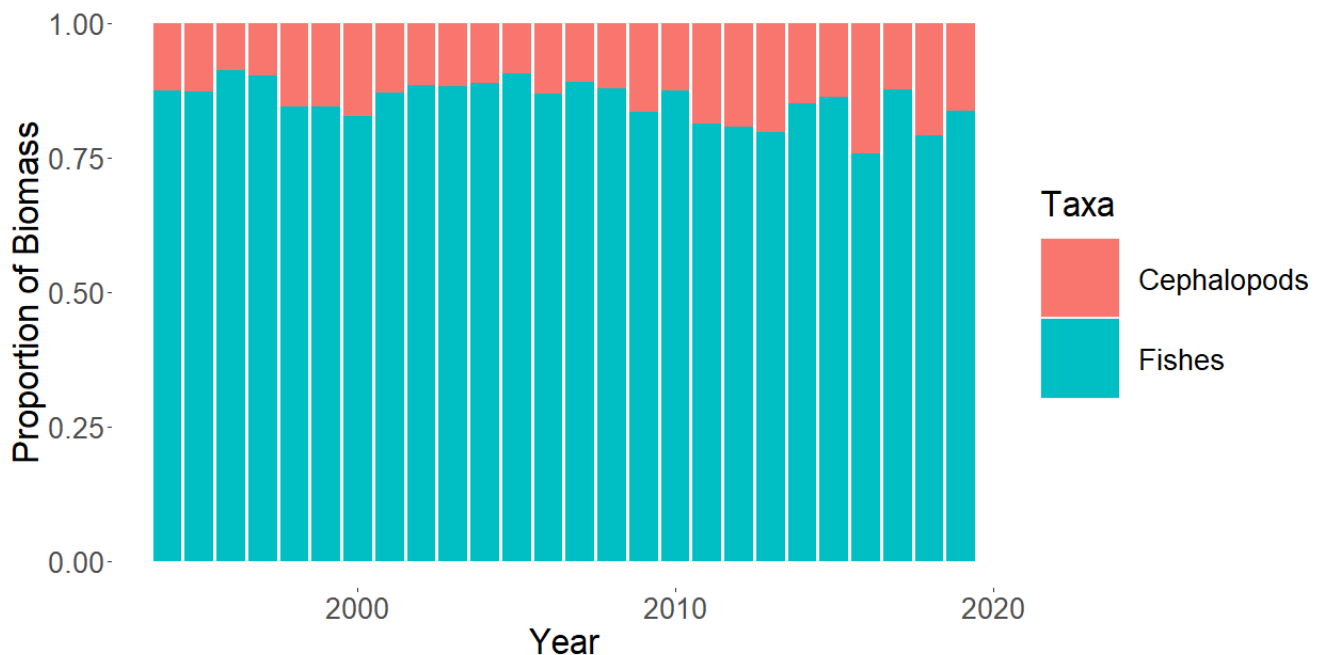


Figure 1.3: Proportion of biomass of cephalopods and fishes in the Western Mediterranean basin, standardised by the sum of biomass of the two taxa groups. Source: Own production with data from MEDITS 1994-2019 - GSA01, GSA06 and GSA07.

1.1.4 Range changes and the “Depth refuge” hypothesis

Increasing pressures can also result in movements of the different species to escape the effects of these stressors. Warming, for instance, has been shown to be highly influential on the distributional shifts. In the marine environment, these shifts match the changes in temperature better than similar displacements recorded in terrestrial communities (Lenoir et al., 2020). Less availability of thermal microrefugia at sea compared to on land, as well as the potential synergic effect with other drivers, appear to be some of the causes behind this pattern (Pinsky et al., 2019; Lenoir et al., 2020). Most of these movements tend to be

latitudinal, with species from southern latitudes migrating towards areas with cooler environments as temperatures surpass their physiological limits (Sunday et al., 2012). In this case, source-sink dynamics are established between warmer, and frequently tropical areas, and colder, temperate or polar areas, where species gains from foreign areas are faster than local species losses (Antão et al., 2020; Gordó-Vilaseca et al., 2023b).

In northern areas, such as the North Sea, it has been consistently shown increases in species richness at both local and regional level due to the northward migrations of southerner species, whose range expansion has been shown to be closely related to the increase in surface temperature (Hiddink and ter Hofstede, 2008). Several species from usually warmer biogeographic areas have shown sudden increases in abundance and ranges since the mid-1990s (Beare et al., 2004), while other species with colder temperature preferences like plaice have experienced latitudinal shifts within the North Sea (Engelhard et al., 2011) (Figure 1.4a).

However, in highly spatially structured environments such as the Mediterranean Sea (Ayata et al., 2018), unexpected distribution shifts can be observed in responses to regional impacts (Sanz-Martín et al., 2024). That is, while meridionalization (i.e. towards north displacement) is regionally expected in the whole region, generalised south and southwest shifts movements of some species are observed in some areas (Sanz-Martín et al., 2024).

Latitudinal displacements are not the only change that has been documented. Another way for marine species to avoid the effects of stressors is to displace towards deeper waters, where both exploitation and temperature are frequently lower. It is estimated that this deepening has been occurring at rates of several metres per decade, partly due to climate change (Dulvy et al., 2008; Lenoir and Svenning, 2015) (Figure 1.4b), while the interacting effect with fishing impact is often difficult to disentangle (Frank et al., 2018,2019; Baudron et al., 2019). On semi-closed systems, such as the Mediterranean Sea, this type of displacement would be expected as the presence of landmass constricts shifts toward northern and cooler areas (Ben Rais Lasram et al., 2010; Chaikin et al., 2022; Sanz-Martín et al., 2024).

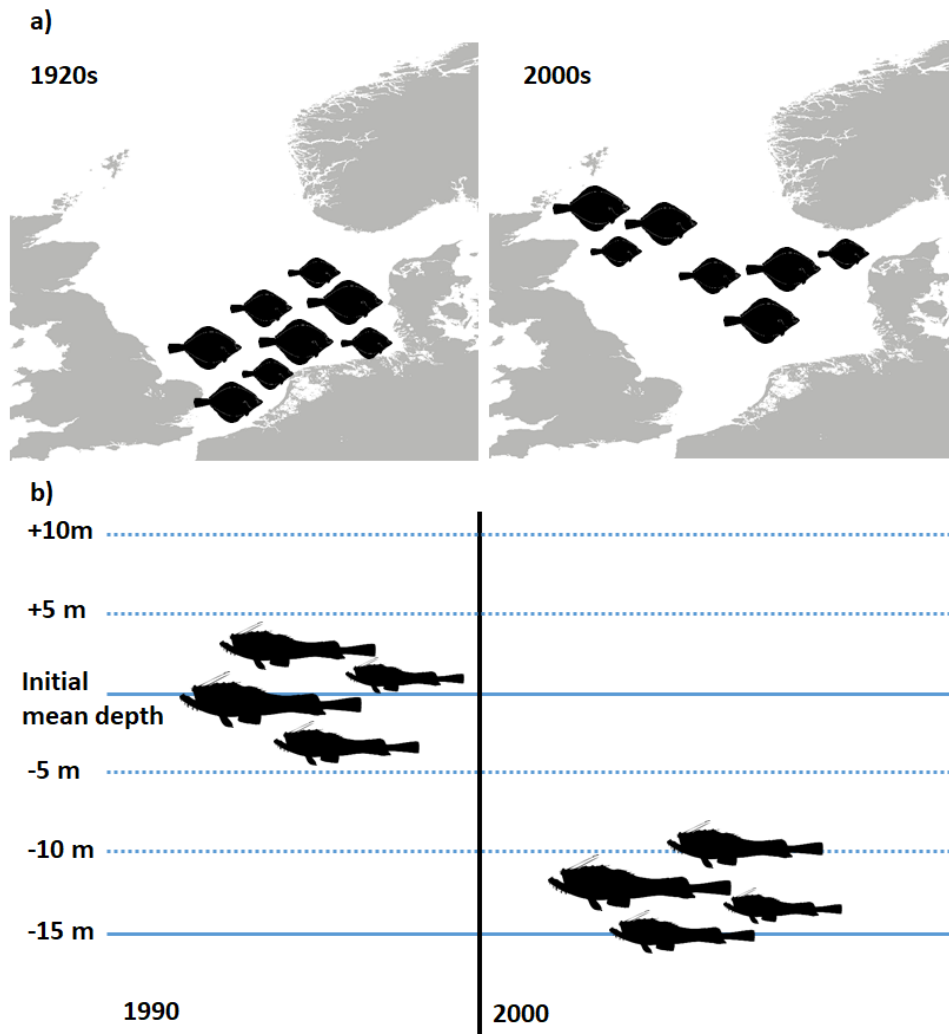


Figure 1.4: Illustrative representation of both types of distribution shifts. On a) latitudinal shifts showing the northward shift of plaice on the North Sea based on results of Engelhard et al., (2011). On b) vertical shifts exemplified by the deepening of anglerfish as reported by Dulvy et al. (2008). Source: Own production.

This bathymetrical shift is the main idea of the Depth refuge hypothesis, which postulates that populations may migrate towards deep waters that can act as a shelter against negative conditions in response to detrimental environmental change or even human impacts (Tyler et al., 2009; Lindfield et al., 2016; Pereira et al., 2018). This is similar to other observed shifts in terrestrial communities, where species move towards less optimal areas as refuge. These areas can be at higher altitudes or even upstream on rivers as it is the case of the Eurasian otter *Lutra lutra* (Ruiz-Olmo et al., 2011; Martínez-Abraín and Jiménez, 2016).

Deep water environments can act as a buffer for environmental conditions as opposed to the surface and they can play the role of “refuge” from harsh environmental changes at the surface (Smith et al., 2014; Pereira et al., 2018; Chaikin et al., 2022) or due to human activity (Petit et al., 2022). These changes can also affect at the level of intraspecies

distribution, for example, with older and larger individuals being abundant in deeper waters as they are less exploited (Lindfield et al., 2014; Audzijonyte and Pecl, 2018; Frank et al., 2018; Sbragaglia et al., 2021). This can have tremendous implications in the population dynamics as removal of BOFFF (Big Old Fat Fecund Female fish) individuals due to fishing can cause reduction of larval productivity and age truncation, which is associated with the increase of environmental sensitivity and less resilient populations (Hidalgo et al., 2011, 2012; Hixon et al., 2014). Distribution changes to deeper areas may be limited by the biological constraints of the species as well as oceanographical limits, such as the end of the continental shelf or the presence of landmass acting as a barrier for latitudinal shifts on semi closed systems (Ben Rais Lasram et al., 2010; Cure et al., 2021; Chust et al., 2024). Other seascape features also contribute to this limitation in movement, especially with bathymetric variation, for example food availability or oxygen concentration, which already establish strong gradients of diversity (Costello and Chaudhary, 2017). These barriers may become a hindrance as the displacement from formerly suitable areas to new ones can eventually result in contraction of spatial ranges and even local extinctions (Chaikin and Belmaker, 2023; Chaikin et al., 2024).

1.2. How to measure ecological change

Ecological indicators can be a useful tool for biodiversity and ecosystem assessments (Rochet and Trenkel, 2003; Tittensor et al., 2014; Shannon and Coll, 2017) and are one of the main basis of the ecosystem-based management approach (Shin and Shannon, 2010; Shin et al., 2010; Lockerbie et al., 2020). These can facilitate the monitoring of the state and evolution of communities and different aspects within them, including composition or trophic ecology (Shannon et al., 2014), as well as facilitate the communication with managers, stakeholders and policy makers (Shin et al., 2010; Shannon et al., 2014; Lockerbie et al., 2020). The combination of different metrics to study the evolution of marine ecosystems provides a unique opportunity to perform a more integrative analysis of the past and current state (Coll et al., 2016). As an illustrative example, the requirements used by the Indiseas project (Shin and Shannon, 2010; Shin et al., 2010, 2012; Bundy et al., 2012) became a reference to establish the criteria to select indicators for integrative analyses. Overall, they must *i)* be based on ecological processes, *ii)* be sensitive and responsive to the specific pressure investigated (such as climate or fishing), and *iii)* to meet strategic criteria such as being easy to interpreter, and communicate (the link between fishing and its effect on the indicator could be clearly understandable).

1.2.1 Biodiversity indicators

For the study of biodiversity, a reference study in terms of methodologies and indicators are the ones based on the BioTIME initiative (Dornelas et al., 2014). BioTIME is a curated database of biodiversity time series that includes data from marine, freshwater and terrestrial systems in order to optimise the estimation of biodiversity metrics (Dornelas et al., 2018). The studies based on BioTIME consider the different aspects of biodiversity, such as alpha biodiversity (the amount of species present within a system) and beta biodiversity (the dissimilarity of species within an area or, in the case of BioTIME, time period) (Figure 1.5a). Despite the global loss of biodiversity (which would correspond to gamma diversity), studies of species richness at local, biogeographic and meta-community scales have often reported no net loss of species richness but rather stable values through time or even increases (McGill et al., 2015). On another hand, increases in the change of ecosystem composition (temporal beta diversity) have been observed with time both locally and globally (Dornelas et al., 2014; Shackell et al., 2012). However, and despite the importance of change in ecosystem composition in terms of alteration of functionality and ecosystem services, as well as the quick rates of change in marine ecosystem (Blowes et al., 2019), beta diversity has not been as well studied as alpha diversity or the regional gamma diversity, especially when it comes to temporal beta diversity.

The beta diversity indicator has two components reflecting the different sources of change in a set of species (Figure 1.5b) (Baselga, 2010): the turnover and the nestedness. The turnover represents the change in identity of the species present in a community, often associated with replacements or invasions. On the other hand, nestedness (or subsetting) represents the loss or addition of species, usually due to extinctions. Beta diversity, and turnover in particular, has been found to be generally sensitive to environmental change (Baselga, 2010; Vale et al., 2021).

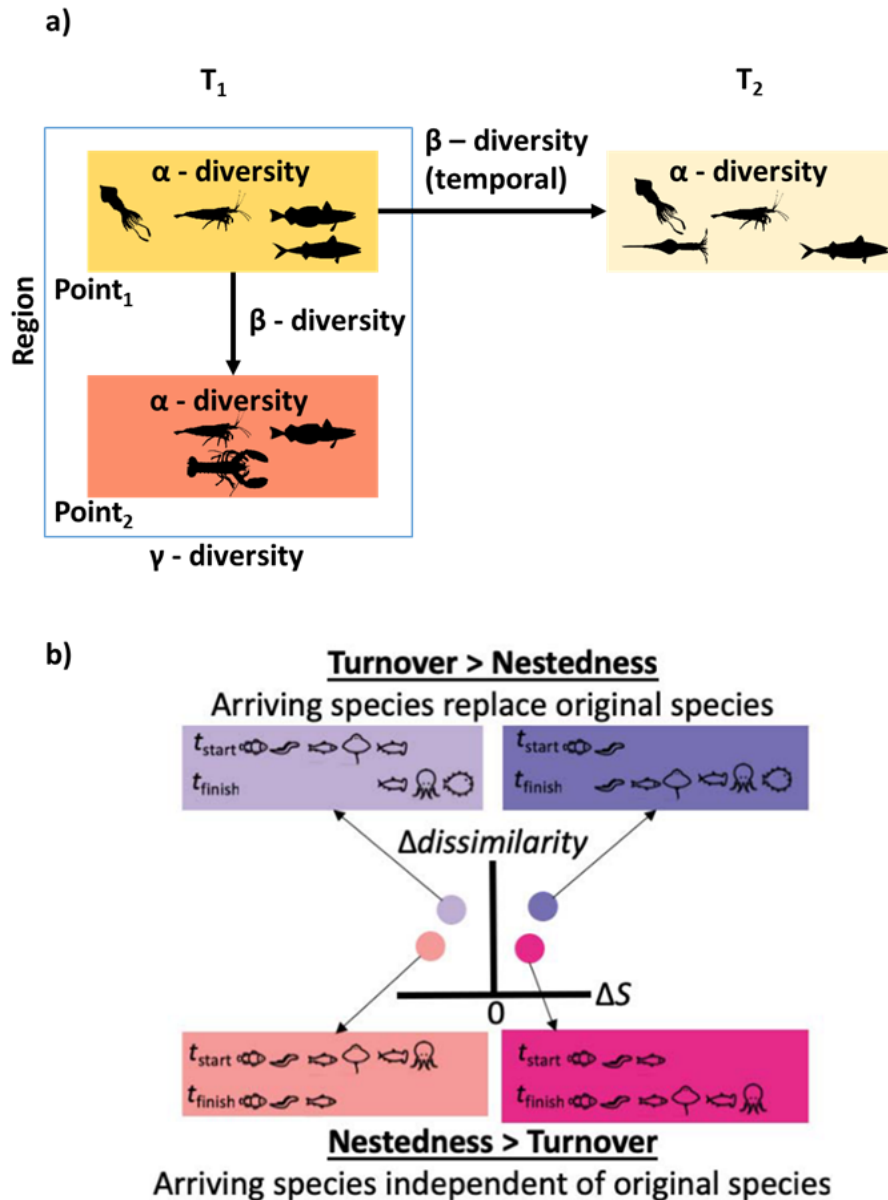


Figure 1.5: Schematic of the different types and components of biodiversity. On a) representation of the three main types of biodiversity, gamma (γ), alpha (α) and beta (β) both in the traditional sense as well as temporal beta diversity. T_1 and T_2 represent different times for the same spatial points. On b) the different components of beta diversity as represented by Blowes et al. (2019) in the context of changes in dissimilarity and species richness. Source: Own production and Blowes et al. (2019).

To account for both the amount of species as well as the overall composition of the ecosystem, it is important to use both traditional species richness (McIntosh, 1967) as well as the temporal beta diversity (Jaccard index) in accordance to the BioTIME methodology (Blowes et al., 2019; Dornelas et al., 2014). Additional indicators can also be used to examine the evenness within the ecosystems using, for example, the Shannon index (Shannon, C.E., Weaver, 1949) and the Pielou index (Pielou, 1966).

1.2.2 Biomass and trophic level indicators

In addition to biodiversity indicators, other indicators have been proposed based on biomass or on trophic levels (Shannon et al., 2014; Coll et al., 2016) and are needed to assess the production as well as the proportion of different groups within the communities.

Biomass-based indicators include total biomass, mean size (using weight as a proxy of size) (Shin et al., 2018) and some trait-dependent ratios such as the biomass of predatory organisms, or *Bpred* (the biomass ratio of species that were considered as predators within one taxon). *Bpred* in particular is an important metric, as the predator species are usually the most affected by pressures such as fisheries (Ferretti et al., 2008). Thus, this indicator has been very sensitive to the impact of fishing due to their life history. It is also an ecologically important indicator due to the weight of predator species on the functioning of the ecosystem, often being keystone species.

Trophic level-based indicators can track different portions of a community attending changes in the relative contribution of different trophic components and levels with space and time. For example, the Trophic Level of the surveyed community (TLc) documents changes on the whole community under monitoring efforts (Shannon et al., 2014). This indicator can also be calculated by filtering for organisms over specific trophic levels such as 3.25 (TL3.25) and 4 (TL4), which corresponds mostly to larger predators. Interrelationship between the different trends of trophic level indicators have been used to document scenarios of fishing exploitation in different areas (Shannon et al., 2014). For example, it is expected that fishing down scenarios would feature declines in these three metrics of trophic level (Pauly et al., 1998). Meanwhile, fishing up and fishing through scenarios can influence the trends differently due to the respective addition of low TL species (Stergiou and Tsikliras, 2011) or progressive addition of high TL species (Essington et al., 2006). Because of this, trophic levels of the whole community and above 3.25 are expected to show stability with fishing through or decline with fishing up processes (Shannon et al., 2014).

1.2.3 Integrative analysis with ecological indicators

Several studies in the literature have evidenced the fact that one indicator is not enough to describe the main changes that marine communities are going through. It is now well accepted that a series of complementing indicators need to be assessed (Shin et al., 2012; Coll et al., 2016; Lockerbie et al., 2020).

For example, the Indiseas project and following studies analysed several ecosystems from temperate, tropical and polar climates using a wide selection of indicators that allowed an in-depth examination of the current state, evolution and pressures these systems were

facing (Shin et al., 2012; Coll et al., 2016). This was achieved by looking at indicators with different ecological significance and the aid of experts in the studied systems for accurate interpretations of the results. As another example, Lockerbie et al. (2016, 2017, 2020) also used several ecological indicators as well as others derived from landings to establish the effect of fisheries and environmental variability on the community by using decision trees applied to several systems such as the Benguela system and the North Catalan Sea.

This integrative approach allowed for better insights on the ecosystem functioning, tracking its changes, the influence of pressures and ultimately aiding in management of resources and decision making.

1.3. Objectives of the PhD

1.3.1 General aim and specific objectives

Taking into account the above context, this PhD aims at contributing to the knowledge about marine biodiversity distribution in a context of global change and biodiversity crisis to address key knowledge gaps identified in terms of under-studied regions, under-examined taxa and under-used indicators.

Therefore, the main aim is to better comprehend the current spatiotemporal changes in biodiversity and how they are influenced by environment and anthropogenic effects by studying Atlantic and Mediterranean marine ecosystems using an integrative analysis of ecological indicators calculated from scientific bottom trawl surveys.

The main aim was achieved with the development of six specific objectives of the PhD, approached in three dedicated chapters:

- 1) To quantify how local and regional biodiversity indicators change along contrasting and heterogenic gradients of climate and fishing conditions (chapters 2.1, 2.2, 2.3);
- 2) To identify which of these indicators and in which regions display temporal trends (chapter 2.1);
- 3) To identify which are the winning and losing taxa along contrasting and heterogeneous gradients of climate and fishing conditions (chapters 2.1, 2.2);
- 4) To determine which are the driving factors impacting the dynamics of winning taxa (chapter 2.2);
- 5) To establish how contrasting marine communities along a global latitudinal gradient respond to global change stressors and test the Depth refuge hypothesis (chapter 2.3);
- 6) To investigate the potential spatiotemporal effects of human exploitation in contrasting marine communities (chapter 2.3).

1.3.2 Structure of the PhD

This thesis is structured in three chapters based on the main aim and several specific objectives.

In **Chapter 2.1** the first and second objectives are addressed within a regional scale study of the Western Mediterranean basin. The variation of the indicators within a regional scale gradient is analysed as well as the temporal trends by taxa and position in the water column. The analysis considers the entire sampled community including fishes, cephalopods and crustaceans of both the benthic and pelagic domain.

This chapter has been published as a peer review publication:

Carlos Veloy, Manuel Hidalgo, Maria Grazia Pennino, Encarnación Garcia, Antonio Esteban, Gregoire Certain, Sandrine Vaz, Angélique Jadaud, María González, Marta Coll,. (2022). *Spatial-temporal variation of the Western Mediterranean Sea biodiversity along a latitudinal gradient.* **Ecological Indicators**, 136: doi:10.1016/j.ecolind.2022.108674

In **Chapter 2.2**. I examine with more detail the first two objectives targeting a specific taxon, the cephalopods, since they are identified as a winning taxa in the first chapter. The third objective is to analyse the response of a selection of indicators to several drivers related to the environment, to human activity as well as to interspecific relationships with both prey and possible competitors and predators.

This chapter has been published as a peer review publication:

Carlos Veloy, Marta Coll, Maria Grazia Pennino, Encarnación Garcia, Antonio Esteban, Cristina García- Ruiz, Gregoire Certain, Sandrine Vaz, Angélique Jadaud, María González, Manuel Hidalgo. (2024). *Understanding the response of the Western Mediterranean cephalopods to environment and fishing in a context of alleged winners of change.* **Marine Environmental Research**, 194: doi:10.1016/j.marenvres.2024.106478

In **Chapter 2.3** objectives 4 and 5 are investigated by looking at a larger gradient that includes several areas within the East Atlantic Ocean and the Western Mediterranean Sea. This chapter tests the Depth refuge hypothesis at the fish community level within a large geographical gradient for the first time. In this study, the responses of several indicators to environmental and human variables are analysed, along with the relationship between indicators, time and depth to test the spatiotemporal interactions of these factors.

This chapter is being prepared for a peer review publication:

Carlos Veloy, Cesc Gordó-Vilaseca, Gregoire Certain, Mark Costello, Antonio Esteban, Tracey Mc Gahey, Encarnación Garcia, Cristina García- Ruiz, Dawit Yemane Ghebrehwet, Maria Grazia Pennino, Angélique Jadaud, Lynne J. Shannon, Sandrine Vaz, Manuel Hidalgo and Marta Coll. *Bathymetric variations of fish indicators along Atlantic and Mediterranean waters*. In preparation.

A final synthesis integrates the main findings of the above chapters (**Chapter 3**) and a set of the most relevant conclusions of this thesis are provided in **Chapter 4**.

1.4. Methodological overview: study areas, data and indicators, and statistical analysis

1.4.1 Study areas

The work developed in this PhD targeted three contrasted regions representative of the East Atlantic coast and the Mediterranean Sea: the North Atlantic system (a temperate to cold, high latitude area), the Western Mediterranean basin (as a temperate-warm area) and the South Africa coast (a warm, low latitude area) (Figure 1.6), which all include several subregional study areas.

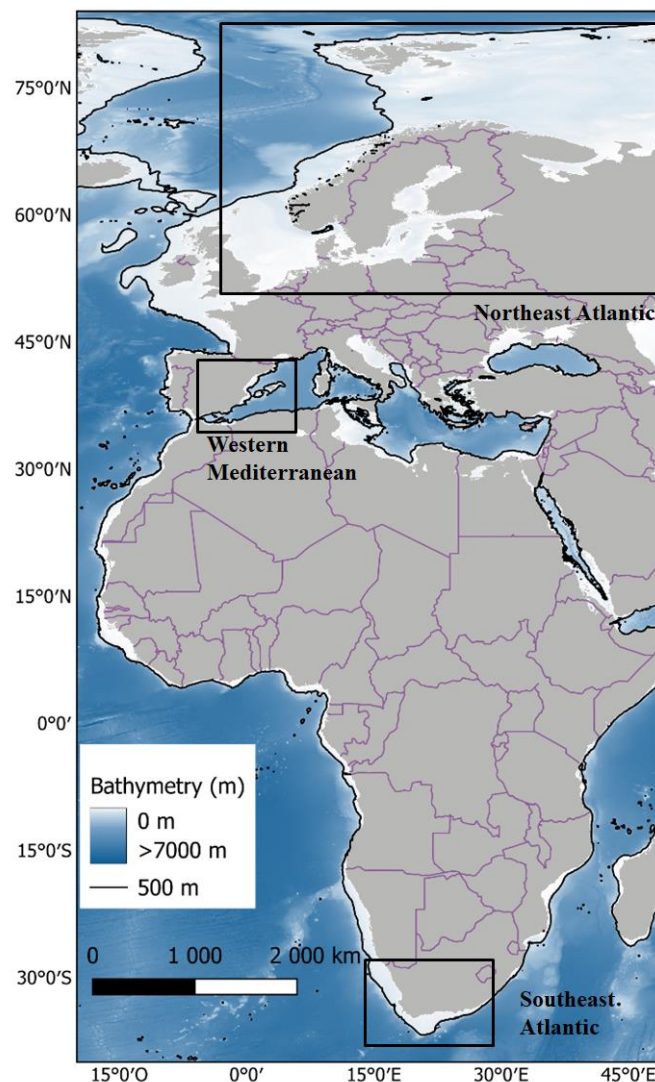


Figure 1.6: Bathymetric map of the East Atlantic, which include the three main study areas. Source: Own production.

Northeast Atlantic

a) Barents Sea

The Barents Sea is a cold shallow area with an ample continental shelf. Atlantic currents moving through the edge of the continental shelf bring warmer waters from the Norwegian Sea and lower latitudes. This oceanic current branches in two and extends through the Barents Sea eastward in the southern and central areas, meanwhile Arctic waters outflow towards the ocean from the northwest (Asplin et al., 2001; ICES, 2021). During recent years, there has been an increase in the inflow of these oceanic waters as well as a decline in sea ice cover contributing to the rapid rates of warming in arctic systems or polar amplification (Rantanen et al., 2022).

On the Barents Sea, displacements at species level have not been detected but at a community level rapid shifts have been recorded, especially in northern parts of this area (Fossheim et al., 2015; Gordó-Vilaseca et al., 2023a). This process has been called borealization, as boreal species have become more abundant replacing the declining arctic species. This change has triggered a replacement of more benthivorous species with low growth rates to more omnivorous and generalist species from boreal regions (Frainer et al., 2017).

b) North Sea

The North Sea ecosystem is characterised by a shallow continental shelf, relatively high primary production and temperate waters with contrasting environmental scenarios in the northern and southern North Sea (ICES, 2022). The northern North Sea is deeper and influenced by Atlantic waters flowing towards the Baltic from the West, with marked seasonality on water stratification (OSPAR Commission, 2000; Capuzzo et al., 2018; ICES, 2022). Meanwhile, the southern area is shallower and influenced by inputs from continental sources and local currents, including water entering through the English Channel, resulting in a perennial mixed water column (ICES, 2022). Historically, this sea has been heavily exploited by fisheries, but there has been a recovery of fish stocks with most commercial species at or below the maximum sustainable yield (MSY) (Engelhard et al., 2011; Fernandes and Cook, 2013; ICES, 2022). Declines in primary production have been reported with important decreases in fish recruitment of several species, such as cod, herring, sandeel or Norway pout, due to bottom up effects (Capuzzo et al., 2018).

During several years, latitudinal shifts have been reported in the Northeast Atlantic area where animals from southern regions move northwards, like in the already described case of the Barents Sea. However, in the case of the North Sea, this change is mostly associated with species from more temperate waters like red gurnards or anchovies in some cases at

exponential rates (Beare et al., 2004). This results in a turnover from large, long-lived species to short-lived and smaller ones (Pecuchet et al., 2017; Beukhof et al., 2019b).

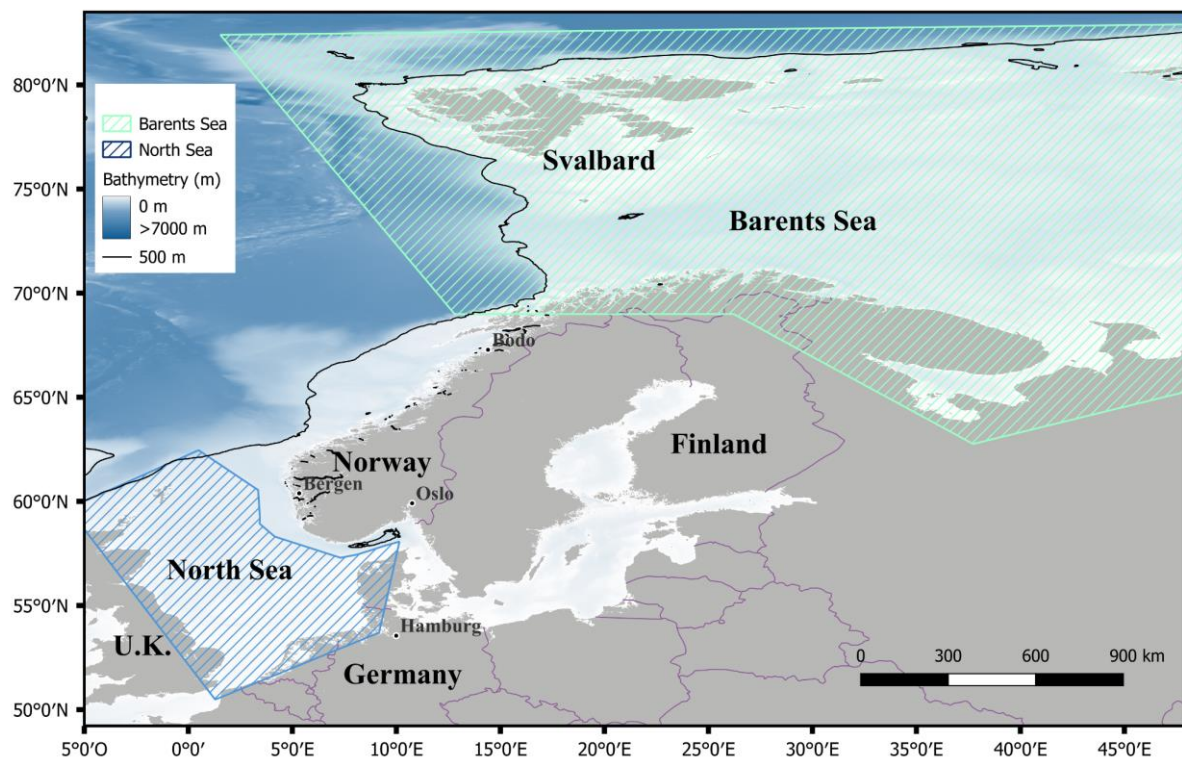


Figure 1.7: Bathymetric map of the Northeast Atlantic including the sampling areas of the North Sea shelf and the Barents Sea. Source: Own production.

c) Western Mediterranean

The Western Mediterranean area represents the most western part of the Mediterranean basin and it borders the Atlantic Ocean. This semi-closed system is a hotspot of marine biodiversity but it is endangered by human activities, directly and indirectly, that cumulatively impact marine ecosystems (Bianchi and Morri, 2000; Coll et al., 2010). Fishing is the main human stressor in these waters, both historically as well as in modern times (Coll et al., 2010; Lotze et al., 2011). Currently, a large percentage of fish stocks are overexploited on the Mediterranean Sea according to the General Fisheries Commission of the Mediterranean (GFCM, FAO, 2022). Pollutants and eutrophication are also other important human pressures in this system, especially on coastal areas (Danovaro, 2003; Micheli et al., 2013), while habitat modification by fishing is also a widespread impact in the whole region (Coll et al., 2012). Besides, alien species also pose a threat to local ecosystems, particularly Indian Ocean species coming through the Suez Canal (also known as Lessepsian fauna) (Bianchi and Morri, 2000).

Biodiversity has been found to be associated with an overall west-east gradient in the Mediterranean basin, with the western parts having more species richness due to higher primary production and colder temperatures while the eastern basin, less productive and warmer, usually shows less species. However, there is some variation to this trend due to regional circumstances (Gaertner et al., 2013).

The Western Mediterranean basin extends from the Gibraltar strait from the Alboran Sea until the Strait of Sicily, although in this study the western portion of the basin is included up to the Gulf of Lion. This basin covers the entire Eastern coasts of the Iberian Peninsula, and as much of the Mediterranean Sea, follows a Southwest-Northeast gradient of production and temperature. Within this system, five subregions were delimited based on their environmental differences:

- The **Alboran Sea**, the southernmost region of the basin, acts as a transitional zone between the Atlantic and the Mediterranean. It is characterised by a very variable primary production due to the inflows from oceanic waters and two persistent anticyclonic gyres.
- The **Valencia Channel**, **Ebro Delta** and **North Catalan Sea** are the subregions located in the central area of the Western Mediterranean, and are characterised by narrow continental shelves that result in deep environments, high temperatures and generally low levels of chlorophyll. Primary production in the Ebro Delta is mainly sustained by the Ebro river, while in the case of the North Catalan Sea the Northern Current flowing south-eastward is the source of enrichment in the area (Estrada, 1996). Furthermore, in the North Catalan Sea, human activity and its impacts are quite prevalent (Coll et al., 2008, 2021; Pennino et al., 2017).
- Finally, the **Gulf of Lion**, the most northern part of the basin, is a shallow, cold water area with high primary production due to the combination of upwelling processes, the flow of nutrients from the Rhône river and their spread through the gulf by the Ligurian current (Nieblas et al., 2014). Landmass at the north of the Gulf acts as a barrier inhibiting further latitudinal displacements of species.

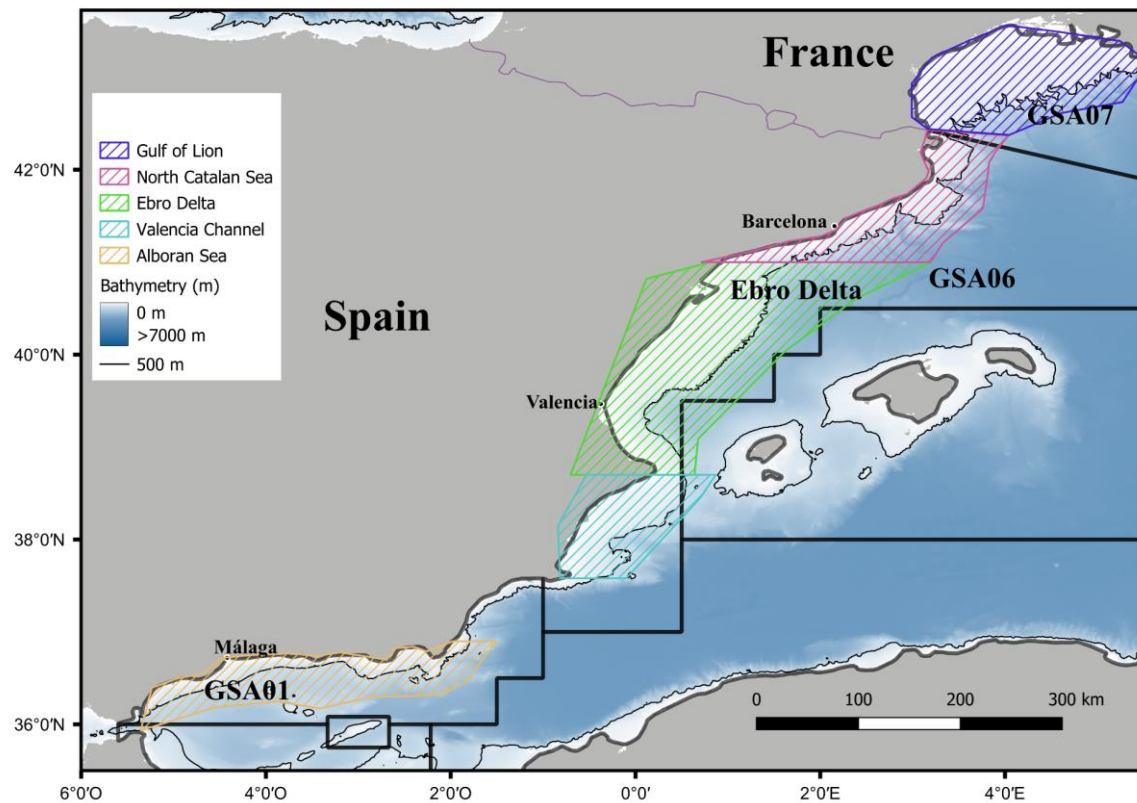


Figure 1.8: Bathymetric map of the Western Mediterranean Sea including the geographical sub-areas (GSAs) and subregions considered in the study, GSA01, GSA06 and GSA07. Source: Own production.

Southeast Atlantic (South Africa)

The South Africa coast is the Southeastern limit of the Atlantic Ocean with the Indian Ocean. It is characterised by high levels of primary productivity as it is part of the Benguela Current Large Marine Ecosystem (BCLME), specifically the southern Benguela. During the last decades it has experienced notable warming of the sea surface (Blamey et al., 2015).

Many upwelling processes occur especially in the western area, where both variability and mean upwelling has increased (Blamey et al., 2015; Kirkman et al., 2016). There has also been described some eastward population shifts mainly affecting small pelagic species, which were caused mostly by fisheries (with two stock crashes between the 1960s and the 2000s), although environment also played a role in some of them (Jarre et al., 2015; Ramírez et al., 2022a, 2022b). Furthermore, and like in the North Atlantic, demersal long-lived species have experienced declines between the 1990s and the 2000s, while fast-growing ones have increased (Atkinson et al., 2011) due to both fishing as well as changes in the upwelling (Blamey et al., 2015).

There are two sub-areas within the South African coast that are influenced by two different currents:

- The **West Coast** area, influenced by the Benguela current. It has a narrow continental shelf and is limited on the north by the Lüderitz upwelling, which is an environmental barrier to the transport of small pelagic organisms, from plankton to small species of nekton (Kirkman et al., 2016).
- The **South Coast**, influenced by the Agulhas current and characterised by a wider continental shelf (Agulhas bank), where upwelling processes over the shelf edge and deep mixing of waters due to the wind patterns influence productivity (Kirkman et al., 2016).

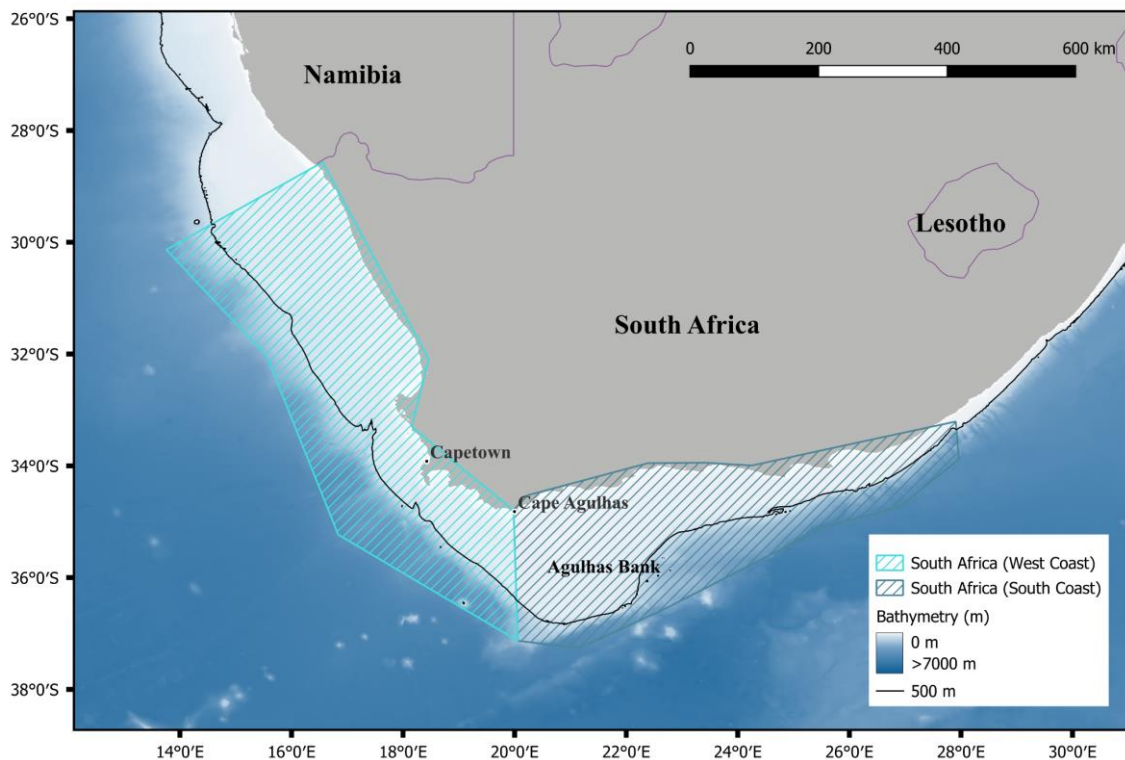


Figure 1.9: Bathymetric map of the South Africa area including the two sampling areas of the West and South Coast. Source: Own production.

1.4.2 Survey and environmental data

The databases resulting from trawling surveys performed on the aforementioned regions (Section 1.4.1) were composed of several geolocalized sample points also identified by haul number and year of the campaign. Several metrics were also recorded for the taxa present in the catch, such as number and weight. In this project those species that were caught and identified up to the species level were considered for analysis. Abundance and weight (expressed as density per km²) were the main variables recorded in these surveys and were used to calculate most of my selected indicators. Presence and absence of

species was used to estimate the different biodiversity indexes, especially Richness and Jaccard (see below section 1.4.3).

Data from the Northeast Atlantic system was gathered using the FishGlob database (Maureaud et al., 2023). This public database standardised data from several fish trawl surveys through the Northern Hemisphere by curating taxonomy information, removing invalid hauls or surveys that did not use otter trawls and standardising units by area. Two surveys included on this database were used in this study. Barents Sea data was collected during the NORBTS campaigns organised by the IMR. These selected samplings were performed with shrimp trawls with 20 mm of mesh size (Maureaud et al., 2023). The study period ranged between 2004 to 2017, due to some uncertainties with species identification in the previous years (Johannesen et al., 2021). North Sea data used in this thesis originated from the DATRAS NS-IBTS trawling surveys by ICES using a GOV Trawl with a mesh size of 20 mm (ICES, 2020). The selected time period spans the years from 1994 to 2020 to be consistent with other study regions, using the seasonal surveys of winter, due to the higher quantity of sampling points

Samples from the Western Mediterranean were sourced by the MEDITS campaigns between 1994-2019. These surveys use a GOC 73 trawling gear with 20 mm of mesh size (Bertrand et al., 2002). MEDITS also establishes several geographical sub-areas (GSA) within the Mediterranean Sea (Spedicato et al., 2020). The GSAs that are included in my study area are GSA1 (corresponding to the Alboran Sea), GSA6 (Valencia Channel, Ebro Delta and North Catalan Sea) and GSA7 (Gulf of Lion).

Finally, South African trawling data was provided by the South African Department of Forestry and Fisheries, which performs trawling surveys using the vessel *Africana* from 1984 (vessel and gear details reviewed by Axelsen and Johnsen (2015)). The study period in this case ranges from 1994 to 2020.

For all caught species, I collected both trait and taxa data from Fishbase and Sealifebase (Froese and Pauly, 2021; Palomares and Pauly, 2021). The goal was to filter the desired groups based on taxa (fishes, cephalopods and crustaceans within the Stomatopoda, Decapoda and Euphausiacea classes) and preferred habitat in the water column (pelagic and benthodemersal) to estimate some of the indicators (see section below).

To examine the causes of change in ecological indicators, several drivers were considered, which reflected various sources of impact, mainly environmental and human related activities (Table 2). The environmental conditions and change were represented by temperature (both sea surface and sea bottom temperature) and chlorophyll-a concentration (as a proxy for primary production). In both cases, reanalysis maps from Copernicus were used, for temperature-related variables GLOBAL_MULTIYEAR_PHY_001_030 and for the primary production GLOBAL_MULTIYEAR_BGC_001_029, (COPERNICUS, 2021). To study the human impact, fishing effort was calculated as the sum of fishing hours per pixel with Global Fishing Watch data (Global Fishing Watch, 2020).

1.4.3 Ecological indicators and analysis

In this study, considering the state of the art in terms of ecological studies, a set of complementary indicators was selected (Table 1.1). This selection included the classic biodiversity indicators, and additional indicators to capture the different facets of ecosystem change. For example, trophic levels and the relative biomass of predators (BPred) or other groups of interest such as pelagic species (BPel) and fishes (BFish).

Trait-based indicators (Bpred and TL) were heavily reliant on the species trophic level, which was taken from the previously mentioned on-line databases. For Bpred, species were qualified as a predator or not. Animals with TL larger than 3.5, maximum total length longer than 20cm (or equivalent measurements) and with active hunting behaviour were eligible for this category, removing both scavenger species as well as those with high TL but small sizes, for example some Syngnathids and Sepiolid.

Table 1.1. Main ecological indicators used in this thesis, their definition, calculation and references.

Indicator		Equation	Reference
Biodiversity indicators			
Species richness (S)	Sum of species (<i>sp</i>) number	Σsp	McIntosh, 1967
Shannon index (H)	Measure of diversity and evenness. p_i is the proportion of individuals belonging to species i in the dataset	$-1 * \Sigma((p_i) * \ln(p_i))$	Shannon & Weaver, 1949
Pielou evenness (J)	Measurement of frequency evenness on an ecosystem. H : Shannon index, S : Species richness	$\frac{H}{\ln(S)}$	Pielou, 1966
Jaccard index (β)	Measurement of community change over time. A & B: different sample sets Components: -Nestedness or subsetting of the sample -Turnover or identity change.	$\frac{ A \cap B }{ A \cup B }$	Dornelas et al., 2014; Blowes et al., 2019
Biomass and trophic level indicators			
Biomass (B) and Abundance (N)	Biomass (B_i) and Abundance (N_i) of surveyed species i .	ΣB_i & ΣN_i	Coll et al., 2016
Mean size (MS)	Mean weight (used as proxy of mean length indicator although less effective). B : biomass, N : abundance.	B/N	Shin et al, 2018
Relative predatory Biomass (BPred)/ Relative biomass indexes	Relationship between biomass of predator species or other considered trait/taxa groups (B_i) and the ecosystem or taxa group (B).	$\frac{\Sigma(B_i)}{B}$	Coll et al., 2016. Other similar indicators were based on BPred
Surveyed community trophic level (TLc)	Mean trophic level of the surveyed species (TL_i). W_i : biomass of species i .	$\frac{\Sigma(TL_i * W_i)}{B}$	Shannon et al., 2014

Mean trophic level of species above 3.25 (TL3.25)	Mean trophic level of species i above 3.25 ($TL_{i,3.25}$)	$\frac{\sum(TL_{i,3.25} * W_{i,3.25})}{B_{3.25}}$
Mean trophic level of species above 4 (TL4)	Mean trophic level of species i above 4 ($TL_{i,4.0}$, top predators)	$\frac{\sum(TL_{i,4.0} * W_{i,4.0})}{B_{4.0}}$

1.4.4 Statistical analysis

To analyse the differences between indicators, as well as the potential impacts of environmental and anthropogenic drivers, this PhD mainly used analysis of variance (ANOVA) and regression analysis, including advanced non-linear regressions such as Generalised Additive Models (GAMs, Hastie and Tibshirani, 1990). This application of GAMs allowed for both high detail spatial analysis and the establishment of relationships between indicator variation and environmental and human impacts.

After the indicators were calculated for the present taxa and trait groups, their spatio-temporal change or their relationship was modelled with several drivers of change in different chapters of this thesis. First, on an initial region scale study, I used a combination of linear regressions and ANOVA models. This was due to differences in the sampling schemes for crustaceans species in the subregions of the Western Mediterranean area, which were underrepresented in the Gulf of Lions and made the application of an ANCOVA model not possible (**Chapter 2.1**). This allowed the comparison of indicator results between the different regions as well as the establishment of temporal trends of a set of ecological indicators.

The following studies performed more in depth analysis looking at the establishment of spatial variation at finer scales and the relationship with drivers (environmental, human impact and interspecific relationships) with the help of GAMs (**Chapters 2.2 and 2.3**). These models, unlike linear regressions or Generalized Linear Models (GLM), assume non-linear relationships with the considered covariates and thus replace the linear predictor of GLMs with an additive predictor (Hastie and Tibshirani, 1990).

The general formula of this type of model is:

$$Y = \sum S_j(X_j)$$

where S_j represents the smooth function of a variable X_j . These smooth functions can be limited in terms of the non-linear complexity by the number of knots assigned, which determine the dimensions represented on the smoother and by extension their degrees of freedom (in this case, to avoid overfitting, I used 3 degrees of freedom or 4 knots). These smoother functions can be unidimensional or bidimensional. Examples used throughout this thesis are $s(\text{SST})$, representing the Sea Surface Temperature, or $s(\text{lon}, \text{lat})$, a classically used bivariate smoother to consider the geographical components. Further,

spatiotemporal interactions in the context of the Depth refuge hypothesis required the use of other bivariate factors. These include the interaction of depth and year/depth to examine the evolution of possible deepening of the communities, or with the fishing effort to study the human effect on ecosystems and their bathymetry in the form of tensor variables (**Chapter 2.3**). The statistical significance of all the selected smoothers is tested with the package *mcgv* (Wood, 2017) with an analysis based on Nychka (1988). Statistical significance was considered for those variables with a p-value below 0.05.

Model selection methods used in the various chapters using GAMs were based on the minimization of Akaike Information Criteria (AIC, Cavanaugh and Neath, 2019) using backwards stepwise or forward stepwise selection intending to the objectives of each Chapter.

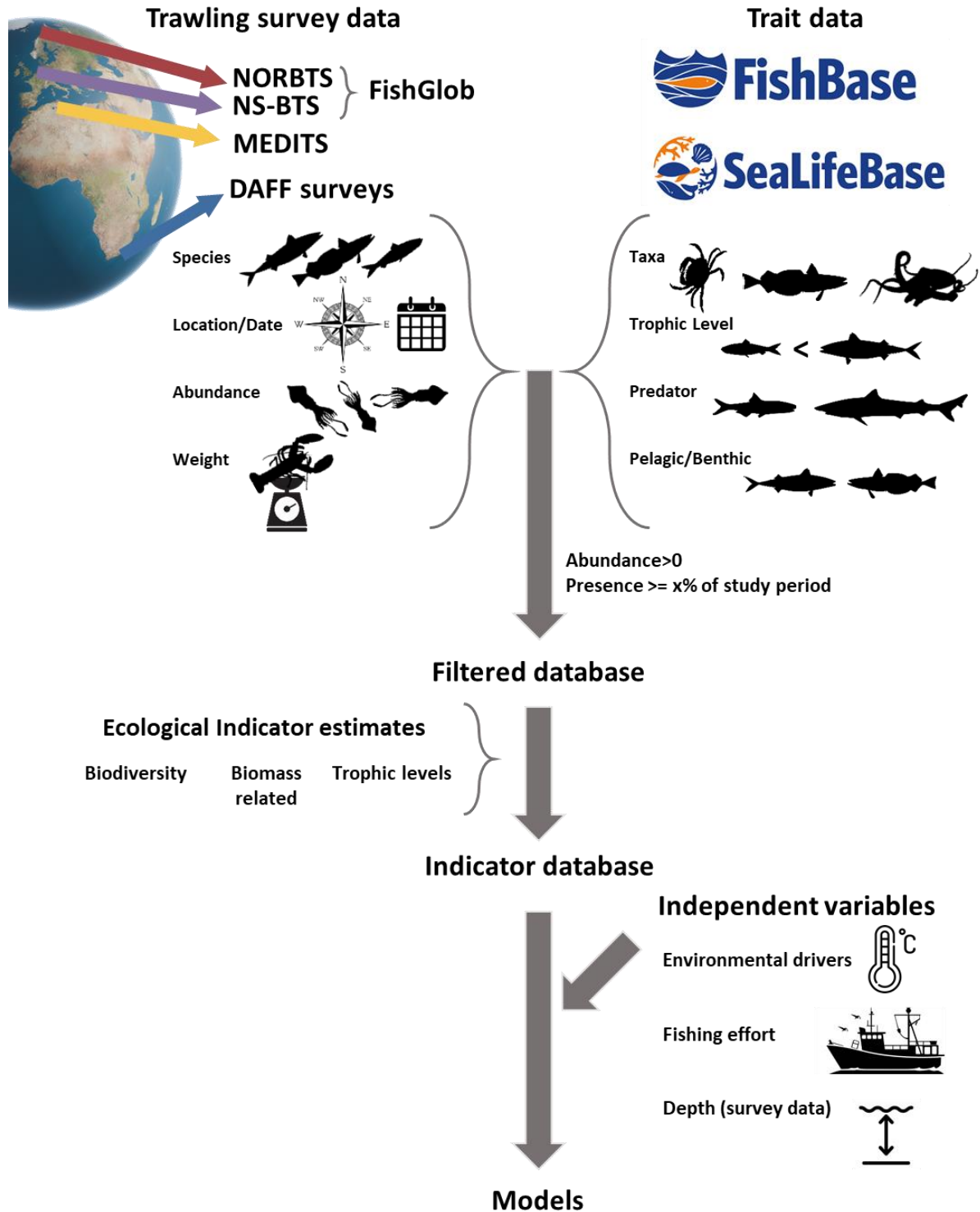
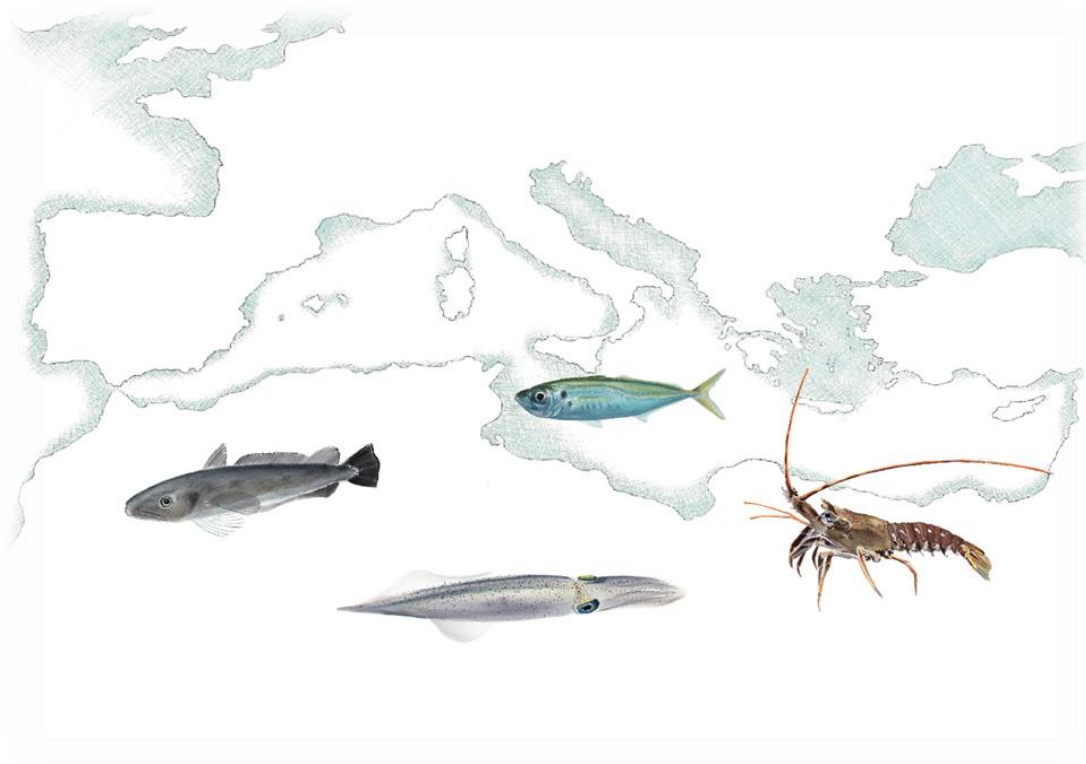


Figure 1.10: Schematic summary of the general workflow used throughout the thesis project. From data and trait sources to data management. Source: Own production.

Chapter 2. Results

2.1. Spatial-temporal variation of the Western Mediterranean Sea biodiversity along a latitudinal gradient

Carlos Veloy, Manuel Hidalgo, Maria Grazia Pennino, Encarnación Garcia, Antonio Esteban, Cristina García- Ruiz, Gregoire Certain, Sandrine Vaz, Angélique Jadaud, Marta Coll



Carlos Veloy, Manuel Hidalgo, Maria Grazia Pennino, Encarnación Garcia, Antonio Esteban, Gregoire Certain, Sandrine Vaz, Angélique Jadaud, María González, Marta Coll. (2022). *Spatial-temporal variation of the Western Mediterranean Sea biodiversity along a latitudinal gradient*. **Ecological Indicators**, 136: <http://doi:10.1016/j.ecolind.2022.108674>

Abstract

The Mediterranean Sea is a large marine ecosystem with high heterogeneity in both environmental and ecological characteristics. It presents clear gradients from north to south and west to east. It is also an important area in terms of biodiversity and conservation of vulnerable species, and it suffers from several cumulative human impacts, such as fishing and climate change. Previous studies have characterized spatial and temporal patterns of species distributions and biodiversity indicators. However, a comprehensive analysis combining a wide representation of biodiversity indicators is still missing. In this study, we examined spatial and temporal changes of marine communities along a latitudinal gradient over the continental shelf ecosystems (25-500 m depth) of the Western Mediterranean Sea, from the Gulf of Lion in the north to the Gibraltar Strait in the south. We used information from the MEDITS trawl scientific surveys from 1994 to 2018, and we calculated relevant indicators to investigate spatial and temporal patterns in the region. We selected several indicators measuring alpha (species richness, Shannon diversity index and Pielou evenness index) and beta (decomposing both turnover and nestedness) diversity, as well as previously studied indicators identified to be sensitive to fishing and climate change impacts (biomass-based and trophic-level based metrics). We assessed differences in these indicators for the surveyed community as a whole and for fish, crustaceans and cephalopods, separately, over five regions. Our results show clear latitudinal gradients in some indicators: we observe a reversed pattern between richness (decreasing from south to north) and biomass trends (increasing from south to north) for the demersal community. We also found a generalized increase in β -diversity in most regions with time, and a decline in the trophic level of the surveyed community. In addition, we identify a remarkable increase in several indicators when only considering the cephalopods group, and a general low environmental status for the North Catalan Sea. We discuss my results considering the differences between regions and taxa related to the fishing activity and environmental dynamics that can act at different scales. This in-depth analysis illustrates how to use a selection of indicators that combine the capacity to detect ecological changes from regional to sub-regional scales.

Keywords

Mediterranean Sea, ecological indicators, fishing impacts, climate change impact, spatial patterns, temporal trends.

2.1.1. Introduction

The Mediterranean Sea is an enclosed sea that was formed around 5 million years ago during the Pliocene when its only natural connection with oceanic waters, the strait of Gibraltar, opened allowing the influx of seawater into the system flooding, at the time, a mostly dried up basin (Coll et al., 2010). This event created a sea with particular features and gradients that have also shaped its own ecosystems and hosts several endemisms (Coll et al., 2010). One of the most characteristic traits of the Mediterranean basin is the northwest to southeast gradient of several physical variables such as higher temperature, and lower salinity and primary production towards the southeast. Biodiversity indicators (e.g., species richness) have also been described to decrease from the west to the east (e.g. Coll et al., 2010; Keller et al., 2016), despite the longitudinal gradient may not be so straightforward as shown in other studies (Gaertner et al., 2007).

Beyond the largely investigated west-east gradients over the whole basin, several regions in the Mediterranean display the combination of regional gradients and mesoscale features representing environmental and ecological spatial variation (Western Mediterranean, Liguria-Tyrrhenian Sea, Adriatic Sea and Aegean Sea among others). In the Western Mediterranean, the area from the Gulf of Lion (north) to the Alboran Sea (south) shows clear different hydrographic and productivity regions that have been used to define distinct environmental provinces (Rossi et al., 2014; Nieblas et al., 2014; D'Ortenzio and d'Alcalá, 2009). Also, in terms of biodiversity, the northwestern areas have been described as more diverse than the southeastern ones (Gaertner et al., 2007; Coll et al., 2010).

In addition to the influence of the environment in the distribution of species and the structure of marine communities (e.g. Navarro et al., 2016; Vilas et al., 2020; Lloret et al., 2021), human activities can contribute to drive the changes in marine ecosystems. The fishing activity in the Mediterranean Sea has been historically very high (Lotze et al., 2006; Coll et al., 2010) and the region is still one of the FAOs fishing areas with the highest percentage of stocks fished at unsustainable or high levels besides the decreasing effort (FAO, 2020). Due to the depletion of marine resources in most shelf fishing grounds and the improvement of technology, part of the fleet has bathymetrically shifted to higher depths (Coll et al., 2014; Farriols et al., 2017).

Other impacts threaten the stability and normal functioning of the ecosystems, such as habitat loss and invasive species, especially Lessepsian fauna migrating from the Suez Canal (Katsenavis et al., 2016; Galil et al., 2017), pollution (Danovaro, 2003) and climate change (Ben Rais Lasram et al., 2010; Lejeusne et al., 2009; Hidalgo et al., 2018). In the case of the Western Mediterranean, their communities face other human related threats aside of overfishing (Fernandes et al., 2017; FAO, 2020) such as eutrophication by discharges as well as accumulation of heavy metals (Danovaro, 2003) that exert most pressure in the coastal areas (Fiorenza et al., 2013). In general, human activities have cumulatively impacted living communities of the Mediterranean in numerous and synergistic ways. For example, marine predators (i.e. large species with a high trophic level) have notably declined from Mediterranean marine ecosystems (Ferretti et al., 2008) with important implications for marine food webs (Sala, 2004; Lotze et al., 2011),

although few species have shown signs of recovery such as the Atlantic Bluefin tuna (Ifremer, 2019) or some vulnerable demersal elasmobranchs (Ramirez-Amaro et al., 2020, Hidalgo et al. 2021).

Previous studies in the Mediterranean Sea have described several spatiotemporal patterns of distribution of biodiversity, both at species, groups of species and the ecosystem level (e.g. Coll et al., 2010, 2012, Navarro et al., 2015; Keller et al. 2016, 2017; Fernandez-Arcaya et al., 2019; Vilas et al., 2020). However, a community-based spatial integrative analysis with a wide range of ecological indicators selected based on their sensitivity to fishing or environmental impacts is still missing to compare patterns in important sub-regional areas in the Mediterranean Sea.

In this study, we fill this gap analyzing the spatiotemporal gradients of marine biodiversity from the Western Mediterranean Sea (from the Gulf of Lion to the Alboran Sea) with the aim to contribute to a better understanding of the changes of marine communities in this region following a continuous latitudinal gradient of environmental change. Using the intermediate scale of environmentally distinct regions over the continuous continental shelf gradient of the Western Mediterranean, we compare several areas according to a selection of indicators considering the multidimensional facets of biodiversity. The importance of such trait-based analysis can be seen in similar studies, such as the one performed in Atlantic waters (Pecuchet et al., 2017, Beukhof et al., 2019). In the latter, the study accounts for the distribution of certain life history traits showing that warmer waters favour opportunistic strategies (short lived and small species with low trophic levels), while colder waters with higher primary production and less variability have a bigger proportion of large long lived species.

Specifically, in my study we selected several indicators with the intention to cover different diversity components and community characteristics combining information of different groups (e.g. pelagic, demersal, predators). First, indicators of biodiversity were used, including beta diversity (hereafter β -diversity). The lack of data about this indicator and its components (turnover or change of identity and nestedness or subsampling) in the region needed to be addressed. This indicator can provide key information about the rates of change in the ecosystem as well as the identity of the change (Dornelas et al., 2014; Blowes et al., 2019). The differentiation in the components of β -diversity also helps to determine which are the underlying ecological processes driving biodiversity change through time, as both have been associated with different phenomena: limited space (Stegen et al., 2013) or high impacted areas (Shackell, et al., 2012) in the case of turnover, or orderly species loss in the case of pure nestedness (Baselga, 2010). Secondly, we added well studied indicators identified to be sensitive to fishing and climate change impacts: biomass-based and trophic-level based metrics (Shin et al., 2012; Bundy et al., 2012; Shannon et al., 2014; Coll et al., 2016; Fu et al., 2019).

Based on the literature available, we hypothesised that different ecological gradients and temporal changes according to different taxonomic groups may emerge, but also we expected to infer other ecological processes for specific taxonomic groups and sub-regions. Finally, my results could reflect as well the spatial-temporal heterogeneity of my study area, providing highly-resolved and novel information about the dynamic components of marine biodiversity in the Western Mediterranean Sea.

2.1.2. Material and Methods

Study area and data set

The study area covers the continental shelf and upper slope of the Western Mediterranean of Spain and France, including depths from 25 m to 500 m (Figure 2.1.1) as it is the stratum with most biodiversity and represents most of the main ecosystems within my region. The data used was collected from the international MEDITS trawl surveys between the years 1994 and 2019 (Spedicato et al., 2020) in 4041 sample stations over 25 years and integrated information of 586 species (Table S2.1.1). The MEDITS program follows a standardized sampling protocol through the entire northern Mediterranean, from the duration of the trawling, the type and specifications of the gear used to the collection and analysis of the biological samples (Bertrand et al., 2002; Spedicato et al., 2019). MEDITS program uses the Geographical Statistical Areas (GSAs) as sampling areas, defined by the General Fisheries Commission for the Mediterranean (GFCM). The chosen area for this study covers the continuous north-south gradient of the Western Mediterranean area ranging from the Gulf of Lion (GSA7), through the Northern Spain (GSA6) to the Northern Alboran Sea (GSA1). The study area was divided in five regions (Figure 1). The GSA6, Valencia Channel (CN), Ebro Delta (DE) and North Catalan Sea (CC), share some similarities, with low chlorophyll levels, deep bathymetry and high sea surface temperature (SST) (Nieblas et al., 2014). CN and DE regions have a relatively wide continental shelf, and DE also receives intakes from several rivers such as the Ebro. The most northern area, the GSA7, Gulf of Lion (GL), features a low SST, shallow bathymetry, extended shelf and high and variable primary production driven by the peculiar oceanographic conditions and the Rhône River. The river generates a layer of high concentrations of nutrients up to a 100 metres in depth, and even deeper during winter due to upwelling processes, that is spread through the area by the Ligurian current allowing fertilization of the whole Gulf (Nieblas et al., 2014)., while CC is characterized by a narrow continental shelf. Finally, the most southern area, GSA1, Northern Alboran Sea (AL), has a high and very variable primary production influenced by the inflow of waters from the Atlantic Ocean and highly dynamic mesoscale processes.

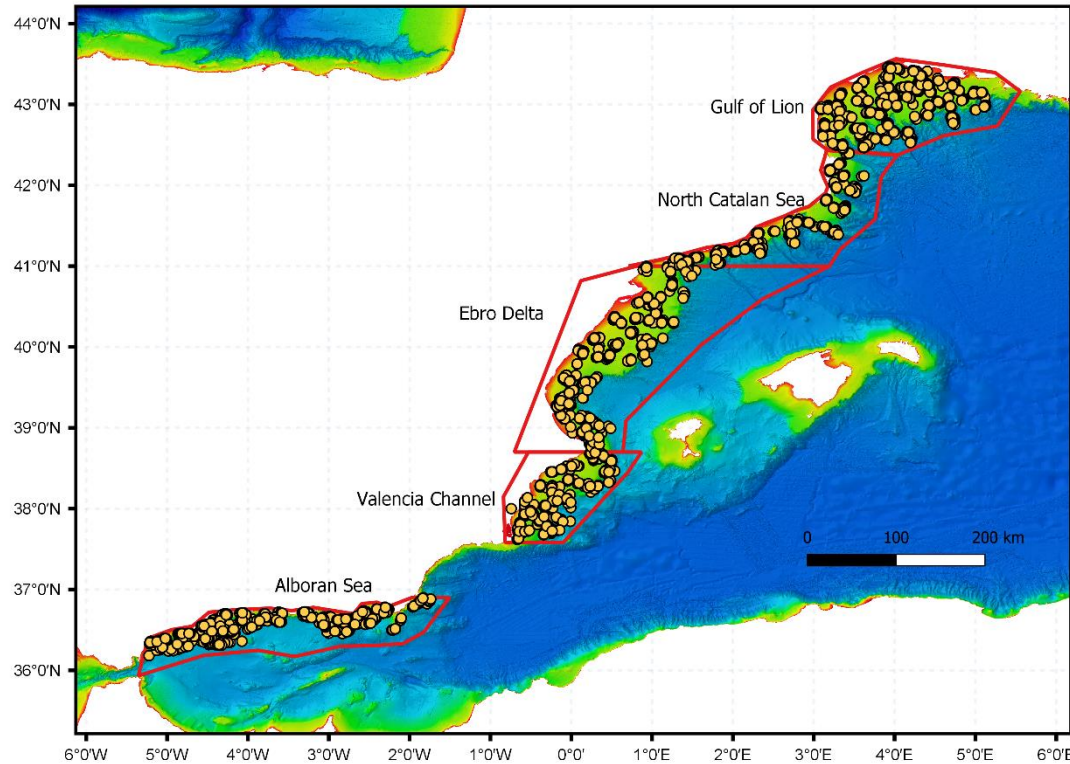


Figure 2.1.1: Map of the study area and its subdivision in regions. Yellow dots represent the sampling stations of MEDITS campaigns used in the analysis.

The data obtained from the surveys was firstly filtered for those registries that reported no individuals, following the protocol established by Dornelas et al. (2014). A second filter was applied to select only those species that appeared in 80% of the time in the temporal series considered. Lastly, for those indicators based on biomass or abundance indices, we also filtered out those species with low and heterogeneous catchability such as gregarious and small pelagic species (e.g., European sardine, *Sardina pilchardus* or boarfish, *Capros aper*). For the indicators based on absence-presence, this criterion was not applied.

For invertebrate species, we faced a challenge related to the heterogeneous sampling protocols among areas. While the surveys carried out in the Spanish Mediterranean areas performed a complete record of both the presence and the biomass of as many species as possible since 1994, in the Gulf of Lion only mandatory species under the MEDITS protocol were sampled until 2012. From this year onwards, the survey started a complete record of other species including crustaceans and cephalopods. To efficiently circumvent this limitation while ensuring the objectives of the study, we considered two separate invertebrate databases: i) first, to analyse the temporal variation, the entire sampling period (1994-2019) was considered but we selected for all the regions only those species sampled before 2012 in GL; ii) second, to perform the spatial analyses, all the species of the demersal community between 2012 and 2019 were used from every region.

Selection of ecological indicators

a) Biodiversity indicators

Different biodiversity metrics of both alpha and beta diversity were calculated (Table 2.1.1). For alpha diversity we focused on two main components of the alpha diversity: species richness (the amount of species present in the community of a region) was measured with the total number of species in the sample (McIntosh, 1967) and the Shannon index (H) (Shannon & Weaver, 1949). For the evenness, we used the Pielou evenness index (J) (Pielou, 1966) since it is constrained by values between 0 and 1, allowing for better comparison between different samples. The β -diversity was calculated with the Jaccard index to assess differences between communities separated with time using the first year of sampling. In the case of the temporal databases, the first year was 1994, while 2012 was used for the spatial database. The two components of β -diversity, turnover and nestedness, were also individually calculated.

Table 2.1.1. Definitions, equations, primary driver of influence (environment, fisheries or both) and references of indicators used in this study. N_i , B_i , W_i and TL_i correspond to Number of individuals, Biomass, Weight and Trophic Level of i species, respectively.

Indicator	Definition	Equation	Primary driver	Reference
Biodiversity indicators				
Species richness (S)	Sum of species (sp) number	Σsp	Both	McIntosh, 1967
Shannon index (H)	Measure of diversity and evenness. p_i is the proportion of individuals belonging to species i in the dataset	$-1 * \Sigma((p_i) * \ln(p_i))$	Both	Shannon & Weaver, 1949
Pielou evenness (J)	Measurement of frequency evenness on an ecosystem. H : Shannon index, S : Species richness	$\frac{H}{\ln(S)}$	Both	Pielou, 1966
Jaccard index (β)	Measurement of community change over time. A & B: different sample sets Components: -Nestedness or subsetting of the sample -Turnover or identity change.	$\frac{ A \cap B }{ A \cup B }$	Both	Dornelas et al., 2014; Blowes et al., 2019
Community and taxa-related indicators				

Biomass (B) and Abundance (N)	Biomass (B_i) and Abundance (N_i) of surveyed species i .	ΣB_i & ΣN_i	Environment	Coll et al., 2016
Mean size (MS)	Mean weight (used as proxy of mean length indicator although less effective). B : biomass, N : abundance.	B/N	Fishing	Shin et al., 2018
Relative predatory Biomass (BPred)	Relationship between biomass of predator species (B_i) and the ecosystem or taxa group (B)	$\frac{\Sigma(B_i)}{B}$	Fishing	Coll et al., 2016
Relative pelagic Biomass (BPel)	Relationship between biomass of pelagic species and the ecosystem		Environment	Based on BPred
Relative fish Biomass (BFish)	Relationship between biomass of fish species and the ecosystem		Fishing	
Relative Cephalopod Biomass (BCeph)	Relationship between biomass of cephalopods and the ecosystem		Both	
Surveyed community trophic level (TLc)	Mean trophic level of the surveyed species (TL_i). W_i : biomass of species i .	$\frac{\Sigma(TL_i * W_i)}{B}$	Environment	Shannon et al., 2014
Mean trophic level of species above 3.25 (TL3.25)	Mean trophic level of species i above 3.25 ($TL_{i,3.25}$)	$\frac{\Sigma(TL_{i,3.25} * W_{i,3.25})}{B_{3.25}}$	Fishing	
Mean trophic level of species above 4 (TL4)	Mean trophic level of species i above 4 ($TL_{i,4.0}$, top predators)	$\frac{\Sigma(TL_{i,4.0} * W_{i,4.0})}{B_{4.0}}$	Fishing	

b) Community and taxa-related indicators

Species were classified in three major taxonomic groups: fishes, crustaceans (only accounting for decapods, stomatopods and euphausiids) and cephalopod mollusks (from now on referred to as cephalopods). For the different species in each group a binary value for two traits (position in the water column, benthopelagic -hereafter referred as pelagic- or demersal species, and feeding type considering the species a predator or not) was also assigned, as well as a trophic level value using FishBase (2020) and SeaLifeBase (2020). For the sake of data uniformity, the trophic level used was the one calculated based on consumed food items as it was the one available for most taxa. Following previous studies, we considered as “predator” those species that had a trophic level higher than 3.5 (Shin et al. 2010). However, we also took into account if they had reported a maximum length greater than 20 cm and actively captured their food. The aim of this

classification was to filter out small organisms like bobtail squids and species that are mostly scavengers such as shrimps.

To assess the state of the ecosystem and of different taxonomic and species groupings, several additional indicators were selected based on the IndiSeas initiative (Shin et al., 2012; Bundy et al., 2012; Coll et al., 2016; Fu et al., 2019, www.indiseas.org) (Table 2.1.1). IndiSeas indicators were initially chosen to track fishing effects on marine ecosystems. Some IndiSeas indicators were also identified as being especially sensitive to changes in primary productivity due to climate variability. Examples of the first type are the relative biomass of predators (BPred), the mean size of the community (MS) and trophic-based indicators such as the trophic levels in the community (TLc), the mean trophic level of the community for species with trophic levels above 3.25 (TL3.25) and the trophic level of the community considering predators above 4 (TL4). Some indicators sensitive to environmental change, such as the total community biomass (B) and the mean trophic level of the entire surveyed community (TLc), were also included (Shannon et al., 2014; Coll et al., 2016).

Data analyses

The heterogeneity of the database did not allow us to develop a complete spatiotemporal analysis (i.e. ANCOVA). Therefore, spatial and temporal analyses were developed separately in two different subsets of the database. To analyse spatial differences among sub-regions, we applied an analysis of variance (ANOVA) to compare the indicator mean values of the different regions across the study area (Figure 1). Afterwards, linear regressions were applied to assess the long-term temporal variation of each indicator. In each region, the different indicators were considered as the dependent variable, and the region was the independent categorical variable for the ANOVA analysis. Before the analyses, we tested that indicators followed the conditions of normality and homogeneity of variances applying the Shapiro and Levene tests, respectively. In the linear regressions, we considered time as the explanatory continuous variable per region. For this purpose, the indicator-time relationship was adjusted assuming a linear relationship between the two variables to compare the rates of increase or decrease (i.e. regression parameter) of the temporal trends. We then compared these trends between different regions for each indicator.

To further test and examine the differences between regions in the ANOVA, we used a Tukey pairwise comparison with 95% confidence intervals. Spatial patterns were summarized by grouping the statistically significant different regions. Two criteria were taken for grouping regions by their mean value: if the region was significantly distinct to the boundary areas or if regions showed significant differences in two pairwise comparisons.

All the indicators were calculated using R version 3.6.3 (R Core Team, 2020). The Jaccard index and its components were calculated using the R package betapart (Baselga, 2012).

2.1.3. Results

We present the summary of spatial and temporal trends for all surveyed species, demersal species and pelagic species using the biodiversity indicators first, and followed by the community and taxa-related indicators (Table 1). For each indicator, a general spatial description is first given followed by the main temporal pattern in the different sub-regions. All statistical results are shown in Supplementary Material (Tables 2.1.3 to 2.1.6).

Biodiversity indicators

Overall, the highest species richness (S) mean values were recorded in the southern areas of the study, the Alboran Sea and in the Channel, where significant differences were found in comparison with the rest of the regions (Table 2.1.2). The surveyed community and fish species richness were also highest in the south (with the exception for all fish and demersal fish richness in the Gulf of Lion), and they presented the lowest values in the North Catalan Sea when considering all and demersal fishes as well as the entire and demersal community ($F_{4,35} = 7.05$; $p < 0.001$) (Table 2.1.2 and 2.1.3; Figures 2.1.2a and 2.1.2b). The species richness showed general and significant increasing temporal trends in almost all areas and with the lowest significant slope values in the Gulf of Lion (slope, $sl = 0.44$, $p < 0.05$, in the surveyed community and $sl = 0.37$, $p < 0.05$, in the demersal community; Figure 2.1.2c, Table 2.1.2). A spatial gradient from north (lower values) to south (higher values) was also observed for cephalopods and crustaceans (Table 2.1.2; Figure 2.1.2e and 2.1.2f), with increasing temporal trends, too.

Both Pielou evenness (Table 2.1.2 and 2.1.3, Figure 2.1.3) and Shannon index showed roughly similar spatial patterns, with the lowest values in the Gulf of Lion. On the contrary, we observed an inverse gradient for cephalopods, where the North Catalan Sea featured the highest values and the Alboran Sea the lowest ($F_{4,35} = 3.741$; $p < 0.05$). Pielou index showed contrasting temporal trends depending on the region with decreasing trend with time in the Gulf of Lions (slope, $sl = -0.02$, $p < 0.001$), while an increase with time was observed for demersal cephalopods in most regions, where significant relationships were reported (slope, $sl = 0.02$, $p < 0.001$; Figure 3f).

Results evidenced that there were no significant spatial differences in β -diversity or its components between different regions (Table 2.1.2, 2.1.3 and 2.1.4). However, β -diversity increased with time showing an upwards trend in many of the regions and groups (Figure 2.1.4). Regarding the β -diversity components, turnover was found to have a significant increase mostly on the North Catalan Sea in many of the considered groups (Tables 2.1.2-2.1.4, Figure 2.1.4e). In contrast, nestedness showed a general significant increase in most regions within all taxa and taxonomic groups, especially in fish (Table 2.1.2, Figure 2.1.4c).

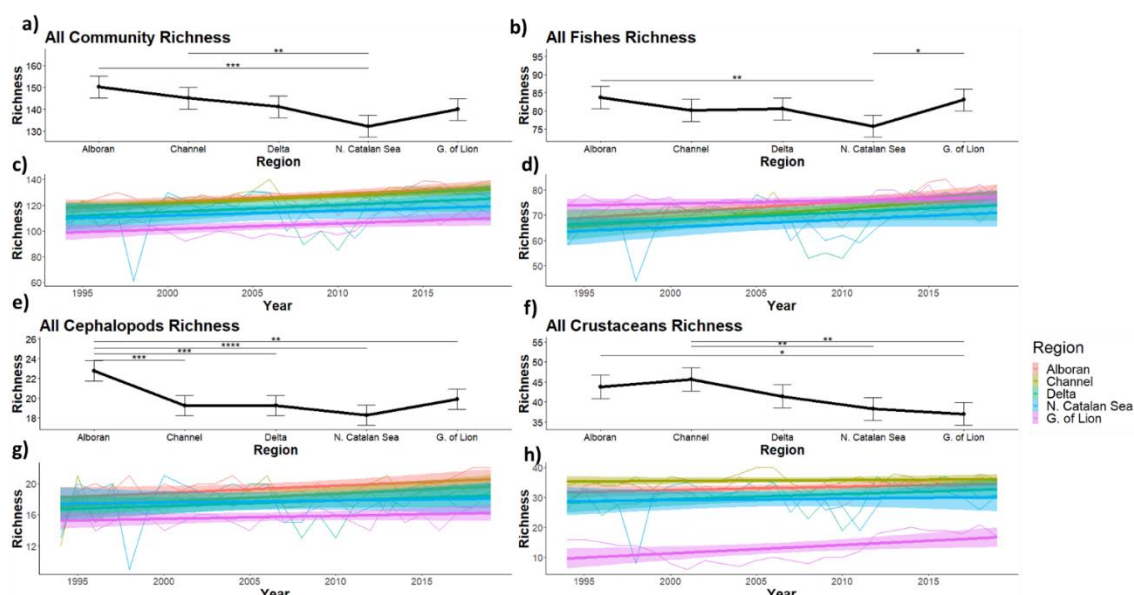


Figure 2.1.2: Temporal trends, pairwise contrast and mean values of species richness (S) for the surveyed community, and for fishes, cephalopods and crustaceans. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate the standard error over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

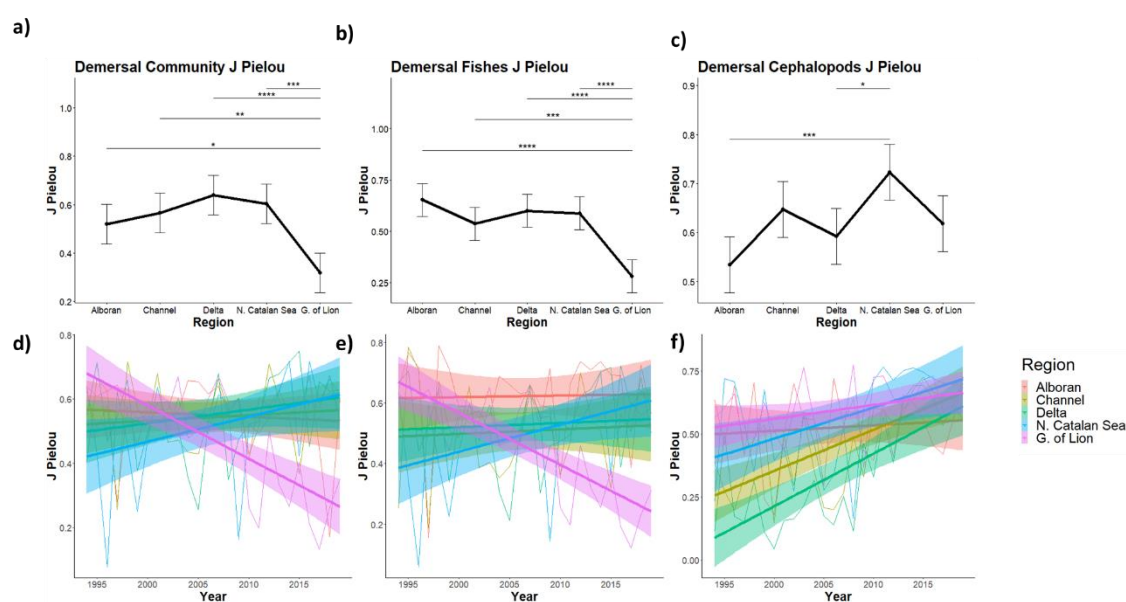


Figure 2.1.3: Temporal trends, pairwise contrast and mean values of Pielou evenness J index for the demersal surveyed community, and for fish and cephalopods. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

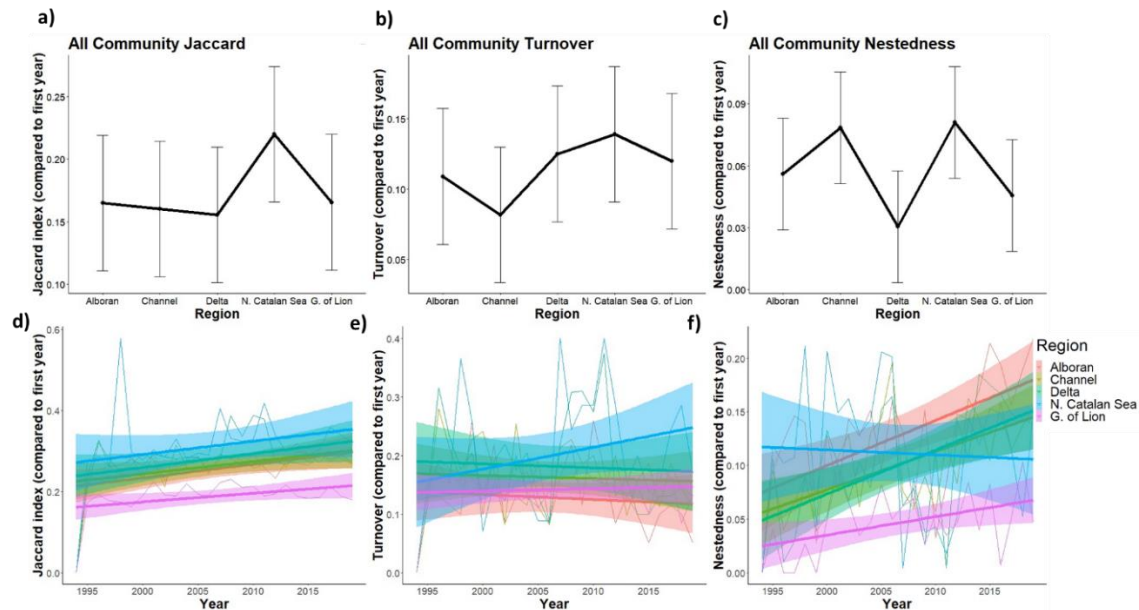


Figure 2.1.4: Temporal trends, pairwise contrast and mean values of β -diversity, turnover and nestedness for the surveyed community. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

Community and taxa-related indicators

The Biomass (B) indices showed a general gradient with a negative south-north pattern, with larger biomass values in the Gulf of Lion (Table 2.1.1, 2.1.2 and 2.1.3). Cephalopods (both all and demersal) showed higher values as well in the Alboran Sea. In contrast, crustaceans showed highest values in the Alboran Sea, while in the other regions values were low. Temporal changes in biomass showed increasing trends specially in cephalopods group and in the Alboran Sea (Table 2.1.2, 2.1.3, 2.1.4, Supplementary Material Table S2.1.3, S2.1.4 and S2.1.5), with few exceptions such as pelagic fishes of the Gulf of Lion that show a clear decreasing trend ($sl=-20.82$, $p<0.05$) (Table 4).

A gradient similar to that of biomass appeared in the surveyed community abundance (N) trends for all regions (Table 2.1.2, 2.1.3, 2.1.4 and S2.1.4), where the Gulf of Lion presented the highest mean values well above those reported for the other regions, while pelagic taxa showed highest values in the south (Table 2.1.4). A temporal pattern of increase taxa was observed (Table 2.1.2 and 2.1.3), with the exception of demersal cephalopods showing declines.

The mean size indicator (MS) was found to have non-significant spatial differences for the majority of groups except for all and demersal fishes and cephalopods (Table 2.1.2 and 2.1.3), which showed significant spatial differences with low values in the Gulf of Lion. However, cephalopods ($F_{4,35}=6.11$, $p\text{-value}<0.001$) did not display a clear gradient, while in the case of fishes all the regions up until the Gulf of Lion showed higher means. Mean size increased with time in various regions with some exceptions such as demersal fishes in the Gulf of Lion and pelagic cephalopods in the Catalan Coast and the Gulf of Lion (Table 2.1.4).

Relative biomass of predators (Bpred) did not display clear gradients for the surveyed community and the fishes (with the exception of the pelagic community), but rather showed low values in both extremes of the study area and higher values in the central regions (Table 2.1.2, Figure 2.1.5a). The pelagic species ($F_{4,35}=4.77$, $p<0.01$) as well as the cephalopods groups (Table 2.1.2, 2.1.3 and 2.1.4) showed south-north gradients with highest biomass values in northern areas. Significant temporal decreasing trends were reported for fishes and the surveyed community, only showing an increasing trend in the pelagic community of the North Catalan Sea and the Gulf of Lion regions (slope, $sl=0.02$, $p<0.001$).

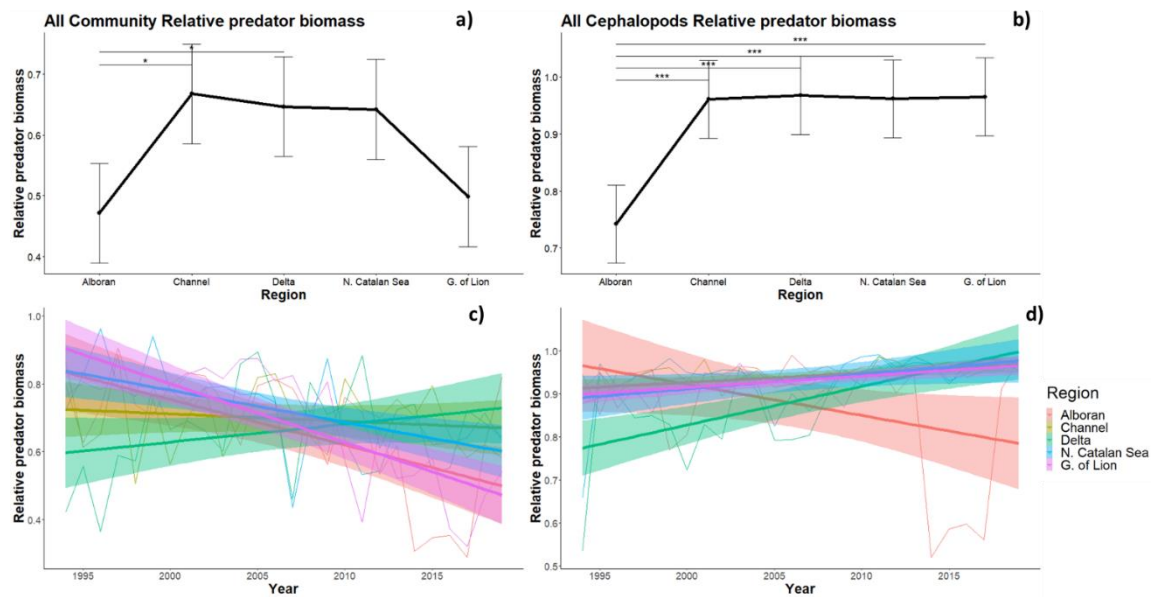


Figure 2.1.5: Temporal trends, pairwise contrast and mean values of Bpred for the surveyed community (left) and cephalopods (right). Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

Results showed how the Relative Fish Biomass (BFish) for the surveyed community was lower in the southern sub-regions than in the northern ones, showing a positive gradient to the north in the study area only interrupted by a decrease in the mean value of the Delta region ($F_{4,35}=7.623$, $p<0.01$) (Supplementary Material Table S2.1.5, Table 2.1.2, Figure 2.1.6a). For all pelagic fish, the highest values were found in the Alboran Sea, while the Delta showed the lowest (Table 2.1.4). In the case of the Relative Cephalopods Biomass (BCeph), there was no discernible pattern although the surveyed community the Gulf of Lion showed the lowest mean value ($F_{4,35}=4.112$, $p<0.01$). Regarding the temporal trends, the biomass of fishes showed a negative trend in the Alboran Sea when considering the surveyed community and demersal species (Table 2.1.2 and 2.1.3), and a negative temporal trend was registered for the pelagic community in the northernmost sub-regions, the Northern Catalan Sea and the Gulf of Lions (Table 2.1.4, Figure 2.1.6c). On the contrary, the Relative Biomass of Cephalopods (BCeph) showed a significant positive relationship with time in the Delta region ($sl=-0.004$, $p<0.05$) when looking at

the demersal species, and a positive increase in the North Catalan Sea (sl=0.02, $p<0.01$) and the Gulf of Lion (sl=0.02, $p<0.001$) when looking at the pelagic community (Table 2.1.4, Figure 2.1.4d).

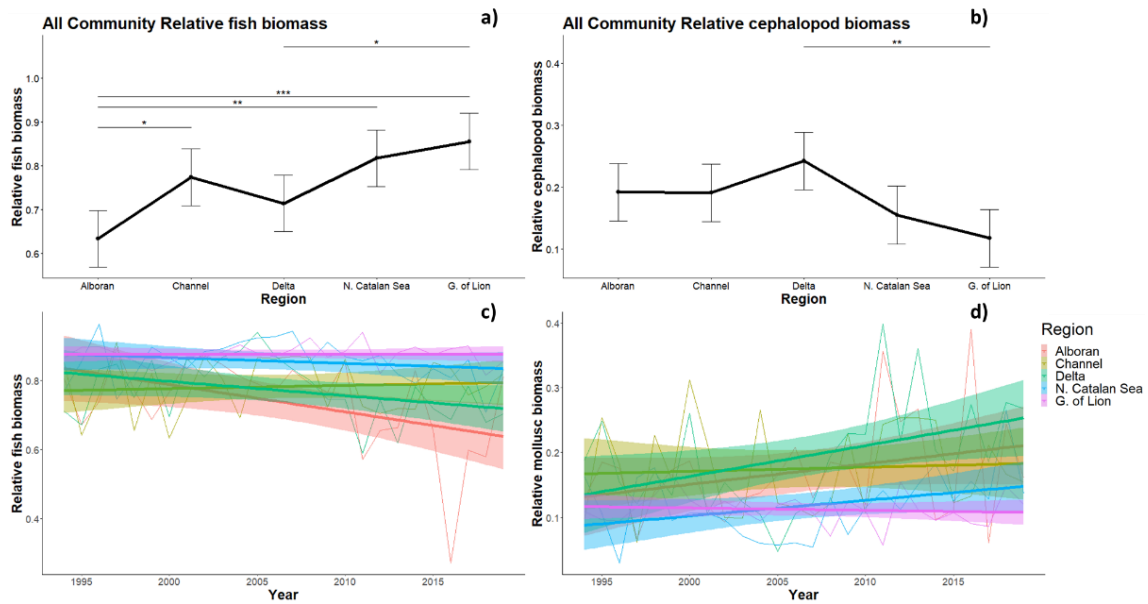


Figure 2.1.6: Temporal trends, pairwise contrast and mean values of BFish (left) and BCeph (right) for the surveyed community. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

Both all surveyed community and the fish community showed lower levels of the TLc and higher levels of TL3.25 in the north (Table 2.1.2, Fig. 2.1.7a). TL4 showed a clear increasing south-north gradient. Cephalopods did not show clear spatial gradients but their maximum values of trophic level indicators were observed in the Delta region. The TLc presented decreasing temporal trends in several regions for all the surveyed community and the fish community, more pronounced in the Gulf of Lions (Table 2, Table 2.1.3, Table 2.1.4; Fig. 2.1.7c). Cephalopods and crustaceans, on the contrary, displayed an increasing trend in both TL3.25 and TLc indicators (Table 2.1.2 and 2.1.3).

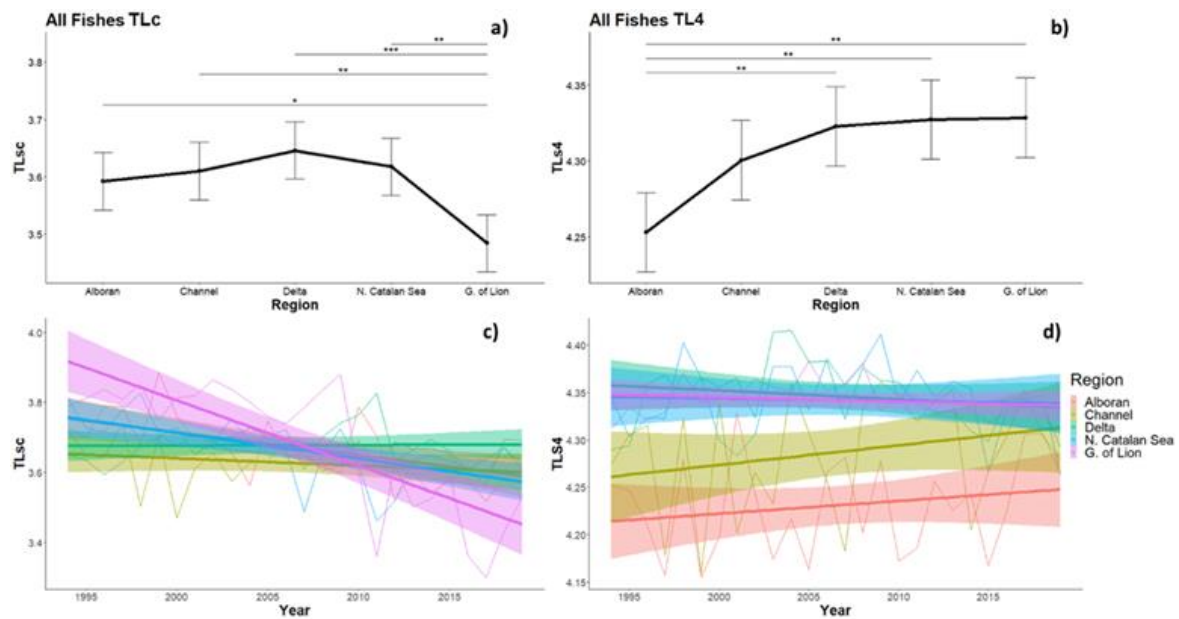


Figure 2.1.7: Temporal trends, pairwise contrast and mean values of TLc (above) and TL4 (below) of all fishes. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

General patterns

Regarding the spatial analyses, four types of gradients were identified in the study area: (i) a clear increase on indicator values from south to north gradient (such as the case of trophic level indicators and the biomass), (ii) a clear decrease from south to north gradients (such as richness and the Shannon Index in some demersal taxa), (iii) gradients interrupted by extreme mean values in one of the regions (such as fish biomass), and (iv) unclear patterns with one or two regions that showed significant differences from the rest (such as TL4 of all and demersal cephalopods and the relative predator biomass of demersal fishes). In addition, my study illustrated that the β -diversity indicators were similar between regions.

Regarding temporal changes, species richness tended to increase with time, while in some cases the Pielou evenness index decreased, less when looking at cephalopods and crustaceans compared to fishes. On the other hand, β -diversity showed an increase with time in most regions, regardless of taxa and species groupings. Nestedness was the component that reported most positive slopes at the expense of turnover, although the North Catalan Sea and the Gulf of Lion regions reported statistically significant increases in turnover in cephalopods and crustaceans.

Biomass indicators showed some declines with time for all surveyed communities and fish communities, including the pelagic species from the northern areas, and increases for cephalopod communities. In fact, cephalopods experienced positive temporal trends in most indicators, species groupings and regions, especially in richness and biomass, where we observed very pronounced slopes in some regions. Trophic level indicators showed

declines when looking at the surveyed community and the fish community in several regions, while they showed increases for cephalopods and crustaceans.

2.1.4. Discussion

In this study, we quantified marine biodiversity and community changes in the Western Mediterranean Sea, and documented contrasting temporal trends and relevant geographic gradients and spatial differences across five sub-regions and taxonomic groups. Our results enabled us to identify which indicators followed continuous geographic gradients, likely influenced by biogeographic features and long-term environmental drivers, and which were more specific to given regions, likely influenced by local fishing impacts and other sub-regional scale processes. The main patterns emerging from my results were associated with taxonomic diversity, β -diversity and its components, relative abundances and biomasses, and trophic level. Our study also reveals emerging characteristic patterns in specific sub-regions and specific taxonomic groups beyond fish (i.e. in the North Catalan Sea and for cephalopods and crustaceans).

Some of the results show similarities to those featured in previous studies (Navarro et al., 2016; Fernandez-Arcaya et al. 2019; Farriols et al., 2020), but we additionally used taxonomic and species groupings (i.e. demersal and pelagic) for this approach and established a regionalization of the gradients. We also computed a wide range of complementary indicators, from classic ones such as species richness and the Shannon index, to more integrative ones such as β -diversity and trophic level-based indicators. As such, my study complements previous studies providing novel results.

According to my results, the richness indicator follows the expected pattern of diversity, decreasing from southern to northern regions. This is a well-described pattern in ecology where warmer areas tend to show larger numbers of species (Worm and Tittensor 2018). This can be explained by environmental gradients such as an increase in temperature or decrease in primary production from the northern to the south most area (Estrada, 1996; Bosc et al., 2004). It is important to notice as well the biogeographical complexity of the Alboran Sea, which represents a confluence of Mediterranean species with the species runoff received from the Atlantic side that can expand northwards along the Iberian Mediterranean coast (Real et al., 2021). When looking at the whole surveyed community and the community of fish (both with all species and the demersal species) this gradient was interrupted by the lowest values appearing in the North Catalan Sea, which matches results found in other studies for non-target finfish as well as analysis of the whole ecosystem (Navarro et al., 2015, Gartner et al., 2007). In both cases, the region reported less species both at spatial grid level and for a regional mean. This pattern could be due to an intense and cumulative human activity in the Catalan Sea area (Taconet et al., 2019), or the reduced area of the continental shelf in this subregion that increases niche and habitat competition.

We also document how the number of species increases in almost all regions with time, although the decrease in richness is rarely documented in the literature and it is usually a sign of the synergy of several human impacts aside from overfishing (Granger et al.,

2015). The increase in my study could be attributed to a decrease in fishing effort, especially of bottom trawlers in some areas (Farriols et al., 2017), or other factors like climate change, which has been linked in temperate systems with an increase in sea temperature and the tropicalization of Mediterranean ecosystems (Antão et al., 2020; Gordo et al., 2021). Indeed, Hidalgo et al. (2021) have recently reported increases of the thermal affinity of these communities, observed for fish, crustacean and cephalopods. However, the causal relationship between richness and any or a combination of these drivers need to be further investigated. It is important to highlight that the number of sampling points per year remained constant with time and results from previous rarefaction curves using the same data show that the sampling effort was sufficient, thus differential sampling effort per year can be ruled out as a possible reason for this trend (Gaertner et al., 2013; Keller et al. 2016).

The lack of statistical significance of the spatial effects for β -diversity could be attributed to the reduced time period analysed in this study (2012-2019), which was applied to compensate for the sampling comparative challenges. It is thus likely that the composition of species has been kept relatively stable over the period used for the spatial analyses. The β -diversity did show, however, temporal significant changes from 1994, with increases over the studied period in most regions, alongside the previously described trends of richness. These increases indicate a lower level of similarity within communities with time, and illustrate the already described pattern of overall change in species but not loss of diversity in natural ecosystems (Dornelas et al., 2014). In all my cases where there were significant temporal relationships in β -diversity, they were mainly associated with a generalized increase of nestedness and a consequent decrease in turnover in most regions. Therefore, in most sectors, nestedness was the main component of biodiversity change, caused by species changes making species-poor sites to resemble a subset of species-rich sites (Baselga, 2010). The region with the highest rate of increase in nestedness over the study period was the Alboran Sea. These results suggest that my studied communities over the different regions became subsets of the original communities by losing or gaining species. This process can be associated with a long term temporal change such as climate change (Vale et al., 2021) and the associated warming of temperate waters as reported for the Mediterranean (Bianchi et al., 2003; Salat et al. 2019), or a higher Atlantic-Mediterranean flux of species through the Gibraltar strait in the case of Alboran (Real et al., 2021).

Changes in primary production dynamics have been recently shown as a potential additional driver because temporal changes in species composition mediated by productivity-driven regime shifts have been reported in the study systems in 2001 and 2009 for the Alboran Sea and Northern Spain, respectively (Hidalgo et al. 2021). While the Mediterranean region could not experience much change in the identity or replacement of species, it could be subjected to losses of different ecosystem functions as β -diversity changes occur in an orderly and non-random manner (Baselga, 2010). Spatial erosion of marine communities due to anthropogenic impacts and a consequent increase in β -diversity has also been observed in other highly impacted areas (Shackell et al., 2012). This process has been previously suggested for the Mediterranean Sea, with higher spatial heterogeneity in its communities due to the long-lasting anthropogenic impact (Hidalgo et al., 2017).

On the contrary, in the North Catalan Sea and the Gulf of Lion, it was the turnover component that dominated the temporal change in β -diversity, consistent with the highest values of beta diversity observed and indicating the replacement of species between sites. In these regions, species replacement seemed to be the most influential driver of biodiversity change and so the change in identity of their communities. The strong dependence of Mediterranean species upon the primary production dynamics (Fu et al. 2018; Hidalgo et al. 2021), and the dynamism of contrasting trophic pathways (Puerta et al. 2015), might trigger strong turnover of species over the North Catalan Sea. In addition, a greater competition in this sub-region is expected as species have to share a smaller ecological space over a narrow continental shelf (Stegen et al., 2013), which could be the reason for this difference of turnover influence. These factors, especially the available space and potential decrease of habitat competition would favour species replacement. The increasing β -diversity is an expected result considering that marine ecosystems usually have high values due to the very mobile species that live within their communities (McGill et al., 2015), including potential biological invaders that could explain the turnover values in areas such as the North Catalan Sea. Meridionalization (or the increase of southern thermophile species due to warming waters) of northern regions such as the North Catalan coast and Gulf of Lion can have an influence as well (Bianchi and Morri, 1993; Boero et al., 2008; Coll et al., 2010; Lloret et al., 2015). However, this process may have a reduced impact in the results since infrequent species were filtered out before analyses. Overall, studies on the β -diversity in the marine environments in general, and in the western Mediterranean in particular, are scarce and my study contributes to filling the gap in the region.

Another of the most relevant patterns observed in this study was the overall high values of abundance and biomass in the Gulf of Lion in contrast to lower ones in the rest of the regions. These spatial patterns are similar to those previously described by Navarro et al. (2015) and partially match those of Fernandez-Arcaya et al. (2019). They also match the macroecological patterns observed in marine ecosystems, where temperate communities tend to show lower rates of biodiversity values and higher biomasses (Worm and Tittensor 2018). This spatial difference can be attributed to the higher primary production in the northern area compared to southern regions (Estrada 1996; Bosc et al. 2004). Interestingly, the lowest levels of biomass and abundance in GSA06 (i.e. Valencia Channel, Ebro Delta and North Catalan Sea) for megafauna in deeper areas (500-800 m) reported in 2012-2015 by Fernandez-Arcaya et al. (2019) match with the identification of lower levels of some of my indicators in the same sub-regions, but at shallower habitats, which can be related with comparatively higher levels of fishing exploitation reported for GSA06 (Fernandez-Arcaya et al. 2019; Taconet et al. 2019).

This study also showed extreme values in several indicators in the Gulf of Lion and the Alboran Sea. This pattern was not recurrent and consistently observed, with different spatial variation observed across the type of indicator or the taxonomic species group. These deviations causing some discontinuous trends may be linked to the heterogeneity in both the north and south most areas seen in environmental drivers or human impacts. A similar case can be seen in the Aegean Sea (Gartner et al., 2007), where diversity is higher than in nearby western seas despite being in the eastern Mediterranean due to an increased amount of nutrients from anthropogenic origin. Both, the Gulf of Lion and the Alboran Sea are the two areas where the environmental gradients suffer more clear

discontinuities, particularly from the primary production and hydrographic perspective (Bosc et al., 2004), which could explain those spatial patterns. In addition, the Alboran Sea has biogeographic singularities in terms of biodiversity as it represents an ecological transition ecosystem between the Atlantic and the Mediterranean (Real et al., 2021). Conversely, these higher values in the extremes could be also a consequence of the lower values in the central area of GA06 related to higher human impacts, as previously discussed.

Regarding results by taxonomic groups, cephalopods and crustaceans showed the most consistent spatial patterns with a north-south gradient in many of their indicators. These patterns correspond to the higher proportion of relative fish biomass in northern bioregions for the surveyed community, and with higher temperatures and lowest primary production in the south (Bosc et al., 2004; Colella et al., 2016). In the case of cephalopods, the increases in most of the study area with time suggest that they may become the “winners” in the region. This increase is consistent with other studies in the Western Mediterranean (Coll et al., 2013; Keller et al., 2016; Hidalgo et al. 2021), and at a global scale (Doubledey et al., 2016; Coll et al., 2020), indicating positive changes of short life-cycle species such as cephalopods under cumulative anthropogenic effects. Cephalopods are fast growing species and are positively affected by increasing temperatures that synergistically interact with the removal of both predators and competitors by fishing, thus allowing boosting production of a few cephalopod species (Keller et al., 2017; Coll et al., 2020). Besides cephalopods, my study also reveals similar patterns in crustaceans, which are generally short life-cycle species compared to most fish, consistent with recent studies in the area (Hidalgo et al. 2021).

Taking into account the different trends in the trophic level-based indicators and their equivalence to the different fishing scenarios proposed by Shannon et al. (2014), the changes in trophic levels observed in my study hint towards a fishing down scenario, especially in the North Catalan Sea. This is in line with previous results investigating trends in specific regions (Coll et al., 2009). In the North Catalan Sea specifically, there has been an increase in species with low trophic level (TLc) and a negative relationship between time and the mean surveyed trophic level above 4. This is probably signalling the intense exploitation reported in the area (Coll et al., 2008; Pennino et al., 2017; Coll et al., 2021). In fact, the indicators analysed in this study picture the North Catalan Sea region as an area with high rates of diversity change, a fishing down process especially notable considering fish, low mean values of richness, abundance and biomass, and decreases in overall biomass and relative biomass of predators. All these values and changes can be associated with overfishing (Shannon et al., 2014) and pollution (Johnston and Roberts, 2009) intensified by the smaller extension of the continental shelf. In southern areas like the Alboran Sea and the Channel, in contrast, some indicators show positive temporal trends (such as the relative biomass of predators and mean surveyed trophic level above 3.25 of crustaceans) and could be related to recoveries of certain species after the decline of fishing effort, as seen for species of chondrichthyans (Ramirez-Amaro et al., 2020, Hidalgo et al. 2021).

Considering my outcomes and the potential limitations of my study, we highlight that some indicators can be prioritized to measure changes in community diversity due to their statistical significance, consistency and responsiveness. Overall, general indicators, such

as species richness, abundance and biomass, were more informative to track long-term spatial and temporal changes in my study area, as they showed more statistically significant relationships and clearer patterns. Others were more complex to interpret, such as evenness and dominance indicators, β -diversity and its components and trophic levels. A reason behind this difficulty of interpretation could be their higher sensitivity to differences between areas and thus their influence by local environmental and human drivers distributed heterogeneously in space.

Our study also highlights that further studies are needed to investigate the dominant mechanistic drivers behind the patterns observed, as well as to elucidate the spatial scale (regional or local) at which these drivers act. Further studies should analyse the effect of cumulative human drivers like fisheries exploitation and/or pollution and environmental factors, such as temperature and primary production, as these are most likely the drivers influencing change. A finer analysis exploring the indicators by depth could also offer more insights as the shelf and slope areas do have different natural communities because of oceanographic conditions and environmental factors, but also face different human impacts (Farriols et al., 2017; Fernandez-Arcaya et al. 2019). In this context, a more detailed spatial analysis is also recommended to confirm those areas with high biodiversity change as well as the most vulnerable areas or those that are most impacted (such as the North Catalan Sea) or may be recovering (such as the Alboran Sea or the Channel). This can be a useful information to be considered for the design and the establishment of marine protected areas (MPAs) and other effective area-based conservation measures (OECMs) for the protection of biodiversity and the sustainable use of marine resources (e.g., Coll et al. 2015; Giménez et al., 2020).

Our study, however, presented some limitations as some traits like the trophic level or the mean size may not capture real changes in the traits but the relative change in biomasses. This is so because the values were taken from available online databases representing information from the entire population. Values from online databases may not be the most suitable due to the oligotrophic and warm environment of the Mediterranean Sea compared to other areas, showing quicker maturation and smaller sizes at maturity for many species due to the temperature size rule (Atkinson, 1994; Silva et al., 2006; Rijn et al., 2017). Another issue is that certain ecosystem functions (e.g. productivity, energy transfer, nutrient cycling) as well as functional groups of ecological importance (such as elasmobranchs, mesopelagic species, or small pelagic fish) are not well captured by my indicators. Lastly, the use of linear effects for the identification of characteristic or recurrent patterns and effects may have masked some non-linear trends that were not considered in favour of analysing long-term effects (Blanchard et al., 2010).

In summary, we have detected spatial gradients and temporal changes in biodiversity indicators through the study area, both at community level and at taxa group level with clear winners (cephalopods) and losers (the North Catalan Sea sub-region) in a context of change. Despite some limitations, this in-depth analysis of the Western Mediterranean ecosystem illustrates the use of a selection of traditional and integrative biodiversity indicators that combine the capacity to detect ecological changes both at a regional and a sub-regional scale.

Acknowledgements

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Table 2.1.2. Summary of the spatial and temporal trends of the taxa (considering all species), in color the regional significant differences (red being the highest mean value, orange and green middle values, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the direction of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. Colors in regional differences are only depicted when there are significant differences by region.

Indicator / region	All community					All fishes					All cephalopods					All crustaceans				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
<i>S</i>	↗	↗			↗	↗	↗				↗	↗								↗
<i>H</i>				↗	↘				↗	↘		↗	↗		↗			↗		
<i>J</i>				↗	↘				↗	↘		↗	↗			↘	↗			
β	↗	↗				↗	↗	↗		↗			↗		↗	↗	↗			
<i>Turnover</i>															↗			↘	↗	
<i>Nestedness</i>	↗	↗	↗			↗	↗	↗		↗		↗						↗		
<i>B</i>	↗	↗					↗				↗	↗	↗	↗		↗	↗			
<i>N</i>					↗										↘					↗
<i>MS</i>	n.s.							↗		↗			↗	↗	↗					
<i>BPred</i>	↘			↘	↘	↘			↘	↘		↗	↗		↗					
<i>BPel</i>			↗							↘		↗	↗	↗	↗					
<i>BFish</i>	↘					NA					NA					NA				
<i>BCeph</i>			↗			NA					NA					NA				
<i>TLc</i>			↗	↘	↘	↘			↘	↘		↗	↗	↗	↗		↗	↗	↗	↘
<i>TL3.25</i>	↘	↘		↘	↘	↘	↘		↘	↘		↗	↗	↗	↗	↗	↗	↗	↗	↘
<i>TL4</i>												↗								

Table 2.1.3. Summary of the spatial temporal trends of the different demersal taxa, in color the regional significant differences (red being the highest mean value, orange and green middle, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the directions of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. Colors in regional differences are only depicted when there are significant differences by region.

Indicator / region	Demersal community					Demersal fish					Demersal Cephalopods					Demersal crustaceans				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
S	↗	↗			↗	↗	↗				↗	↗								↗
H				↗	↘				↗	↘		↗	↗	↗	↗			↗		
J					↘				↗	↘		↗	↗	↗				↗		
β	↗	↗				↗	↗	↗		↗			↗		↗		↗			
Turnover															↗			↘		
Nestedness	↗	↗	↗		↗	↗	↗	↗				↗								
B	↗	↗					↗				↗	↗	↗			↗	↗			
N					↗					↗			↘	↘	↘		↗			↗
MS	n.s.								↗	↘		↗	↗	↗	↗	n.s.				
BPred	↘			↘	↘	↘			↘	↘		↗	↗		↗					
BFish	↘					NA					NA					NA				
BCeph						NA					NA					NA				
TLc	↘			↘	↘	↘			↘	↘							↗	↗	↗	↘
TL3.25	↘					↘			↘							↗	↗	↗	↗	↘
TL4																NA				

Table 2.1.4. Summary of the spatial temporal trends of the different benthic-pelagic taxa, in color the significant regional differences (red being the highest mean value, orange and green middle, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the direction of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. * Beta diversity and its components were disregarded for pelagic invertebrates because of the small number of species. Colors in regional differences are only depicted when there are significant differences by region.

Indicator / region	<i>Pelagic community</i>					<i>Pelagic fish</i>					<i>Pelagic Cephalopods</i>					<i>Pelagic crustaceans</i>				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
<i>S</i>													↗	↗					↘	
<i>H</i>					↗	↗				↗						↘			↘	NA
<i>J</i>					↗	↗				↗						↘				NA
β					↗					↗	*					*				
<i>Turnover</i>				↗																
<i>Nestedness</i>	↗		↗		↗	↗		↗		↗										
<i>B</i>		↗	↗		↗					↘		↗	↗	↗	↗					
<i>N</i>				↘	↘					↘		↗	↗	↗	↗					
<i>MS</i>	↗	↗	↗		↗									↘	↘					
<i>BPred</i>				↗	↗			↗			↘					NA				
<i>BFish</i>				↘	↘	NA					NA					NA				
<i>BCeph</i>				↗	↗	NA					NA					NA				
<i>TLc</i>				↗	↗						NA									
<i>TL3.25</i>			↗			↘			↘	↘	NA									
<i>TL4</i>											NA					NA				

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2.2. Understanding the response of the Western Mediterranean cephalopods to environment and fishing in a context of alleged winners of change

Carlos Veloy, Marta Coll, Maria Grazia Pennino, Encarnación Garcia, Antonio Esteban, Cristina García- Ruiz, Gregoire Certain, Sandrine Vaz, Angélique Jadaud, María González, Manuel Hidalgo



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Abstract

Increasing impacts of both fisheries and climate change have resulted in shifts in the structure and functioning of marine communities. One recurrent observation is the rise of cephalopods as fish recede. This is generally attributed to the removal of main predators and competitors by fishing, while mechanistic evidence is still lacking. In addition, climate change may influence cephalopods due to their high environmental sensitivity. We aim to unveil the effects of different anthropogenic and environmental drivers at different scales focusing on the cephalopod community of the Western Mediterranean Sea. We investigate several ecological indicators offering a wide range of information about their ecology, and statistically relating them with environmental, biotic and fisheries drivers. Our results highlight non-linear responses of indicators along with spatial differences in their responses. Overall, the environment drivers have greater effects than biotic and local human impacts with contrasting effects of temperature across the geographic gradient. We conclude that cephalopods may be impacted by climate change in the future while not necessarily through positive warming influence, which should make us cautious when referring to them as generalized winners of current changes.

Keywords

Cephalopods, ecological indicators, fishing, climate change, anthropogenic impact, β -diversity.

2.2.1. Introduction

Global change causes several negative impacts reported worldwide on marine ecosystems, while it can favour some taxonomic groups. Numerous studies on different areas and species have identified cephalopods as potential winners in the marine environment, while the generalization of this pattern is still pending of conclusive proof. This trend, observed at both regional (Keller et al., 2016; Veloy et al., 2022) and global scales (Doubleday et al., 2016), may be largely influenced by the favouring conditions of climate change (such as warming) and interspecific relationships with other diminishing and competing taxa such as fishes of higher trophic level. Cephalopods have a great ecological importance for their top-down control mechanisms due to their strong predatory role and high trophic levels (Anderson et al., 2011; Eddy et al., 2017). Therefore, an understanding of the factors that affect the cephalopod community, as well as the increase of dominance in the ecosystem, can aid to better understand the current state and expected changes of marine ecosystems.

The overexploitation of fishes, as one of the main predators of cephalopods (Caddy and Rodhouse, 1998; Hastie et al., 2009; Staudinger et al., 2013), has been proposed as an important factor in the increase of this taxonomic group. Indeed, the decrease of fish production results in fishing fleets switching from declining fish stocks towards invertebrates, including cephalopods. In fact, the landings on cephalopods is rising worldwide (FAO, 2020; Ospina-Alvarez et al., 2022). The south of Europe, particularly Spain, is among the countries with more local cephalopod supply available per capita alongside Republic of Korea, Japan and Taiwan (Hunsicker et al., 2010; Ospina-Alvarez et al., 2022), which makes south European stocks potentially more at risk. In the Mediterranean Sea, while many assessed fish stocks are already heavily exploited, the lack of generalized assessment of cephalopods limits the capacity to assess their current health status (FAO, 2022). Furthermore, for these invertebrates, metrics such as the Maximum Sustainable Yield (MSY) are not well adapted to them compared to fishes. This is mainly due to poor data as well as the problems their short life-strategy poses to modelling (Arkhipkin et al., 2021), which represent a long-lasting challenge for the current and future management.

It is also known that cephalopods are highly sensitive to environmental factors (e.g. Arvanitidis et al., 2002; Forsythe, 2004; Pierce et al., 2008) (see list of references and associated mechanisms and observations reviewed and shown in the Supplementary Material Table S1). They also have a great degree of plasticity observed through their different life cycles and species (Arvanitidis et al., 2002; Otero et al., 2009; Pierce et al., 2008). This plasticity results in unexpected responses to certain environmental factors that vary by both taxa and study area with, for instance, differential responses in adult body size to warming across taxa and regions. Both increase in body size and younger maturation and, therefore, smaller adult size and shorter lifespan, have all been reported to be favoured by warming conditions (Forsythe, 2004; Hatfield, 2000; Pecl and Jackson, 2008). High sea surface temperatures (SSTs) generally benefit cephalopods at a population level allowing them to increase their abundance and even their spatial distribution range in some cases (van der Kooij et al., 2016). Primary production also

plays a similar role benefitting cephalopod populations mostly related to upwelling processes, particularly in early life stages, allowing higher survival rates due to the associated increase in secondary production (Bakun and Csirke, 1998; Lauria et al., 2016; Otero et al., 2009; Puerta et al., 2016b). However, in some systems there is a negative relationship between certain species of cephalopods and primary production, mostly due to lagged responses, as paralarva are released during the less intense periods of upwelling (i.e. less productive) to ensure they remain near the coast (Otero et al., 2009), in agreement with the ‘optimal environmental window’ hypothesis (Cury and Roy, 1989).

The Mediterranean Sea is a semi-enclosed sea, characterized by oligotrophic nature and warming increasing temperatures (Coll et al., 2010). It is an important region as a biodiversity hotspot (Coll et al., 2010; Costello et al., 2010), but with many marine resources still overexploited by fishing (FAO, 2022). The local marine ecosystem is also subjected to quick changes due to climate change (Hidalgo et al., 2018; Lejeusne et al., 2010), increased sensitivity to natural variability in primary production (Fu et al., 2018; Hidalgo et al., 2022a), the effects of invasive alien species such as the Lessepsian fauna (Galil et al., 2017) and of pollution (Danovaro, 2003; Pennino et al., 2020). Recent studies analysing marine biodiversity changes in space and time have shown divergent patterns according to the taxonomic groups investigated in this semi-enclosed sea (Carmezim et al., 2022; Pennino et al., 2024; Veloy et al., 2022). One example of these differences is the case of fishes and cephalopods: while the former have been shown to decrease with time, likely related to fisheries activity impacts (Farriols et al., 2020), cephalopods have been shown to be a prolific group (Ciércoles et al., 2018; Keller et al., 2017a; Puerta et al., 2016b; Quetglas et al., 2016).

In the Mediterranean Sea, some relationships between the different environmental drivers, the bathymetric gradient, and the cephalopod community have been already confirmed. For instance, the bathymetric pattern of species richness gradient has been shown to peak nearing the continental shelf break (Keller et al., 2017b). Environmental factors such as SST and primary production can have a positive relationship with species richness as well as biomass (Supplementary Material Table S2.2.1). In contrast, human impacts have been shown to have a negative influence on the cephalopod richness in non-target species, while a non-linear response (increasing richness at low and upper levels of exploitation) also observed (Navarro et al., 2015; Vilas et al., 2019). These findings are in line with reported higher biomass of cephalopods with lower levels of predators and higher levels of fishing (Coll et al., 2013), and in areas with relative warmer waters (Navarro et al., 2015). However, the responses of cephalopods to direct and indirect variables have been shown to differ depending on the studied species and region (Keller et al., 2017b; Puerta et al., 2016a, 2016b, 2015), in part due to short life cycle and their high capacity to adapt to local and regional environmental conditions (Moreno et al., 2002; Pierce et al., 2008).

Most of past and recent research has focused on direct quantitative approaches to study cephalopod populations taking biomass and abundance as main metrics (Hastie et al., 2009; Hatfield, 2000; Otero et al., 2009; Puerta et al., 2016b) (Supplementary Material Table S1), while little is known about other community and biodiversity indicators, or other indicators informing on their function on the ecosystems. In addition, the analyses of drivers causing variation on β -diversity or other community and trophic-based

indicators have not been widely investigated. The combination of these indicators may provide valuable information regarding the geographic and temporal evolution of this taxon, the mechanisms of change and potential implications on the ecosystem functioning attending to environmental and anthropogenic drivers in given areas.

Our hypothesis is that cephalopods, being short-lived organisms, respond more profoundly to the environment than to other drivers, although they can be influenced by local human activities such as fishing (Navarro et al., 2015; Nieblas et al., 2014; Puerta et al., 2016b). Furthermore, these factors could influence competition as well as food availability represented by the predatory fishes and crustaceans, respectively (Puerta et al., 2016a). Thus, the main objective of this study is to investigate local and regional scale drivers of spatial change in the cephalopod community of the West Mediterranean Sea in terms of a set ecological indicators and relate them to environmental, human and biotic drivers. This study follows the results of a regional analysis that showed important increases of cephalopods indicators in the region (Veloy et al., 2022), selecting those indicators that have shown most significant spatial variation.

2.2.2. Materials and Methods

Sampling and study area

We used cephalopods data collected from annual trawling surveys performed within the Mediterranean International Trawl Survey (MEDITS) program between 2013 and 2019 with 1296 unique sampling points (Supplementary Material Table S2), as this period allowed us to get a complete time series of the forcing variables of interest. A common sampling protocol was used in the entire study area, standardizing duration of the hauls as well as gear type and its specifications (Bertrand et al., 2002; Spedicato et al., 2020).

The General Fisheries Commission of the Mediterranean (GFCM) adopted several divisions of the surveyed area denominated Geographical Sub-Areas (GSAs). We focused on the continuous area of the Western Mediterranean, ranging from the Alboran Sea to the Gulf of Lion, corresponding to GSA1 (Northern Alboran Sea), GSA6 (Northern Spain) and GSA7 (Gulf of Lion)(Figure 2.2.1). These three areas display continuous subareas with contrasting hydrographical characteristics: i) the northern Alboran Sea is an area influenced by the influx of Atlantic waters and thus has a high and variable primary production; ii) the Northern Spain, including Valencia Channel, Ebro Delta and North Catalan Sea, is characterized by low values of chlorophyll-a concentration (although the Ebro Delta receives nutrients from continental sources) and high temperature but differ in the width of their continental shelves; and iii) the Gulf of Lion, a shallow area with an extended continental shelf as well as lower SST characterized by variable but high productivity due to its local oceanography (Rhône river input and wind induced coastal upwelling) (Bosc et al., 2004; Estrada, 1996; Nieblas et al., 2014). These subareas divisions have been used in previous studies (Veloy et al., 2022). Because the depth range between 25 and 500 m is the one with the most diversity of taxa, only sample points from those depth ranges (corresponding to the continental shelf and upper slope area) were considered.

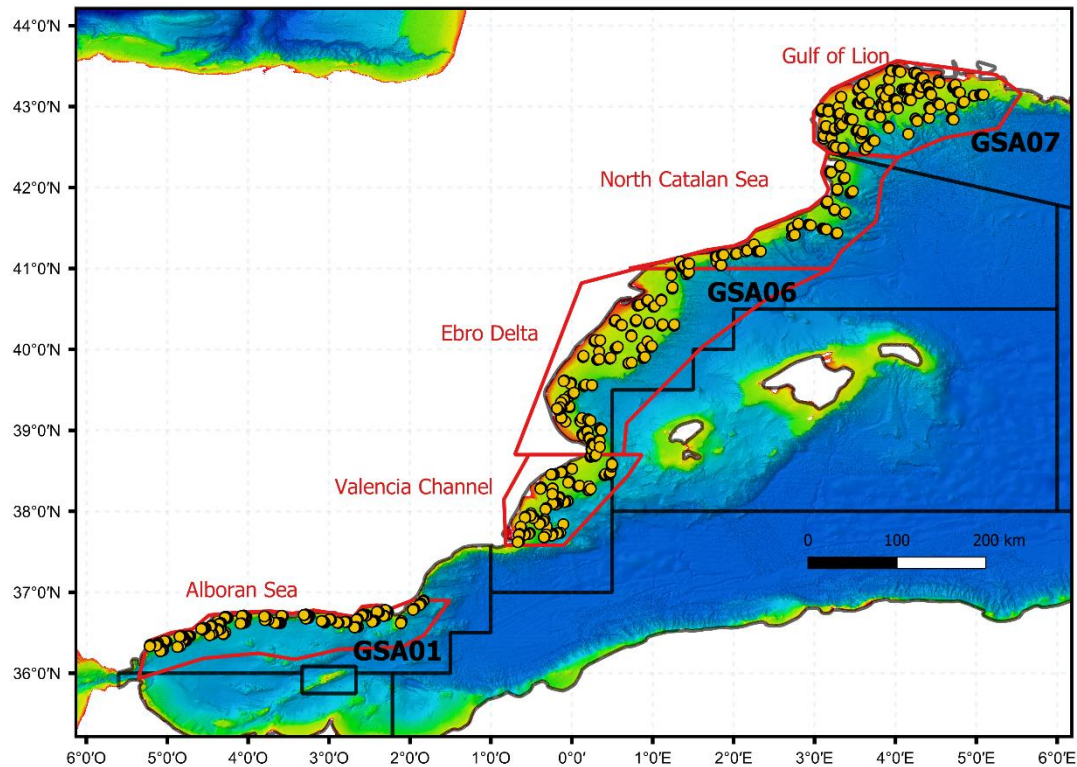


Figure 2.2.1: Western Mediterranean area with the considered subregions (in red), GSA areas (in black) and sampling points of the MEDITS trawling survey used in this study.

Indicators and drivers of change

We used three groups of indicators: (a) traditional biodiversity indicators such as species richness and β -diversity (Jaccard index); (b) community indicators such as biomass, mean size (both of these transformed into logarithm in this study) and relative biomass of predators within the cephalopods (B_{pred}); and (c) trophic level indicators as $TL_{3.25}$ and TL_4 (Table 2.2.1). These indicators were selected based on criteria used in previous studies (Veloy et al., 2022) and the Indiseas project (Coll et al., 2016; Shannon et al., 2014; Shin et al., 2018), such as measurability and data availability (must be estimated routinely and have time-series available), ecological significance and sensitivity to different drivers.

To calculate B_{pred} we labelled as “predator” those species of cephalopods with Trophic Level (TL) above 3.5 that were reported as having maximum sizes larger than 20 cm of total length or equivalent measurements. Trophic levels were obtained from different online databases (Froese and Pauly, 2021; Palomares and Pauly, 2021). After assigning this trait data, those species present in less than 80% of the temporal series were discarded from the study (Supplementary Material Table S2.2.3).

The drivers (independent variables) (Table 2.2.2, Figure 2.2.2) were classified into four categories depending on the information they provided: (a) depth as a structural and static driver (note that geographic smoother were explicitly avoided; see explanation below) (b) dynamic environmental variables (Sea Surface Temperature (SST), and Chlorophyll-a

(Chl-a), (c) dynamic human drivers (Fishing effort) and (d) dynamic biotic variables (Relative biomass of predatory fishes (Fish B_{pred}) and crustacean biomass as a prey indicator). These independent variables were selected because they have shown to be very influential on cephalopod populations, as well as allow to explore different types of change (anthropogenic and natural) (Supplementary Material Table S2.2.1).

Environmental and human drivers were obtained from reanalysis data of physic and biochemistry parameters of the Mediterranean provided by COPERNICUS (2021) with a resolution of 0.04 degrees and from Global Fishing Watch (2019) data with a resolution of 0.01 degree, respectively. The study period selected within the databases is between 2013 to 2019. In the case of the environmental drivers, data was used to calculate yearly means per sample point (i.e. grid cell), while for fishing effort the daily data was processed to get the yearly sum of the total fishing hours per grid cell using previously established methods (Taconet et al., 2019). While the use of lagged variables, specially for the environmental ones, have been featured in other studies (Keller et al., 2017a), we only used data from the same year because the focus of the study was to understand the spatial variation of the community and adding a temporal dimension could complicate the interpretation of the results attending to the spatiotemporal dependence of processes and data.

Lastly, biotic data was extracted from the data available in a previous study (Veloy et al., 2022). The Fish B_{pred} considered a similar criterion of predator as it was described previously for predatory cephalopods (i.e., *Octopus vulgaris*, *Loligo forbesii*). Both fishing effort and the biomass of crustaceans was transformed using the logarithm.

The biotic data derived from MEDITS and the drivers investigated were interpolated into a grid with a resolution of 0.25 degrees over the study area (Figure 2.2.2).

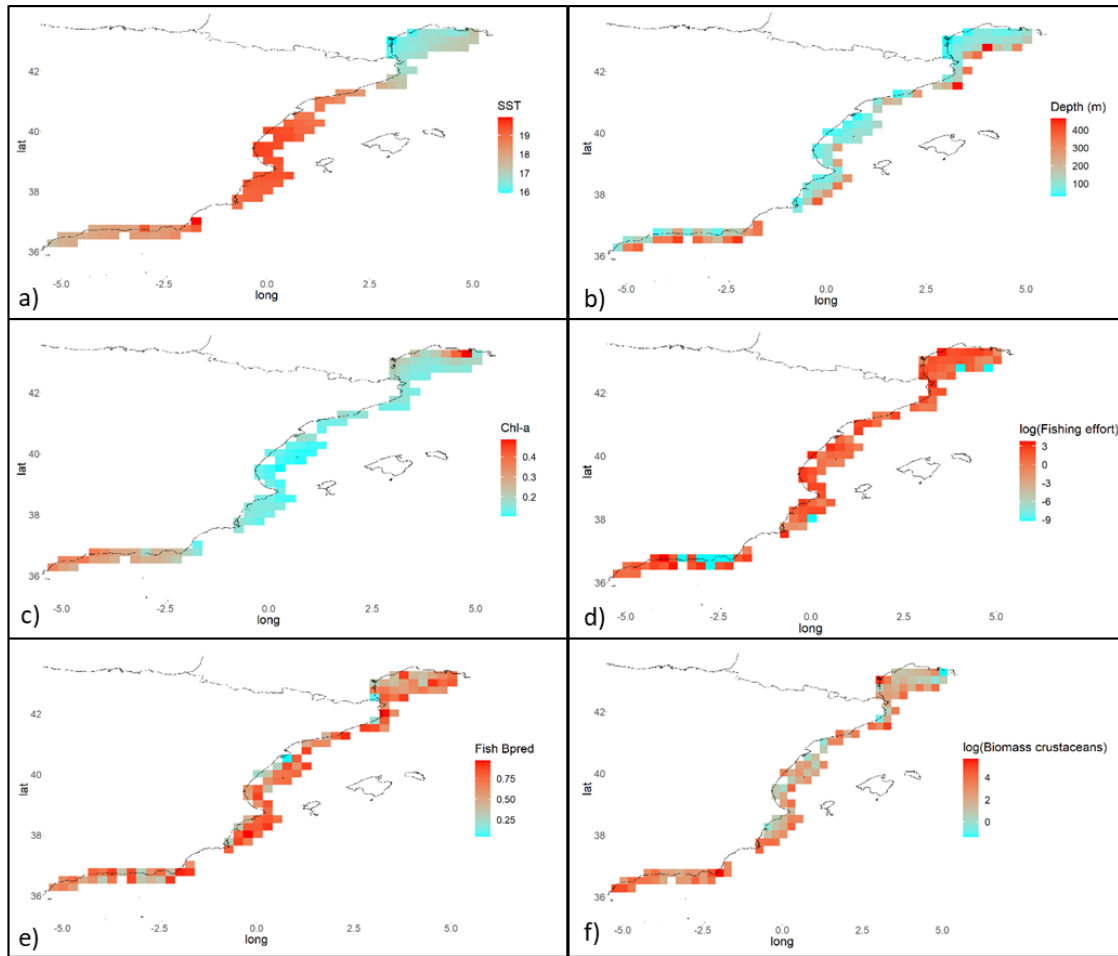


Figure 2.2.2: Spatial variation of the different independent variables considered for this study. Values represent the mean of the time period. a) SST ($^{\circ}\text{C}$), b) Depth (m), c) Chl-a (mg/m^3), d) $\log(\text{Fishing Effort})$, e) Fish B_{pred} , f) $\log(\text{Biomass crustaceans})$.

Data analysis

Firstly, correlation matrices were used to preliminary check the correlation between drivers and all the ecological indicators. The final selection of independent variables (Table 2) featured indicators of each category (environment, human or biological) that were complementary: SST, Chl-a, Fishing Effort, Fish B_{pred} and Biomass of crustaceans.

Secondly, we applied General Additive Modelling (GAM) (Wood, 2006) to each indicator to evaluate the regional influence of environmental and anthropogenic drivers as univariate smoother along with depth as a structural variable (i.e. persistent influence). GAM models were considered for the study due to their premise of a non-predefined functional form of the effect and their capacity to determine non-linear effects, allowing a more complete understanding of the effects and the response capacity of all the indicators. We also took into account the ease of interpretation of the relationships between each indicator and the drivers on an individual level as well as the efficiency to study the residuals, as opposed to other methods. One-dimensional non-parametric smoothing functions used included cubic splines with up to a maximum of 3 degrees of freedom (i.e. 4 knots) to avoid model overfitting and obtain meaningful functional forms

of the effects. All the models were calculated using Gaussian distribution with the exception of the Richness model, where a Poisson distribution was used. Model selection was done comparing the models with all the independent variables with those where the non-statistically significant variables were sequentially removed (Supplementary Material Table S2.2.5). An important element in my modelling approach is that we explicitly avoided the use of a geographic bi-variate smoother (latitude, longitude) to allow environmental factors to capture the potential spatial variability.

To distinguish whether the drivers investigated were geographically structured or whether they represented a larger scale impact at the scale of the studied region, we investigated the partial residuals of all covariates and models according to the five distinct sub-regions continuously spread over the three contiguous GSAs: GSA1, GSA6 and GSA7. We indicate in the results when it is meaningful based on the overlapping of the residuals of different sub-regions. Finally, we present the spatial predictions of the models using the independent variables as predictors.

All indicators and analysis were calculated with R version 4.2.2 (R Core Team, 2022). Jaccard index and its components were calculated using the R package betapart (Baselga and Orme, 2012) and the GAM models were obtained using mgcv (Wood, 2011).

Table 2.2.1. Dependent variables used in the study and information they provide about the state of cephalopods and the communities they are part of.

Indicators	Information about cephalopods/ecosystem	Data source	Indicator source
Biodiversity indicators			
Richness	Number of cephalopod species present	MEDITS data; Veloy et al., 2022	McIntosh, 1967
B-diversity (Jaccard index)	Temporal change of the cephalopod subset of the ecosystem	MEDITS data; Veloy et al., 2022	Blowes et al., 2019; Dornelas, 2014
Biomass and size			
Total biomass of cephalopods (Biomass)	Weight of all cephalopods (transformed to logarithm)	MEDITS data; Veloy et al., 2022	Coll et al., 2016
Relative predatory cephalopod biomass (B_{pred})	Fraction of cephalopods that are considered predators	MEDITS data; Veloy et al., 2022	Coll et al., 2016
Mean Size	Weight of the average cephalopod as a proxy for size (transformed to logarithm)	MEDITS data; Veloy et al., 2022	Shin et al., 2018; Forsythe, 2004
Trophic level indicators			

TL _{3.25}	Mean trophic level of cephalopods above 3.25	MEDITS data; Veloy et al., 2022	Shannon et al., 2014
TL ₄	Mean trophic level of cephalopods above 4	MEDITS data; Veloy et al., 2022	Shannon et al., 2014

Table 2. Independent variables used in the study and sources of origin.

Variable	Definition	Data source	Variable source
Structural driver			
Depth	Depth at sea bottom	MEDITS data	
Environmental drivers			
SST	Sea Surface Temperature	COPERNICUS, 2021	COPERNICUS, 2021
Chl-a	Primary production	COPERNICUS, 2021	COPERNICUS, 2021
Human impact drivers			
Fishing effort	Number of yearly hours that vessels spent fishing on an area, (human pressure) (transformed to logarithm)	Global Fishing Watch 2021	Anderson et al., 2011; Caddy and Rodhouse, 1998
Biotic drivers			
Fish B _{pred}	Fraction of fishes that are considered predators (competitors and predators of cephalopods)	MEDITS data; Veloy et al., 2022	Coll et al., 2016; Veloy et al. (2022)
Crustacean biomass	Weight of all sampled crustaceans from the order Malacostraca, excluding amphipods and isopods (cephalopod main prey) (transformed to logarithm)	MEDITS data; Veloy et al., 2022	Puerta et al., 2015; Veloy et al. (2022)

2.2.3. Results

Biodiversity indicators

Cephalopods' richness showed positive relationships with SST above 18 °C, a linear influence of the biomass of crustaceans, as well as a maximum of species at depths of 150-300 m (Figure 2.2.3, Table 2.2.3). Spatially, it presented lower values in northern areas, characterized by low temperatures and low values of crustacean biomass. Richness showed maximum values on the southernmost area of GSA6, where all those drivers show higher values. Interestingly, SST displayed a spatial segregation of partial residuals while the other drivers showed a regional effect (i.e. overlapping distribution, Supplementary

Material Figure S2). Maximum species richness values were observed south of the Ibiza Channel and a heterogeneous pattern emerged in the Alboran Sea and the Ebro delta.

β -diversity showed a nonlinear relationship with SST with a maximum value around 17 °C followed by a decrease (Figure 2.2.3, Table 2.2.3). It showed a negative relationship with Chl-a until 0.4 mg/m³ from which β -diversity increased. It also showed a positive non-linear relationship with fishing effort and a negative relationship with fish B_{pred} and depth. Spatial patterns were roughly opposite to the ones found for richness, with the highest values found in the northern areas and the lowest on the south of GSA6 on the Valencia Channel. The partial residuals of the effects showed the highest values of this index in the Gulf of Lion and North Catalan Sea, which are areas with the lowest SST (Figure 4).

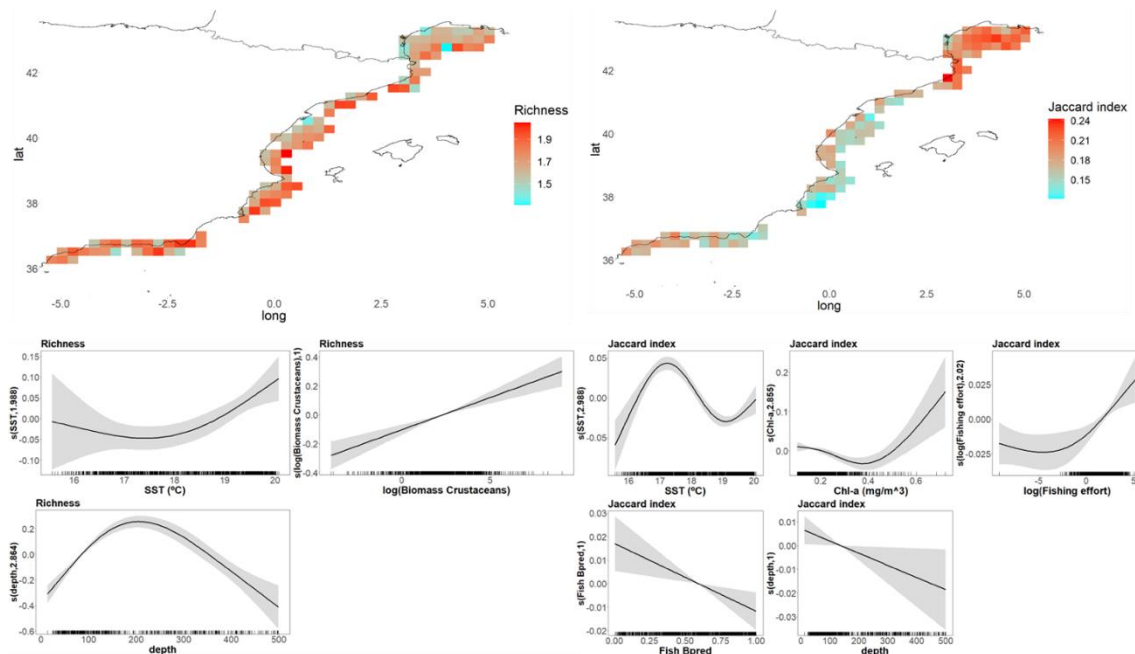


Figure 2.2.3: Spatial variation and smoothing effect of species richness (left) and β -diversity (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

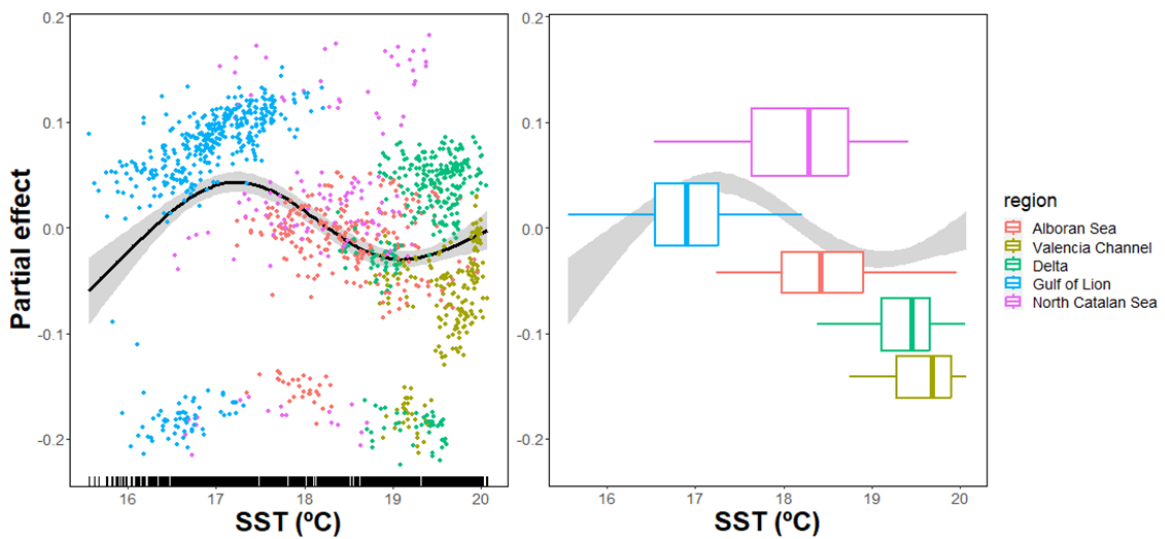


Figure 2.2.4: Residuals (left) and boxplots (right) of the partial effect of SST on the Jaccard index. The shaded areas of the partial plot indicate the 95% confidence interval.

Biomass and mean size

A decreasing trend was found between total cephalopods biomass and SST, reaching a minimum between 17 °C and 18 °C and a small increase at 19 °C (Figure 2.2.5, Table 2.2.3). It also showed a non-linear increasing trend with biomass of crustaceans and with Fish B_{pred} , with a maximum value at ratios stabilized around 0.5 in the latter case. On the other hand, cephalopods biomass decreased with Chl-a and particularly with depth. The highest values were found in the shallow areas of the Gulf of Lion and the deep areas in central Northern Spain (i.e. Ebro Delta). The partial residuals of the effects of SST showed that the Catalan Coast and the Gulf of Lion areas were associated with the highest values of the indicator as well as the decrease in cephalopods biomass (Figure 2.2.6).

SST had a negative effect on B_{pred} until 18.5 °C and of Chl-a until 0.3 mg/m³ (Figure 5, Table 2.2.3). Residuals on the SST model showed a geographical pattern of this effect (Figure 2.2.6), where the Gulf of Lion and the Catalan Sea were associated to higher values of B_{pred} and the residuals of the rest of the independent variables were more homogeneously distributed (Supplementary Material Figure S5). B_{pred} showed a nonlinear decreasing trend with depth and biomass of crustaceans, while fish B_{pred} had a positive linear relationship with this metric. Areas from the north had higher ratios of predators than southern areas such as the Alboran Sea (GSA1) showing a gradient between the former and the Gulf of Lion (Figure 5).

Mean Size (Figure 2.2.7, Table 2.2.3) had a negative nonlinear relationship with Chl-a and depth, and a dome-shaped relationship with SST with a maximum at 18 °C. It also had a clear positive relationship with fish B_{pred} . Highest mean sizes appeared in GSA6 areas, on grid cells where primary production was low and the ratio of predatory fishes was high.

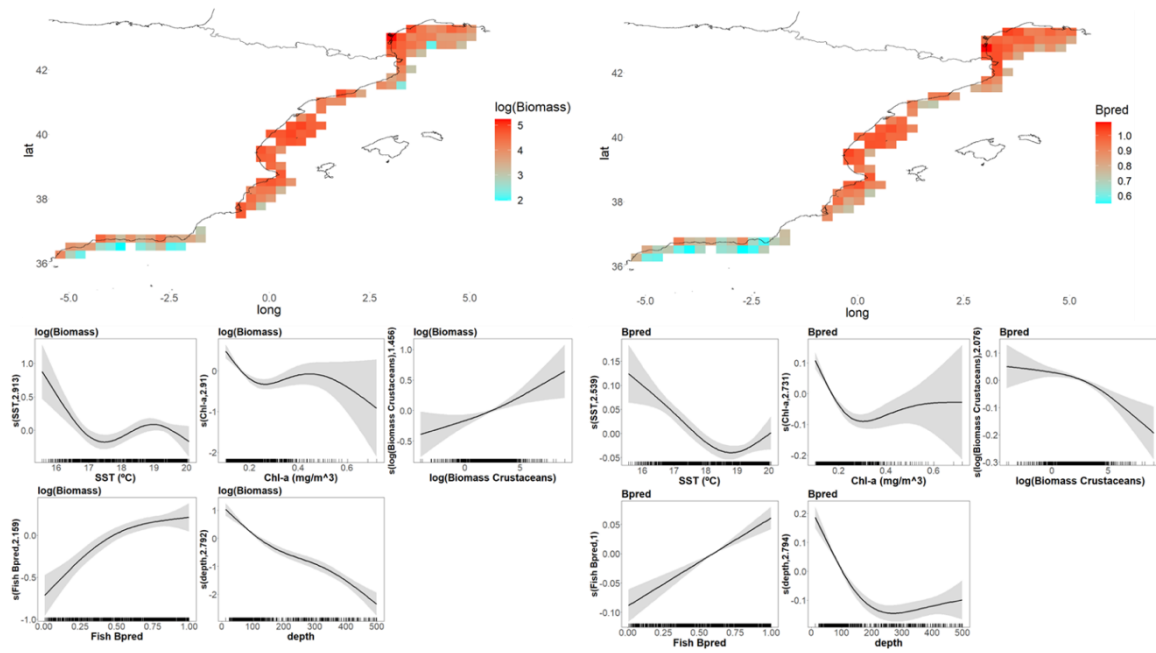


Figure 2.2.5: Spatial variation and smoothing effect of the Biomass (log scale, left) and B_{pred} (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

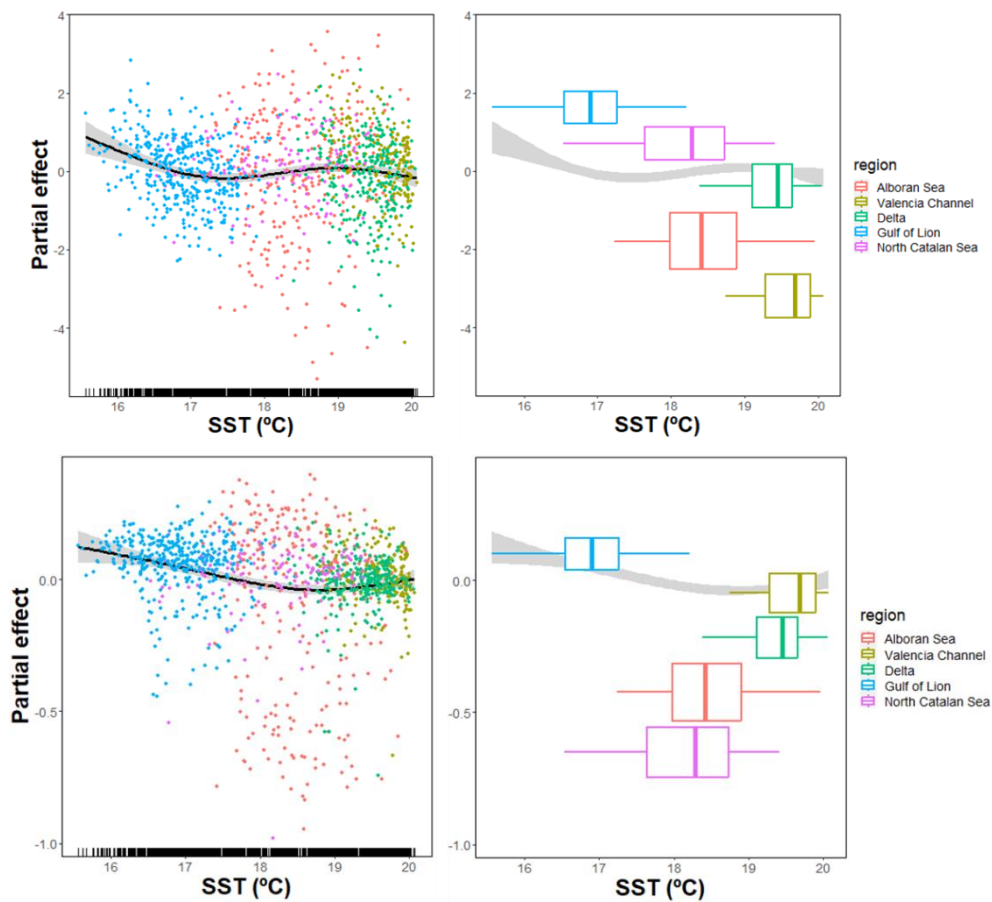


Figure 2.2.6: Residuals (left) and boxplots (right) for SST of the Biomass (log scale, upper row) and B_{pred} (lower row) models. The shaded areas of the partial plot indicate the 95% confidence interval.

Trophic level indicators

$TL_{3.25}$ presented a linear negative relationship with biomass of crustaceans (Figure 8, Table 3). Meanwhile, for SST and depth, these relationships were positive but non-linear. The highest values of $TL_{3.25}$ were found within the cells of GSA6, an area with generally high SST and biomass of crustaceans (Figure 2.2.8). Partial residuals seem to confirm this trend as the values of the residuals of the regions of the Valencia Channel and Ebro delta are higher than the other regions (Supplementary Material Figure S2.2.6).

For TL_4 , Chl-a also showed a dome-shaped influence with a maximum near 0.4 mg/m^3 . SST showed a positive relationship with TL_4 , while the biomass of crustaceans and depth had a negative relationship. The highest values of TL_4 were found in the shallow waters and comparatively in the south, being associated with high productivity, intermediate values of SST and low values of biomass of crustaceans (Figure 2.2.8). Some high values of TL_4 were also found on sparse cells corresponding to temperate shallow waters in the Gulf of Lion.

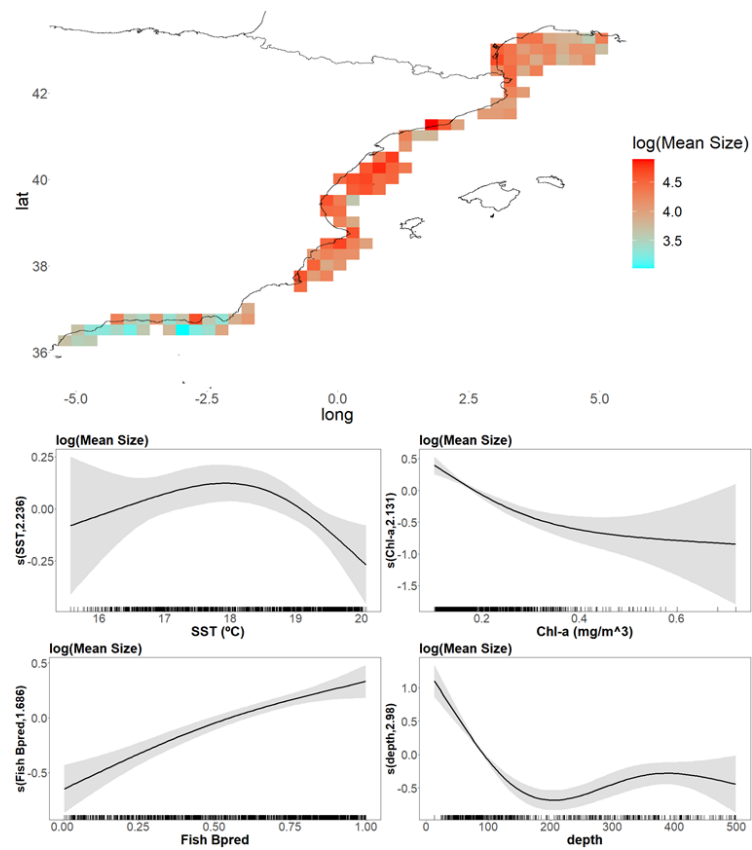


Figure 2.2.7: Spatial variation and smoothing effect of the Mean Size (log scale). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

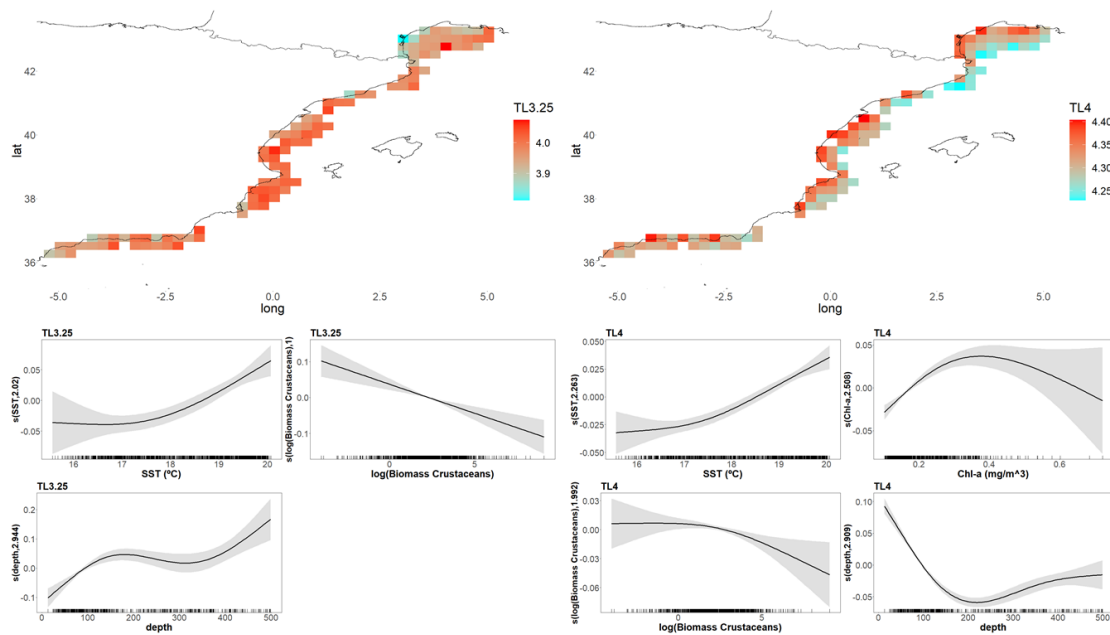


Figure 2.2.8: Spatial variation and smoothing effect of mean trophic level above 3.25 (left) and 4 (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

Table 2.2.3: GAM models summary for each ecological indicator. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. edf = Estimated degrees of freedom of univariate smoothers; %DV = Deviance explained (percentage).

Indicator	Drivers	Intercept	edf	%DV
Richness		1.697 ± 0.012		23.6
	SST		1.988***	
	Log(Biomass crustaceans)		1***	
	Depth		2.864***	
B-diversity (Jaccard index)		0.183 ± 0.002		10.9
	SST		2.988***	
	Chl-a		2.855***	
	Log(Fishing effort)		2.020***	
	Fish B_{pred}		1**	
	Depth		1 *	
Log(Biomass)		3.988 ± 0.312		25
	SST		2.913***	
	Chl-a		2.910***	
	Log(Biomass crustaceans)		1456 **	
	Fish B_{pred}		2.159***	
	Depth		2.792 ***	
B_{pred}		0.878 ± 0.005		27.5

	SST	2.539***	
	Chl-a	2.731***	
	Log(Biomass crustaceans)	2.076***	
	Fish B _{pred}	1***	
	Depth	2.794 ***	
Log(Mean Size)		4.079 ± 0.031	10.02
	SST	2.236*	
	Chl-a	2.131***	
	Log(Fishing effort)	1.442	
	Fish B _{pred}	1.686***	
	Depth	2.980***	
TL_{3.25}		3.977 ± 0.005	8.82
	SST	2.020***	
	Log(Biomass crustaceans)	1***	
	Depth	2.944***	
TL₄		4.328 ± 0.002	34.5
	SST	2.263***	
	Chl-a	2.508***	
	Log(Fishing effort)	2.706	
	Log(Biomass crustaceans)	1.992 **	
	Depth	2.909***	

Overall trends

In most of the dependent variables, SST showed a change of trend between 17 °C and 19 °C, corresponding mostly with the transition area of the Catalan coast between the Gulf of Lion and the Ebro delta broad shelf (Figure 2.2.1). Values on the indicators switched from a descending curve to an ascending one and were associated with the spatial gradient of this variable, corresponding to three thermal areas. Chl-a showed a similar pattern, with an inflection point that indicates a change in response between 0.3 and 0.4 mg/m³, which is mainly associated with the extreme areas in the Gulf of Lion and the Alboran Sea (Supplementary Material Figures S2.2.3 and S2.2.4). The effects on cephalopods' indicators were mainly associated with the geographic pattern of these two covariates, although in the case of Chl-a it seems to show a reduced geographical component in some indicators unlike SST, where a large geographic effect is apparent. These shifts in trends experienced between the Alboran Sea must be taken with caution, since the effects and the mechanisms behind them are not the same as those found in the Gulf of Lion-Catalan Coast area. This is due to its particularities as a transitional zone between the Atlantic and the Western Mediterranean and the influence of the ocean in its oceanography and the high turnover of species in this ecosystem. Those indicators showing a larger influence by environmental variables were β -diversity and B_{pred}, which revealed gradients alongside the Western Mediterranean coast. When looking at the partial residuals of β -diversity and B_{pred}, the spatial effect responsible for these gradients was visible and associated to SST, as values from each region are structured in differentiated clusters along the thermal gradient (Supplementary Material Figures S2.2.1 to S2.2.5).

Those indicators most influenced by other types of variables, both biotic and human, showed less clear spatial patterns in the effects, likely indicating regional impacts. This was revealed by the partial residuals of all the regions, which were distributed in a more homogenous way along the curve of the smoothing effect with no differences between the regions. This would correspond to more heterogeneous effects on the indicators selected going beyond regional environmental gradients. Examples of these effects are fishing effort on β -diversity or Biomass of crustaceans on Richness.

Overall, GSA1 had lower values in most indicators than the ones in the rest of the study area, except for TL₄. The GSA6 area presented intermediate or high values for the different indicators, with the exception of the areas adjacent to the Ebro delta (e.g. Biomass, B_{pred}) and Valencia channel (e.g. β -diversity). Grid cells within the Valencia channel area tended to have lower values than those in the rest of the GSA6 region. GSA7 showed high values for many indicators compared to the rest of the Western Mediterranean, like Biomass or B_{pred}.

2.2.4. Discussion

This study provides a multidimensional perspective of the cephalopod community to further comprehend their ecology and role in marine ecosystems. Previous studies examined the interactions between this taxon and drivers at a species level (Miyahara et al., 2005; Moreno et al., 2014; Otero et al., 2009; Xavier et al., 2016; among others) or considered different types of cephalopods such as squids and octopus represented by a single species (e.g. Puerta et al., 2015) (see Supplementary Material Table S2.2.1 for further details in a summarized review performed for the present study). While others studies have focused on the community analysing the variation of species composition (Keller et al., 2017a), we here investigated the cephalopod community from a different perspective: using a set of complementary ecological indicators that offer a wider picture about this diverse group along with their response to both environmental drivers and anthropogenic pressures. Our study brings novel elements to the spatial nature of the impacts of both environmental and human drivers, whether they present regionally heterogeneous or geographically effects structured in gradients. In fact, while spatial patterns of the indicators were already hinted at in a recent study (Veloy et al., 2022), we here identify the main responsible drivers of the known regional patterns including those observed at a finer scale. For instance, values of the biomass of predatory cephalopods display a positive south-north gradient (mainly due to the effect of SST), while TL_{3.5} displays maximum values on the southern parts of GSA6 and intermediate ones on the northern areas. On the other hand, β -diversity, which was not showing any significant spatial effects when looking at a regional scale in past studies, revealed a positive south-north gradient in my study, mainly driven by the SST gradient.

Species richness has been suggested to follow large geographical gradients, with particular latitudinal variation along the Mediterranean Sea (Coll et al., 2010; Navarro et al., 2015; Veloy et al., 2022). However, at a regional scale, my study did not show marked geographical trends, highlighting maximum values around the Valencia Channel. This is

consistent with recent unpublished studies evidencing a regional southern displacement of the demersal community in the Iberian Peninsula following sub-regional pathways of climate velocity (Sanz-Martín et al., 2024). These could increase local responses of diversity in southern regions of GSA6 associated with local displacements to avoid sub-optimal thermal habitats. In fact, richness and β -diversity appear to have complementary patterns, with cells showing high values of β -diversity generally having low species richness and vice versa (Pennino et al., 2024). This is especially apparent in GSA6 and GSA7. Some areas with the lowest values of richness tended to be associated with low biomass of crustaceans and low SST, similarly to what was found in recent studies (Keller et al., 2016; Oesterwind et al., 2022; Vilas et al., 2019), which are likely related to lower food availability.

Fishing impact was only observed to have a significant effect on β -diversity, which is consistent with previous studies suggesting the erosion of the spatial structure of communities with a consequent decrease in connectivity between putative meta-communities (Hidalgo et al., 2017; Shackell et al., 2012). The exploitation pressure, especially in large species with more fecundity and mobility, could trigger the destabilization of northern ecosystems and also explain a smaller number of species at a local and regional level. This mechanism has been particularly observed in the GSA6 (Hidalgo et al., 2022b; Pennino et al., 2024; Veloy et al., 2022).

The biomass of the cephalopod community was found to be very influenced by environmental drivers, which had a marked geographical effect likely driven by SST. Our results show that SST displays a generally negative relationship with cephalopod biomass, with the colder areas of the Western Mediterranean having more biomass than warmer ones consistent with recent studies (Schickele et al., 2021). Interestingly, in areas such as the Portugal shelf the trend is inverse to my observations, yet it shares a similar threshold of change at 17 °C in surface waters for *L. vulgaris* (Moreno et al., 2014). In the Mediterranean area, differences in responses between cephalopod taxa were also noted with some species associated with cooler waters, while others thrive on warmer environments (Keller et al., 2017b; Puerta et al., 2014). These variations in the non-stationary environmental effects among species could affect the response of the overall group related with the variation of species composition of cephalopods community in different areas, and ultimately limiting a regional global response of the cephalopods community to warming.

Cephalopod biomass appears to be positively influenced by crustacean biomass, showing a close link between cephalopods population and prey availability. It is consistent with species-specific relationships of cephalopods in my study area (Puerta et al., 2015), being notable that prey and predators have similar spatial patterns as it can be seen as well in GSA7. Biomass of predators (fishes) also result in higher biomass of cephalopods, reaching an optimum at intermediate values, which could suggest that higher values could keep stable cephalopod biomass likely due to high pressure from predators (Bakun and Csirke, 1998). Although we here considered crustaceans as the prey item of cephalopods, larger species (specially squids) may also tend to prey more on fishes in oceanic ecosystems (Lordan et al., 1998). However, at a Mediterranean scale, previous studies support that even on relatively large species, crustaceans are present to some degree on their diet (Puerta et al., 2015). Previous research and the smaller sizes of the cephalopod

species found in the study area may support that the proportion of piscivory might not be high enough to alter the results and their interpretation in the present study.

The biological and environmental drivers on mean size, meaning the high biomass of crustaceans, high B_{pred} of fishes and low primary productions, are similar to those observed in the Eastern Mediterranean (Arvanitidis et al., 2002). However, it is possible that the negative relationship between mean size and Chl-a could be due to an indirect effect of fishes over cephalopods. As observed at species level, it could be a consequence of the competition with other fishes during paralarval phases (Keller et al., 2017b; Puerta et al., 2015), decreasing food availability and therefore limiting survival and growth. This would also be especially notable in areas with high SST, which increases growth rates on hatchlings at the cost of shortening maturation and lifespan (Hatfield, 2000; Pecl and Jackson, 2008). On such systems and with reduced food availability, paralarvae do not benefit from the faster metabolic rates resulting in a smaller size at adulthood (Pecl and Jackson, 2008; Pierce et al., 2008; Xavier et al., 2016). At a community level, lower mean size seems to suggest that there are more small-sized species in those areas, where fish B_{pred} is lower. Small cephalopods, such as sepiolids or the genus *Allotheutis*, are present on the diet of more fish species than larger cephalopods, thus fish predation or its reduction would play a bigger role in their dynamics (Daly et al., 2001; Velasco et al., 2001). We can also remark on the possible contribution that recruits may have on my selected indicators. As seasonal recruitment peaks of some species occur during the sampling season, between May and June (Pierce et al., 2010; Tursf et al., 1995) and also has shown spatial variability between areas due to regional environmental conditions (Puerta et al., 2016b).

TL_{3.25} was found to be associated with low biomass of crustaceans as well as areas with low ratios of predator fishes. The trophic level of TL₄ was also related to low biomass of crustaceans. The reason behind could be the competition with fishes as well as their possible predation pressure. The observed decline of fishes due to high exploitation levels would indirectly favour higher trophic levels in cephalopods, especially as seen with TL_{3.25} (Caddy and Rodhouse, 1998; Coll et al., 2010; Hastie et al., 2009; Pennino et al., 2017). This may support the hypothesis of cephalopod replacement in response to the removal of fishes, especially at high trophic levels.

Out of all drivers, fishing effort was the least influential driver as it only showed significant effects on the β -diversity. In general, cephalopods seem to be less sensitive to direct human local impacts than to environmental ones, which may be linked to their short life strategy that also make them less susceptible to be affected by the continuous pressure of fishing (Quetglas et al., 2016). The biology of this group becomes both an advantage and a hindrance, as this greater dependence on environmental factors can make them more susceptible to climate variations. One example could be warming, which has been shown to affect cephalopods at species level (Forsythe, 2004; Georgakarakos et al., 2002; Xavier et al., 2016), and at a community level in this study. The response observed to an increasing SST is either negative for some of the key indicators, such as the total biomass of cephalopods or the biomass of predatory cephalopods, or becomes negative after reaching a certain temperature threshold like in mean size. It is worth acknowledging, however, that in the case of this last indicator it could be also caused by peaks in recruitment of species like *Eledone cirrhosa* (Tursf et al., 1995), which is also fairly

abundant in the database analysed. This is especially relevant in my study area, as northward migrations and expansions in response to increasing SST (i.e. meridionalization) are limited by landmass on the Gulf of Lion region.

The selection of indicators shown in this manuscript also responds to the need of the EU's Marine Strategies Framework Directive (MSFD) to assess the state of marine communities. These ecological metrics were complementary to some of the proposed descriptors within the framework, specifically for D1 and D4 related to both biodiversity as well as trophic ecology (IEO and MAGRAMA, 2012a, 2012b). This study takes into account some indicators not considered in the current MSFD work, such as the β -diversity, that can be useful to better understand the different components of biodiversity from local to regional scales. Other chosen indicators correspond to already established metrics and objectives. For instance, B_{pred} is equivalent to the descriptor 4.2 (proportion of species on high levels of the trophic chain). Meanwhile, trophic level indicators help to assess the state of the trophic chain of the taxa of study. Overall, the use of various indicators highlights the relevance of this study to inform future policy recommendations.

These results also call for caution when referring to cephalopods as general winners to expected warming. While they have been thriving compared to other taxa such as fishes, and in spite of their opportunistic lifestyle, the observed responses of indicators to SST suggest that detrimental effects could be expected, particularly in geographically localized areas with higher warming. Based on these results lower values of biomass, mean size and ratio of predator species could be observed in the aforementioned areas. It is also important to consider that this study reflects the mean response for the entire Cephalopoda class, therefore differences between species sometimes turn into opposite responses to the same environmental pressures attending to their life history characteristics (e.g. benthopelagic o benthic habitat), as it is the case of *Illex coindetii* and *Eledone cirrhosa* (Puerta et al., 2014). In the Western Mediterranean basin, the squid was associated with colder waters while the aforementioned octopod was seen to displace towards warmer environments. This is also relevant in terms of fisheries management as the increase in fishing effort might affect cephalopod communities by changing their relative species composition with a differential effect of those inhabiting in the benthic or the pelagic realm.

It is worth noticing that the results may represent a snapshot of the community since the MEDITS data samples are only from one season (in the summer, between May and June). Some of the considered factors have shown different effects during summer and winter on some cephalopod species. For example, significant effects of primary production were reported on warmer seasons for two cephalopod species while fisheries played a significant role in their winter distribution (Lloret-Lloret et al., 2021). Thus the spatial distribution of the indicators could vary along the year showing seasonal patterns of migration due to some species tend to move towards northern regions during summer (Lloret-Lloret et al., 2021; Vilas et al., 2019), while it is also possible that the seasonal turnover of species may maintain the community properties and indicators stable (Moranta et al., 2008). Changes in community composition have not been studied as this work only aimed to analyze the cephalopod community as a whole. Despite this, the results might still hint at some changes in the composition of this subset of the Western Mediterranean community. Forecasts of future scenarios would be difficult as other

possibly influential drivers (such as stratification of the water column), as well as the potential adaptive processes of the different species have not been taken into account (Hidalgo et al. 2018).

In summary, we have been able to describe relationships between key aspects of the cephalopod ecology with environmental, human and biotic drivers of change. Our results highlight that the cephalopod community of the Western Mediterranean will likely continue to change, mainly due to changes in environmental conditions related to climate change, such as an increase in sea warming or changes in primary production. However, these changes will not necessarily result in boosted cephalopod populations. Drivers related to the structure of the biotic community, such as prey availability and the concurrence of competitors, can also influence cephalopods future dynamics, illustrating that this taxon is highly dependent on different ecosystems compartments and the whole ecosystem structure and functioning. We conclude that to ensure a sustainable fisheries management of the cephalopods community within the study area an ecosystem-based approach is needed, considering the subregional differences within larger regions.

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Data Availability statement

The data underlying this article were provided by IEO under licence / by permission. Data can be shared on request to the IEO.

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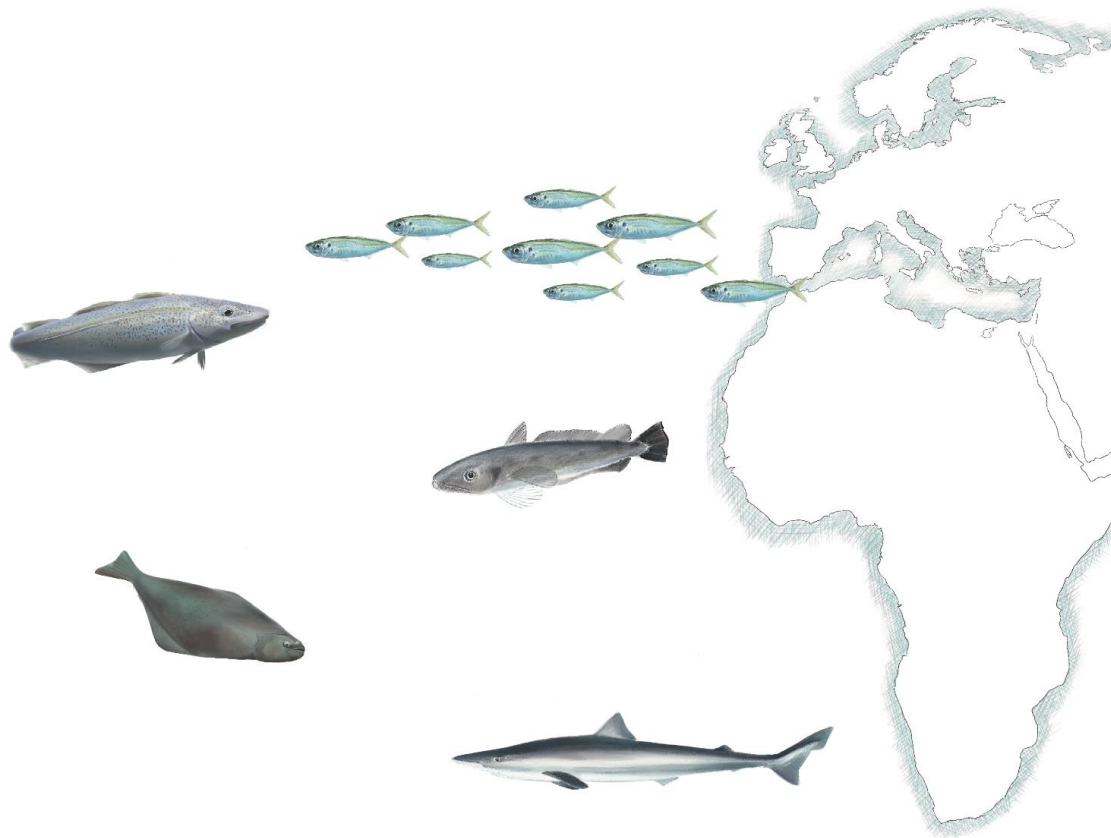
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2.3. Bathymetrical variations of fish community indicators along Atlantic and Mediterranean waters

Carlos Veloy, Cesc Gordó-Vilaseca, Gregoire Certain, Mark Costello, Antonio Esteban, Tracey McGahey, Encarnación García, Cristina García-Ruiz, Dawit Yemane Ghebrehiwet, Maria Grazia Pennino, Angélique Jadaud, Lynne J. Shannon, Sandrine Vaz, Manuel Hidalgo, Marta Coll



In preparation

Abstract

Climate change affects production, phenology, and distribution of marine life, triggering consequences in the structure and functioning of ecosystems. Most of the distribution shifts described are either latitudinal or longitudinal, and mainly focus on occurrence, abundance or biomass of species. While vertical changes are also recorded at sea, and some species move to colder deeper waters, there is still a need to understand the ecological implications of these changes. In this study, we examine the spatiotemporal variation of community indicators with depth in contrasting fish communities along the Northeast Atlantic, Mediterranean Sea and South Africa. To do that, we calculated a set of indicators representing production, biodiversity and trophic ecology aspects using data from bottom trawl surveys. Using non-linear regression models, we explored the patterns of variation of these indicators between and within study areas, the temporal trends of the indicators' distributions with depth, as well as the potential influence of fishing impact in the depth distribution. Heterogeneous temporal changes of the bathymetric distribution of indicators emerged in almost all the indicators and areas with system-specific contractions or expansions of the indicators values towards coastal or deeper areas. Temperature related drivers showed the most significant effects, while the effect of fishing effort on the bathymetric distribution of ecological indicators was observed in specific regions such as the Mediterranean Sea. Overall, regional areas' characteristics had a larger effect on bathymetric changes than large scale environmental processes and gradients.

Keywords

Biodiversity, fishes, ecological indicators, bathymetry, environmental and anthropogenic impacts

2.3.1. Introduction

Modifications of the marine communities are one of the most consistent effects of climate change on ecosystems. These ranged from directional shifts of dominance or species contribution (Laurans et al., 2004; Fossheim et al., 2015; Doubleday et al., 2016), variations on critical ecological processes such the mean phenology (Ramírez-Amaro et al., 2020) as well as the modification of the species distribution (Rubenstein et al., 2023). This last effect has been mostly associated with latitudinal and longitudinal changes of their range, triggering tropicalization and deborealization processes worldwide as species move away from the equator or temperate areas to colder waters (Lenoir et al., 2020; McLean et al., 2021; Gordó-Vilaseca et al., 2023b, 2023a; Chust et al., 2024). However, unexpected subregional responses have also been reported (Sanz-Martín et al., 2024). Beyond large geographic displacements due to shifts in temperature gradients, there is still a general lack of knowledge on how local diversity along with other ecosystem-dependent properties respond to temperature variation, and how consistent are these patterns across contrasting ecosystems facing different climatic conditions and bathymetric profiles.

In terrestrial environments, altitudinal range shifts of species can also change, so does the depth range in marine ecosystems (Pereira et al., 2018; Freitas et al., 2021; Chaikin et al., 2022). Thus, the bathymetric dimension should be accounted for in the spatial movements of fish communities (Rubenstein et al., 2023). Recent literature already reports certain gradients and significant downslope trends in fish distributions (i.e. deepening) with consequences on the bathymetric organisation of communities (Dulvy et al., 2008; Thatje, 2021). However, there is still a generalized lack of understanding of how the vertical profile of community characteristics and properties have historically changed according to contemporary impact of natural and anthropogenic pressures. Changes of marine communities with depth could result in modifications of ecosystem functions due to the differential shifts of bathymetric range of the species within the community (Cure et al., 2021). However, there is a lack of studies that investigated depth-related modifications on multiple community properties across contrasting ecosystems.

Richness in marine ecosystems usually shows a dome-shape relationship with depth, with taxa-dependent differences in the peak of maximum number of species (Pineda and Caswell, 1998; Keller et al., 2016; Pereira et al., 2018). This ecological gradient may be the result of environmental filtering, selection and complementarity of species with different traits, but also due to a random distribution of species between two limits resulting in a parabolic relationship (Pineda and Caswell, 1998). Moreover, in deep waters, harsh conditions such as lower temperatures, higher pressure, lower amount of nutrients and hypoxia are limiting factors for a high number of species (Costello and Chaudhary, 2017). Although there is some degree of tolerance depending on species life history (Thatje, 2021), depth also represents a physiological constraint limiting the bathymetric distribution of many species (Costello et al., 2010; Lin and Costello, 2023).

Bathymetric shifts in distribution have been, however, proposed to be a response to different stress factors, which is often known as the “Depth refuge hypothesis”. Moving deeper in the water column could compensate for rising temperatures in shallower waters

(Smith et al., 2014; Pereira et al., 2018). However, fishing can produce in some cases confounding patterns to this process, as fishing pressure is usually higher at shallow than deep waters. This can erode the spatial distributions of species inducing a bathymetric pattern where biomass and richness of fish are higher at deeper ecosystems, where fishing pressure generally decreases (Tyler et al., 2009; Ciannelli et al., 2013; Frank et al., 2018; Petit et al., 2022). Thus, deeper environments can act both as a protection for further climate and fishing impacts as well as a reservoir for future recolonizations of shallower waters after depletion or local extinctions (Smith et al., 2014; Frank et al., 2018; Mindel et al., 2018). In addition, in the context of climate change, estimates quantifying the deepening of species range between 3-6 metres/decade on average, and up to 10 metres for some species in sensitive areas such as the North Sea (Dulvy et al., 2008). Physical barriers such as continental landmasses could exacerbate this process as they limit potential latitudinal migrations, like in semi-enclosed systems such as the Mediterranean Sea. However, there are not many studies reporting consistent depth displacements (but see Delgado et al., 2018; and Sanz-Martín et al., 2024).

Directional community displacements causing borealization and deborealization have already been observed in the North Atlantic ecosystems (e.g. Fossheim et al., 2015; Gordó-Vilaseca et al., 2023b, 2023a). Therefore, we may expect an increase in richness and mean size in the coldest latitudes due to climate change and resulting northward migrations. This includes potential variations in the trophic level of communities mirroring changes in the community composition. For example, this could be caused by a possible reduction of predators or a shift to shorter lived species in some boreal areas (Beukhof et al., 2019a), or an increase in large higher trophic level species in the Arctic ones (Kortsch et al., 2015). It is also expected that the interaction between fishing effort and depth will be negative in shallow areas, contributing to the deepening of high values of indicators (Frank et al., 2018).

To obtain a broad picture of this phenomenon, we developed a cross-comparison of different ecological indicators representing biodiversity, production, and trophic ecology of latitudinally contrasting communities, covering temperate and high latitudinal regions of the East Atlantic and the Mediterranean Sea.

In this study, we analysed the potential variations over depth and time of several ecological indicators of fish communities with the goal of understanding their change with bathymetry. We tested these changes along with the indicators responses to changes in environmental conditions (sea surface temperature, bottom temperature, and primary production) and fishing effort. We also aimed at identifying whether fishing effort displacements to deeper waters, observed in several regions (Farriols et al., 2017), have played a role or not in bathymetric changes in community properties overall. All these results will help to disentangle how these processes occur through a large oceanic scale.

2.3.2. Material and Methods

Three latitudinally contrasting ecosystems

The study was conducted in five regions: Barents Sea and North Sea in the North Atlantic, Western Mediterranean Sea, and the west and east south African coast in the Benguela current system (Figure 2.3.1).

The North Atlantic contains a marked temperature gradient from the North Sea to the Barents Sea, with colder waters in the latter. This area has undergone structural community changes in recent years derived from northward shifts of several species in both areas (Perry et al., 2005; Gordó-Vilaseca et al., 2023a). In the case of the Barents Sea, this has resulted in an increase in the richness of the community (Kortsch et al., 2015; Frainer et al., 2021; Gordó-Vilaseca et al., 2023b). Similar processes were seen in the North Sea, where both fishing and climate change have led to the reduction of long-lived high trophic level species in favour of smaller, short-lived fishes with lower trophic levels (Beukhof et al., 2019a), along with an increase in more southern species in detriment of boreal ones (Beare et al., 2004; Engelhard et al., 2011).

The Western Mediterranean Sea is a generally oligotrophic environment, although there is marked regional variation due to regional key oceanographic features (Estrada, 1996; Nieblas et al., 2014; Colella et al., 2016; Ayata et al., 2018). For instance, within the most western part of the Western Mediterranean basin, both the southern and northern areas, which correspond to the Alboran Sea and the Gulf of Lion, tend to have higher levels of primary production. This is due to the influx of Atlantic waters in the case of the Alboran Sea and, the discharge of rivers like the Rhone, the presence of a wide continental shelf in the north and the occurrence of deep, wind-driven, convection events in winter that influence the primary production dynamics in the case of the Gulf of Lion (Estrada, 1996; Nieblas et al., 2014; Macias et al., 2018). Sea Surface Temperature (SST) mostly follows a north-south positive gradient, with the exception of the Alboran sea reporting cooler waters than its adjacent areas due to the influence of the Atlantic inflow (Nieblas et al., 2014). Prior studies show differences between northern and southern regions with the former showing higher values of biomass (Navarro et al., 2015; Keller et al., 2016; Veloy et al., 2022), mainly due to the temperature gradients. In addition, local factors such as human impact and the variation of primary production due to differences in nutrient inputs were shown to affect the spatial patterns of certain ecological indicators (Veloy et al., 2022), and recently reported southern and deepening displacements of the demersal community due to local climate impacts (Sanz-Martín et al., 2024).

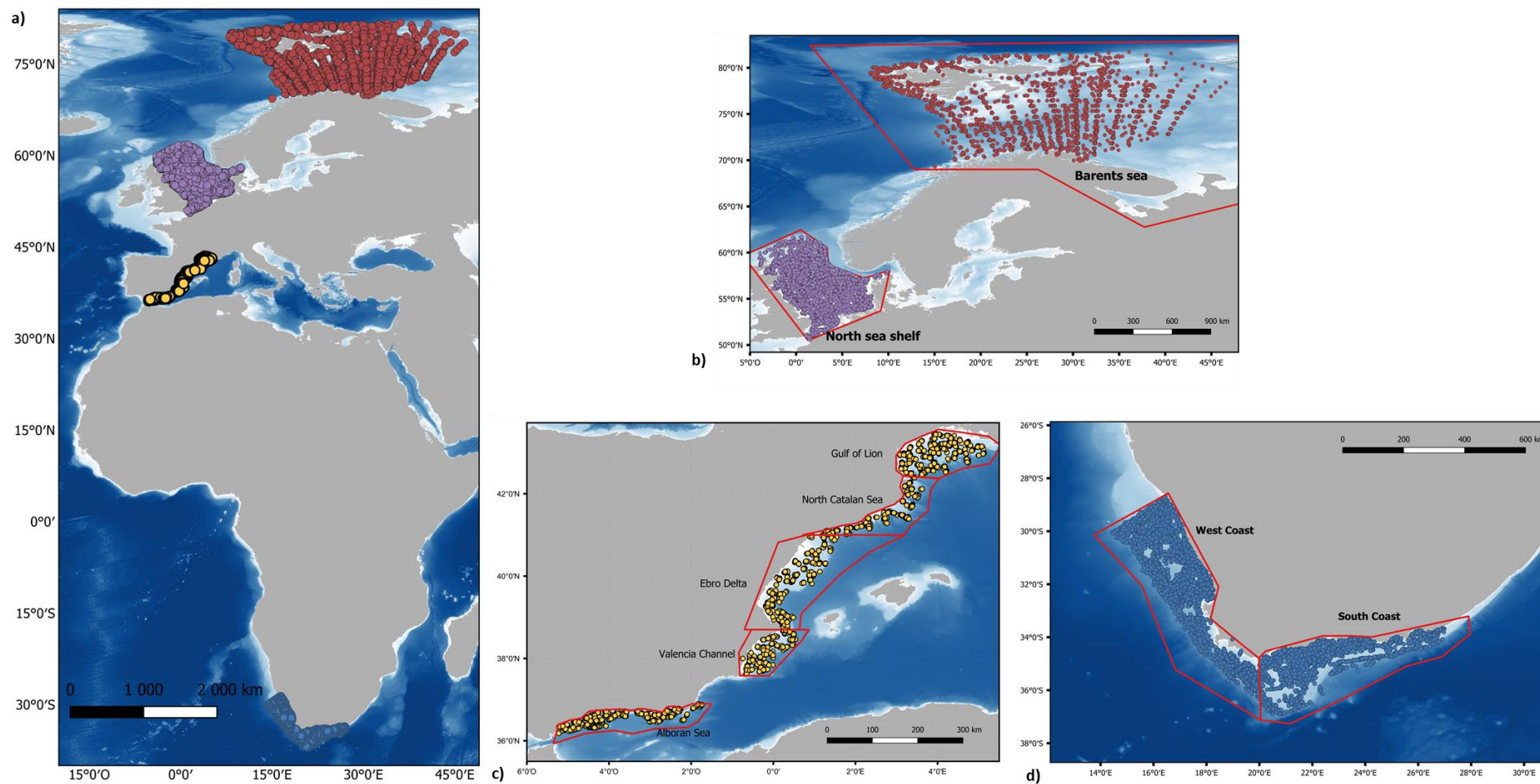


Figure 2.3.1: a) Study areas within the East Atlantic latitudinal gradient, and sample points and region divisions of the b) North Atlantic, c) Western Mediterranean and d) South Africa areas. Colours correspond to the source of the trawling survey data, MEDITS (yellow), DATRAS (purple), NORBTS (red) and DAAF (blue).

The South African coast is part of the Benguela Current Large Marine Ecosystem (BCLME), which is characterized by high levels of primary productivity as well as environmental variability that makes it a reservoir of biomass for many taxa (Yemane et al., 2015). This area has experienced warming of its sea surface temperature (SST) over last decades as well as increases in variation and upwellings (Blamey et al., 2015; Kirkman et al., 2016). The West coast is more influenced by the Benguela Current specially at the shelf edge while the South coast is influenced by the warmer Agulhas current (Kirkman et al., 2015) and represents the South-Eastern limit between the Atlantic and the Indian Ocean. Species from the West Coast area also use the South coast as a spawning ground (Kirkman et al., 2016). Areas within the South African coast have higher richness than neighbour areas from Angola (Yemane et al., 2015). Population shifts within this system have been mostly influenced by human activity. A first shift was related to the sardine stock crash in the 60s caused mainly by fishing rather than just environment, while a later shift towards eastern waters during the mid-1990s and 2000s was caused by environmental factors and accentuated by fishing effort (Jarre et al., 2015). During following years, the extent of optimal habitats for small pelagics, as well as their catches, decreased on the West coast while increases were observed on the South coast evidencing a temporal change in environmental conditions (Ramírez et al., 2022). These regime-shifts causing displacements in small pelagics were also likely associated to changes in the composition of demersal species in the area (Atkinson et al., 2011).

Data sources

Different bottom trawl surveys were used to access the fish community data (Figure 2.3.1). North Atlantic areas were gathered from the NOR-BTS and NS-IBTS surveys, accessed through the FishGlob database (Maureaud et al., 2023). Data from the Western Mediterranean Area was gathered from the MEDITS trawl surveys (Bertrand et al., 2002; Spedicato et al., 2020; Jadaud and Certain, 1994). Lastly, South African trawl data was provided from surveys by the South African Department of Agriculture, Forestry and Fisheries (DAFF) (Axelsen and Johnsen, 2015). Those surveys that used similar gears and sampling methods to the MEDITS survey (GOC 73 trawling gear with 20 mm of mesh size) (Bertrand et al., 2002) were selected, when possible, to account for similar species assemblages. A bathymetric range for the data from 10 to 500 metres was considered due to common data availability across areas and standardization (Supplementary Material table 2.3.1). To homogenise data across time within each region, and to avoid the effect of seasonality, samples were selected from seasons with most sample points and that covered surface when several seasonal surveys are available: Winter in the North Sea, Summer in the Barents Sea and the South Africa West Coast and Autumn in the South Coast. On the other hand, MEDITS surveys were only performed during Spring (Supplementary Material table 2.3.1).

Trait data was obtained to calculate the ecological indicators (section below) and included species trophic levels, maximum size and feeding strategies. This data was gathered from Fishbase database, using both the website (Froese and Pauly, 2021) as well as the R package rfishbase (Chamberlain et al., 2023).

Ecological indicators

Several ecological indicators were selected based both on prior studies as well as the criteria for adequate metrics considered in projects such as Indiseas (ecological significance, measurability, data availability and sensitivity to drivers) (Shannon et al., 2014; Coll et al., 2016; Fu et al., 2018; Veloy et al., 2022, 2024) (Table 1). Overall, various indicators that can be classified within three groups were calculated: (i) biodiversity metrics (species richness and temporal beta diversity), (ii) community biomass indicators (total biomass, mean size, and relative biomass of predator taxa, or Bpred), and (iii) trophic level (TL) indicators (both the community trophic level, or TLc, and the trophic level of the community including organisms with TL equal or higher than TL4).

Following previous studies (Veloy et al., 2022, 2024), for the biomass of predators (Bpred) certain conditions that a species should meet to be considered a predator were established: (i) it had to be a species with trophic level (TL) above 3.5, (ii) its maximum length should be equal or above 20 cm, and (iii) it must actively hunt on macrofauna. With these criteria, both species that could be considered scavengers as well as small fishes with high reported values of TL such as some species from the Syngnathidae family were successfully filtered out.

Table 2.3.1. Dependent variables used in the study and information they provide about the state of the communities. Trawling data includes records from several scientific trawling surveys (NORBTS, DATRAS, MEDITS, DAFF)

Indicators	Information about ecosystem		Data source	Indicator definition
Biodiversity indicators				
Richness	Number of fish species present		Trawling data; Veloy et al., 2022	McIntosh, 1967
Temporal diversity (Jaccard index)	β -	Difference in assemblage composition between two adjacent years.	Trawling data; Veloy et al., 2022	Blowes et al., 2019; Dornelas et al., 2014
Biomass and size				
Total biomass (Biomass)	Weight of all specimens		Trawling data; Veloy et al., 2022	Coll et al., 2016
Relative biomass of predators (Bpred)		Fraction of fish biomass from predator species	Trawling data; Veloy et al., 2022	Coll et al., 2016
Mean Size	Weight of the average fish		Trawling data; Veloy et al., 2022	Shin et al., 2018

Trophic level indicators			
TLc	Mean trophic level of the community	Trawling data; Veloy et al., 2022	Shannon et al., 2014
TL4	Mean trophic level of fishes above 4	Trawling data; Veloy et al., 2022	Shannon et al., 2014

Spatial-temporal drivers

Several drivers of change as independent variables were used (Table 2.3.2): (i) environmental drivers, which included Sea Surface Temperature and Sea Bottom Temperature (SST and SBT) and the concentration of Chlorophyll a (Chl-a); (ii) human impact drivers considering the intensity of fishing effort. Environmental data was obtained from Copernicus products GLOBAL_MULTIYEAR_BGC_001_029 and GLOBAL_MULTIYEAR_PHY_001_030 (COPERNICUS, 2021) from 1994 to 2020 and with a resolution of 0.25 and 0.1 degrees respectively. Fishing effort data was obtained from Global Fishing Watch (GFW) (Global Fishing Watch, 2020) and was calculated as the sum of all the fishing hours of bottom trawlers per cell per year. As some years of the surveys were not present in the GFW database (as it includes only from 2013 to 2019), we considered fishing effort as a cumulative driver that did not vary with time but only in space to identify those areas and depths with consistently higher fishing effort. We thus calculated the sum of fishing hours on each raster cell and standardized it with the maximum value present in each study area for the whole time series.

Table 2.3.2. Independent variables used in the study and sources of origin.

Indicators	Definition	Data source
Structural driver		
Depth	Depth at sea bottom	Trawling survey data
Environmental drivers		
SST	Sea Surface Temperature	COPERNICUS, 2021
SBT	Sea Bottom Temperature	COPERNICUS, 2021
Chl-a	Primary production (concentration of Chlorophyll-a)	COPERNICUS, 2021
Human impact drivers		

Fishing effort	Total number of hours that trawling vessels spent fishing on an area, standarized (human pressure)	Global Fishing Watch 2019
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Statistical analysis

The effect of environmental variables on each indicator was modelled fitting General Additive Models (GAMs, Hastie and Tibshirani, 1990) to each indicator and study area (Table 2.3.1). Structural, environmental and anthropogenic impacts were used as independent variables (Table 2.3.2), along with temporal and bathymetric interactions. One dimensional nonparametric smoothing functions were used to assess the effect of SST and SBT and Chl-a, with a maximum of 3 degrees of freedom (i.e. 4 knots) to avoid model overfitting (Wood, 2017). To analyse the temporal changes in depth distribution of the indicators, we added a tensor smoothing function between depth and year (except on the beta diversity models, as it was calculated per region). Finally, a tensor smoother was also applied to assess the interaction between fishing effort and depth for all the indicators. We included a two-dimensional smoothing function to account for the geographic effect (i.e., latitude and longitude), which represents the remaining variance not explained by the rest of covariates and being spatially structured.

Models for all indicators and regions were calculated using Gaussian distribution, except for richness for which a Poisson distribution was used. Due to the differences in the environment, study area and sampling in all the regions, one model per indicator and region was developed. This allowed checking with more detail the relationships between drivers and indicators, and then comparing the functional form of the different uni- and bivariate effects across ecosystems. The final models were selected using a forward model selection, choosing those models with the lowest value of the Akaike Information Criterion (AIC) (Burnham and Anderson, 2002).

The statistical analysis was performed with R version 4.2.2 (R Core Team, 2022). Beta diversity was calculated using the R package betapart (Baselga and Orme, 2012) and the GAM models were developed using mgcv package (Wood, 2017).

2.3.3. Results

The best fitting models of all the indicators and regions are summarized in Table 2.3.3 with the model selection presented in the Supplementary Material Table S2.3.2, where the AIC scores are also included. A summary of the overall results is shown on Table 2.3.4.

Table 2.3.3: GAM models summary for each ecological indicator and region; Dev. Expl. = Deviance explained. In bold, selected variables that showed significant effects (p-value<0.05).

Indicator	Region	Dev. Expl.	Intercept	Model formula
Richness	Barents Sea	0.206	2.374±0.006	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	North Sea shelf	0.342	2.598±0.003	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	Western Mediterranean	0.145	3.118±0.004	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	South Africa (West Coast)	0.689	2.664±0.006	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	South Africa (South Coast)	0.364	2.807±0.006	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
Jaccard index	Barents Sea	0.693	0.19±0.001	(year)+(SST)+(SBT)+(long,lat)
	North Sea shelf	0.416	0.279±0	(year)+(long,lat)
	Western Mediterranean	0.62	0.35±0.001	(year)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	South Africa (West Coast)	0.106	0.01±0	(year)+(SST)+(long,lat)
	South Africa (South Coast)	0.156	0.025±0	(year)+(SST)+(depth, Fishing effort)
Biomass	Barents Sea	0.246	6.86±0.021	(year,depth)+(Chl.a)+(SST)+(SBT)+(long, lat)
	North Sea shelf	0.233	7.462±0.011	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	Western Mediterranean	0.233	5.751±0.015	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	South Africa (West Coast)	0.338	8.282±0.021	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	South Africa (South Coast)	0.173	8.68±0.021	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
Bpred	Barents Sea	0.414	0.088±0.003	(year,depth)+(SST)+(SBT)+(depth, Fishing effort)+(long,lat)
	North Sea shelf	0.215	0.108±0.002	(year,depth)+(SST)+(SBT)+(long,lat)
	Western Mediterranean	0.398	0.662±0.003	(year,depth)+(SST)+(SBT)+(depth, Fishing effort)
	South Africa (West Coast)	0.104	0.068±0.002	(year,depth)+(SST)+(depth, Fishing effort)+(long,lat)

	South Africa (South Coast)	0.241	0.076±0.003	(year,depth)+(SBT)+(depth,Fishing effort)+(long,lat)
Mean Size	Barents Sea	0.366	-2.1±0.017	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth,Fishing effort)+(long,lat)
	North Sea shelf	0.31	2.984±0.008	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth,Fishing effort)+(long,lat)
	Western Mediterranean	0.121	-3.698±0.012	(year,depth)+(Chl.a)+(SST)+(SBT)+(depth,Fishing effort)+(long,lat)
TLc	Barents Sea	0.351	4.008±0.004	(year,depth)+(Chl.a)+(SST)+(SBT)+(long,lat)
	North Sea shelf	0.351	3.591±0.002	(year,depth)+(SST)+(SBT)+(long,lat)
	Western Mediterranean	0.248	3.714±0.003	(year,depth)+(SST)+(SBT)+(depth,Fishing effort)+(long,lat)
	South Africa (West Coast)	0.177	3.91±0.003	(year,depth)+(Chl.a)+(SST)+(depth,Fishing effort)+(long,lat)
	South Africa (South Coast)	0.353	3.82±0.003	(year,depth)+(SST)+(SBT)+(depth,Fishing effort)+(long,lat)
TL4	Barents Sea	0.231	4.247±0.001	(year,depth)+(SST)+(SBT)+(depth,Fishing effort)+(long,lat)
	North Sea shelf	0.156	4.318±0.001	(year,depth)+(long,lat)
	Western Mediterranean	0.027	4.352±0.01	(Chl.a)+(SST)+(depth,Fishing effort)+(long,lat)
	South Africa (West Coast)	0.092	4.34±0.002	(year,depth)+(SST)+(depth,Fishing effort)+(long,lat)
	South Africa (South Coast)	0.284	4.272±0.002	(SST)+(SBT)+(depth,Fishing effort)+(long,lat)

Temperature and primary production effects

Overall, temperature related drivers were the ones with most significant effects and present in the majority of selected models. Both temperature covariables (SST and SBT) showed mostly nonlinear relationships with the indicators, with heterogeneous responses of all ecological indicators across regions. However, some general patterns were detected.

Regarding SST, richness increased with increasing temperature, especially in the Northern Hemisphere (Figure 2.3.2a). In the west and south African coast, richness decreased at the highest SST, with a tipping point at 18 °C, while the general trend was negative in the Western Mediterranean (Figure 2.3.2a). Jaccard also showed a generalised increase with SST in the Barents Sea and showed also a positive relationship in the Mediterranean (Figure 2.3.2b). Biomass, on the other hand, showed negative trends in the Northern Hemisphere (Figure 2.3.2c). The biomass of predators (Bpred) showed a generalised positive influence of SST (Figure 2.3.2d). Mean size and TL indicators showed opposed patterns between the Barents Sea and the North Sea (Figure 2.3.2e). TL4

indicators showed opposite patterns in the West and East south African coast (Figure 2.3.2g).

Regarding SBT, richness showed similar general relationships than those found with SST, although region-specific thresholds were different in some areas (Figure 2.3.3). Biomass in the South African regions reported negative relationships over a large range of variation in the SBT (Figure 2.3.3c). In the North Sea and Western Mediterranean regions, SBT was positively related to biomass. SBT and Bpred showed negative trends in all regions except South Africa (Figure 2.3.3d), which contrasted with previous results with SST. Mean size and trophic level indicators presented regional variability and showed either unclear relationships or possible latitudinal gradients of responses, including some opposite trends to those seen for SST (Figure 2.3.2 and Figure 2.3.3).

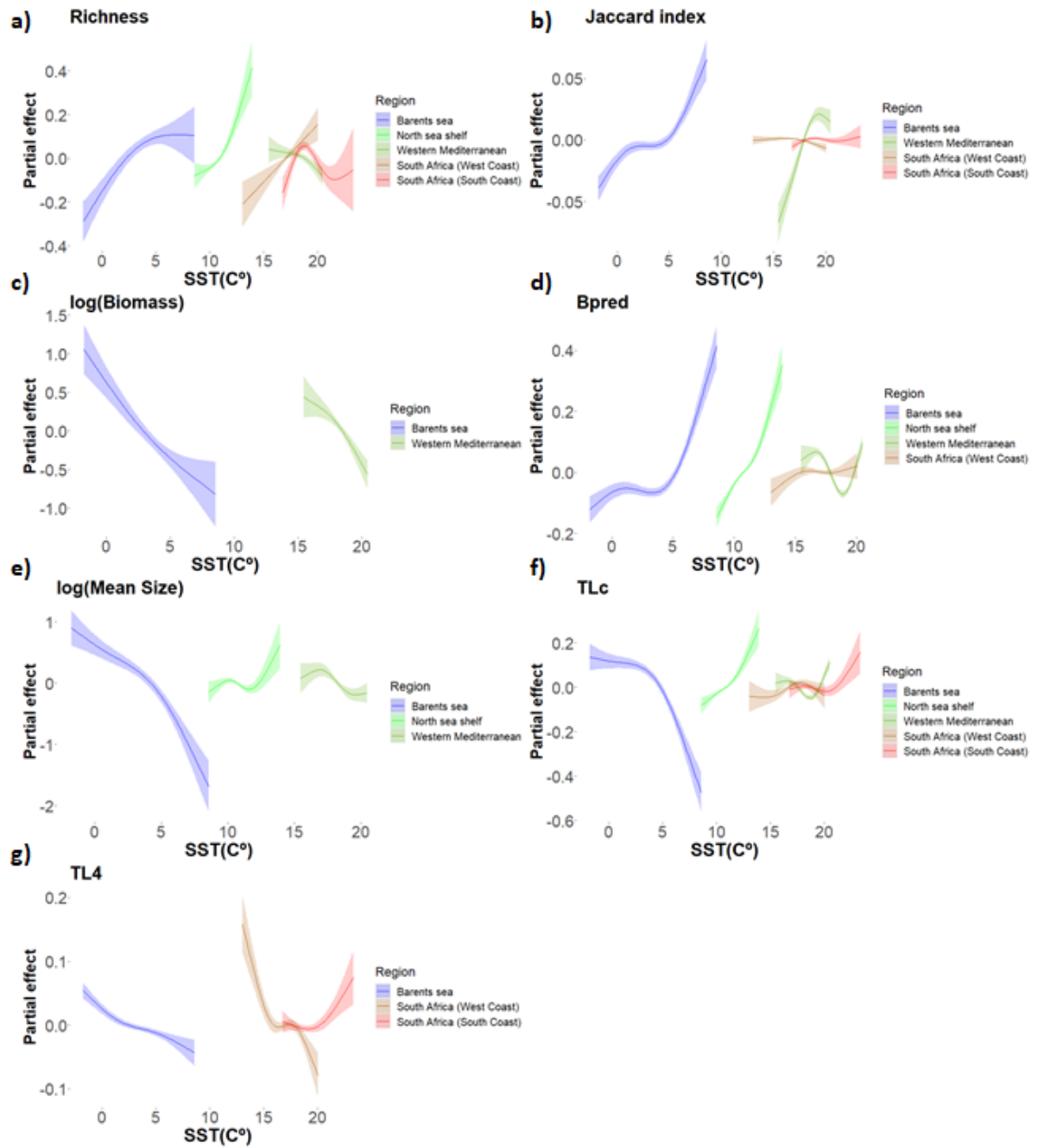


Figure 2.3.2: Partial effect (individual effect of the smooth variable on the model) of SST on the different models for each indicator (a-g) comparing the response of the different regions.

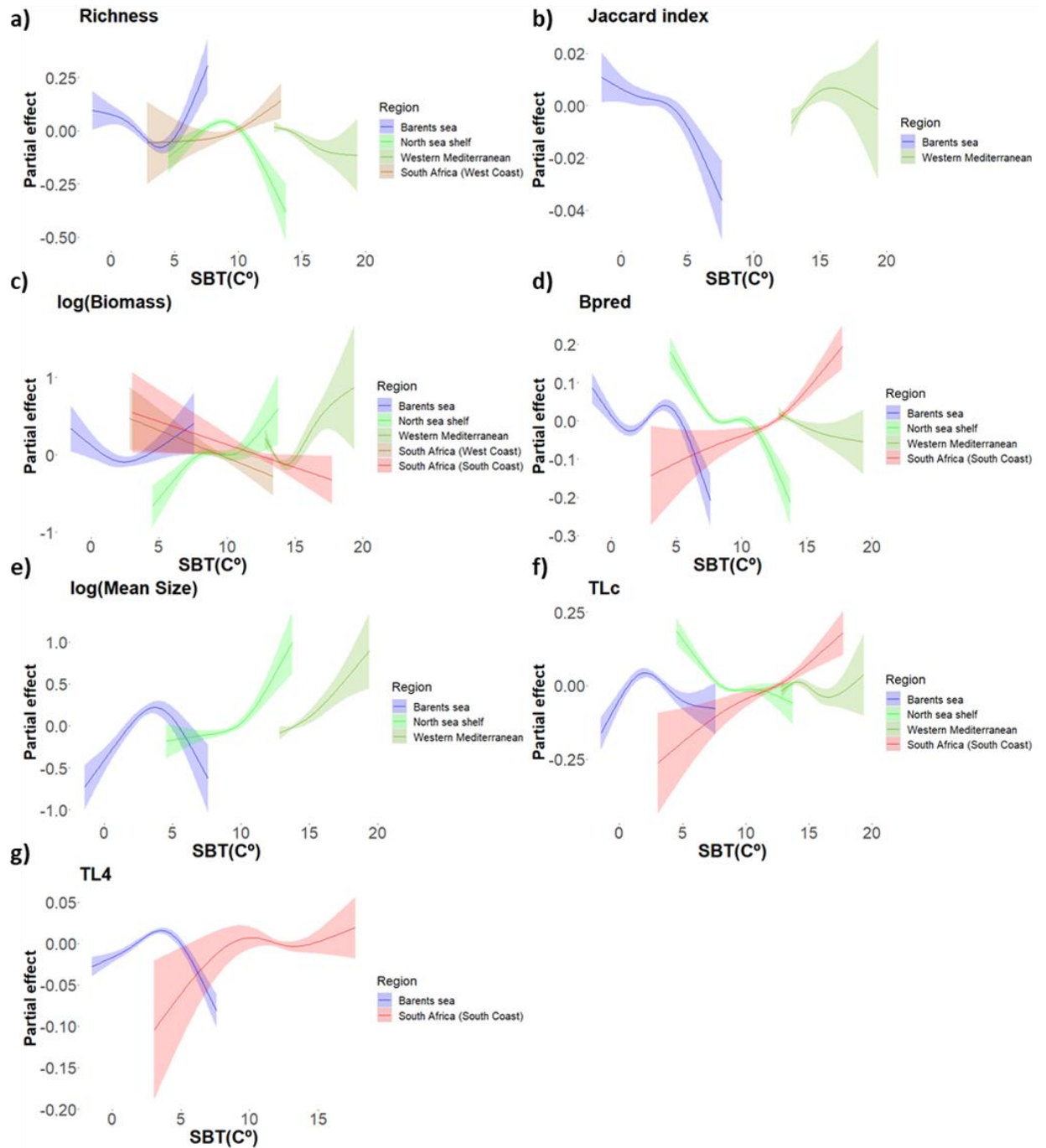


Figure 2.3.3: Partial effect of SBT on the different models for each indicator (a-g) comparing the response of the different regions.

Ecological indicators were overall less responsive to Chl-a concentration. A significant effect was observed in fewer models and, when included in the best models, the functional relationship was highly variable across regions. However, moderate dependence of some indicators upon Chl-a variation was shown in some regions, with certain consistency observed in the functional form of Chl-a effect across indicators within the same ecosystem (Figure 2.3.4). For instance, in the Barents Sea the relationship displayed a similar parabolic pattern in almost all indicators with Chl-a. The same occurred in the

Benguela ecosystems, with South African areas having mostly consistent relationships across most indicators, negative in the west and positive in the east coast (Figure 2.3.4a and 2.3.4b).

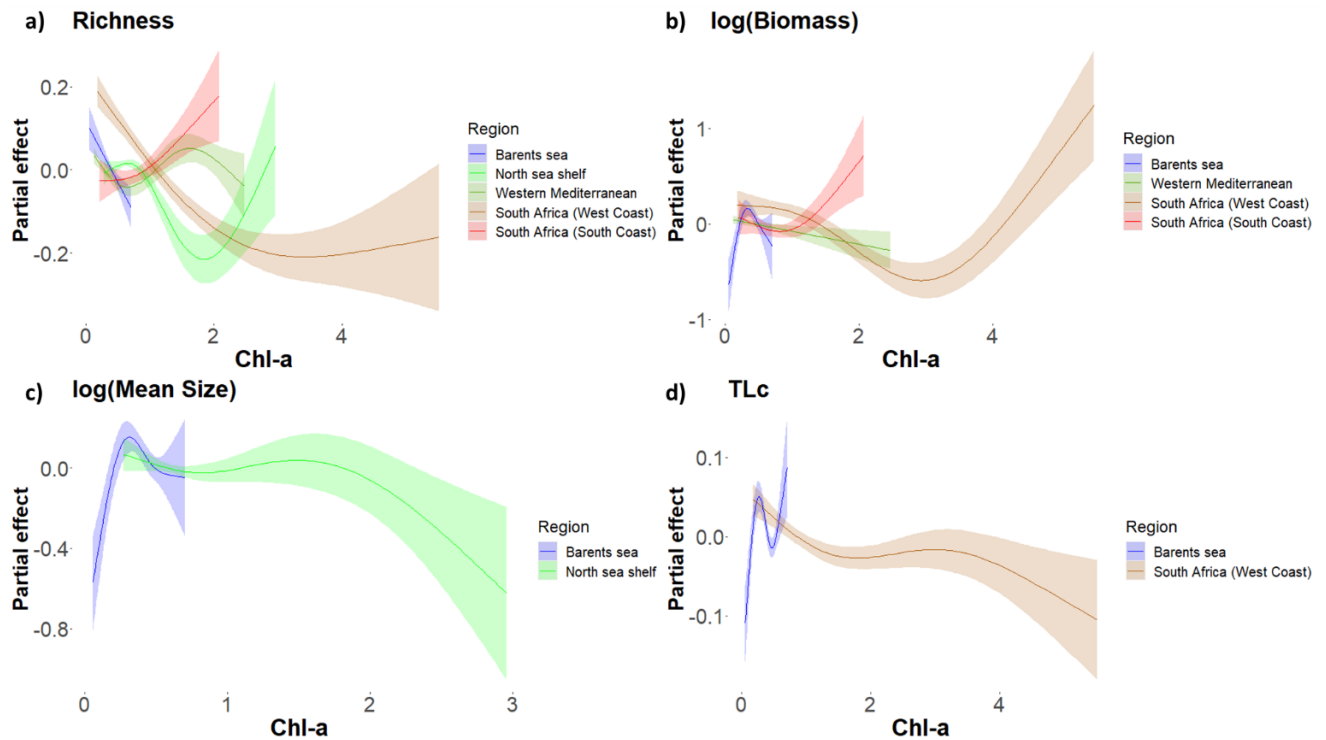


Figure 2.3.4: Partial effect of Chl-a on the different models for each indicator (a-cd) comparing the response of the different regions.

Interactions between time, depth and fishing effort

We found bathymetric changes with time in most indicators, although no progressive deepening or shallowing patterns generally emerged; changes were important but region dependent. Differences on how depth influences indicators over time were observed, such as those seen for Bpred or TL4 (Figure 2.3.5c and 2.3.5f). Some of the ecological indicators showing temporal bathymetric responses were associated with contractions on the depth range where higher values of the indicator appeared. For example, the depth range where values of TLc of the Western Mediterranean and biomass of the South Africa West Coast were lower increased with time, yet TLc also showed some expansions such as the ones seen in the Barents Sea or the South coast of South Africa (Figure 2.3.5e).

In other indicators and regions, constant bathymetric structuring was reported. This was the case of richness, which peaked at around 200 m depth in the Barents Sea, North Sea, and Western South African coast, while it declined from surface to 150 m in the Western Mediterranean Sea and the South African southern coast. No major temporal trends were detected in the depth patterns of richness. Exceptions were a slight increase in shallow richness as well as a deepening of high values in the Mediterranean Sea, as well as an overall increase in the Barents Sea richness across time. Biomass distributions across

depth also remained fairly constant across several study areas, though a deepening with time in the Western South African coast was observed.

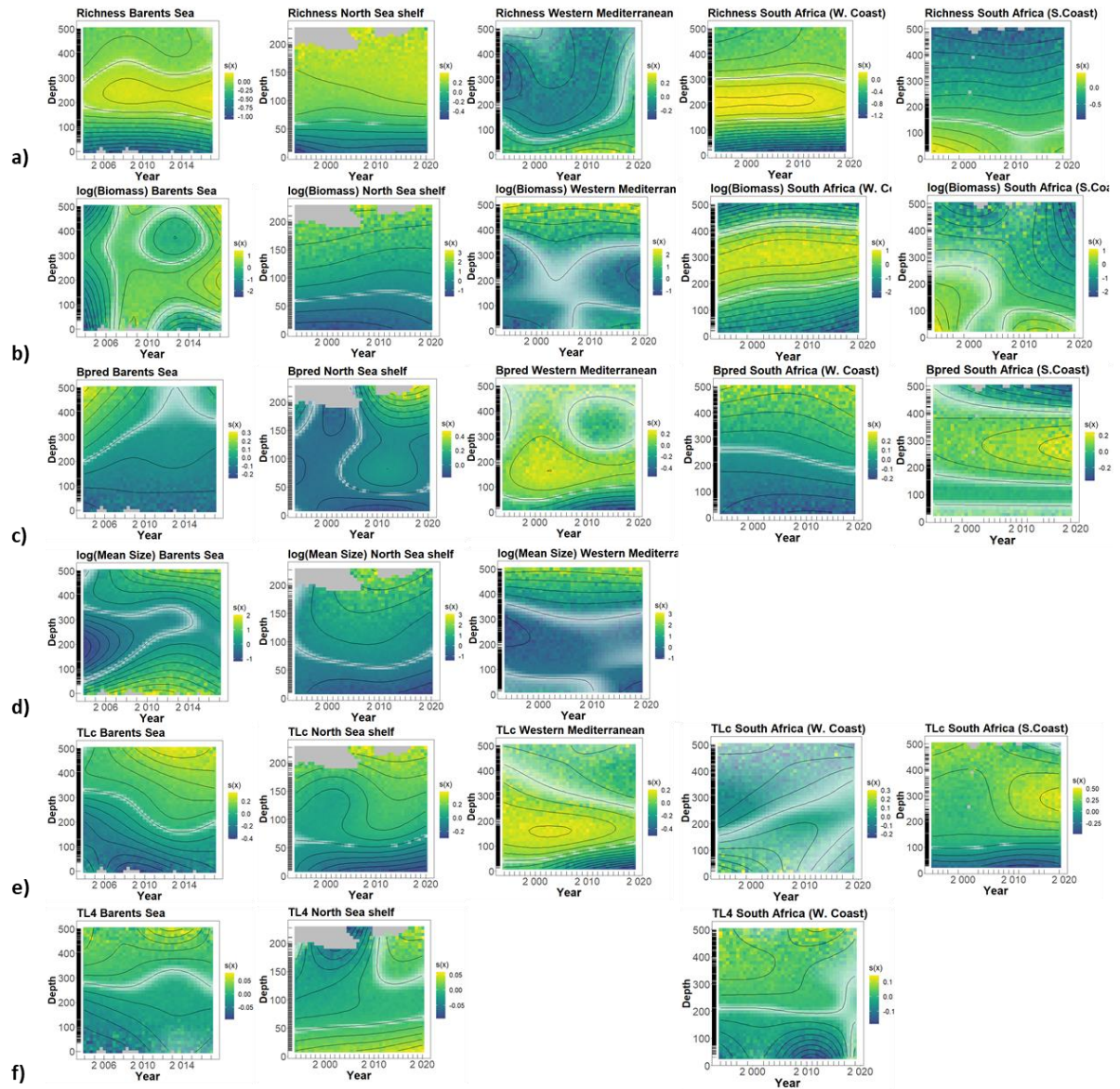


Figure 2.3.5: Partial effect of the interaction between depth and year on the models for the different indicator models (a-f) and regions.

In contrast, the effect of fishing effort on the bathymetric distribution of ecological indicators was more consistent across regions although selected in fewer models (Table 2.3.3). Higher fishing effort tended to exacerbate negative effects in some ecological indicators, showing a synergistic effect with depth (Figure 2.3.6). This was observed with the richness of the Western Mediterranean and the South African region. Fish biomass also reported low values in shallow waters and high levels of fishing effort in the southern South African coast, and in deeper waters in the North Sea shelf and the Western

Mediterranean, where negative effects were observed across all depths. Indeed, the Western Mediterranean displayed the strongest influence by fishing effort with negative effects even at relatively low levels of fishing. Finally, the biomass of predators in the Barents Sea was highly responsive to fishing pressure, declining initially with depth but also at shallow waters with increasing fishing effort (Figure 2.3.6). Responses and bathymetric distribution of other ecological indicators were highly region dependent.

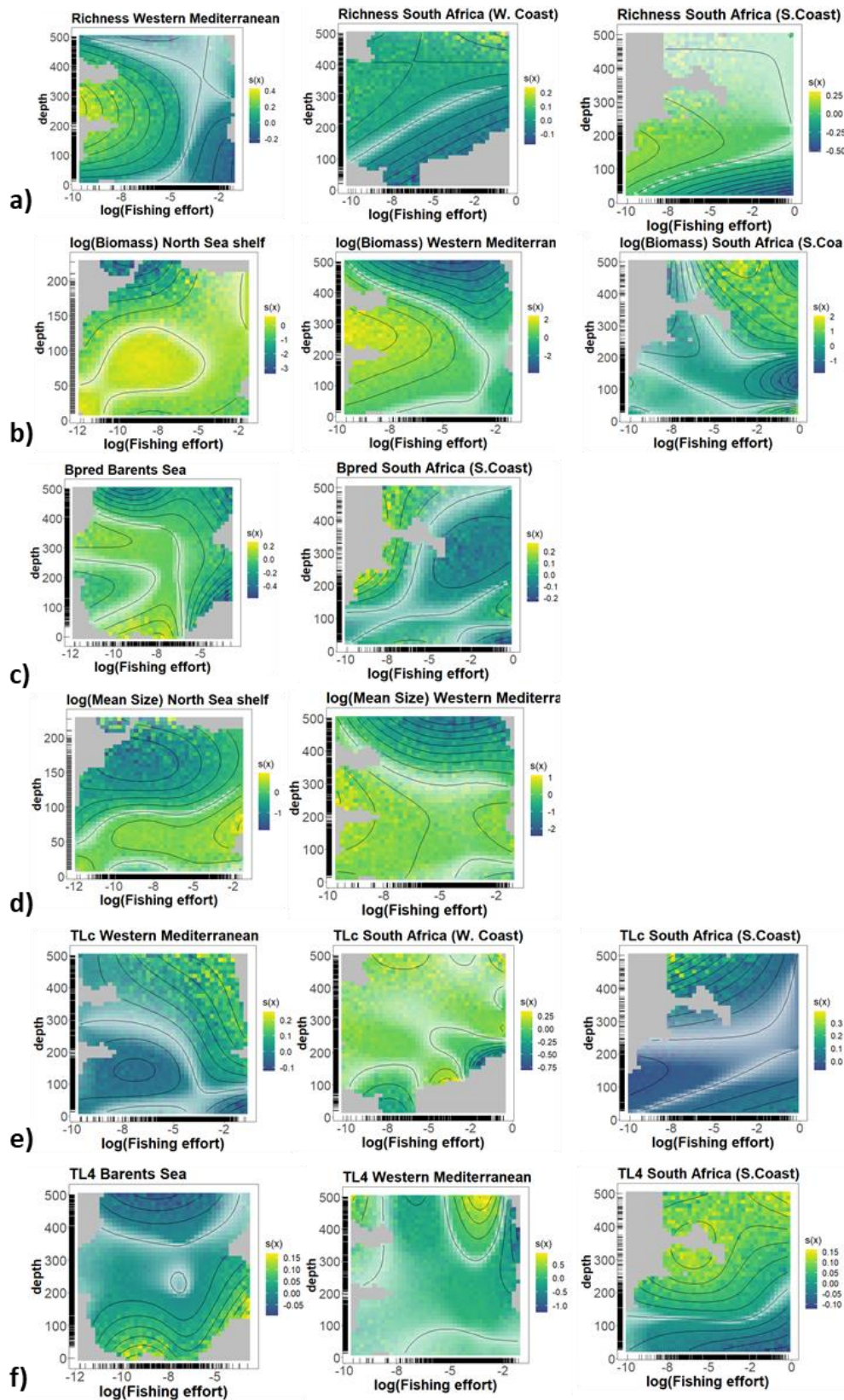


Figure 2.3.6: Partial effect of the interaction between Depth and Fishing effort in the models for the different indicator models (a-f) and regions. White shadow marks the line where the trend shifts from positive to negative, which is also the line where the partial effect of the interaction is zero.

Table 2.3.4. Summary of the partial effects of the considered drivers in the models of the Barents Sea (BSea), North Sea shelf (NSS), Western Mediterranean (WMed), South Africa west coast (SAw) and South Africa south coast (SAs). In dark grey variables not included on the GAM model or with no significant effect ($p\text{-value}>0.05$), in light grey tensors with constant effects, not showing interaction between the variables. In green and red, positive and negative trends of smoothers. Icons represent the different shape of the functional forms of the environmental smoothers (lineal, logarithmic, exponential, parabolic and bimodal).

	Lineal	Logarithmic	Exponential	Parabolic	Bimodal
Positive					
Negative					

Indicator	Area	depth/year	FE/depth	SST	SBT	Ch-a
Richness	BSea	N	NA			
	NSS	N	NA			
	WMed	Deepening	Low fishing+medium depth			
	SAw	N	High fishing+high depths			
	SAs	N	Low fishing+low depth			
Jaccard index	BSea	NA	NA			
	NSS	NA	NA			
	WMed	NA	N			
	SAw	NA	N			
	SAs	NA	N			
Biomass	BSea	Other	NA			
	NSS	N	Low fishing+medium depths			

	WMed	N	Low fishing+medium depths			
	SAw	Deepening	NA			
	SAs	Shallowing	Other			
Bpred	BSea	Decrease deep	Other			
	NSS	Increase deep	NA			
	WMed	Deepening (Decrease shallow)	NA			
	SAw	N	N			
	SAs	Increase at medium	Low fishing+low depths			
Mean Size	BSea	Other	N			
	NSS	N	High fishing+low depths			
	WMed	N	Low fishing+medium depths			
TLc	BSea	Shallowing	NA			
	NSS	N	NA			
	WMed	Deepening (Decline at shallow)	Low fishing+medium depths			
	SAw	N	N			
	SAs	Shallowing	N			
TL4	BSea	Increase deep	High fishing+high depths			
	NSS	Increase deep (Increase shallow)	NA			
	WMed	NA	Other			
	SAw	Decrease shallow (and increase deep)	N			
	SAs	NA	N			

2.3.4. Discussion

This study illustrates several consistent trends of ecological indicators through a comparison of contrasting systems over a large latitudinal gradient, but also heterogeneous responses to drivers between the considered regions emerge. Results also evidence a diversity of regional-dependent processes associated with dynamic and static environmental drivers influencing the indicators. The combination of results of all the indicators explored here offers an extensive picture that helps understanding the effect of environmental drivers and finishing on the different components of the ecosystems and their temporal and bathymetric evolution.

Among all indicators, trophic levels and biomass-related indicators presented temporal change in their bathymetric distribution in most regions. Meanwhile, richness seemed to be most responsive to environmental drivers, followed by TLc. This could suggest that trophic dynamics are one of the most sensitive aspects, along with biodiversity, to the regional environmental variation within marine ecosystems. Trophic indicators appear to be more prone to bathymetric variation than the other indicators. Resulting alterations in trophic ecology could leave ecosystems more vulnerable to the effects of human action, further impacting the overall trophic structure of the system (Jackson et al., 2001; Perry et al. 2011).

The key role of temperature

Temperature was the most influential environmental factor, consistent with the widely reported effects of temperature changes in both surface and bottom on marine ecosystems (Sunday et al., 2012; Freitas et al., 2021). Besides some heterogeneous responses to warming, opposite effects of surface and bottom temperature were detected associated with different aspects of the region. Surface temperatures were more associated to large scale thermal gradients over the globe (Hillebrand, 2004; Costello and Chaudhary, 2017), and thus providing more consistent and generally linear responses across regions. By contrast, the indicators yield heterogeneous non-linear responses over the regions with bottom temperature, which better represents regional oceanography. For example, richness and Bpred showed positive trends in most regions with SST, but presented more diverse trends with SBT as this driver seems to signal better the different ecological processes occurring in each area.

Temperature effect (both surface and bottom) in the indicators of the North Atlantic represents how the thermal gradient regionally influences the transition between different communities. In the Barents Sea, the increase in richness with temperature is accompanied by an increase in predator relative biomass, which could be the result of expanding higher trophic species, or a decline of lower trophic levels. However, the overall reduction in biomass and mean size points towards the latter, similar to what was reported by Kortsch et al. (2015). Moreover, we detected a decline in overall trophic level with temperature at the warmest edge of the study area, complementing the reported expansion of generalist species in the Arctic section of the Barents Sea (Kortsch et al., 2015; Frainer et al., 2021; Gordó-Vilaseca et al., 2023a, 2023b). At around 5 °C, the

effect of SBT on several indicators shifts from positive to negative, suggesting a different effect of temperature in colder or warmer waters in areas where polar and Atlantic waters converge. Previous research in the area detected a different effect of temperature in Arctic and boreal species, with the former increasing their maximum length with temperature, and the latter becoming smaller (Lavin et al., 2022). Our results suggest that different responses to temperature may apply at the community level.

In the North Sea, surface temperature was also positively correlated with several indicators, although SBT gave a more complex picture of the system. Richness, Bpred and Trophic Level decreased with SBT, while biomass and mean size increased. This points to a homogenization of the system towards lower trophic level species, increasing overall biomass and showing a decline in richness (Magurran et al., 2015; Jones et al., 2023). These fishes, despite being larger on average in areas with colder SBT, are of lower trophic level, mainly below 3.5, align with previous changes in trait composition of the ecosystem towards fast growing species (Beare et al., 2004; Pecuchet et al., 2018; Beukhof et al., 2019b; Montanyès et al., 2023).

On the contrary, in the north-western Mediterranean Sea, ecological indicators showed a general negative relationship to SST, suggesting that warming is negatively affecting fish communities in the area. This is an expected result, as climate related impacts (and warming in particular) have been documented as one of the largest threats to fish resources in the area as well as a potential source of decrease of fish diversity (Hidalgo et al., 2018, 2022). Moreover, the increase in temporal beta diversity indicates an increased temporal variability of the fish community. This is in line with previous studies reporting increases in temporal beta diversity investigating multiple taxa in the basin, and considering the increase in nestedness (Veloy et al., 2022) this observed trend could be possibly due to losses of diversity at local scales. The effect of SST and SBT on Bpred and TLc followed a similar pattern and showed a temperature threshold after which the trend changes, with the trophic level and the relative presence of predator species increasing. Coupled with the trends on biomass, this could be attributed to the diminishing proportion of species of low trophic levels as it is the case with species like sardine due to cumulative impacts of high fishing pressure and climate change (Coll et al., 2019; Ramírez et al., 2021).

The South Africa region seems to be a special case in thermal influence due to the confluence of warm and cold currents in the intermediate and deep waters of the Benguela system, representing a very large range of variation. The contrasted differences between both South and West areas are manifested by the sometimes-opposite trends in the indicators, recorded mainly associated with the relationship with SST. Overall, the South Coast presented positive values with temperature while West Benguela featured negative trends. This difference in community response can be related to major ecological modifications in the ecosystem such as the eastward shift of pelagic fishes and the displacement of some other demersal species after them (Blamey et al., 2015; Shannon et al., 2020; Yemane et al., 2020). The trends observed on TL4, for instance, could be explained by the increase in fast-growing species reported on the West coast as the demersal fish assemblage has been shown to be heavily influenced by temperature (Atkinson et al., 2011; Blamey et al., 2015).

On the other hand, it is important to consider that because SBT generally decreases with bathymetry, it may also act as a proxy for depth, although the relationship between depth and SBT varies between and through regions. Decreases in some indicators with higher values of SBT could reinforce in some cases the results and conclusions about the partial effects of bathymetric variation. This can be the case, for instance, for richness in the Western Mediterranean or biomass in the North Sea.

Role of productivity

Primary production was a less influential factor compared with temperature, but it reflected the spatial changes of primary production in the different regions. We found that concentrations of chlorophyll of 2 mg/m³ acted as a threshold in most of the regions, beyond which changes in trends (increases or decreases) were reported. In the case of the North Sea, for instance, this point was associated with an increase in richness and a decrease in mean size while in the Western Mediterranean, it was linked with a decrease of richness. In the Mediterranean, this could be partly explained by the latitudinal gradient in the basin that results in lower richness and biomass in the Gulf of Lion, in spite of the highest primary production of the region (Navarro et al., 2015; Veloy et al., 2022). Another possible reason for this is the higher number of cumulative impacts in coastal areas, negatively affecting the fishes and counteracting the positive effects of the coast's high productivity (Navarro et al., 2015).

The Barents Sea and the two South African regions showed prominent and consistent effects of primary production in indicators, suggesting a close link between primary producers, community structure and ecosystem functioning. The opposite trends were observed in South Africa, with the Southern area reporting positive responses and the Western coast negative values. These observations can be related to the differences in Benguela currents, upwellings and the resulting displacement dynamics recorded in prior literature, especially in small pelagics (Blamey et al., 2015; Jarre et al., 2015). This could explain the negative trends in the Western Coast. Nonlinear effects in the Barents Sea were observed as well, possibly related to the boreal and polar transition previously discussed (Fossheim et al., 2015; Kortsch et al., 2015; Frainer et al., 2021; Lavin et al., 2022).

The role of time, depth and fishing

Instead of generalized depth patterns, region-specific effects of bathymetry were detected, with clear temporal changes in most indicators. However, contrary to expectations of overall trends showing deepening or shallowing, these results display evidence of expansion and contraction processes, or concentrations, without a clear homogeneous trend across regions. Thus, results seem to partially fit the Depth refuge hypothesis with some modifications. The possible discrepancies as well as the reported heterogeneity can be the result of both the use of several indicators, as opposed to just abundance and biomass like in previous studies (Lindfield et al., 2014; Cure et al., 2021), and the inclusion of the whole fish community. Some of these observed processes, mainly contractions and expansions of depth range, fit bathymetric evolutions previously proposed for deepening displacements (Chaikin et al., 2022).

The resulting patterns of changes in the bathymetric range can be grouped into three categories: (i) expansions and (ii) contractions, which are either increases or decreases in

the depth ranges, as can be seen respectively for the TL of the Barents Sea and biomass of the South African West Coast, and (iii) concentrations, which can be associated to a strengthening of the community due to the increase of high values in certain indicators, without a clear change in the bathymetric range of the values; this third pattern is observed in indicators such as Bpred in the North Sea shelf.

The contractions were usually associated with smaller depth ranges of positive indicator values. One of the reasons is that potential changes in regional oceanographic features could be playing an important role in determining the bathymetric shifts of several ecological indicators with time (Ciannelli et al., 2013). The study areas with less surface in the continental shelf (the Western Mediterranean and the Benguela system regions) showed the strongest contractions. Limitations of the latitudinal displacement may play a role, as climate-induced geographic shift can be limited by the European landmass in the Western Mediterranean (Ben Rais Lasram et al., 2010; Sanz-Martín et al., 2024) or by a lack of continental shelf (Kitchel et al., 2022) in South Africa. The North Sea and Barents Sea, on the other hand, experienced fewer deepening processes due to their generally limited depth. Their extended shelf also allows marine communities to experience longitudinal shifts besides the latitudinal ones (Perry et al., 2005; Engelhard et al., 2011; Fossheim et al., 2015; Gordó-Vilaseca et al., 2023a).

In the Barents Sea, we found that many indicators related to trophic ecology and size (such as Bpred, mean size, TLc and TL4) showed the highest values in deep waters, which likely reflects the ecology of several demersal species, some of which expanded into Arctic latitudes in recent years (Fossheim et al., 2015; Kortsch et al., 2015; Frainer et al., 2021). The lack of a clear trend in bathymetry across time in most indicators suggests that no clear deepening has occurred, but rather a geographic displacement. Arctic species have been shown to be highly responsive to warming (Gordó-Vilaseca et al., 2023a), and seeking refugia at deeper waters could be a strategy of acclimatisation. The absence of this strategy may be an indicator of Arctic species vulnerability that deserves further investigation. On the contrary, boreal species at these temperatures and latitudes are not expected to seek refugia deeper, as it is probably not too warm for them to leave shallow waters, and they may benefit from the warming as their thermal habitat expands (Fossheim et al., 2015).

Similarly, ecological indicators in the North Sea had a positive relationship with depth, some of which increase with time. Our results suggest that North Sea deeper waters are in a better conservation state than shallow areas, as most commercial fisheries primarily operate in the southern area (Engelhard et al., 2015). Our study aligns with other studies that have previously reported and widespread deepening of the fish community in the North Sea from 1980 to 2004 (Perry et al., 2005; Dulvy et al., 2008). Up to what degree are fish deepening a result of fishing pressure or fishing preference (especially high in the North Sea for high trophic species such as cod or haddock) (Engelhard et al., 2015; Frank et al., 2018), or a climate-warming induced response remains a matter of debate (Frank et al., 2018, 2019; Baudron et al., 2019).

In the Western Mediterranean, the results align with previously reported richness increases after 2010 (Farriols et al., 2019), mostly at shallow depths but also expanding into deeper waters in recent years (Pennino et al., 2024). These patterns are also similar

to previously reported high values of richness in shallow waters for commercial fishes and elasmobranchs (Navarro et al., 2015). A higher biomass of these groups at these depths would explain the peak in Bpred and TLc at intermediate depth (Navarro et al., 2015; Keller et al., 2016). Still, most of the community biomass was concentrated in deeper waters, which could be the result of high fishing pressure at shallower waters, without a selective depletion of species.

In South Africa, indicators' relationship to depth gradients were not homogenous and sometimes even opposite, highlighting differences in community dynamics between both areas. Medium depths and deep waters were associated with higher richness, biomass, higher trophic levels and proportion of predators, specially the depth range between 100-400 metres, as observed in most communities due to the confluence of deep and shallow communities and similar to previously reported patterns in the area (Yemane et al., 2020). Deepening of biomass and contraction was congruent with bathymetric movements reported in the region, as demersal species were found to increase their mean depth (Yemane et al., 2014; Jarre et al., 2015). Some of the possible factors that drive these movements may be related to the intense fishing effort and environmental variability experienced through the last decades, which have triggered distribution shifts in numerous species (Jarre et al., 2015; Kirkman et al., 2016).

Overall, the impacts of fishing on ecological indicators were most noticeable in the Western Mediterranean, where negative correlation to increasing fishing effort was observed for several ecological indicators across all depths, even with small increments of fishing. In the case of biomass and mean size a negative interaction with depth may be observed, as higher levels of fishing effort result in negative responses at more shallow depths. As the effect is more notable than on shallow waters, it might point at higher sensitivity of communities below 300 m. These effects seem to be in line with previous literature widely reporting the numerous ecosystems impact of overfishing in the Mediterranean Sea (Coll et al., 2012; Tsikliras et al., 2015; Farriols et al., 2017; FAO, 2022). In South Africa regions this effect of fisheries is noticeable especially in shallow waters, and can be seen in richness and TL4 of the South Coast, suggesting negative effects of exploitation in those depths. The effect of fisheries in the other areas was less clear. However, as these analyses are based on community metrics, results may overlook the effect of fishing on single species. It is also important to consider that in this study the impacts of fisheries have been studied from a spatial point of view, signalling those areas consistently exploited, as the temporal dimension was not considered in this study due to the standardization applied. The evolution in fishing effort should be accounted for in future studies, as this aspect of the current methodology might be a limitation in our analysis.

Overall patterns

According to the results, sea temperature and fishing have important effects on the fish populations as they influence many of their indicators. These analyses also report remarkable bathymetric changes due to either a displacement of population towards deeper waters, the removal or decrease of shallow water populations, and the strengthening of communities in deep waters. Overall, these results are generally in accordance to previously established patterns and ecological trends in the different described regions (Dulvy et al., 2008; Kirkman et al., 2015; Navarro et al., 2015; Gordó-

Vilaseca et al., 2023b; Sanz-Martín et al., 2024) as well as with some of the expected patterns of deepening within the Depth refuge hypothesis (Tyler et al., 2009; Chaikin et al., 2022).

This refuge effect of deep waters was observed to some degree in all the regions. However, this study also highlights that bathymetric responses are heterogeneous across study areas and may hint to a more significant effect of regional conditions and local circumstances than large scale gradients when it comes to the displacement and deepening of communities. Regional features such as the amount of fishing exploitation, relative rates of warming or primary production, and physical limits to both horizontal and vertical shifts are some of the factors that may condition changes in the indicators analysed (Ben Rais Lasram et al., 2010; Coll et al., 2010; Kirkman et al., 2016; ICES, 2021, 2022; FAO, 2022). The Western Mediterranean basin is likely the most evident case, where we see the combined impacts of sea warming and high impact of fishing interacting in the response of several indicators (Farriols et al., 2017, Veloy et al. 2024).

Our results, being community-wide, blur the effect of the thermal tolerances and affinities of individual species (Chaikin et al., 2022; Ouled-Cheikh et al., 2022). As a consequence, within the same system we can observe differential movements based on specific taxa, with shallowing of warm water species and deepening of cold water fishes (Dulvy et al., 2008). Fishing impacts can be further studied considering separately the commercial or non-commercial status of species or taxa groups, especially important in areas where fishing has played an important role, such as the Western Mediterranean or the North Sea (Fernandes et al., 2017; FAO, 2022; ICES, 2022).

Conclusions

This study identified several types of bathymetric changes with time within the selection of ecological indicators and studied regions. However, homogenous patterns of bathymetrical change were not found between study areas, nor even between adjacent areas like the South African subregions. These results highlight that regional variation may be more relevant in the processes of deepening and community change than large scale gradients and effects, evidencing the need of combining large scale drivers with regional pressures and environmental indicators to have a complete comprehension of ecosystems changes.

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2.4. Summary of Results

In the previous three sections (**Chapters 2.1. to 2.3.**), I examined the spatial and temporal variation of several indicators within three large marine areas along contrasting latitudinal gradients as well as their potential relationships with different environmental drivers and human pressure to assess historical community changes with possible implications to ecosystem structure and functioning. In **Chapter 2.1.**, I identified contrasting responses on different ecological metrics calculated on several taxa (fish, cephalopods and crustaceans together and separately) in terms of temporal trends and spatial patterns in different regions of the Western Mediterranean Sea. Fish indicators mostly showed decreasing trends while invertebrates displayed certain increases. Focusing on the cephalopods community, an alleged “winning” taxa in the Western Mediterranean basin, in **Chapter 2.2.** I assessed which drivers were most influential to describe a subset of indicators that reflected key aspects of cephalopod biology and ecology. This group was shown to have several negative relationships with SST, making their winner status from the first chapter somehow questionable in the future. Finally, in **Chapter 2.3.** I zoomed out to analyse a larger area of the Eastern Atlantic and Mediterranean Sea, and focused on several ecological indicators describing the fish community. I evaluated their evolution with depth and time and tested the Depth refuge hypothesis along with the potential role of fishing impact and environmental drivers (temperature and primary production change).

Chapter 2.1

In this chapter, regional variation of a set of complementary ecological indicators in five sub areas within the Western Mediterranean basin and its temporal variation from 2012 to 2019 were examined. I aimed to analyse the differences between the responses of three taxa groups (fishes, cephalopods and crustaceans) and two groups inhabiting contrasting habitat (demersal and pelagic species), including the entire community.

Species richness showed high values on the southeastern areas of the basin, namely the Alboran Sea and the Valencia Channel, being a common result in all of the examined groups, with the exception of fishes and particularly demersal fishes, with higher species richness in the Gulf of Lion. In the North Catalan Sea, on the other hand, indicators consistently displayed the lowest values for most taxa. β -diversity did not show marked spatial differences, but showed positive trends in almost all taxa and regions. Nestedness was the most influential component of β -diversity and showed an increase with time. Turnover showed mixed temporal trends, while it increased in the North Catalan Sea. Other complementary biodiversity indexes (such as Shannon H' index and Pielou index) showed similar spatial patterns with higher values in the south of the Western Mediterranean compared to the north. For most cephalopods and crustaceans, ecological indicators displayed increasing temporal trends.

Latitudinal gradients were evident in fish biomass and abundance, showing a generalized negative south-to-north pattern, with higher values in the Gulf of Lion. However, cephalopods and crustaceans displayed different responses, with either high values in the

Alboran Sea or an inverted pattern. Overall, fish biomass and abundance increased over the study period. Meanwhile the relative Fish biomass indicator showed a positive south-to-north gradient that was only interrupted by the Ebro Delta, and decreases over time in regions with a significant relationship, evidencing a generalized decrease of fish in the Mediterranean with time. Conversely, relative cephalopod biomass exhibited an opposite regional pattern and statistically significant increases over time, particularly in the community component with a stronger pelagic behaviour.

Mean Size did not exhibit significant regional differences in most groups, except for fishes and cephalopods. However, it mostly showed positive trends over time. Trophic level indicators showed marked gradients, with opposite maximums observed for TL_c and higher trophic levels in both the community and fishes. Typically, fishes and cephalopods exhibited negative trends in these indicators, while invertebrates showed positive trends.

In general, several types of gradients were observed, including clear latitudinal gradients, gradients interrupted by peaks or low mean values of an indicator in certain regions (mostly the North Catalan Coast), and unclear spatial patterns. Another common finding across the basin was that cephalopods experienced most positive temporal trends on most indicators and regions, particularly in Richness, and the different trophic levels indicators. In contrast, fish exhibited decreases over time in some of those indicators.

The Relative biomass of predators (B_{pred}) did not exhibit clear gradients for the surveyed community and the fishes (except for the pelagic component of the community), but rather showed low values in both extremes of the study area (Alboran Sea and Gulf of Lion) and higher values in the central regions. Pelagic species and cephalopods displayed south-north gradients with the highest B_{pred} values in northern areas. Significant temporal decreasing trends of this ratio were reported for fishes and the surveyed community, with only the pelagic community in the North Catalan Sea and the Gulf of Lion regions showing an increasing trend.

Chapter 2.2

Considering cephalopods as potential 'winning' taxa groups in the Western Mediterranean basin, richness in this group showed a positive relationship with temperature, indicating a regional gradient in thermal effects, although depth also played a significant role. Spatially, northern areas exhibited lower values, while maximum richness was found in southern locations. β -diversity was also positively associated with Sea Surface Temperature (SST) and positively correlated with both Fishing effort and Fish B_{pred} . This indicator also displayed a roughly opposite spatial pattern compared to richness.

Temperature had mostly a detrimental effect on cephalopod biomass, although it showed a slight increase after 18°C. This indicator was positively correlated with Fish B_{pred} but negatively correlated with both depth and Chl-a. The highest values were observed in the Gulf of Lion and the Ebro delta, suggesting a regional effect of their drivers. Cephalopod B_{pred} exhibited parabolic relationships with both SST and Chl-a, with the Gulf of Lion and the Catalan Sea associated with higher values, supporting a regional gradient in these

effects. This was further evidenced by the spatial distribution of the indicator, where northern areas had higher values of Bpred, indicating a positive south-north gradient. Mean size showed a negative relationship with depth and Chl-a and increased with SST up to 18°C. Areas with low primary production and high ratios of predatory fishes were associated with higher mean sizes.

Trophic level indicators responded similarly to SST and crustacean biomass for both TL4 and TL3.25, showing increases in TL with SST and a negative relationship with crustacean biomass. However, they exhibited contrasting trends with depth, being positive for TL3.25 and negative for TL4. Additionally, TL4 showed a parabolic relationship with Chl-a, peaking at 0.4 mg/m³. At the spatial scale, the Valencia Channel and the Ebro had the highest values of TL3.25, while the shallow areas of the Gulf of Lion had the highest TL4.

In summary, SST emerged as the most influential factor in this study, significantly affecting most indicators. Many non-linear relationships showed a threshold between 17°C and 19°C, indicating a transition from positive to negative effects, likely between the Gulf of Lion and the Ebro Delta through the North Catalan coast. Chl-a also showed a significant impact in fewer models, with tipping points around 0.3-0.4 mg/m³, notably affecting the Gulf of Lion and the Alboran Sea. These drivers, especially SST, strongly influenced cephalopod indicators. Indicators more affected by these environmental factors exhibited apparent gradients across the Western Mediterranean, with structured clusters of residuals associated with different regions. Conversely, indicators influenced by other drivers showed less clear spatial gradients, with residuals distributed more uniformly along the model curve. Generally, positive south-north gradients were observed, with southern areas such as the Alboran Sea having low values in most indicators (except TL4) intermediate to high values in most of the Northern Spanish coast, and high values in the Gulf of Lion, particularly in biomass.

Chapter 2.3

Regarding the large-scale comparison of indicators, temperature emerged as the most influential environmental factor, with both SST and SBT showing significant effects in the majority of models. Some general responses to these drivers were observed, such as an increase in Richness with temperature in the North Atlantic areas, but with thresholds beyond which this indicator decreased. These tipping points were identified at ca. 12 °C for SBT, affecting the North Sea shelf and Western Mediterranean, and at 18 °C for SST, impacting the Western Mediterranean and the South Africa West coast. Additionally, responses to SST and SBT were sometimes opposite in certain indicator models. For instance, Bpred generally exhibited a positive correlation with SST, whereas for SBT, most regions showed a negative relationship with this temperature.

Primary production, represented by the concentration of chlorophyll-a, emerged as the least significant environmental driver among the three considered. In most models, it was not included, and where it appeared, the relationship was not statistically significant (p -value > 0.05). Nevertheless, common patterns were observed in those models, including

the presence of a parabolic relationship in most indicators in several areas (e.g., the Barents Sea), as well as contrasting and consistent trends between the two regions of the South Africa coast.

The bathymetric distribution of indicator values changed with time in almost half of the models, where the interaction between depth and year had significant effects. In other cases, the bathymetric distribution remained constant through the considered time periods, exhibiting different patterns in the study regions. In indicators showing temporal variation, stratified responses were more frequent than displacement of indicator values. When displacement occurred (deepening or shallowing), it was usually followed by a contraction of the depth range where maximum values occur, as observed in biomass in the South Africa West Coast or Trophic level in the Western Mediterranean. No consistent temporal variations common to the study areas and indicators were found; instead, the responses of the models were region-dependent. Lastly, the effect of fishing was consistent across the bathymetric distribution in the study region. High levels of fishing were often associated with negative effects on the indicators, synergistically interacting with depth (with the lowest values appearing in areas corresponding to deeper waters and high exploitation). Richness and biomass were the indicators most influenced by the interaction of fishing and depth. This was particularly evident in the Western Mediterranean, where a negative effect of fishing appeared across all depths, showing positive effects on indicators such as biomass and richness at intermediate depths and very low levels of fishing effort.

Chapter 3. Summary of Discussion

The main objective of this thesis was to determine ecosystem changes at regional and oceanic scales within a large region following a contrasting latitudinal gradient, and using a multi-indicator approach. Three representative areas were selected as case studies: the North Atlantic system, the Western Mediterranean basin, and the South Africa coast (Southern Benguela). The discussion summary is divided into several main questions addressed in this thesis: the information gathered from selected indicators (objective 2), spatiotemporal changes in these communities (objectives 1 and 5), the differential responses of taxa and trait groups (objective 3), the role of considered drivers in these changes (objective 4), and the possible implications of observed trends and changes (objective 6). Finally, limitations of this study and future research directions in this field are also discussed.

3.1. Complementary information of indicators used

The wide selection of indicators used in this thesis proved to be complementary and useful in obtaining a holistic view of the communities' state, distribution and dynamics over time. Out of the several ecological indicators initially considered in **Chapter 2.1**, seven of them were deemed most relevant due to the biological information provided, representation of the three indicator categories, emergence of significant trends, and lack of correlation. These included Species Richness, Beta Diversity, Biomass, Biomass of predators, Mean Size, and Trophic Level indicators. This final selection of indicators was used in **Chapters 2.2** and **2.3**.

Biodiversity metrics have been crucial for assessing ecosystem status, providing an intuitive way to compare different communities and their ecological and health stages. Species richness, representing a fundamental metric, is one of ecology's oldest measures (McIntosh, 1967). While it is often linked to ecosystem health and functioning, higher richness alone does not reflect aspects like species dominance or evenness addressed in **Chapter 2.1** with Shannon and Pielou (Pielou, 1966; Shannon, Weaver, 1949), or temporal and spatial species turnover (Dornelas et al., 2014; McGill et al., 2015). Global or regional trends in richness may differ from local scales (Dornelas, 2014). Since all chapters address larger scales, beta diversity and its components are crucial for assessing temporal biodiversity changes. In **Chapter 2.1**, alongside richness increases, temporal beta diversity and its nestedness component also increased, possibly indicating species loss in the Western Mediterranean at local scales. **Chapter 2.2** reported similar increases in both indicators in response to temperature, but nearly opposite spatial trends with higher values of beta-diversity in areas with low values of richness such as the Gulf of Lion (Pennino et al., 2024). Another contrast was fishing effort's significant impact on beta diversity, likely eroding community connectivity (Shackell et al., 2012; Hidalgo et al., 2017).

Biomass and related indicators serve as measures of ecosystem productivity. However, Biomass alone, when considering the entire ecosystem, may not necessarily indicate

richer or healthier communities. While global patterns show that productive systems are associated with communities with higher numbers of species and/or a dominance of a group of species (M. Hidalgo, Pers. Comm.), values and trends of both Richness and Biomass can be misaligned or even opposite in some cases like in temperate ecosystems (Worm and Tittensor, 2018). This phenomenon was observed in productive areas with low species diversity in this thesis, such as the Gulf of Lion in the Western Mediterranean Sea (Estrada, 1996; Navarro et al., 2015), as discussed in **Chapters 2.1** and **2.2**. It may also result from a process of homogenization (Magurran et al., 2015), especially when there is a marked decrease in richness accompanied by an increase in biomass of dominant species. On **Chapter 2.3**, homogenization of the North Sea shelf can be inferred from the response of both Richness and Biomass to temperature, exhibiting opposite trends with SBT.

Other indicators that utilise Biomass to estimate the relative proportions of certain groups are useful for determining changes in the ecosystem at a more specific level. Low levels of Bpred or Bfish, for instance, would be associated with ecosystems populated by a low number of predators and fishes. The North Catalan Coast exhibited the lowest values in Bpred for the entire community, especially for fishes, which is representative of very impacted communities particularly due to overfishing, as observed in **Chapter 2.1**.

However, the patterns and trends of Biomass (and to a lesser degree, Richness) should be considered when examining these types of indicators. Otherwise, reductions in relative biomass may be mistakenly attributed to the removal of species or biomass when, in fact, this decrease could be the result of increases in Biomass of species belonging to other groups. This phenomenon can be observed in **Chapter 2.3**, as it is theorised that the proportion of predators in the North Sea in response to SBT may not decrease due to the removal of predators, but because of the introduction of more individuals of low trophic level species. This would also explain the increase in biomass as well as the negative trend of TLc and is similar to the expected shift in function from long-lived species to short-lived ones (Beukhof et al., 2019a).

Mean size was also a useful indicator for providing additional information regarding the communities besides informing about the good state of a taxa group, like it was seen in marine invertebrates in **Chapter 2.1**. It can also signal either changes in mass at a community level (more representation of larger species) or increases in size at the individual level across species. In **Chapter 2.2**, the mean size of cephalopods appeared to decrease in response to some drivers such as SST, and some possible mechanisms for decreasing mean size at these two levels were proposed. Among them, effects of chlorophyll-a and temperature could hinder cephalopod paralarvae, resulting in adult sizes becoming smaller (Pecl and Jackson, 2008; Pierce et al., 2008). Additionally, decrease in this indicator could be caused by an increase in the population of certain small species due to the reduction of their predators (Daly et al., 2001; Velasco et al., 2001). Similarly, in **Chapter 2.3**, variations of Mean Size in the Barents Sea were associated with possible increases in size at species level with temperature (Lavin et al., 2022).

Trophic ecology indicators served to determine the fishing scenarios that ecosystems were experiencing. The interrelationships between different trophic levels have been explored previously by Shannon et al. (2014), and while they provide an approximation of the events affecting the ecosystem, these scenarios also depend on the type of species inhabiting the ecosystem or included in the database, and fishing strategies and developments. Based on the results of **Chapter 2.1**, regions like the North Catalan Sea were considered to be experiencing cases of a “fishing down the food web” scenario, as the trophic level of the entire community and TL3.25 decreased.

Furthermore, trophic levels were also good indicators of changes in ecosystem identity. Variations in these indicators not only hinted at modifications in the food web but could also be a signal of more profound changes like those observed in **Chapter 2.3** for Northeast Atlantic areas related to latitudinal migrations. Distributional changes of communities due to northward migrations (Fossheim et al., 2015; Kortsch et al., 2015; Frainer et al., 2021; Gordó-Vilaseca et al., 2023a) could be also detected by the responses in trophic levels and by considering the characteristics of the species. For instance, increases on TLc or TL4 in the Barents Sea could be related to the incoming boreal species, whose increasing representation on the total biomass as well as their higher omnivory in comparison to polar species would result in higher levels on these indicators (Kortsch et al., 2019).

3.2. Spatiotemporal change: environmental gradients vs local/regional responses

In the current context of global change, it is important to study and understand the changes in the distribution of natural communities as it can provide useful information and insights on how ecosystems will respond, how exploited resources will be affected, and how to manage fishing activity accordingly under scenarios of climate change. Variations in community indicators were studied both over time (**Chapters 2.1** and **2.3**) and across space (**Chapters 2.1**, **2.2**, and **2.3**).

The analysis of temporal changes in the marine realm is a useful tool for determining geographic displacements and other expected changes in ecosystem dynamics and function. At the regional scale, results of this PhD show that the trends in indicators are highly dependent on local impacts and system characteristics, as observed in both **Chapter 2.1** and **Chapter 2.3**. However, common regional patterns were found for some taxa in **Chapter 2.1**, hinting at possible generalized processes over the whole Western Mediterranean. For example, the loss or decrease of fishes in the Western Mediterranean, likely a consequence of impacts such as overexploitation or warming, or the rise of invertebrates as possible 'winners,' partly due to the removal of fishes from the systems (Caddy and Rodhouse, 1998; Doubleday et al., 2016).

Other important temporal trends observed included various bathymetric structural variations reported in **Chapter 2.3**, such as deepening and contraction of indicators' depth ranges or increases with depth. For instance, the contractions were usually associated with limited continental shelf space, and thus potentially less areas for displacement (Ben Rais Lasram et al., 2010), while the strengthening was linked to favourable conditions like the reduction of fishing effort in the North Sea (ICES, 2022).

Regarding horizontal variations, latitudinal gradients are one of the most prevalent spatial patterns found at scales ranging from regional to oceanic and planetary (Hillebrand, 2004; Mittelbach et al., 2007; Worm and Tittensor, 2018). In the Western Mediterranean, these gradients were manifested in the values of several indicators for the whole community, fishes, cephalopods, and crustaceans. The observed values tended to match the temperature gradient observed through the basin, with colder waters in the Gulf of Lion at the north reporting lower values on indicators such as richness than southern areas. In other indicators, however, values followed the inverse gradient, reaching maximum values at the northern limit of the basin. Processes like differing levels of primary production (Estrada, 1996; Nieblas et al., 2014) were behind this reversal of the generally positive north-south gradient, which often trigger unexpected directional movements in the distributional changes of species (Sanz-Martín et al., 2024).

In **Chapter 2.2**, using a higher spatial resolution, indicators like Richness showed latitudinal gradients for the cephalopods taxa similar to those found in **Chapter 2.1**. Still, the effect of the regions was manifested in the models' residuals, highlighting the regionalization of the effects over the whole area. This differentiation between areas was the main reason behind some of the interrupted gradients and discontinuous patterns described in **Chapter 2.1**. The influence of more localized processes like human-related impacts, the oceanography of the area, sub-regional effect of climate change and nutrient inputs from continental sources resulted in an apparent breaking of the generalized gradient. In the Western Mediterranean, identified causes of the patterns observed were the intense human activity in the North Catalan Sea, the influx of nutrients from the Ebro Delta, and the Atlantic inflow currents in the Alboran Sea (Estrada, 1996; Bosc et al., 2004; Nieblas et al., 2014; Taconet et al., 2019). Regional characteristics also seem to play a certain role on larger scales based on the results of **Chapter 2.3**. While responses and ranges of SST on the GAM models did fit the established large-scale latitudinal gradients, for the other drivers, the trends and ranges were more influenced by local processes.

Bathymetry was also shown as another important source of spatial variation. Species distribute and concentrate at different depths based on the match between their life history and the environmental variables, and this is reflected in changes in ecological indicators. One of the most generalized patterns related to this is the hump-shaped relationship between richness and depth (Pineda and Caswell, 1998; Keller et al., 2017), which was also observed in cephalopods of the Western Mediterranean in **Chapter 2.2**, and in other ecosystems (**Chapter 2.3**). Depth influenced all indicators and showed marked gradients in some of them, such as TL4. Similar to the conspicuous latitudinal patterns, these

gradients were heavily influenced by other environmental drivers like temperature or productivity and the common confluence of communities as species with large depth ranges overlap at intermediate depths (Pineda and Caswell, 1998; Keller et al., 2016; Costello and Chaudhary, 2017; Pereira et al., 2018).

3.3. Responses of different groups: expected ‘winners’ may not always win

Biological characteristics often determine the response to impacts, either helping species cope, resist, or even thrive under certain conditions. However, some life history characteristics can also weaken their populations and make them more sensitive to other stressors (Jackson et al., 2001; Jennings et al., 1998). In terms of taxonomic groups, fishes were the taxa that most consistently reported negative trends, especially on key indicators (such as Bpred and trophic levels). This process was more exacerbated in the Western Mediterranean, where several negative trends were reported on indicators such as various trophic levels (**Chapter 2.1**). Based on these results, fishes were categorized as a ‘losing taxon’. Meanwhile, invertebrates, and cephalopods in particular, seemed to fare better, with positive trends in several indicators within the Western Mediterranean signalling increases in richness, biomass, trophic level, and proportion of predators. This can be due to both positive responses to warming and a decrease in predation and competitive pressure from fishes (Caddy and Rodhouse, 1998; Hastie et al., 2009; Staudinger et al., 2013), as many small species of cephalopods were well represented in the diets of several fish species (Daly et al., 2001; Velasco et al., 2001). Having identified cephalopods as possible winners, **Chapter 2.2** was dedicated to further investigate whether this status held up.

However, when looking at their relationship with different stressors, results show that future warming could result in negative consequences for their dynamics and production, as SST trends showed impacts on several indicators. For instance, biomass, Bpred and mean size had negative responses to SST. This aligns with previously established effects of temperature on the physiology of these invertebrates (Forsythe, 2004; Pecl and Jackson, 2008; Pierce et al., 2008; Xavier et al., 2016). Increasing temperatures could result in the alteration of certain dynamics, especially when coupled with low food availability that could counteract the benefits of a faster metabolism (Hatfield, 2000; Pierce et al., 2008). Based on this, and considering the thermal influence on indicators as a regional effect, it can be concluded that declaring that a group is a ‘winner’ of global change is not so clear. This is especially relevant when considering the responses to current spatial gradients taking the future differential warming into account. The same pressures that initially allow species to thrive can result in diminishing returns after surpassing certain environmental thresholds.

Further insights into the bathymetric movements of fishes reaffirmed their ‘losing’ situation established in **Chapter 2.1** for the Western Mediterranean. The relationship

between depth and fishing effort often displayed very marked negative effects on the indicators even at relatively low intensities in **Chapter 2.3** in line with the global concern of fishing impacts on marine ecosystems (FAO, 2022; Fernandes et al., 2017; Lotze et al., 2006). Indeed, this is also in line with the history of degradation in the Mediterranean Sea making the system very sensitive to natural fluctuations of the environment (Lotze et al., 2006; Coll et al., 2010; Fu et al., 2019; Hidalgo et al. 2022), but also to small variations on human pressures (**Chapter 2.3**). In other areas, several fish indicators underwent processes of contraction of the depth ranges that reported high values. Some of those ecological indicators also displayed negative trends with environmental factors such as temperature.

Future ecological processes involving changes in fish communities can be inferred based on these results on selected indicators and the current knowledge of the study areas examined in this thesis. One of the most notable being the community shifts in the Barents and North Sea, which are related to the warming of both seas and the consequential latitudinal migrations (Beare et al., 2004; Engelhard et al., 2011; Gordó-Vilaseca et al., 2023a). Results of **Chapter 2.3**, especially those related to trophic levels and proportions of predators, seem to point to these displacements. In the Barents Sea, modelled indicators show a transition to higher trophic level communities with larger fishes, in accordance with known processes of borealization (Fossheim et al., 2015; Frainer et al., 2021). The Arctic community, characterized by small herbivorous demersal fishes and trophic webs with a low number of links, would be progressively replaced by boreal fishes with a higher degree of omnivory (and thus trophic level), larger sizes, and more trophic links between organisms (Frainer et al., 2021). This trend seems to fit the results of this thesis, although in the case of drivers like SBT and chlorophyll-a, clear thresholds were detected. These thresholds could correspond to the transitional areas where Arctic and boreal fauna converge, as the initial positive response in TL fits the increase in links on trophic webs. Additionally, positive responses of Arctic species, like an increase in size with initial warming, could also contribute to these threshold values (Lavin et al., 2022). At the Mediterranean scale, a similar process has been observed in the last cold refugia of the Mediterranean, the Adriatic Sea (Sguotti et al., 2022; Cali, 2024).

In the North Sea, the distribution of boreal fishes changed northwards. Thus, species from warmer climates, characterized by lower trophic levels and generally life histories associated to ‘faster growth’ (Beare et al., 2004; Beukhof et al., 2019b), would move towards the system causing the observed trends in indicators, especially in response to SBT. On the other hand, the reported increases in indicators such as Bpred in deep waters could be the consequence of measures to reduce fishing effort taken into action during the last decades on the North Sea, as well as the effects that these activities had on the bathymetric distribution of taxa and size classes (Frank et al., 2018; ICES, 2022).

One aspect to consider is that the studies within this thesis cover the demersal community as a whole, and while different groupings were used, certain responses of some trait/functional groups or more species-specific responses might escape these analyses in favour of mean responses. For instance, in cephalopods, despite the general trends

observed for SST, some species may have more affinity to warm waters than colder ones. These differences result in contrasting distributional patterns between species such as *Illex coindetti* (associated with colder waters) and *Eledone cirrhosa* (from warmer waters) (Puerta et al., 2014). Species-specific affinities to certain environmental conditions could also result in variations in vertical movements. Fishes from warmer waters have been seen to experience shallowing in the North Sea, while cold-water species shift towards deeper waters (Dulvy et al., 2008). Adding the commercial status of species to the analyses could also provide more insight into the effects of fishing on the community, helping to untangle responses like the positive effect at high levels of fishing effort of some indicators in **Chapter 2.3**.

3.4. Environment, fisheries and their role in ecosystem change

Environment and fisheries were both seen as driving forces to explain both spatial variation and temporal evolution in ecological indicators, as proxies of the communities as a whole.

Out of all the studied drivers, temperature was the most influential factor in all areas for both cephalopods and fishes, as observed in both **Chapter 2.2** and **2.3**. In addition, in **Chapter 2.1**, some of the selected indicators indirectly hinted at the influential role temperature. This can be seen in the regional differences of the fish communities in the colder regions of the Western Mediterranean basin (Gulf of Lion and Alboran Sea) and the warmer regions, ranging between the Valencia Channel and the North Catalan Sea. In **Chapter 2.2**, when examining cephalopods in detail, it was evident that across the globe, there are multiple responses to warming at physiological and ecological levels (Pierce et al., 2008; Schickele et al., 2021; see review Table S2.2.1 in Supplementary Material). One of the main effects of warming is the speeding up of life cycles, often resulting in lower mean sizes (Hatfield, 2000; Pecl and Jackson, 2008; Audzijonyte et al., 2024). Due to the ectothermic nature of most marine species, as well as fewer limitations to displacement than terrestrial animals, their latitudinal range could cover most, if not all, of their thermal range (Sunday et al., 2012). Because of this, warming has been shown to influence latitudinal migrations as a mechanism to cope with temperatures surpassing the thermal affinities of organisms (Lenoir and Svenning, 2015; Lenoir et al., 2020). Bathymetric movements were also seen to be another mechanism to avoid the negative effects of warming (**Chapter 2.3**), as observed recently local scale in other Atlantic and Mediterranean areas (Delgado et al., 2018; Marina Sanz-Martín et al., 2024; Chaikin et al., 2022).

In contrast, primary production was seen as one of the less influential factors regarding ecosystemic change, and often its variability did not represent overarching global

gradients. Rather, it signalled more regional-scale processes influenced by oceanography and inflows of nutrients, oceanic currents, upwellings, or continental inflows from rivers (Nieblas et al., 2014; Kirkman et al., 2016). This is manifested in the variations observed both in the model residuals of chlorophyll-a in **Chapter 2.2** and the ranges of the partial response of GAM models in **Chapter 2.3**.

When it comes to human impacts, fishing effort showed mixed results in both cephalopods and fishes. Bottom trawlers did not show significant effects on the Mediterranean cephalopods indicators (Quetglas et al., 2016), with the exception of Beta diversity, indicating increased temporal variability with higher fishing activity and a decrease in the community connectivity (Shackell et al., 2012; Hidalgo et al., 2017). In fishes, the ecological indicators showed diverse responses to the interaction between fishing effort and depth. The most notable ones were found in the Western Mediterranean, where the effects of fishing effort were negative for richness and biomass above very low levels of exploitation and were especially negative beyond the 100-200 m depth range. These impacts of fisheries in the Western Mediterranean area have been widely studied and are related to the broad overexploitation of the Mediterranean system and historical fishing intensity (Lotze et al., 2006; Fernandes et al., 2017; FAO, 2022).

3.5. Possible consequences of community change

One of the main aspects studied through this thesis is the variation of several taxonomic groups of the ecosystem, either through changes in their relative presence or prevalence, (**Chapter 2.1** and **2.2**) or distributional shifts (**Chapter 2.3**). These types of disruptions often caused by environmental processes or human pressures can alter the functions and dynamics within the community (Maureaud et al., 2019). As a result, different ecosystem processes and services could be compromised, most notably food availability for humans as populations of commercial species decline species (Lotze et al., 2006; Fernandes et al., 2017; FAO, 2022; Hidalgo et al., 2022). Fishes, for example, have been shown to be subjected to processes of fishing down on the Western Mediterranean in **Chapter 2.1**.

In cases of winning taxa, however, the initially positive changes they face due to favourable environmental and ecological conditions could greatly benefit fisheries exploiting these species being the case, for instance, for cephalopods (Caddy and Rodhouse, 1998; Doubleday et al., 2016). Despite this, negative effects can also result in more vulnerable populations as they can be at higher risk of overexploitation, but also becoming more sensitive to natural fluctuations of the environment as they are made more dependent on external drivers (Quetglas et al., 2016; Hidalgo et al., 2022). More so considering the effect of fishing on the variation of the cephalopod community seen on **Chapter 2.2**. With the importance that these invertebrates have for fisheries in Spanish

waters (Ospina-Alvarez et al., 2022), worsening conditions for these animals could make stock management and sustainable exploitation of this resource very difficult.

Other profound changes documented in this PhD were related to shifts in the overall trophic ecology and proportion of predator species. These changes signalled severe modifications at the community level in some of the regions studied on **Chapter 2.3**. The indicator responses were linked with notable rearrangements of the overall species composition towards species with higher thermal preferences and the consequential effects on functional ecology. Shifts from polar to boreal communities in the Barents Sea as well as the increase in lower trophic level species in the North Sea are examples of these changes, which may have notable consequences in the energy flows of the aforementioned systems as seen in previous studies (Kortsch et al., 2019; Frainer et al., 2021).

Another important implication of results from this thesis is the differential effect of global change on the contrasting selected, and often neighbouring, areas. Those areas with species with limited room for movement, both horizontal, as in the case of landmass obstruction as well as latitudinal limit, and vertical on areas with narrow continental shelves, were the ones reporting more negative changes on **Chapter 2.3**. These geographical features would act as barriers limiting displacement and resulting in reduced productivity and even local extinctions (Chaikin and Belmaker, 2023; Kitchel et al., 2022; Ben Rais Lasram et al., 2010). On the contrary, the distributional shifts as well as the variations on the bathymetrical pattern can lead to redistribution of fisheries with the associated socioeconomic challenges this can entail (Ramirez et al., 2022a). An example of this is the South African fisheries of small pelagics, which have been forced to move towards eastern waters with the negative outcome this added cost had on small fisheries (Atkinson et al., 2011; Jarre et al., 2013). Deepenings and latitudinal migrations on the West Coast of South Africa could also have important effects in terms of transboundary and straddling fish stocks (Jarre et al., 2015).

3.6. Study limitations, current gaps and future research

Although this thesis aimed to develop a holistic analysis of marine community metrics and functionality, there are still certain methodological and knowledge gaps that could be addressed further in future studies.

Different sampling origins corresponding to multiple campaigns resulted in both heterogeneity of sampling methodology (which, when possible, was standardized by selecting trawls with similar gears) and an unequal availability of the data used (Bertrand et al., 2002; Axelsen and Johnsen, 2015; ICES, 2020). Even within the same trawling

campaign, different areas have shown notable differences in the species registered. For example, the case of the Gulf of Lion within the MEDITS surveys, which only monitored a limited number of crustacean species until 2012. Besides the FishGlob initiative (Maureaud et al., 2023) further effort in surveys standardization and data availability are still needed.

In terms of trait analysis, the traits used in this study were few and, on purpose, simplified (mostly TL and the predator nature), facilitating the synthesis of the multi-indicator analysis while compromising a more exhaustive functional analysis in favour of covering most of the ecosystem. This was mainly due to some species not having other trait data available in accessible databases (Froese and Pauly, 2021; Palomares and Pauly, 2021). This is the case for some cephalopods and crustaceans, and it is particularly relevant for small species. As a consequence, the functional variability that could allow for more complete results and assessments, such as the study of the fast-slow continuum (Winemiller, 2005; Beukhof et al., 2019b) or the variation of more concrete functional groups (Maureaud et al., 2019), was not fully reflected.

The assemblage of ecological indicators (both the initial selection used in **Chapter 2.1.** and the final one for **Chapters 2.2** and **2.3**) was suitable for the objectives of the thesis. However, other indicators could be added to these analyses to further expand the resulting knowledge. Newly developed indicators such as Trophic Variance, which measures the variability of trophic levels within a trophic web (Miguel Vivas, Pers. Comm.), or relative biomasses of other considered traits, could be considered. Lastly, one aspect that could be expanded in the future is the use of metrics of functional diversity (Petchey and Gaston, 2002; Mason et al., 2005), which was disregarded in favour of other indicators.

For the purpose of explaining different aspects of ecosystem diversity and functioning, several drivers of change were considered, most notably environmental variables and fishing effort as a human impact. This selection took into account some basic but ubiquitous and prevalent impacts. Yet, there are multiple variables that could deeply influence the spatiotemporal changes of ecosystems that were unaccounted for, such as oxygen concentration (Breitburg et al., 2018; Lavin et al., 2022) or ice cover in the case of the Barents Sea (Halpern et al., 2015; Kortsch et al., 2019). Furthermore, environmental and human drivers do not have isolated effects on communities but often act synergically. These joint effects can be more pernicious to organisms than the sum of the parts, as illustrated, for example, in the safe operating space analysis (Ramírez et al., 2021). Including additional indicators in future studies, as well as considering their interactions, can help explain ecosystem variation further.

Another aspect to consider is the effect of seasonality. These analyses merely represented a snapshot of the community and do not reflect the yearly variations of the species as part of their life cycles. Spatial distribution of marine taxa can vary throughout the year, for example, due to displacements motivated by foraging or reproduction, as seen in previous studies of the Western Mediterranean (Vilas et al., 2019; Lloret-Lloret et al., 2021). Seasonality can also affect recruitment and spawning processes of certain species of cephalopods (Tursf et al., 1995; Pierce et al., 2010), which could influence both biomass

and mean size responses to drivers. At community level ecological properties tend to be more stable within the year (Moranta et al., 2008). However, the role that seasonality may have in biodiversity indicators at regional scales is still partially unknown. Finally, future research should include more functional groups based on both taxonomy and a wider assembly of traits, allowing the establishment of more animal groups whose response to change might be of interest (such as commercial species, elasmobranchs, long-lived species, different families of cephalopods, etc.). Expansion of the current study area is also an ideal goal. This could allow a more comprehensive and larger view of the response to change. Expanding our results could be feasible with the aid of the FishGlob database (Maureaud et al., 2023), as well as other external sources of data (Hidalgo Pers. Comm.).

Chapter 4. Summary of Conclusions

The main conclusions that can be extracted from this PhD thesis are the following:

- 1) The Western Mediterranean basin showed different regional gradients and temporal trends of marine biodiversity when analysing a portfolio of complementary indicators representing the demersal and pelagic community;
- 2) The Northern areas of the Western Mediterranean with higher primary production were associated with communities dominated by higher biomass but lower species richness;
- 3) Temporal β -diversity showed positive trends, especially for its nestedness component, indicating a generalized loss of species from the Western Mediterranean study area with time;
- 4) More impacted regions, such as the North Catalan Sea, tended to disrupt the general latitudinal gradient, likely due the cumulative impacts of human activities but also to the transitional position between the Gulf of Lion and the Ebro Delta, which are influenced by different primary production dynamics;
- 5) Winning and losing taxa were identified based on the trends and patterns observed for some ecological indicators. Fishes were the apparent “losers” while invertebrates (mainly cephalopods) were identified as “winners” of change;
- 6) At finer scales, indicators based on cephalopods data followed a south-north latitudinal gradient, being mostly influenced by the overall regional effect of sea surface temperature;
- 7) Ecological indicators that were most influenced by non-environmental variables, such as mean size, did not show marked regional effects nor regional gradients;
- 8) Sea surface temperature was often linked to non-linear relationships with cephalopods dynamics, showing negative trends above a temperature threshold of 17-19 °C;
- 9) Fishing effort was the least influential variable to describe indicators for cephalopods, only showing significant effects with the temporal β -diversity and therefore could be linked to the community variability;
- 10) Despite the positive effects of fish declines and sea warming on cephalopods dynamics, overall results indicating cephalopods as “winners” of change are debatable due to non-linear trends and future temperature changes associated with heterogeneous responses in space;
- 11) Analyzing a large latitudinal gradient (that included the Northeast Atlantic, the Western Mediterranean and South Africa) I observed that biomass and trophic level-based indicators for the fish community were the ones most sensitive to bathymetric changes;
- 12) Marked temporal changes in the bathymetric variation of ecological indicators were found. However, these changes were region-dependent, as illustrated by differences between both South African areas analyzed;

Summary of Conclusions

- 13) Overall, sea surface temperature was the most consistent driver associated with the latitudinal gradients of ecological indicators for the fish community, while sea bottom temperature displayed regional effects;
- 14) The most evident contractions of indicators with depth range were associated to areas where longitudinal displacement was limited such as the Western Mediterranean and South Africa;
- 15) Fishing effort interaction with depth was most notable in the Western Mediterranean Sea, where biomass and species richness indicators were high for intermediate depths and low levels of fishing, showing lower levels at shallower and deeper areas.

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Annex I - Supplementary Material

Supplementary Material – Chapter 2.1

Table S2.1.1. Number of sample points per region and taxa considered for the temporal and the spatial analysis

	AL	CN	DE	CC	GoL	All
Temporal analysis (1994-2019)						
Community	654	544	834	479	1530	4041
Fishes	654	544	834	479	1530	4041
Cephalopods	654	542	477	834	1526	4033
Crustaceans	650	538	826	472	884	3370
Spatial analysis (2012-2019)						
Community	290	226	329	152	470	1467
Fishes	290	226	329	152	470	1467
Cephalopods	290	226	329	151	479	1466
Crustaceans	288	223	329	152	465	1457

Table S2.1.2. Total number of species per region and taxa

	AL	CN	DE	CC	GoL	All
Community	370	354	345	330	336	586
Fishes	222	210	204	195	196	338
Cephalopods	40	35	40	35	40	58
Crustaceans	108	109	101	100	100	186

Table S2.1.3. Slope parameter of time and its statistical significance of the linear regressions of all taxa. N.S.: non-significant effects (p-value>0.05). *: p-value<0.05. **: p-value<0.01. *: p-value<0.001**

	Community					Fishes					Cephalopods					Crustaceans				
	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL
S	0.62 **	0.59 ***	0.55 N.S.	0.38 N.S.	0.45 *	0.42 ***	0.45 ***	0.3 N.S.	0.3 N.S.	0.13 N.S.	0.09 *	0.1 *	0.07 N.S.	0.03 N.S.	0.04 N.S.	0.11 N.S.	0.03 N.S.	0.18 N.S.	0.06 N.S.	0.28 *
H	-2.81e-03 N.S.	0.02 N.S.	0.02 N.S.	0.04 *	-0.08 ***	0.02 N.S.	0.01 N.S.	0.01 N.S.	0.04 *	-0.07 ***	9.20e-03 N.S.	0.04 ***	0.05 ***	0.02 N.S.	0.02 *	-0.01 N.S.	0.01 N.S.	0.03 *	-2.97e-03 N.S.	0.01 N.S.
J	-1.17e-03 N.S.	4.63e-03 N.S.	4.10e-03 N.S.	7.84e-03 *	-0.02 ***	4.08e-03 N.S.	1.73e-03 N.S.	1.98e-03 N.S.	8.43e-03 *	-0.02 ***	2.06e-03 N.S.	0.01 ***	0.02 ***	7.60e-03 N.S.	5.83e-03 N.S.	-3.42e-03 N.S.	2.83e-03 N.S.	8.00e-03 N.S.	-1.83e-03 N.S.	1.33e-03 N.S.
β I/F	3.36e-03 *	3.04e-03 *	3.41e-03 N.S.	3.27e-03 N.S.	2.12e-03 N.S.	2.74e-03 *	3.12e-03 *	5.35e-03 **	2.38e-03 N.S.	2.84e-03 **	3.21e-03 N.S.	2.63e-03 N.S.	5.89e-03 *	2.76e-03 N.S.	5.37e-03 **	5.15e-03 **	3.19e-03 *	-2.95e-03 N.S.	6.05e-03 N.S.	-4.86e-03 N.S.
Turnover I/F	-8.43e-04 N.S.	-5.26e-04 N.S.	-6.89e-04 N.S.	3.73e-03 N.S.	4.04e-04 N.S.	-1.81e-03 N.S.	-1.71e-03 N.S.	1.82e-03 N.S.	1.04e-03 N.S.	1.64e-03 N.S.	-9.57e-04 N.S.	-2.35e-03 N.S.	3.40e-03 N.S.	3.62e-03 N.S.	4.21e-03 *	3.16e-03 N.S.	2.58e-03 N.S.	-7.97e-03 *	8.58e-03 **	-3.20e-03 N.S.
Nestedness I/F	4.20e-03 **	3.56e-03 **	4.10e-03 **	-4.63e-04 N.S.	1.71e-03 *	4.56e-03 ***	4.83e-03 ***	3.53e-03 **	1.34e-03 N.S.	1.20e-03 *	4.17e-03 N.S.	4.98e-03 *	2.49e-03 N.S.	-8.60e-04 N.S.	1.16e-03 N.S.	2.00e-03 N.S.	6.17e-04 N.S.	5.01e-03 **	-2.53e-03 N.S.	-1.65e-03 N.S.
B	616.43 *	538.78 **	247.99 N.S.	-170.49 N.S.	220.06 N.S.	214.91 N.S.	411.27 **	109.2 N.S.	-198.01 N.S.	197.96 N.S.	172.65 **	116.88 **	128.17 **	33.28 *	7.21 N.S.	228.88 **	10.63 *	10.63 N.S.	-5.76 N.S.	14.89 N.S.

N	24773.61 N.S.	11389.87 N.S.	-5839.54 N.S.	-25415.5 9 N.S.	139431. 58 ***	-2330.1 5 N.S.	14869. 11 N.S.	-3497.6 4 N.S.	-24158. 93 N.S.	137610. 56 ***	731.0 4 N.S.	365.7 8 N.S.	-3750.6 8 N.S.	-667.31 N.S.	-2321.4 3 *	26372. 72 N.S.	-3845.0 2 N.S.	1408.7 8 N.S.	-589.35 N.S.	4142.4 5 **
MS	0.5 N.S.	0.33 N.S.	0.6 **	0.61 *	-0.83 ***	0.31 N.S.	0.06 N.S.	0.41 *	0.47 N.S.	-0.82 ***	1.75 N.S.	2.1 N.S.	2.46 ***	3.55 **	2.62 ***	0.66 *	0.04 N.S.	-2.11e- 03 N.S.	-0.04 N.S.	-0.35 N.S.
Bpred	-0.01 **	-2.18e-03 N.S.	5.27e-03 N.S.	-9.47e- 03 **	-0.02 ***	-0.01 ***	-3.81e- 03 N.S.	2.32e- 03 N.S.	-0.01 ***	-0.02 ***	-7.22e- 03 N.S.	2.18e- 03 **	8.95e- 03 ***	3.41e- 03 N.S.	2.65e- 03 **	7.44e- 05 N.S.	2.31e- 04 N.S.	-1.17e- 03 N.S.	3.73e- 05 N.S.	1.21e- 03 N.S.
TLc	-3.90e-03 N.S.	-6.08e-04 N.S.	4.04e-03 *	-4.60e- 03 *	-0.02 ***	-6.54e- 03 **	-2.05e- 03 N.S.	1.66e- 04 N.S.	-7.35e- 03 ***	-0.02 ***	-5.67e- 04 N.S.	4.04e- 03 *	0.01 ***	5.25e- 03 *	3.73e- 03 **	3.84e- 03 N.S.	5.62e- 03 **	7.19e- 03 ***	4.86e- 03 **	-6.43e- 03 **
TL3.25	-0.05 **	-0.02 **	-0.01 N.S.	-0.03 **	-0.03 ***	-0.06 ***	-0.03 **	-0.02 N.S.	-0.04 **	-0.04 ***	-5.67e- 04 N.S.	4.04e- 03 *	0.01 ***	5.25e- 03 *	3.73e- 03 **	4.85e- 03 *	3.52e- 03 ***	7.03e- 03 ***	3.31e- 03 *	-6.74e- 03 **
TL4	7.64e-04 N.S.	2.56e-03 N.S.	-5.60e-04 N.S.	-2.76e- 04 N.S.	-3.85e- 04 N.S.	1.34e- 03 N.S.	2.07e- 03 N.S.	-9.23e- 04 N.S.	-2.73e- 04 N.S.	-4.58e- 04 N.S.	-1.82e- 05 N.S.	2.53e- 03 *	6.50e- 04 N.S.	2.01e- 03 N.S.	9.51e- 04 N.S.	NA	NA	NA	NA	NA
BPel	6.67e-05 N.S.	1.64e-03 N.S.	4.93e-03 **	1.40e-03 N.S.	1.47e- 04 N.S.	3.40e- 04 N.S.	8.33e- 04 N.S.	5.28e- 05 N.S.	-6.49e- 04 N.S.	-6.04e- 04 ***	-2.78e- 04 N.S.	7.60e- 03 **	0.02 **	9.75e- 03 *	5.72e- 03 **	-3.22e- 03 N.S.	-3.79e- 03 N.S.	-1.37e- 04 N.S.	-1.67e- 03 N.S.	-6.33e- 04 N.S.
BFish	-7.86e-03 *	9.23e-04 N.S.	-4.14e-03 N.S.	-1.67e- 03 N.S.	-3.69e- 06 N.S.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
BMolusc	3.16e-03 N.S.	6.31e-04 N.S.	4.74e-03 *	2.41e-03 N.S.	-3.56e- 04 N.S.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table S2.1.4. Slope parameter of time and its statistical significance of the linear regressions of demersal taxa. N.S.: non-significant effects (p-value>0.05). *: p-value<0.05. **: p-value<0.01. ***: p-value<0.001

	Demersal Community					Demersal Fishes					Demersal Cephalopods					Demersal Crustaceans				
	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL
S	0.6 ***	0.6 ***	0.46 N.S.	0.37 N.S.	0.37 *	0.39 ***	0.46 ***	0.24 N.S.	0.25 N.S.	0.07 N.S.	0.09 *	0.1 *	0.04 N.S.	-1.03e-03 N.S.	0.02 N.S.	0.12 N.S.	0.05 N.S.	0.18 N.S.	0.11 N.S.	0.29 *
H	-3.64e-03 N.S.	0.01 N.S.	0.02 N.S.	0.04 *	-0.07 ***	6.32e-03 N.S.	9.75e-03 N.S.	7.96e-03 N.S.	0.04 *	-0.07 ***	9.35e-03 N.S.	0.05 ***	0.06 ***	0.03 *	0.02 *	-2.46e-03 N.S.	1.09e-03 N.S.	0.03 **	-8.96e-03 N.S.	0.02 N.S.
J	-1.40e-03 N.S.	1.74e-03 N.S.	4.25e-03 N.S.	7.75e-03 N.S.	-0.02 ***	5.13e-04 N.S.	1.48e-03 N.S.	1.39e-03 N.S.	8.89e-03 *	-0.02 ***	2.19e-03 N.S.	0.02 ***	0.02 ***	0.01 *	5.50e-03 N.S.	-1.09e-03 N.S.	1.64e-04 N.S.	8.49e-03 **	-4.05e-03 N.S.	3.31e-03 N.S.
β I/F	3.43e-03 *	3.53e-03 *	3.29e-03 N.S.	3.25e-03 N.S.	1.11e-03 N.S.	3.24e-03 *	3.93e-03 *	5.82e-03 **	2.98e-03 N.S.	1.71e-03 *	3.25e-03 N.S.	2.57e-03 N.S.	5.14e-03 *	2.17e-03 N.S.	4.82e-03 *	4.16e-03 N.S.	3.33e-03 *	-3.31e-03 N.S.	5.02e-03 N.S.	-5.42e-03 N.S.
Turnover I/F	-8.80e-04 N.S.	-4.29e-04 N.S.	-7.19e-04 N.S.	3.19e-03 N.S.	-4.50e-04 N.S.	-1.43e-03 N.S.	-1.43e-03 N.S.	2.40e-03 N.S.	1.31e-03 N.S.	7.93e-04 N.S.	-1.01e-03 N.S.	-2.48e-03 N.S.	3.55e-03 N.S.	3.80e-03 N.S.	4.62e-03 *	9.54e-04 N.S.	1.95e-03 N.S.	-6.63e-03 *	6.55e-03 N.S.	-3.44e-03 N.S.
Nestedness I/F	4.31e-03 **	3.96e-03 ***	4.01e-03 ***	6.04e-05 N.S.	1.56e-03 *	4.67e-03 ***	5.36e-03 ***	3.41e-03 ***	1.67e-03 N.S.	9.14e-04 N.S.	4.26e-03 N.S.	5.04e-03 *	1.58e-03 N.S.	-1.63e-03 N.S.	2.00e-04 N.S.	3.21e-03 N.S.	1.37e-03 N.S.	3.32e-03 N.S.	-1.52e-03 N.S.	-1.98e-03 N.S.
B	563.28 *	490.34 **	157.69 N.S.	-181.76 N.S.	210.96 N.S.	190.35 N.S.	394.39 **	105.53 N.S.	-189.59 N.S.	218.78 N.S.	143.3 **	83.03 *	41.9 *	12.76 N.S.	-22.86 N.S.	229.63 *	12.92 **	10.27 N.S.	-4.93 N.S.	15.04 N.S.

N	33135.72 N.S.	15039.62 N.S.	-8057.17 N.S.	-20068. 17 N.S.	141728 .43 ***	3049.23 N.S.	12636. 11 N.S.	-3269.2 2 N.S.	-19473. 4 N.S.	140225. 41 ***	-535.9 8 N.S.	-309.5 5 N.S.	-5287.9 8 *	-953.4 *	-2771.6 1 **	30622. 47 N.S.	2713.0 7 *	500.04 N.S.	358.64 N.S.	4274.6 3 **
MS	0.29 N.S.	0.21 N.S.	0.57 **	0.44 N.S.	-0.88 ***	-0.27 N.S.	5.29e- 03 N.S.	0.38 N.S.	0.32 N.S.	-0.87 ***	3.34 N.S.	3.8 **	3.42 ***	5.5 ***	3.02 ***	0.82 *	0.02 N.S.	0.02 N.S.	-0.1 N.S.	-0.51 *
Bpred	-0.01 ***	-2.33e-03 N.S.	3.68e-03 N.S.	-0.01 ***	-0.02 ***	-0.01 ***	-3.20e- 03 N.S.	2.33e- 03 N.S.	-0.01 ***	-0.02 ***	-7.29e- 03 N.S.	1.97e- 03 *	9.29e- 03 ***	3.02e- 03 N.S.	2.56e- 03 **	7.15e- 05 N.S.	2.05e- 04 N.S.	-1.21e- 03 N.S.	2.79e- 05 N.S.	1.17e- 03 N.S.
TLc	-4.51e-03 *	-1.62e-03 N.S.	8.74e-04 N.S.	-6.35e- 03 ***	-0.02 ***	-6.79e- 03 **	-1.84e- 03 N.S.	1.67e- 04 N.S.	-7.68e- 03 ***	-0.02 ***	5.07e- 04 N.S.	-4.96e- 05 N.S.	1.90e- 03 N.S.	-4.27e- 04 N.S.	6.44e- 04 N.S.	3.05e- 03 N.S.	3.79e- 03 ***	7.20e- 03 ***	4.09e- 03 *	-6.73e- 03 **
TL3.25	-3.63e-03 *	-8.37e-04 N.S.	-1.10e-04 N.S.	-2.42e- 03 N.S.	3.36e- 04 N.S.	-5.67e- 03 **	-1.75e- 03 N.S.	-1.53e- 03 N.S.	-3.30e- 03 *	1.22e- 03 N.S.	5.07e- 04 N.S.	-4.96e- 05 N.S.	1.90e- 03 N.S.	-4.27e- 04 N.S.	6.44e- 04 N.S.	4.85e- 03 *	3.52e- 03 ***	7.03e- 03 ***	3.31e- 03 *	-6.74e- 03 **
TL4	6.86e-04 N.S.	2.24e-03 N.S.	-8.91e-04 N.S.	-2.98e- 04 N.S.	-4.66e- 04 N.S.	1.52e-03 N.S.	2.07e- 03 N.S.	-9.20e- 04 N.S.	-2.71e- 04 N.S.	-4.58e- 04 N.S.	1.89e- 04 N.S.	1.40e- 03 N.S.	-5.14e- 04 N.S.	1.95e- 04 N.S.	4.75e- 04 N.S.	NA	NA	NA	NA	NA
BFish	-8.39e-03 *	1.66e-03 N.S.	-2.09e-04 N.S.	7.23e- 05 N.S.	6.59e- 04 N.S.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
BMolusc	2.92e-03 N.S.	-5.17e-04 N.S.	6.50e-04 N.S.	5.88e- 04 N.S.	-1.04e- 03 N.S.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table S2.1.5. Slope parameter of time and its statistical significance of the linear regressions of pelagic taxa. N.S.: non-significant effects (p-value>0.05).

*: p-value<0.05. **: p-value<0.01. ***: p-value<0.001

	Pelagic Community					Pelagic Fishes					Pelagic Cephalopods					Pelagic Crustaceans				
	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL	AL	CN	DE	CC	GoL
S	0.02 N.S.	-0.02 N.S.	0.09 N.S.	0.01 N.S.	0.07 N.S.	0.03 N.S.	-4.44e-03 N.S.	0.07 N.S.	0.04 N.S.	0.06 N.S.	5.47e-03 N.S.	4.44e-03 N.S.	0.03 **	0.03 *	0.02 N.S.	-0.01 N.S.	-0.02 N.S.	-8.28e-05 N.S.	-0.08 ***	-2.85e-17 N.S.
H	5.05e-03 N.S.	8.97e-05 N.S.	-1.97e-04 N.S.	0.01 N.S.	0.02 **	0.02 *	-0.02 N.S.	0.02 N.S.	0.02 N.S.	8.27e-03 **	-8.82e-04 N.S.	-2.39e-03 N.S.	6.52e-03 N.S.	-4.20e-04 N.S.	-4.15e-04 N.S.	-0.02 **	-2.56e-03 N.S.	3.34e-03 N.S.	-0.02 *	NA
J	1.38e-03 N.S.	1.63e-04 N.S.	-2.52e-05 N.S.	2.33e-03 N.S.	8.77e-03 *	0.01 *	-7.14e-03 N.S.	9.77e-03 N.S.	0.01 N.S.	3.93e-03 *	-1.27e-03 N.S.	-3.44e-03 N.S.	9.41e-03 N.S.	-6.07e-04 N.S.	-5.98e-04 N.S.	-0.02 **	1.69e-03 N.S.	6.91e-03 N.S.	-5.62e-03 N.S.	NA
β I/F	3.12e-03 N.S.	3.82e-04 N.S.	3.92e-03 N.S.	3.32e-03 N.S.	7.64e-03 **	1.22e-03 N.S.	-2.03e-04 N.S.	3.41e-03 N.S.	8.93e-05 N.S.	7.44e-03 **	2.74e-03 N.S.	2.22e-03 N.S.	0.02 **	0.01 *	0.01 N.S.	0.01 ***	2.08e-03 N.S.	1.63e-03 N.S.	0.02 ***	NA
Turnover I/F	-3.04e-04 N.S.	-1.07e-03 N.S.	-1.61e-03 N.S.	8.39e-03 **	4.97e-03 N.S.	-3.09e-03 N.S.	-2.74e-03 N.S.	-2.01e-03 N.S.	1.39e-03 N.S.	5.70e-03 N.S.	NA	NA	NA	NA	NA	0.02 **	-1.71e-04 N.S.	NA	NA	NA
Nestedness I/F	3.43e-03 *	1.45e-03 N.S.	5.53e-03 *	-5.07e-03 N.S.	2.67e-03 N.S.	4.30e-03 **	2.54e-03 N.S.	5.42e-03 *	-1.30e-03 N.S.	1.74e-03 N.S.	2.74e-03 N.S.	2.22e-03 N.S.	0.02 **	0.01 *	0.01 N.S.	-2.91e-03 N.S.	2.25e-03 N.S.	1.63e-03 N.S.	0.02 ***	NA
B	53.16 N.S.	48.44 **	90.3 **	11.27 N.S.	9.1 N.S.	24.56 N.S.	16.88 N.S.	3.67 N.S.	-8.42 N.S.	-20.82 **	29.35 N.S.	33.85 **	86.27 **	20.52 *	30.07 **	-0.75 N.S.	-2.29 N.S.	0.39 N.S.	-0.97 N.S.	-0.14 N.S.

N	-8362.1 N.S.	-3649.75 N.S.	2217.63 N.S.	-5347.43 N.S.	- 2296.84 *	- 5379.3 8 N.S.	2233 N.S.	- 228.42 N.S.	- 4685.5 3 N.S.	- 2614.85 *	1267. 02 N.S.	675.3 3 ***	1537.3 **	286.09 **	450.19 ***	- 4249. 74 N.S.	-6558.08 N.S.	1017.2 9 N.S.	- 1116.7 8 N.S.	-126.33 N.S.
MS	0.71 *	0.39 **	1.19 *	0.97 N.S.	1.22 **	0.98 N.S.	0.08 N.S.	0.13 N.S.	0.18 **	-0.05 N.S.	-1.57 N.S.	-1.36 N.S.	-1.13 N.S.	-2.61 *	-3.89 ***	0.3 N.S.	-2.17e- 03 N.S.	4.25e- 03 N.S.	0.01 N.S.	-4.33e- 03 N.S.
Bpred	2.35e-03 N.S.	0.01 N.S.	0.01 N.S.	0.02 **	0.02 ***	6.51e- 04 N.S.	2.14e- 05 N.S.	7.27e- 03 *	-7.70e- 05 N.S.	1.06e- 03 N.S.	-0.01 **	- 8.52e- 04 N.S.	-1.96e- 04 N.S.	- 1.36e- 07 N.S.	-1.11e- 05 N.S.	NA	NA	NA	NA	NA
TLc	2.98e-03 N.S.	0.01 N.S.	0.01 N.S.	0.02 **	0.02 ***	-6.35e- 05 N.S.	-6.45e- 04 N.S.	1.35e- 03 N.S.	1.19e- 03 N.S.	2.35e- 04 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	1.04e- 03 N.S.	3.40e-04 N.S.	3.39e- 04 N.S.	5.37e- 04 N.S.	-5.69e- 17 N.S.
TL3.25	-0.06 N.S.	1.90e-03 N.S.	0.05 *	-0.02 N.S.	-0.01 N.S.	-0.05 *	-6.90e- 03 N.S.	1.48e- 03 N.S.	-0.04 *	-0.02 ***	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	NA	NA	NA	NA	NA
TL4	-1.04e-03 N.S.	1.63e-04 N.S.	1.95e-05 N.S.	-6.62e- 05 N.S.	1.26e- 05 N.S.	0.06 N.S.	0.02 N.S.	-0.04 N.S.	0.03 N.S.	-0.01 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	3.87e- 17 N.S.	NA	NA	NA	NA	NA
BFish	-4.56e-03 N.S.	-6.82e-03 N.S.	-0.01 N.S.	-0.02 *	-0.02 **	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
BMolusc	5.34e-03 N.S.	0.01 N.S.	0.01 N.S.	0.02 **	0.02 ***	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Table S2.1.6. F-value and statistical significance of the different ANCOVA models. N.S.: non-significant effects (p-value>0.05). *: p-value<0.05. **: p-value<0.01. *: p-value<0.001**

	Community			Fishes			Cephalopods			Crustaceans		
	All	Demersal	Pelagics	All	Demersal	Pelagics	All	Demersal	Pelagics	All	Demersal	Pelagics
S	7.009 ***	5.757 **	17.438 ***	4.35 **	4.955 **	10.109 ***	11.226 ***	13.027 ***	7 ***	6.548 ***	5.783 **	18.637 ***
H	10.701 ***	9.525 ***	4.115 **	15.61 ***	13.245 ***	3.378 *	2.541 N.S.	3.382 *	5.841 **	9.553 ***	14.981 ***	4.058 **
J	10.812 ***	9.725 ***	1.922 N.S.	15.676 ***	13.541 ***	2.417 N.S.	3.741 *	6.145 ***	5.841 **	11.293 ***	17.199 ***	3.666 *
β I/F	0.986 N.S.	1.205 N.S.	3.889 *	0.755 N.S.	2.218 N.S.	3.434 *	2.281 N.S.	2.319 N.S.	7 ***	2.848 *	2.148 N.S.	7.755 ***
Turnover I/F	0.821 N.S.	0.931 N.S.	5.392 **	1.082 N.S.	1.721 N.S.	5.479 **	1.76 N.S.	1.823 N.S.	NA	1.291 N.S.	1.721 N.S.	1 N.S.
Nestedness I/F	2.617 N.S.	2.635 N.S.	1.233 N.S.	3.174 *	1.182 N.S.	3.026 *	0.472 N.S.	0.128 N.S.	7 ***	3.91 **	3.487 *	8.311 ***
B	25.049 ***	30.39 ***	2.313 N.S.	31.554 ***	34.314 ***	2.692 *	3.436 *	7.01 ***	2.606 N.S.	5.636 **	5.455 **	10.515 ***
N	21.316 ***	21.781 ***	3.55 *	32.542 ***	33.329 ***	2.31 N.S.	8.705 ***	15.616 ***	2.481 N.S.	2.632 N.S.	2.483 N.S.	1.552 N.S.
MS	4.714 **	5.205 **	1.716 N.S.	9.527 ***	8.338 ***	1.511 N.S.	6.11 ***	4.44 **	2.063 N.S.	1.791 N.S.	1.715 N.S.	2.118 N.S.

Bpred	5.228 **	4.77 **	6.55 ***	3.349 *	3.777 *	2.958 *	8.659 ***	7.324 ***	6.589 ***	7.49 ***	7.543 ***	NA
TLc	6.909 ***	6.021 ***	6.52 ***	6.361 ***	6.486 ***	2.835 *	3.223 *	0.788 N.S.	NA	2.513 N.S.	2.553 N.S.	0.766 N.S.
TL3.25	1.036 N.S.	13.736 ***	1.979 N.S.	0.917 N.S.	20.064 ***	1.43 N.S.	3.223 *	0.788 N.S.	NA	2.333 N.S.	2.328 N.S.	3.046 *
TL4	10.559 ***	8.56 ***	2.331 N.S.	6.109 ***	5.662 **	4.033 **	0.864 N.S.	1.928 N.S.	NA	NA	NA	NA
BPel	4.616 **	NA	NA	3.128 *	NA	NA	4.834 **	NA	NA	3.454 *	NA	NA
BFish	4.112 **	2.82 *	4.71 **	NA	NA	NA	NA	NA	NA	NA	NA	NA
BMolusc	7.623 ***	9.151 ***	2.461 N.S.	NA	NA	NA	NA	NA	NA	NA	NA	NA

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Table S2.2.1. Effects of selected independent variables (drivers) related to cephalopods on the dependent variables (indicators) on different study areas.

Driver	Indicator	Study area	Direction of change	Mechanism and observations	Published research paper
Mediterranean Sea					
Chl-a	Richness	Mediterranean Sea	Positive (after threshold)	Inverted bell shape with inflection point at 0.4mg/m ³ .	(Keller et al., 2016)
SST	Richness	Mediterranean Sea	Positive	Below average diversity below 14-16°C.	(Keller et al., 2016)
SST	Biomass	Mediterranean and Northeast Atlantic	Negative	Scenarios of SST increase limit environment suitability of several species of cephalopods.	(Schickele et al., 2021)
Chl-a	Biomass	Western Mediterranean	Positive		(Puerta et al., 2016)
Chl-a	Biomass	Western Mediterranean	Negative	High levels of primary production can benefit small pelagic fishes resulting in competition with planktonic phases.	(Keller et al., 2017)
Chl-a, Fishing effort	Richness	Western Mediterranean	Negative	Significant negative effect of Chl-a in non-target species and of fishing for target species.	(Navarro et al., 2015)
SST, Fishing effort	Biomass	Western Mediterranean	Positive	Significant effect of SST in target cephalopods and significant positive effect of fishing in non-target species.	(Navarro et al., 2015)
SST	Richness	Western Mediterranean	Positive		(Vilas et al., 2019)
SST	Mean Size	Western Mediterranean Sea/Saharan Bank	Negative	Low SST lengthens growth period and delays maturation resulting in larger sizes despite of slower growth rates.	(Pierce et al., 2008)
SST	Biomass	Western Mediterranean	Mixed	Differing effects of temperature in species, <i>I. coindetti</i> more associated with cooler waters while <i>E. cirrhosa</i> is more associated with warmer SST.	(Puerta et al., 2014)
Biomass Crustaceans	Biomass	Western Mediterranean	Positive	Crustacean (prey) density increases cephalopod density.	(Puerta et al., 2015)
Chl-a	Biomass	Central Mediterranean	Positive	For squid species primary production increases hatchling survival.	(Lauria et al., 2016)
Chl-a	Biomass	Central Mediterranean	Negative	This negative relationship between primary production and abundance of octopus may be	(Lauria et al., 2016)

					result of a lagged response to upwellings.	
Chl-a	Biomass	North Aegean Sea		Positive	Spatial distribution of certain squid species was positively correlated with areas with high productivity.	(Valavanis et al., 2004)
SST	Mean Size	Eastern Mediterranean, Northeast Atlantic		Mixed	Flexibility of response in different areas. In Eastern Mediterranean positively correlated with length and weight. On the NE Atlantic the relationship is negative, showing life cycle flexibility.	(Arvanitidis et al., 2002)
SST	Biomass	Eastern Mediterranean		Mixed	Catch of loliginids positively related to SST while ommaestrophids had a negative correlation.	(Georgakarakos et al., 2002)
Chl-a	Mean Size	Eastern Mediterranean		Negative	Negatively correlated with weight in Greek waters.	(Arvanitidis et al., 2002)

Other Areas						
SST	Mean Size	Lab and in the wild		Positive		(Forsythe, 2004)
Fishing effort, Fish Bpred	Biomass	Worldwide		Positive	Overexploitation of fishes increases cephalopod catches due to removal of competitors and predators.	(Caddy and Rodhouse, 1998)
SST, Chl-a	Mean Size	General		Positive	The combined effect of abundant food supply and fast growth rates allows bigger adult sizes.	(Pierce et al., 2010)
SST	Mean Size	General		Negative	In <i>S. officinalis</i> , high temperatures result in an increase in oxygen consumption, amount of yolk used for metabolism and therefore reduced hatchling size.	(Xavier et al., 2016)
SST	Biomass	Northeast Atlantic		Positive		(Pierce et al., 2008)
Fishing effort	Biomass	Northeast Atlantic		Positive		(Hastie et al., 2009)
Chl-a	Biomass	Galician coast		Positive	Zooplankton availability increases success of recruitment.	(Pierce et al., 2008)

SST	Biomass	Portugal shelf	Negative (after threshold)	Nonlinear relationship between temperature and juvenile abundance of <i>L. forbesii</i> in the nursery areas, with an optimum value of 17°C.	(Moreno et al., 2014)
SST	Mean Size	Scottish waters	Negative (after threshold)	Size peaks at 11°C, after that temperature there is a decrease in body size during summer.	(Viana, 2007)
SST	Biomass	Scottish waters	Negative (after threshold)	Optimal temperature of 10°C after which there is a negative response.	(Viana, 2007)
SST	Richness	North Sea	Positive	Higher richness levels with increasing temperatures partly due to northward migrations.	(Oesterwind et al., 2022)
SST	Biomass	North Sea	Positive	Detected increase of biomass during period of historical maximum of SST.	(Oesterwind et al., 2022)
Fishing effort	Biomass	Saharan Bank	Positive	Replacement of overexploited finfish.	(Pierce et al., 2008)
Fish Bpred	Biomass	Northwest Atlantic	Negative	High predatorial pressure could decimate populations during spawning migrations.	(Bakun and Csirke, 1998)
SST	Mean Size	Southwest Atlantic	Negative	Reduced hatchling size and time to maturity.	(Pecl and Jackson, 2008)
SST	Mean Size	Falkland Islands	Positive	High SST at hatching accelerates growth rates.	(Hatfield, 2000)
SST	Biomass	Pacific	Positive	Paralarval exposure to low SSTs lead to reduction in stock abundance. Maximal survival rate of hatchlings between 19.5–23°C in <i>T. pacificus</i> .	(Rosa et al., 2011)
SST	Biomass	Pacific	Positive	In <i>S. oualaniensis</i> there is an increase of CPUE between 24-26°, decrease between 26-27° and after 27° there is a surge in CPUE remaining at high levels. This increase explains most of its variation.	(Yu et al., 2019)
Chl-a	Biomass	Pacific	Positive	CPUE rises between 0.05–0.20 mg of Chl-a for <i>S. oualaniensis</i> .	(Yu et al., 2019)
SST	Biomass	Sea of Japan	Positive	Increase in squid landings of <i>T. rhombus</i> with temperature due to recruitment success.	(Miyahara et al., 2005)

Table S2.2.2. Number of sampling points in the Western Mediterranean Area during the time period of the study (2013-2019)

Year	Sample points
2013	177
2014	179
2015	181
2016	189
2017	190
2018	188
2019	197
TOTAL	1298

Table S3. Number of cephalopod species found in the study area by GSA and year during at least 80% of the considered time period.

No. species of	2013	2014	2015	2016	2017	2018	2019	TOTAL
GSA01	22	22	22	23	24	24	25	26
GSA06	25	21	23	22	22	21	22	25
GSA07	20	17	18	16	18	19	21	24
TOTAL	26	26	26	27	27	27	27	27

Table S4 List of cephalopod species found in the study area during the 2013 to 2019 period and their trait data. Predator tags those species that can be considered predators with a value of 1 and TL represents the Trophic level of the species. Species that appear in less than 80% of the timeframe (in grey) were discarded.

Species name	Predator	TL
<i>Abralia veranyi</i>	0	NA
<i>Adinaefiola ligulata</i>	0	3.4
<i>Alloteuthis media</i>	0	3.47

<i>Alloteuthis subulata</i>	1	4.5
<i>Ancistroteuthis lichtensteini</i>	0	NA
<i>Bathypolipus arcticus</i>	1	3.4
<i>Bathypolypus sponsalis</i>	1	3.65
<i>Brachioteuthis riisei</i>	1	3.2
<i>Callistoctopus macropus</i>	1	3.53
<i>Chroteuthis veranii</i>	1	4.04
<i>Eledone cirrhosa</i>	1	3.7
<i>Eledone moschata</i>	0	3.98
<i>Heteroteuthis dispar</i>	0	3.6
<i>Histioteuthis bonnellii</i>	1	4.16
<i>Histioteuthis reversa</i>	1	4.11
<i>Illex coindetii</i>	1	4.34
<i>Loligo forbesii</i>	1	4.29
<i>Loligo vulgaris</i>	0	4.5
<i>Macrotritopus defilippi</i>	0	NA
<i>Neorossia caroli</i>	0	NA
<i>Octopus salutii</i>	0	4.17
<i>Octopus vulgaris</i>	1	3.74
<i>Onychoteuthis banksii</i>	0	3.79
<i>Pteroctopus tetracirrhus</i>	0	3.73
<i>Rondeletiola minor</i>	1	3.7
<i>Rossia macrosoma</i>	1	4.04
<i>Scaevurgus unicolor</i>	0	NA
<i>Sepia elegans</i>	1	3.84
<i>Sepia officinalis</i>	1	3.71
<i>Sepia orbigynana</i>	0	4.16
<i>Sepietta neglecta</i>	0	3.41
<i>Sepietta obscura</i>	0	NA
<i>Sepietta oweniana</i>	0	3.45

<i>Sepiola affinis</i>	0	3.4
<i>Sepiola intermedia</i>	1	NA
<i>Sepiola robusta</i>	0	3.99
<i>Stoloteuthis leucoptera</i>	0	NA
<i>Todarodes sagittatus</i>	0	4.4
<i>Todaropsis eblanae</i>	0	4.25

Table S2.2.5 GAM Model selection for the different indicators, based on AIC and explained deviance of the different models. Variables in bold correspond to statistically significant drivers for the corresponding indicator.

Indicator	Model formula	AIC	%DV
Richness	SST + log(Biomass crustaceans) + depth	5284.429	23.6
	SST + Chl-a + log(Biomass crustaceans) + depth	5285.326	23.7
	SST + Chl-a + log(Biomass crustaceans) + Fish Bpred + depth	5286.715	23.8
	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + Fish Bpred + depth	5287.612	24
B-diversity (Jaccard index)	SST + Chl-a + log(Fishing effort) + Fish Bpred + depth	-2661.66	10.9
	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + Fish Bpred + depth	-2660.68	11.1
Log(Biomass)	SST + Chl-a + log(Biomass crustaceans) + Fish Bpred + depth	4025.13	25
	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + Fish Bpred + depth	4026.146	25.1
Bpred	SST + Chl-a + log(Biomass crustaceans) + Fish Bpred + depth	-673.689	27.5
	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + Fish Bpred + depth	-671.695	27.5
Log(Mean Size)	SST + Chl-a + log(Fishing effort) + Fish Bpred + depth	4032.673	10.2
	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + Fish Bpred + depth	4034.105	10.3
	SST + Chl-a + Fish Bpred + depth	4035.012	9.87
	SST + Chl-a + log(Biomass crustaceans) + Fish Bpred + depth	4036.79	9.92
TL _{3,25}	SST + log(Biomass crustaceans) + depth	-556.157	8.82
	SST + Chl-a + log(Biomass crustaceans) + depth	-554.415	8.84
	SST + Chl-a + log(Biomass crustaceans) + Fish Bpred + depth	-553.207	8.9
	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + Fish Bpred + depth	-552.532	8.99
TL ₄	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + depth	-3354.97	34.5
	SST + Chl-a + log(Biomass crustaceans) + depth	-3353.91	34.2
	SST + Chl-a + log(Fishing effort) + log(Biomass crustaceans) + Fish Bpred + depth	-3353.85	34.6
	SST + Chl-a + log(Biomass crustaceans) + Fish Bpred + depth	-3353.05	34.3

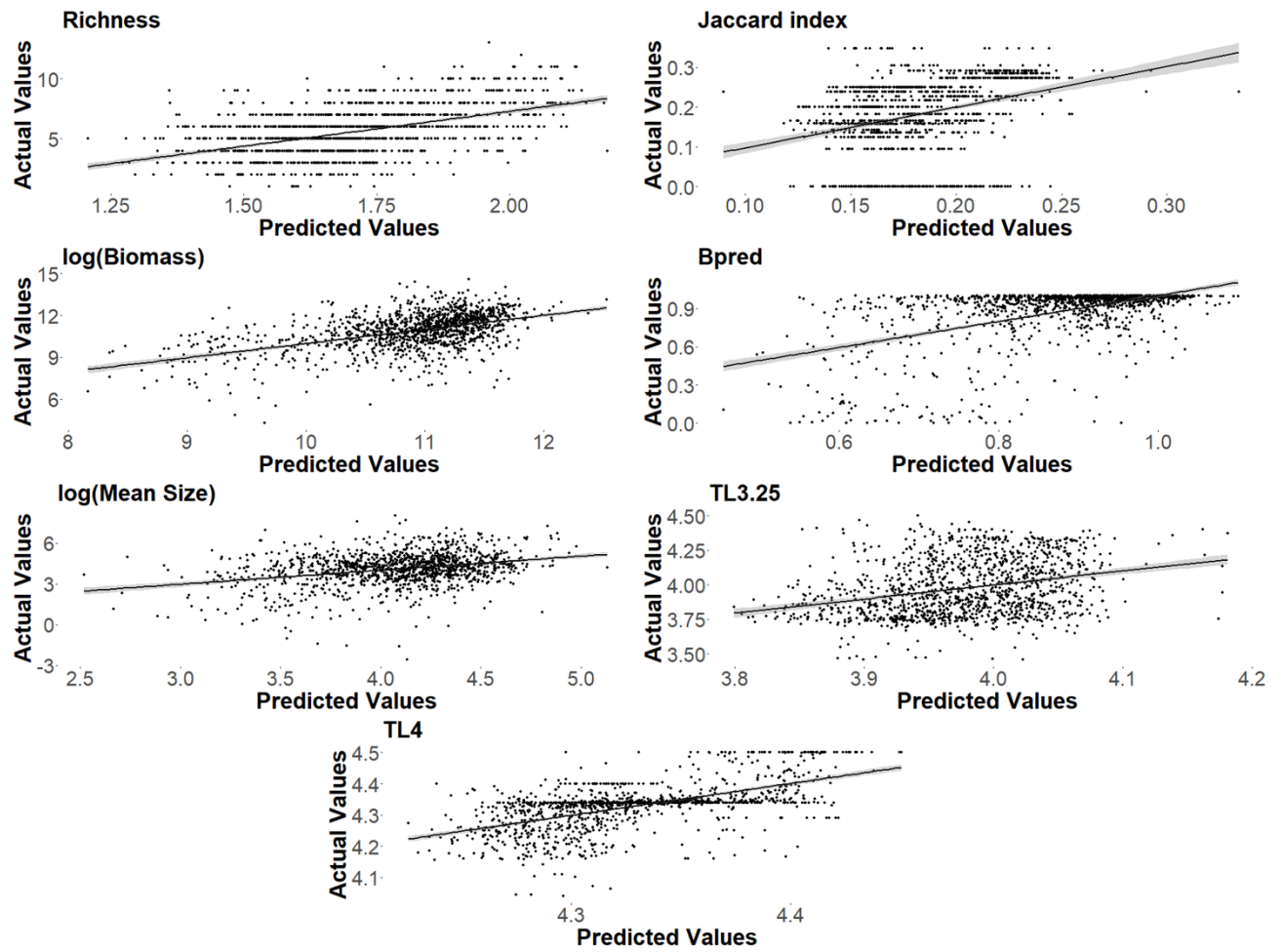


Figure S2.2.1: Fitted vs Predicted values of the selected models for the different indicators

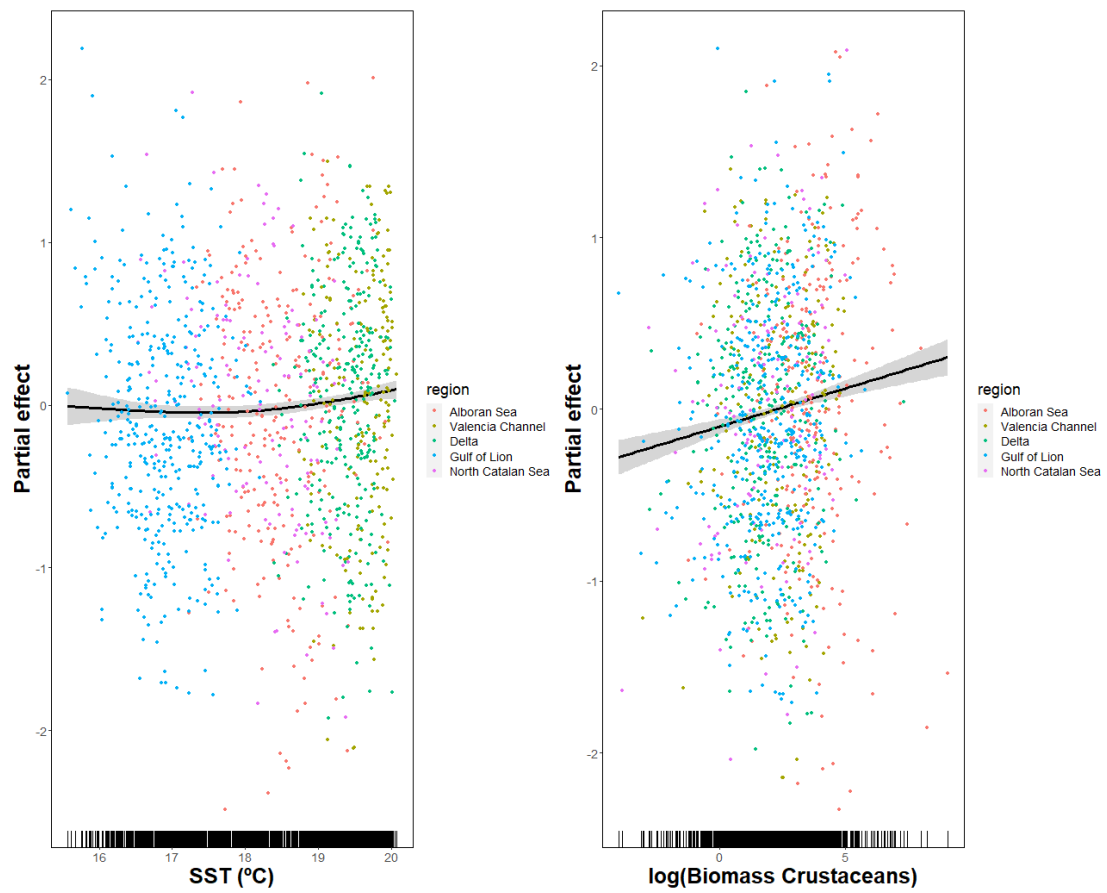


Figure S2.2.2: Partial residuals for SST (left) and Biomass of Crustaceans (right) of the Richness model. The shaded areas indicate the 95% confidence interval.

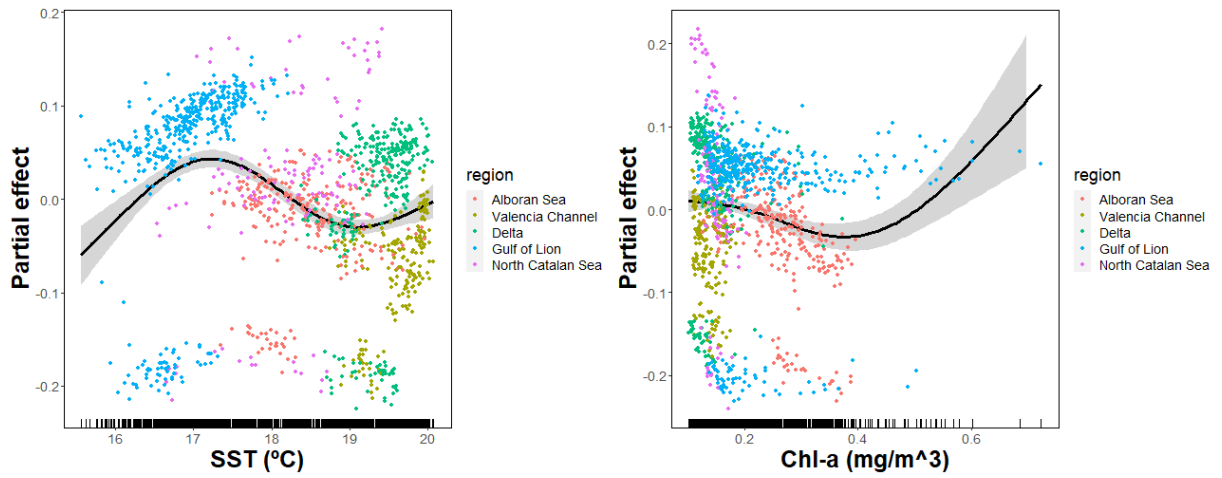


Figure S2.2.3: Partial residuals for SST (left) and Chl-a (right) of the Jaccard index model. The shaded areas indicate the 95% confidence interval.

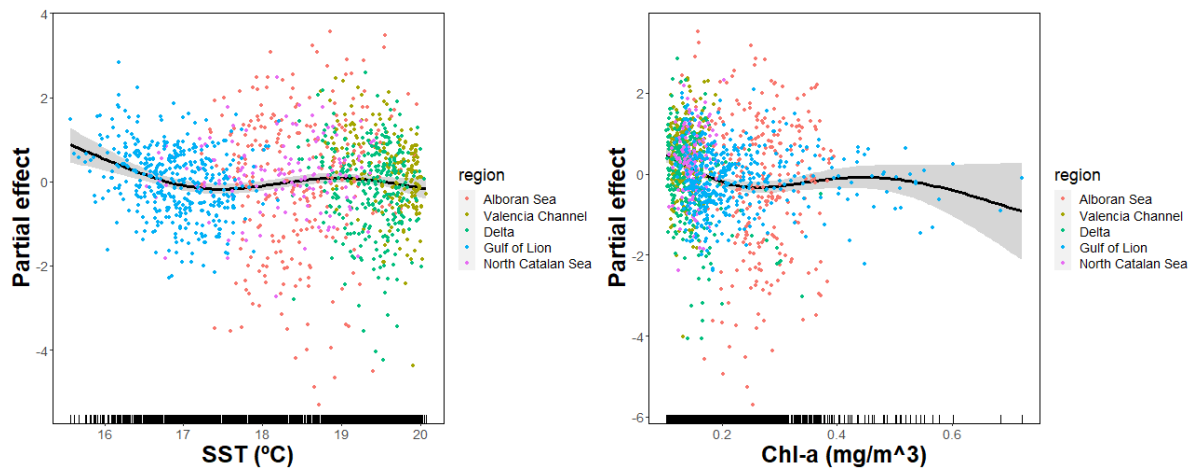


Figure S2.2.4: Partial residuals for SST (left) and Chl-a (right) of the Biomass model. The shaded areas indicate the 95% confidence interval.

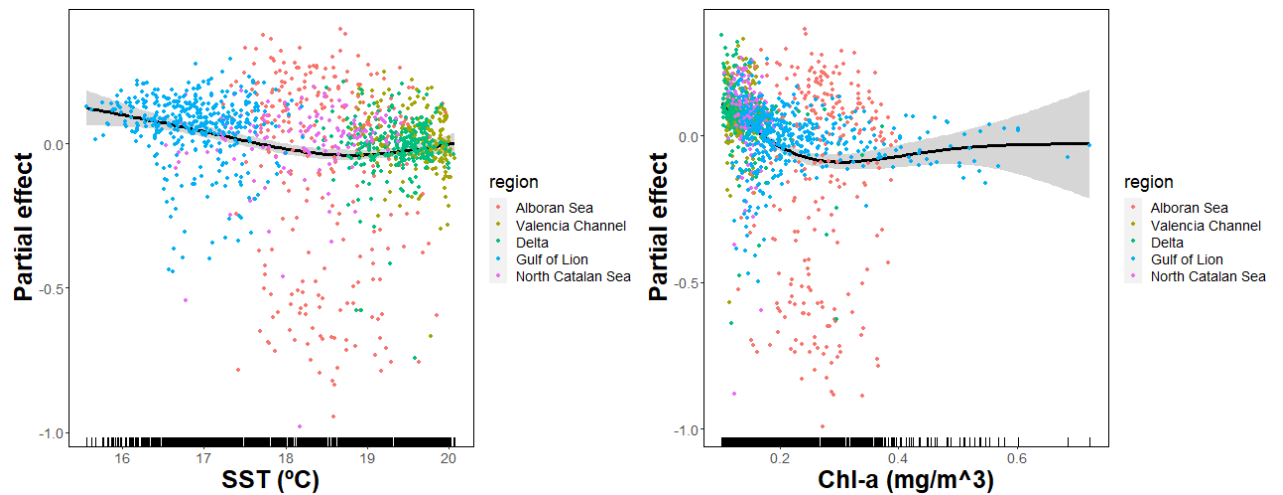


Figure S2.2.5: Partial residuals for SST (left) and Chl-a (right) of the Bpred model. The shaded areas indicate the 95% confidence interval.

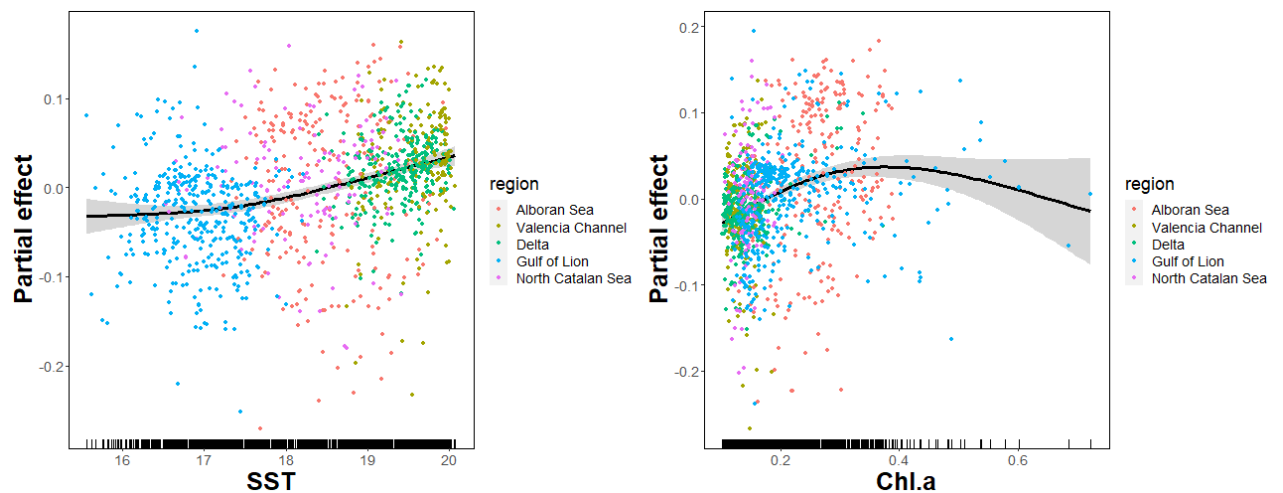


Figure S2.2.6: Partial residuals for SST (left) and Chl-a (right) of the TL₄ model. The shaded areas indicate the 95% confidence interval.

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Supplementary Material – Chapter 2.3

Table S2.3.1. Survey information of the regions considered in this study including number of sampling points, depth range, surveyed years and the selected season.

Region	Samplepoints	Depth range	Years	Season
Barents Sea	2890	33-500 m	2004-2017	Summer
North Sea	8727	10-500 m	1994-2020	Winter
Western Mediterranean	4056	13-500 m	1994-2019	Spring
South Africa West coast	2216	20-500 m	1994-1997,1999,2002-2017,2019	Summer
South Africa South coast	1623	27-500 m	1994-1997,1999,2003-2011, 2014-2016,2019	Autumn

Table S2.3.2. Selection and statistical summary of the best three GAM models for Barents Sea, North Sea, Western Mediterranean (WMed), South Africa west coast (SAw) and South Africa south coast (SAs) for each indicator. In bold the selected model based on the lowest AIC value.

Indicator	Region	Model formula	AIC	D.V.	Intercept
Richness	Barents Sea	Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	13920.84	0.206	2.374±0.006
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	13920.86	0.206	2.374±0.006
		Richness~s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	13948.23	0.191	2.375±0.006
	North sea	Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	43328.71	0.342	2.598±0.003
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	43379.08	0.337	2.599±0.003
		Richness~s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	43379.99	0.336	2.599±0.003
	WMed	Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	20528.36	0.145	3.118±0.004
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)	20530.7	0.143	3.118±0.004
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	20537.57	0.141	3.118±0.004
	SAw	Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	10908.86	0.689	2.664±0.006
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	10913.73	0.687	2.665±0.006
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	10917.14	0.686	2.664±0.006
	SAs	Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	8839.53	0.364	2.807±0.006
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	8839.898	0.362	2.807±0.006
		Richness~te(year,depth,k=4)+s(Chl.a,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	8877.905	0.342	2.807±0.006
B-diversity		B-diversity~s(year,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-10485.6	0.693	0.19±0.001

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	Barents Sea	B-diversity~s(year,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-10482	0.694	0.19±0.001
		B-diversity~s(year,k=4)+s(SST,k=4)+s(long,lat,k=4)	-10466.5	0.69	0.19±0.001
	North sea	B-diversity~s(year,k=4)+s(long,lat,k=4)	-29979	0.416	0.279±0
		B-diversity~s(year,k=4)	-29972.5	0.415	0.279±0
		B-diversity~s(year,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-29655.4	0.437	0.279±0
	WMed	B-diversity~s(year,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-12531.4	0.62	0.35±0.001
		B-diversity~s(year,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-12527.9	0.618	0.35±0.001
		B-diversity~s(year,k=4)+s(SST,k=4)+s(long,lat,k=4)	-12521.1	0.617	0.35±0.001
	SAw	B-diversity~s(year,k=4)+s(SST,k=4)+s(long,lat,k=4)	-13999.9	0.106	0.01±0
		B-diversity~s(year,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-13999	0.107	0.01±0
		B-diversity~s(year,k=4)+s(SST,k=4)	-13996.5	0.103	0.01±0
	SAs	B-diversity~s(year,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)	-8541.12	0.156	0.025±0
		B-diversity~s(year,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)	-8539.51	0.156	0.025±0
		B-diversity~s(year,k=4)+s(SST,k=4)	-8537.84	0.151	0.025±0
Biomass	Barents Sea	Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	8731.102	0.246	6.86±0.021
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	8732.313	0.247	6.86±0.021
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(long,lat,k=4)	8736.346	0.244	6.86±0.021
	North sea	Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	24846.13	0.233	7.462±0.011
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	24846.42	0.233	7.462±0.011
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	24866.22	0.231	7.462±0.011
	WMed	Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	8766.784	0.233	5.751±0.015
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)	8789.409	0.227	5.751±0.015
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	8795.281	0.226	5.751±0.015
	SAw	Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	6114.267	0.338	8.282±0.021
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	6115.005	0.337	8.282±0.021
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	6117.942	0.335	8.282±0.021
	SAs	Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	4087.604	0.173	8.68±0.021
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	4090.472	0.17	8.68±0.021
		Biomass~te(year,depth,k=4)+s(Chl.a,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	4090.519	0.169	8.68±0.021
Bpred	Barents Sea	Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-2775.65	0.414	0.088±0.003
		Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-2765.77	0.408	0.088±0.003
		Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)	-2748.66	0.407	0.088±0.003
	North sea	Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-8505.58	0.215	0.108±0.002
		Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-8484.45	0.223	0.108±0.002

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		Bpred~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-8427.93	0.217	0.108±0.002
	WMed	Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)	-1440.27	0.398	0.662±0.003
		Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-1438.19	0.398	0.662±0.003
		Bpred~te(year,depth,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)	-1436.14	0.397	0.662±0.003
	SAw	Bpred~te(year,depth,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-3985.57	0.104	0.068±0.002
		Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-3984.08	0.104	0.068±0.002
		Bpred~te(year,depth,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-3979.89	0.1	0.068±0.002
	SAs	Bpred~te(year,depth,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-2619.89	0.241	0.076±0.003
		Bpred~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-2618.84	0.242	0.076±0.003
		Bpred~s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-2605.83	0.231	0.076±0.003
Mean Size	Barents Sea	Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	7525.521	0.366	-2.1±0.008
		Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	7531.824	0.363	-2.1±0.008
		Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	7584.265	0.352	-2.1±0.008
	North sea	Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	20181.42	0.31	-2.984±0.01
		Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	20205.12	0.307	-2.984±0.01
		Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	20209.03	0.307	-2.984±0.01
	WMed	Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	7411.656	0.121	-3.698±0.01
		Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	7423.607	0.116	-3.698±0.01
		Mean Size~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	7434.142	0.115	-3.698±0.01
Tlc	Barents Sea	Tlc~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-1431.03	0.351	4.008±0.004
		Tlc~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-1429.55	0.353	4.008±0.004
		Tlc~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(long,lat,k=4)	-1381.76	0.338	4.008±0.004
	North sea	Tlc~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-5544.33	0.351	3.591±0.002
		Tlc~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+s(SBT,k=4)+s(long,lat,k=4)	-5499.2	0.352	3.591±0.002
		Tlc~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-5497.89	0.353	3.591±0.002
	WMed	Tlc~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-1908.84	0.248	3.714±0.003
		Tlc~te(year,depth,k=4)+s(SST,k=4)+s(SBT,k=4)+te(Fishing effort,depth,k=4)	-1905.7	0.247	3.714±0.003
		Tlc~te(year,depth,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-1900.9	0.245	3.714±0.003
	SAw	Tlc~te(year,depth,k=4)+s(Chl.a,k=4)+s(SST,k=4)+te(Fishing effort,depth,k=4)+s(long,lat,k=4)	-2827.73	0.177	3.91±0.003

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		$TLc \sim te(year, depth, k=4) + s(Chl.a, k=4) + s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-2827	0.178	3.91±0.003
		$TLc \sim te(year, depth, k=4) + s(Chl.a, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-2820.19	0.174	3.91±0.003
	SAs	$TLc \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-1777.62	0.353	3.82±0.003
		$TLc \sim te(year, depth, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-1770.62	0.349	3.82±0.003
		$TLc \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + s(long, lat, k=4)$	-1769.02	0.347	3.82±0.003
TL4	Barents Sea	$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-9585.66	0.231	4.247±0.001
		$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4)$	-9567.92	0.226	4.247±0.001
		$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + s(long, lat, k=4)$	-9567.48	0.222	4.247±0.001
	North sea	$TL4 \sim te(year, depth, k=4) + s(long, lat, k=4)$	-24625.8	0.156	4.318±0.001
		$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + s(long, lat, k=4)$	-24569.2	0.18	4.318±0.001
		$TL4 \sim te(year, depth, k=4) + s(SBT, k=4) + s(long, lat, k=4)$	-24530.5	0.175	4.318±0.001
	WMed	$TL4 \sim s(Chl.a, k=4) + s(SST, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	6207.712	0.027	4.352±0.01
		$TL4 \sim s(Chl.a, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	6208.573	0.026	4.352±0.01
		$TL4 \sim s(Chl.a, k=4) + s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	6209.576	0.027	4.352±0.01
	SAw	$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-4338.39	0.092	4.34±0.002
		$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-4336.67	0.092	4.34±0.002
		$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + te(Fishing\ effort, depth, k=4)$	-4332.94	0.087	4.34±0.002
	SAs	$TL4 \sim s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-4165.27	0.284	4.272±0.002
		$TL4 \sim te(year, depth, k=4) + s(SST, k=4) + s(SBT, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-4163.8	0.287	4.272±0.002
		$TL4 \sim s(SST, k=4) + te(Fishing\ effort, depth, k=4) + s(long, lat, k=4)$	-4161.06	0.279	4.272±0.002

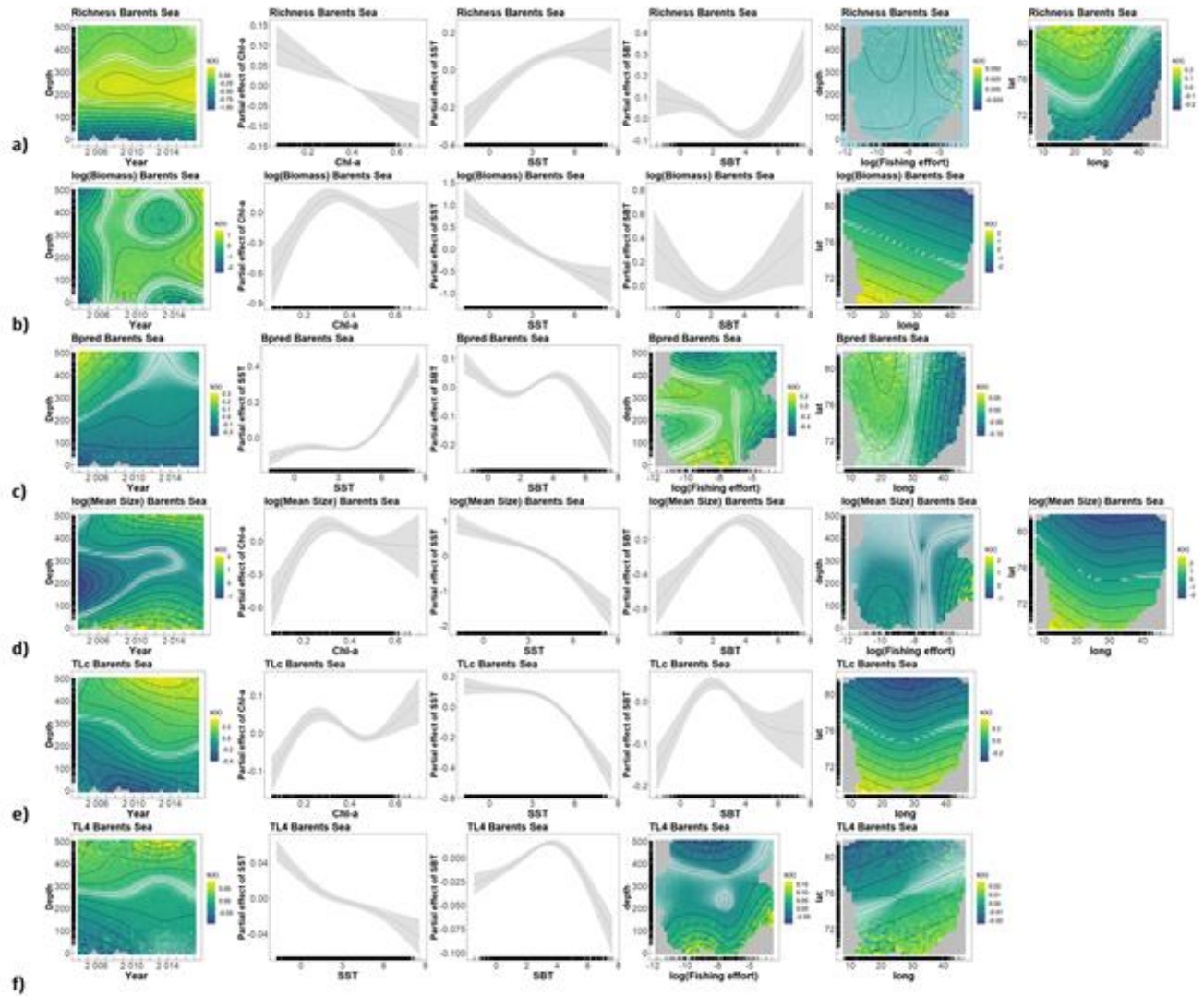


Figure S2.3.1: Partial effects of all the variables selected on the models for the different indicators (a-f) on the Barents Sea region. Blue shaded plots represent independent variables with non-significant effects that were included on the model.

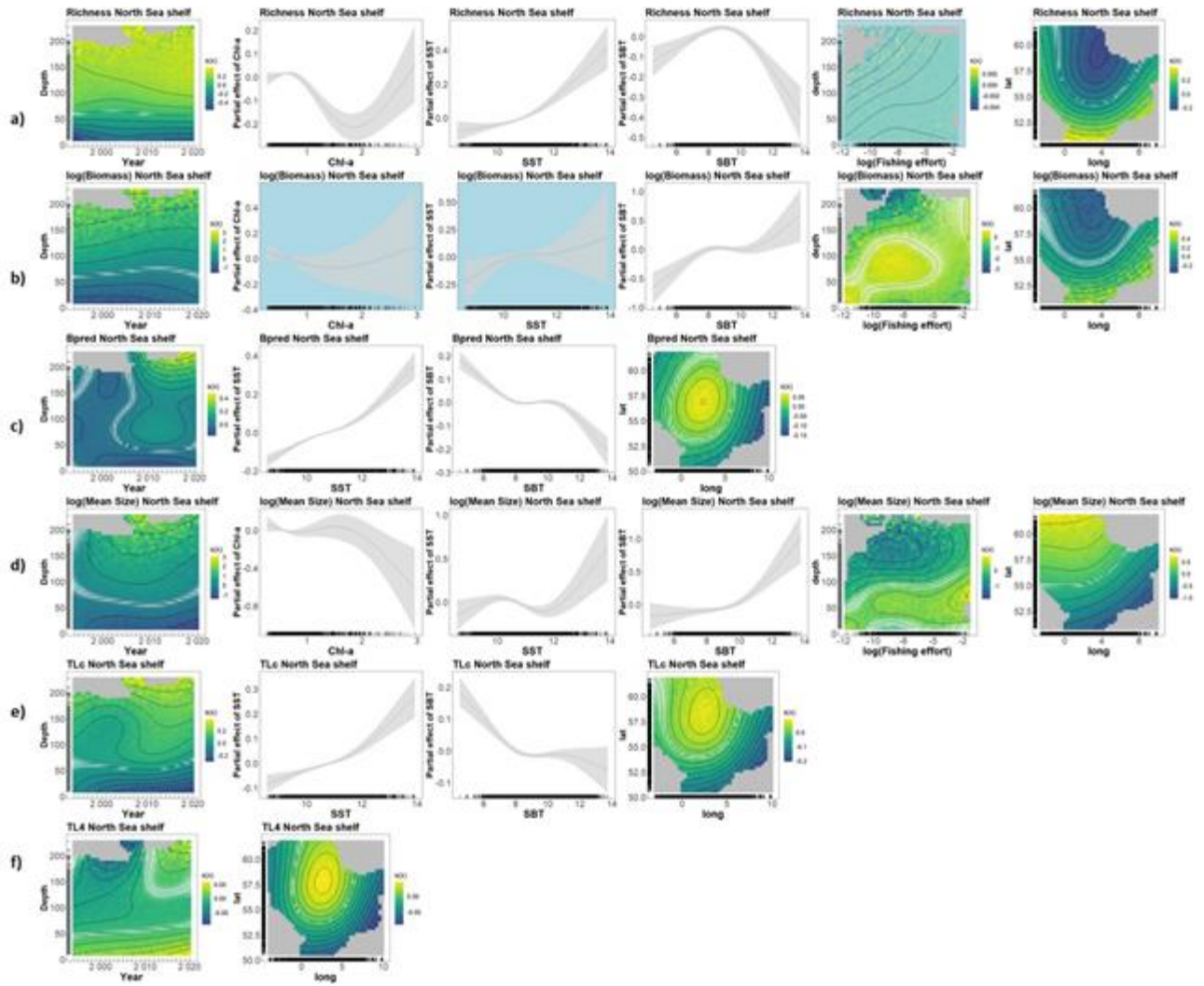


Figure S2.3.2: Partial effects of all the variables selected on the models for the different indicators (a-f) on the North Sea shelf region. Blue shaded plots represent independent variables with non-significant effects that were included on the model.

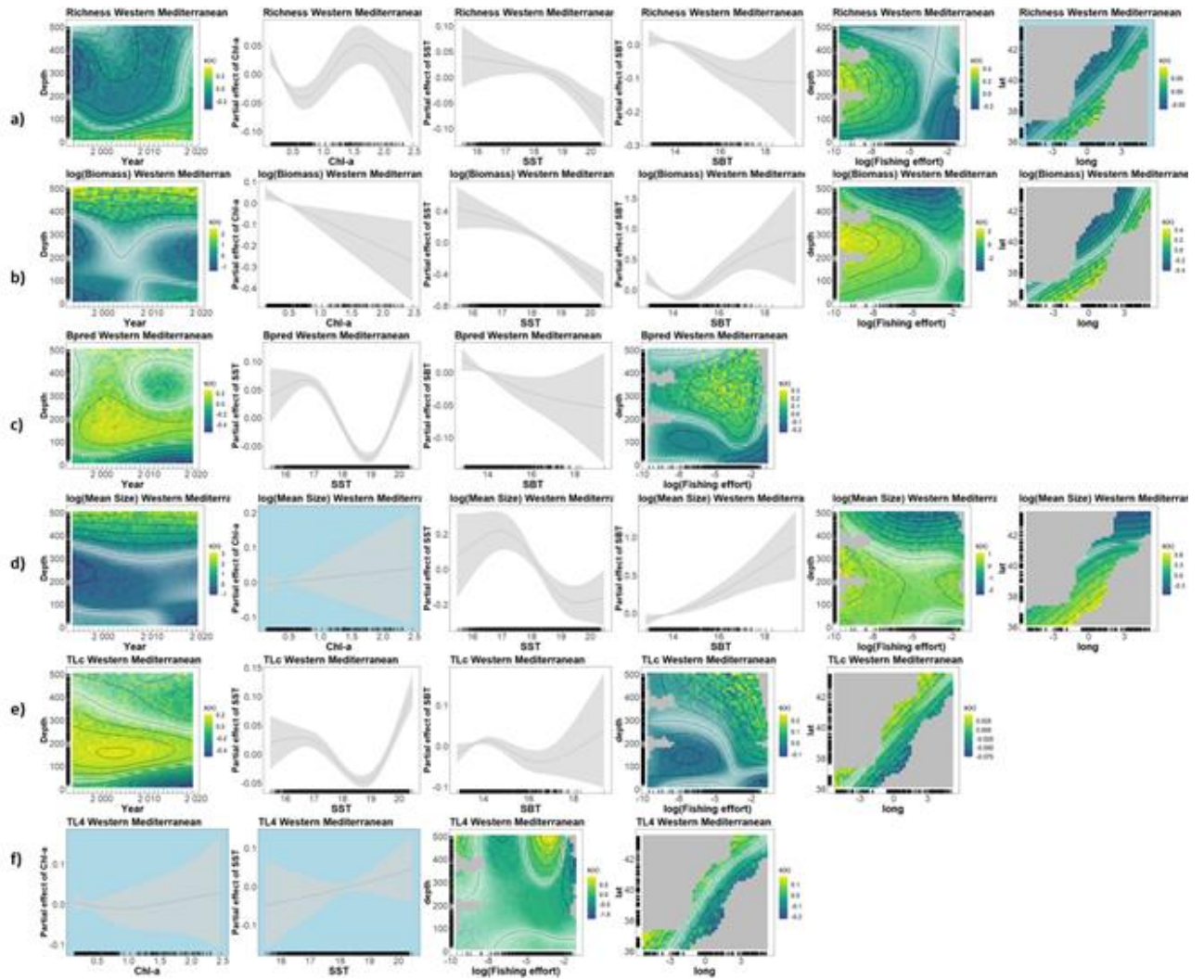


Figure S2.3.3: Partial effects of all the variables selected on the models for the different indicators (a-f) on the Western Mediterranean region. Blue shaded plots represent independent variables with non-significant effects that were included on the model.

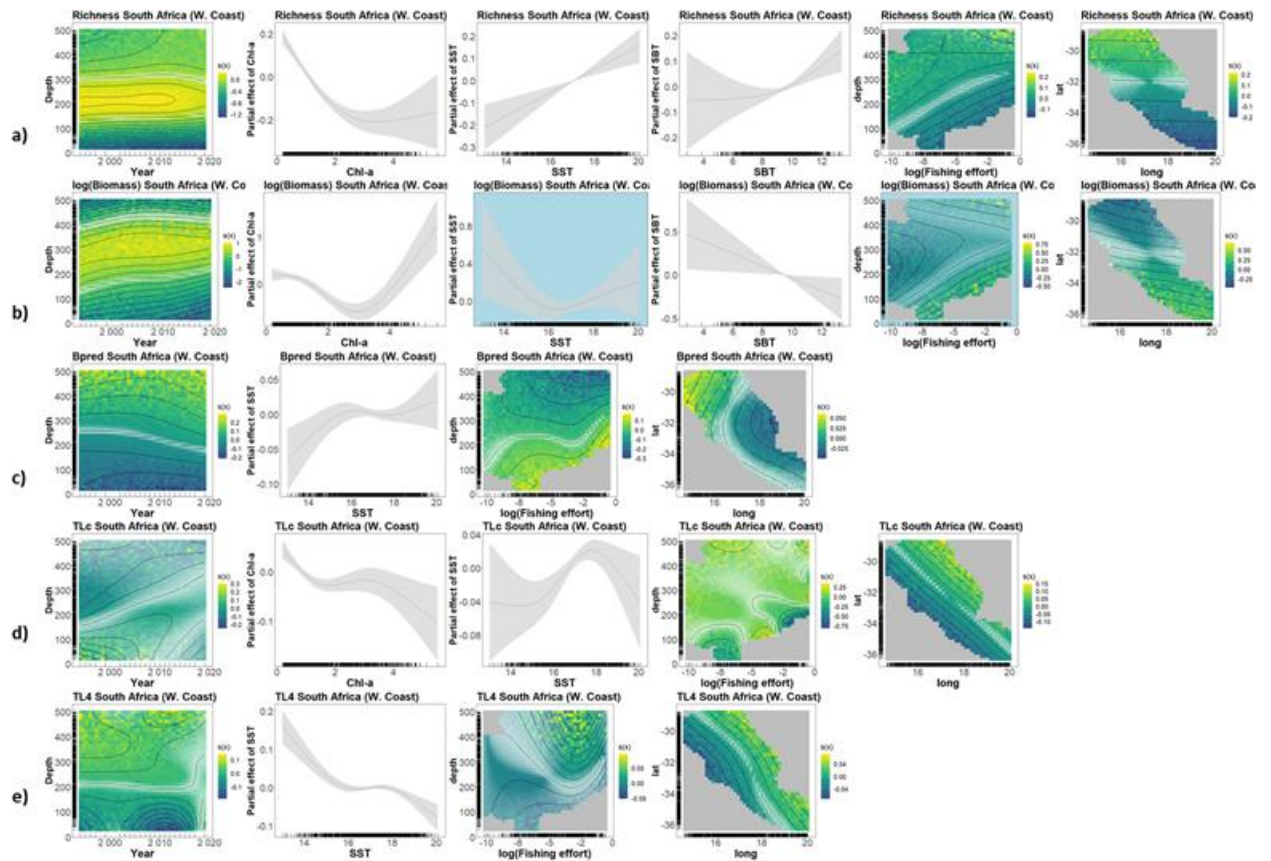


Figure S2.3.4: Partial effects of all the variables selected on the models for the different indicators (a-e) on the South Africa West Coast region. Blue shaded plots represent independent variables with non-significant effects that were included on the model.

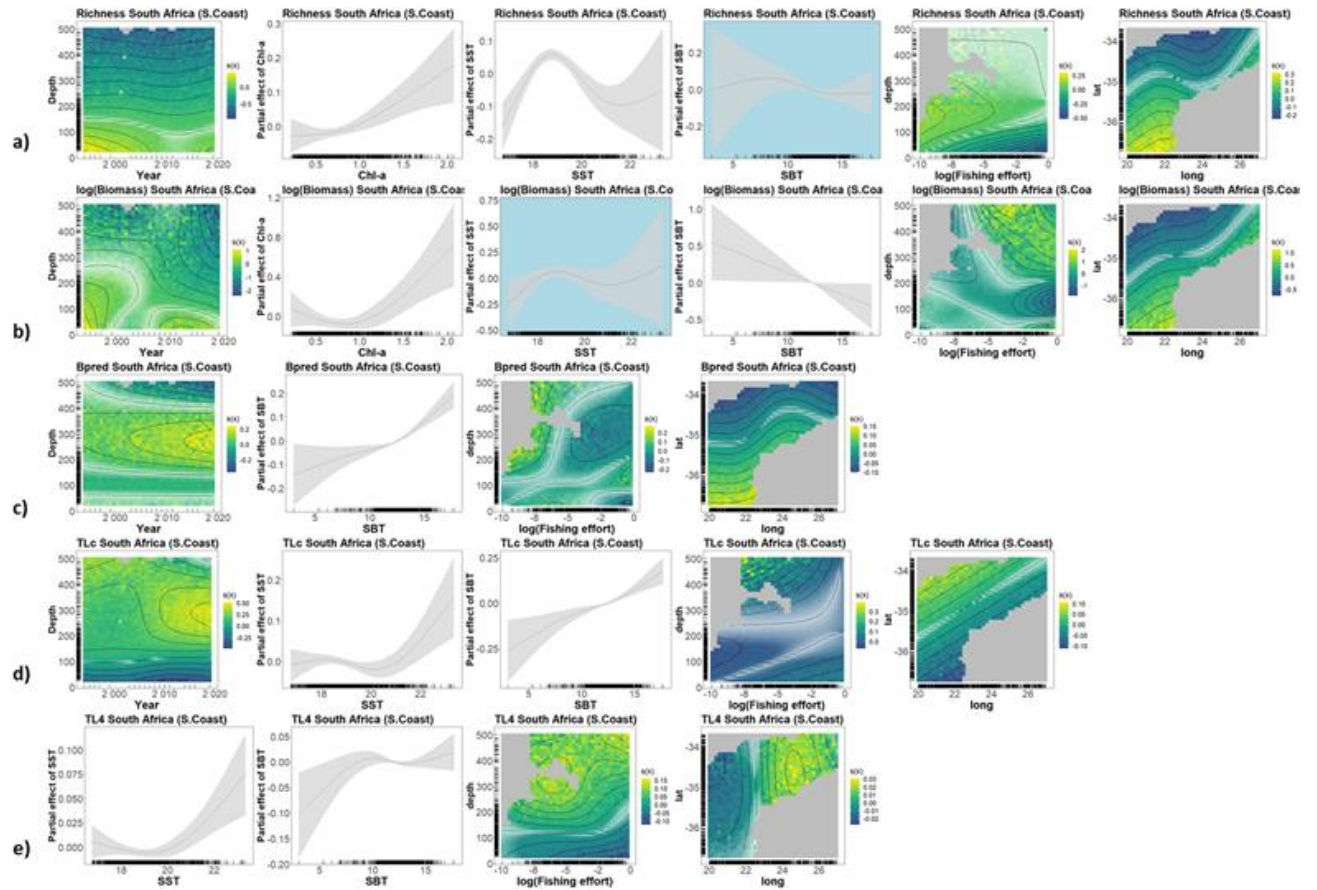
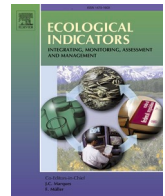


Figure S2.3.5: Partial effects of all the variables selected on the models for the different indicators (a-e) on the South Africa South Coast region. Blue shaded plots represent independent variables with non-significant effects that were included on the model.

Annex II – Published Articles



Spatial-temporal variation of the Western Mediterranean Sea biodiversity along a latitudinal gradient

Carlos Veloy^{a,*}, Manuel Hidalgo^b, Maria Grazia Pennino^c, Encarnación García^d, Antonio Esteban^d, Cristina García-Ruiz^e, Gregoire Certain^f, Sandrine Vaz^f, Angélique Jadaud^f, Marta Coll^a

^a Institute of Marine Sciences (ICM-CSIC), Passeig Marítim de la Barceloneta, n° 37-49, 08003 Barcelona, Spain

^b Instituto Español de Oceanografía (IEO-CSIC) (Palma), Ecosystem Oceanography Group (GRECO), Muelle de Poniente, s/n Aptdo, 291, 07015 Palma de Mallorca, Spain

^c Instituto Español de Oceanografía (IEO-CSIC) (Vigo), Subida a Radio Faro, 50-52 36390 Vigo, Spain

^d Instituto Español de Oceanografía (IEO-CSIC) (Murcia), Calle el Varadero, 1, 30740 San Pedro del Pinatar, Spain

^e Instituto Español de Oceanografía (IEO-CSIC) (Málaga), Puerto Pesquero, s/n Aptdo, 285, 29640 Fuengirola, Spain

^f MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France

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ABSTRACT

The Mediterranean Sea is a large marine ecosystem with high heterogeneity in both environmental and ecological characteristics. It presents clear gradients from north to south and west to east. It is also an important area in terms of biodiversity and conservation of vulnerable species, and it suffers from several cumulative human impacts, such as fishing and climate change. Previous studies have characterized spatial and temporal patterns of species distributions and biodiversity indicators. However, a comprehensive analysis combining a wide representation of biodiversity indicators is still missing. In this study, we examined spatial and temporal changes of marine communities along a latitudinal gradient over the continental shelf ecosystems (25–500 m depth) of the Western Mediterranean Sea, from the Gulf of Lion in the north to the Gibraltar Strait in the south. We used information from the MEDITS trawl scientific surveys from 1994 to 2018, and we calculated relevant indicators to investigate spatial and temporal patterns in the region. We selected several indicators measuring alpha (species richness, Shannon diversity index and Pielou evenness index) and beta (decomposing both turnover and nestedness) diversity, as well as previously studied indicators identified to be sensitive to fishing and climate change impacts (biomass-based and trophic-level based metrics). We assessed differences in these indicators for the surveyed community as a whole and for fish, crustaceans and cephalopods, separately, over five regions. Our results show clear latitudinal gradients in some indicators: we observe a reversed pattern between richness (decreasing from south to north) and biomass trends (increasing from south to north) for the demersal community. We also found a generalized increase in β -diversity in most regions with time, and a decline in the trophic level of the surveyed community. In addition, we identify a remarkable increase in several indicators when only considering the cephalopods group, and a general low environmental status for the North Catalan Sea. We discuss our results considering the differences between regions and taxa related to the fishing activity and environmental dynamics that can act at different scales. This in-depth analysis illustrates how to use a selection of indicators that combine the capacity to detect ecological changes from regional to sub-regional scales.

1. Introduction

The Mediterranean Sea is an enclosed sea that was formed around 5

million years ago during the Pliocene when its only natural connection with oceanic waters, the strait of Gibraltar, opened allowing the influx of seawater into the system flooding, at the time, a mostly dried up basin

* Corresponding author at: Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas (ICM-CSIC), P. Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain and Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain.

E-mail address: veloy@icm.csic.es (C. Veloy).

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(Coll et al., 2010). This event created a sea with particular features and gradients that have also shaped its own ecosystems and hosts several endemisms (Coll et al., 2010). One of the most characteristic traits of the Mediterranean basin is the northwest to southeast gradient of several physical variables such as higher temperature, and lower salinity and primary production towards the southeast. Biodiversity indicators (e.g., species richness) have also been described to decrease from the west to the east (e.g. Coll et al., 2010; Keller et al., 2016), despite the longitudinal gradient may not be so straightforward as shown in other studies (Gaertner et al., 2007).

Beyond the largely investigated west-east gradients over the whole basin, several regions in the Mediterranean display the combination of regional gradients and mesoscale features representing environmental and ecological spatial variation (Western Mediterranean, Liguria-Tyrrhenian Sea, Adriatic Sea and Aegean Sea among others). In the Western Mediterranean, the area from the Gulf of Lion (north) to the Alboran Sea (south) shows clear different hydrographic and productivity regions that have been used to define distinct environmental provinces (Rossi et al., 2014; Nieblas et al., 2014; d'Ortenzio and d'Alcalá, 2009). Also, in terms of biodiversity, the northwestern areas have been described as more diverse than the southeastern ones (Gaertner et al., 2007; Coll et al., 2010).

In addition to the influence of the environment in the distribution of species and the structure of marine communities (e.g. Navarro et al., 2016; Vilas et al., 2019; Lloret-Lloret et al., 2021), human activities can contribute to drive the changes in marine ecosystems. The fishing activity in the Mediterranean Sea has been historically very high (Lotze et al., 2006; Coll et al., 2010) and the region is still one of the FAOs fishing areas with the highest percentage of stocks fished at unsustainable or high levels besides the decreasing effort (Fao, 2020; FAO, 2020A). Due to the depletion of marine resources in most shelf fishing grounds and the improvement of technology, part of the fleet has bathymetrically shifted to higher depths (Coll et al., 2014; Farriols et al., 2017).

Other impacts threaten the stability and normal functioning of the ecosystems, such as habitat loss and invasive species, especially Lessepsian fauna migrating from the Suez Canal (Katsanevakis et al., 2016; Galil et al., 2017), pollution (Danovaro, 2003) and climate change (Ben Rais Lasram et al., 2010; Lejeune et al., 2010; Hidalgo et al., 2018). In the case of the Western Mediterranean, their communities face other human related threats aside of overfishing (Fao, 2020; Fernandes et al., 2017; FAO, 2020A) such as eutrophication by discharges as well as accumulation of heavy metals (Danovaro, 2003) that exert most pressure in the coastal areas (Fiorenza et al., 2013). In general, human activities have cumulatively impacted living communities of the Mediterranean in numerous and synergistic ways. For example, marine predators (i.e. large species with a high trophic level) have notably declined from Mediterranean marine ecosystems (Ferretti et al., 2008) with important implications for marine food webs (Sala, 2004; Lotze et al., 2011), although few species have shown signs of recovery such as the Atlantic Bluefin tuna (Ifremer, 2019) or some vulnerable demersal elasmobranchs (Ramírez-Amaro et al., 2020; Hidalgo et al. 2021).

Previous studies in the Mediterranean Sea have described several spatiotemporal patterns of distribution of biodiversity, both at species, groups of species and the ecosystem level (e.g. Coll et al., 2010, 2012, Navarro et al., 2015; Keller et al. 2016, 2017a; Fernandez-Arcaya et al., 2019; Vilas et al., 2019). However, a community-based spatial integrative analysis with a wide range of ecological indicators selected based on their sensitivity to fishing or environmental impacts is still missing to compare patterns in important sub-regional areas in the Mediterranean Sea.

In this study, we fill this gap analyzing the spatiotemporal gradients of marine biodiversity from the Western Mediterranean Sea (from the Gulf of Lion to the Alboran Sea) with the aim to contribute to a better understanding of the changes of marine communities in this region following a continuous latitudinal gradient of environmental change.

Using the intermediate scale of environmentally distinct regions over the continuous continental shelf gradient of the Western Mediterranean, we compare several areas according to a selection of indicators considering the multidimensional facets of biodiversity. The importance of such trait-based analysis can be seen in similar studies, such as the one performed in Atlantic waters (Pecuchet et al., 2017; Beukhof et al., 2019). In the latter, the study accounts for the distribution of certain life history traits showing that warmer waters favour opportunistic strategies (short lived and small species with low trophic levels), while colder waters with higher primary production and less variability have a bigger proportion of large long lived species.

Specifically, in our study we selected several indicators with the intention to cover different diversity components and community characteristics combining information of different groups (e.g. pelagic, demersal, predators). First, indicators of biodiversity were used, including beta diversity (hereafter β -diversity). The lack of data about this indicator and its components (turnover or change of identity and nestedness or subsampling) in the region needed to be addressed. This indicator can provide key information about the rates of change in the ecosystem as well as the identity of the change (Dornelas et al., 2014; Blowes et al., 2019). The differentiation in the components of β -diversity also helps to determine which are the underlying ecological processes driving biodiversity change through time, as both have been associated with different phenomena: limited space (Stegen et al., 2013) or high impacted areas (Shackell, et al., 2012) in the case of turnover, or orderly species loss in the case of pure nestedness (Baselga, 2010). Secondly, we added well studied indicators identified to be sensitive to fishing and climate change impacts: biomass-based and trophic-level based metrics (Shin et al., 2012; Bundy et al., 2012; Shannon et al., 2014; Coll et al., 2016; Fu et al., 2019).

Based on the literature available, we hypothesised that different ecological gradients and temporal changes according to different taxonomic groups may emerge, but also we expected to infer other ecological processes for specific taxonomic groups and sub-regions. Finally, our results could reflect as well the spatial-temporal heterogeneity of our study area, providing highly-resolved and novel information about the dynamic components of marine biodiversity in the Western Mediterranean Sea.

2. Methods

2.1. Study area and data set

The study area covers the continental shelf and upper slope of the Western Mediterranean of Spain and France, including depths from 25 m to 500 m (Fig. 1) as it is the stratum with most biodiversity and represents most of the main ecosystems within our region. The data used was collected from the international MEDITS trawl surveys between the years 1994 and 2019 (Spedicato et al., 2020) in 4041 sample stations over 25 years and integrated information of 586 species (Appendix table A1). The MEDITS program follows a standardized sampling protocol through the entire northern Mediterranean, from the duration of the trawling, the type and specifications of the gear used to the collection and analysis of the biological samples (Bertrand et al., 2002; Spedicato et al., 2020). MEDITS program uses the Geographical Statistical Areas (GSAs) as sampling areas, defined by the General Fisheries Commission for the Mediterranean (GFCM). The chosen area for this study covers the continuous north-south gradient of the Western Mediterranean area ranging from the Gulf of Lion (GSA7), through the Northern Spain (GSA6) to the Northern Alboran Sea (GSA1). The study area was divided in five regions (Fig. 1). The GSA6, Valencia Channel (CN), Ebro Delta (DE) and North Catalan Sea (CC), shares some similarities, with low chlorophyll levels, deep bathymetry and high sea surface temperature (SST) (Nieblas et al., 2014). CN and DE regions have a relatively wide continental shelf, and DE also receives intakes from several rivers such as the Ebro. The most northern area, the GSA7, Gulf of Lion (GL),

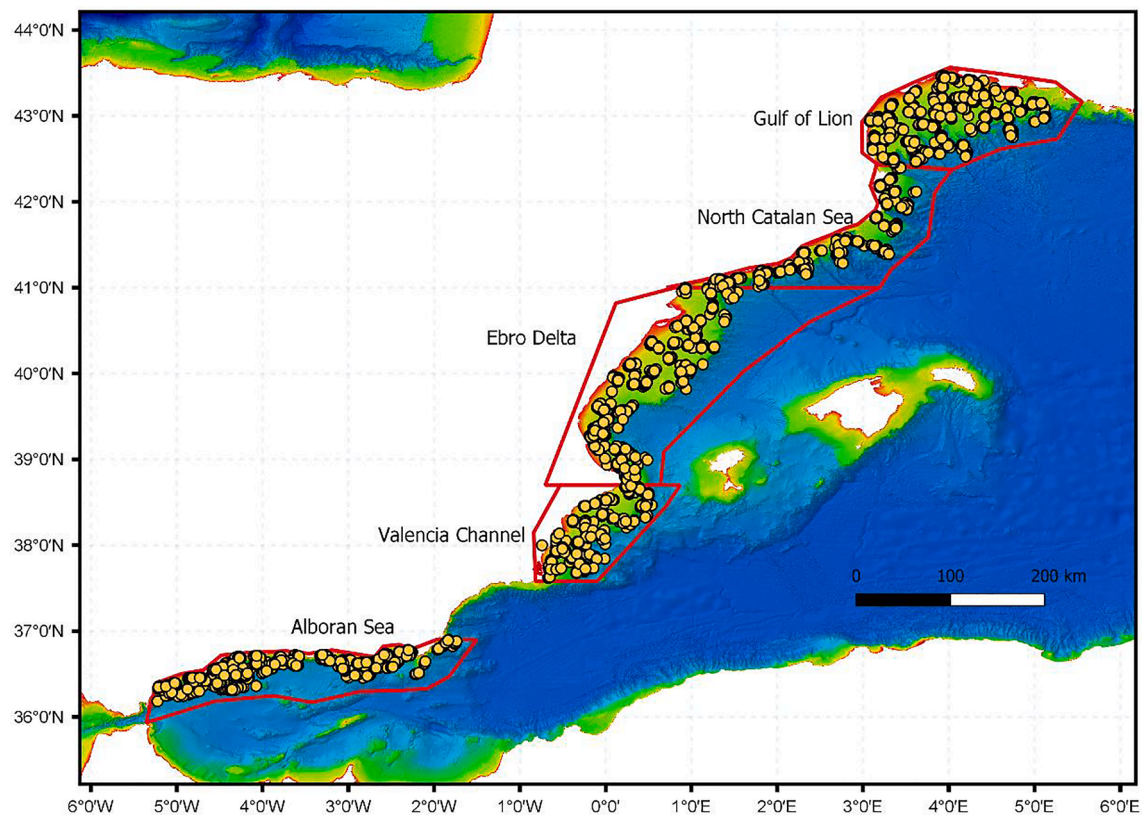


Fig. 1. Map of the study area and its subdivision in regions. Yellow dots represent the sampling stations of MEDITS campaigns used in the analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

features a low SST, shallow bathymetry, extended shelf and high and variable primary production driven by the peculiar oceanographic conditions and the Rhône River. The river generates a layer of high concentrations of nutrients up to a 100 m in depth, and even deeper during winter due to upwelling processes, that is spread through the area by the Ligurian current allowing fertilization of the whole Gulf (Nieblas et al., 2014), while CC is characterized by a narrow continental shelf. Finally, the most southern area, GSA1, Northern Alboran Sea (AL), has a high and very variable primary production influenced by the inflow of waters from the Atlantic Ocean and highly dynamic mesoscale processes.

The data obtained from the surveys was firstly filtered for those registries that reported no individuals, following the protocol established by Dornelas et al. (2014). A second filter was applied to select only those species that appeared in 80% of the time in the temporal series considered. Lastly, for those indicators based on biomass or abundance indices, we also filtered out those species with low and heterogeneous catchability such as gregarious and small pelagic species (e.g., European sardine, *Sardina pilchardus* or boarfish, *Capros aper*). For the indicators based on absence-presence, this criterion was not applied.

For invertebrate species, we faced a challenge related to the heterogeneous sampling protocols among areas. While the surveys carried out in the Spanish Mediterranean areas performed a complete record of both the presence and the biomass of as many species as possible since 1994, in the Gulf of Lion only mandatory species under the MEDITS protocol were sampled until 2012. From this year onwards, the survey started a complete record of other species including crustaceans and cephalopods. To efficiently circumvent this limitation while ensuring the objectives of the study, we considered two separate invertebrate databases: i) first, to analyse the temporal variation, the entire sampling period (1994–2019) was considered but we selected for all the regions only those species sampled before 2012 in GL; ii) second, to perform the spatial analyses, all the species of the demersal community between

2012 and 2019 were used from every region.

2.2. Selection of ecological indicators

a) Biodiversity indicators

Different biodiversity metrics of both alpha and beta diversity were calculated (Table 1). For alpha diversity we focused on two main components of the alpha diversity: species richness (the amount of species present in the community of a region) was measured with the total number of species in the sample (McIntosh, 1967) and the Shannon index (H) (Shannon and Weaver, 1949). For the evenness, we used the Pielou evenness index (J) (Pielou, 1966) since it is constrained by values between 0 and 1, allowing for better comparison between different samples. The β -diversity was calculated with the Jaccard index to assess differences between communities separated with time using the first year of sampling. In the case of the temporal databases, the first year was 1994, while 2012 was used for the spatial database. The two components of β -diversity, turnover and nestedness, were also individually calculated.

b) Community and taxa-related indicators

Species were classified in three major taxonomic groups: fishes, crustaceans (only accounting for decapods, stomatopods and euphausiids) and cephalopod mollusks (from now on referred as cephalopods). For the different species in each group a binary value for two traits (position in the water column, benthopelagic -hereafter referred as pelagic- or demersal species, and feeding type considering the species a predator or not) was also assigned, as well as a trophic level value using FishBase (Froese and Pauly, 2021) and SeaLifeBase (Palomares and Pauly, 2021). For the sake of data uniformity, the trophic level used was the one calculated based on consumed food items as it was the one available for most taxa. Following previous studies, we considered as “predator” those species that had a trophic level higher than 3.5 (Shin and Shannon, 2010). However, we also took into account if they had

Table 1

Definitions, equations, primary driver of influence (environment, fisheries or both) and references of indicators used in this study. N_i , B_i , W_i and TL_i corresponds to Number of individuals, Biomass, Weight and Trophic Level of i species, respectively.

Indicator	Definition	Equation	Primary driver	Reference
Biodiversity indicators				
Species richness (S)	Sum of species (sp) number	Σsp	Both	McIntosh, 1967
Shannon index (H)	Measure of diversity and evenness. p_i is the proportion of individuals belonging to species i in the dataset	$-1 * \Sigma (p_i * \ln(p_i))$	Both	Shannon and Weaver, 1949
Pielou evenness (J)	Measurement of frequency evenness on an ecosystem. H : Shannon index, S : Species richness	$H / \ln(S)$	Both	Pielou, 1966
Jaccard index (β)	Measurement of community change over time. A & B: different sample sets Components: -Nestedness or subsetting of the sample -Turnover or identity change.	$ A \cap B / A \cup B $	Both	Dornelas et al., 2014; Blowes et al., 2019
Community and taxa-related indicators				
Biomass (B) and Abundance (N)	Biomass (B_i) and Abundance (N_i) of surveyed species i .	ΣB_i & ΣN_i	Environment	Coll et al., 2016
Mean size (MS)	Mean weight (used as proxy of mean length indicator although less effective). B : biomass, N : abundance.	B/N	Fishing	Shin et al., 2018
Relative predatory Biomass (BPred)	Relationship between biomass of predator species (B_i) and the ecosystem or taxa group (B)	$\frac{\Sigma(B_i)}{B}$	Fishing	Coll et al., 2016
Relative pelagic Biomass (BPel)	Relationship between biomass of pelagic species and the ecosystem		Environment	Based on BPred
Relative fish Biomass (BFish)	Relationship between biomass of fish species and the ecosystem		Fishing	
Relative Cephalopod Biomass (BCeph)	Relationship between biomass of cephalopods and the ecosystem		Both	
Surveyed community trophic level (TLsc)	Mean trophic level of the surveyed species (TL_i). W_i : biomass of species i .	$\frac{\Sigma(TL_i * W_i)}{B}$	Environment	Shannon et al., 2014
Mean trophic level of species above 3.25 (TLs3.25)	Mean trophic level of species i above 3.25 ($TL_{i,3.25}$)	$\frac{\Sigma(TL_{i,3.25} * W_{i,3.25})}{B_{3.25}}$	Fishing	
Mean trophic level of species above 4 (TLs4)	Mean trophic level of species i above 4 ($TL_{i,4.0}$, top predators)	$\frac{\Sigma(TL_{i,4.0} * W_{i,4.0})}{B_{4.0}}$	Fishing	

reported maximum length greater than 20 cm and actively capture their food. The aim of this classification was to filter out small organisms like bobtail squids and species that are mostly scavengers such as shrimps.

To assess the state of the ecosystem and of different taxonomic and species groupings, several additional indicators were selected based on the IndiSeas initiative (Shin et al., 2012; Bundy et al., 2012; Coll et al., 2016; Fu et al., 2019; Indiseas, 2020) (Table 1). IndiSeas indicators were initially chosen to track fishing effects on marine ecosystems. Some IndiSeas indicators were also identified as being especially sensitive to changes in primary productivity due to climate variability. Examples of the first type are the relative biomass of predators (BPred), the mean size of the community (MS) and trophic-based indicators such as the trophic levels in the community (TLsc), the mean trophic level of the community for species with trophic levels above 3.25 (TLs3.25) and the trophic level of the community considering predators above 4 (TLs4). Some indicators sensitive to environmental change, such as the total community biomass (B) and the mean trophic level of the entire surveyed community (TLsc), were also included (Shannon et al., 2014; Coll et al., 2016).

2.3. Data analyses

The heterogeneity of the database did not allow us to develop a complete spatiotemporal analysis (i.e. ANCOVA). Therefore, spatial and temporal analyses were developed separately in two different subsets of the database. To analyse spatial differences among sub-regions, we applied an analysis of variance (ANOVA) to compare the indicator mean values of the different regions across the study area (Fig. 1). Afterwards, linear regressions were applied to assess the long-term temporal variation of each indicator. In each region, the different indicators were considered as the dependent variable, and the region was the independent categorical variable for the ANOVA analysis. Before the analyses, we tested that indicators followed the conditions of normality and homogeneity of variances applying the Shapiro and Levene tests, respectively. In the linear regressions, we considered time as the explanatory continuous variable per region. For this purpose, the indicator-time relationship was adjusted assuming a linear relationship between the

two variables to compare the rates of increase or decrease (i.e. regression parameter) of the temporal trends. We then compared these trends between different regions for each indicator.

To further test and examine the differences between regions in the ANOVA, we used a Tukey pairwise comparison with 95% confidence intervals. Spatial patterns were summarized by grouping the statistically significant different regions. Two criteria were taken for grouping regions by their mean value: if the region was significantly distinct to the boundary areas or if regions showed significant differences in two pairwise comparisons.

All the indicators were calculated using R version 3.6.3 (R Core Team, 2021). The Jaccard index and its components were calculated using the R package betapart (Baselga and Orme, 2012).

3. Results

We present the summary of spatial and temporal trends for all surveyed species, demersal species and pelagic species using the biodiversity indicators first, and followed by the community and taxa-related indicators, as in Table 1. For each indicator, a general spatial description is first given followed by the main temporal pattern in the different sub-regions. All statistical results are shown in Appendix Tables A3 to A6.

3.1. Biodiversity indicators

Overall, the highest species richness (S) mean values were recorded in the southern areas of the study, the Alboran Sea and in the Channel, where significant differences were found in comparison with the rest of the regions (Table 2). The surveyed community and fish species richness were also highest in the south (with the exception for all fish and demersal fish richness in the Gulf of Lion), and they presented the lowest values in the North Catalan Sea when considering all and demersal fishes as well as the entire and demersal community ($F_{4,35} = 7.05$; $p < 0.001$) (Tables 2 and 3; Fig. 2a and 2b). The species richness showed general and significant increasing temporal trends in almost all areas and with the lowest significant slope values in the Gulf of Lion (slope, $sl = 0.44$, p

Table 2

Summary of the spatial and temporal trends of the taxa (considering all species), in color the regional significant differences (red being the highest mean value, orange and green middle values, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the direction of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. Colors in regional differences are only depicted when there are significant differences by region.

Indicator / region	All community					All fishes					All cephalopods					All crustaceans				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
S	↗	↗			↗	↗	↗			↗	↗	↗			↗	↗	↗			↗
H				↗	↘				↗	↘		↗	↗		↗			↗		
J				↗	↘				↗	↘		↗	↗		↗	↘	↗			
θ	↗	↗				↗	↗	↗		↗			↗		↗	↗	↗			
Turnover															↗			↘	↗	
Nestedness	↗	↗	↗			↗	↗	↗		↗		↗						↗		
B	↗	↗					↗				↗	↗	↗	↗		↗	↗			
N					↗										↘					↗
MS	n.s.									↗			↗	↗	↗					
BPred	↘			↘	↘	↘			↘	↘		↗	↗	↗	↗					
BPel			↗							↘		↗	↗	↗	↗					
BFish	↘					NA					NA					NA				
BCeph			↗			NA					NA					NA				
TLsc			↗	↘	↘	↘			↘	↘		↗	↗	↗	↗		↗	↗	↗	↘
TLs3.25	↘	↘		↘	↘	↘	↘		↘	↘		↗	↗	↗	↗	↗	↗	↗	↗	↘
TLs4												↗								

Table 3

Summary of the spatial temporal trends of the different demersal taxa, in color the regional significant differences (red being the highest mean value, orange and green middle, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the directions of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. Colors in regional differences are only depicted when there are significant differences by region.

Indicator / region	Demersal community					Demersal fish					Demersal Cephalopods					Demersal crustaceans				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
S	↗	↗			↗	↗	↗			↗	↗	↗			↗	↗	↗			↗
H				↗	↘				↗	↘		↗	↗	↗	↗			↗		
J					↘				↗	↘		↗	↗	↗	↗			↗		
θ	↗	↗				↗	↗	↗		↗			↗		↗	↗	↗			
Turnover															↗			↘		
Nestedness	↗	↗	↗		↗	↗	↗	↗		↗		↗						↗		
B	↗	↗					↗				↗	↗	↗	↗		↗	↗			
N					↗					↗			↘	↘	↘		↗			↗
MS	n.s.									↘		↗	↗	↗	↗	n.s.				
BPred	↘			↘	↘	↘			↘	↘		↗	↗	↗	↗					
BFish	↘					NA					NA					NA				
BCeph						NA					NA					NA				
TLsc	↘			↘	↘	↘			↘	↘							↗	↗	↗	↘
TLs3.25	↘					↘			↘							↗	↗	↗	↗	↘
TLs4																NA				

< 0.05, in the surveyed community and $sl = 0.37$, $p < 0.05$, in the demersal community; Fig. 2c, Table 2). A spatial gradient from north (lower values) to south (higher values) was also observed for cephalopods and crustaceans (Table 2; Fig. 2e and f), with increasing temporal trends, too.

Both Pielou evenness (Tables 2 and 3, Fig. 3) and Shannon index showed roughly similar spatial patterns, with the lowest values in the Gulf of Lion. On the contrary, we observed an inverse gradient for cephalopods, where the North Catalan Sea featured the highest values and the Alboran Sea the lowest ($F_{4,35} = 3.741$; $p < 0.05$). Pielou index showed contrasting temporal trends depending on the region with decreasing trend with time in the Gulf of Lions (slope, $sl = -0.02$, $p < 0.001$), while an increase with time was observed for demersal cephalopods in most regions, where significant relationships were reported (slope, $sl = 0.02$, $p < 0.001$; Fig. 3f).

Results evidenced that there were no significant spatial differences in β -diversity or its components between different regions (Tables 2, 3 and 4). However, β -diversity increased with time showing an upwards trend

in many of the regions and groups (Fig. 4). Regarding the β -diversity components, turnover was found to have a significant increase mostly on the North Catalan Sea in many of the considered groups (Tables 2–4, Fig. 4e) in contrast, nestedness showed a general significant increase in most regions within all taxa and taxonomic groups, especially in fish (Table 2, Fig. 4c).

3.2. Community and taxa-related indicators

The Biomass (B) indices showed a general gradient with a negative south-north pattern, with larger biomass values in the Gulf of Lion (Tables 1, 2 and 3). Cephalopods (both all and demersal) showed higher values as well in the Alboran Sea. In contrast, crustaceans showed highest values in the Alboran Sea, while in the other regions values were low. Temporal changes in biomass showed increasing trends specially in cephalopods group and in the Alboran Sea (Tables 2, 3, 4, Appendix Table A3, A4 and A5), with few exceptions such as pelagic fishes of the Gulf of Lion that show a clear decreasing trend ($sl = -20.82$, $p < 0.05$)

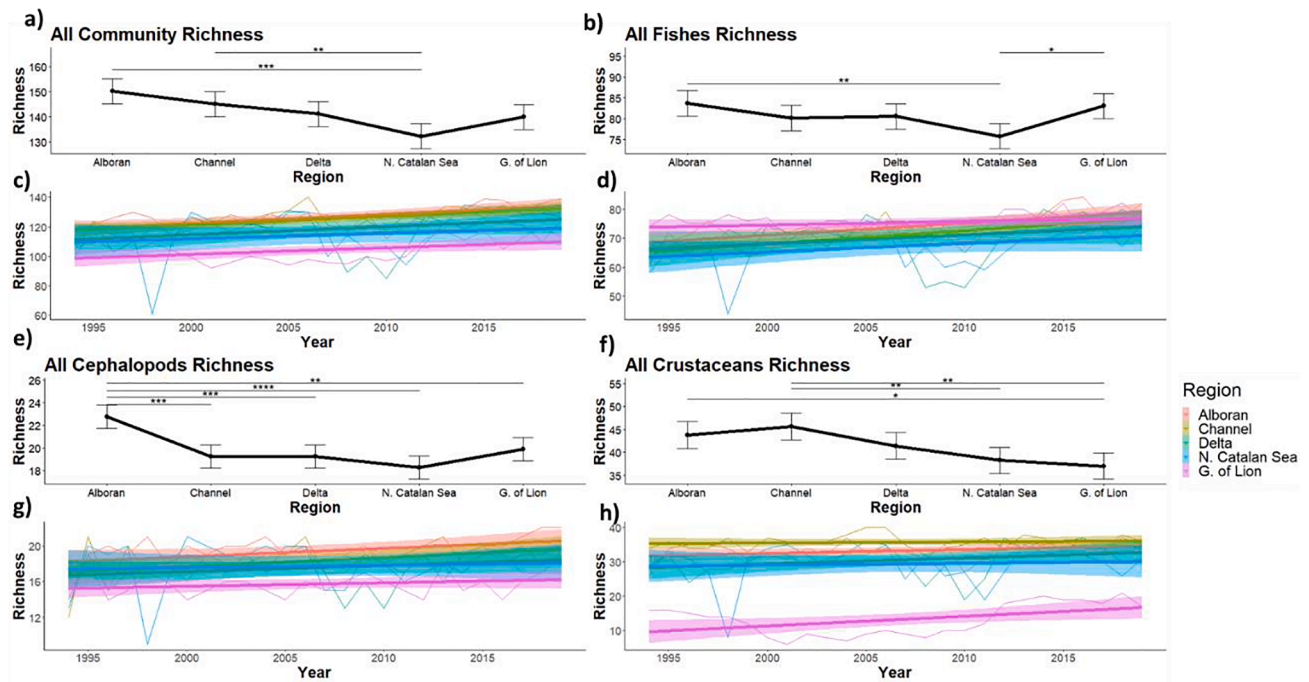


Fig. 2. Temporal trends, pairwise contrast and mean values of species richness (S) for the surveyed community, and for fishes, cephalopods and crustaceans. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate the standard error over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

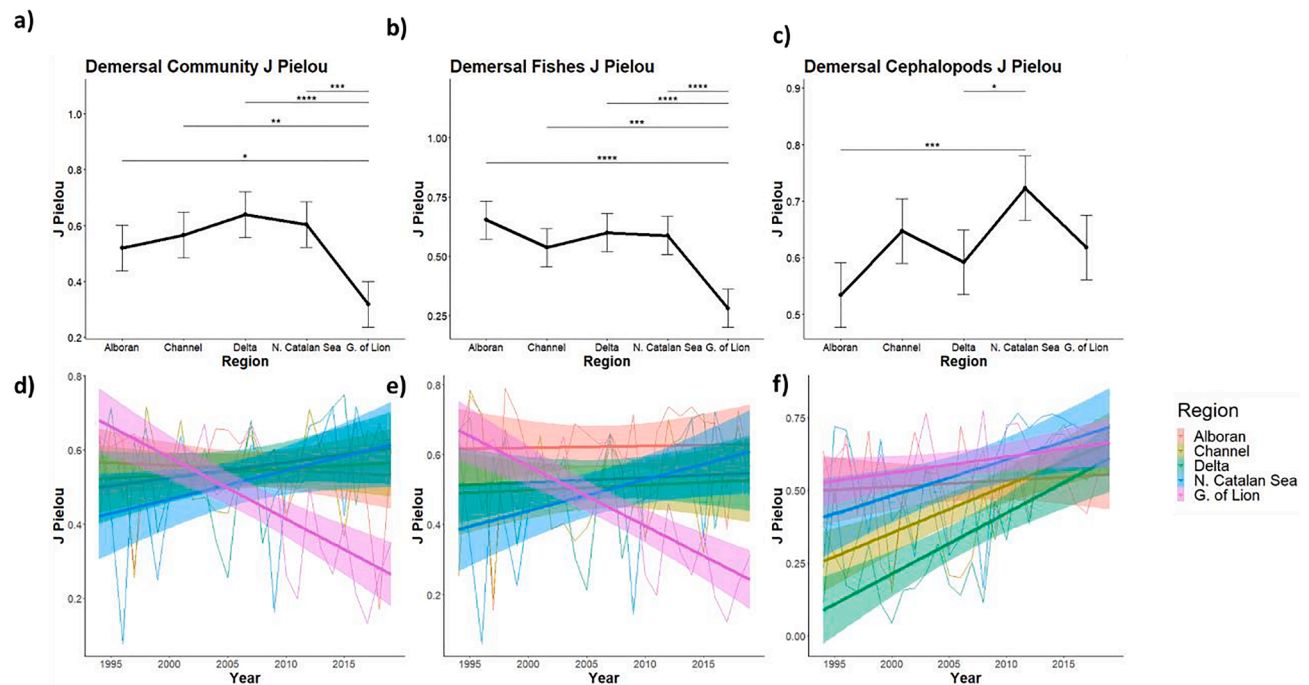


Fig. 3. Temporal trends, pairwise contrast and mean values of Pielou evenness J index for the demersal surveyed community, and for fish and cephalopods. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

(Table 4).

A gradient similar to that of biomass appeared in the surveyed community abundance (N) trends for all regions (Tables 2, 3, 4 and Appendix Table A6), where the Gulf of Lion presented the highest mean values well above those reported for the other regions, while pelagic taxa showed highest values in the south (Table 4). A temporal pattern of

increase was observed (Tables 2 and 3), with the exception of demersal cephalopods showing declines.

The mean size indicator (MS) was found to have non-significant spatial differences for the majority of groups except for all and demersal fishes and cephalopods (Tables 2 and 3), which showed significant spatial differences with low values in the Gulf of Lion. However,

Table 4

Summary of the spatial temporal trends of the different benthic-pelagic taxa, in color the significant regional differences (red being the highest mean value, orange and green middle, blue the lowest). Indicators in white represent no significant spatial differences. Arrows indicate the direction of the slope in the linear models (increase or decrease) when a significant temporal effect is detected. NA: Indicator not applicable to this group. * Beta diversity and its components were disregarded for pelagic invertebrates because of the small number of species. Colors in regional differences are only depicted when there are significant differences by region.

Indicator / region	Pelagic community					Pelagic fish					Pelagic Cephalopods					Pelagic crustaceans				
	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL	AL	CN	DE	CC	GL
S																				
H																				
J																				
θ																				
Turnover																				
Nestedness																				
B																				
N																				
MS																				
BPred																				
BFish																				
BCeph																				
TLsc																				
TLs3.25																				
TLs4																				

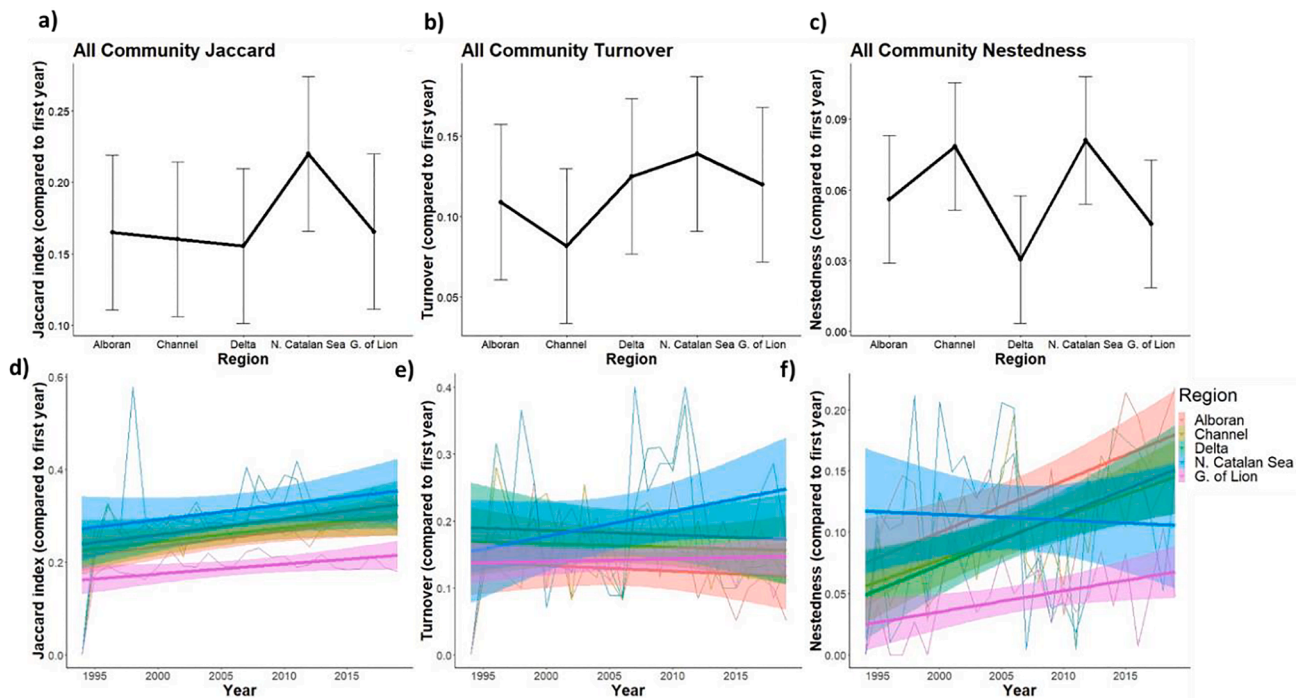


Fig. 4. Temporal trends, pairwise contrast and mean values of β -diversity, turnover and nestedness for the surveyed community. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

cephalopods ($F_{4,35} = 6.11$, p -value < 0.001) did not display a clear gradient, while in the case of fishes all the regions up until the Gulf of Lion showed higher means. Mean size increased with time in various regions with some exceptions such as demersal fishes in the Gulf of Lion and pelagic cephalopods in the Catalan Coast and the Gulf of Lion (Table 4).

Relative biomass of predators (BPred) did not display clear gradients for the surveyed community and the fishes (with the exception of the pelagic community), but rather showed low values in both extremes of the study area and higher values in the central regions (Table 2, Fig. 5a). The pelagic species ($F_{4,35} = 4.77$, $p < 0.01$) as well as the cephalopods

groups (Tables 2, 3 and 4) showed south-north gradients with highest biomass values in northern areas. Significant temporal decreasing trends were reported for fishes and the surveyed community, only showing an increasing trend in the pelagic community of the North Catalan Sea and the Gulf of Lion regions (slope, $sl = 0.02$, $p < 0.001$).

Results showed how the Relative Fish Biomass (BFish) for the surveyed community was lower in the southern sub-regions than in the northern ones, showing a positive gradient to the north in the study area only interrupted by a decrease in the mean value of the Delta region ($F_{4,35} = 7.623$, $p < 0.01$) (Appendix Table A5, Table 2, Fig. 6a). For the pelagic community, the highest values were found in the Alboran Sea,

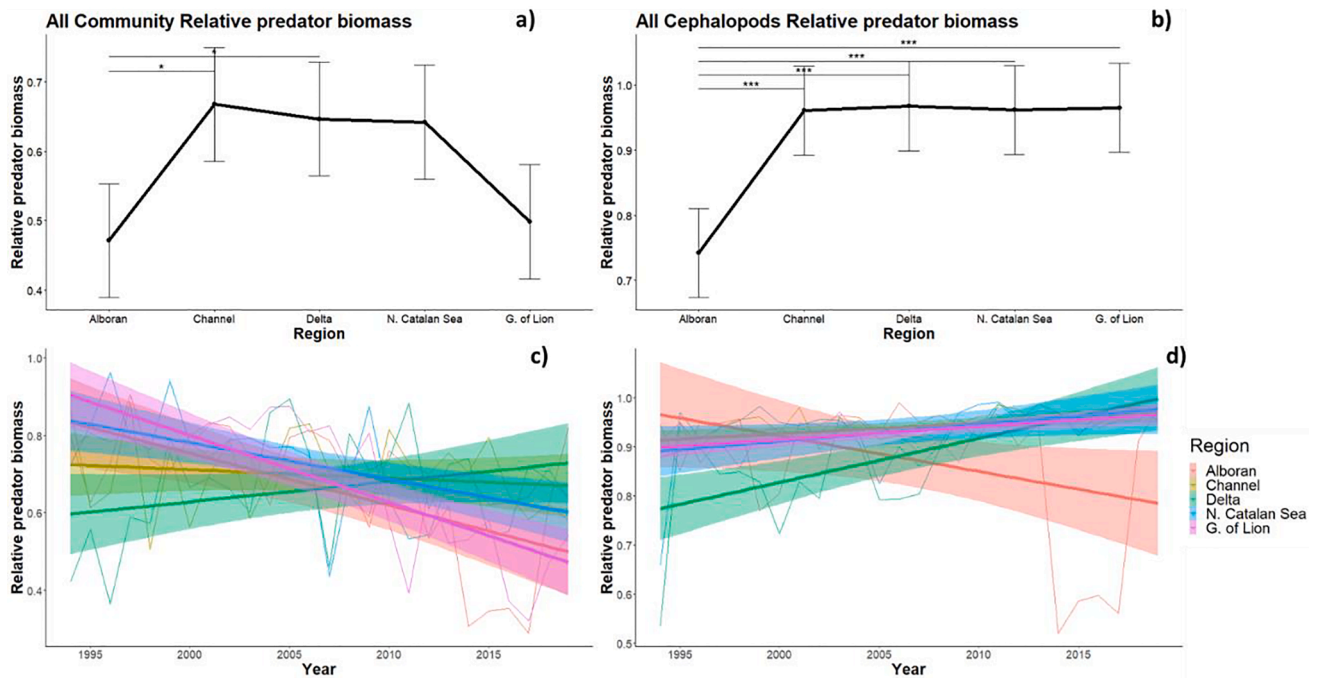


Fig. 5. Temporal trends, pairwise contrast and mean values of Bpred for the surveyed community (left) and cephalopods (right). Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

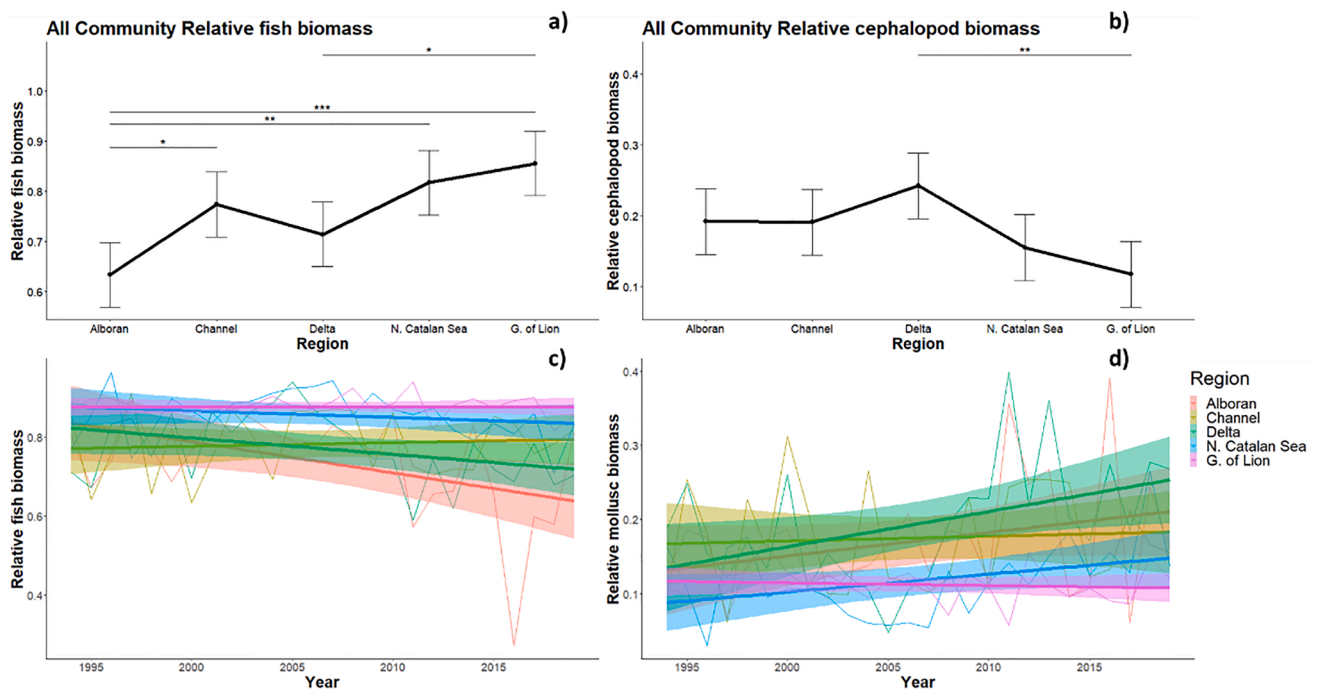


Fig. 6. Temporal trends, pairwise contrast and mean values of BFish (left) and BCeph (right) for the surveyed community. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

while the Delta showed the lowest (Table 4). In the case of the Relative Cephalopods Biomass (BCeph), there was no discernible pattern although the surveyed community the Gulf of Lion showed the lowest mean value ($F_{4,35} = 4.112$, $p < 0.01$). Regarding the temporal trends, the biomass of fishes showed a negative trend in the Alboran Sea when considering the surveyed community and demersal species (Tables 2 and

3), and a negative temporal trend was registered for the pelagic community in the northernmost sub-regions, the Northern Catalan Sea and the Gulf of Lions (Table 4, Fig. 6c). On the contrary, the Relative Biomass of Cephalopods (BCeph) showed a significant positive relationship with time in the Delta region ($sl = -0.004$, $p < 0.05$) when looking at the demersal species, and a positive increase in the North Catalan Sea ($sl =$

0.02, $p < 0.01$) and the Gulf of Lion ($sl = 0.02$, $p < 0.001$) when looking at the pelagic community (Table 4, Fig. 4d).

Both all surveyed community and the fish community showed lower levels of the TLsc and higher levels of TL3.25 in the north (Table 2, Fig. 7a). TLs4 showed a clear increasing south-north gradient. Cephalopods did not show clear spatial gradients but their maximum values of trophic level indicators were observed in the Delta region. The TLsc presented decreasing temporal trends in several regions for all the surveyed community and the fish community, more pronounced in the Gulf of Lions (Tables 2, 3 and 4; Fig. 7c). Cephalopods and crustaceans, on the contrary, displayed an increasing trend in both TLs3.25 and TLsc indicators (Tables 2 and 3).

3.3. General patterns

Regarding the spatial analyses, four types of gradients were identified in the study area: (i) a clear increase on indicator values from south to north gradient (such as the case of trophic level indicators and the biomass), (ii) a clear decrease from south to north gradients (such as richness and the Shannon Index in some demersal taxa), (iii) gradients interrupted by extreme mean values in one of the regions (such as fish biomass), and (iv) unclear patterns with one or two regions that showed significant differences from the rest (such as TLs4 of all and demersal cephalopods and the relative predator biomass of demersal fishes). In addition, our study illustrated that the β -diversity indicators were similar between regions.

Regarding temporal changes, species richness tended to increase with time, while in some cases the Pielou evenness index decreased, less when looking at cephalopods and crustaceans compared to fishes. On the other hand, β -diversity showed an increase with time in most regions, regardless of taxa and species groupings. Nestedness was the component that reported most positive slopes at the expense of turnover, although the North Catalan Sea and the Gulf of Lion regions reported statistically significant increases in turnover in cephalopods and crustaceans.

Biomass indicators showed some declines with time for all surveyed

communities and fish communities, including the pelagic species from the northern areas, and increases for cephalopod communities. In fact, cephalopods experienced positive temporal trends in most indicators, species groupings and regions, especially in richness and biomass, where we observed very pronounced slopes in some regions. Trophic level indicators showed declines when looking at the surveyed community and the fish community in several regions, while they showed increases for cephalopods and crustaceans.

4. Discussion

In this study, we quantified marine biodiversity and community changes in the Western Mediterranean Sea, and documented contrasting temporal trends and relevant geographic gradients and spatial differences across five sub-regions and taxonomic groups. Our results enabled us to identify which indicators followed continuous geographic gradients, likely influenced by biogeographic features and long-term environmental drivers, and which were more specific to given regions, likely influenced by local fishing impacts and other sub-regional scale processes. The main patterns emerging from our results were associated to taxonomic diversity, β -diversity and its components, relative abundances and biomasses, and trophic level. Our study also reveals emerging characteristic patterns in specific sub-regions and specific taxonomic groups beyond fish (i.e. in the North Catalan Sea and for cephalopods and crustaceans).

Some of our results show similarities to those featured in previous studies (Navarro et al., 2016; Fernandez-Arcaya et al. 2019; Farriols et al., 2020), but we additionally used taxonomic and species groupings (i.e. demersal and pelagic) for our approach and established a regionalization of the gradients. We also computed a wide range of complementary indicators, from classic ones such as species richness and the Shannon index, to more integrative ones such as β -diversity and trophic level-based indicators. As such, our study complements previous studies providing novel results.

According to our results, the richness indicator follows the expected pattern of diversity, decreasing from southern to northern regions. This

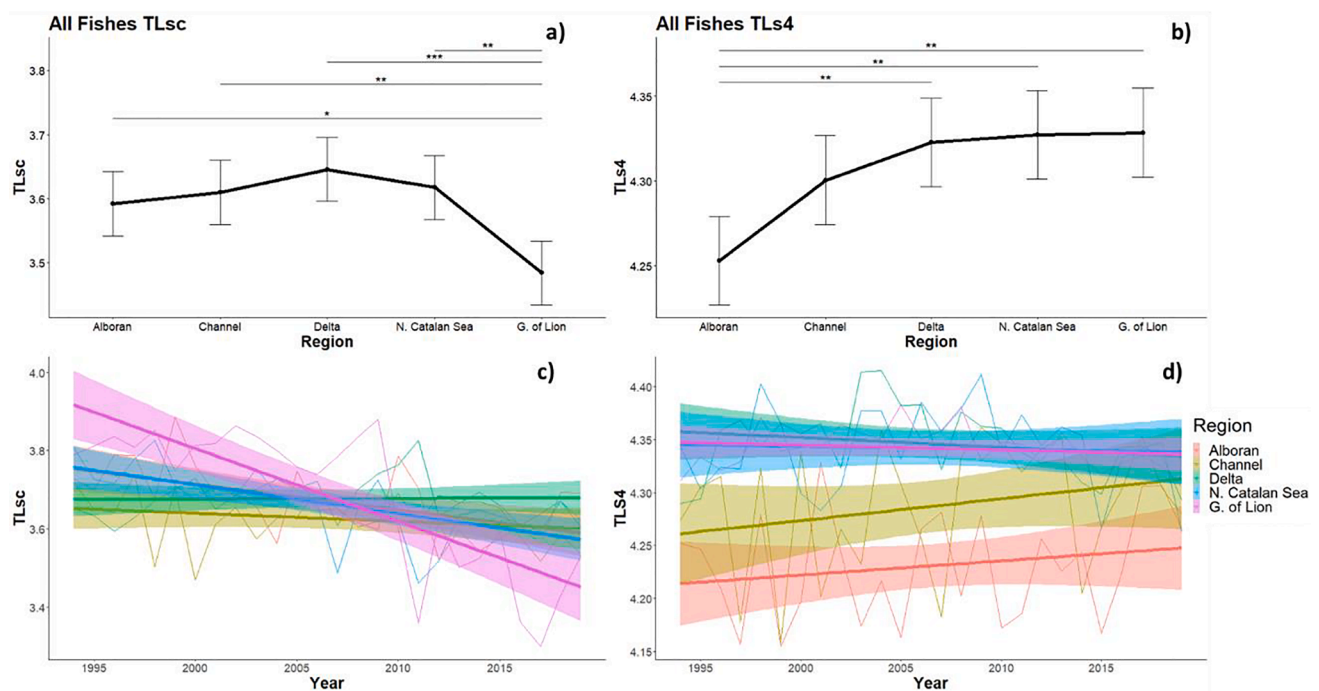


Fig. 7. Temporal trends, pairwise contrast and mean values of TLsc (above) and TLs4 (below) of all fishes. Lines over two or more area levels indicate significant pairwise differences according to the Tukey test. Error bars indicate standard errors over given regions in the spatial analyses, while shaded areas represent the smooth conditional means on the temporal regressions.

is a well-described pattern in ecology where warmer areas tend to show larger number of species (Worm and Tittensor 2018). This can be explained by environmental gradients such as an increase in temperature or decrease in primary production from the northern to the south most area (Estrada, 1996; Bosc et al., 2004). It is important to notice as well the biogeographical complexity of the Alboran Sea, which represents a confluence of Mediterranean species with the species runoff received from the Atlantic side that can expand northwards along the Iberian Mediterranean coast (Real et al., 2021). When looking at the whole surveyed community and the community of fish (both with all species and the demersal species) this gradient was interrupted by the lowest values appearing in the North Catalan Sea, which matches results found in other studies for non-target finfish as well as analysis of the whole ecosystem (Navarro et al., 2015; Gaertner et al., 2007). In both cases, the region reported less species both at spatial grid level and for a regional mean. This pattern could be due to an intense and cumulative human activity in the Catalan Sea area (Taconet et al., 2019), or the reduced area of the continental shelf in this sub-region that increases niche and habitat competition.

We also document how the number of species increases in almost all regions with time, although the decrease in richness is rarely documented in the literature and it is usually a sign of the synergy of several human impacts aside from overfishing (Granger et al., 2015). The increase in our study could be attributed to a decrease in fishing effort, especially of bottom trawlers in some areas (Farriols et al., 2017), or other factors like climate change, which has been linked in temperate systems with an increase in sea temperature and the tropicalization of Mediterranean ecosystems (Antão et al., 2020; Gordó-Vilaseca et al., 2021). Indeed, Hidalgo et al. (2021) have recently reported increases of the thermal affinity of these communities, observed for fish, crustacean and cephalopods. However, the causal relationship between richness and any or a combination of these drivers need to be further investigated. It is important to highlight that the number of sampling points per year remained constant with time and results from previous rarefaction curves using the same data show that our sampling effort was sufficient, thus differential sampling effort per year can be ruled out as a possible reason for this trend (Gaertner et al., 2013; Keller et al. 2016).

The lack of statistical significance of the spatial effects for β -diversity could be attributed to the reduced time period analysed in this study (2012–2019), which was applied to compensate for the sampling comparative challenges. It is thus likely that the composition of species has been kept relatively stable over the period used for the spatial analyses. The β -diversity did show, however, temporal significant changes from 1994, with increases over the studied period in most regions, alongside the previously described trends of richness. These increases indicate a lower level of similarity within communities with time, and illustrates the already described pattern of overall change in species but not loss of diversity in natural ecosystems (Dornelas et al., 2014). In all our cases where there were significant temporal relationships in β -diversity, they were mainly associated with a generalized increase of nestedness and a consequent decrease in turnover in most regions. Therefore, in most sectors, nestedness was the main component of biodiversity change, caused by species changes making species-poor sites to resemble a subset of species-rich sites (Baselga, 2010). The region with the highest rate of increase in nestedness over the study period was the Alboran Sea. These results suggest that our studied communities over the different regions became subsets of the original communities by losing or gaining species. This process can be associated with a long term temporal change such as climate change (Vale et al., 2021) and the associated warming of temperate waters as reported for the Mediterranean (Bianchi and Morri, 2003; Salat et al. 2019), or a higher Atlantic-Mediterranean flux of species through the Gibraltar strait in the case of Alboran (Real et al., 2021).

Changes in primary production dynamics have been recently shown as a potential additional driver because temporal changes in species composition mediated by productivity-driven regime shifts have been

reported in the study systems in 2001 and 2009 for the Alboran Sea and the Northern Spain, respectively (Hidalgo et al. 2021). While the Mediterranean region could not experience much change in the identity or replacement of species, it could be subjected to losses of different ecosystem functions as β -diversity changes occur in an orderly and non-random manner (Baselga, 2010). Spatial erosion of marine communities due to anthropogenic impacts and a consequent increase in β -diversity has also been observed in other highly impacted areas (Shackell et al., 2012). This process has been previously suggested for the Mediterranean Sea, with higher spatial heterogeneity in its communities due to the long-lasting anthropogenic impact (Hidalgo et al., 2017).

On the contrary, in the North Catalan Sea and the Gulf of Lion, it was the turnover component that dominated the temporal change in β -diversity, consistent with the highest values of beta diversity observed and indicating the replacement of species between sites. In these regions, species replacement seemed to be the most influential driver of biodiversity change and so the change in identity of their communities. The strong dependence of Mediterranean species upon the primary production dynamics (Fu et al., 2018; Hidalgo et al. 2021), and the dynamism of contrasting trophic pathways (Puerta et al. 2015), might trigger strong turnover of species over the North Catalan Sea. In addition, a greater competition in this sub-region is expected as species have to share a smaller ecological space over a narrow continental shelf (Stegen et al., 2013), which could be the reason of this difference of turnover influence. These factors, especially the available space and potential decrease of habitat competition would favour species replacement. The increasing β -diversity is an expected result considering that marine ecosystems usually have high values due to the very mobile species that live within their communities (McGill et al., 2015), including potential biological invaders that could explain the turnover values in areas such as the North Catalan Sea. Meridionalization (or the increase of southern thermophile species due to warming waters) of northern regions such as the North Catalan coast and Gulf of Lion can have an influence as well (Bianchi and Morri, 1993; Boero et al., 2008; Coll et al., 2010; Lloret et al., 2015). However, this process may have a reduced impact in our results since infrequent species were filtered out before analyses. Overall, studies on the β -diversity in the marine environments in general, and in the western Mediterranean in particular, are scarce and our study contributes to fill the gap in the region.

Another of the most relevant patterns observed in this study was the overall high values of abundance and biomass in the Gulf of Lion in contrast to lower ones in the rest of the regions. These spatial patterns are similar to those previously described by Navarro et al. (2015) and partially match those of Fernandez-Arcaya et al. (2019). They also match the macroecological patterns observed in marine ecosystems, where temperate communities tend to show lower rates of biodiversity values and higher biomasses (Worm and Tittensor 2018). This spatial difference can be attributed to the higher primary production in the northern area compared to southern regions (Estrada 1996; Bosc et al. 2004). Interestingly, the lowest levels of biomass and abundance in GSA06 (i.e. Valencia Channel, Ebro Delta and North Catalan Sea) for megafauna in deeper areas (500–800 m) reported in 2012–2015 by Fernandez-Arcaya et al. (2019) match with the identification of lower levels of some of our indicators in the same sub-regions, but at shallower habitats, which can be related with comparatively higher levels of fishing exploitation reported for GSA06 (Fernandez-Arcaya et al. 2019; Taconet et al. 2019).

Our study also showed extreme values in several indicators in the Gulf of Lion and the Alboran Sea. This pattern was not recurrent and consistently observed, with different spatial variation observed across the type of indicator or the taxonomic species group. These deviations causing some discontinuous trends may be linked to the heterogeneity in both the north and south most areas seen in environmental drivers or human impacts. A similar case can be seen in the Aegean Sea (Gaertner et al., 2007), where diversity is higher than in nearby western seas despite being in the eastern Mediterranean due to an increased amount

of nutrients from anthropogenic origin. Both, the Gulf of Lion and the Alboran Sea are the two areas where the environmental gradients suffer more clear discontinuities, particularly from the primary production and hydrographic perspective (Bosc et al., 2004), which could explain those spatial patterns. In addition, the Alboran Sea has biogeographic singularities in terms of biodiversity as it represents an ecological transition ecosystem between the Atlantic and the Mediterranean (Real et al., 2021). Conversely, these higher values in the extremes could be also a consequence of the lower values in the central area of GA06 related to higher human impacts, as previously discussed.

Regarding results by taxonomic groups, cephalopods and crustaceans showed the most consistent spatial patterns with a north–south gradient in many of their indicators. These patterns correspond to the higher proportion of relative fish biomass in northern bioregions for the surveyed community, and with higher temperatures and lowest primary production in the south (Bosc et al., 2004; Colella et al., 2016). In the case of cephalopods, the increases in most of the study area with time suggest that they may become the “winners” in the region. This increase is consistent with other studies in the Western Mediterranean (Coll et al., 2013; Keller et al., 2016; Hidalgo et al. 2021), and at a global scale (Doubleday et al., 2016; Coll et al., 2021), indicating positive changes of short life-cycle species such as cephalopods under cumulative anthropogenic effects. Cephalopods are fast growing species and are positively affected by increasing temperatures that synergistically interact with the removal of both predators and competitors by fishing, thus allowing boosting production of a few cephalopod species (Keller et al., 2017b; Coll et al., 2021). Besides cephalopods, our study also reveals similar patterns in crustaceans, which are generally short life-cycle species compared to most fish, consistent with recent studies in the area (Hidalgo et al. 2021).

Taking into account the different trends in the trophic level-based indicators and their equivalence to the different fishing scenarios proposed by Shannon et al. (2014), the changes in trophic levels observed in our study hint towards a fishing down scenario, especially in the North Catalan Sea. This is in line with previous results investigating trends in specific regions (Coll et al., 2009). In the North Catalan Sea specifically, there has been an increase in species with low trophic level (TLsc) and a negative relationship between time and the mean surveyed trophic level above 4. This is probably signalling the intense exploitation reported in the area (Coll et al., 2008; Pennino et al., 2017; Coll et al., 2021). In fact, the indicators analysed in this study picture the North Catalan Sea region as an area with high rates of diversity change, a fishing down process especially notable considering fish, low mean values of richness, abundance and biomass, and decreases in overall biomass and relative biomass of predators. All these values and changes can be associated with overfishing (Shannon et al., 2014) and pollution (Johnston and Roberts, 2009) intensified by the smaller extension of the continental shelf. In southern areas like the Alboran Sea and the Channel, in contrast, some indicators show positive temporal trends (such as the relative biomass of predators and mean surveyed trophic level above 3.25 of crustaceans) and could be related to recoveries of certain species after the decline of fishing effort, as seen for species of chondrichthyans (Ramírez-Amaro et al., 2020; Hidalgo et al. 2021).

Considering our outcomes and the potential limitations of our study, we highlight that some indicators can be prioritized to measure changes in community diversity due to their statistical significance, consistency and responsiveness. Overall, general indicators, such as species richness, abundance and biomass, were more informative to track long-term spatial and temporal changes in our study area, as they showed more statistically significant relationships and clearer patterns. Others were more complex to interpret, such as evenness and dominance indicators, β -diversity and its components and trophic levels. A reason behind this difficulty of interpretation could be their higher sensitivity to differences between areas and thus their influence by local environmental and human drivers distributed heterogeneously in space.

Our study also highlights that further studies are needed to

investigate the dominant mechanistic drivers behind the patterns observed, as well as to elucidate the spatial scale (regional or local) at which these drivers act. Further studies should analyse the effect of cumulative human drivers like fisheries exploitation and/or pollution and environmental factors, such as temperature and primary production, as these are most likely the drivers influencing change. A finer analysis exploring the indicators by depth could also offer more insights as the shelf and slope areas do have different natural communities because of oceanographic conditions and environmental factors, but also face different human impacts (Farriols et al., 2017; Fernandez-Arcaya et al. 2019). In this context, a more detailed spatial analysis is also recommended to confirm those areas with high biodiversity change as well as the most vulnerable areas or those that are most impacted (such as the North Catalan Sea) or may be recovering (such as the Alboran Sea or the Channel). This can be a useful information to be considered for the design and the establishment of marine protected areas (MPAs) and other effective area-based conservation measures (OECMs) for the protection of biodiversity and the sustainable use of marine resources (e.g., Coll et al. 2015; Giménez et al., 2020).

Our study, however, presented some limitations as some traits like the trophic level or the mean size may not capture real changes in the traits but the relative change in biomasses. This is so because the values were taken from available online databases representing information from the entire population. Values from online databases may not be the most suitable due to the oligotrophic and warm environment of the Mediterranean Sea compared to other areas, showing quicker maturation and smaller sizes at maturity for many species due to the temperature size rule (Atkinson, 1995; Silva et al., 2006; van Rijn et al., 2017). Another issue is that certain ecosystem functions (e.g. productivity, energy transfer, nutrient cycling) as well as functional groups of ecological importance (such as elasmobranchs, mesopelagic species, or small pelagic fish) are not well captured by our indicators. Lastly, the use of linear effects for the identification of characteristic or recurrent patterns and effects may have masked some non-linear trends that were not considered in favour of analysing long-term effects (Blanchard et al., 2010).

In summary, we have detected spatial gradients and temporal changes in biodiversity indicators through the study area, both at community level and at taxa group level with clear winners (cephalopods) and losers (the North Catalan Sea sub-region) in a context of change. Despite some limitations, this in-depth analysis of the Western Mediterranean ecosystem illustrates the use of a selection of traditional and integrative biodiversity indicators that combine the capacity to detect ecological changes both at a regional and a sub-regional scale.

CRedit authorship contribution statement

Carlos Velay: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Visualization. **Manuel Hidalgo:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Visualization. **Maria Grazia Pennino:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Encarnación García:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Antonio Esteban:** Resources. **Cristina García-Ruiz:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Gregoire Certain:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Sandrine Vaz:** Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Angélique Jadaud:** Investigation, Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Marta Coll:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

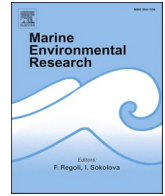
Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.108674>.

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Understanding the response of the Western Mediterranean cephalopods to environment and fishing in a context of alleged winners of change

Carlos Veloy^{a,*}, Marta Coll^a, Maria Grazia Pennino^b, Encarnación García^c, Antonio Esteban^c, Cristina García-Ruiz^d, Gregoire Certain^e, Sandrine Vaz^e, Angélique Jadaud^e, María González^c, Manuel Hidalgo^f

^a Institute of Marine Science (ICM-CSIC), Passeig Marítim de La Barceloneta, N° 37-49, 08003, Barcelona, Spain

^b Instituto Español de Oceanografía (IEO-CSIC) (Madrid), Calle del Corazón de María, 8, 28002, Madrid, Spain

^c Instituto Español de Oceanografía (IEO-CSIC) (Murcia), Calle el Varadero, 1, 30740, San Pedro del Pinatar, Spain

^d Instituto Español de Oceanografía (IEO-CSIC) (Málaga), Puerto Pesquero, s/n Aptdo. 285, 29640, Fuengirola, Spain

^e MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France

^f Instituto Español de Oceanografía (IEO-CSIC) (Balears), Ecosystem Oceanography Group (GRECO), Moll de Ponent, 07015, Palma, Spain

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ABSTRACT

Increasing impacts of both fisheries and climate change have resulted in shifts in the structure and functioning of marine communities. One recurrent observation is the rise of cephalopods as fish recede. This is generally attributed to the removal of main predators and competitors by fishing, while mechanistic evidence is still lacking. In addition, climate change may influence cephalopods due to their high environmental sensitivity. We aim to unveil the effects of different anthropogenic and environmental drivers at different scales focusing on the cephalopod community of the Western Mediterranean Sea. We investigate several ecological indicators offering a wide range of information about their ecology, and statistically relating them with environmental, biotic and fisheries drivers. Our results highlight non-linear changes of indicators along with spatial differences in their responses. Overall, the environment drivers have greater effects than biotic and local human impacts with contrasting effects of temperature across the geographic gradient. We conclude that cephalopods may be impacted by climate change in the future while not necessary through positive warming influence, which should make us cautious when referring to them as generalized winners of current changes.

1. Introduction

Global change causes several negative impacts reported worldwide on marine ecosystems, while it can favour some taxonomic groups. Numerous studies on different areas and species have identified cephalopods as potential winners in the marine environment, while the generalization of this pattern is still pending of conclusive proofs. This trend, observed at both regional (Keller et al., 2016; Veloy et al., 2022) and global scales (Doubleday et al., 2016), may be largely influenced by the favouring conditions of climate change (such as warming) and interspecific relationships with other diminishing and competing taxa such as fishes of higher trophic level. Cephalopods have a great ecological importance for their top-down control mechanisms due to their strong predatory role and high trophic levels (Anderson et al., 2011; Eddy et al., 2017). Therefore, an understanding of the factors that

affect the cephalopod community, as well as the increase of dominance in the ecosystem, can aid to better understand of the current state and expected changes of marine ecosystems.

The overexploitation of fishes, as one of the main predators of cephalopods (Caddy and Rodhouse, 1998; Hastie et al., 2009; Staudinger et al., 2013), has been proposed as an important factor in the increase of this taxonomic group. Indeed, the decrease of fish production results in fishing fleets switching from declining fish stocks towards invertebrates, including cephalopods. In fact, the landings on cephalopods is rising worldwide (FAO, 2020; Ospina-Alvarez et al., 2022). The south of Europe, particularly Spain, is among the countries with more local cephalopod supply available per capita alongside Republic of Korea, Japan and Taiwan (Hunsicker et al., 2010; Ospina-Alvarez et al., 2022), which makes south European stocks potentially more at risk. In the Mediterranean Sea, while many assessed fish stocks are already

* Corresponding author.

E-mail address: veloy@icm.csic.es (C. Veloy).

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heavily exploited, the lack of generalized assessment of cephalopods limits the capacity to assess their current health status (FAO, 2022). Furthermore, for these invertebrates, metrics such as the Maximum Sustainable Yield (MSY) are not well adapted to them compared to fishes. This is mainly due to poor data as well as the problems that their short life-strategy poses to modelling (Arkhipkin et al., 2021), which represent a long-lasting challenge for the current and future management.

It is also known that cephalopods are highly sensitive to environmental factors (e.g. Arvanitidis et al., 2002; Forsythe, 2004; Pierce et al., 2008) (see list of references and associated mechanisms and observations reviewed and shown in the [Supplementary Material Table S1](#)). They also have a great degree of plasticity observed through their different life cycles and species (Arvanitidis et al., 2002; Otero et al., 2009; Pierce et al., 2008). This plasticity results in unexpected responses to certain environmental factors that vary by both taxa and study area with, for instance, differential responses in adult body size to warming across taxa and regions. Both increase in body size and younger maturation and, therefore, smaller adult size and shorter lifespan, have all been reported to be favoured by warming conditions (Forsythe, 2004; Hatfield, 2000; Pecl and Jackson, 2008). High sea surface temperatures (SSTs) generally benefits cephalopods at a population level allowing them to increase their abundance and even their spatial distribution range in some cases (van der Kooij et al., 2016). Primary production also plays a similar role benefitting cephalopod populations mostly related to upwelling processes, particularly in early life stages, allowing higher survival rates due to the associated increase in secondary production (Bakun and Csirke, 1998; Lauria et al., 2016; Otero et al., 2009; Puerta et al., 2016b). However, in some systems, there is a negative relationship between certain species of cephalopods and primary production, mostly due to lagged responses, as paralarva are released during the less intense periods of upwelling (i.e. less productive) to ensure they remain near the coast (Otero et al., 2009), a process in agreement with the 'optimal environmental window' hypothesis (Cury and Roy, 1989).

The Mediterranean Sea is a semi-enclosed sea, characterized by oligotrophic nature and warming increasing temperatures (Coll et al., 2010). It is an important region as biodiversity hotspot (Coll et al., 2010; Costello et al., 2010), but with many marine resources still overexploited by fishing (FAO, 2022). The local marine ecosystem is also subjected to quick changes due to climate change (Hidalgo et al., 2018; Lejeune et al., 2010), increased sensitivity to natural variability in primary production (Fu et al., 2018; Hidalgo et al., 2022a), the effects of invasive alien species such as the Lessepsian fauna (Galil et al., 2017) and of pollution (Danovaro, 2003; Pennino et al., 2020). Recent studies analysing marine biodiversity changes in space and time have shown divergent patterns according to the taxonomic groups investigated in this semi-enclosed sea (Carmezim et al., 2022; Pennino et al., 2024; Veloy et al., 2022). One example of these differences is the case of fishes and cephalopods: while the former have been shown to decrease with time, likely related to fisheries activity impacts (Farriols et al., 2020), cephalopods have been shown to be a prolific group (Ciércoles et al., 2018; Keller et al., 2017a; Puerta et al., 2016b; Quetglas et al., 2016).

In the Mediterranean Sea, some relationships between the different environmental drivers, the bathymetric gradient, and the cephalopod community have been already confirmed. For instance, the bathymetric pattern of species richness gradient has been shown to peak nearing the continental shelf break (Keller et al., 2017b). Environmental factors such as SST and primary production can have a positive relationship with species richness as well as biomass ([Supplementary Material Table S1](#)). In contrast, human impacts have been shown to have a negative influence on the cephalopod richness in non-target species, while a non-linear response (increasing richness at low and upper levels of exploitation) has been also observed (Navarro et al., 2015; Vilas et al., 2019). These findings are in line with reported higher biomass of cephalopods with lower levels of predators and higher levels of fishing (Coll et al., 2013), and in areas with relative warmer waters (Navarro

et al., 2015). However, the responses of cephalopods to direct and indirect variables have been shown to differ depending on the studied species and region (Keller et al., 2017b; Puerta et al., 2015, 2016a, 2016b), in part due to short life cycle and their high capacity to adapt to local and regional environmental conditions (Moreno et al., 2002; Pierce et al., 2008).

Most of past and recent research has focused on direct quantitative approaches to study cephalopod populations taking biomass and abundance as main metrics (Hastie et al., 2009; Hatfield, 2000; Otero et al., 2009; Puerta et al., 2016b) ([Supplementary Material Table S1](#)), while little is known about other community and biodiversity indicators, or other indicators informing on their function on the ecosystems. In addition, the analyses of drivers causing variation on β -diversity or other community and trophic-based indicators have not been widely investigated. The combination of these indicators may provide valuable information regarding the geographic and temporal evolution of this taxon, the mechanisms of change and potential implications on the ecosystem functioning attending to environmental and anthropogenic drivers in given areas.

Our hypothesis is that cephalopods, being short-lived organisms, respond more profoundly to the environment than to other drivers, although they can be influenced by local human activities such as fishing (Navarro et al., 2015; Nieblas et al., 2014; Puerta et al., 2016b). Furthermore, these factors could influence competition as well as food availability represented by the predatory fishes and crustaceans, respectively (Puerta et al., 2016a). Thus, the main objective of this study is to investigate local and regional scale drivers of spatial change in the cephalopod community of the West Mediterranean Sea in terms of a set ecological indicators and relate them to environmental, human and biotic drivers. This study follows the results of a regional analysis that showed important increases of cephalopods indicators in the region (Veloy et al., 2022), selecting those indicators that have shown most significant spatial variation.

2. Materials and methods

2.1. Sampling and study area

We used cephalopods data collected from annual trawling surveys performed within the Mediterranean International Trawl Survey (MEDITS) program between 2013 and 2019 with 1296 unique sampling points ([Supplementary Material Table S2](#)), as this period allowed us to get a complete time series of the forcing variables of interest. A common sampling protocol was used in the entire study area, standardizing duration of the hauls as well as gear type and its specifications (Bertrand et al., 2002; Spedicato et al., 2020).

The General Fisheries Commission of the Mediterranean (GFCM) adopted several divisions of the surveyed area denominated Geographical Sub-Areas (GSAs). We focused on continuous area of the Western Mediterranean, ranging from the Alboran Sea to the Gulf of Lion, corresponding to GSA1 (Northern Alboran Sea), GSA6 (Northern Spain) and GSA7 (Gulf of Lion) ([Fig. 1](#)). These three areas display a continuous geographic area with contrasting hydrographical characteristics: i) the northern Alboran Sea is an area influenced by the influx of Atlantic waters and thus has a high and variable primary production; ii) the Northern Spain, including Valencia Channel, Ebro Delta and North Catalan Sea, is characterized by low values of chlorophyll-a concentration (although the Ebro Delta receives nutrients from continental sources) and high temperature but differ in the width of their continental shelves; and iii) the Gulf of Lion, a shallow area with an extended continental shelf as well as lower SST characterized by variable but high productivity due to its local oceanography (Rhône river input and wind induced coastal upwelling) (Bosc et al., 2004; Estrada, 1996; Nieblas et al., 2014). These subareas division have been used in previous studies (Veloy et al., 2022). Because the depth range between 25 and 500 m is the one with most diversity of taxa, only sample points

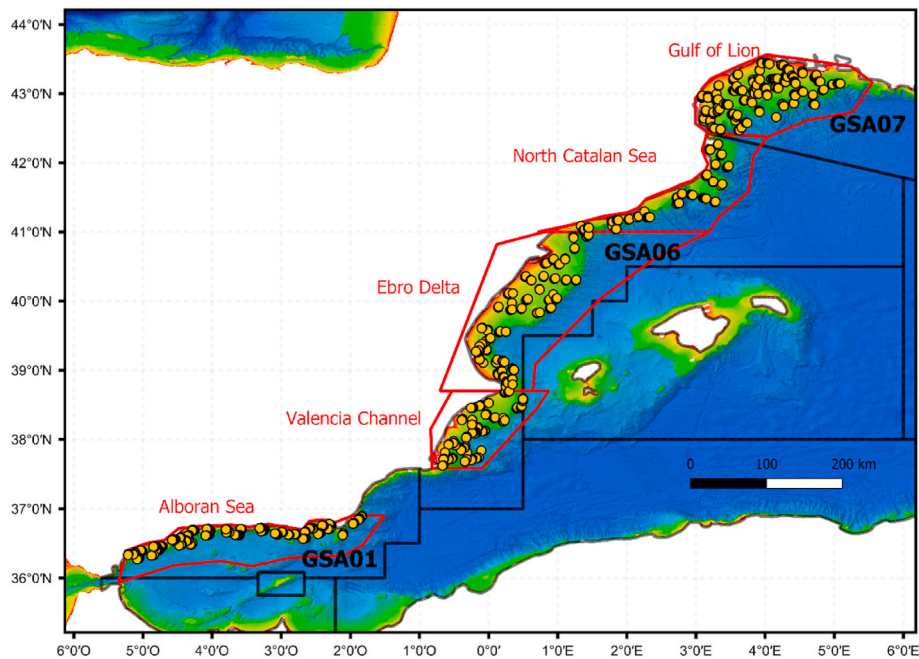


Fig. 1. Western Mediterranean area with the considered subregions (in red), GSA areas (in black) and sampling points of the MEDITS trawling survey used in this study.

from those depth ranges (corresponding to the continental shelf and upper slope area) were considered.

2.2. Indicators and drivers of change

We used three groups of indicators: (a) traditional biodiversity indicators such as species richness and β -diversity (Jaccard index); (b) community indicators such as biomass, mean size (both of these transformed into logarithm in this study) and relative biomass of predators within the cephalopods (B_{pred}); and (c) trophic level indicators as $TL_{3.25}$

Table 1
Dependent variables used in the study and information they provide about the state of cephalopods and the communities they are part of.

Indicators	Information about cephalopods/ecosystem	Data source	Indicator source
Biodiversity indicators			
Richness	Number of cephalopod species present	MEDITS data; Veloy et al. (2022)	McIntosh (1967)
B-diversity (Jaccard index)	Temporal change of the cephalopod subset of the ecosystem	MEDITS data; Veloy et al. (2022)	Blowes et al. (2019); Dornelas (2014)
Biomass and size			
Total biomass of cephalopods (Biomass)	Weight of all cephalopods (transformed to logarithm)	MEDITS data; Veloy et al. (2022)	Coll et al. (2016)
Relative predatory cephalopod biomass (B_{pred})	Fraction of cephalopods that are considered predators	MEDITS data; Veloy et al. (2022)	Coll et al. (2016)
Mean Size	Weight of the average cephalopod as a proxy for size (transformed to logarithm)	MEDITS data; Veloy et al. (2022)	Shin et al. (2018); Forsythe (2004)
Trophic level indicators			
$TL_{3.25}$	Mean trophic level of cephalopods above 3.25	MEDITS data; Veloy et al. (2022)	Shannon et al. (2014)
TL_4	Mean trophic level of cephalopods above 4	MEDITS data; Veloy et al. (2022)	Shannon et al. (2014)

and TL_4 (Table 1). These indicators were selected based on criteria used in previous studies (Veloy et al., 2022) and the Indiseas project (Coll et al., 2016; Shannon et al., 2014; Shin et al., 2018), such as measurability and data availability (must be estimated routinely and have time-series available), ecological significance and sensitivity to different drivers.

To calculate B_{pred} we labelled as “predator” those species of cephalopods with Trophic Level (TL) above 3.5 that were reported as having maximum sizes larger than 20 cm of total length or equivalent measurements. Trophic levels were obtained from different online databases (Froese and Pauly, 2021; Palomares and Pauly, 2021). After assigning this trait data, those species present in less than 80% of the temporal series were discarded from the study (Supplementary Material Table S3).

The drivers (independent variables) (Table 2, Fig. 2) were classified into four categories depending on the information they provided: (a) depth as a structural and static driver (note that geographic smoother were explicitly avoided; see explanation below) (b) dynamic environmental variables (Sea Surface Temperature (SST), and Chlorophyll-a (Chl-a), (c) dynamic human drivers (Fishing effort) and (d) dynamic biotic variables (Relative biomass of predatory fishes (Fish B_{pred}) and crustacean biomass as a prey indicator). These independent variables were selected because they have shown to be very influential on cephalopod populations, as well as they allow to explore different types of change (anthropogenic and natural) (Supplementary Material Table S1).

Environmental and human drivers were obtained from reanalysis data of physic and biochemistry parameters of the Mediterranean provided by COPERNICUS (2021) with a resolution of 0.04° and from Global Fishing Watch (2019) data with a resolution of 0.01° , respectively. The study period selected within the databases is between 2013 and 2019. In the case of the environmental drivers, data was used to calculate yearly means per sample point (i.e. grid cell), while for fishing effort the daily data was processed to get the yearly sum of the total fishing hours per grid cell using previously established methods (Taconet et al., 2019). While the use of lagged variables, specially for the environmental ones, have been featured in other studies (Keller et al., 2017a), we only used data from the same year because the focus of the study was to understand the spatial variation of the community and

Table 2
Independent variables used in the study and sources of origin.

Variable	Definition	Data source	Variable source
Structural driver			
Depth	Depth at sea bottom	MEDITS data	
Environmental drivers			
SST	Sea Surface Temperature	COPERNICUS (2021)	COPERNICUS (2021)
Chl-a	Primary production	COPERNICUS (2021)	COPERNICUS (2021)
Human impact drivers			
Fishing effort	Number of yearly hours that vessels spent fishing on an area, (human pressure) (transformed to logarithm)	Global Fishing Watch 2021	Anderson et al. (2011); Caddy and Rodhouse (1998)
Biotic drivers			
Fish B _{pred}	Fraction of fishes that are considered predators (competitors and predators of cephalopods)	MEDITS data; Veloy et al. (2022)	Coll et al. (2016); Veloy et al. (2022)
Crustacean biomass	Weight of all sampled crustaceans from the order Malacostraca, excluding amphipods and isopods (cephalopod main prey) (transformed to logarithm)	MEDITS data; Veloy et al. (2022)	Puerta et al. (2015); Veloy et al. (2022)

adding a temporal dimension could complicate the interpretation of the results attending to the spatiotemporal dependence of processes and data.

Lastly, biotic data was extracted from the data available in a previous study (Veloy et al., 2022). The Fish B_{pred} considered a similar criterion of predator as it was described previously for predatory cephalopods (i.e., *Octopus vulgaris*, *Loligo forbesii*). Both fishing effort and the biomass of crustaceans was transformed using the logarithm.

The biotic data derived from MEDITS and the drivers investigated were interpolated into a grid with a resolution of 0.25° over the study area (Fig. 2).

2.2.1. Data analysis

Firstly, correlation matrices were used to preliminary check the correlation between drivers and all the ecological indicators. The final selection of independent variables (Table 2) featured indicators of each category (environment, human or biological) that were complementary: SST, Chl-a, Fishing Effort, Fish B_{pred} and Biomass of crustaceans.

Secondly, we applied General Additive Modelling (GAM) (Wood, 2006) to each indicator to evaluate the regional influence of environmental and anthropogenic drivers as univariate smoother along with depth as a structural variable (i.e. persistent influence). GAM models were considered for the study due to their premise of non predefined functional form of the effect and their capacity to determine non-linear effects, allowing a more complete understanding of the effects and the response capacity of all the indicators. We also took into account the ease of interpretation of the relationships between each indicator and the drivers on an individual level as well as the efficiency to study the residuals, as opposed to other methods. One-dimensional non-parametric smoothing functions used included cubic splines with up to a maximum of 3 degrees of freedom (i.e. 4 knots) to avoid model overfitting and obtain meaningful functional forms of the effects. All the models were calculated using Gaussian distribution with the exception of the Richness model, where a Poisson distribution was used. Model selection was done comparing the models with all the independent variables with those where the non-statistically significant variables were sequentially removed (Supplementary Material Table S5). An

important element in our modelling approach is that we explicitly avoided the use of a geographic bi-variate smoother (latitude, longitude) to allow environmental factors to capture the potential spatial variability.

To distinguish whether the drivers investigated were geographically structured or whether they represented a larger scale impact at the scale of the studied region, we investigated the partial residuals of all covariates and models according to the five distinct sub-regions continuously spread over the three contiguous GSAs: GSA1, GSA6 and GSA7. We indicate in the results when it is meaningful based on the overlapping of the residuals of different sub-regions. Finally, we present the spatial predictions of the models using the independent variables as predictors.

All indicators and analysis were calculated with R version 4.2.2 (R Core Team, 2022). Jaccard index and its components were calculated using the R package betapart (Baselga and Orme, 2012) and the GAM models were obtained using mgcv (Wood, 2011).

3. Results

3.1. Biodiversity indicators

Cephalopods' richness showed positive relationships with SST above 18 °C, a linear influence of the biomass of crustaceans, as well as a maximum of species at depths of 150–300 m (Fig. 3, Table 3). Spatially, it presented lower values in northern areas, characterized by low temperatures and low values of crustacean biomass. Richness showed maximum values on the southernmost area of GSA6, where all those drivers show higher values. Interestingly, SST displayed a spatial segregation of partial residuals while the other drivers showed a regional effect (i.e. overlapping distribution, Supplementary Material Fig. S2). Maximum species richness values were observed south the Ibiza Channel and a heterogeneous pattern emerged in the Alboran Sea and the Ebro Delta.

β-Diversity showed a nonlinear relationship with SST with a maximum value around 17 °C followed by a decrease (Fig. 3, Table 3). It showed a negative relationship with Chl-a until 0.4 mg/m³ from which β-diversity increased. It also showed a positive non-linear relationship with fishing effort and a negative relationship with fish B_{pred} and depth. Spatial patterns were roughly opposite to the ones found for richness, with the highest values found in the northern areas and the lowest on the south of GSA6 on the Valencia Channel. The partial residuals of the effects showed the highest values of this index in the Gulf of Lion and North Catalan Sea, which are areas with the lowest SST (Fig. 4).

3.2. Biomass and mean size

A decreasing trend was found between total cephalopods biomass and SST, reaching a minimum between 17 °C and 18 °C and a small increase at 19 °C (Fig. 5, Table 3). It also showed a non-linear increasing trend with biomass of crustaceans and with Fish B_{pred}, with a maximum value at ratios stabilized around 0.5 in the latter case. On the other hand, cephalopods biomass decreased with Chl-a and particularly with depth. The highest values were found in the shallow areas of the Gulf of Lion and the deep areas in central Northern Spain (i.e. Ebro Delta). The partial residuals of the effects of SST showed that the Catalan Coast and the Gulf of Lion areas were associated with the highest values of the indicator as well as the decrease on cephalopods biomass (Fig. 6).

SST had a negative effect on B_{pred} until 18.5 °C and of Chl-a until 0.3 mg/m³ (Fig. 5, Table 3). Residuals on the SST model showed a geographical pattern of this effect (Fig. 6), where the Gulf of Lion and the Catalan Sea were associated to higher values of B_{pred} and the residuals of the rest of the independent variables were more homogeneously distributed (Supplementary Material Fig. S5). B_{pred} showed a nonlinear decreasing trend with depth and biomass of crustaceans, while fish B_{pred} had a positive linear relationship with this metric. Areas from the north had higher ratios of predators than southern areas such as

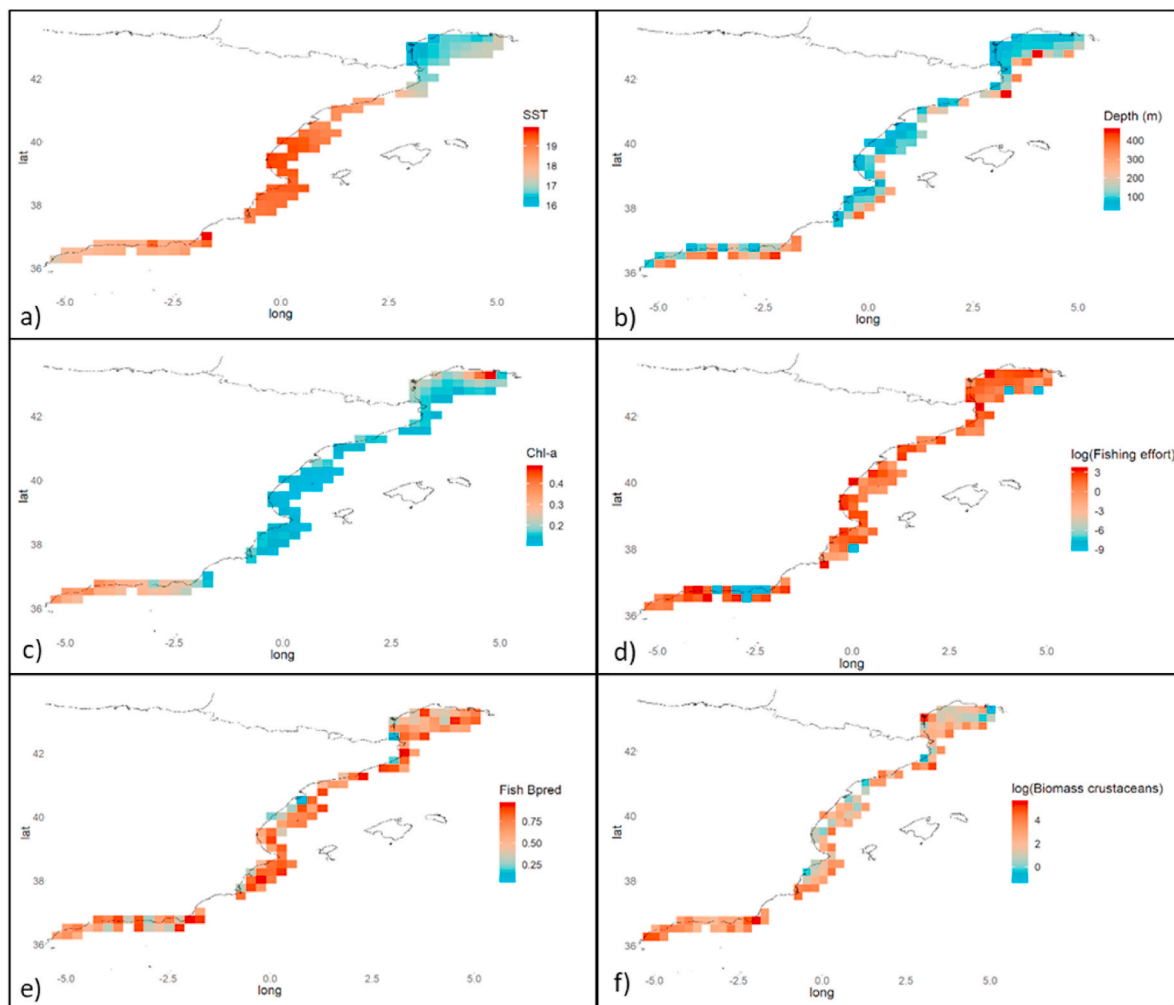


Fig. 2. Spatial variation of the different independent variables considered for this study. Values represent the mean of the time period. a) SST (°C), b) Depth (m), c) Chl-a (mg/m³), d) log (Fishing Effort), e) Fish B_{pred} , f) log (Biomass crustaceans).

the Alboran Sea (GSA1) showing a gradient between the former and the Gulf of Lion (Fig. 5).

Mean Size (Fig. 7, Table 3) had a negative nonlinear relationship with Chl-a and depth, and a dome-shaped relationship with SST with a maximum at 18 °C. It also had a clear positive relationship with fish B_{pred} . Highest mean sizes appeared in GSA6 areas, on grid cells where primary production was low and the ratio of predatory fishes was high.

3.3. Trophic level indicators

$TL_{3.25}$ presented a linear negative relationship with biomass of crustaceans (Fig. 8, Table 3). Meanwhile, for SST and depth, these relationships were positive but non-linear. The highest values of $TL_{3.25}$ were found within the cells of GSA6, an area with generally high SST and biomass of crustaceans (Fig. 8). Partial residuals seem to confirm this trend as the values of the residuals of the regions of the Valencia Channel and Ebro Delta are higher than the other regions (Supplementary Material Fig. S6).

For TL_4 , Chl-a also showed a dome-shaped influence with a maximum near 0.4 mg/m³. SST showed a positive relationship with TL_4 , while the biomass of crustaceans and depth had a negative relationship. The highest values of TL_4 were found in the shallow waters and comparatively in the south, being associated with high productivity, intermediate values of SST and low values of biomass of crustaceans (Fig. 8). Some high values of TL_4 were also found on sparse cells corresponding to temperate shallow waters in the Gulf of Lion.

3.4. Overall trends

In most of the dependent variables, SST showed a change of trend between 17 °C and 19 °C, corresponding mostly with the transition area of the Catalan coast between the Gulf of Lion and the Ebro Delta broad shelf (Fig. 1). Values on the indicators switched from a descending curve to an ascending one and were associated with the spatial gradient of this variable, corresponding to three thermal areas. Chl-a showed a similar pattern, with an inflection point that indicated a change in response between 0.3 and 0.4 mg/m³, which is mainly associated to the extreme areas in the Gulf of Lion and the Alboran Sea (Supplementary Material Figs. S4 and S5). The effects on cephalopods' indicators were mainly associated with the geographic pattern of these two covariates, although in the case of Chl-a it seems to show a reduced geographical component in some indicators unlike SST, where a large geographic effect is apparent. These shifts in trends experienced between the Alboran Sea must be taken with caution, since the effects and the mechanisms behind them are not the same as those found in the Gulf of Lion-Catalan Coast area. This is due to its particularities as a transitional zone between the Atlantic and the Western Mediterranean and the influence of the ocean in its oceanography and the high turnover of species in this ecosystem. Those indicators showing a larger influence by environmental variables were β -diversity and B_{pred} , which revealed gradients alongside the Western Mediterranean coast. When looking at the partial residuals of β -diversity and B_{pred} , the spatial effect responsible for these gradients was visible and associated to SST, as values from each region are

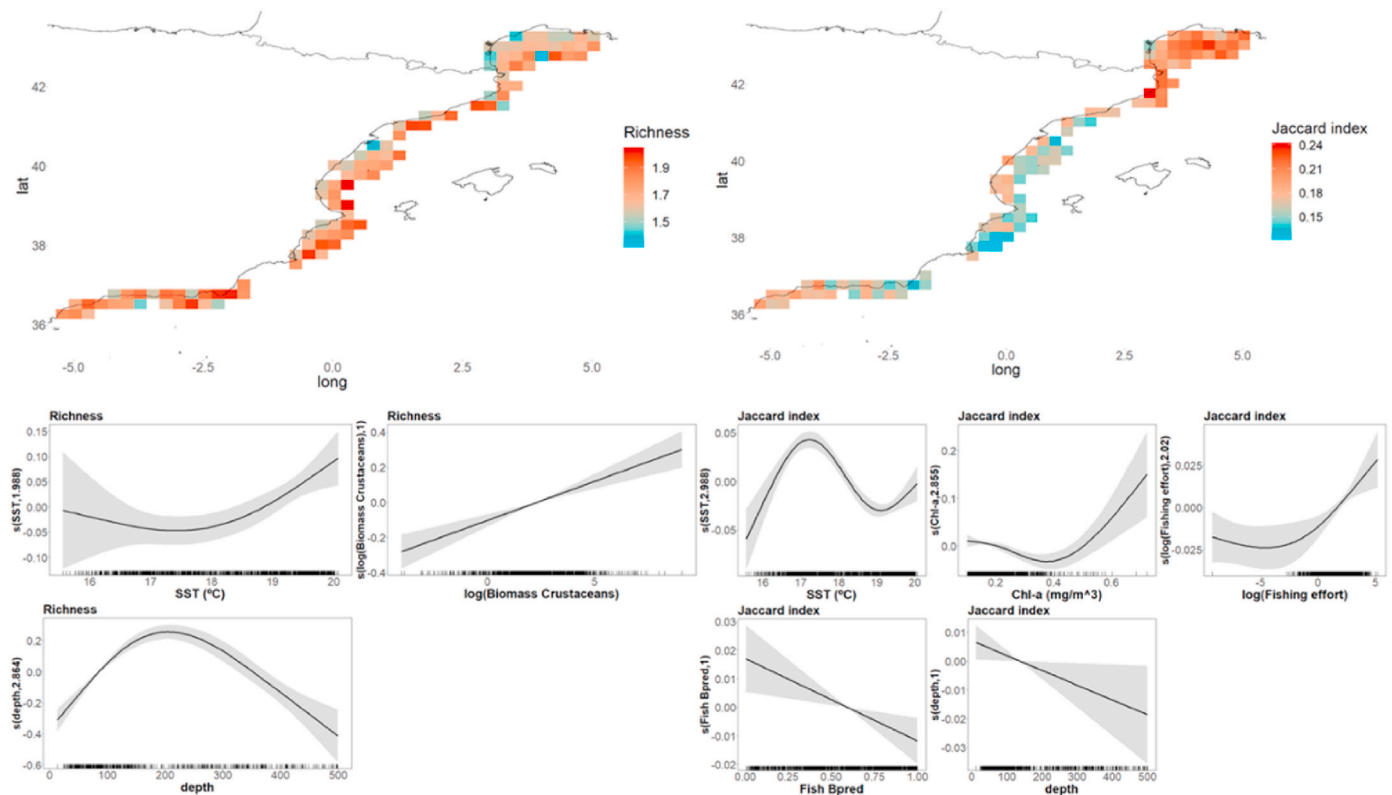


Fig. 3. Spatial variation and smoothing effect of species richness (left) and β -diversity (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

structured in differentiated clusters along the thermal gradient (Supplementary Material Figs. S2-S6).

Those indicators most influenced by other types of variables, both biotic and human, showed less clear spatial patterns in the effects, likely indicating regional impacts. This was revealed by the partial residuals of all the regions, which were distributed in a more homogenous way along the curve of the smoothing effect with no differences between the regions. This would correspond to more heterogeneous effects on the indicators selected going beyond regional environmental gradients. Examples of these effects are fishing effort on β -diversity or Biomass of crustaceans on Richness.

Overall, GSA1 had lower values in most indicators than the ones in the rest of the study area, except for TL₄. GSA6 area presented intermediate or high values for the different indicators, with the exception of the areas adjacent to the Ebro Delta (e.g. Biomass, B_{pred}) and Valencia channel (e.g. β -diversity). Grid cells within the Valencia channel area tended to have lower values than those in the rest of the GSA6 region. GSA7 showed high values for many indicators compared to the rest of the Western Mediterranean, like Biomass or B_{pred} .

4. Discussion

This study provides a multidimensional perspective of the cephalopod community to further comprehend their ecology and role in marine ecosystems. Previous studies examined the interactions between this taxon and drivers at a species level (Miyahara et al., 2005; Moreno et al., 2014; Otero et al., 2009; Xavier et al., 2016; among others) or considered different types of cephalopods such as squids and octopus represented by a single species (e.g. Puerta et al., 2015) (see Supplementary Material Table S1 for further details in a summarized review performed for the present study). While others studies have focused on the community analysing the variation of species composition (Keller et al., 2017a), we here investigated the cephalopod community from a

different perspective: using a set of complementary ecological indicators that offer a wider picture about this diverse group along with their response to both environmental drivers and anthropogenic pressures. Our study brings novel elements to the spatial nature of the impacts of both environmental and human drivers, whether they present regionally heterogeneous or geographically effects structured in gradients. In fact, while spatial patterns of the indicators were already hinted in a recent study (Veloy et al., 2022), we here identify the main responsible drivers of the known regional patterns including those observed at a finer scale. For instance, values of the biomass of predatory cephalopods display a positive south-north gradient (mainly due to the effect of SST), while TL_{3.5} displays maximum values on the southern parts of GSA6 and intermediate ones on the northern areas. On the other hand, β -diversity, which was not showing any significant spatial effects when looking at a regional scale in past studies, revealed a positive south-north gradient in our study, mainly driven by the SST gradient.

Species richness has been suggested to follow large geographical gradients, with particular latitudinal variation along the Mediterranean Sea (Coll et al., 2010; Navarro et al., 2015; Veloy et al., 2022). However, at a regional scale, our study did not show marked geographical trends, highlighting maximum values around the Valencia Channel. This is consistent with recent unpublished studies evidencing a regional southern displacement of the demersal community in the Iberian Peninsula following sub-regional pathways of climate velocity (Sanz-Martín et al., 2024). These could increase local responses of diversity in southern regions of GSA6 associated to local displacements to avoid sub-optimal thermal habitats. In fact, richness and β -diversity appear to have complementary patterns, with cells showing high values of β -diversity generally having low species richness and vice versa (Pennino et al., 2024). This is especially apparent in GSA6 and GSA7. Some areas with the lowest values of richness tended to be associated with low biomass of crustaceans and low SST, similarly to what was found in recent studies (Keller et al., 2016; Oosterwind et al., 2022; Vilas et al.,

Table 3

GAM models summary for each ecological indicator. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. edf = Estimated degrees of freedom of univariate smoothers; %DV = Deviance explained (percentage).

Indicator	Drivers	Intercept	edf	%DV
Richness		1.697 ± 0.012		23.6
	SST		1.988***	
	Log (Biomass Crustaceans)		1***	
	Depth		2.864***	
B-diversity (Jaccard index)		0.183 ± 0.002		10.9
	SST		2.988***	
	Chl-a		2.855***	
	Log (Fishing effort)		2.020***	
	Fish B _{pred}		1**	
	Depth		1*	
Log(Biomass)		3.988 ± 0.312		25
	SST		2.913***	
	Chl-a		2.910***	
	Log (Biomass crustaceans)		1456**	
	Fish B _{pred}		2.159***	
	Depth		2.792***	
B_{pred}		0.878 ± 0.005		27.5
	SST		2.539***	
	Chl-a		2.731***	
	Log (Biomass crustaceans)		2.076***	
	Fish B _{pred}		1***	
	Depth		2.794***	
Log(Mean Size)		4.079 ± 0.031		10.02
	SST		2.236*	
	Chl-a		2.131***	
	Log (Fishing effort)		1.442	
	Fish B _{pred}		1.686***	
	Depth		2.980***	
TL_{3,25}		3.977 ± 0.005		8.82
	SST		2.020***	
	Log (Biomass crustaceans)		1***	
	Depth		2.944***	
TL₄		4.328 ± 0.002		34.5
	SST		2.263***	
	Chl-a		2.508***	
	Log (Fishing effort)		2.706	
	Log (Biomass crustaceans)		1.992**	
	Depth		2.909***	

2019), which are likely related to lower food availability.

Fishing impact was only observed to have a significant effect on β -diversity, which is consistent with previous studies suggesting the erosion of the spatial structure of communities with a consequent decrease in connectivity between putative meta-communities (Hidalgo et al., 2017; Shackell et al., 2012). The exploitation pressure, especially in large species with more fecundity and mobility, could trigger the destabilization of northern ecosystems and also explain a smaller number of species at a local and regional level. This mechanism has been particularly observed in the GSA6 (Hidalgo et al., 2022b; Pennino et al., 2024; Veloy et al., 2022).

The biomass of the cephalopod community was found to be very influenced by environmental drivers, which had a marked geographical

effect likely driven by SST. Our results show that SST displays a generally negative relationship with cephalopod biomass, with the colder areas of the Western Mediterranean having more biomass than warmer ones consistent with recent studies (Schickele et al., 2021). Interestingly, in areas such as the Portugal shelf the trend is inverse to our observations, yet it shares a similar threshold of change at 17 °C in surface waters for *L. vulgaris* (Moreno et al., 2014). In the Mediterranean area, differences in responses between cephalopod taxa were also noted with some species associated to cooler waters, while others thrive on warmer environments (Keller et al., 2017b; Puerta et al., 2014). These variations in the non-stationary environmental effects among species could affect the response of the overall group related with the variation of species composition of cephalopods community in different areas, and ultimately limiting a regional global response of the cephalopods community to warming.

Cephalopod biomass appears to be positively influenced by crustacean biomass, showing a close link between cephalopods population and prey availability. It is consistent with species-specific relationships of cephalopods in our study area (Puerta et al., 2015), being notable that prey and predators have similar spatial patterns as it can be seen as well in GSA7. Biomass of predators (fishes) also result in higher biomass of cephalopods, reaching an optimum at intermediate values, which could suggest that higher values could keep stable cephalopod biomass likely due to high pressure from predators (Bakun and Csirke, 1998). Although we here considered crustaceans as the prey item of cephalopods, larger species (specially squids) may also tend to prey more on fishes in oceanic ecosystems (Lordan et al., 1998). However, at a Mediterranean scale, previous studies supports that even on relatively large species, crustaceans are present to some degree on their diet (Puerta et al., 2015). Previous research and the smaller sizes of the cephalopod species found in the study area may support that the proportion of piscivory might not be high enough to alter the results and their interpretation in the present study.

The biological and environmental drivers on mean size, meaning the high biomass of crustaceans, high B_{pred} of fishes and low primary productions, are similar to those observed in the Eastern Mediterranean (Arvanitidis et al., 2002). However, it is possible that the negative relationship between mean size and Chl-a could be due to an indirect effect of fishes over cephalopods. As observed at species level, it could be a consequence of the competition with other fishes during paralarval phases (Keller et al., 2017b; Puerta et al., 2015), decreasing food availability and therefore limiting survival and growth. This would also be especially notable in areas with high SST, which increases growth rates on hatchlings at the cost of shortening maturation and lifespan (Hatfield, 2000; Pecl and Jackson, 2008). On such systems and with reduced food availability, paralarvae do not benefit from the faster metabolic rates resulting in a smaller size at adulthood (Pecl and Jackson, 2008; Pierce et al., 2008; Xavier et al., 2016). At a community level, lower mean size seems to suggest that there are more small-sized species in those areas, where fish B_{pred} is lower. Small cephalopods, such as sepiolids or the genus *Allotheutis*, are present on the diet of more fish species than larger cephalopods, thus fish predation or its reduction would play a bigger role in their dynamics (Daly et al., 2001; Velasco et al., 2001). We can also remark the possible contribution that recruits may have on our selected indicators. As seasonal recruitment peaks of some species occur during the sampling season, between May and June (Pierce et al., 2010; Tursf et al., 1995) and also has shown spatial variability between areas due to regional environmental conditions (Puerta et al., 2016b).

TL_{3,25} was found to be associated to low biomass of crustaceans as well as areas with low ratios of predator fishes. The trophic level of TL₄ was also related to low biomass of crustaceans. The reason behind could be the competition with fishes as well as their possible predation pressure. The observed decline of fishes due to high exploitation levels would indirectly favour higher trophic levels in cephalopods, especially as seen with TL_{3,25} (Caddy and Rodhouse, 1998; Coll et al., 2010; Hastie

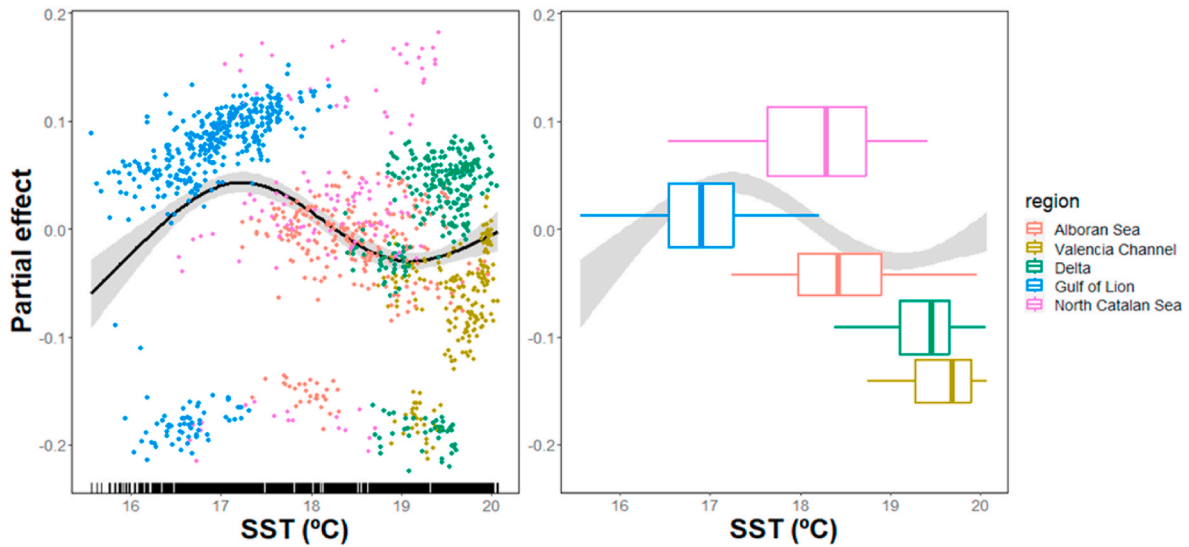


Fig. 4. Residuals (left) and boxplots (right) of the partial effect of SST on the Jaccard index. The shaded areas of the partial plot indicate the 95% confidence interval.

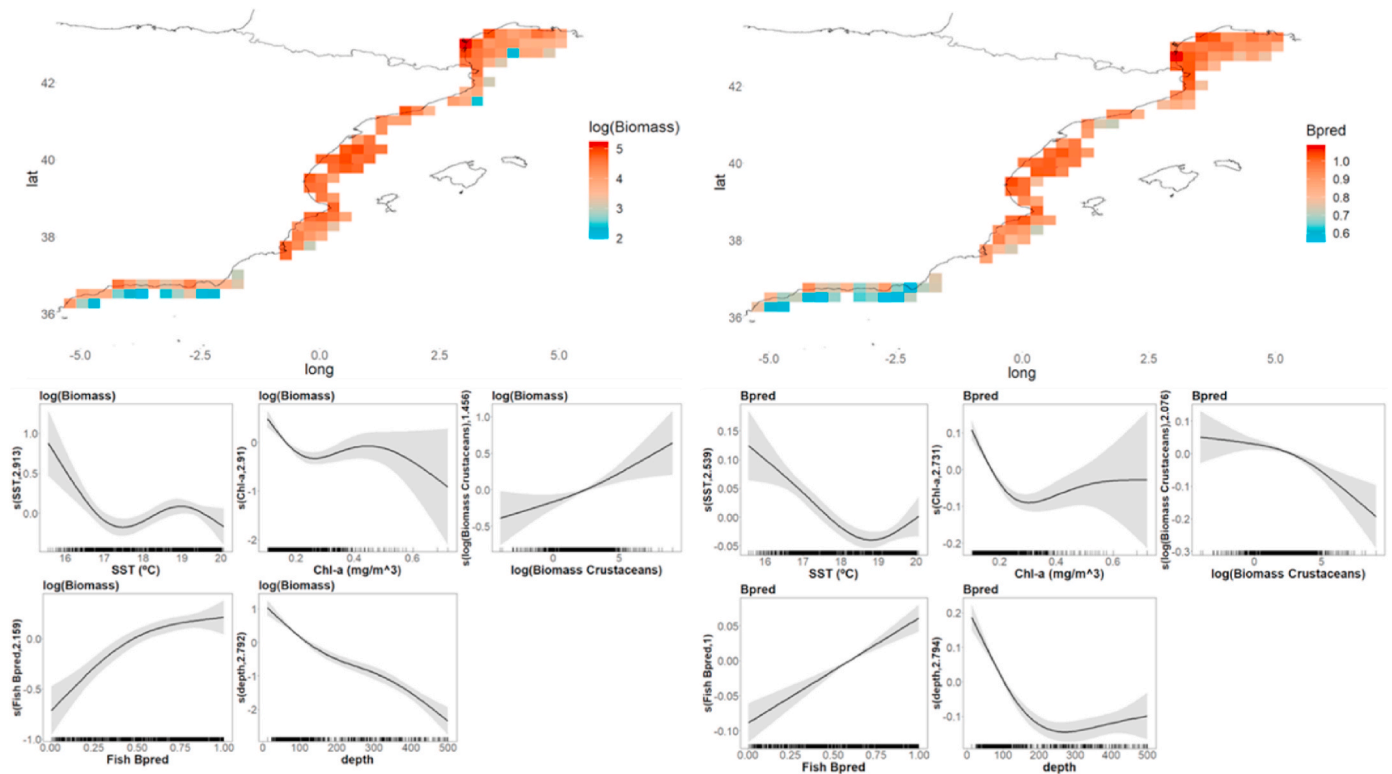


Fig. 5. Spatial variation and smoothing effect of the of Biomass (log scale, left) and Bpred (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

et al., 2009; Pennino et al., 2017). This may support the hypothesis of the cephalopod replacement in response to the removal of fishes, especially at high trophic levels.

Out of all drivers, fishing effort was the least influential driver as it only showed significant effects on the β -diversity. In general, cephalopods seem to be less sensitive to direct human local impacts than to environmental ones, which may be linked to their short life strategy that also make them less susceptible to be affected by the continuous pressure of fishing (Quetglas et al., 2016). The biology of this group becomes both an advantage and a hindrance, as this greater dependence on environmental factors can make them more susceptible to climate

variations. One example could be warming, which has been shown to affect cephalopods at species level (Forsythe, 2004; Georgakarakos et al., 2002; Xavier et al., 2016), and at a community level in this study. The response observed to an increasing SST is either negative for some of the key indicators, such as the total biomass of cephalopods or the biomass of predatory cephalopods, or becomes negative after reaching certain temperature threshold like in mean size. It is worth to acknowledge, however, that in the case of this last indicator it could be also caused by peaks in recruitment of species like *Eledone cirrhosa* (Tursi et al., 1995), which are also fairly abundant in our data. This is especially relevant in our study area, as northward migrations and

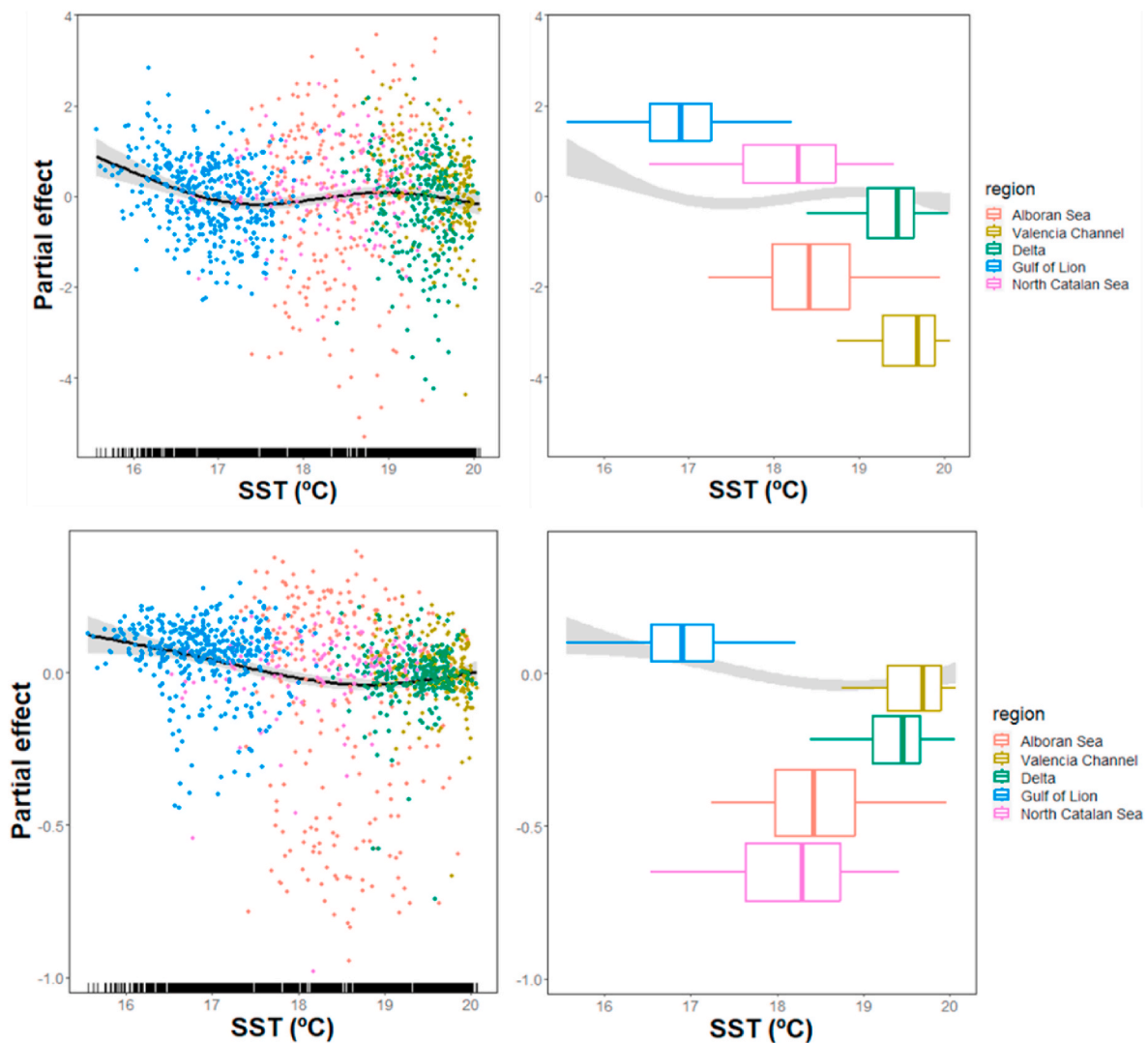


Fig. 6. Residuals (left) and boxplots (right) for SST of the Biomass (log scale, upper row) and B_{pred} (lower row) models. The shaded areas of the partial plot indicate the 95% confidence interval.

expansions in response to increasing SST (i.e. meridionalization) are limited by landmass on the Gulf of Lion region.

The selection of indicators shown in this manuscript also responds to the need of the EU's Marine Strategies Framework Directive (MSFD) to assess the state of marine communities. These ecological metrics were complementary to some of the proposed descriptors within the framework, specifically for D1 and D4 related to both biodiversity as well as trophic ecology (IEO and MAGRAMA, 2012a; 2012b). This study takes into account some indicators not considered in the current MSFD work, such as the β -diversity, that can be useful to better understand the different components of biodiversity from local to regional scales. Other chosen indicators correspond to already established metrics and objectives. For instance, B_{pred} is equivalent to the descriptor 4.2 (proportion of species on high levels of the trophic chain). Meanwhile, trophic level indicators help to assess the state of the trophic chain of the taxa of study. Overall, the use of various indicators highlights the relevance of our study to inform future policy recommendations.

Our results also call for caution when referring to cephalopods as general winners to expected warming. While they have been thriving compared to other taxa such as fishes, and in spite of their opportunistic lifestyle, the observed responses of indicators to SST suggest that detrimental effects could be expected, particularly in geographically localized areas with higher warming. Based on our results lower values

of biomass, mean size and ratio of predator species could be observed in the aforementioned areas. It is also important to consider that this study reflects the mean response for the entire Cephalopoda class, therefore differences between species sometimes turn into opposite responses to the same environmental pressures attending to their life history characteristics (e.g. benthopelagic or benthic habitat), as it is the case of *Illex coindetii* and *Eledone cirrhosa* (Puerta et al., 2014). On the Western Mediterranean basin, the squid was associated with colder waters while the aforementioned octopod was seen to displace towards warmer environments. This is also relevant in terms of fisheries management as the increase in fishing effort might affect cephalopod communities by changing their relative species composition with a differential effect of those inhabiting in the benthic or the pelagic realm.

It is worth noticing that our results may represent a snapshot of the community since the MEDITS data samples are only from one season (in the summer, between May and June). Some of the considered factors have shown different effects during summer and winter on some cephalopod species. For example, significant effects of primary production were reported on warmer seasons for two cephalopod species while fisheries played a significant role in their winter distribution (Llor-et-Lloret et al., 2021). Thus the spatial distribution of the indicators could vary along the year showing seasonal patterns of migration due to some species tend to move towards northern regions during summer

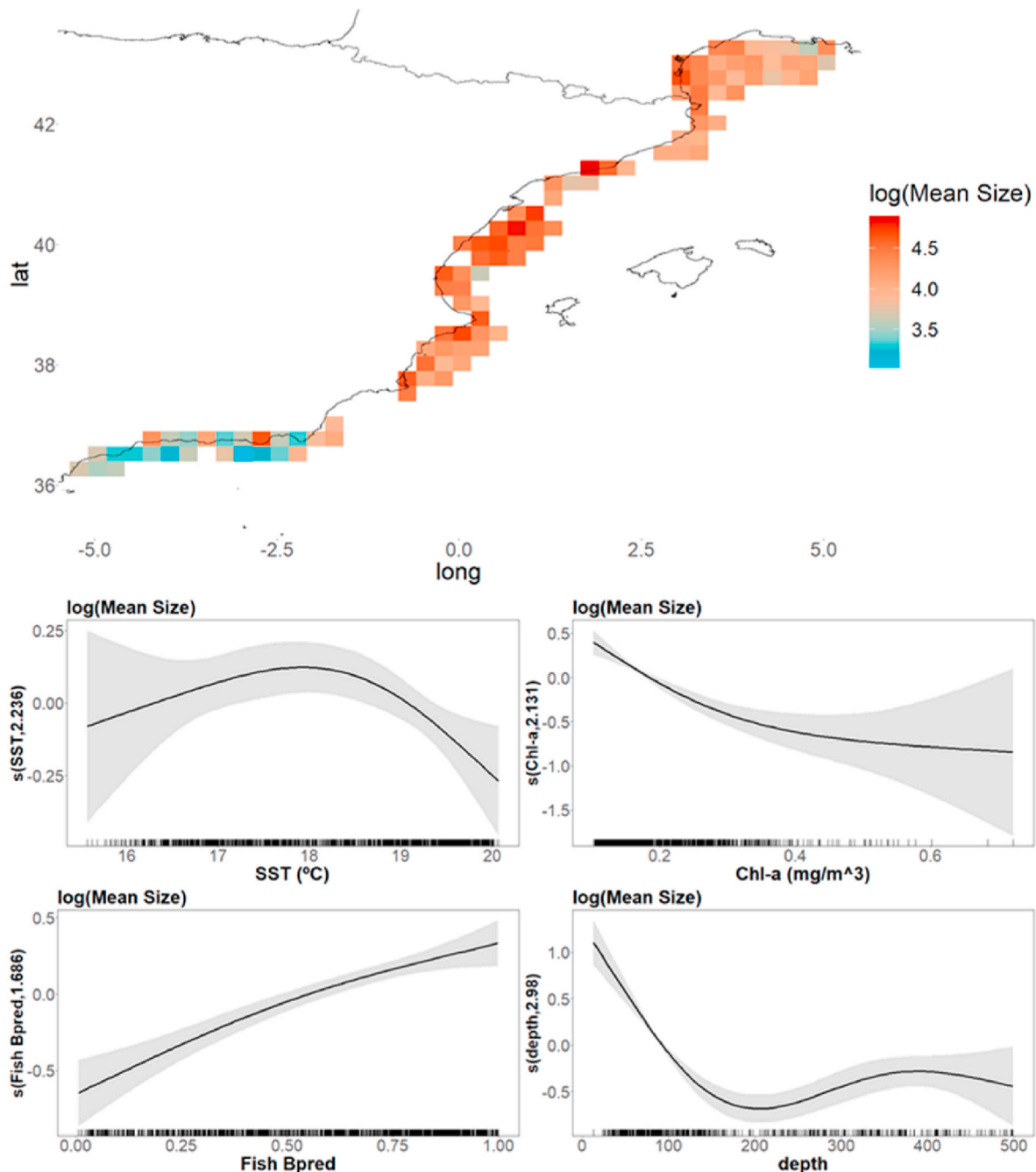


Fig. 7. Spatial variation and smoothing effect of the Mean Size (log scale). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

(Lloret-Lloret et al., 2021; Vilas et al., 2019), while it is also possible that the seasonal turnover of species may maintain the community properties and indicators stable (Moranta et al., 2008). Changes in community composition have not been studied as this work only aimed to analyze the cephalopod community as a whole. Despite this, the results might still hint at some changes in the composition of this subset of the Western Mediterranean community. Forecasts of future scenarios would be difficult as other possibly influential drivers (such as stratification of the water column), as well as the potential adaptive processes of the different species have not been taken into account (Hidalgo et al., 2018).

In summary, we have been able to describe relationships between key aspects of the cephalopod ecology with environmental, human and biotic drivers of change. Our results highlight that the cephalopod community of the Western Mediterranean will likely continue to change,

mainly due to changes in environmental conditions related to climate change, such as an increase in sea warming or changes in primary production. However, these changes will not necessary result in boosted cephalopod populations. Drivers related to the structure of the biotic community, such as prey availability and the concurrence of competitors, can also influence cephalopods future dynamics, illustrating that this taxon is highly dependent to different ecosystems compartments and the whole ecosystem structure and functioning. We conclude that to ensure a sustainable fisheries management of the cephalopods community within the study area an ecosystem-based approach is needed, considering the subregional differences within larger regions.

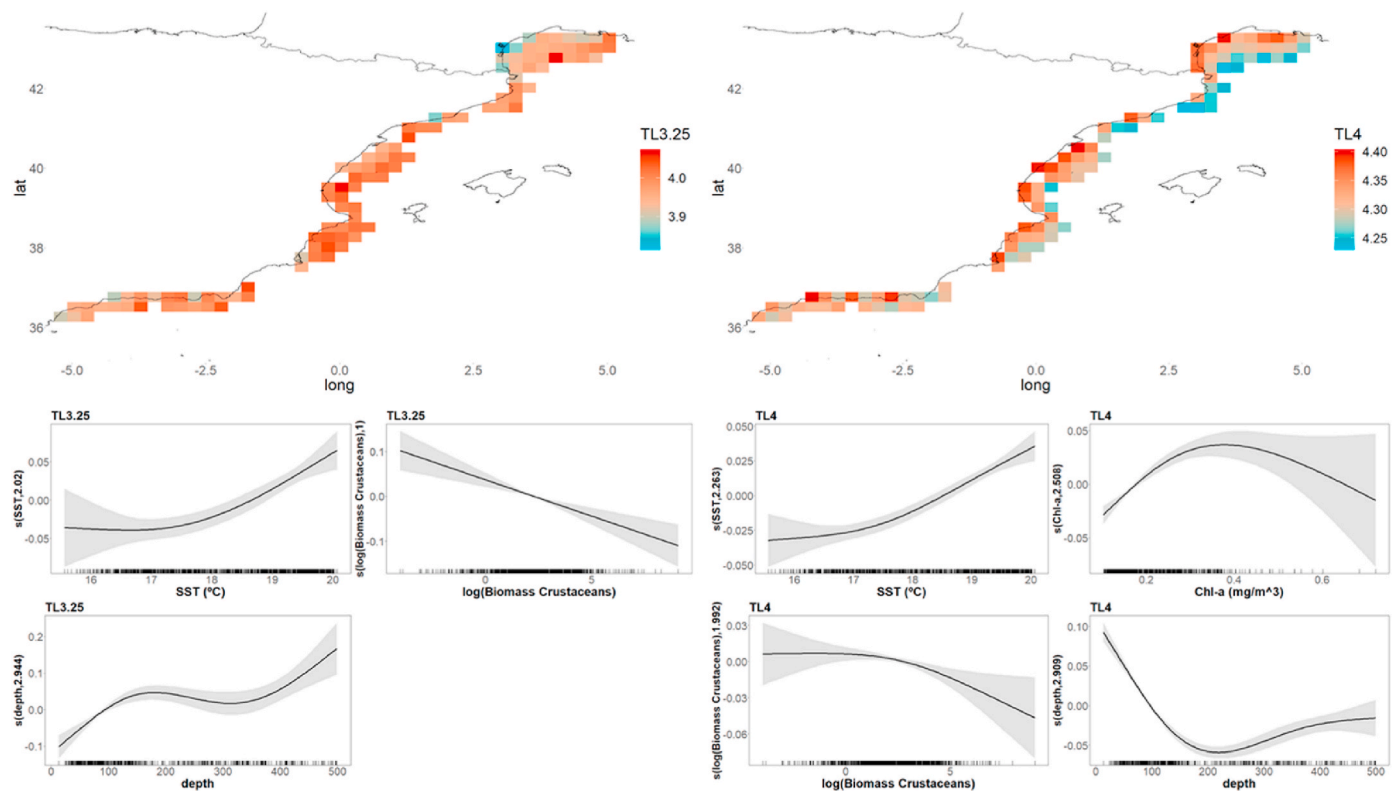


Fig. 8. Spatial variation and smoothing effect of mean trophic level above 3.25 (left) and 4 (right). Dashed areas indicate the 95% confidence intervals and the Y axis indicates degrees of freedom of the smoother.

CRediT authorship contribution statement

Carlos Veloy: Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marta Coll:** Data curation, Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Maria Grazia Pennino:** Investigation, Resources, Writing – review & editing. **Encarnación García:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Antonio Esteban:** Resources. **Cristina García-Ruiz:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Gregoire Certain:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Sandrine Vaz:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Angélique Jadaud:** Investigation, Resources, Writing – original draft, Writing – review & editing. **María González:** Writing – original draft, Writing – review & editing. **Manuel Hidalgo:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Conceptualization, Data curation, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2024.106478>.

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