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EFECTOS DEL CAMBIO CLIMÁTICO Y LA PESCA SOBRE LOS ECOSISTEMAS DEMERSALES

UNA APROXIMACIÓN AL IMPACTO DE LAS PRESIONES ANTROPOGÉNICAS EN LAS COMUNIDADES DEL MAR CANTÁBRICO Y EL MEDITERRÁNEO ESPAÑOL

PhD THESIS

EFFECTS OF CLIMATE CHANGE AND FISHING ON DEMERSAL ECOSYSTEMS

AN APPROACH TO HUMAN IMPACTS ON NORTH EAST ATLANTIC AND SPANISH MEDITERRANEAN COMMUNITIES

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I dedicate this work to every person concerned about achieving a sustainable, healthy relationship with the global ocean.

PREFACE

This thesis was submitted as part of the requirements for the achievement of the degree of Doctor of Philosophy (PhD) at the Universidad de Cantabria (UNICAN). The research presented in this thesis was carried out in the Oceanographic Center of Santander of Instituto Español de Oceanografía (CSIC), between March 2019 and April 2023. The thesis was supervised by Dr. Antonio Punzón. The pre-doctoral contract that enabled the completion of the PhD study was funded in its most part by the Government of Cantabria, with additional support provided by the Instituto Español de Oceanografía within the CICLICA project, which also sponsored a research stay at the University of Trømso (UiT, Norway), in collaboration with Dr. Laurene Pecuchet and Dr. Raul Primicerio. This contract also made possible the participation in other national and international projects such as the ERDEM project (Assessment of Demersal Resources through Direct Methods in ICES areas), Marine Strategies Framework Directive (MSFD), INTEMARES, VADAPES, IMPALHA and the ICES working group COMEDA.

SUMMARY OF CONTENTS

This thesis has investigated the response to climate change and fishing of the marine communities inhabiting the bentho-demersal realm of Cantabrian and Western Mediterranean seas, northern and eastern coasts of Iberian Peninsula. Chapter 1 provides a general background for the research, by discussing the context in which its hypotheses were raised, the state of the field of knowledge and a broad description of the study areas. Chapter 2 introduces the research by explaining the construction of a community index from the most explored ecological trait of a species distribution, the temperature of affinity. Through the study of other ecological features of the community, Chapter 3 approaches the Spanish Mediterranean and Cantabrian communities' biogeographical evolution in space and time. Whereas Chapter 4 explores past trends of a selection of fish species in Cantabrian bentho-demersal community and its resilience dynamics leading to abrupt reorganizations, Chapter 5 goes into the spatio-temporal dynamics of the communities' sensitivity to both fishing and warming. Chapter 6 briefs the main conclusions reached by the different studies of the thesis and Chapter 7 contains the bibliography examined for its completion.

RESUMEN

En los últimos años, el calentamiento global ha sido confirmado como uno de los factores ambientales con más influencia en la reorganización de las comunidades marinas. Además, éstas están expuestas a otras presiones de origen ambiental o antropogénico, entre las que destaca la presión pesquera. Para conservar el buen funcionamiento de los ecosistemas marinos y facilitar un uso sostenible de los servicios que proveen es necesario que su gestión se realice desde un enfoque ecosistémico. Este tipo de gestión debe apoyarse en estudios científicos que aspiren a entender, cada vez mejor, los procesos que subyacen a dichas reorganizaciones ecológicas. Esta tesis contiene varias aproximaciones en esta línea de investigación, analizando la conexión entre los cambios composicionales observados en las comunidades y el desplazamiento de las especies en busca de sus condiciones ambientales óptimas, atendiendo también otros mecanismos ecológicos que se encuentran tras estos cambios, en concreto, aquellos relacionados con la sensibilidad y la resiliencia de las comunidades.

Ante los niveles actuales de calentamiento, las comunidades bentónicas y demersales se están viendo cada vez más dominadas por especies de afinidades térmicas altas, ya sean de origen alóctono o autóctono. Estos procesos se han denominado "tropicalización" y "meridionalización", respectivamente. Los desplazamientos motivados por el seguimiento del nicho térmico preferido por las especies no sólo se reflejan en la temperatura de afinidad de las comunidades, sino también en otros indicadores ecológicos como la salinidad, la latitud, la profundidad o los rangos de distribución. Un estudio sobre la *Community Weighted Mean Temperature* (CWMT o Temperatura Media de la Comunidad), un indicador que permite analizar la relación entre la preferencia térmica de las comunidades de peces demersales y la temperatura ambiental, posibilitó la identificación de cierta variabilidad espacio-temporal coherente con el proceso de calentamiento del Mar Cantábrico (sur del Golfo de Vizcaya). En esta región, una clasificación de los lances de más de tres décadas de campañas oceanográficas anuales, en base a la CWMT, discriminó las comunidades en tres tipos: cálidas, templadas y frías. Mientras que el área ocupada por las comunidades cálidas se ha expandido, las comunidades más frías se han contraído. Como este indicador pareció reflejar fielmente las dinámicas de la comunidad en cuanto a la temperatura ambiental, su estudio fue complementado con la exploración de la media y la varianza a nivel de comunidad de otras propiedades ecológicas del nicho de las especies, en este caso relacionadas con la posición media de las especies en latitud y profundidad así como los valores medios de la salinidad, la temperatura superficial preferida por las especies y sus rangos de tolerancia térmica. En este estudio se analizaron las comunidades demersales de dos ecosistemas regionales en el Mar Cantábrico y el Mar Mediterráneo español, caracterizados por una distinta exposición al calentamiento de las aguas. El estudio de los distintos indicadores mostró cómo los procesos de tropicalización y meridionalización de ambas comunidades se parecen en varios aspectos, pese a ciertas diferencias regionales. En

las últimas décadas, la contribución relativa de especies con rangos de tolerancia térmica amplios y mayores distribuciones en latitud ha aumentado en las comunidades demersales del Cantábrico. De la misma forma, y en lo que hemos considerado una posible señal de una "flexibilización" de las comunidades, la tropicalización de las comunidades mediterráneas está caracterizada por un aumento relativo de los rangos de distribución más amplios.

La interacción entre el cambio climático y la pesca en áreas explotadas se suma a la lista de factores estresantes como otro elemento generador de cambio. Esto complica esclarecer de una manera exacta los mecanismos de respuesta de los ecosistemas a las presiones a las que se ven sometidos. Cuando estos dos procesos se dan al mismo tiempo en un mismo lugar, eventualmente generan cambios en la composición específica de las comunidades marinas, así que, para aproximarnos a los posibles efectos combinados del cambio climático y la pesca en el Mar Cantábrico, analizamos la evolución temporal de la comunidad de peces demersales en el período 1983-2018. Las dinámicas temporales observadas fueron asociadas a las de la actividad pesquera y una selección de factores ambientales en la zona. A través de análisis multivariante y modelado aditivo y no aditivo, se estudió un índice de la comunidad, en el que se identificaron al menos dos regímenes ecológicos distintos que fueron interpretados como la respuesta no lineal de una comunidad templada a su contexto ambiental. El marco de un *Integrated Resilience Assessment* (IRA o Evaluación Integrada de la Resiliencia) sirvió para evaluar el mecanismo de respuesta del sistema a sus principales presiones ambientales y antropogénicas. Un importante declive en la presión pesquera en el área de estudio después de los años 90 fue asociado a una transición gradual de este sistema biológico, erosionando a largo plazo la resiliencia del sistema a sus estresores externos, lo que alrededor de 2010 supuso un cambio de régimen ecológico abrupto y, probablemente, irreversible.

Por último se estudiaron los patrones espacio-temporales de la sensibilidad al calentamiento y a la pesca de arrastre de las comunidades cantábricas y mediterráneas. En una aproximación preliminar para identificar las comunidades más sensibles y comprender sus mecanismos de respuesta a los principales impulsores del ecosistema demersal, se llevó a cabo una evaluación basada en el marco de un *Vulnerability Assessment* (VA o Evaluación de la Vulnerabilidad). Este estudio reveló un cambio en la composición de las comunidades en cuanto a sus especies más sensibles. Hasta el comienzo de la década de los 2000, en la región cantábrica, las comunidades bento-demersales experimentaron un aumento relativo de las especies sensibles a la pesca, paralelamente a una disminución de las especies más sensibles al calentamiento. Los indicadores de sensibilidad en las comunidades cantábricas muestran valores relativamente altos, en contraste con los de las comunidades mediterráneas españolas, que han experimentado una disminución abrupta en la abundancia relativa de las especies sensibles a cualquiera de las dos presiones, estabilizándose después del año 2000 con respecto a la sensibilidad de las comunidades al calentamiento, pero no a la pesca. La pérdida de las especies más vulnerables, más acentuada en la región mediterránea, se presenta como un hallazgo esperable en un ecosistema obligado a lidiar con una alta inestabilidad ambiental. Los resultados de este estudio han permitido plantear nuevas preguntas de investigación y han servido para destacar el valor de utilizar un enfoque basado en los atributos funcionales de las especies en vez del enfoque taxonómico, a la hora de analizar los componentes de la vulnerabilidad de los sistemas biológicos.

Esta tesis muestra lo intrincadamente que las comunidades marinas están sujetas a su ambiente y a variables antropogénicas, cuyo efecto se traduce en las preferencias ambientales de la comunidad, así como en su composición taxonómica y funcional. Estos efectos a menudo han supuesto respuestas abruptas del ecosistema y por todo ello, esperamos que los estudios aquí contenidos sirvan de base para futuras investigaciones y, en última instancia, ayuden a informar mejor las decisiones de una gestión con enfoque ecosistémico, que facilite una relación más sostenible con los océanos.

ABSTRACT

Global warming is at present an undeniable driver of marine communities' reorganizations. Marine ecosystems are also exposed to other pressures of environmental and anthropogenic origin, among which the many forms of fishing stand out. In order to protect the functioning of these ecosystems and allow a sustanaible access to the services they provide, a well informed ecosystem-based management depends on the sustained generation of scientific assessments. This thesis aims at a better understanding of the processes that underly such reorganizations through different approaches, by analyzing the connection between observed compositional changes and the species tracking of their preferred niche conditions, and by examining other ecological mechanisms that underlay such changes, in particular those related to the marine communities' sensitivity and resilience.

Under the current levels of warming, benthic and demersal communities are experiencing processes of tropicalization and meridionalization, becoming increasingly dominated by species of warmer affinities. The species tracking of their preferred thermal niche does not only reflect in the communities' preferred temperature, but might also mirror in other ecological indicators such as the preferred salinity, latitude, depth and ranges of distribution of the biotic assemblages. A study carried on the Community Weighted Mean Temperature (CWMT), an indicator that allows linking the thermal preference of demersal fish communities with environmental temperature, has allowed the identification of relevant spatio-temporal variability coherent with the warming trends of the Cantabrian Sea (Southern Bay of Biscay). In this region, a classification based on the CWMT discriminated three communities: warm, temperate and cold. While the area occupied by the warm communities has expanded, the cold communities have contracted. As this indicator seemed to properly capture the community dynamics regarding environmental temperature, its study was complemented by exploring the mean and variance of other ecological traits, this time related to the mean position of the species in latitude and depth, as well as to the mean values of the species preferred salinity, temperature at bottom and ranges of thermal tolerance. This study, that covered two regional ecosystems in the temperate East-Atlantic and the Mediterranean Sea, characterized by a distinct exposure to warming, revealed the two communities' tropicalization procceses resemble in many respects, with regional differences that regard not only mean values but also the variance of the communities' ecological preferences. In the last decades, the bentho-demersal communities inhabiting the Cantabrian Sea have accommodated higher abundances of species with wider thermal ranges of distribution and species with wider areas of distribution in latitude. Similarly, in what we have considered part of a 'flexibilitation' process, the tropicalization experienced by Mediterranean communities features a general widening of the community's ecological ranges.

The interaction between climate change and fishing in exploited areas adds up to the list of community stressors as an additional driver of change, making the unraveling of response mechanisms a complex matter of study. The co-occurrence of these processes eventually induces changes in the specific composition of marine communities, so, in this sense, the temporal evolution of the demersal fish community of Cantabrian Sea in the period 1983-2018 was analyzed and the observed dynamics were associated to those of fishing and a selection of environmental features in the area. A community index was explored through multivariate analysis and non-additive modeling, revealing two distinct decadal-scale regimes that suggested a non-linear response of the community to its environment. The Integrated Resilience Assessment framework enabled the approach to the response mechanism of the system to its main environmental and anthopogenic stressors. An important decline in fishing pressure in the studied region after the 1990s was associated with a gradual transition of this biological system, which further on could have eroded the system's resilience towards its external stressors, leading to a discontinuous response expressed as an abrupt, possibly irreversible shift in the 2010s.

Finally, the spatio-temporal patterns of the Cantabrian Sea and Spanish Mediterranean communities' sensitivity to fishing (i.e., trawling) and warming were studied. As a preliminary attempt to identify the most sensitive communities and understand their response mechanisms to the demersal ecosystem's main drivers, a straightforward assessment based on the Vulnerability Assessment framework, revealed a turnover in the communities' composition in terms of their sensitive species. Until the beginning of the 2000s decade, in the Cantabrian region the bentho-demersal communities have experienced a relative increase of species sensitive to fishing, paralleled by a decrease in those more sensitive to warming. The sensitivity indicators in the Cantabrian communities show relatively high values, contrastingly to those of the Spanish Mediterranean communities, which have experienced steep decreases in the relative abundance of sensitive species to either stressor, stabilizing after year 2000 respecting the communities' sensitivity to warming, but not to fishing. The loss of the most vulnerable species, more accentuated in the Mediterranean region, comes up as an expected finding in an ecosystem compelled to cope with high environmental instability. The findings of this study allowed raising new research questions and have highlighted the value of using trait-based approaches to analyze the vulnerability components of a biological system.

This thesis shows how intricately marine communities are subject to their environmental and anthropogenic drivers, whose effect can be noticed in their niche related features and in their trait and species composition. These effects often lead to wide ecosystem responses; therefore, the studies contained here will hopefully serve as basis for future research and ultimately help scientists better inform ecosystem-based management decisions that allow a sustainable relationship with the oceans.

LIST OF PUBLICATIONS

This PhD thesis is based on the following research articles and scientific conference contributions:

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The following publication represents a minor contribution to the research of this thesis and was not included as an independent chapter:

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TABLE OF CONTENTS

CHAPTER 1. INTRODUCTION TO THE RESEARCH 16

1.1 Motivations of the research 16

1.2 State of the art 21

1.3 Study areas 25

1.4 Objectives of the thesis 33

CHAPTER 2. TRACKING CLIMATE DRIVEN RANGE SHIFTS: COMMUNITY WEIGHTED MEAN TEMPERATURE (CWMT) 36

2.1 Introduction 36

2.2 Material and methods 37

2.3 Results 40

2.4 Discussion 46

2.5 Supporting information 50

CHAPTER 3. ATLANTIC AND MEDITERRANEAN COMMUNITIES' CLIMATE DRIVEN RANGE SHIFTS 56

3.1 Introduction 56

3.2 Material and methods 58

3.3 Results 61

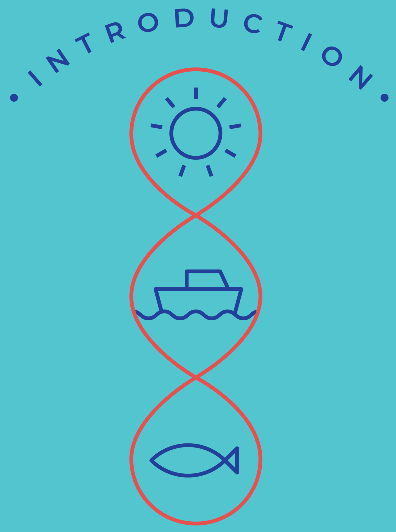
3.4 Discussion 68

3.5 Supporting information 74

CHAPTER 4. ANTHROPOGENIC DRIVEN TRANSITIONS IN THE DEMERSAL ECOSYSTEM OF CANTABRIAN SEA 82
4.1 Introduction 82
4.2 Material and methods 84
4.3 Results 90
4.4 Discussion 97
4.5 Supporting information 103
CHAPTER 5. DEVELOPMENT OF INDICATORS OF THE COMMUNITIES' SENSITIVITY TO CLIMATE CHANGE AND FISHING 114
5.1 Introduction 114
5.2 Material and Methods 116
5.3 Results 125
5.4 Discussion 129
5.5 Supporting information 135
CHAPTER 6. CONCLUSIONS 144
6.1 Shifting spatial distributions 144
6.2 Regime shifts and resilience dynamics 145
6.3 Communities' sensitivity to climate change and fishing 146
CHAPTER 7. REFERENCES 150
ANNEX 1 174

EFFECTS OF CLIMATE CHANGE AND
FISHING ON DEMERSAL ECOSYSTEMS

AN APPROACH TO HUMAN IMPACTS ON
NORTH EAST ATLANTIC AND SPANISH
MEDITERRANEAN COMMUNITIES



CHAPTER

01

INTRODUCTION TO THE RESEARCH

CHAPTER 1. INTRODUCTION TO THE RESEARCH

1.1 MOTIVATIONS OF THE RESEARCH

1.1.1 CLIMATE CHANGE AND FISHING IMPACTS ON MARINE ECOSYSTEMS

Human-induced climate change has driven most ecosystems to accommodate to unprecedented bio-physical conditions. As oceans absorb more than 90% of the energy the Earth system cannot balance, they buffer the impacts of warming on terrestrial ecosystems. As a direct consequence of the Earth's Energy Imbalance absorption the oceans' heat content and carbon dioxide increases, creating a series of environmental anomalies that widely affect organisms depending on them. The impacts of climate change on marine ecosystems are diverse and have shown to be even faster in marine than in terrestrial systems (Pinsky et al., 2019). The warming of sea surface has not stopped since the 80s, reaching the highest ever recorded levels in year 2021 (Cheng et al, 2022), and even in the most stringent Representative Concentration Pathway (RCPs)[1] and Shared Socioeconomic Pathway (SSPs)[2] scenarios, oceans are expected to continue absorbing heat as a consequence of their large thermal inertia (Yang and Zhu, 2011). In this context of rapidly progressing climate change impacts, considerable scientific effort is being devoted to understanding its effects on marine life, acknowledging the role of human populations both as active drivers of change but also as subject to its outcomes.

Oceans buffering capacity is rapidly decreasing and as a consequence, the continuous take up of CO_2, is expected to accelerate their chemistry change (Jiang et al, 2019). This process will especially affect the most vulnerable marine ecosystems (VME), and those with an eroded resilience. Most future projections anticipate a likely reduction of marine ecosystems' resilience to adjust to climate change impacts, generated by alterations in both the range of environmental factors and their rate of change (IPCC, 2021). Hence the importance of efficiently managing the anthropogenic impact so ecosystems can maintain, and even enhance, their resilience, as has often been pointed out by ecologists (Folke, 2006; Möllmann et al, 2009; Lindegren et al., 2016; Wu et al., 2017). Although the protection of ecosystems through management initiatives such as the establishment of Marine Protected Areas (MPAs) or the reduction of exploitation rates have been evidenced as effective measures in building resilience (Jennings, 2009; Neubauer et al., 2013; Sumaila and Tai, 2020), globally, less than

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[1] RCP-based scenarios are the International Panel on Climate Change's (IPCC's) adopted theoretical greenhouse gas concentration trajectories. They are named RCP2.6, RCP4.5, RCP6.0 and RCP8.5 according to the level of radiative forcing (in watts per square meter, or W m-2) they predict as a result from the scenario by the year 2100.

[2] SSP-based scenarios are the International Panel on Climate Change's (IPCC's) adopted theoretical Shared Socioeconomic Pathway. They describe the socioeconomic trends underlying the RCP scenarios.

8% of the ocean is treated as a Marine Protected Area and almost half of North East Atlantic and 90% of Mediterranean stocks are still nowadays fished unsustainably (Sumaila and Tai, 2020). What is more, according to the IPCC latest Assessment Report (AR), in most protected areas there is not the minimum needed stewardship to contribute to reducing damage from, or increasing resilience to, climate change (IPCC, 2021). Studies and efforts aimed at understanding and securing ecological resilience are still an urgent ingredient for oceans' sustainability.

Climate change impacts often interact with other drivers of communities' variability, either of natural (such as the natural variability of marine currents) or anthropogenic origin. Between the plethora of human pressures acting in combination with climate change over marine communities, the many forms of fishing stand out as the most stressful factors (Pauly et al., 2002), trawling being the central, most impacting gear. In many cases, a climate-driven state of collapse was reached due to a weakening of the system's resilience facilitated by unsustainable fishing (Scheffer et al., 2001; Miller et al., 2010; Möllmann and Diekmann, 2012). As fishing differentially removes large individuals and older spawners from a population, it can impair its biodiversity, reproductive fitness and the average size of the remaining stock. At larger scales, it simplifies marine food-webs, rendering them more vulnerable (Pauly et al, 2002) and when not properly governed, fishing erodes the communities' equilibria and might enable other persistent stressors to drive the system towards unstable statuses (Miller et al., 2010).

In this setting, reliably mitigating the effects of fishing and climate change is limited by the current poor understanding of how anthropogenic stressors and natural disturbance interact to influence ecological processes. Complex interactions between stressors often generate non-linear, additive and synergistic cumulative responses (Levin and Lubchenco, 2008; Wu et al, 2017). To adequately understand the observed changes in marine systems, the modeling of biophysical interactions needs to consider the effects of exploitation and resolve key climate-fishing interactions (Perry et al., 2010). And ultimately, in order to tackle governance, resilience and uncertainty of the interacting impacts between climate change and fishing, research needs to work together with suitable institutional responses.

RESILIENCE AND VULNERABILITY

Resilience is a concept that ecology has inherited from the physics (Holling, 1973).While it can be defined in multiple ways, in this document it is understood as the ability of an individual, a community, or a complex system to maintain its key properties and adaption capacity after an stressful event (Holling, 1973; Scheffer et al., 2001; Folke, 2006). In many studies, it has been considered to be highly related to the occurrence of catastrophic, irreversible shifts, and defined as the amount of disturbance ecosystems can undertake before shifting to alternative states (Gallopín, 2006; Dakos and Hastings, 2013). In Figure 1, its relation to other fundamental concepts in conservation sciences, such as vulnerability and sensitivity, is summarized. The deterioration of resilience leads to the material risk, as ecological thresholds are reached in terms of the ecosystems ability to adapt to changes, and they may be driven towards new equilibria and modes of stability (Scheffer et al., 2009). The switchover of a biological community or a whole ecosystem to a new stable configuration might carry significant losses of ecological and economic functions (Scheffer et al., 2001). An example of this is how a major reorganization of the Mediterranean assemblages in the mid-1990s associated to the synchronicity of changes in the exposure (climatic oscillations) and an erosion of resilience, led to a new functional configuration that conferred the communities a higher sensitivity to regional changes (Vasilakopoulos et al., 2017; Hidalgo et al., 2022c). In this sense, further research on the resilience dynamics of ecological communities specific to each of their stressors is paramount, as well as on their sensitivity to external stressors. These two qualities of the ecosystems combined with information on the degree of exposure to their potential hazards, can assist the identification of communities close to suffering irreversible shifts that need to be monitored as a top priority.

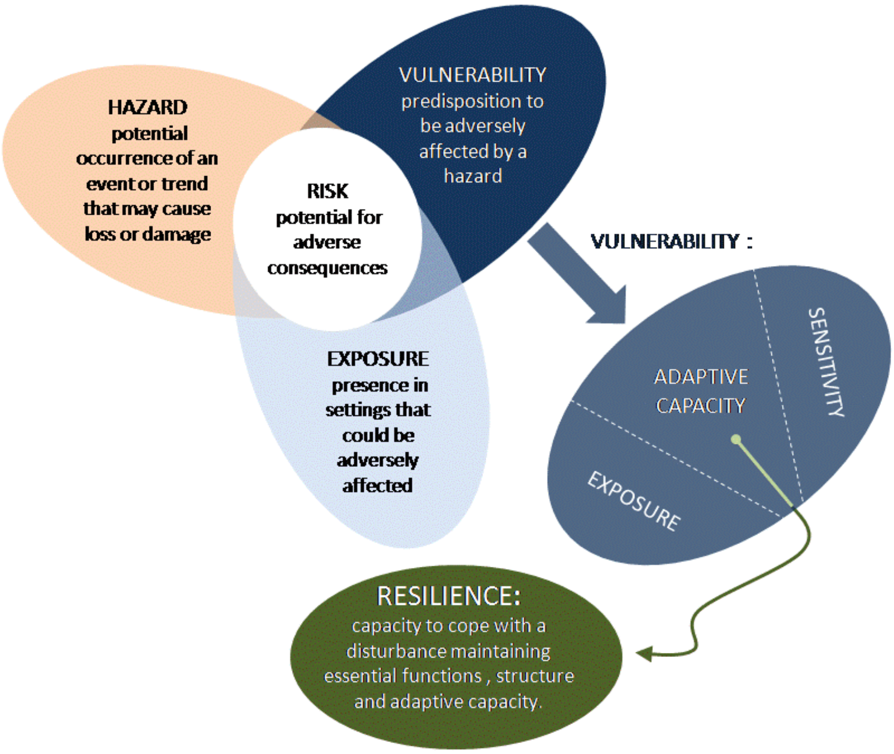


Figure 1. Main elements of the IPCC AR5 conceptual framework linked with the main components of vulnerability and ecological resilience. (Modified from IPCC, 2019)

1.1.2 EFFECTS OF CLIMATE CHANGE AND FISHING ON COMMUNITIES' BIOGEOGRAPHY AND REGIME SHIFTS

The mechanisms of climate-driven changes on marine ecosystems have been widely explored. A classification of these mechanisms in fish populations that could be extended to whole marine communities, categorizes climate-driven impacts as a result of either one or more than one of the following processes: (i) physiological responses to changes in environmental parameters, such as temperature, (ii) behavioral responses, such as distributional range displacements to avoid unfavorable conditions, (iii) population dynamics, such as changes in the rates of mortality, growth, reproduction and dispersal, which could result in the establishment of new populations in new areas, or abandonment of traditional sites, and (iv) wider changes at ecosystem level, i.e. shifts in productivity or trophic interactions (Rijnsdorp et al, 2009). The interaction between climate change and fishing in exploited areas adds up to this list as an additional driver of change, making the unraveling of response mechanisms the complicated matter of study it is. The co-occurrence of these processes eventually induces changes in the specific composition of marine communities. In the research contained in this thesis, we analyzed the connection between observed compositional changes and the species tracking of their preferred niche conditions, but also examined other ecological mechanisms that underlay such changes, in particular those related to communities' sensitivity and resilience.

BIOGEOGRAPHICAL SHIFTS

In reference to the behavioral response of shifting distributions, along the shift of climate zones poleward, entire communities adapt by following their thermal niches, sometimes exploring the limits of their distribution (IPCC, 2021). The joint effect of biological and ecological processes at various organizational levels is behind the displacement of the species centers of gravity towards their mean preferred conditions, changes in populations' spatial distributions, changes in species migration patterns, etc (Perry et al., 2005, Langan et al., 2021). For example, optimum spawning rates of a particular population might be found at a certain spot in its distribution area and minimized at the edges. Species that can disperse will typically respond to warming via abundance changes, depth and geographic shifts (Fossheim et al., 2015), thus, the distributional patterns and rates of shifting ranges are in general species-specific (Pinsky et al., 2013).

The study of the biogeographical affinities of the species shaping a community has shown a useful tool for the identification of the pervasiveness of climate change effects on marine communities (Perry et al., 2005; Poloczanska et al., 2013; Fogarty et al., 2017; Lenoir et al., 2020; Punzón et al., 2021), as well as for the estimation and forecasting of biotic velocities (i.e., the rates of species distribution shifts; Burrows et al., 2014; Alabia et al., 2018; Palacios-Abrantes et al., 2022). But the community's response in terms of its biogeography does not only depend on its species' tracking their preferred niche conditions, but also on the contribution of the species' life history strategies, their size structure and the communities' inner dynamics, which might result in contrasting responses of different communities to similar drivers (Ter Hofstede et al., 2010; Pecuchet et al., 2016; Hidalgo et al., 2017; Hidalgo et al., 2022b). Therefore, detailed evaluations of spatial shifts that aim at unequivocally disentangling the contribution of each factor are critical challenges for evaluating ecosystem's vulnerability to climate changes (Alabia et al., 2018).

REGIME SHIFTS

Depending on the ecosystem's internal structure and level of exposure to external pressures, its response can take different forms, which are ultimately determined byits ability to maintain its equilibria, or, in other words, its resilience. The identification of persistent switches to alternative states, which could imply the loss of the ecosystem's functionalities, is central for a proper assessment of the biological resources prone to be exploited for human leverage. When the reaction of the system takes the form of a sudden, high-amplitude event, and it is detectable in multiple aspects of its physical and biological components, it is considered an ecological 'regime shift' (Scheffer et al., 2001; Collie et al., 2004; Lees et al., 2006). In its more statistical expression, it consists of a transition to a new stability landscape or basin of attraction and its occurrence has important management implications as it has, in many cases, implied irreversible losses.

The quantitative definition of a regime shift carries some controversy, since its occurrence in modeling has been both inferred from smooth, quasi-linear, responses to stressors (Collie et al., 2004), as well as from non-linear, and discontinuous relationships between the forcing and the response variables, the latter being the form most commonly found in literature. The three types of system's response related to regime shifts are illustrated in Figure 2. In summary, when the shift of a complex system is caused by a sudden large external force, it takes the form of a continuous, smooth trend. But when small perturbations cause large changes, it is due to the reach of a tipping point or a system's critical threshold, which might produce an abrupt response. If over a range of external conditions, the system shows more than one stable state, then the system's response is discontinuous. Only in the case of a discontinuous response of the system to its forcing variables, signs of hysteresis can be found (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Lees et al., 2006; Scheffer et al., 2009); hysteresis implies the existence of alternative stable states and it is an attribute of some systems that in the switching to a new stability landscape (or system tendency) retain some of their previous structure, which allows them to recover if the stressor is mitigated. In this last case, the response curve would fold backwards in a fold-bifurcation with two tipping points (Tsimara et al., 2021).

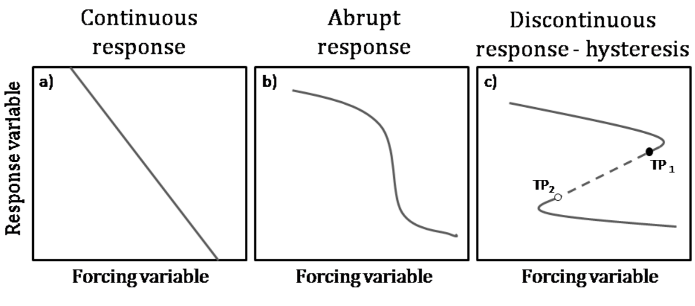


Figure 2. Types of system responses classified as regime shifts. a) A smooth shift. Response is linear and only one equilibrium exists for each condition. b) An abrupt shift. In it there is only one stable state, but the system shows hysteresis: when the initial conditions are restored, the system doesn't recover completely. c) A discontinuous regime shift. The difference with an abrupt regime shift emerges when the forcing variable is reversed (Lees et al., 2006). In these cases, the equilibrium curve is folded

backwards and two stable equilibria can exist for a given condition. TP_1 and TP_2 indicate the critical tipping points, the black circle depicting the critical threshold at which the forward reaction occurs and the open circle the lower critical threshold at which the reverse reaction would occur. The dashed middle section is unstable and represents the border between the basins of attraction of the two alternative stable states, represented by the upper and lower branches. (Modified from Lees, 2006)

1.1.3 SIGNIFICANCE OF THE RESEARCH

One of the most crucial challenges faced by ecologists is the prediction of climate change impacts on ecosystems through the changes in community composition (De Bello et al., 2021). The geographical displacement of communities and the occurrence of ecological regime shifts can have deep implications over global ecological stability, eventually affecting how humans access and make use of ocean services (Palacios-Abrantes et al., 2022). This may go as far as to a point where, facilitated by ecological connectivity, changes at apparently remote or unexploited ecological levels conduct large ecosystem turnovers. Therefore, approaching in the most accurate way how these reorganizations have taken place in the past can help aim for a realistic adaptive management of present and future scenarios. This PhD thesis intends to be a small but significant contribution to the wide field of Quantitative Ecology and Ecosystem Functioning from an Ecosystemic Approach.

1.2 STATE OF THE ART

To approach the state of populations in this thesis we have used geo-referenced abundance data from bottom trawl surveys. Often, marine scientists lack independent population estimates of the species abundances, and the data used for estimating trends which will ultimately be used to support management decisions comes directly from fisheries, instead of scientific surveys.

The analysis of time series is present in most studies of ecosystem's response to external pressures (Jassby and Powell, 1990). Trends in data are typically forced by persistent effects, the modeling of these trends through linear or non-linear, additive and non-additive, fixed or mixed models, typically allows a detailed study of the time series (Zuur et al., 2007). The observation of cyclical and seasonal trends and the identification of non-linearities yield considerable information of a system's inner mechanisms. Together with the identification of spatial effects (such as habitat availability and quality) and intra-population dynamics, tools developed for the study of time series are each day more abundant and informative.

1.2.1 TRAIT-BASED APPROACHES

Trait-based ecology aims to understand how the species characteristics that affect their fitness, and generally measurable at the individual level, influence their ecological roles and their responses to environmental changes (Lavorel and Garnier, 2002; Bremner et al., 2006; Violle et al., 2007). The Biological Traits Approach (BTA) assumes that species that share similar life cycle traits, and reproduction, morphological and behavioral attributes are expected to have similar responses to external stressors, regardless of the taxonomy affinity (de Juan et al., 2020). However, so far, the most common approaches for studying ecosystem functioning and community structure have been taxonomy-based (De Bello et al., 2021). Although the taxonomic approach contributes to this same purpose by observing spatio-temporal changes in species diversity and composition, non-taxonomic approaches can provide a mechanistic understanding of observed ecological patterns and assist studies on these patterns across ecosystems. Trait-based methodologies have assisted research on communities' biogeographical shifts and assessments of vulnerability to pressures such as fishing or climate change.

ECOLOGICAL FEATURES

While not being considered as proper 'traits', as they are not computed on the individual level (see De Bello et al., 2021), species' environmental properties are frequently referred to in literature as 'ecological traits' or 'eco-traits', and as such we have treated them in the present document. The use of environment-species associations has often helped understand the species' displacements due to their biogeographical affinities. A common method for the estimation of species' mean ecological features or environmental preferences is explained in the Material and Methods sections of chapters 2 and 3. Its inference assumes that the ecological niche of a species can be described by its mean position and breadth along various environmental axes (Thuiler et al., 2005). Although this assumption and the application of ecological traits as proxies for a species environmental affinity have been questioned in repeated occasions (Zeleny and Schaffers, 2012; Regos et al., 2019; De Bello et al., 2021 and references therein), their use has shown to be a straightforward approach to assess shifting niches (Arndt and Schembri, 2015; Devictor et al., 2003). At a community level the environment-species associations are often used to investigate the community's turnover regarding changes in its mean ecological features. The use of eco-traits relies on marine organisms being constrained to a specific range of optimal environmental conditions, directly related to a sufficient access to the essential resources of either one of an organism's life processes. An example of this mechanism is the supply of oxygen by ventilation and circulation that can only take place within a species' specific thermal range (Pörtner, 2002; Drinkwater et al., 2010). The most studied environmental preference has undoubtedly been temperature, which comes as the most relevant environmental inductor of distributional changes at large scales (Collie et al., 2008; Cheung et al., 2010, 2013; Punzón et al., 2021; Sanz-Martín et al., *under revision*). Yet, other stressors acting at a more local scale can have a large impact on the community's composition and are too often ignored, whereas to get a more holistic understanding of ecological change it is crucial to study beyond the thermal realm of the niche (Lenoir and Svenning, 2015; Delgado et al., 2018).

TRAIT-BASED VULNERABILITY ASSESSMENTS

With the aim of reducing the impact of fishing and the risks posed by climate change on the most vulnerable species and communities, trait-based approaches to vulnerability were developed. While the modeling of population and environmental data can provide important insights in ecological mechanisms, trait-based climate change vulnerability assessments (CCVAs) are being used to identify the most vulnerable parts of marine systems, including both exploited organisms and exploiting communities (Stortini et al., 2015; Foden et al., 2019; Bueno-Pardo et al., 2021). The vulnerability of a species to a stressor is a function of an external factor, the exposure, and two intrinsic factors, the sensitivityand adaptive capacity of the species, which are determined by biological and ecological characteristics or traits (Butt et al., 2022). Quantifying and projecting the sensitivity and adaptive capacity of the species, assemblages or even habitats, into future scenarios, can ultimately enable the establishment of effective management. Therefore, the interest in trait-based vulnerability assessments to numerous stressors, at many ecological levels and spatio-temporal scales, has increased among managers, planners, policy makers, and researchers.

Frameworks for the assessment of vulnerability to climate change (such as the Climate Change Vulnerability Assessments, CCVA, or the VPWA, when they only consider vulnerability to projected warming) often rely on expert judgment to estimate which characteristics of the species are more related to their vulnerability, such as the level of exposure to environmental change, or their resilience. Independently of the type of trait data used, whether they are qualitative, categorical or quantitative, thresholds need to be defined to determine categories ranked according to sensitivity or vulnerability. Then, trait categories' scores or ranks are usually combined either qualitatively or semi-quantitatively to allocate species into categories of vulnerability (Foden et al., 2019).

In a similar approach, several studies have analyzed communities' sensitivity to fishing impacts through trait-based indices (de Juan and Demestre, 2012; González-Irusta et al., 2018). These indices classify species according to the sensitivity to the fishing activities their traits confer them. The use of expert judgment to score trait categories according to their sensitivity or adaptive capacity carries certain vagueness and uncertainty, as the consideration of an organism as belonging to one or another category and the threshold after which trait values are categorized are sometimes subjective and can vary among studies. Some studies have addressed this issue through bootstrapping (Spencer et al., 2019) or 'fuzzy logic', by which the degree of membership of an organism to one or more than one trait category is defined by a gradation, instead of classifying it as either 'true' or 'false' (Cheung et al., 2005; Jones and Cheung, 2018). However, these approaches are limited by the high degree of uncertainty about the links between species' traits and climate change and fishing impacts, as well as for the lack of high quality, reliable, species-level data for desired traits (Foden et al., 2019).

1.2.2 STUDY OF REGIME SHIFTS AND RESILIENCE

CATASTROPHIC TRANSITIONS AND STUDIES ON RESILIENCE

Regarding the study and forecast of regime shifts, in order to test the existence of alternative stable states in either terrestrial or aquatic ecosystems, researchers most often apply multivariate ordination techniques on time series or spatially aggregated data of one or multiple variables, whether biotic, environmental or both (Möllmann and Diekmann, 2012). Said multivariate methods go from those that apply a dimension reduction on the data series and look for abrupt changes in main tendencies, to techniques specifically designed for the analysis of discontinuities. Among the former, two commonly used reduction techniques for the study of regime shifts are the normalized principal component analysis (PCA), a tool that decomposes the variability of the dataset into new theoretical variables (the principal components or dimensions) (Hemery et al., 2007; Mollmann & Diekmann, 2012; Cabrero et al., 2019; Bode et al., 2020) and the non-metric multidimensional scaling, which rescales data and provides visual representations of similar or dissimilar observations (MDS; Auber et al, 2015; Bode et al., 2020). PCA's new variables are linear but orthogonal composites of the originals and thus, they can simplify complex datasets that include correlated variables. Not only can these new variables be modeled or analyzed with specific regime detection techniques, but their graphical representation often hints for more than one persistent state. Among the techniques specifically designed for the analysis of discontinuities, the chronological clustering is a cluster technique constrained to group sequential samples (Legendre et al., 1985) that has also been applied to detect significant differences between periods in biological or ecological data (Weijerman et al., 2005).

As for formal hypothesis-testing methods used for the analysis of discontinuities, the Sequential regime shift detection method (STARS; Rodionov, 2004) is often found in the literature. The STARS conducts a sequential t-test that signals the possibility of a shift in the mean level or the variance (for which an F-test is then carried). For each new observation STARS performs a test to determine the validity of the null hypothesis, the existence of a regime shift. To avoid spurious detection of regime shifts, all these methodologies (chronological clustering and STARS both explained in more detail in Chapter IV) are commonly used as complementary to each other and to other methods, such as the regime shift analysis (RSA; Ebbesmeyer et al., 1991), Bayesian change-point analyses (Erdman and Emerson, 2007; Kortsch et al., 2012), multivariate multiscale–split moving window boundary analyses (MMS–SMW; Beaugrand & Reid, 2012) and the detection through modeling of significant accelerations in the rate of change of ecological time series (Lindegren et al., 2012 and references therein), among others.

Successfully predicting ecological regime shifts is still a challenge, and it can take many years before a shift can be detected, as different components of the ecosystem sometimes react asynchronously before the ecological response can be detected and understood. The methodologies proposed for this intent aim at a better understanding of the ecological assemblages' internal dynamics as well as the link between the drivers and the system's response (deYoung et al., 2008). This allows the identification of early-warning signals, before the system reaches a critical threshold or tipping point, at which it would abruptly shift. Such signals can take the form of abrupt changes in system indicators, such as diversity indices, the loss of functional diversity, a destabilization of fishing stocks, stepwise changes across different trophic levels, etc (Beaugrand, 2004) but also, as pointed out by Scheffer et al. (2009), a slowing down in the recovery of a system from small perturbations can be an indicator of how close a system is to a tipping point. In this regard, the assessment of a system's resilience comes as a key instrument for the prevention of catastrophic transitions.

Given the difficulty in monitoring natural systems by systematically testing recovery rates, quantitatively evaluating resilience under changing ecological baselines remains an emerging field of study (Scheffer et al, 2009; Wu et al, 2017). Further in this text (Chapter IV), a framework for the evaluation of resilience in a biotic community, the Integrated Resilience Assessment, or IRA (Vasilaopoulos et al., 2017) is explained in detail. The IRA is built on the idea proposed by Van Nes & Scheffer (2007) of directly measuring resilience as the distance of a variable from its tipping point value (Vasilakopoulos and Marshall, 2015). In addition to this, other methods for the evaluation of a natural system's resilience have been developed. Examples found in literature are the previously mentioned identification of a critical slowing down in the response of a system to its stressors (Scheffer et al., 2009), the estimation of the probabilities of population recovery, either experimentally (Dai et al., 2013) or through the simulation of trajectories towards different system states (Mumby et al., 2014), or the ITRA, a variation of the IRA that evaluates the temporal dynamics and resilience of the trait composition of an assemblage (Tsimara et al., 2021).

1.3 STUDY AREAS

The research contained in this thesis are set on two study areas, the Cantabrian and Spanish Mediterranean seas. In order to prevent repetitions, their main characteristics are explained in this section.

1.3.1 CANTABRIAN SEA

The first of the two areas of interest to this thesis' studies corresponds to the northern continental shelf of the Iberian Peninsula (i.e. ICES divisions VIIIc and the northern part of IXa). Although the study area comprises both Cantabrian Sea and Galician waters, for simplicity we have treated the entire region as Cantabrian Sea. It is a region located in the Southern Bay of Biscay, in the temperate North East (NE) Atlantic Ocean. It is a shelf sea that covers an approximate area of 20000 km^2 (Figure 3).

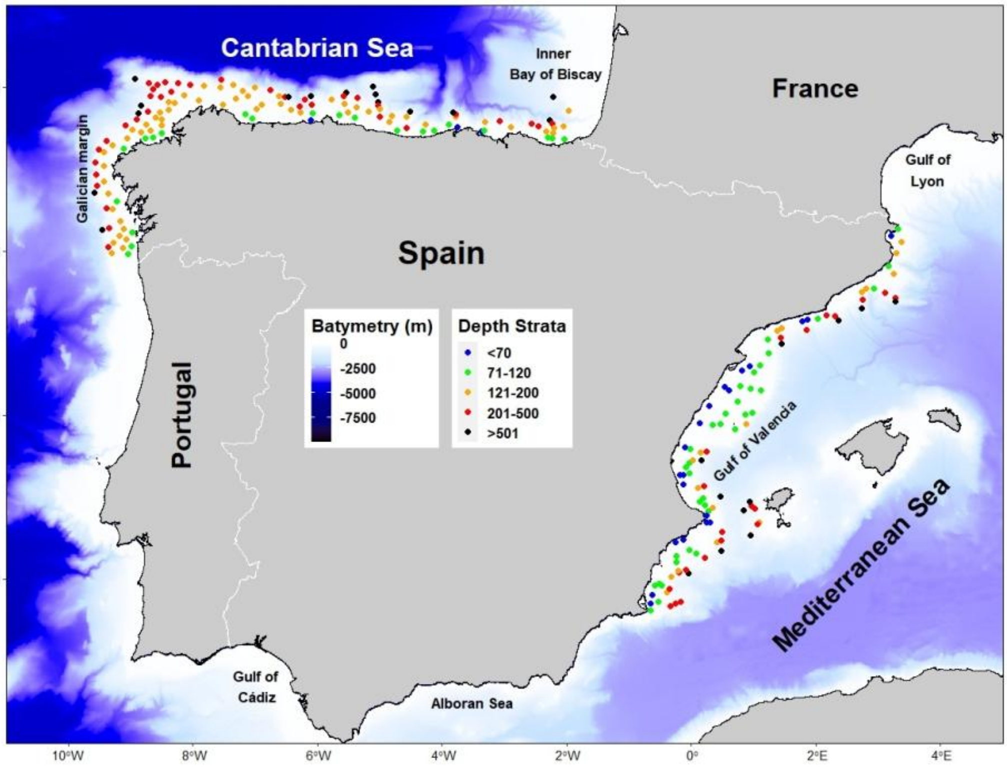


Figure 3.Samples in the study area by depth strata and year (1983 to 2020).

GEOGRAPHICAL, OCEANOGRAPHIC AND ECOLOGICAL CONTEXTS

SEAFLOOR MORPHOLOGY AND GEOLOGY

Cantabrian Sea is characterized by a narrow continental shelf (between 12 and 30 km) and a pronounced transition between the shelf and the deep sea resulting in a steep slope. Due to this area's multiple geographic features, such as capes, estuaries and canyons, the Cantabrian slope is a highly heterogeneous environment (Borja et al., 2019). The type of seabed on the inner Bay of Biscay's shelf is mainly composed of rocky or sandy substrata, muddier towards the outer shelf, while the Galician margin is characterized by fine sands and muddy sand bottoms (Serrano et al., 2008).

OCEANOGRAPHIC AND CLIMATE CONTEXT

The region has a temperate climate, with an annual temperature range around 9.5–12.5°C that increases towards the inner Bay of Biscay, due to this area's warmer summers (Tasker, 2008). The most characteristic oceanographic features over the Southern Bay of Biscay have been related to two important teleconnection patterns, the North Atlantic Oscillation (NAO) and the East Atlantic pattern (EA). NAO and EA are two North Atlantic pressure dipoles, the first often related to extreme climate changes and the second associated to a high degree of variability of sea surface temperature (SST) (Borja et al., 2019 and references therein).

In spring and summer, easterly winds favor coastal upwelling along the coast, with a higher persistence and continuity on the Northwest coast (Galician waters), which makes it a highly productive area (Llope et al., 2006; Gil, 2008).

Warming trends associated to human-induced climate change have been identified in the area both at sea surface and at bottom. They consist in gradual increases that started in the 1980s consequence of an increasing air temperature and insolation (Gómez-Gesteira et al., 2008; Tasker, 2008; Chust et al, 2022). Until the mid-2000s, the North Atlantic basin had experienced the world's greatest warming rates, but shortly after an intense mixing and cooling event in the winter of 2005, during the so-called global warming hiatus, the warming at surface stopped and large amounts of heat were transferred in this basin from upper to deeper levels. This deepening of heat had consequences in the thermohaline properties at every level in the Cantabrian Sea water column (Prieto et al, 2015; Somavilla et al., 2016). After a while, in the first years of the 2010s decade, a freshening originated in North Atlantic waters restored the previous rates of heat absorption at surface and at present, warming of Cantabrian Sea's water column from the surface down to 1000 m is in the order of 0.2 °C (Chust et al., 2022). In addition, in the last decades, extreme events related to precipitation, river flows, extreme wave heights and wind speed have increased their occurrence in the area, although their attribution to climate change has not been confirmed (Chust et al., 2022).

BENTHO-DEMERSAL ECOSYSTEM

The wide range of habitats found in this area is reflected in the biological richness and diversity of the communities inhabiting them. These communities are mostly composed of temperate species, although species characteristic of cold waters (such as Laminariaceae species) are also frequent, as are also warm water species. The latter are mostly found in the south-eastern area of the Bay, including species of Mediterranean origin, due to the warmer summer temperatures in the area (Borja et al., 2019). In general, the biodiversity in coastal areas is higher and more variable, while diversity at the central continental shelf is more stable, probably due to the homogeneity of the continental shelf strata in terms of geomorphology and their greater exposure to trawling pressure (Sánchez and Serrano, 2003).

The bentho-demersal community, which is the focus of the studies in this thesis, encompasses not only the epi- and endo-benthic organisms, but also the demersal species, those related to the sea bottom during the adult stages of their life cycle (Rijnsdorp et al., 2009). In the recent years, the bentho-demersal communities at Iberian Atlantic waters have accommodated climate change impacts in various ways. More than 50% of the demersal species with temperate biogeographical affinities have increased their abundance (Punzón et al., 2016), a process known as meridionalization and further analyzed in Chapters 2 and 3 of this document. The tropicalization of the community, i.e., the increasing occurrence of warm-affinity species of southern and/or tropical origin, has also been evidenced in the area

(Bañón et al., 2010, 2017; Punzón et al., 2016, 2021). Eastward areas, which are less influenced by upwelling, have been associated with a greater risk for fisheries productivity, due to greater warming impacts on the composition and biomass of plankton (Bode et al., 2012; Mendo et al., 2020). Important fisheries in the area are experiencing the effects of oceanographic changes related to climate change and it is projected they undergo further changes. Examples of this are the advancement of anchovy's spawning peak at a rate of 5.5 days/decade and the general increase of its spawning activity, probably associated to shifting phytoplankton abundance (Chust et al., 2011; Erauskin-Extramiana et al., 2019). Similarly, the timing of the peak of catches of Northeast Atlantic mackerel (*Scomber scombrus*) has shifted forward up to a month in the last two decades (Punzón and Villamor, 2009; Rodríguez-Básalo et al., 2022).

ANTHROPOGENIC PRESSURES: FISHING

There is a long history of intense fishing activities in the southern Bay of Biscay (Punzón et al., 2016). The main fishing gears used for demersal and pelagic species are otter and pair trawling, long-line, purse seine and gillnets. The main commercial species fished in the area are anchovy, sardine, hake, horse mackerel, angler and tuna (Mendo et al., 2020; Punzón et al., 2016). As has been observed in other areas of the Northeast Atlantic, several commercial species suffered relevant declines in their stock due to overexploitation, which led in some cases to temporal fishing bans, e.g. the collapse of the anchovy stock in the beginning of the 2000s decade followed by a ban that allowed its recovery (Lazkano et al., 2013). Until the 2010s the yield of fisheries in the Bay of Biscay was sustained by increasing the effort and shifting fishing grounds, heavily impacting the populations, as seen on the reduction of size and mean trophic level of landed fish (Guénette and Gascuel, 2012; Arroyo et al., 2019). However, the enforcement of specific regulations has reduced the mortality of the main commercial species and triggered the recovery of many of the stocks (Modica et al., 2014; Arroyo et al., 2017). By the end of the 2010s decade, bentho-demersal communities in this region were in a much better status (Fernandes and Cook, 2013; Gascuel et al., 2016; Arroyo et al., 2017).

MONITORING PROGRAM IN THE AREA

In Cantabrian Sea, different monitoring programs have been carried out in the last decades, resulting in the availability of long-term series of data. The Cantabrian Sea bentho-demersal community has been sampled every autumn from 1983 to 2022 (with the exception of year 1987) by the Instituto Español de Oceanografía (CSIC) using a standardized methodology (ICES International Bottom Trawl Surveys, ICES, 2017). These surveys follow a random sampling scheme stratified to the area, with three bathymetric depth strata (70–120 metres, 121–200 metres, 201–500 metres) and five geographical sectors delimited by the main geographical features: at the Galician margin, western region of Cantabrian Sea, the geographical sectors are 'Miño River-Cape Finisterre' (MF) and 'Cape Finisterre-Cape

Estacas' (FE), and North of Cantabrian Sea the geographical sectors are 'Cape Estacas-Cape Peñas' (EP), 'Cape Peñas-Cape Ajo' (PA), and 'Cape Ajo-Bidasoa River' (AB) (Figure 3Figure). The sampling unit, also referred to in this text as 'haul', consists of bottom trawls of 30 minutes at 3 knots, using a standard 'baca' 44/60 otter trawl gear with 10 mm cod-end mesh size. The mean horizontal and vertical opening of the net is 18.9 and 2.0 m, respectively. After each haul is performed, every caught species is identified, weighted, counted and measured. Not all species in the community were used in the subsequent studies; therefore, in every chapter's Material and Methods section a brief summary on the survey and the species selection is included.

1.3.2 SPANISH MEDITERRANEAN SEA

The research contained in chapters 3 and 5 of this thesis also looks at ecological processes in the area of western Mediterranean that runs along the Iberian Margin. This area has been treated here as Spanish Mediterranean Sea, and it corresponds to the eastern Balearic Sea associated to the Iberian Peninsula coast, excluding the most southern tail of the Spanish Mediterranean coast, the Alboran Sea. The Spanish Mediterranean is characterized by large-scale environmental gradients, including surface and intermediate water masses temperature as well as diverse primary productivity regimes resulting from the confluence of deep ocean convection from the Gulf of Lion, riverine nutrient inputs by the Ebro river and submesoscale and frontal processes (Ramirez-Romero et al., 2020).

GEOGRAPHICAL, OCEANOGRAPHIC AND ECOLOGICAL CONTEXTS

SEAFLOOR MORPHOLOGY AND GEOLOGY

Northwest Mediterranean has a diverse topography, with canyons, islands, deep areas, and wide shelves (Ramirez-Romero et al., 2020). The continental shelf varies in its width along the Spanish coast (Massutí and Reñones, 2005; Mérigot et al., 2007). For example, at the Gulf of Valencia there is an important accumulation of sediments related to the Iberian orogeny, and a network of canyons runs across it and Catalonia slopes, merging at depth into a channel through which most of the Ebro sediments are transported into the abyssal plain. Towards the French borders, north of the study area, the Gulf of Lion is characterized by numerous canyons that cut into the river Rhone's sediments. These areas have a very diverse geomorpholy that acts as a refuge for spawners of many exploited Mediterranean species (IUCN, 2012).

OCEANOGRAPHIC AND CLIMATIC CONTEXT

Spanish Mediterranean waters have a complex oceanography, with Atlantic surface currents and deep Mediterranean waters coming from the Alboran Sea, south of the study area. High activity fronts (i.e., highly variable heat and wind fluxes) coexist with upwelling areas, rendering significant regionalization and heterogeneity in biological diversity (García-Ruiz et al, 2015; Ramírez-Romero et al., 2020). The confluence of Atlantic waters coming through the Strait of Gibraltar with saltier resident waters from the North, in parallel to the influence of river flows (the Ebro and the Rhone), trigger the relatively high primary production levels in this sub-basin (Hidalgo et al., 2017). The deep ocean convection around Gulf of Lion and the riverine inputs makes the Spanish area of Mediterranean Sea exceptional in terms of secondary production and fisheries (Ramírez-Romero et al., 2020 and references therein).

Partly due to its semi-enclosed nature, the Mediterranean basin is a considered a 'hotspot' of climate change (Calvo et al., 2011). It shows a hydrological residence time of about 100 years, a great capacity to store heat (Marbà et al., 2015) and a warming rate of two to three times the global oceans' (Vargas-Yáñez et al., 2008; D'Amen et al., 2022). Temperature and salinity at intermediate and deep layers of the Western Mediterranean have increased in the last century and warming of these layers accelerated since the 50s. The temperature and salinity trends for the 1943-2015 period at the intermediate layers are 0.002 °C/yr and 0.001 yr^{-1}, respectively, while deep layers have warmed and increased their salinity at a rate of 0.004 °C/yr and 0.001 yr^{-1} (Vargas-Yáñez et al., 2017).

BENTHO-DEMERSAL ECOSYSTEM

Temperature and salinity of the water masses flowing through the Strait of Gibraltar are important drivers of communities' variability in the Western Mediterranean, but the influence of trawling on the composition and diversity of fish and invertebrate assemblages has also been evidenced (Cartes et al., 2009; García-Ruiz et al., 2015; Piroddi et al., 2017). Studies on the Mediterranean's zonation patterns have associated these with different faunistic composition of Mediterranean's assemblages, mostly related to the width of the shelf break and the access to food (García-Ruiz et al., 2015 and references therein). Between the Gulf of Lion (up-north from our study area) and the Strait of Gibraltar (south from our study area) several works have pointed out an increase in number of species with depth until right after the continental shelf (Gaernet et al., 2005; Massutí and Reñones, 2005; Mérigot et al., 2007), after which the relationship between bathymetry and number of species turns negative (Gaertner et al., 2005). In general, demersal communities along the Spanish Mediterranean coast are bathymetrically and geographically segregated, so, in contrast to communities in the Atlantic Ocean, communities inhabiting different strata might respond discordantly to similar drivers (Farriols et al., 2015; Hidalgo et al., 2017).

In terms of biogeographical distribution, in the Spanish Mediterranean, the presence of species with typical Atlantic distribution increases towards Alboran Sea (south of the study area), including Atlantic-African and Atlantic-European species (García-Ruiz et al., 2015). Although Mediterranean Sea displays a high percentage of narrowly distributed, endemic species, (Coll et al., 2010), most of Mediterranean coastal waters have already been colonized by alien species of Indo-Pacific or Lessepsian origin (Coll et al., 2010; García-Ruiz et al., 2015), which have even spread to our study area (Bianchi, 2013).

Climate change is also strongly affecting Mediterranean marine biota and ecosystems, mostly through processes linked to warming. The increase of maximum water temperature associated to global warming has been related to the degradation of benthic habitats in this area (Chefaoui et al., 2018). It is reflected, for example, in the higher rates of mortality of *Posidonia oceanica*, an endemic marine habitat-forming phanerogam, whose threat is projected to reach functional extinction levels (Moranta et al., 2006; Chefaoui et al., 2018). Another critical cue of climate change is seen in the population dynamics of the previously mentioned endemic species. This fauna tracks the migration of its isotherms in order to maintain its thermal niche, but unlike endemic species in other areas, Mediterranean endemisms have a limited scope to adapt by shifting their biogeographical range poleward (Marbà et al., 2015). Furthermore, Mediterranean bentho-demersal communities are also experiencing meridionalization and tropicalization processes, mainly reflected in the northward expansion of native thermophilic species and the heavier input of alien species through the Suez Canal and the Strait of Gibraltar. Under various scenarios of sea warming, the predicted biotic response to rising SST is characterized by significant increases of alien invertebrates and fishes (both demersal and pelagic), while relative abundance of native fish and vulnerable species is expected to decrease (Corrales et al, 2018).

ANTHROPOGENIC PRESSURES: FISHING

Mediterranean resources are exploited by fisheries from the twenty-two countries that border the Mediterranean Sea. The yield for total fisheries and aquaculture catches has increased over the last decades, although catch of wild stocks has declined since the 1990s (Hilmi et al., 2022). Unlike other regions of the Mediterranean, the fisheries of the western-most sub-area show certain stability in their catches. While in the eastern sub-areas an excessive fishing-mortality has driven catches to decrease, the more stable catches in the West have been associated to the exploitation of new species and the expansion to deeper fishing grounds (Piroddi et al., 2017).

A 'fishing-down' effect, associated to overexploitation, has been observed in the trophic level of the catch of the Western Mediterranean fisheries (Piroddi et al., 2017). This process consists in a decrease of top predator and large-sized fish abundances, which are replaced by species from lower trophic levels (Pauly et al., 1998). Also, in certain areas of Mediterranean Sea, overfishing has been held accountable for the success of alien fauna, mainly due to the depletion of certain predator species (Corrales et al., 2018). Spanish Mediterranean fisheries are highly dependent on recruitment, as a big proportion of their catch is composed of juveniles (Mendo et al., 2020). This, in conjunction with the overexploited state of some stocks (FAO, 2018) and a low adaptive capacity, makes Spanish Mediterranean fisheries highly vulnerable to climate change impacts (Mendo et al., 2020; Aragâo et al., 2021).

MONITORING PROGRAM IN THE AREA

As part of the MEDITS trawl survey program, conducted to evaluate the status of demersal resources of the Mediterranean Sea, the marine ecosystem of the Spanish Mediterranean region has been sampled yearly since 1994. For the studies contained in this thesis, we used information obtained from scientific bottom trawl surveys carried in the geographical sub-area 6 (GSA) every early summer (May-June), from 1994 to 2019. The surveys intend to produce basic information on the population distribution and demographic structure of the continental shelf, so they follow a stratified random sampling scheme with five depth strata, covering from 50 to 800 m deep (Spedicato et al., 2019). The sampling gear is a bottom trawl designed for experimental fishing with scientific purposes, and has average horizontal and vertical openings of 19.5 and 2.5 m, respectively, and a codend mesh size of 20 mm (Bertrand et al., 2002). Haul duration is 30 minutes and the standard fishing speed is 3 knots on the ground (Spedicato et al., 2019). After each haul, catch is identified taxonomically, weighted, counted and length is measured. In our analyses we used density (in number of individuals of a species) per haul standardized by swept area (i.e. number of individuals/km^2). As not all species in the community were included in our studies, a brief summary on the survey and the species selection has been added to each chapter's Material and Methods section.

1.4 OBJECTIVES OF THE THESIS

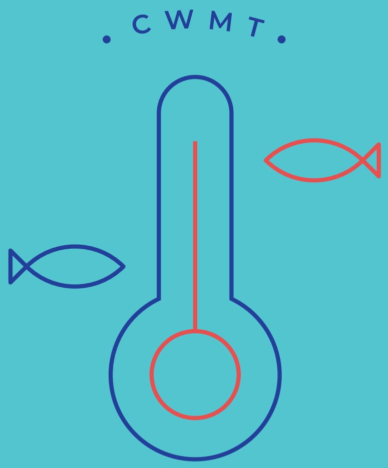
HYPOTHESIS

The alterations evidenced at Cantabrian and Mediterranean marine ecosystems in the last 40 years involve changes in commercial species richness and abundance, as well as generalized increases in the abundance of southern species and changes in the trophic and size structure of the communities. With this in mind we hypothesize these are all signs of a pervasive change in the demersal ecosystem, related to the widespread effects of climate change and fishing, which reflects in the biogeographical and functional display of the demersal communities.

OBJECTIVES

In order to determine how demersal communities around Iberian Peninsula have undertaken the last decades' changes in their main external stressors, warming and fishing, the following specific objectives have been met:

- Analyze how communities have incorporated climate change impacts in terms of their biogeography, first through the study of communities' mean thermal affinity and then expanding the approach to acknowledge the multivariate nature of species niches (chapters 2 and 3).
- Analyze and characterize the response of the Cantabrian Sea biotic system to the effects of climate change and fishing pressure, identifying possible discontinuities (regime shifts) and exploring their causal drivers (Chapter 4).
- If discontinuous responses to drivers were found, assess Cantabrian demersal community's ecological resilience and identify signs of hysteresis (Chapter 4).
- Approach the communities' sensitivity to external stressors throughout the design of sensitivity indicators that integrate the biological and ecological attributes of the species shaping the Cantabrian and Spanish Mediterranean bentho-demersal communities.



CHAPTER

02

TRACKING CLIMATE DRIVEN RANGE SHIFTS - CWMT

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CHAPTER 2. TRACKING CLIMATE DRIVEN RANGE SHIFTS: COMMUNITY WEIGHTED MEAN TEMPERATURE (CWMT)

2.1 INTRODUCTION

Global warming is modifying species distributions at an unprecedented rate in marine environments (Cheung et al., 2009; Burrows et al, 2011), challenging species to cope with increasing temperatures. Among the most commonly described changes, the abundance distribution and ranges of marine species are shifting toward higher latitudes, causing tropicalization (Horta e Costa et al., 2014), meridionalization (Punzón et al., 2016) and borealization (Fossheim et al., 2015) in the ecosystems, which become increasingly dominated by species with warmer affinities (Tasker, 2008; Lenoir et al., 2011; Simpson et al., 2011). Species ranges also shift toward higher depths, due to physical constraints such as substrate types (Dulvy et al., 2008; Hofstede et al., 2010; Punzón et al., 2016). The species tracking of their preferred thermal niche is among the first consequences of the increasing sea water temperatures. In fact, 80% of the observed changes in marine species distributions is consistent with the expected impact of global warming, and phenological changes also comply (in over 75% of the reported cases) with the altered climate seasonality (Poloczanska et al., 2013). In addition to these responses, resilience mechanisms such as phenological plasticity and adaptation capacities could counterbalance the effect of global warming at the population level, decreasing the risk of local extinctions (Simpson et al., 2011).

Although species are the common unit of study in most climate change studies, the cumulative effect of these changes in species distributions can also be reflected in the fish assemblages and communities (Lucey and Nye, 2010; Kleisner, 2016), which may be displaced from their original distribution ranges (Fossheim et al., 2015). An early index to characterize these displacements was the Preferred Temperature of the Community (PTC), calculated by weighting the species preferred temperature by their annual abundance (Collie et al., 2008). Based on the most numerous species in the community, the PTC was able to characterize shifts in the communities towards species with warmer affinities, mirroring the increasing water temperature in the ecosystems (Collie et al., 2008; Lucey and Nye, 2010). However, the PTC was built upon 19% of the community richness (Collie et al., 2008), and thus these promising results might be over-conservative. In fact, first sightings of species outside their usual geographical range can be considered an early indication of climate-related shifts (Fogarty et al., 2017) and rare species can significantly contribute to changing the community functioning. Along this line, Cheung et al. (2013) developed the Mean Temperature of the Catch (MTC), calculated by weighting the preferred temperature of all exploited species by their annual catch. This index revealed the relationship between the structure of the commercial catches and the changes in Sea Surface Temperature (SST) in several large marine ecosystems (Cheung et al., 2013). However, issues related to resources accessibility, fleet targets, fisheries regulations and management or misreporting (Pauly et al., 2013; Payne, 2013; Pauly and Zeller, 2016) remained unaddressed with this index, hampering its ecological interpretation. More recently, Peristeraki et al. (2019) analyzed the spatial and inter-annual patterns of MTC of demersal assemblages from bottom trawl surveys along the northern Mediterranean, without looking at temporal trends in most of the area. These authors concluded the recent bottom temperature increases observed in the Mediterranean have not caused an immediate response in the structure of their demersal and benthic communities.

Building on these, we have analyzed the Community Weighted Mean Temperature (CWMT), an index to track the effect of warming in fish communities. CWMT is based on all fish species in the community and calculated by weighting the mean temperature of their distributions by their abundance. Its performance was assessed in the Cantabrian Sea (Southern Bay of Biscay) using 32 years of data from International Bottom Trawl Surveys in the area (1983-2015). Species-specific responses to the increasing water temperatures (González-Pola et al., 2005; Gómez-Gesteira et al., 2008), have been recently documented in the area, with a generalized increase in the frequencies of occurrence and abundances of species with warmer affinities and a shift of the species centers of gravity towards deeper areas in the last decades (Punzón et al., 2016). In addition, the heterogeneous oceanography of the Cantabrian region offered a perfect setting to explore how CWMT varies at different spatial scales along the space-time continuum and responds to the interannual variation of the regional hydrography and long-term warming. Finally, we evaluated the speed of CWMT's changes.

2.2 MATERIAL AND METHODS

2.2.1 STUDY AREA AND FISH COMMUNITY DATA

The study area is the Cantabrian Sea, set on the Southern Bay of Biscay, a shelf sea on the Northeast Atlantic covering an approximate area of 20000 km^2 (Figure 1). This area is characterized by an apparent gradient in ocean exposure from Southwest to Northeast, which can be seen, for example, in the higher temperatures towards the inner Bay of Biscay (Tasker, 2008). During the spring and summer, the easterly winds favor coastal upwelling along the Cantabrian coast (Gil, 2008). These winds are more persistent and continuous in time on the Northwest coast (Galician waters) that on the northern slope of the Bay of Biscay, resulting in a decrease of the strength of the upwelling from the Southwest to the Northeast (Llope et al., 2006).

During the last decades warming trends have been identified both at surface waters (Gómez-Gesteira et al., 2008; Tasker, 2008) and while upwelling intensity has generally increased, the number of days under upwelling conditions has decreased (Alvarez et al., 2011). These trends in water temperature and upwelling intensity have contrasting effects on the phytoplankton communities, whose productivity in the Southern Bay of Biscay has remained stable over the last decades (Otero et al., 2018, Beca-Carretero et al., 2019).

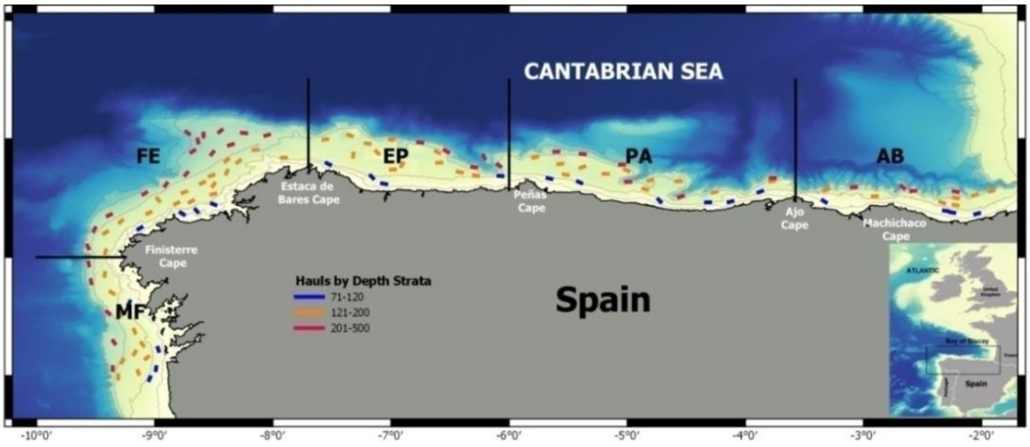


Figure 1. Samples in the study area by depth strata and year (1983 to 2015).

For this study we used data from the sampling of the bentho-demersal fish community carried at DEMERSALES annual surveys, which adhere to the ICES standardized methodology for International Bottom Trawl Surveys (ICES, 2017). Data covered the period 1983 to 2015 (except for 1987). The surveys follow a random sampling scheme stratified to the area, with three bathymetric depth strata (70–120 m, 121–200 m, 201–500 m) and five geographical sectors: Miño River- Cape Finisterre (MF), C. Finisterre- C. Estaca (FE), C. Estaca-C. Peñas (EP), C. Peñas-C. Ajo (PA) and C. Ajo-Bidasoa River (AB) (Figure 1). The characteristics of the sampling methodology are explained in the Study areas section in Chapter 1. All fish species in the community were used in subsequent analysis, except for those few species which were ambiguously identified along the time series (family Gobiidae and Myctophidae) and those whose occurrence was considered incidental (further details in Punzón et al., 2016). Thus, the whole community comprised 69 fish species, most of them typically demersal (71%), but also including a few species considered benthic with high vertical mobility (16%) and a few species considered pelagic (13%).

2.2.2 TEMPERATURE OF THE WATER COLUMN

Temperature data for the water column was obtained from the ocean physics reanalysis product ‘Atlantic-Iberian Iberian Biscay Irish- Ocean Physics Reanalysis’, generated and provided by the CMEMS IBI-MFC (see Sotillo et al., 2016 for a detailed description). The model provided monthly means of temperature for 50 different depth ranges, between 0.5 and 5698 m deep for the period 2002 to 2015, with a high spatial resolution (0.028º x 0.028º). Since the fish community is sampled in early autumn (September-October) a mean value for the previous 5 months (June to October) was calculated for each depth range in gridded layers of 5x5 nm resolution. This temporal window was selected because it features a season with stable environmental conditions (e.g. temperature and upwelling) previous to the survey. Subsequently, we computed the Mean Temperature of the Water Column Temperature (MTW) and the delta temperature (ΔMTW; difference between maximum and minimum temperature of the water column) of the first 1000 m, based on a set of 17 depths. Computing an integrated value of temperature for the whole water column, the MTW accounted for the main oceanographic features conferring spatial variability to the system. Initially we explored the bottom temperature, following previous studies on fish distribution (González-Irusta and Wright, 2017; Morato, et al., 2020), but in our study area this variable failed to capture the longitudinal gradients in the water column present in the area (Llope et al., 2006), a gradient mirrored by the demersal fish community (Serrano et al., 2011). For this reason, in this work we used the MTW and the ΔMTW instead of proxies for bottom temperature. As the MTW did not cover the entire study period, we obtained as well temperature profiles from the ocean reanalysis (ECMWF Ocean Reanalysis System 4, ORAS4) (Balmaseda et al., 2013). This reanalysis provides monthly temperature data at 42 pressure levels from 5 to 5000 m with higher vertical spacing towards the bottom (1959-present). However, the coarser spatial resolution of 1°x1° of this reanalysis would not allow for a detailed spatial analysis of temperature changes. The ORAS4 reanalysis has been systematically presented together with data from oceanographic sections in the Bay of Biscay for the study of hydrographic and circulation changes in the mid-latitudes of the Eastern North Atlantic (Somavilla et al. 2016, 2017). These previous comparisons serve as an important validation of the data, as gridded datasets accuracy is in general affected by either model errors in ocean reanalysis data (Balmaseda et al., 2013) or the gap-filling strategy in climatological data (Cheng and Zhu, 2015). To assess low frequency temperature changes in the study, we also calculated the annual average of temperature in the depth range between 300 and 600 m deep, excluding from this average the surface mixed layer depth affected by strong seasonality. The climatological maximum winter mixed layer in the area is within 250 m depth, and so we named this average temperature Temperature Below Winter Mixed Layer (TBWML).

2.2.3 THE COMMUNITY WEIGHTED MEAN TEMPERATURE (CWMT)

The Community Weighted Mean Temperature (CWMT) was calculated in each haul as:

$$CWMT_i = \sum Tpref_s * W_{si} \Big/ \sum W_{si}$$

Where $CWMT_i$ is the Community Weighted Mean Temperature in haul i, the $Tpref_s$ is the preferred temperature of species and W_{si} is the biomass in weight of species s in the haul i.

The preferred temperature was calculated for each species by spatially weighting the mean water bottom temperature and the species probability of occurrence (Table Supp. 1). The distribution ranges and probabilities of occurrence for all fish species were obtained from the bioclimatic envelope models developed by AQUAMAPS (Kaschner et al., 2016). This approach, despite its simplicity, overcomes some of the limitations of previous indices based on the species preferred temperatures, such as the lack of information on the temperature affinities of each species in the scientific literature (as used in Collie et al., 2008). In addition, we considered the overall distribution range of each species, avoiding the bias of considering only the temperatures within the study area (as did Lucey and Nye, 2010) and we used the water temperature at the sea bottom, which is more determinant for benthic-demersal communities, particularly when including deep species (Hiddink and Hofstede, 2008). Nevertheless, these preferred temperatures should be considered a proxy for the temperature affinity of the species, rather than the optimum temperature for the species.

Statistics of Community Weighted Mean Temperature (CMWT) by depth range and geographical sector were estimated based on the CWMT by haul. In order to compare it with the MWT and study possible correlation between them, the spatial distribution of CWMT for the study period (2002-2015) was calculated as the mean value for each sample station. In order to represent the index (CWMT) at a finer resolution we used the Universal Kriging Analysis. The Universal Kriging was computed using the function autofitVariogram, from the package automap (Hiemstra et al., 2008), to compute the variogram, and the function krige, from the package gstat (Pebesma, 2004), to do the kriging, using depth as covariate.

To estimate the evolution in time of CWMT for the total area and by geographical sector a General Additive Model (GAM; Hastie and Tibshirani, 1990) was performed. To analyze the trends in the spatial distribution over time, the CWMT by haul was classified using k-means algorithm to discriminate distinct geographical areas. K-means stores k centroids that are later used to define clusters.

The analyses were performed using R (R Development Core Team, 2018). The GAM was performed using the 'mgcv' library without limiting the degrees of freedom of the smoothers and assuming a gaussian distribution (Wood, 2011), and the k-means classification was performed using 'classInt' library (Bivand, 2018).

2.3 RESULTS

The spatial pattern displayed by the Mean Temperature of the Water Column (MTW) over the continental shelf reflects the regional oceanography of the southern Bay of Biscay, generally increasing either in mean and/or maximum values from Southwest to Northeast, towards the inner Bay of Biscay (Figure Supp. 1 and Figure 2A). Across the depth strata, the MTW decreased (T^e 70-120 = 14.32, T^e 120-200 = 13.98, T^e 200-500 = 13.82) (Figure Supp. 2A), but aggregating the MTW data by depth stratum and geographical sector, this temperature decline with depth was only apparent in the Cantabrian Sea towards the inner Bay of Biscay, but not in the westernmost sectors (Figure Supp. 3). Based on the temperature of the water column, the ΔT^e (difference between maximum and minimum water column temperature), is minimum in the shelf of the Galician waters, mainly in MF (Figure 2B).

Meanwhile in the Cantabrian Sea the ΔT^e has a pattern according with depth strata, minimum in the shallow strata and maximum in the deep one (Figure 2B).

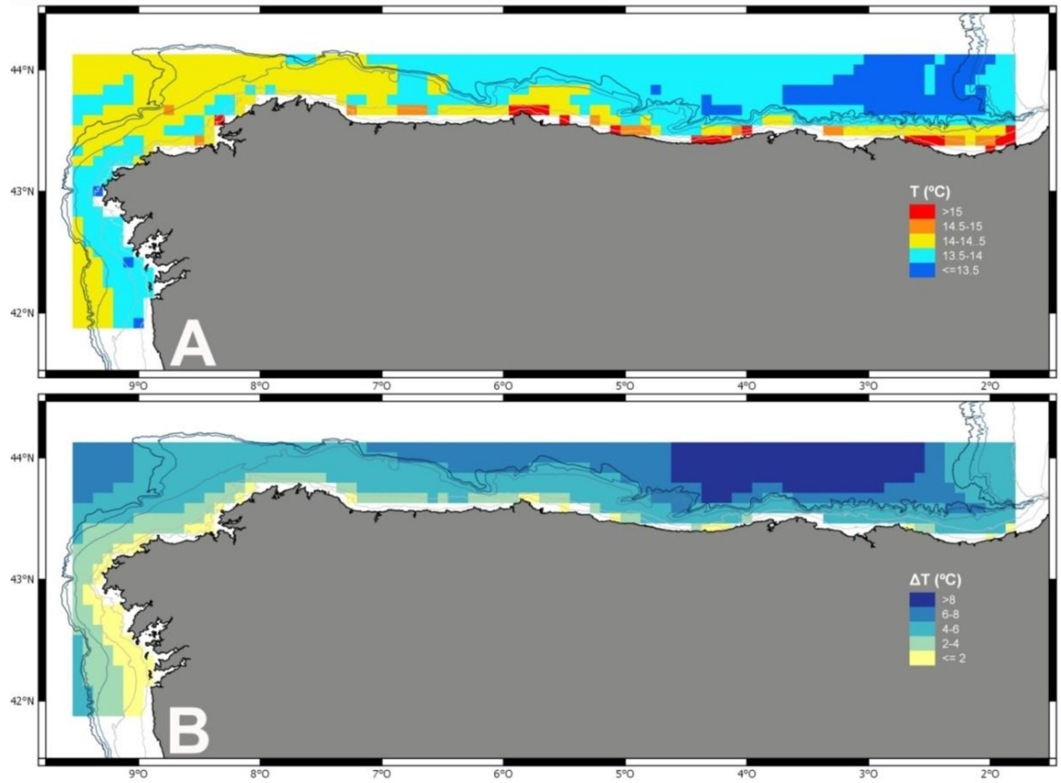


Figure 2. Spatial distribution of the Mean Temperature of the Water column (MTW) (A) and increment (difference between maximum and minimum water column temperature) of MTW over the period 2002-2015 (B).

The median values of the community weighted mean temperature (CWMT) showed a similar trend to the observed in the MTW, with a generalized increase from the Southwest of the study area to the inner Bay of Biscay in the Northeast (Figure 3A), with CWMT values significantly differing between Galician waters (MF and FE sectors) and the north sectors of Cantabrian Sea (EP, PA and AB sectors). The CWMT also decreased across depth strata ($CWMT_{70\text{-}120}$ = 11.04, $CWMT_{120\text{-}200}$ = 8.06, $CWMT_{200\text{-}500}$ = 7.35) (Figure 3B). Aggregating the results by geographical sector and depth strata (Figure 3C), the CWMT patterns were geographically distinct; in Galician waters the changes in CWMT with depth were not clear, with no significant differences at all between the two deepest strata (120-200 and 200-500), while in the Cantabrian Sea differences in CWMT were significant along the depth gradient (Figure 3C). Comparing the distributions of MTW and CWMT, the spatial patterns displayed by both metrics were quite similar (Figure 2A, Figure 4, and Figure Supp. 4). The Pearson correlation between CWMT and MTW was 0.372 (interval confidence = 0.29-0.44, p = 2.2e-16).

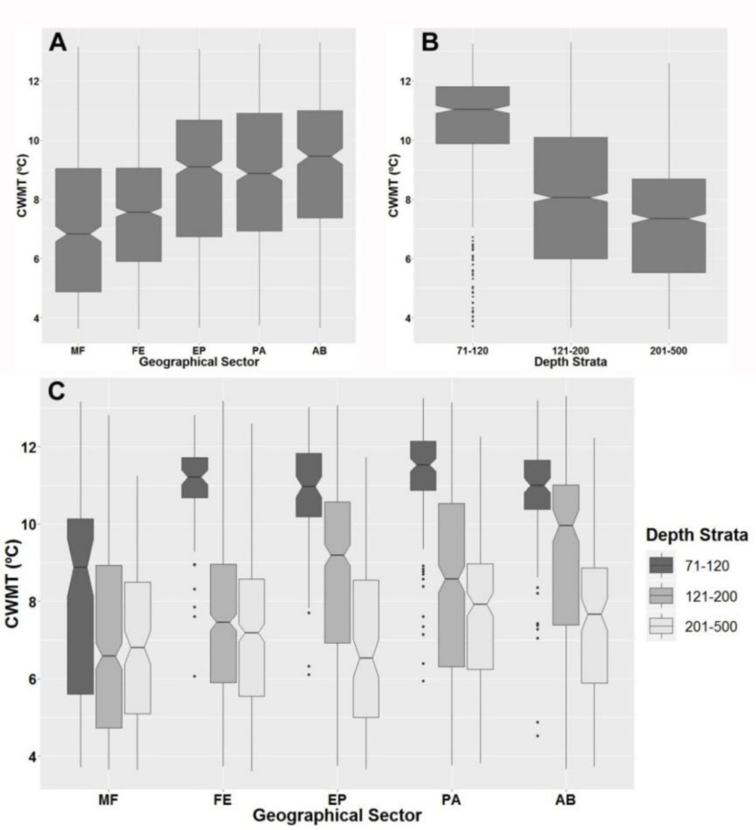


Figure 3. CWMT by geographical sector (A), by depth strata (B) and by geographical sector and depth strata combined (C). The boxes represent the interquartile range (IQR), the line is the median and the notches are its confidence interval. The lines of the whiskers extend 1.5 IQR and outliers are identified as points beyond the whiskers.

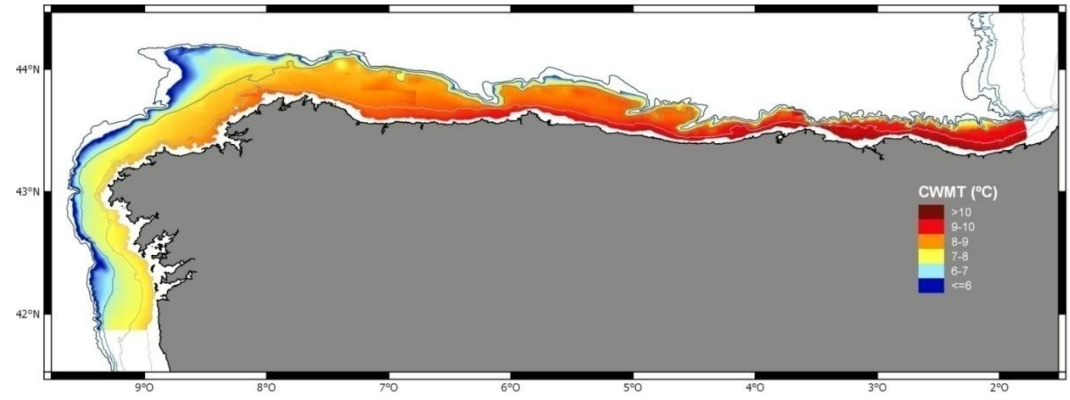


Figure 4. Spatial distribution of the CWMT between 2002-2015.

The annual trend for CWMT for the whole area (Figure 5B) matches the annual trend of the TBWML (Figure 5A). Neither of the two series showed any temporal autocorrelation. The Pearson correlation coefficient between the time series was 0.613 (interval confidence = 0.339-0.794, $p < 0.001$). Our analysis revealed a clear temporal pattern in the CWMT (CWMT~year, p<2e-16) (Figure 5B), heterogeneous among geographic sectors (Figure 6), with an annual rate of increase of the CWMT of 0.04 °C/yr. Sectors in the West displayed lower, but more fluctuating patterns compared to sectors in the East, with the patterns between the sub-regions MF, FE and EP temporally asynchronized from AB's pattern sinceafterthe mid-90s. The Pearson correlation between the CWMT andthe TBWML in the western areas (sectors MF and FE) was 0.522 (interval confidence = 0.212-0.78, $p < 0.001$); and between the CWMT and the TBWML in the northeastern areas (EP and AB), it was 0.5918 (interval confidence = 0.30-0.78, $p=0.00036$).

We identified the species involved in the observed temporal trends, based on their contribution to the CWMT (Figure 5C). The proportion of species with cooler preferred temperatures decreased over time, particularly blue whiting (*Micromesistius poutassou*), which despite its high interannual variability is one of the dominant species in the community. On the other hand, the species with warmer preferred temperatures, a pool of species including *Scyliorhinus canicula*, *Pagellus acarne* and *Lepidorhombus boscii*, increased over time (Figure 5B). The exceptional increases of CWMT in 1994 and 2008 were caused by different communities (Figure 5). The first peak was related to the increase in the abundance of a few species with warmer preferred temperatures, particularly *Macroramphosus scolopax* and *Trachurus trachurus*, while the second one was caused by a steep decrease in *M. poutassou* and a generalized gain in abundance of species with warmer preferred temperatures (Figure 5).

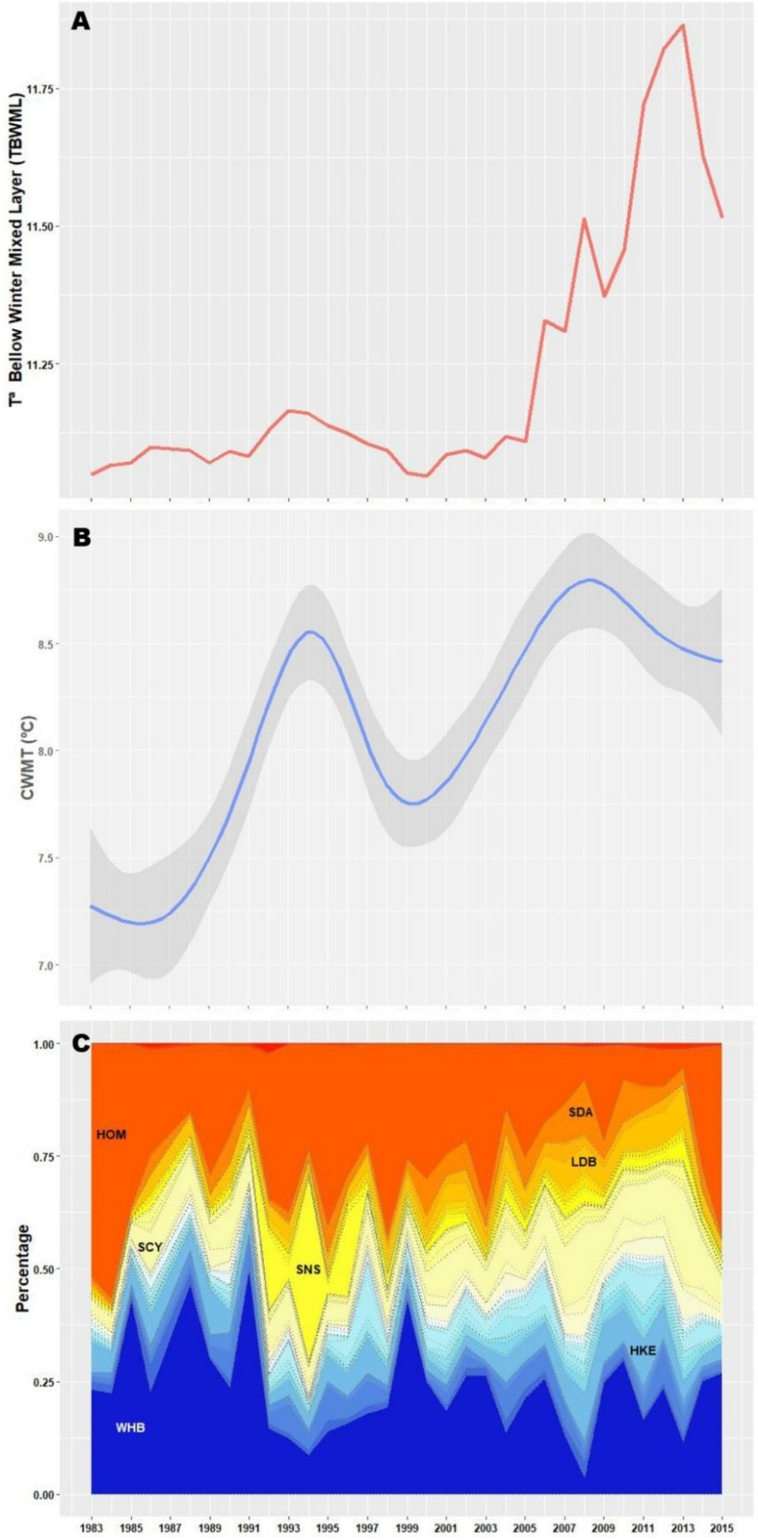


Figure 5. Annual Temperature BelowWinter Mixed Layer (TBWML) (A), annual changes in CWMT (results of the Generalized Additive Model) (B) and relative abundances of the different fish species in the community annually (C). The color of each species reflects the mean temperature of the species, with blue being the coolest and red the warmest (see Table Suppl. 1). Species code: *Micromesistius poutassou* (WHB), *Scyliorhinus canicula* (SCY), *Merluccius merluccius* (HKE), *Trachurus trachurus* (HOM), *Macroramphosus scolopax* (SNS), *Pagellus acarne* (SDA), *Lepidorhombus boscii* (LDB).

In the temporal trends of the CWMT by geographic sector, we observed that the generalized increase identified for the whole study area varied among regions, the geographical sectors of inner Bay of Biscay (PA and AB) displaying a more stable increase, while Galician waters sectors (MF and FE) displayed higher rates of increment and higher variability (Figure 6). The peaks of CWMT in 1994 and 2008 corresponded with high values of CWMT in Galician waters, when the CWMT was quite homogeneous between regions (i.e. 8-9°C on average). On the other hand, CWMT strongly varied between geographic sectors (by approximately 5°C), reflecting the steep CWMT gradient from the Southwest (Galician Waters) to the Northeast (inner Bay of Biscay).

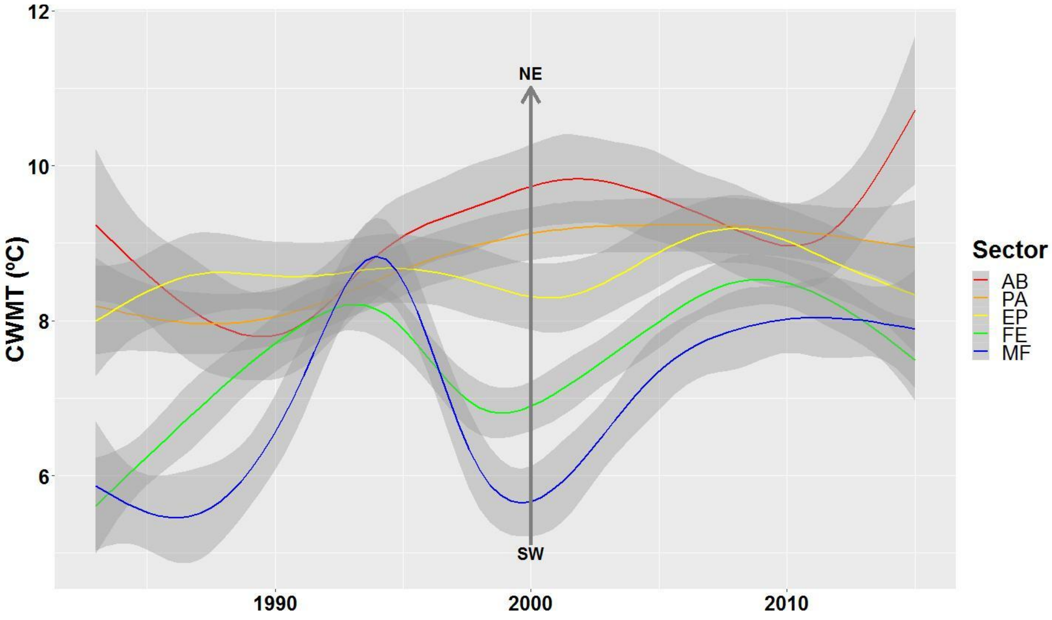


Figure 6. Variability in the annual changes of CWMT represented by geographical sector (results from the Generalized Additive Model).

To analyze the spatio-temporal trends of the CWMT, we classified CWMT by haul in three groups by the k-mean method. The CWMT range by groups was: Cold ≤ 6.64°C; 6.64°C < Temperate ≤ 9.58°C; Warm > 9.58°C. Figure Supp. 5 shows the spatial distribution of the community types for all time series, where the warm community is in the littoral area of the Cantabrian Sea geographical sectors and scarcely in the north of Galician Waters. In the geographical sectors of the Galician waters the temperate community is the most important. Spatial interpolation was estimated for every year from data by haul, and every cell was classified to estimate the occupied area by CWMT range groups. In Figure 7 we show the trend by CWMT range groups. The trends for warm and cold CWMT groups were significant (warm, $p=0.0013$; cold, $p=0.0014$). The slope for the warm CWMT group was 268.41 km^2 per year, and for the cold group was -155.39 km^2 per year.

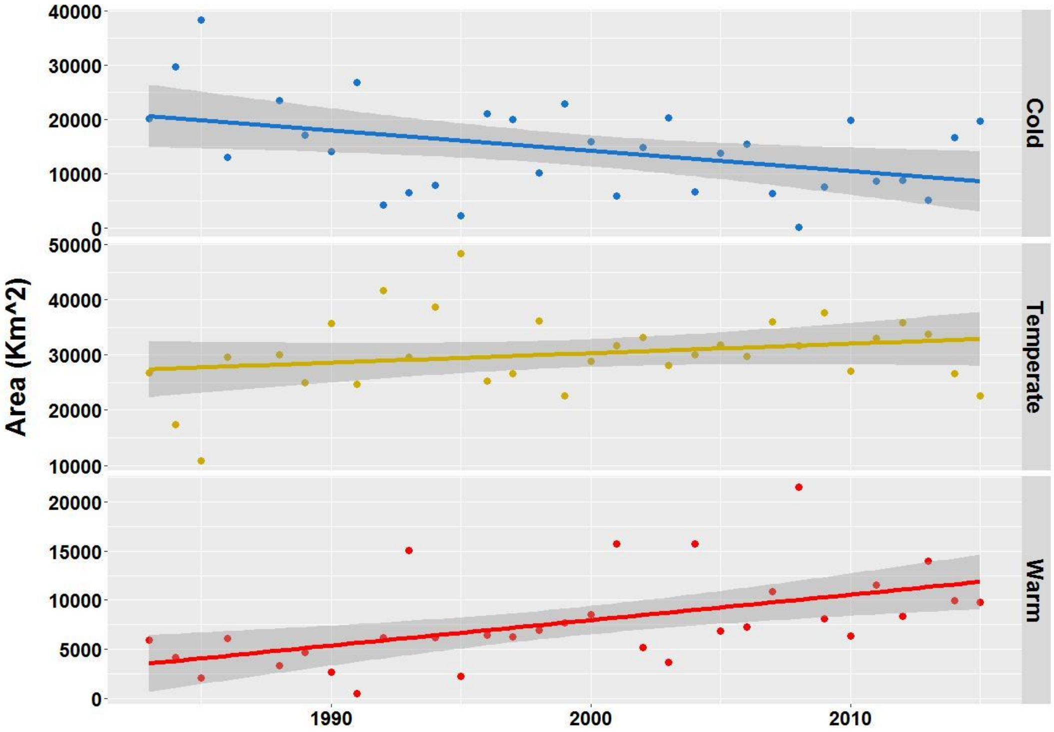


Figure 7. Trends in the spatial occupation of the community types: warm (p = 0.0013, r2 = 0.3, slope = 268.409), temperate (p = 0.1768, r2 = 0.06, slope = -121.348) and cold (p = 0.0144, r2 = 0.18, slope = -155.389).

2.4 DISCUSSION

The community weighted mean temperature (CWMT) showed a good agreement with the Mean Temperature of the Water Column (MTW) and Temperature Below Winter Mixed Layer (TBWML), reproducing its space-time trends in the study area, i.e. (i) an increase from the southwest to the northeast (towards the inner Bay of Biscay); (ii) a decrease with depth (except in the Southwestern area, characterized by intense upwelling); (iii) a general increase over the time series; (iv) temporal fluctuations declined when moving from SW to NE regions; and (v) from the mid-90s, a higher synchrony between the three westernmost sectors, which contrasts with the asynchrony observed in the eastern sectors (PA and AB). The Mean Temperature of the Water Column (MTW) was able to capture the main space-time patterns in sea temperature described for the southern Bay of Biscay, such as the increasing temperature values towards the inner Bay of Biscay (from SW to NE) and decreases with depth. This gradient mirrors the regional oceanography, as it matches the decrease in upwelling intensity (from SW to NE) and the increase in water stratification following the same direction (Valdés et al., 2007; Gil, 2008). Indeed, the westernmost sectors of the study area, with similar MTW values across the depth strata, show a temperature profile characteristic of upwelling ecosystems (Chavez and Messie, 2009) with a well-mixed water column and lacking a temperature gradient in depth (Bode et al., 2009). In the area, we also found a generalised increment along the time series on sea surface and intermediate water temperatures (González-Pola et al., 2005; Gómez-Gesteira et al., 2008; Tasker, 2008). This suggests that the CWMT responds to the temperature of the water column as a combination of the thermal niches (*sensu* Magnuson et al., 1979) of the species that constitute the fish community. In fact, temperature can be considered as one of the multiple dimensions of a species niche, understanding the niche as a multidimensional combination of both biotic and abiotic variables which provide an appropriate environment for a given species (Hutchinson, 1978). With temperature displaying marked spatial gradients in latitude, longitude and depth, the thermal niche arises as a fundamental factor in the distribution of fish species (Pörtner and Peck, 2010; Righton et al., 2010; Brugue et al., 2016; Kleisner et al., 2017).

The spatial variability in CWMT observed in the present study should be expected. Changes in the structure of fish and invertebrate communities along the West-East axis of the Southern Bay of Biscay had been described in previous studies (Sanchez and Serrano, 2003; Serrano et al, 2006, 2011), particularly an increase in biodiversity towards the Cantabrian Sea (central and eastern sub-regions of the study area). In addition, the decrease in CWMT along the depth gradient in the Cantabrian Sea is paralleled by a clear succession of the fish and invertebrate communities (Sánchez and Serrano, 2003; Serrano et al, 2011). Anyhow, in the westernmost sectors (Galician waters), where CWMT values remain constant along the depth gradient, this in-depth structure of the fish communities is not as apparent (Fariña et al., 1997) and can only be acknowledged if considering fish and invertebrate fauna together (Serrano et al, 2008). The strong agreement between CWMT and the community variability described in the aforementioned studies, suggests that longitude and depth are proxies for the spatial temperature gradients, notwithstanding the additive effect of other local environmental factors along these geographical variables and/or the spatial autocorrelation of the community structure (Currie, 2007). The long-term increment in CWMT indicates that the fish community is increasingly dominated by the species with warmer affinities, reflecting the increase in abundance and frequency of occurrence of temperate species with Lusitanian affinities (Punzón et al., 2016), and supporting the meridionalization hypothesis for this ecosystem, as an increase in the abundance of native fauna with southern affinities. The increase in CWMT over time is more evident in the inner part of the Bay of Biscay than in the SW zone. This may be related to the dampening effect of the upwelling on ocean warming, particularly in coastal areas (Santos et al., 2012). Indeed, SST warming in the SW area has been estimated as of 0.15°C per decade (Gómez-Gesteira et al., 2011) while in the inner Bay of Biscay SST warming estimates reach 0.26°C per decade (Goikoetxea et al., 2009).

Changes in fish communities tracking the increasing water temperature have been described using different indices in several large ecosystems (Collie et al., 2008; Lucey and Nye, 2010; Cheung et al., 2013; Keskin and Pauly, 2014; Tsikliras and Stergiou, 2014, Vasilakopoulos et al., 2017). At a finer spatial scale, we demonstrate that the long-term increases in CWMT in the southern Bay of Biscay persist over sub-regional and local scales, although showing different degrees of variability. CWMT variability was least at the inner bay and increases towards the West, driven mainly by the variability in the abundance of blue whiting (*M.*

poutassou) which dominates the community when the CWMT reaches lower values. Blue whiting is a cold-water migratory species with a wide distribution in the Northeast Atlantic, whose abundance in the area is probably determined by its population dynamics over the whole Northeastern Atlantic rather than by the regional oceanography in the southern Bay of Biscay. On the other hand, the increase in CWMT over the time series responds to the increasing abundance of a pool of species with temperate and warm affinities (*S. canicula*, *L. boscii*, *P. acarne*, *C. aper*, *Raja clavata*, etc), rather than a unique species (Punzón et al., 2016). Despite the increasing abundance of these species, no distributional shifts were identified (Punzón et al., 2016). In particular, the dominant warm water species, horse mackerel (*T. trachurus*) also seemed to decline over time, but the population distribution of this species ranges over a much larger area than our study site, and thus, its abundance might not be as influenced by the regional oceanography in the Southern Bay of Biscay. The distribution of this species in the study area also seems to be stable in time, without significant changes in latitude, longitude or depth (Punzón et al., 2016). The exceptionally high CWMT of 1994 and 2008 could be responding to oceanographic processes that improved the recruitment of some of these species. For instance, Sánchez and Serrano (2003) found that a moderate Poleward Current together with a high upwelling index favored a good recruitment of hake (*Merluccius merluccius*) and possibly other demersal species on the Cantabrian Sea shelf.

The distribution pattern of the three thermal communities identified by CWMT, attributes the warm communities to the coastal inner Bay of Biscay, the temperate communities to the continental shelves and Galician coastal areas under the influence of the upwelling, and the cold communities to the shelf break and deep waters. Along the time series, we recorded an increase in the distribution area of the warm communities and a retraction of the cold communities in response to the increasing temperatures of the Southern Bay of Biscay. These trends provide further evidence for the phenomena of meridionalization of temperate ecosystems (Punzón et al., 2016), in line with the increasing proportion of species with temperate affinities in the landings of the North-East Atlantic large marine ecosystem (Cheung et al., 2013).

The benthic-demersal fish communities analyzed in the present study responded to the temperature at different spatio-temporal scales reflecting: (i) the observed warming trends in the water column; (ii) the local oceanographic processes; and (iii) their internal structure. Therefore, the CWMT proves to be a good indicator of changes in marine communities, reflecting both its spatial and temporal variability. In fact, the CWMT captured the community dynamics even in absence of species replacements or migration of new species into the Bay of Biscay, while these events have been commonly reported in cold-temperate fish communities subject to similar rates of warming (Perry et al., 2005; Collie et al., 2008; Hofstede et al., 2010). The biogeographical zone can be the key difference between these studies; this study is set in a warm-temperate province, while previous studies took place in cold-temperate provinces, responding to the hypothesis of Hiddink and Hofstede (2008), who suggested that changes in species richness would preferentially occur in temperate and cold latitudes, in relation to warmer latitudes. Therefore, we hypothesize the existence of a gradient in the rate of change of communities between warm-provinces and cold provinces, faster at higher latitudes. CWMT could thus be a useful tool to further investigate this hypothesis and a test of the performance of this index on a latitudinal range of marine ecosystems could allow evaluating the generality of our findings. The rate of change of the communities in the Southern Bay of Biscay suffices to deeply impact the economic activities founded on benthic-demersal resources. This highlights the importance of predicting the evolution of the demersal ecosystem under different scenarios of climate change, with the aim to implement adaptation and mitigation tools.

2.5 SUPPORTING INFORMATION

APPENDIX 1: SUPPORTING TABLES

Table Supp. 1. Biogeographical guilds, habitat from Fishbase and surface and bottom (used in this paper) preferred temperature calculated from Fishbase.

			Pref. Temp. (ºC)	
Species	**Biogeographic guild**	**Habitat**	**Surface**	**Bottom**
Acantholabrus palloni	Lusitanian	---	16.47	8.92
Argentina sphyraena	Lusitanian	bathydemersal	12.17	9.48
Argyropelecus hemigymnus	Atlantic	bathypelagic	20.27	4.28
Arnoglossus imperialis	Lusitanian	demersal	23.86	12.95
Arnoglossus laterna	Lusitanian	demersal	13.62	10.42
Bathysolea profundicola	Lusitanian	bathydemersal	20.33	9.65
Blennius ocellaris	Lusitanian	demersal	17.41	12.44
Boops boops	Lusitanian	demersal	22.45	13.06
Buglossidium luteum	Lusitanian	demersal	12.64	10.79
Callionymus lyra	Lusitanian	demersal	11.97	10.41
Callionymus maculatus	Lusitanian	demersal	11.91	9.60
Capros aper	Lusitanian	demersal	14.87	10.93
Cepola macrophthalma	Lusitanian	demersal	17.34	12.92
Chelidonichthys cuculus	Lusitanian	demersal	12.94	10.34
Chelidonichthys lucerna	Lusitanian	demersal	12.55	10.28
Chelidonichthys obscurus	Lusitanian	demersal	18.62	13.50
Chimaera monstrosa	Atlantic	bathydemersal	13.25	8.52
Chlorophthalmus agassizi	Atlantic	bathydemersal	21.79	10.06
Coelorinchus caelorhincus	Atlantic	benthopelagic	23.59	10.27
Conger conger	Lusitanian	demersal	14.61	10.14
Echiodon dentatus	Mediterranean	demersal	19.23	11.34
Etmopterus spinax	Atlantic	bathydemersal	20.08	9.77
Eutrigla gurnardus	Lusitanian	demersal	11.71	9.51
Gadiculus argenteus	Lusitanian	pelagic-oceanic	15.47	10.70
Gaidropsarus macrophthalmus	Lusitanian	demersal	12.85	8.40
Gaidropsarus vulgaris	Lusitanian	demersal	11.91	9.85
Galeus sp	Lusitanian	demersal	15.02	10.50
Helicolenus dactylopterus	Atlantic	bathydemersal	19.01	9.93
Hexanchus griseus	Atlantic	bathydemersal	20.44	10.79
Labrus mixtus	Lusitanian	reef-associated	12.73	10.63
Lampanyctus crocodilus	Atlantic	bathypelagic	16.68	5.49
Lepidopus caudatus	Atlantic	benthopelagic	17.45	9.78
Lepidorhombus boscii	Lusitanian	demersal	15.46	11.15
Lepidorhombus whiffiagonis	Lusitanian	demersal	11.79	9.49
Lepidotrigla dieuzeidei	African	demersal	18.79	13.49
Leucoraja naevus	Lusitanian	demersal	12.33	9.80
Lophius budegassa	Lusitanian	demersal	14.64	10.81
Lophius piscatorius	Lusitanian	demersal	16.76	11.05
Macroramphosus scolopax	Lusitanian	demersal	19.89	11.21
Malacocephalus laevis	Atlantic	bathydemersal	22.94	8.36
Maurolicus muelleri	Atlantic	bathypelagic	13.73	7.74
Merluccius merluccius	Lusitanian	demersal	16.90	12.83
Microchirus variegatus	Lusitanian	demersal	15.20	11.48
Micromesistius poutassou	Atlantic	demersal	13.47	9.09
Molva macrophthalma	Lusitanian	demersal	14.47	10.40

Table Supp. 1. (cont.) Biogeographical guilds, habitat from Fishbase and surface and bottom (used in this paper) preferred temperature calculated from Fishbase.

Species	Biogeographic guild	Habitat	Pref. Temp. (ºC)	
			Surface	Bottom
Mullus surmuletus	Lusitanian	demersal	13.49	10.69
Pagellus acarne	Lusitanian	benthopelagic	18.91	12.33
Pagellus bogaraveo	Lusitanian	benthopelagic	16.75	11.47
Pagellus erythrinus	Lusitanian	benthopelagic	18.59	12.84
Phycis blennoides	Lusitanian	benthopelagic	14.28	10.41
Raja clavata	Lusitanian	demersal	17.69	9.15
Raja montagui	Lusitanian	demersal	14.81	12.03
Sardina pilchardus	Lusitanian	pelagic-neritic	17.66	13.36
Scomber colias	Lusitanian	pelagic-neritic	23.12	14.02
Scomber scombrus	Atlantic	pelagic-neritic	10.53	6.78
Scorpaena loppei	Lusitanian	demersal	18.57	10.15
Scorpaena notata	Lusitanian	demersal	19.67	12.70
Scorpaena scrofa	Lusitanian	demersal	21.14	13.74
Scyliorhinus canicula	Lusitanian	demersal	17.06	12.14
Scyliorhinus stellaris	Lusitanian	demersal	15.04	11.87
Serranus cabrilla	Lusitanian	demersal	21.96	13.23
Solea solea	Lusitanian	demersal	12.98	10.99
Spondyliosoma cantharus	Lusitanian	benthopelagic	17.14	11.41
Trachinus draco	Lusitanian	demersal	14.07	11.23
Trachurus mediterraneus	Lusitanian	pelagic-oceanic	18.23	13.43
Trachurus trachurus	Lusitanian	pelagic-neritic	15.56	11.15
Trigla lyra	Lusitanian	demersal	21.65	12.72
Trisopterus luscus	Lusitanian	benthopelagic	11.70	9.96
Trisopterus minutus	Lusitanian	benthopelagic	11.06	9.26
Zeus faber	Lusitanian	benthopelagic	16.59	11.72

APPENDIX 2: SUPPORTING FIGURES

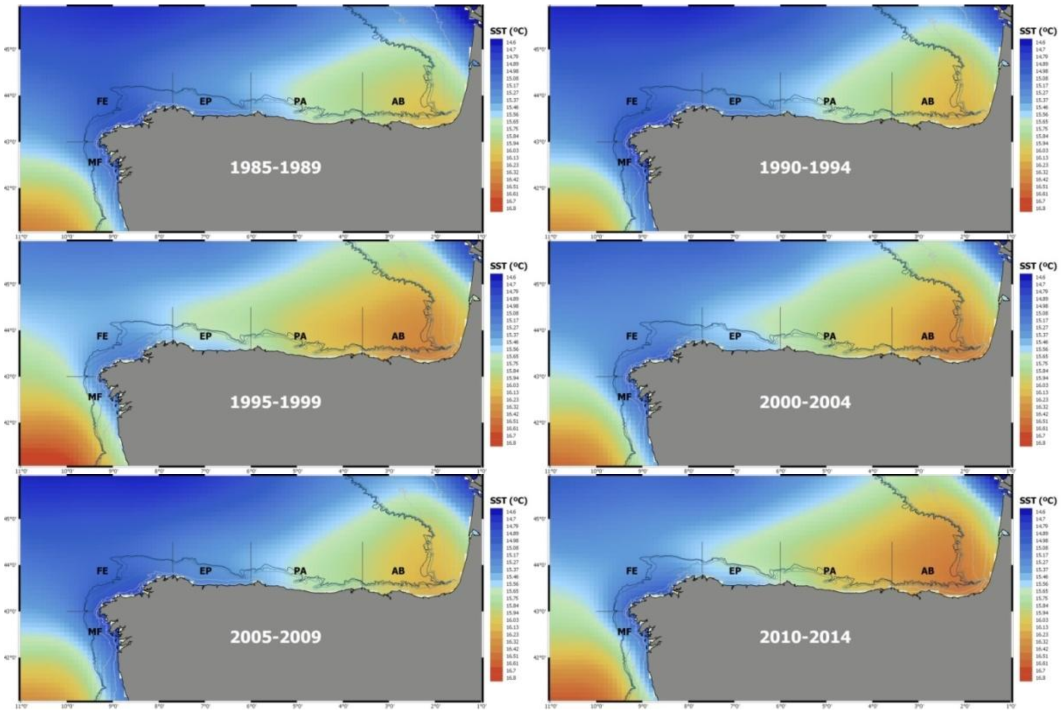


Figure Supp. 1. SST from 1985 to 2015 in the study area. Source: OCLE (http://ocle.ihcantabria.com/)

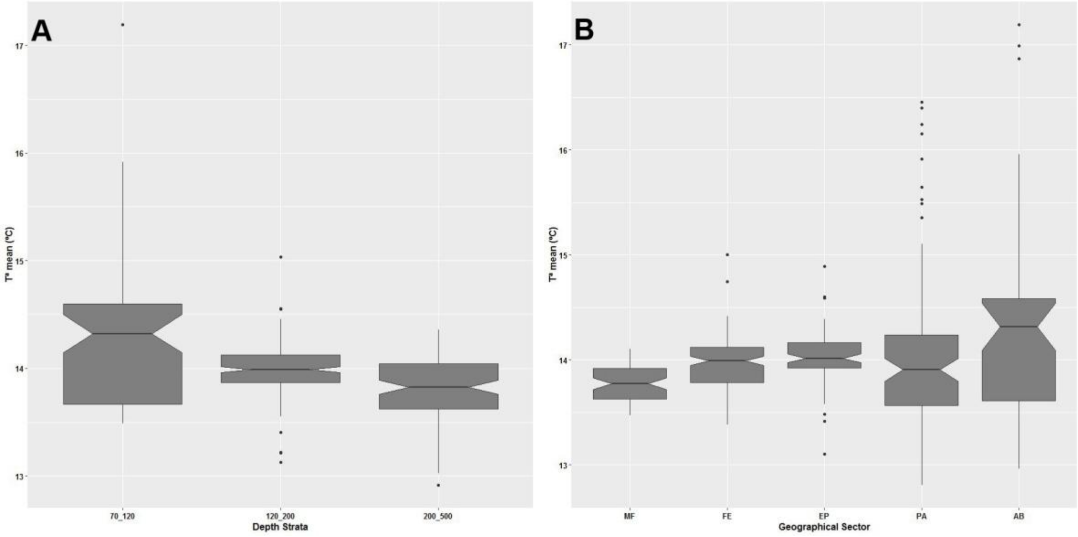


Figure Supp. 2. Mean Temperature of the Water column (MTW) by depth strata (A) and sector (B). The boxes represent the interquartile range (IQR), the line is the median and the notches are its confidence interval. The lines of the whiskers extend 1.5 IQR and outliers are identified as points beyond the whiskers.

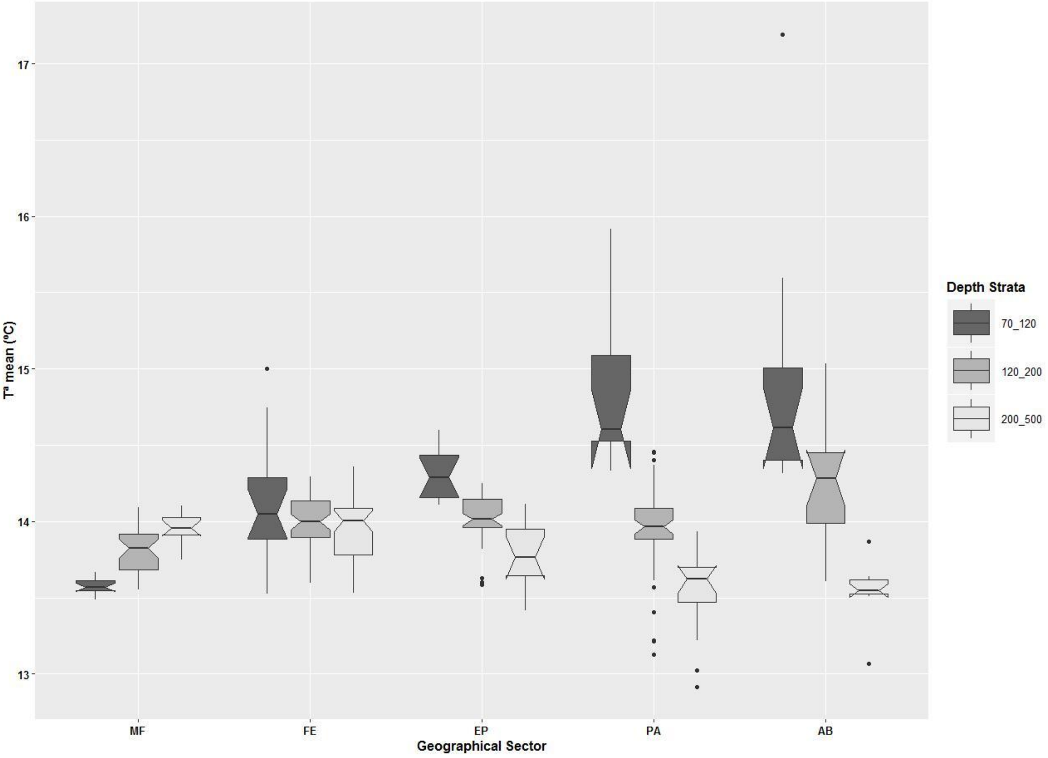


Figure Supp. 3. MTW by geographical sector and depth strata. The boxes represent the interquartile range (IQR), the line is the median and the notches are its confidence interval. The lines of the whiskers extend 1.5 IQR and outliers are identified as points beyond the whiskers.

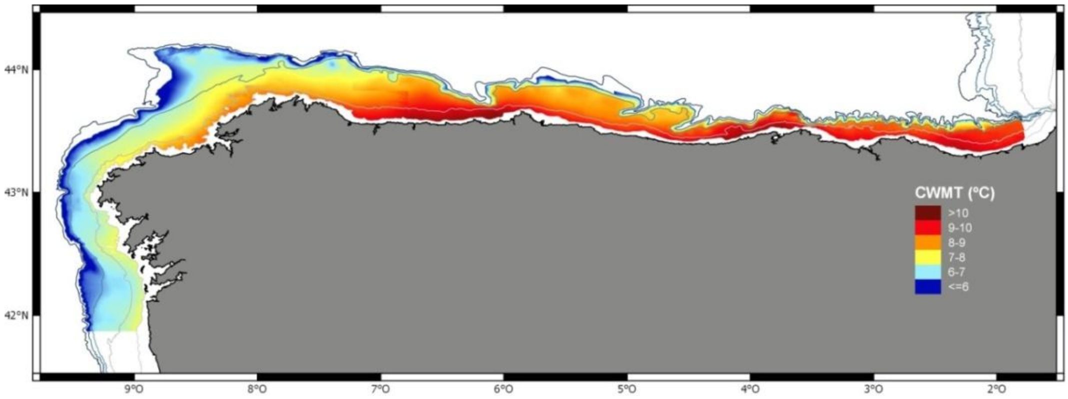


Figure Supp. 4.Spatial distribution of the Community Weighted Mean Temperature (CWMT) over the study period.

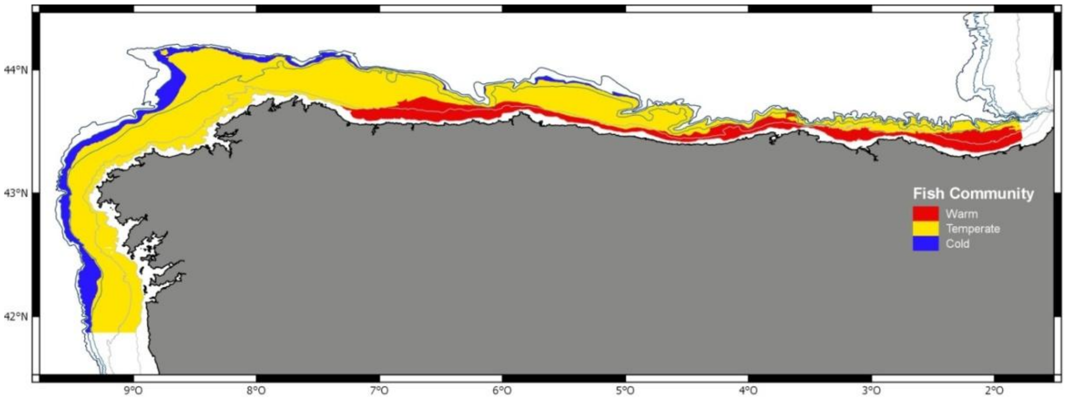
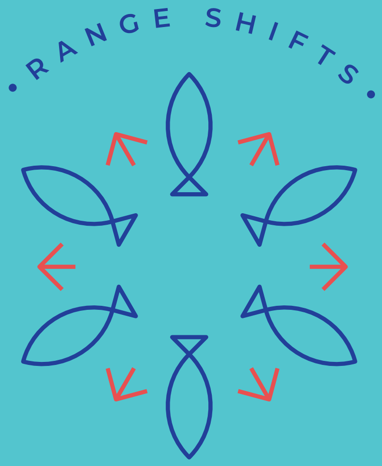


Figure Supp. 5. Spatial distribution by community types: Cold, ≤6.64°C; Temperate, >6.64 and ≤ 9.58°C; Warm, >9.58°C



CHAPTER

03

ATLANTIC AND MEDITERRANEAN COMMUNITIES’ CLIMATE DRIVEN RANGE SHIFTS

A modified version of this chapter has been submitted for publication as the research article ‘Community’s ecological traits reflect spatio-temporal variability of climate change impacts’ by Polo, J., Punzón, A., Hidalgo, M., Pecuchet., L., Sainz-Bariáin, M., González-Irusta, J.M., Esteban, A., García, E., Vivas, M., Gil de Sola, L. & López-López, L. to Ecological Indicators.

CHAPTER 3. ATLANTIC AND MEDITERRANEAN COMMUNITIES' CLIMATE DRIVEN RANGE SHIFTS

3.1 INTRODUCTION

As a consequence of the anthropogenic, long-lasting changes in oceanographic features, most marine ecosystems in the globe have readjusted their structure and function to increasing temperatures, which for many North East (NE) Atlantic ecosystems has implied ecological regime shifts at various levels, from population (Goikoetxea and Irigoien, 2013; Cabrero et al., 2019) and community (Auber et al., 2015; Hidalgo et al., 2022c; Tsimara et al., 2022) to ecosystem level (Möllmann and Diekmann, 2012; Alheit et al., 2019; Bode et al., 2020; IPCC, 2022). The species tracking of their suitable temperature regimes ultimately affects the width, depth and latitude of a community's coverage. Although it is generally expected that marine organisms will redistribute towards cooler (poleward and deeper) regions as a result of climate change, exceptions that result from local variations in temperature, trophic dynamics, species life history and interactions with other stressors are common (ICES, 2017; Molinos et al., 2018; Punzón et al., 2021; Sanz-Martín et al., *under revision*).

Climate change impacts display relevant spatial variability, which has been evidenced around the Iberian Peninsula even at the sub-regional scale (Aragão et al., 2022). On ecosystems associated to the Atlantic Ocean and the Mediterranean Sea this variability comes from contrasting exposure and sensitivity to climate change impacts, along with a cumulative interaction with other stressors, such as fishing. On one side, the communities associated to the Atlantic shelf of Iberian Peninsula, while recovering from long term overfishing (Modica et al., 2014; Hidalgo et al., 2017; Arroyo et al., 2019; Punzón et al., 2021) are also experiencing the impacts of a sea surface warming rate of 0.23 °C per decade (Chust et al., 2022). Regional climate change projections for the southern Bay of Biscay also indicate decreases in surface salinity and a deepening of the winter mixing layer, two processes that have been going on so far and could be leading increases in nutrients and oxygen concentrations identified at sea surface (Erauskin-Extramiana et al., 2019; Chust et al., 2019, 2022). The effect of these impacts on populations and communities has been recognized in the area in several aspects, for example, in the niche tracking and earlier migration of the Northeast Atlantic albacore (Dufour et al., 2010; Chust et al., 2019), in changes in the spawning period of anchovy and mackerel in the Bay of Biscay (Punzón and Villamor, 2009; Erauskin-Extramiana et al., 2019; Rodríguez-Básalo et al., 2022) and as complex ecological regime shifts at various levels (Bode et al., 2020; Polo et al., 2022), to name a few. In general terms, deeper areas have experienced a much subtle and progressive increase of mean temperatures, but still show clear evidences of meridionalization, i.e. increase in the abundance of native fauna with southern affinities (Punzón et al., 2016 and references therein), reflected in the rising Community Weighted Mean Temperature of the Cantabrian bentho-demersal community (Punzón et al., 2021).

In contrast to the Atlantic communities, fishing impacts on Mediterranean fish stocks and communities are large and ongoing (Arroyo et al., 2019; Farriols et al., 2019; FAO, 2022). Fishing pressure in combination with several additional anthropogenic drivers makes Mediterranean populations and communities highly responsive to natural environmental variability (e.g. Hidalgo et al., 2011, 2022c; Quetglas et al., 2013). Mediterranean communities have shown to respond to global change heterogeneously in space, with a clear east to west gradient (Hidalgo et al., 2017; Farriols et al., 2019; D'Amen et al., 2022). Over the whole Mediterranean basin, the sea is warming at a rate of 0.35°C per decade (Pastor et al., 2020), fostering not only the meridionalization, but also the tropicalization (increase in warm-affinity native and non-native species, respectively) of the communities and ecosystems (Bianchi, 2013; Fogarty et al., 2017 and references therein; Vasilakopoulos et al, 2017; Hidalgo et al., 2017, 2022c). The diversity of impacts related to climate change in this region also includes changes in the vertical mixing affecting primary production regimes (Macias et al., 2018), changes in the thermohaline circulation, the local hydrography (Ser-Giacomi et al., 2020), the strength of winter weather events (Gaertner et al., 2018) and an increasing frequency and intensity of marine heatwaves (Darmaraki et al. 2019).

The use of ecological traits or niche features to assess the extent of shifting niches at a community level has typically been focused on temperature, sometimes overlooking other aspects of the species' niche. Examples of indicators based on the preferred temperature of the assemblage are the Community's Temperature Index (CTI; Devictor et al., 2008; Cheung et al., 2013), the Preferred Temperature of the Catch (PTC) or the Mean Temperature of the Catch (MTC; Cheung et al., 2013). All these were designed in order to characterize eventual species turnover from cold-adapted to warm-adapted species, which would cause a change in the community's mean thermal preference.

In this research, we have aimed at a broad, more comprehensive look into the spatio-temporal insights of distribution shifts beyond the relative increase in thermophilic species. We have approached the shifting niches of two impacted bentho-demersal communities by analyzing simultaneously the mean and variance of the frequency distribution of various ecological traits, revealing the specific means in which ecosystems are experiencing climate change impacts (Fossheim et al, 2015; Pecuchet et al., 2016; Beukhof et al, 2019; Husson et al., 2022). Building on the recently published Community Weighted Mean Temperature (Punzón et al., 2021), we computed the Community Weighted Mean and Variance of sea bottom and surface temperatures, salinity, mean depth, latitude and species range size (i.e., area occupied) along with four descriptors of the communities' distributional ranges, i.e., surface and bottom thermal tolerance ranges as well as latitudinal and depth ranges. Our expectation was that the spatio-temporal analyses of these indicators of communities' weighted mean and variance of the ecological niche would provide additional evidence of the response mechanisms of demersal communities to human-induced environmental variability.

3.2 MATERIAL AND METHODS

3.2.1 DATA AND DATA TREATMENT

SURVEY DATA

Species abundance data (number of individuals per km^2) for the most common 246 vertebrate and invertebrate species of the demersal Spanish Mediterranean and Cantabrian Sea (i.e., southern Bay of Biscay) communities were gathered from two bottom-trawl surveys carried on the Iberian Peninsula continental shelf, over a geographic scale with substantial longitudinal, latitudinal, and depth gradients. We settled on this set of species after filtering each survey database to keep species that occurred persistently along the time series (at least 12 years), which were widely distributed in the study areas (at least appeared in 12 hauls each year) and which attained a minimum abundance per haul and thus contributed significantly to the total abundance of the community. Although rare species can have important impacts for the functioning of the ecosystem (e.g., keystone species), here we are interested in studying the overall changes in community composition in terms of abundance, thus rare species were excluded from the analyses by only keeping species with an abundance value over the first decile.

The study areas encompass the Cantabrian Sea, extending from southern Bay of Biscay to north-west of the Spanish shelf, between the mouths of Miño and Bidasoa rivers, and the Mediterranean geographical subarea 6 (GSA6), the eastern Balearic Sea associated to the Iberian Peninsula coast. In the Bay of Biscay, bottom-trawl survey DEMERSALES has been conducted every autumn by the Spanish Oceanography Institute (IEO) since 1983 (with the exception of 1987). In the Spanish Mediterranean ecosystem the MEDITS bottom trawl survey has sampled the bentho-demersal ecosystem every early summer since 1994. Both surveys use similar sampling protocols (DEMERSALES is standardized by IBTS while MEDITS is standardized according to CGPM) and present matching spatial coverage and resolution. To ensure consistency in the identification of invertebrates across the surveys in the Cantabrian region, we only analyzed hauls for the period 1994-2020. Therefore, the surveys cover the periods 1994-2020 (26 years) for DEMERSALES and 1994-2019 (25 years) for MEDITS. Both surveys follow a stratified random sampling scheme with five depth strata (more detailed explanations on the surveys are included in Chapter 1; Spedicato et al., 2019; ICES, 2022). In our analyses we used density (in number of individuals of a species) per haul standardized by swept area (i.e. number of individuals/km^2).

ENVIRONMENTAL PREFERENCES DATA

As descriptors of the species niche we collected an initial set of 31 ecological traits obtained from the bioclimatic envelope models developed by AQUAMAPS (Kaschner et al., 2019) and presence data from the Ocean Biogeographic Information System database (OBIS, 2019). For each species, we estimated its global distribution area as those cells in which it had a probability of occurrence over 50%. Based on this distribution we computed the mean value as well as the 0.1 and 0.9 quantiles for each variable, which will be referred to as minimum and maximum values from now onwards. Ranges for some of the ecological traits were computed by subtracting the minimum (10^{th} quantile) to the maximum (90^{th} quantile). We downloaded data on parameters commonly used to characterize the environmental preferences of demersal species such as sea surface (SST) and bottom (SBT) temperatures (mean, minimum (min.) and maximum (max.) values) and salinity (mean, min. and max. SSS), as well as data associated to the species distribution range, such as occupied area (expressed in km^2), latitude (mean, min., max. and latitudinal range) and sea surface and bottom temperature tolerance ranges (STT and BTT, respectively). Additionally, we calculated the depth (mean, min., max. and depth range) based on the species presence records (OBIS, 2019) and the digital bathymetry provided by EMODNET (http://www.emodnet-bathymetry.eu). For the species lacking a model in AQUAMAPS, we overlapped presence data with the AQUAMAPS environmental dataset, to obtain similar environmental data. We approached the species' environmental preferences following the procedure described by Punzón et al (2021), considering the overall distribution range of each species, thus avoiding the bias of taking in consideration only parameters within the study area. Nevertheless, these environmental preferences should be considered as a proxy for the affinity of the species for specific environmental conditions, rather than the exact optimum niche properties.

3.2.2 COMMUNITY-WEIGHTED MEAN NICHE TRAITS ANALYSES

To characterize the bentho-demersal communities within each haul in terms of their ecological properties, we computed mean ecological values at the community level (CWM) as well as the community-weighted variance (CWV) of the niche traits. The CWM described the average value of a niche trait in a community, whereas the CWV describes the spread of the trait values within the community. Note that a shifting CWV along a gradient would indicate an increasing or decreasing variability in the species' niche traits, but it would not reveal the direction of change. Changes in CWM along the same gradient would provide this insight. Both indexes were computed by weighting the ecological trait value of each single species by its abundance at a given sampling station, following the community-weighted mean trait value approach (Grime, 1998). Prior to undertaking any modeling approach for the study of CWM and CWV, data which were markedly right skewed were log-transformed to approach normally distributed variables. After that, variables were standardized via function *decostand* in R package vegan (Oksanen et al., 2020). For the final analyses in this work, we selected a final set of ten variables and avoided the most correlated and collinear ones computing the Pearson coefficients for every variable combination. To explore spatio-temporal patterns, we mapped the smoothed values of CWM and CWV and fitted General Additive Models (GAMs; Hastie and Tibshirani, 1990) using the gam function in R package mgcv (Wood, 2011), assuming a gaussian distribution and limiting the degrees of freedom of the smoothers to 4.

3.2.3 CLASSIFICATION OF THE COMMUNITIES

Once the bentho-demersal communities at each haul were characterized by their community-weighted environmental preferences, we looked for similarity patterns across each studied area separately, to assess whether the response to climate change was spatially and/or temporally clustered. For this purpose, a non-hierarchical cluster technique, Partitioning Around Medoids (PAM, Kaufman and Rousseauw, 1986), was performed on the CWM composition of the hauls. We prioritized the identification of changes in the direction of the communities and focused this and the following analyses in the mean (CWM) over the variance (CWV) values of the traits. The cluster algorithm divided the datasets into k clusters, building each cluster around a median sample of the dataset (medoid). The integer k that endured well-separated clusters was identified by computing the Silhouette width (Rousseeuw, 1987; Pollard and Van der Laan, 2005) and the minimum sum of square errors within clusters (SSE). To assess temporal changes in the communities' composition in terms of their niche traits, we computed the yearly anomalies regarding the mean proportion of stations classified as Cluster 2 by subtracting from the number of Cluster 2 hauls for a specific year the mean number of Cluster 2 hauls for the whole series. The clustering results were also plotted over a Principal Component analysis (PCA) biplot for each study area. The two first principal dimensions (Dim.1 and Dim.2) of the CWM of Cantabrian and Mediterranean PCAs provided information on the metrics of the communities' niche dimensions, the variance of their geographical range and the extent of the species tolerance to changes in physical conditions. To assess the communities' niche spatio-temporal variability, every CWM niche property was investigated simultaneously through the analysis of the first principal dimensions. The sampling stations' scores (coordinates) of the first and second principal dimensions were used to approach the extent or magnitude of the changes that have taken place in both studied communities, while the inspection of the CWM loadings (contribution of the weighted niche properties to the principal dimensions) gave an idea on the nature of those changes. We used function PCA in R package FactoMineR (Lê et al., 2008) to conduct the PCA, which we based on the correlation matrix following Jolliffe and Cadima (2016).

3.2.4 COMMUNITIES' RATE OF CHANGE IN TERMS OF THEIR NICHE TRAITS

Each haul was assigned to its corresponding cell in a grid of 0.05° longitude and 0.05° latitude. C-squares were used for grid construction and as spatial indexing system (Rees, 2003). To unveil the spatio-temporal trends in CWM environmental preferences we constructed linear regression models for each time series of the first dimension of the CWM PCA (Dim. 1) in each C-square cell using year as a predictor. To build these models, we only kept C-square cells with a minimum of 5 sampling events along the time series. This meant that from the 425 grid cells sampled in the Cantabrian Sea (3417 sampling stations) only 174 remained (2875 sampling stations), and from the 375 C-squares sampled in Mediterranean Sea (2177 sampling stations in total), 142 cells (1670 sampling stations) were suited for the linear regression modeling. For a correct inference of the slope and p-value of each cell trend along the studied period, we accounted for the 'nestedness' of the data (the fact that hauls belonging to a single C-square could be spatially dependent) by explicitly including the model of the C-square nested effects in Generalized Linear Models constructed as follows:

$Dim\ 1 \sim \beta + year/C\text{-}square + \varepsilon$

We assumed a normal distribution of residuals and 'identity' as the link function.

The slope of the models indicated if there was a directional positive or negative change in the studied parameter in the respective C-square cell. Finally, principal component analyses (PCAs) were applied to the temporal trends to identify similarities, spatial patterns and spatio-temporal trends between the CWMs.

All data handling and quantitative analyses were performed using R version 4.1.0.

3.3 RESULTS

3.3.1 COMMUNITY-WEIGHTED NICHE TRAITS

The temporal and spatial patterns of the community-weighted mean and variance of the studied ecological traits revealed major similarities between study areas, although some traits did show regional divergence (Figure 1 and Table Supp. 1). Regarding temporal trends, the Cantabrian bentho-demersal community showed a rising CWM surface thermal affinity (SST), although at bottom (SBT), the rise only takes place after year 2000. The Spanish Mediterranean CWM SST and SBT showed an initial apparent decrease that lifted after mid-2000s. The community's salinity (CWM SSS) affinity values in Cantabrian Sea have decreased, while the Mediterranean's CWM SSS declined across the time series. As for the thermal ranges inhabited by the Cantabrian community, the range of tolerance to surface temperatures (CWM STT) increased while bottom thermal range (CWM BTT) showed an upward trend. The range of surface temperature tolerated by the Mediterranean community widened steadily along the series, having last decade's increase been sharper for these communities' bottom temperature tolerance range.

The mean area occupied by the species structuring the Cantabrian community (CWM area) showed an increasing trend. The Spanish Mediterranean CWM area showed a moderate increasing trend. CWM latitude of both Cantabrian and Spanish Mediterranean communities have generally decreased along the study periods, with a short increasing phase in the Mediterranean region that reversed by year 2000 and is mirrored by CWM depth. In the Cantabrian region, CWM depth has no clear trend. The latitudinal layout, i.e. the distributional range in latitude, of the species forming the Cantabrian communities shifted from a relatively smooth negative trend around low values to an increase towards a wider latitudinal range right after year 2000, tendency mirrored by the Spanish Mediterranean communities. In parallel, at Cantabrian Sea the depth range of the community (CWM depth range) has fluctuated, similarly to the Mediterranean communities. In both regions CWM depth ranges widened initially and contracted after year 2000.

Variances of certain community traits (mid-column of Figure 1 and Table Supp. 1) showed similar temporal patterns between areas. In the Cantabrian communities the CWV of every trait has experimented fluctuating but apparent increases, except for thermal affinity at bottom (CWV SBT), that has decreased from the beginning of the series, showing, however, a recent upward trend that started around 2010, and the range of distribution in depth (CWV depth range), which has fluctuated but at present shows values that do not differ from its initial ones. Spanish Mediterranean communities eco-traits' CWV did not display clear temporal trends, but fluctuated, at the exception of CWM BTT and CWM mean latitude, which increased during the study period, similarly to the Cantabrian communities.

The CWM trait values varied spatially (right column of Figure 1). The lowest values of CWM surface and bottom temperatures (SST and SBT) are observed in the communities associated to the Cantabrian Sea, with lower values at the western part of the study area, the Galician margin, and increasing towards the eastern part, the inner Bay of Biscay. CWM SBT reflects the bathymetry of both areas for its most part, with the exception of the areas of the Galician margin typically influenced by upwelling, and the mid latitudes of the Spanish Mediterranean coast, where communities feature affinity to warmer waters even at higher depths. CWM salinity showed higher values at lower depths in both areas and its lowest values in the Spanish Mediterranean communities, with considerable spatial heterogeneity. The thermal ranges inhabited by the species are narrower and more spatially variable in the Mediterranean area.

In terms of traits related to the species distributional ranges, the communities are composed of species with wider ranges of distribution the further from the coast line in both areas, with distinct higher values in the southern regions of the Mediterranean Sea. CWM depth appeared to be generally shallower in the Mediterranean communities, inner Bay of Biscay and Cantabrian coastal communities. Both CWM depth and depth range mostly reproduce the bathymetry and geographic gradients in both areas. Spanish Mediterranean communities show much lower CWM latitude. While on average these communities are only 5° of latitude apart, their CWM latitude varied by as much as 15° in many cases. Communities in the westernmost edge of Cantabrian Sea are those with distribution ranges wider in depth but more limited distributions in latitude. The Mediterranean communities had generally higher CWM latitudinal ranges and lower CWM depth ranges than the Atlantic community, with a strong heterogeneous gradient.

3.3.2 CLASSIFICATION OF SAMPLING STATIONS

The most reasonable grouping pattern for both Cantabrian and Mediterranean seas CWM datasets were identified as a k=2 (Figure Supp. 1 and Figure Supp. 2). The environmental preferences typifying each cluster group were determined and are stated in Figure 2 and plotted in Figure Supp. 3 in the Supporting Information. In the Cantabrian region stations with higher CWM bottom and surface thermal affinities, narrower depth range and smaller area occupied are grouped together in Cluster 1. The second cluster comprises stations characterized by much lower community weighted mean bottom temperatures and stations with higher relative abundance of species with extensive distribution areas and able to tolerate wider depth ranges. CWM thermal ranges (STT and BTT), salinity, latitude and depth slightly differ between groups, but differences are not decisive. The two different groups seem to coexist in time (Figure 2A) and space (Figure Supp. 4 in Supporting Information). As for the Spanish Mediterranean bentho-demersal communities, they were also clustered in two main community types (Figure 2 B). Firstly, PAM grouped together sampling stations with higher CWM bottom thermal affinity and salinity, smaller area of distribution and narrower latitudinal range as well as thermal tolerance ranges. Stations classified as the second group, mostly found in the second half of the studied time series, have lower CWM preferred bottom temperature, wider latitudinal range and lower values of CWM depth and latitude, meaning they display higher relative abundance of species inhabiting more southern, shallower waters. In the communities of this region, the two groups are more distinctively distributed in time and space.

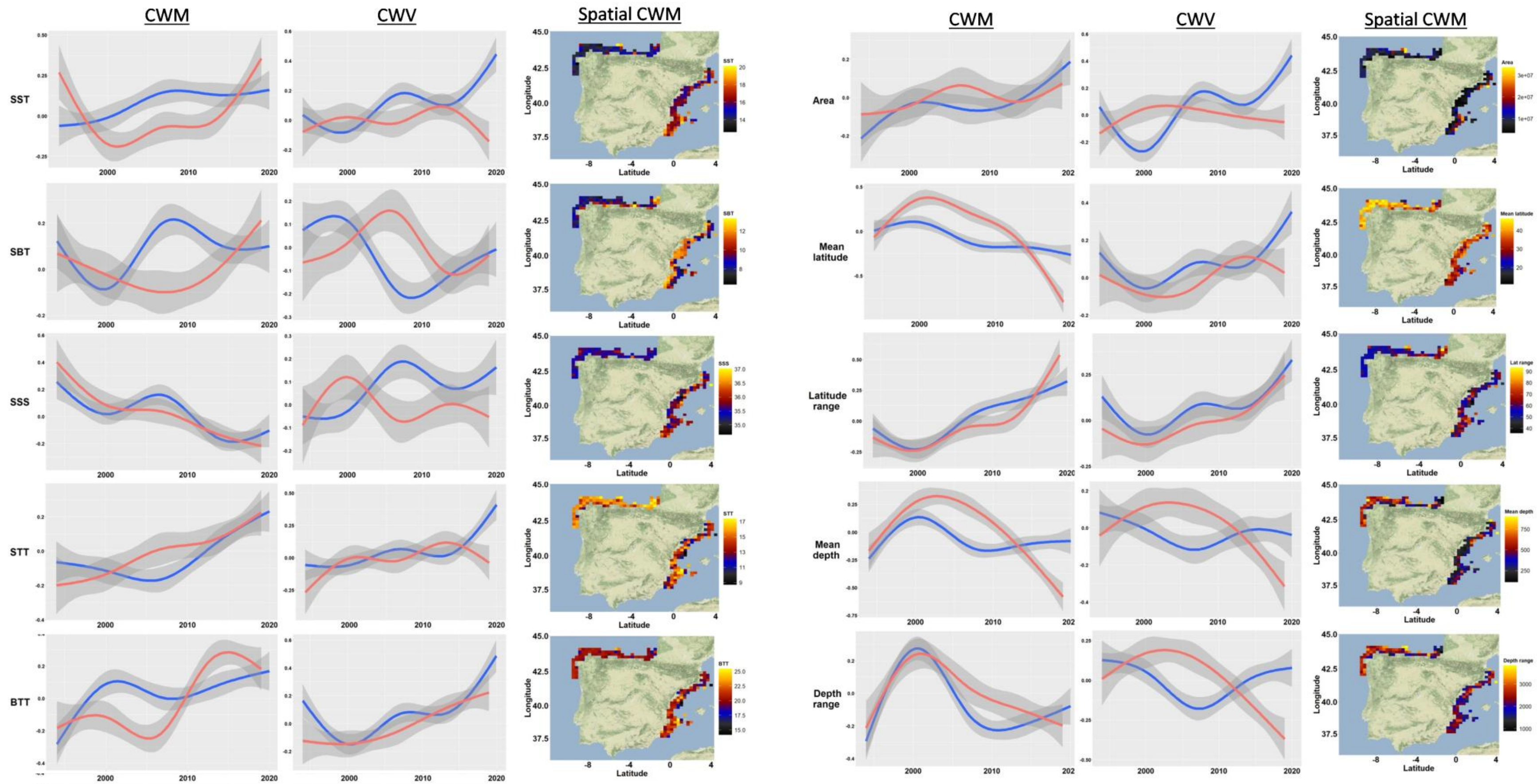
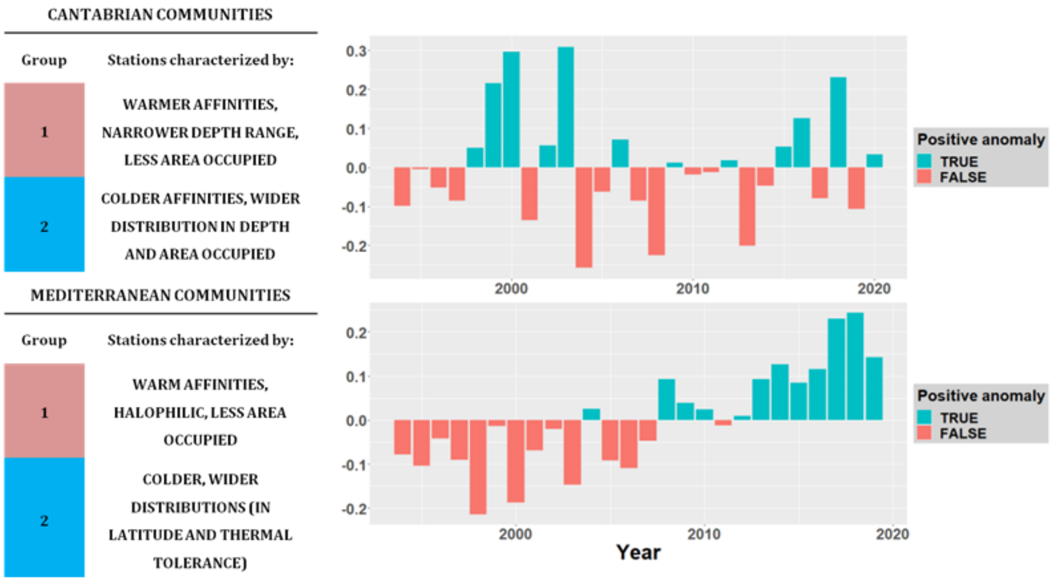


Figure 1. Community-weighted mean values (CWM) and community-weighted variance (CWV) of sea surface and bottom temperature (SST and SBT, respectively), sea surface salinity (SSS), surface and bottom temperature tolerance ranges (STT and BTT, respectively) and area occupied (Area), latitude (Mean latitude) and latitudinal range (Latitude range), depth (Mean depth) and depth range (Depth range). Blue line and red line represent the observed changes in community-weighted means (left column) and variances (right column) in the Cantabrian and Mediterranean seas, respectively, and the grey area represents the 95% confidence interva



CANTABRIAN COMMUNITIES

Group	Stations characterized by:
1	WARMER AFFINITIES, NARROWER DEPTH RANGE, LESS AREA OCCUPIED
2	COLDER AFFINITIES, WIDER DISTRIBUTION IN DEPTH AND AREA OCCUPIED

MEDITERRANEAN COMMUNITIES

Group	Stations characterized by:
1	WARM AFFINITIES, HALOPHILIC, LESS AREA OCCUPIED
2	COLDER, WIDER DISTRIBUTIONS (IN LATITUDE AND THERMAL TOLERANCE)

Figure 2. Annual anomalies regarding the mean proportion of stations classified as Cluster 2 for the whole series, and environmental properties characterizing Cantabrian (A) and Mediterranean (B) cluster groups.

The first dimension (Dim. 1) of the Principal Components Analysis on the CWM niche properties accounted for 34.1% of variation in the Cantabrian data and 40.5% of variation in Spanish Mediterranean data. Cantabrian Sea communities are distributed along a gradient defined by their preferred bottom temperature, the surface temperature range of tolerance and the area occupied by the species (Figure 3 and Figure 4). Thus, this dimension defined by the PCA marks, on one side, sampling stations defined by species with wider distributions, broad thermal ranges of tolerance (at surface and at bottom) and spread across larger areas and depth ranges; and on another side, stations with higher mean thermal affinity at bottom and higher community mean salinity. After year 2005, the community shifted towards wider distribution ranges in extension as well as in thermal, depth and latitudinal range (top Figure 4). Also, the Cantabrian community has undergone an increase in mean surface thermal affinity (top Figure 4).

In the Spanish Mediterranean Sea, the communities have a strictly monotonic increasing trend in their first dimension, transitioning from stations with a higher CWM SBT, CWM SSS, and narrow CWM distributional ranges (in depth, latitude and area), towards stations characterized by larger CWM temperature ranges of tolerance and wider latitudinal expansion. The ecological traits that most contribute to the first axis of variation of Mediterranean data refer to the thermal range of tolerance and the latitudinal range, while the second axis mostly segregates stations with higher CWM latitude and depth and low surface temperature (more dominant at the beginning of the time series) from stations with higher surface thermal affinity and lowest CWM depths and latitudes (ecological traits whose dominance increased throughout the study period, (bottom Figure 4).

The integrity of the groups identified by the clustering technique in both studied datasets was corroborated in the PCA, as shown in top and bottom Figure 3.

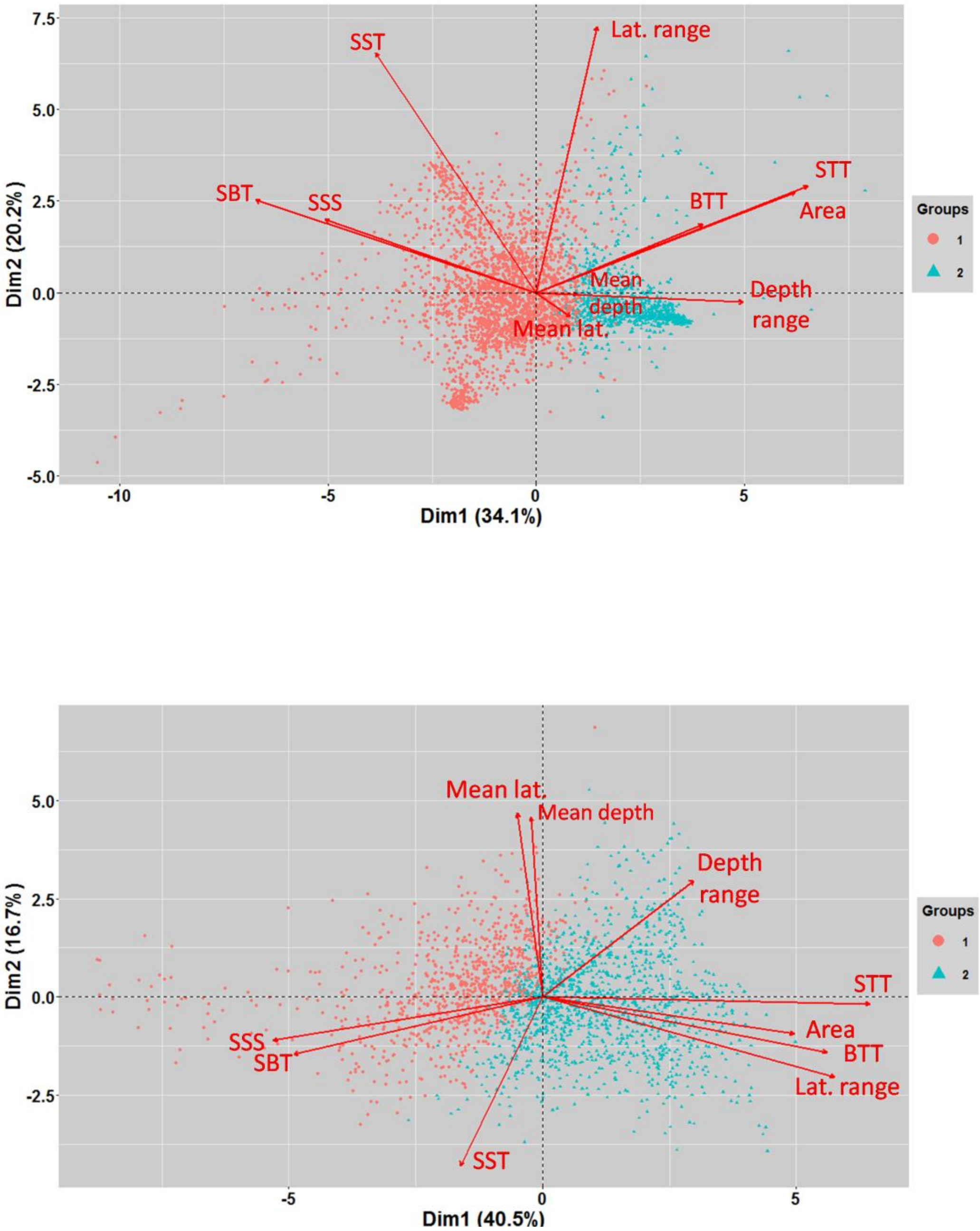
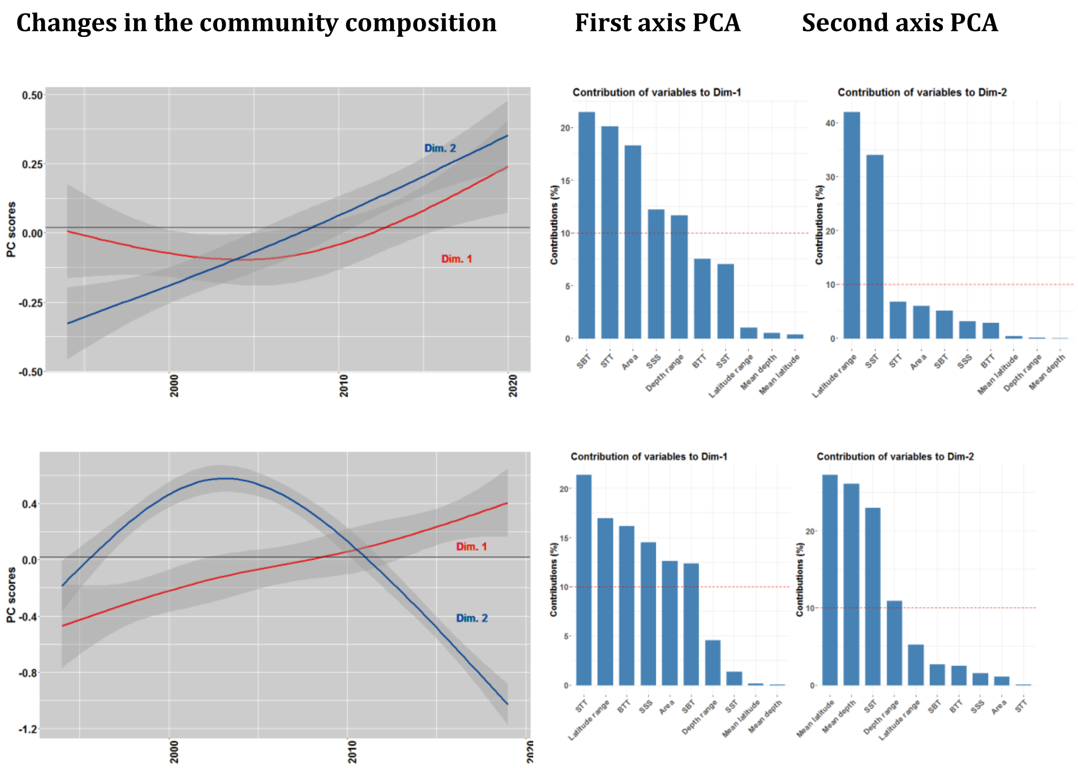


Figure 3. Principal component analysis of Cantabrian (top) and Spanish Mediterranean (bottom) sampling stations. Stations are colored according to the cluster groups described in Figure 2.



Changes in the community composition **First axis PCA** **Second axis PCA**

Figure 4. Cantabrian (top) and Spanish Mediterranean (bottom) observed changes in community composition across the time series (left plots). Red line shows the evolution of the first principal component of the PCA, and blue line represents the temporal changes of the second dimension of the PCA. Main five contributing ecological traits to first and second axis of the PCA are represented in the two right plots.

3.3.3 SPATIO-TEMPORAL CHANGES OF THE COMMUNITIES IN TERMS OF THEIR NICHE PREFERENCES

The temporal changes of the bentho-demersal communities' ecological traits (summarized as Dim. 1, the first dimension of the CWM traits PCA) varied spatially (Figure 5). This figure only displays the coefficients of the significant temporal models (to visualize also non-significant models see Figure Supp. 5). The communities inhabiting the Cantabrian Sea presented a negative trend in 33% of the surveyed C-squares. In these cells, mostly allocated in the shallower sub-regions of this region, there has been a shift towards more thermophilic communities, with a species composition more limited in their ranges of distribution. Only the 5% of the cells showed the opposite trend, i.e., towards wider ranges of distribution in depth, wider thermal niches and affinity for colder waters. These communities are located in deeper waters of the inner Bay of Biscay. Most of the Mediterranean C-squares analyzed, approximately a 70%, showed a displacement towards a species composition with wider distributions in latitude, wider thermal ranges and area occupied, and affinity for colder temperatures. This trend has been more pronounced in communities inhabiting deeper areas.

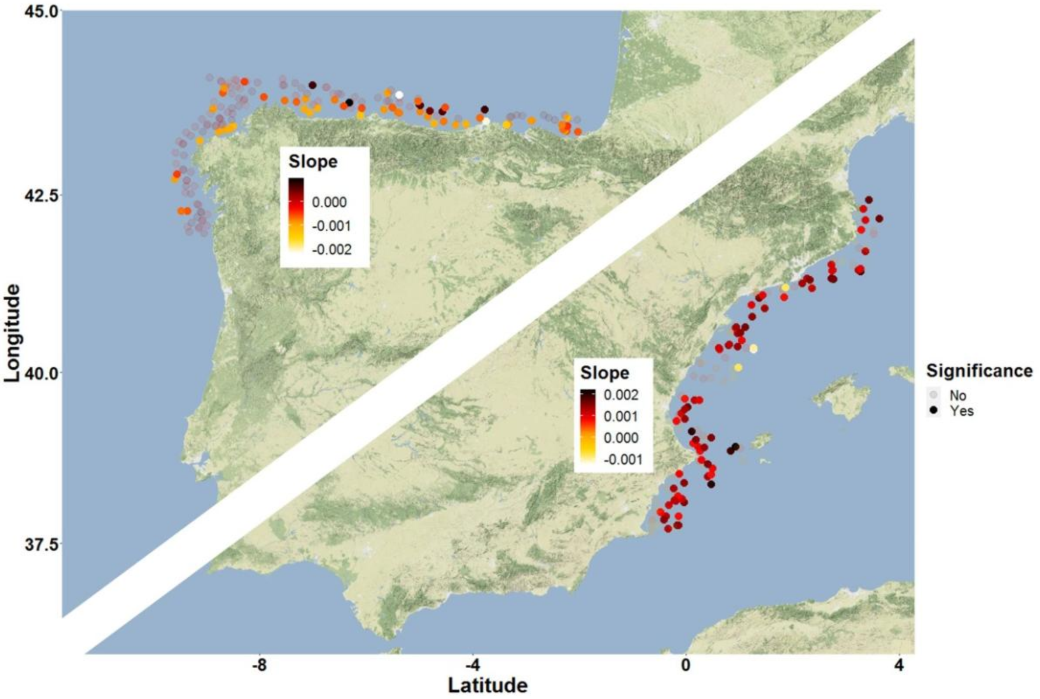


Figure 5. Spatial distribution of communities change in terms of their species ecological traits. Colored points indicate the direction of change across the time series, the dominant ecological traits towards which communities have shifted, as obtained from the coefficients of the first dimensions (Dim. 1) models for Cantabrian Sea and Spanish Mediterranean Sea communities. Non-significant models are indicated with a semi-transparent point. Darker dots correspond to C-squares with positive trends, i.e. towards higher values in the first axis of the PCA, and yellow and white cells are those in which the GLM models had a negative trend, which in both areas reflects an evolution towards stations dominated by warm-affinity, more restrictively distributed species. Note that the scales in the Cantabrian Sea and the Spanish Mediterranean are independent.

3.4 DISCUSSION

Global change is driving major changes in the location of suitable habitat for many species worldwide and Iberian marine ecosystems are no exception. Our findings have revealed that shifts in species distributions of bentho-demersal communities around Iberian Peninsula are ubiquitous and prevalent. We have studied two communities known to be closely tracking changes in sea surface temperature and have found their tropicalization processes resemble in many respects and are not limited to the increasing contribution of warm-affinity species, but also affect their distributional ranges, with regional differences that regard not only mean values but also the variance of communities ecological preferences or traits. In the last decades, the composition of the Cantabrian Sea bentho-demersal communities, in the North-East (NE) Atlantic, have shifted its mean thermal affinity in the process of accommodating higher abundances of species with lower latitudes and wider latitude ranges of distribution. In parallel, it stands out how the Spanish Mediterranean communities' tropicalization process features a general widening of the community's ecological ranges. Both regions have also experienced a high variation in most of the studied niche related preferences, mostly noticeable from the 2000s decade. Differences in communities' response might arise from the biotic systems' different adaptive capacity, which we argue are mostly a result of their climatic and physical environment and their demographic structure, which imply different coping mechanisms to external disturbances.

Temperature is one of the main axes of the ecological niche space, as it serves as proxy for distributional features such as latitude and depth and it is a determinant factor of the distribution of species (Kleisner et al., 2017). The temperature of preference of a biotic assemblage is expected to show a direct response to warming; therefore, it has been the species ecological trait the most commonly used to assess range shifts and turnover of species in warming environments at the community level (e.g. Cheung et al., 2013; Vasilakopoulos et al., 2017; Morley et al., 2018). In this respect, we identified an increase in Cantabrian Sea CWM surface temperature and both surface and bottom thermal ranges, indicating not only that Cantabrian communities are changing in terms of their preferred temperature, but also increasing and diversifying their thermal tolerance. In addition, CWM latitude is decreasing, reflecting the community's hosting of species from lower mean latitudes, a known process in the area and the expected response as some populations progressively meet the limits of their thermal niche (Ter Hofstede et al., 2010; Le Marchand et al., 2020; Chaudhary et al., 2021). It is also in line with Punzón et al. (2021), who documented a decrease in Atlantic cold-favoring species in the Cantabrian community parallel to a thriving of Lusitanian warm-favoring species. In contrast, our results showed temporal fluctuations in the Spanish Mediterranean bentho-demersal CWM SST and SBT. This is differing to the results of Hidalgo et al. (2022c), who found the community had undergone a widespread rise in the relative contribution of thermophilic fish and invertebrate species. This increase, which would be expected at an area with significantly higher warming trends (D'Amen and Azurro, 2020), is only discernible in our results after the mid-2000s, at a time in which the widening of Spanish Mediterranean CWM sea surface thermal range also took off for the thermal range at bottom. Around this period, between the late 90s and mid-2000s, a regime shift across various trophic levels has been observed (Tsimara et al., 2021; Hidalgo et al., 2022c). Hidalgo et al. (2022c) associated it mostly to primary production dynamics facilitated by a long-term continuous anthropogenic degradation. We can infer the pervasiveness of this shift from the change in tendency of many of the Mediterranean's community niche traits studied here. CWM and variance of mean depth and latitude of Mediterranean communities, for example, started reflecting a relative increase in shallower species from lower latitudes, which also implied more variability in preferred latitudes but narrower depth ranges (CWM Depth Range) as well as fewer variability in terms of mean depth (Depth's CWV).

In this same line, a shifting point also arose during the first decade of 2000 for most of the niche traits (e.g., CWM SBT, SSS, BTT, Area, Mean latitude and Lat. Range and Mean Depth and Depth Range) in the Cantabrian Sea communities. This change matches a regime shift that has been interpreted as a response to the combination of a changing environment and the release from a historically severe fishing pressure (Polo et al., 2022) as well as a cue of a more global ecological regime shift in NE Atlantic (Hemery et al., 2008; Luczak et al., 2011;

Auber et al., 2015; Bode et al., 2020). In our study, it translates as minor changes in the biotic system's dynamics, which is driven towards a period with no consistent trends in bottom thermal affinities and a rise of preferred bottom temperatures as well as a decrease in the community weighted mean depth range. The period after year 2000 is characterized by a decrease in fishing efforts, and thus the relieve of large effects of fishing in the community, but also by a sharper emergence of warming effects (Punzón et al., 2016, 2020; Polo et al., 2022). The expansion appreciated in the area occupied, the surface thermal range and latitudinal range of the communities in this second period complements the most straightforward expectation, which would be a response mostly characterized by a steeper rise of thermal affinities. The increase of mean and variance of surface temperature tolerance within the community is observed in both study areas, and it reflects the increasing relative contribution of species with eurythermal niches. These species would be favored at the expense of more stenothermal organisms, as a tolerance to wide temperature ranges would allow them to settle and succeed more easily in rapidly warming environments than species heavily constrained in their thermal tolerances (Dhalke et al, 2020). In the Mediterranean communities, these sharp increases in mean thermal ranges could be due to the increasing abundances of 'flexible' species, with larger niche breadths, which would allow communities to better cope with environmental extremes and environmental instability (Sexton et al., 2017).

We might find more on this 'flexibilitation' of niche breadths at other community features, such as CWM depth and depth ranges, salinity and distribution in latitude. It is noteworthy that the preferred depths of the Spanish Mediterranean species pool are generally shallower than the Cantabrian Sea's (along with narrower depth ranges). In the Galician margin of Cantabrian Sea CWM depth values typical from upper-slope communities (500-750 m) extend to coastal areas, while in the most southern communities of Spanish Mediterranean show CWM depths of continental shelves (250 m) that extend to the upper slope. The increase of shallow water species at depth in this area of Mediterranean Sea might relate to the increase in the relative contribution of species of Atlantic origin (Navarro-Barranco et al., 2019; Real et al., 2021). Atlantic species entering the Mediterranean through the Strait of Gibraltar are generally species with preference for shallow depths, given the barrier effect of this shallow corridor for deep biota, and show narrow bathymetric ranges but broad in latitude, which makes them more easily adapted to new environments (Real et al., 2021). This turnover is indeed one of the characteristics of the previously mentioned regime shift described by Tsimara et al. (2021) and has also been observed by Sainz-Martín et al. (*under revision*), whom associated it to a displacement in the centers of gravity of key species in the community towards higher depths and linked this configuration of the communities, mainly composed of species with shallower distributions, to higher sensitivity to natural environmental variability (e.g. changes in primary production). In their study, Sanz-Martin et al. (*under revision*) also identified key demersal species shifting their abundance distributions in accordance to sub-regional patterns of warming. They studied climate velocity and climate trajectories in the Western Mediterranean ecosystem and described a local maximum of warming in the Gulf of Valencia, in the middle of their (and our) study area, where climate trajectories originated and diverged to the North and the South. In our results the Gulf of Valencia came out as the area with higher CWM SBT, suggesting a sub-regional adaptation of the communities to higher warming rates.

Among the key ecological traits for marine species, salinity is also considered to have an important role in structuring benthic communities and has been previously related to shifts in biomass (Neumann et al., 2016; Weinert et al., 2016). Within the Cantabrian Sea bentho-demersal communities, CWM salinity has decreased, although its variance increased, an ecological variation apparently disconnected from fluctuations in the environmental salinity, which has not substantially changed in the area during the studied period (Chust et al., 2022). In the Spanish Mediterranean, on the other hand, the steep decrease in CMW salinity over time contrasts with the increase in environmental salinity described in the area from surface to deep waters (Vargas-Yáñez et al., 2017). Given the decoupling of the ecological indicator of CWM salinity from actual in-situ salinity values, the appreciated decreases in the Mediterranean region are probably another sign of a higher dominance in the community of flexible species with mainly Atlantic distributions, and thus lower mean salinities, with respect to more stenoic, endemic Mediterranean species, with higher mean salinity affinities. The climate-driven range contraction for a large number of native species in the western Mediterranean Sea was predicted by Albouy et al. (2013) and might be also reflected in the decreases of certain community traits' variance, i.e. thermal affinity at bottom, mean depth and depth range. This means that while better adapted species are increasing in abundance, abundance of other non-adaptive species is lost.

Regarding the ecological traits directly related to the geographical distribution, processes driving both Cantabrian Sea and Spanish Mediterranean communities are alike once more. Community Weighted Mean (CWM) area did not show any consistent pattern, although a slight increase could be hinted in the Cantabrian communities and latitudinal and depth ranges showed opposing responses. Latitudinal ranges within the community are generally increasing and diversifying (i.e., increasing in variance), while depth ranges are generally decreasing and homogenizing (i.e., decreasing in variance). These contrasting patterns suggest that species with wide latitudinal distributions have had an adaptive advantage under changing conditions, unlike species with wider depth distributions, which could be related to the fact that adaptability along the depth gradient has a physiological limit that demersal species might have already exhausted (Rutterford et al., 2015). In fact, large latitudinal distributions are commonly related to some sort of structuring at the meta-population level, providing species with increased phenotypic plasticity and thus a higher capacity to adapt to changing conditions at the regional scale (Sultan and Spencer, 2002). High phenotypic plasticity to adapt to novel environments, i.e. environmental generalists, is a common characteristic of species moving into new environments or experiencing strong environmental change, with large, generalist, motile species assumed to have the greatest advantage (Frainer et al., 2017). While only pertaining to ecological traits, our results also suggest that having a wide latitudinal distribution could have indirectly conferred species an adaptive advantage under changing environments.

When combining the CWM traits into a multivariate indicator (through its first dimension, Dim. 1), contrasting temporal dynamic patterns between Cantabrian and Spanish Mediterranean communities emerged. Cantabrian stations confirmed a generalized meridionalization, trending towards an increased predominance of warmer affinities, narrower ranges and distribution areas. Conversely, the Mediterranean stations showed an increasing predominance of wider distributions (both in latitudinal and thermal values) hinting for a complex mechanism of temperate communities at accommodating climate change, in which the environmentally constrained species are replaced by more cosmopolitan ones. These tendencies are not spatially even in neither area. In Cantabrian Sea, communities along the depth gradient have followed opposite directions. Shallower stations have shifted towards a more thermophilic composition whilst the communities associated to the outer continental margin (in the inner Bay of Biscay as well as the Galician margin) were driven towards wider thermal and depth ranges and higher predominance of species with wide distributional range areas. This comes up as expected, since assemblages inhabiting the coastal areas are generally more exposed to climate change impacts than those in the open ocean, either by the quicker exchange of heat from and to the atmosphere or by the increased frequency of exceptional storm events and freshwater runoff from terrestrial flooding (Whiteley et al., 2018; Simões et al, 2021). The communities associated to the westernmost area of the Cantabrian Sea (Galician margin) are somehow protected from the loss of their most sensitive species (those less tolerant to environmental changes or already inhabiting their thermal limits), due to not only a more direct contact to a larger water mass, but also to spring and summer upwelling, an oceanographic phenomenon known to soothe the annual warmest extremes in the area (Lavín et al., 2006; Santos et al., 2012). In the Mediterranean, CWM ecological traits follow a more consistent trend at the local scale, with most sampling stations displaying positive trends and thus undergoing the described change towards species with larger latitudinal ranges and colder temperature affinities. This generalized widening of most distributional ranges in Mediterranean bentho-demersal communities might be yet another sign of the projected reductions in abundances of endemic and native species (Albouy et al., 2013). Despite it being a generalized progression, it also shows some bathymetrical segregation, deep stations in the Catalonian margin and Ibiza Channel show the highest rates of change while at the central Gulf of Valencia there is a cluster of sampling stations where trends are not significant, which pinpoints once again the singularity of this area, where the highest climate warming velocities in the study area take place (Sanz-Martín et al., *under revision*).

As part of our effort to analyze general patterns of the communities' niche, we have studied large temporal trends in two areas known to have certain heterogeneity in their exposure to external perturbations as well as in their ecosystem structure. Studies that analyze marine communities' niche reorganizations at a more local scale and integrating regional dynamics are still needed and could probably help achieve a more accurate picture of ecosystems' responses to anthropogenic impacts, which is of central importance for adaptive approaches to ecosystem management (Aragâo et al., 2022). Our approach attempted at a wide, multivariate look of how environment determines communities' distribution, but our analysis did not directly explore cause-effect relations neither considered fishing pressure as a possible driver of these complex community changes. Also, the studied CWM ecological preferences have proved to be a good indicator of the community dynamics, but they are calculated based only on the most frequent and abundant organisms in the communities, thus not reflecting immediate immigration-extinction dynamics or the entry or leakage of non-indigenous species (NIS), a rare phenomenon in the Cantabrian Sea (Punzón et al., 2016) but quite common in the Mediterranean region, where the rate of detection of NIS has accelerated after the year 2000 (Coll et al., 2010; Arndt & Schembri, 2015; Marbà et al., 2015).

The ecological indicators studied here might be useful for ecological forecasting. Since climatic predictions for these two areas highly differ, we would expect most indicators to follow different temporal trajectories. On one side, warming in Cantabrian Sea is projected in various RCP/SSP scenarios to slow down due to a debilitating Atlantic meridional overturning circulation (Gierz et al., 2015). Also, the spatial continuity of Atlantic communities might make them more adaptive to changing conditions, i.e., they could sustain a more pervasive effect of global impacts (Shackell et al., 2012; Hidalgo et al., 2017; Polo et al., 2022). Mediterranean Sea perspectives are more severe; it is one of the most responsive regions to climate change and is expected to be affected by many climatic risks along with a warming average of 2.8°C by 2080–2099 (Albouy et al., 2013; Hidalgo et al. 2022b). Mediterranean's marine fauna highly contributes to the world's marine biodiversity through, among others, many endemic species. We encourage further studies that elaborate on the specific effects of this biogeography shifts on taxonomy and biomass dynamics at a species level, and to properly assess the extent of the transition into a 'tropicalized', cosmopolitan community effects, which might already be affecting the ecosystems' functionalities. At a time in which marine ecosystems are increasingly affected by anthropogenic-driven pressures, notably climate change, it is primordial to understand marine community responses to these pressures to better anticipate and mitigate ecosystem changes.

3.5 SUPPORTING INFORMATION

APPENDIX 1: SUPPORTING TABLES

Table Supp. 1. Summary of the community-weighted mean (CWM) and variance (CWV) tendencies of the studied niche traits for Cantabrian and Spanish Mediterranean bentho-demersal communities. Up arrows (↗) refer to upward trends and down arrows (↘) to downward trends. Hyphen (-) represents features with no clear trend.

Niche traits:	**Cantabrian Sea**		**Spanish Mediterranean Sea**	
	CWM	**CWV**	**CWM**	**CWV**
Sea Surface Temperature	↗	↗	↘↗	-
Sea Bottom Temperature	-	↘	↘↗	↗↘
Surface Temperature Tolerance range	↗	↗	↗	- (↗)
Bottom Temperature Tolerance range	↗	↘↗	↗	↗
Sea Surface Salinity	↘	↗	↘	-
Area occupied	↗	↗	-	-
Mean latitude	↘	↗	↘	-
Latitude range	↗	↗	↗	↗
Mean Depth	-	-	↗↘	↗↘
Depth Range	↗↘	-	↗↘	↗↘

APPENDIX 2: SUPPORTING FIGURES

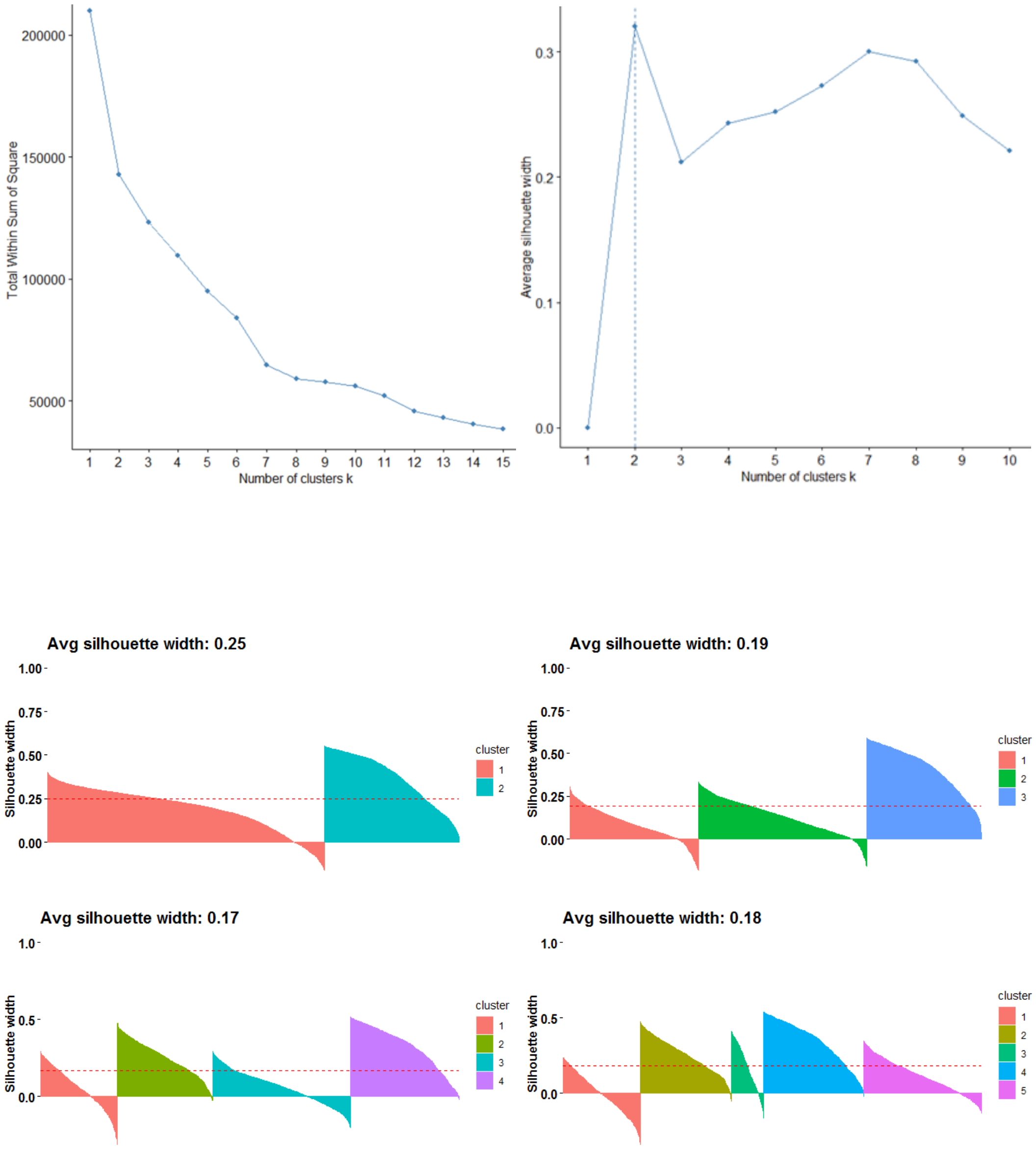


Figure Supp. 1. Elbow method (left) and overall Silhouette Width (right and lower figure) results indicating the optimal number of clusters at a k=2 for Cantabrian Sea sampling stations data. As methods produced different optimal grouping (k values), we based our decision on the observation of the Average Silhouette width, higher for 2 clusters. The plot visually displays a measure of how close each point in a cluster is to points in neighbor. A higher coefficient corresponds to samples being further from one another. Negative values reflect the amount of samples that might have been wrongly assigned.

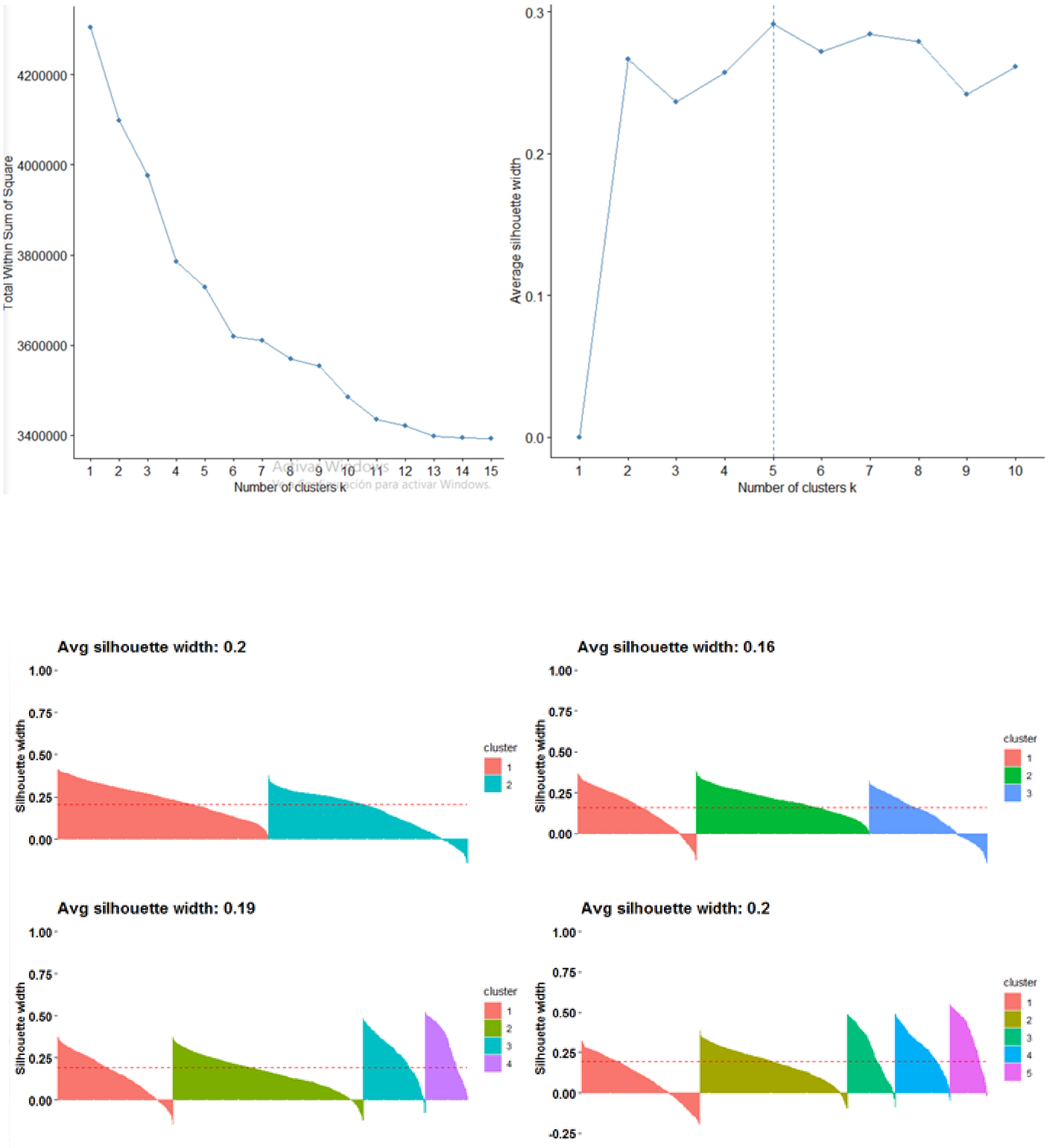


Figure Supp. 2. Elbow method (left) and overall Silhouette Width (right and lower figure) results indicating the optimal number of clusters at a k=2 for Spanish Mediterranean Sea sampling stations data. As methods produced different optimal grouping (k values), we based our decision on the observation of the Average Silhouette width, higher for 2 and 5 clusters. The plot visually displays a measure of how close each point in a cluster is to points in neighbor. A higher coefficient corresponds to samples being further from one another. Negative values reflect the amount of samples that might have been wrongly assigned.

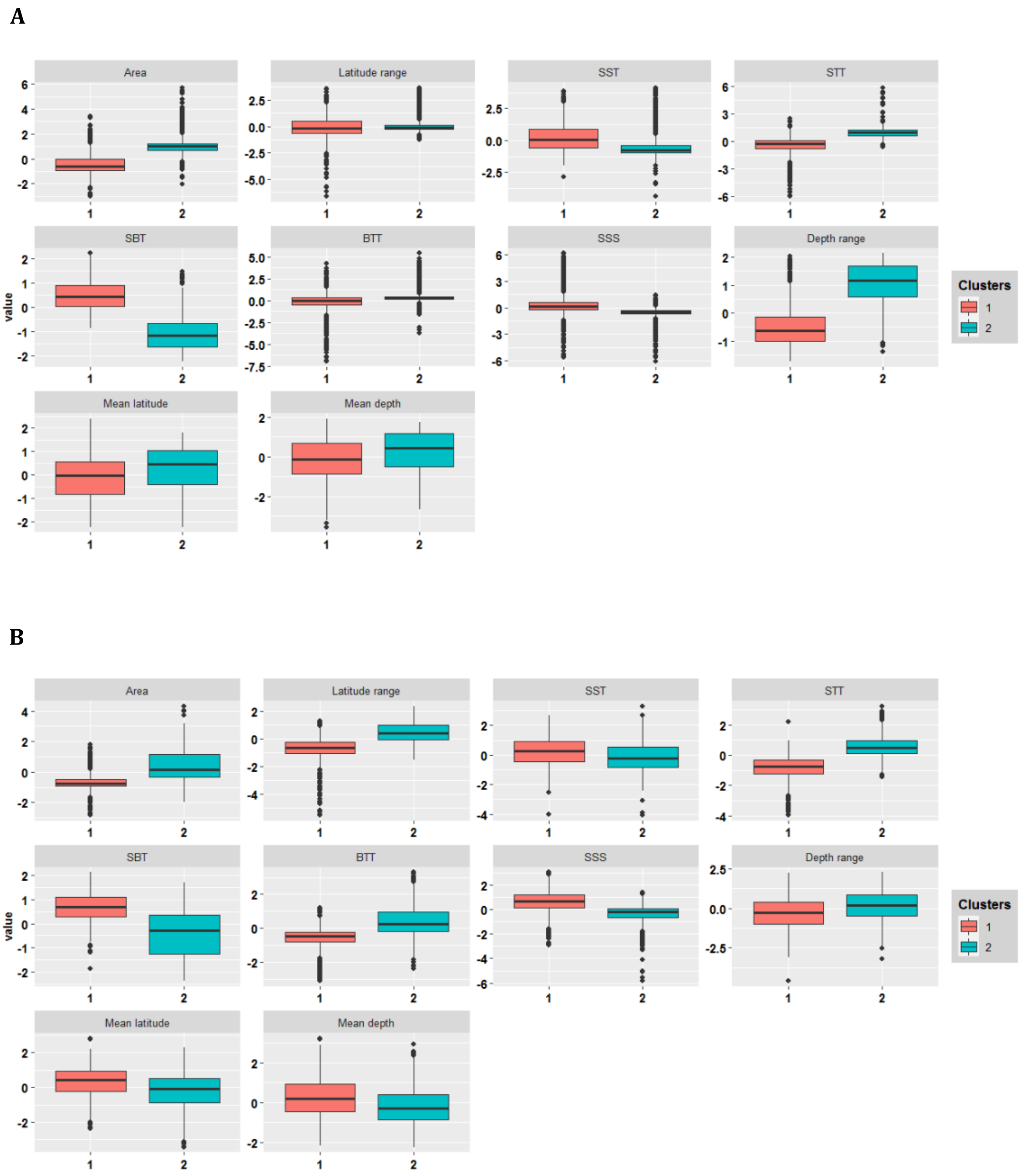


Figure Supp. 3. Environmental properties for each of the two clusters of Cantabrian (A) and Spanish Mediterranean (B) sampling stations.

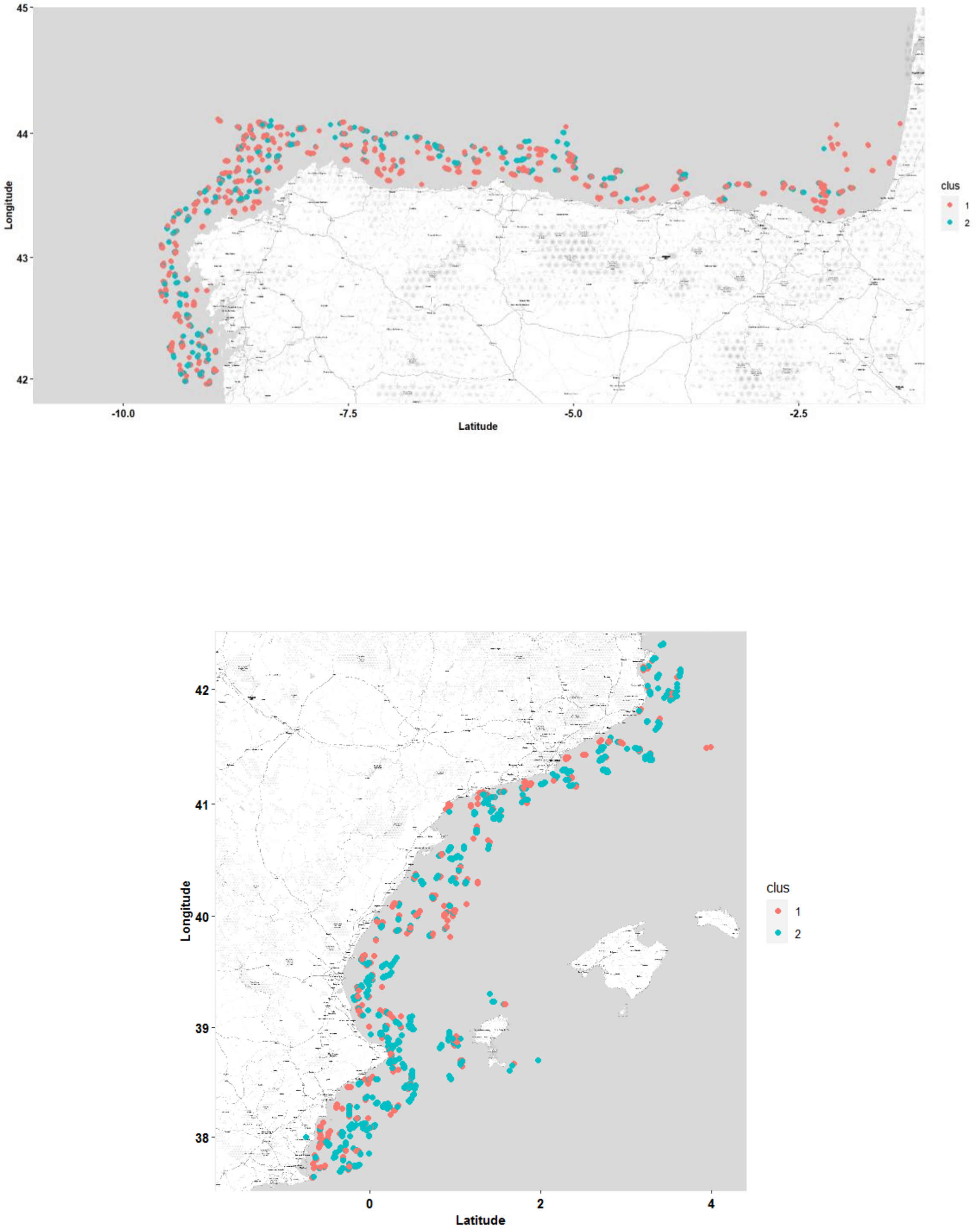


Figure Supp. 4. Spatial display of sampling stations colored according to their classification as Cluster 1 (red) or Cluster 2 (blue), for both study areas, Cantabrian Sea (top) and Spanish Mediterranean Sea (bottom).

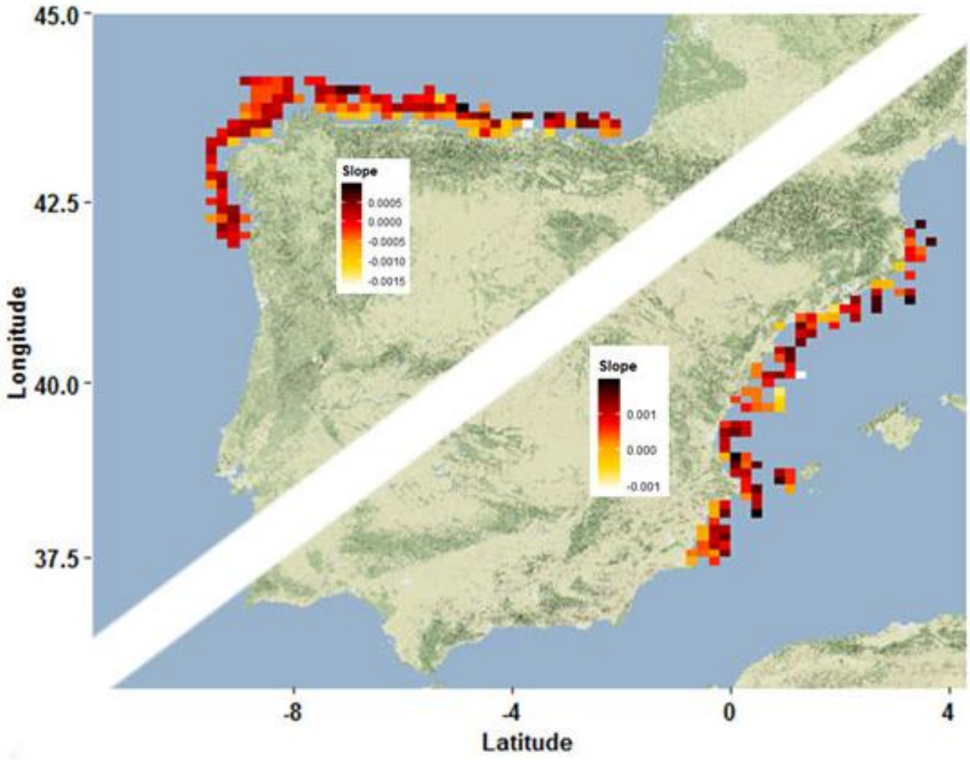
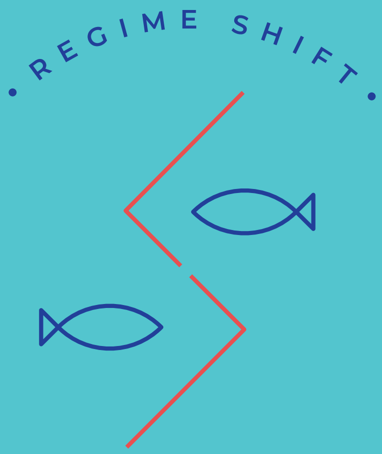


Figure Supp. 5. Spatial arrangement of communities' changes in terms of their environmental preferences, as obtained from the coefficients of every model, including non-significant (p-value > 0.05), for Cantabrian and Spanish Mediterranean communities. The gradient shown in the map is the result of plotting the mean coefficient of neighbour C-squares. Dark colors represent a tendency of the communities at that given area towards species with wider distributional ranges and colder-affinities.



CHAPTER

04

ANTHROPOGENIC DRIVEN TRANSITIONS IN THE DEMERSAL ECOSYSTEM OF CANTABRIAN SEA

A modified version of this chapter has been published as the research article 'Environmental and anthropogenic driven transitions in the demersal ecosystem of Cantabrian Sea.', by Polo, J., Punzón, A., Vasilakopoulos, P., Somavilla, R., & Hidalgo, M., in 2022 in the ICES Journal of Marine Science, vol. 79(7), 2017-2031.

CHAPTER 4. ANTHROPOGENIC DRIVEN TRANSITIONS IN THE DEMERSAL ECOSYSTEM OF CANTABRIAN SEA

4.1 INTRODUCTION

Natural systems often fluctuate around an average state dependent on the stability and/or variability of its external conditions. Such ‘stable states’ refer to dynamic regimes with a defined range of deviations from an attractor over time (Scheffer and Carpenter, 2003; Vasilakopoulos and Marshall, 2015). Whether the system exhibits a smooth continuous reaction to changes in its stressors or if, at some point, abruptly shifts from its main tendency and basin of attraction is a major management and conservation concern, as it determines the timing for the enforcement and extent of regulatory measures for preventing undesirable impacts in habitats and communities inhabiting them.

The development of a methodological framework for the study of abrupt shifts, also referred to as ‘critical transitions’, (Scheffer et al., 2009; Mollman and Diekmann, 2012 and references therein; Vasilakopoulos et al., 2017) has been used to define the mechanisms of natural systems’ response to their stressors, with an emphasis on detecting non-linear behaviors that may lead to the alternation of different ecological regimes once a critical threshold or ‘tipping point’ is exceeded. A critical or utility threshold is the point in an ecological system at which small changes in environmental conditions produce substantial change (Samhouri et al., 2010, 2017). In recent years, many wide-scale sudden shifts in several biological and environmental systems of North East (NE) Atlantic have been reported, attributed to a range of factors, both climatic and anthropogenic (Choi et al., 2005; Weijerman et al., 2005; Möllmann et al, 2009; Vasilakopoulos and Marshall, 2015). Hence, it comes as a relevant management issue to clarify whether a change of pattern in the structure and function of an ecological community is due to a natural intrinsic variability or represents the non-linear amplification of stochastic physical forcing (Deyoung, 2008), often fostered by anthropogenic impact.

Until the mid-2000s, the upper layers of NE Atlantic acted as a main heat storage basin, but at that point, driven by extraordinary convective mixing events, the heat and salt gained slowly over the years, started being passed on to deeper levels and stored in the deeper ocean (Balmaseda et al., 2013; Somavilla et al., 2016). This trend went on until the mid-2010s, when salinity trends were reversed accompanied by above average temperatures (Lavín et al., 2020). As a general display of global warming in the area, Cantabrian Sea exhibited an increase in intermediate waters temperature and salinity during the period 1992-2003 (González-Pola et al., 2005). Over the periods 1978-1982 and 2003-2007 the temperature increase reached up to 0.8 to 1° C (Tasker, 2008). Cantabrian Sea corresponds to the subtropical boreal transition subprovince between the Atlantic boreal and the northern subtropical subprovinces, thus, life in this marine area may be highly sensitive and respond rapidly to small shifts in climate (Blanchard, 2005).

Furthermore, the temperate character of Cantabrian Sea has favored the development of important mixed demersal fisheries mainly engaged on pair and otter trawling (Abad et al., 2010; Castro et al., 2010; Punzón et al., 2010). As a consequence of increasing effort and capacity, a generalized regime of stocks depletion was reached around the late-80s, which led to decreases in catches and yields of the traditionally exploited species, similar to those observed in other fishing grounds (Worm et al., 2009). However, due to the progressive implementation of fisheries management in the Atlantic Iberian waters within the framework of ICES (yearly TAC limits on landings and quotas (Castro et al., 2012), the 2002 reform of the EU's Common Fisheries Policy (Fernandes and Cook, 2013) and regional-specific management actions (Abad et al., 2010)), a rapid decline in landings reflected a recovery in species associated with demersal-benthic habitats (Fernandes and Cook, 2013; Modica et al., 2014; Fernandes et al., 2017; Hidalgo et al., 2017; Arroyo et al., 2019; Preciado et al., 2019).

Recent research has reported numerous alterations in the structure and function of Cantabrian Sea's ecosystem, some related to wide-scale climatic changes, mainly increasing temperatures (Perry et al., 2005; ICES, 2008; Tasker, 2008; Punzón and Villamor, 2009; Punzón et al., 2016, 2021), and other regional scaled anthropogenic stressors, such as the retirement of high levels of fishing pressure (Modica et al., 2014; Arroyo et al., 2017, 2020), as well as to their combined or synergistic effects. These studies hinted on the various scales at which either single or combined stressors have impacted Cantabrian Sea's ecosystem, but none has yet acknowledged the ecosystem's thresholds and resilience dynamics, which we stress as ecological features determinant when taking any management actions.

With the aim of contributing to the understanding of the concurrent effects of environmental and anthropogenic forces on complex natural systems, this study analyzes a temperate demersal community's main tendencies and response to its main potential stressors. Through univariate and multivariate methods, as well as the application of an Integrated Resilience Assessment (IRA) (Vasilakopoulos and Marshall, 2015; Vasilakopoulos et al., 2017) on biomass estimates from a scientific survey, we argue that additive effects of anthropogenic pressures such as fishing and sea warming have eroded the resilience of this complex natural system, making it more vulnerable to abrupt shifts. In particular, a combination of continuous and discontinuous response mechanisms to fishing have been key to the evolution of the Cantabrian Sea's biological system in the last 40 years.

4.2 MATERIAL AND METHODS

4.2.1 STUDY AREA

Cantabrian Sea (Nort East Atlantic) is located between the Bay of Biscay and Atlantic Iberian waters (see Figure Supp. 1). While it is often treated as a compact system in terms of geological, climatic and ecological features, it can be understood as the union of two distinct subareas: on the eastern side, the southern Bay of Biscay, and on the western side, the Galician waters or Iberian Atlantic area. Given it comprises a very heterogeneous environment and represents a subtropical/boreal transition zone, typical temperate-water species occur together with those of northern origin (Sánchez and Olaso, 2004), including many species of commercial interest.

A weak circulation pattern in comparison with the main currents in the North East Atlantic basin (Blanchard and Vandermeirsch, 2005) and east component winds in spring and summer, which favor the appearance of upwelling, stand out as the main environmental patterns in the Bay of Biscay. The most important upwelling phenomena are found in the western area, in the waters of Galicia, and they decrease in intensity to the east. Upwelling events and the Iberian Poleward Current (IPC, also known as 'Navidad' current) are the most common and important hydrographic events in Galicia and the Cantabrian Sea, both showing high seasonal and interannual variability (Koutsikopoulos and Le Cann, 1996) while NAO (North Atlantic Oscillation index) and EA (Eastern Atlantic pattern) act as the leading modes of variability for the whole Eastern North Atlantic Central Waters and are known to affect marine populations of the European seas (Quinzán et al., 2020).

4.2.2 DATA

To represent the biotic dimension of the ecosystem, a set of 63 fish species was selected from the Demersales survey data bank. This standardized bottom trawl survey (ICES International Bottom Trawl Survey Working Group, IBTSWG) provides data since 1983 and keeps sampling the area every autumn (September-October), except for 1987. It follows a stratified random sampling scheme, with five geographical sectors and five depth strata, in which sampling stations are selected randomly from 5x5 nautical miles rectangles, the number of hauls per stratum being proportional to the surface area available for trawling (ICES, 2017). The sampling unit consists on bottom trawls of 30 min at 3 knots, using a standard 'baca' 44/60 otter trawl gear with 10 mm cod-end mesh size. Catch processing and sorting are done following the IBTS procedures: species are sorted to species level, each species catch is weighed and a representative sample counted. Instead of using species abundance information (number of individuals), in our analyses we used biomass (in grams) per haul standardized by swept area (i.e. g/km^2), to avoid giving a disproportionate weight to small and abundant species compared to larger and less abundant species. To avoid misidentifications and possible misestimates, we selected those species that were at least identified in 30 hauls out of the average 126 hauls conducted yearly (Punzón et al., 2016).

In year 2013, the sampling vessel used in the survey was replaced, and despite the calibration operations between the new and the old vessel, the gear used in 2013 had a heavier footrope that entailed a more benthic catch (higher catchabilities for many benthic species). However, since 2014, the gear geometry was recalibrated, so from then on the survey data are coherent with the values reached previously (ICES, 2021). After testing for it we found the results of our study were not majorly affected by 2013's data, so we present analyses based on the complete series. Species that are typically associated to the pelagic environment (e.g. anchovy, mackerel, etc) were removed from the analyses to avoid possible biases caused by changes in catchability independent of sampling. In order to reduce the effect of outliers and homogenize the scale of the biological variables, each biomass value was standardized by subtracting the species mean and dividing it by the species standard deviation over the whole time series (Z-scores standardization).

With the aim of identifying the main stressors and mechanisms affecting the demersal ecosystem 13 variables were explored (Table Supp. 1 and Figure Supp. 2). The final set of variables was selected based on the following criteria: length of the covered period, representativeness for a specific ecosystem component or a specific driver and low correlation with other variables (Figure Supp. 2 and Figure Supp. 3). A Redundancy Analysis (RDA I in the following section) on the species and abiotic data sets also served the purpose of avoiding correlated and collinear variables (Möllmann et al., 2009). Since the abiotic variables showed different scales, they were standardized by means of function decostand-standardize, which standardizes values to zero mean and unit variance, in R package vegan (Oksanen et al., 2019). The final abiotic environment of the Cantabrian Sea is represented by four stressors: two regional hydroclimatic variables (annual mean sea surface temperature -SST-, and salinity below the winter mixed layer -SBwML-), one global index (NAO index) and one variable that acts as proxy for fishing pressure (F_{com}), all of them are described below.

Weekly satellite-derived sea surface temperature data (OISST, https://www.ncdc.noaa.gov/oisst) from 1983 to 2018 have been used to obtain annual SST averaged values for the two main subareas (Galician margin and Bay of Biscay) i.e. mean SST was calculated for each 1°x1° grid in the subarea, and the averaged value for the whole are in the corresponding year calculated. SST was used as a proxy of the effect of surface temperature variability on demersal sources. Annual mean temperatures are increasing as a consequence of warming occurring especially during summer months (Borja et al., 2019).

To account for physical events that have taken place at mid-layers in the area (Balmaseda et al., 2013; Somavilla et al., 2016; Lavín et al., 2020), the annual average salinity in the depth range between 300 and 600 m depth was calculated, excluding from this average the surface mixed layer depth affected by strong seasonality. The climatological maximum winter mixed layer in the area is within 250 m depth, and so we named this variable 'Salinity Below the winter Mixed Layer' (SBwML). Salinity data to calculate this index was obtained from salinity profiles from the ocean reanalysis (ECMWF Ocean Reanalysis System 4, ORAS4) (Balmaseda et al., 2013). The ORAS4 reanalysis provides monthly temperature, salinity, current and sea level data at 42 pressure levels from 5 to 5000 m with higher vertical spacing towards the bottom and a spatial resolution of 1°x1°.

Data for the main pattern of atmospheric variability in the Euro-Atlantic sector, NAO and winter NAO indices, were provided by the Climate Analysis Section, NCAR. The North-Atlantic Oscillation (NAO) has been previously considered to best explain variability in community composition and ecological regime shifts (Attrill and Power, 2002; Alheit et al., 2005), as have other large scale patterns of variability (e.g., the Atlantic Multidecadal Oscillation -AMO-, the Pacific Decadal Oscillation -PDO- or El Niño-Southern Oscillation -ENSO-) (Newman et al., 2016; Bode et al. 2020). These global teleconnecting patterns are related by means of pantropical interactions and modulate one another (Cai et al., 2019; Zhang et al., 2019), so when discussing NAO's influence on the studied area, we are indirectly referring to the variability of other global climatic patterns.

As an approximation to the community removal rate, we used the assemblage-averaged fishing mortality (F_{com}). We followed Modica et al. (2014) approximation to obtain the region specific F_{com}, based on five commercial species data: *Lophius piscatorius*, *L. budegassa*, *Merluccius merluccius*, *Lepidorhombus boscii* and *L. whiffiagonis*. Therefore, to better inform target setting under the Marine Strategy Framework Directive (MSFD), we used the MSY reference points, $F_{s,msy}$ for each species. F_{com} was calculated as

$$F_{com,Y} = \frac{\sum_{s=1}^{5} {F_{s,Y}}\Big/{F_{s,msy}}}{5}$$

where $F_{s,Y}$ is the fishing mortality estimates for each species in year Y, and $F_{s,msy}$ is each species maximum sustainable yield (MSY) reference point. The species reference points and annual stock assessment were downloaded from R package icesSAG (Millar et al., 2019).

All data handling and quantitative analyses were performed using R version 4.1.0.

4.2.3 DATA ANALYSIS

The biological time series had annual resolution and covered the period 1983-1986 and 1988-2018. Data for the missing year, 1987, were filled with the average of 1986 and 1988 in order to have an even spacing between annual mean estimates (Möllman et al., 2009).

We applied multivariate analysis methods proposed in the Integrated Ecosystem Assessment (IEA) framework (Möllmann et al., 2009; Möllmann and Diekmann, 2012; Levin and Möllmann, 2015). The purpose of the first section of the study was to better understand the general trends of the demersal community, simplify it and look for potential regime shifts. A heatmap helped visualize the biotic system's temporal evolution, while Principal

Components Analysis (PCA) was used to identify general trends on the time series and create a composite system variable, PCsys, the first principal component, which reduced the complexity of the species biomass data. Chronological clustering and sequential t-test analysis of regime shifts (STARS) were used to compare outcomes with the multivariate analyses results and contrast them with the previously detected patterns.

For a better understanding of the system's response to its main stressors, in the second section, we applied a Redundancy Analysis (RDA), and fitted additive and non-additive models on each system (PCsys) -stressor relationship following the approach of the Integrated Resilience Assessment (IRA) framework (Vasilakopoulos and Marshall, 2015; Vasilakopoulos et al., 2017). The IRA also allowed the estimation of the resilience dynamics of the studied community through the construction of a folded stability landscape.

REGIME SHIFT IDENTIFICATION

We visualized the temporal biomass trends of each species in the data set reducing the data complexity into a heatmap. In it, species annual mean biomass data were categorized into quintiles and ordered according to their preferred temperature (as a proxy for the temperature affinity of the species). The preferred temperature index was estimated following the methodology described by Punzón et al. (2021) and trends were analyzed using linear regression on R statistical language (R Core Team, 2021).

PCA (Zuur et al., 2007) allowed for a preliminary detection of system's shifting trends expressed as deviations from the mean values of the data. This simplification technique does not clarify any mechanisms of the system's response to changes in its environment. The main outputs of PCA are the principal components (PC scores or eigenvectors) which, plotted against time, show the underlying pattern of a specific component and thus if and when a sudden change occurred (Weijermann, 2005). Also, the PCA estimates the loadings of the species, i.e. the extent to which the original variables (in this case species) are related to the principal components. When performing this analysis, we focused on the variability between years and whether it was possible to establish different profiles or clusters. Two years would be close to each other if the relative contribution of the species' biomass were similar. It also allowed us to summarize the biomass data into an index or composite variable that could subsequently be analyzed against the abiotic drivers.

We selected the environmental and anthropogenic stressors to be used in further analyses through an analysis of the covariates correlation jointly with a redundancy analysis (RDA). The RDA is a constrained version of PCA that models response variables as a function of explanatory variables and quantifies its associations (Zuur et al., 2007). It was selected as the proper constrained multivariate analysis after carrying a Detrended Correspondence Analysis (DCA), which produced the length of gradient of the ordination axis that hinted on the use of either a linear ordination technique (such as RDA and PCA), when the length was lower than 3, or unimodal (such as the Correspondence Analysis, CA) when it was higher

(Hill and Gauch, 1980; Leps and Smilauer, 1999). The function for DCA is included in R package *vegan* (Oksanen et al., 2019). RDA was performed on the species data set and an initial abiotic dataset, consisting of 13 explanatory variables (Table Supp. 1). The implementation of RDA for this purpose (RDA I) is described in Supporting Information.

As part of the effort to identify possible shifts of tendency in the survey data, instead of a typical clustering technique, which could ensemble non-successive years, we applied a chronological clustering to our biomass data (Legendre et al., 1985), a clustering variation that runs on ordered successive samples like time series. For this, after creating a similarity matrix combining samples into clusters, based on a permutation test and pre-defined significance and connectedness levels (Legendre et al., 1985), we used the Constrained Incremental Sums of Squares ('coniss' method, Grimm, 1987) as agglomeration method.

We also applied the sequential t-test analysis of regime shifts (STARS) (Rodionov, 2005) to the biotic composite variable (PCsys), extracted from the biotic data PCA, as well as on the final selection stressors (see below). This method estimates a Regime Shift Index (RSI), i.e. a cumulative sum of normalized anomalies relative to each value of the time series analyzed, and uses it to confirm or reject the null hypothesis of a regime shift at that year (Rodionov, 2006). Here, we set the cut-off length, the time scale in which shifts are detected, at 15 years and did the RSI estimation at a probability level p of 0.05, accounting for red noise through Ordinary Least Squares (OLS). The 3.2 version of this regime detection tool was downloaded from http://www.beringclimate.noaa.gov/regimes.

SYSTEM-STRESSOR RELATIONSHIP

Once the final environmental and anthropogenic stressors were singled out, a second RDA (RDA II) provided a preliminary visualization of the stressors connection to the evolution of the time series. To study the goodness of fit, RDA II adjusted R-squared (adj-R^2) fit was calculated. R-squared measures the amount of explained variation, but it tends to 'reward' the inclusion of many explanatory variables, so the adjusted R-squared served as an unbiased version of this regression statistic.

The Integrated Resilience Assessment (IRA) framework builds on the study of the multivariate development of natural systems proposed in the IEA by applying non-additive modeling on the system-stressor couple and quantifying ecological resilience to build stability landscapes. In the IRA framework the relationship between PCsys and its drivers is assessed using PCsys as response variable in generalized additive models (GAMs) and threshold-GAMs (TGAMs) (Cianelli et al., 2004). Each of the four stressors with 0, 1 and 2 year lags were used as explanatory variables in separate models. Testing potential lagged effect of the stressors was designed to detect a potential delayed response of the sampled biomass by species. GAMs are models that assume additive and stationary relationships between the response and explanatory variables while TGAMs are GAMs adjusted to account for abrupt changes in the response mechanism (Ciannelli et al. 2004). The basic GAM function used is included in R package mgcv (Wood, 2011). The ‘genuine’ cross-validatory squared prediction error (gCV), a modification of generalized cross validation proposed by Cianelli et al. (2004) that makes the goodness of fit of GAMs and TGAMs comparable, was computed for model selection and estimation of the threshold year. The optimal most explicative model was selected between every GAM and TGAM of PCsys’ response to its stressors as well as the composite stressor variable with 0, 1 and 2 years lag. When the biotic-abiotic system relationship was found to be non-stationary, the threshold year was identified by minimizing the gCV after running the model for every possible threshold year (Vasilakopoulos et al., 2017).

Following Jolliffe and Cadima (2016) and Weijerman (2005), the PCA and RDA were conducted based on the correlation matrix instead of the covariance coefficients. We used functions PCA and rda in R packages *FactoMineR* (Lê et al., 2008) and *vegan* (Oksanen et al., 2019), respectively.

RESILIENCE ASSESSMENT

The methodology for the resilience quantification and folded stability landscape estimation is based on the theory of critical transitions (Scheffer et al., 2001; Van Nes and Scheffer, 2007; Scheffer et al., 2009) and the related implementation within the IRA framework (Vasilakopoulos and Marshall, 2015; Vasilakopoulos et al., 2017). The fitted lines or branches of the optimal model in terms of both gCV and adjusted-R^2 were considered as the attractors of the system. Resilience for every year (t) was then estimated as the sum of two components: *vComp*, the vertical component, measured along the system axis as the negative distance from the attractor, and *hComp*, the horizontal component, measured along the stressor axis as the distance from the tipping point (Vasilakopoulos and Marshall, 2015). *vComp* and *hComp* are related to the resistance and precariousness of the system, respectively (Walker et al., 2004). Resilience at a given year was therefore estimated as $Res_t = vComp_t + hComp_t$.

The greater the Res_t estimates are, the further away from a ‘hilltop’ the system lies, being less likely for it to shift to an alternate basin of attraction, conversely, at a tipping point, Res_t would be zero. The folded stability landscape was subsequently constructed through linear interpolation of all Res_t values onto a 100 x 100 grid.

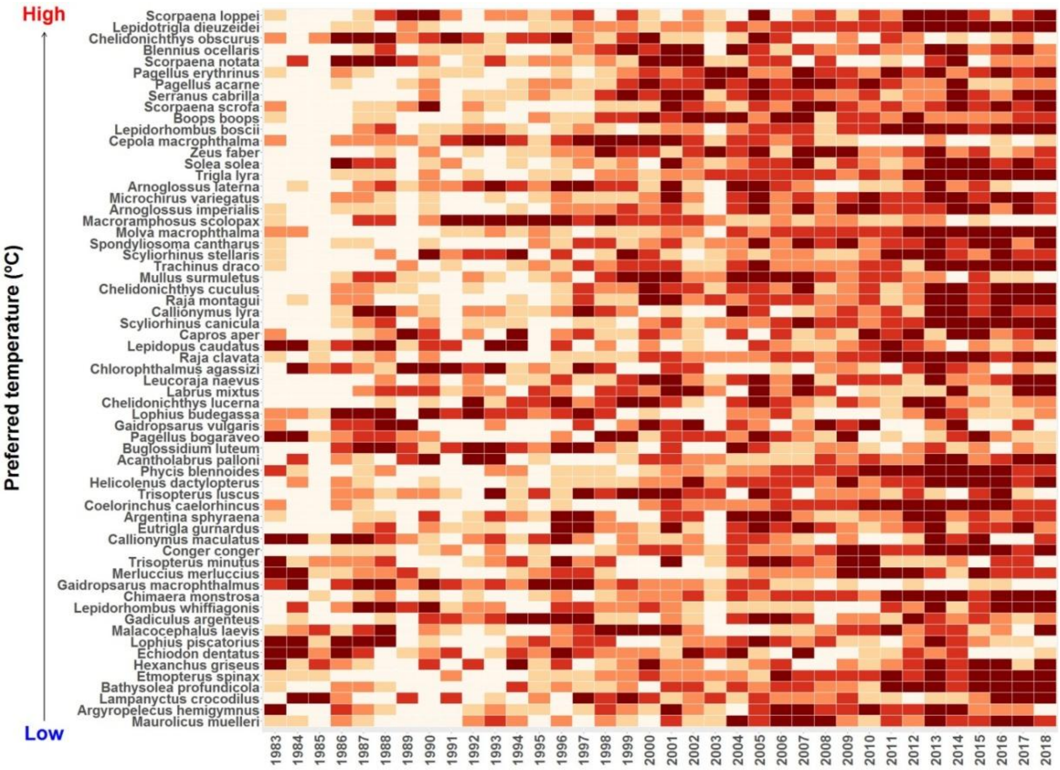


Figure 1. Heatmap of species annual mean biomass evolution. Time series were transformed into quintiles, and each quintile was given a specific tone of orange, highest quintiles symbolized by the darkest orange and white representing the lowest values of the variable. Arrow on the side informs that warmer affinity species are located in the upper side of the heatmap, and colder affinity species in the lower side.

4.3 RESULTS

4.3.1 REGIME SHIFT IDENTIFICATION

In 1983-2018 there was a general increase in most species' biomass (Figure 1). The increasing trend was slightly more evident for species with a higher preferred temperature (top rows of the figure). When analyzed via linear regression (Figure Supp. 8**¡Error! No se encuentra el origen de la referencia.**) the most thermophilic species trends showed almost twice the slope (0.041 g/km^2.year^{-1}) than those associated to a lower preferred temperature (0.022 g/km^2.year^{-1}). In the PCA applied to the species data matrix, PC1 and PC2 explained 32.6% and 9.5% of the variation, respectively (Figure 2A). The output of the biotic system PCA was visualized by plotting PC yearly scores along the PC1 and PC2 axes on a two-dimensional figure (Figure 2A). These results suggested a gradual change: years 2011-2018 were grouped together while the rest of the series appeared to reflect a more progressive transition. Graphical representation of both principal components annual trends (Figure 2B) unveiled a directional transition of the PC1 during the whole series. As a composite biotic variable, we used the first principal component of the analysis (PC1, or PCsys when used as biomass composite variable), as it explained a high variance (32.6% of the information contained in the original biomass dataset) and captured the directional change in the system.

When sorting the 63 species according to their loadings in PC1 and PC2 (Figure Supp. 7), the most contributive species to PC1 were *Raja clavata*, *Chelidonichthys cuculus*, *Lepidorhombus boscii*, *Scyliorhinus canicula*, *Chimaera monstrosa*, *Etmopterus spinax*, *Microchirus variegatus*, *Conger conger*, *Lepidotrigla dieuzeidei*, *Bathysolea profundicola*. This group appears to have experienced a distinct increase of their biomass starting in the late 1990s that boosted after year 2011.

A

B

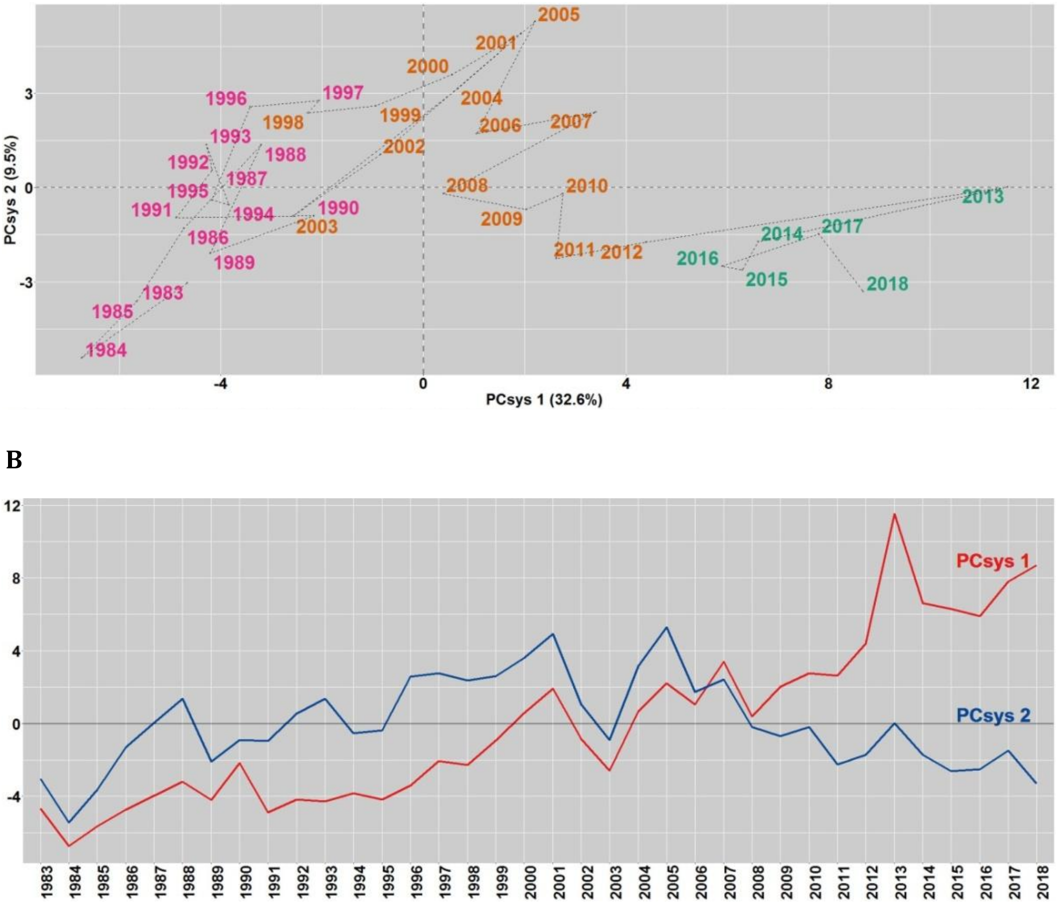


Figure 2. Biotic system's Principal Component Analysis (A) Dashed line represents the time trajectory of PC1 vs PC2 of the PCA based on the correlation matrix. Years are colored in accordance to the clusters produced by CONISS chronological clustering (see Figure 5). B) Yearly PC-scores along the first two principal components of the PCA carried out for the Cantabrian Sea bentho-demersal system.

The results of the methods applied for the explanatory variable selection, the correlation calculation and RDA I, are presented in Supporting Information and in Figure Supp. 2 and Figure Supp. 4, respectively. The final dataset of possible drivers was set to 4 variables (F_{com}, SST, NAO and SBwML), all of them considered representative of the main environmental and anthropogenic stressors (Figure 3).

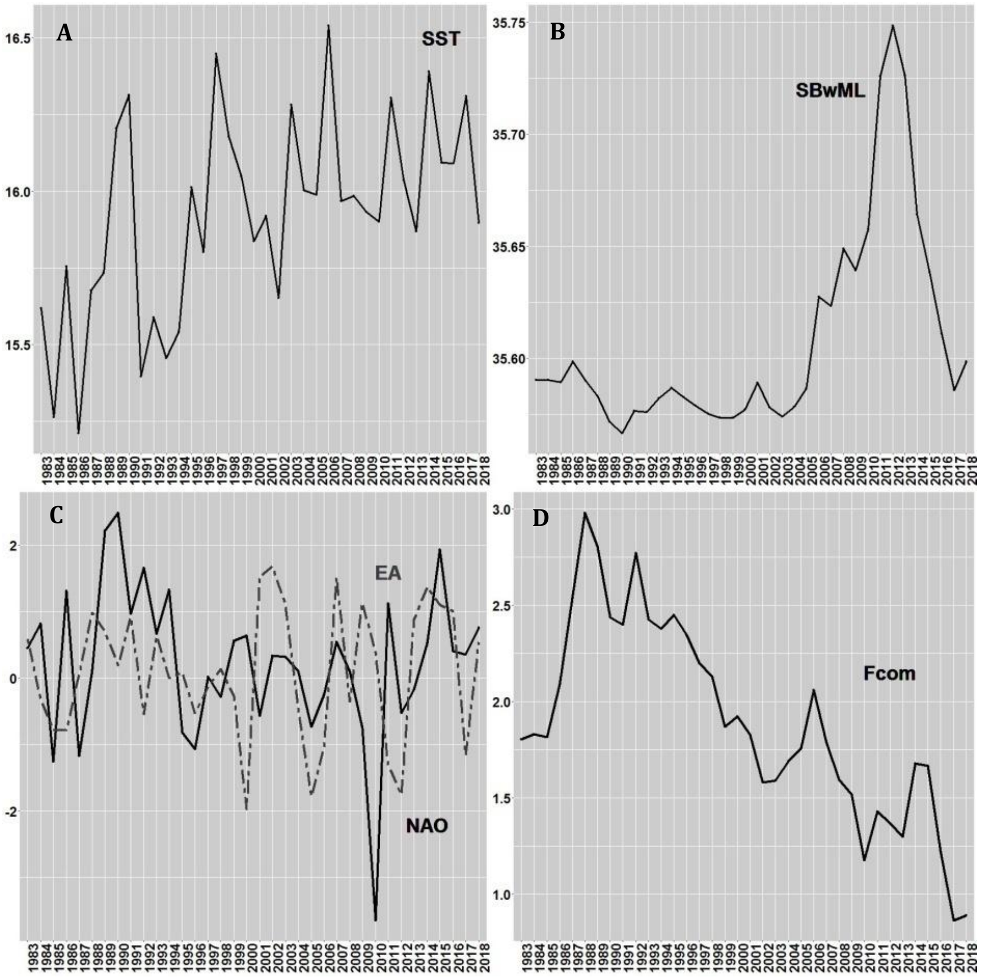


Figure 3. Abiotic variables evolution. A) Annual mean sea surface temperature (SST) B) Salinity below winter mixed layer C) Annual mean North-Atlantic Oscillation (NAO index) and winter average Eastern-Atlantic pattern indexes (wEA, dashed line) D) Community averaged fishing mortality index (F_{com}) evolution along the time series.

In the studied area, annual mean SST showed a fluctuating increase until year 2004, after which its rise stabilized (Figure 3A). Salinity below the winter mixed layer stratum remained stable until 2005, when it increased until reaching its peak in 2012, slowly after which it went back to its baseline. During the beginning of the time series (until year 1998) NAO and EA indexes presented equal phases, and in periods 1998-2002 and 2009-2012 they were opposite. The latter behavior was associated with larger anomalies in the North Atlantic jet stream. Also, from year 1998 onwards, NAO's signal weakened, starting a period we will further refer to as a 'non-NAO' period. This went on until an outstanding negative NAO episode in 2010 associated with extremely cold European climate events. As for F_{com}, its striking decrease (Figure 3D), started in 1988 and reached its lowest value in 2017. According to RDA I results, neither upwelling, ENSO index nor mixed layer depth (winter minimum nor the annual mean) explained a significant amount of variance, so they weren't used in posterior analyses (STARS, GAM/TGAM fitting and the resilience assessment). Since ChlA data started in year 1998, they weren't incorporated to the main analyses so they wouldn't compromise the length of the series.

The resulting triplot of the RDA fitted for the final set of stressors (RDA II) is presented in Figure 4 and its numerical output included as supporting information. The triplot summarizes the main patterns of variation in the species abundance data and visually relates them to the explanatory variables. The first and second constrained axis in RDA II (RDA 1 and RDA 2) explained, respectively 24.6 % and 4 % of the total variance (inertia), which was more than the variance explained by the unconstrained axis (PC1 and PC2 of the redundancy analysis explain together 18 %). This confirms that the biotic dataset is mainly structured by the covariates included in the analysis. F_{com} and SST exhibited opposite roles on the displaying of the years' scores in the RDA plot, and the same applies to NAO and SBwML. Warming trends in the area oppose to the F_{com} tendency (Figure 3A and 3D), with a correlation coefficient of -0.3. SBwML also exhibited a slight correlation with the fishing pressure variable, with a correlation coefficient of -0.5 (Figure Supp. 3).

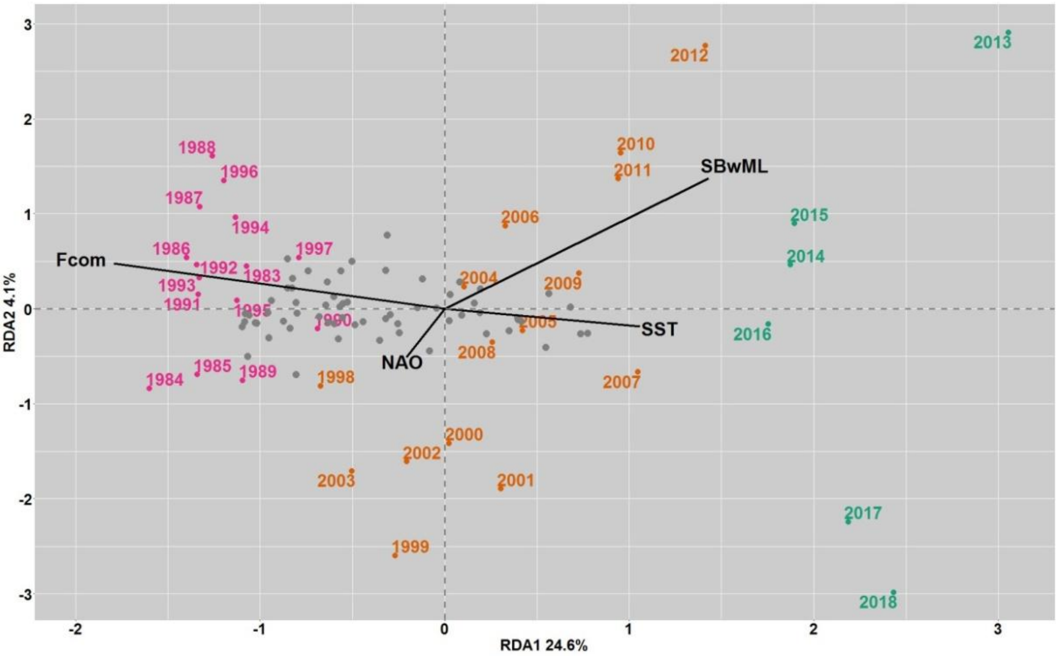


Figure 4. RDA II triplot. The explained variance of the two first axes of RDAII, i.e. the sum of all so-called canonical eigenvalues for the constrained axes divided by total variance (inertia), is 28.7 % and the model adjusted R2 is 25.3 %. The arrow length and direction corresponds to the variance explained by the variable. The angle between black lines reflects the correlations between explanatory variables. The narrower the angle, the stronger the correlation. Years are colored in accordance to the clusters produced by CONISS chronological clustering (see Figure 5).

In terms of years-environmental relations, it appears that F_{com} influence is major on the left side of the plot (years 1983-1999), its highest values associated with the start of the PCsys time series. The effect on the PCsys of SBwML and the SST parameter are mainly linked to the right side of the plot (years 2012-2018) (Figure 4). The triplot shows that NAO mildly related to intermediate years in the period 1998-2010, matching a 'non-NAO' period (in which NAO index exhibited low absolute values).

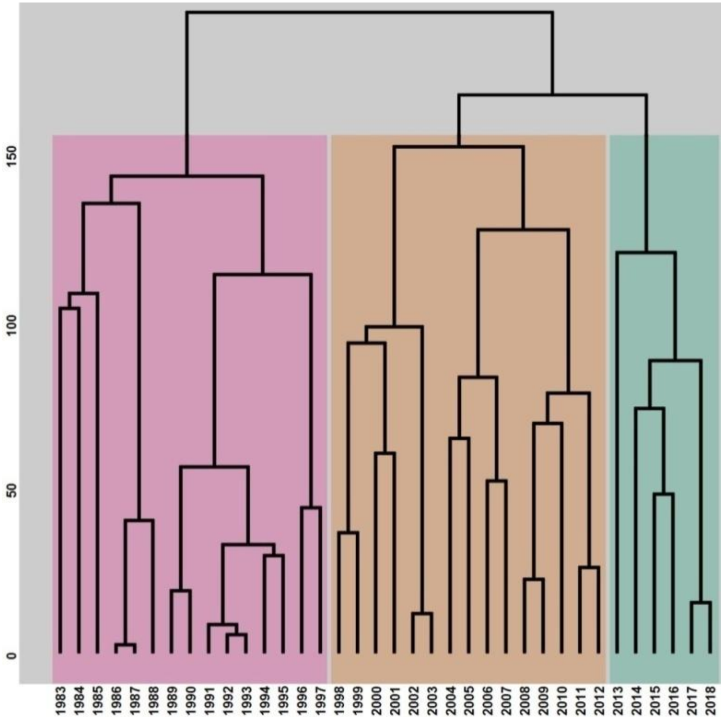


Figure 5. Dendrogram of the chronological clustering applied using the ‘coniss’ method (Constrained Incremental Sums of Squares) on the 63 demersal species time series. The three periods identified by the analysis are colored differently and colors are used coherently in subsequent analyses.

The dendrogram (Figure 5), produced through a chronological clustering, grouped together years 1983-1997 and 1998 until the end of the series. Apart from this main break in the time series, years 1998-2012 formed a secondary group inside the second period.

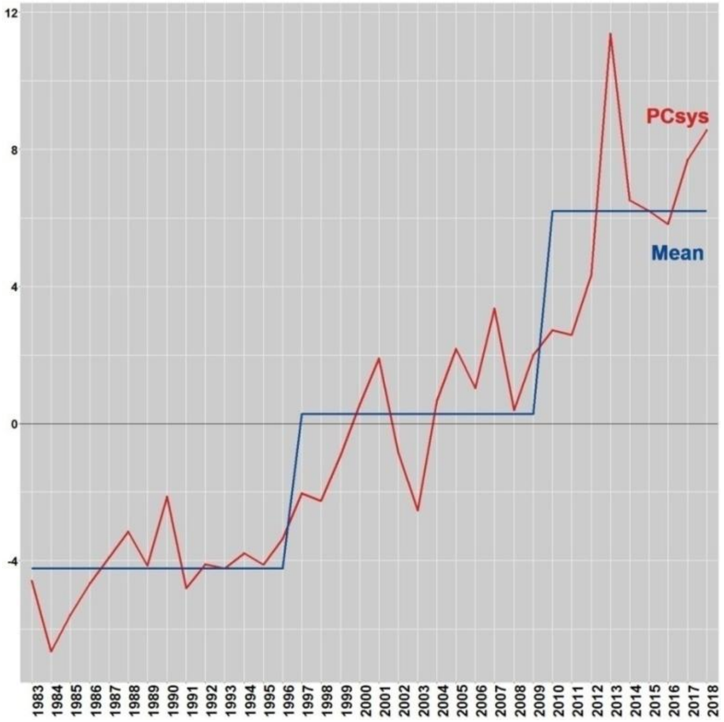


Figure 6. Plot of STARS applied on the PCsys. Blue line shows the stepwise trend containing the regime shift in the mean detected by STARS method. Red line represents the first principal component of the PCA of the biotic system.

A similar pattern was identified when STARS was applied on the biomass composite variable (PCsys), which produced high Regime Shift Indices (RSI) for years 1997 (RSI = 0.967) and 2010 (RSI = 1.125) (Figure 6). The mean detected by STARS showed a stepwise trend containing two transitions, which seem to adjust consistently to the biotic index along the time series. There is a gradual leap around year 1997 and a second abrupt transition around year 2010 (Figure 6). F_{com} series produced a signal of two possible shifting tendencies in years 1999 and 2016, while SST had significant RSI values for year 1995. STARS applied on NAO did not produce any RSI, while SBwML showed a moderate RSI for year 2006 (Figure Supp. 5).

4.3.2 SYSTEM-STRESSOR RELATIONSHIP

Through the comparison of the fits of additive (continuous) and non-additive (discontinuous) statistical models on the system-stressor relationship, this section of the analyses focused on assessing the type of system's response. For the inclusion of PCsys and the lagged and non-lagged stressors in models we used the time series starting in year 1988. This was decided based on 1987 data being an estimation for both PCsys and F_{com} as the average of adjacent years, and first and foremost, due to the perception in the model plots of the whole time series, of years 1983 to 1986 differing substantially from the subsequent ones in PCsys values, which hinted they could be the tail of an older state.

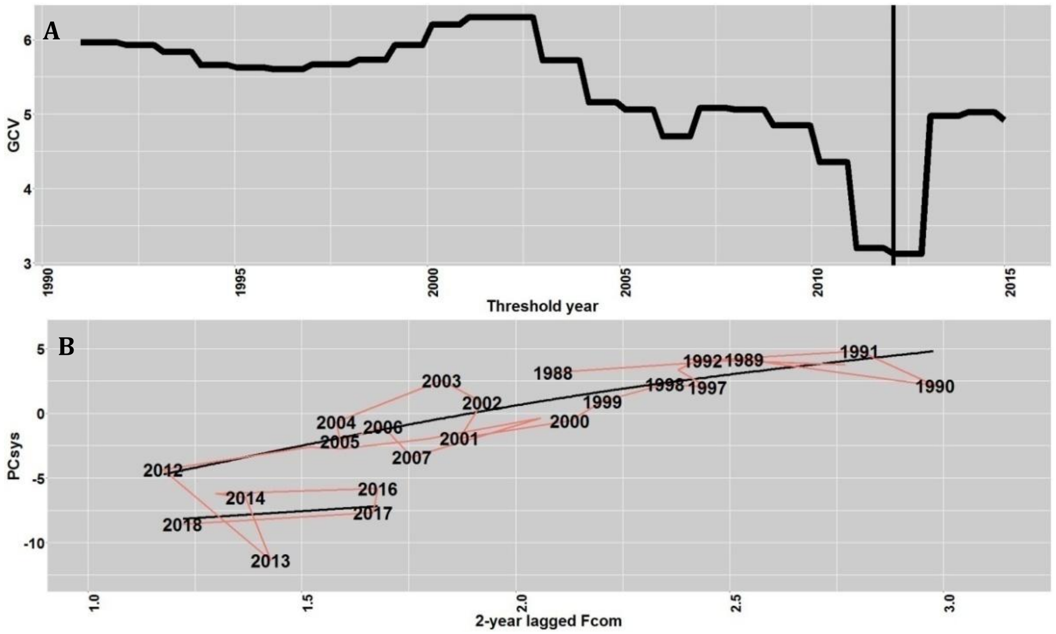


Figure 7. A) Fitting of TGAM on –PCsys and 2-year lagged F_{com} relationship. Black lines indicate the fitted TGAMs and red line the chronological path of the series. B) GCV values of TGAM with threshold year fitted on the relationship between system state indicator (Pcsys) and 2-year lagged F_{com}.

The optimal fit for the system index (PCsys) – stressor relationship was a TGAM with 2-year lagged F_{com} and a utility threshold in year 2012. The threshold year (2012) lied at a local minimum of F_{com}, as predicted by the theory of critical transitions. This model yielded an adjusted-R^2 of 87.6 % and the lowest gCV among all models examined (a gCV value of 0.22)

(Table 1). As shown in Figure 7, the model plot describes the first part of the series as a period in which the system had a smooth linear relationship with F_{com}; the late 1990s gradual regime shift of the system revealed by STARS and chronological clustering being a continuous response to the change in F_{com}. Around year 2012, the system abruptly exited the previous system-stressor coupling and entered a new regime with a new, weaker, relationship with F_{com}.

Table 1. Numerical output of GAM and TGAM fits for every stressor relationship to the biotic index. The model with minimum gCV is highlighted in red and corresponds to that of a 2-year lagged F_{com} discontinuous response of PCsys with a utility threshold in year 2012.

Stressor	Lag	Fits	gCV	Threshold year
SST	0	TGAM (R^2adj. = 78.1%)	0.383	2010
		GAM (R^2adj. = 19.1%)	0.865	
	1 year	TGAM (R^2adj.= 73%)	0.562	2011
		GAM (R^2adj. = 20.4%)	0.865	
	2 years	TGAM (R^2adj.= 74.4%)	0.681	2011
		GAM (R^2adj. = 20.7%)	0.859	
F_{com}	0	TGAM (R^2adj. = 86.3%)	0.223	2012
		GAM (R^2adj. = 68.5%)	0.330	
	1 year	TGAM (R^2adj. = 84.8%)	0.257	2012
		GAM (R^2adj. = 66.6%)	0.372	
	2 years	TGAM (R^2adj.= 87.6%)	0.220	2012
		GAM (R^2adj. = 71.2%)	0.354	
Salinity below ML	0	TGAM (R^2adj.= 84.1%)	0.375	2012
		GAM (R^2adj. = 39.6%)	0.710	
	1 year	TGAM (R^2adj.= 81.9%)	0.292	2012
		GAM (R^2adj. = 50.5%)	0.572	
	2 years	TGAM (R^2adj.= 78.8%)	0.366	2013
		GAM (R^2adj. = 61.9%)	0.459	
NAO	0	TGAM (R^2adj.= 67.8%)	0.883	2010
		GAM (R^2adj. < 0 %)	1.079	
	1 year	TGAM (R^2adj.= 70.8%)	0.569	2011
		GAM (R^2adj. = < 0 %)	1.051	
	2 years	TGAM (R^2adj.= 72.1%)	0.478	2011
		GAM (R^2adj. = < 0 %)	1.086	

4.3.3 RESILIENCE ASSESSMENT

Figure 8 represents the folded stability landscape of the bentho-demersal community of the Cantabrian Sea in response to F_{com}. The PCsys-F_{com} plot exhibits two basins of attraction around the TGAM branches identified earlier (Figure 7), which correspond to this complex natural system's two regimes (system-stressor couplings), and two tipping points (F1 and F2). PCsys values for years 1985-1987 have been added to the graph without estimating their resilience, as they likely reflect the 'tail' of an older state, as explained earlier.

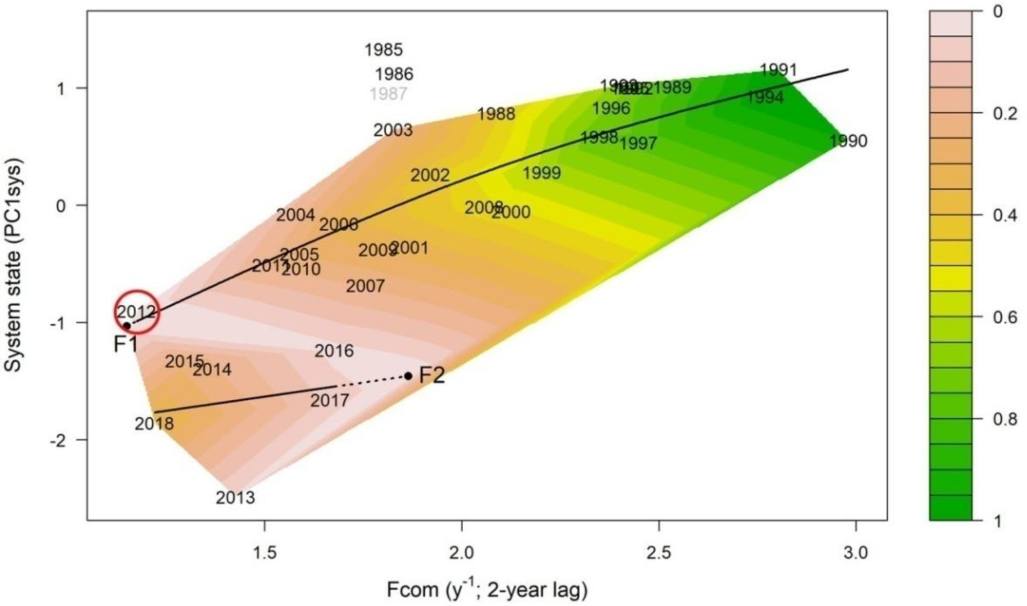


Figure 8. Folded stability landscape and relative resilience estimates. The system's change has a horizontal component in which conditions (2-year lagged F_{com}) change, and a vertical component which represents system's state changes. Dotted black line indicates the possible extensions of the linear attractors (mean numerical properties of the system for a given period). F1 and F2 are indicating the tipping points assumed location. Threshold year 2012 is highlighted by a red circle.

The resilience of the system's initial regime decreased along F_{com}'s initial decline, which went from its highest values at the beginning of the series on to 2012, when the first tipping point was reached (Figure 8). Around 2012 a local minimum in F_{com} values matched a point in which the system's recovery capacity was weakened, leading to the abrupt change of the system state, also reflected by CONISS and STARS, as well as the change in the system-stressor relationship. Hereafter, the system entered a 'shorter' regime, unfolding around a weaker attractor with lower resilience values. Nevertheless, there were clear signs of hysteresis after this regime shift: in years 2015-2016 the system experienced similar F_{com} values to those that had taken place in the second half of the 2000s without returning to its previous state (Figure 8).

4.4 DISCUSSION

Through a combination of multivariate analysis and non-additive modeling, we interpreted the temporal development of a temperate demersal community. Main patterns were observed and associated with specific anthropogenic and environmental covariates. The analysis revealed a double shift of the biological system in the late 1990s and early 2010s, primarily resulting of a continuous and a discontinuous responses, respectively, to fishing pressure and the effect of sea warming. We suggest the existence of an initial phase (during the 1988-2011 period), in which the bentho-demersal fish community was changing sharply but gradually in response to a declining fishing effort, and responded linearly to its impact. During that time, the mitigation of fishing pressure's effects overlapped with the emergence of a changing environment's impacts, which drove the biological system to a point of low resilience at which the studied community, being presumably mostly climate-driven, exited its previous strong coupling with fishing (i.e., the change towards a less steep slope of the system-F_{com}'s interaction). Our analyses provide evidence that the Cantabrian ecosystem still appears to be in a dynamic and directional progression. The resilience of the demersal community has been eroding over time and at its current state is prone to shift as conditions continue to change with a warming climate.

The analysis of demersal fish biomass trends showed a global increase in species abundances with two marked shifts, detected by STARS and the chronological clustering in the late 1990s decade and early 2010s. In a scenario characterized by the release of a historically severe fishing impact, we understand these shifts as responses to a combination of changes in forcing. On one side, in the late 1990's, fishing impact on the North-East Atlantic ecosystems had softened, as progressive enforcement of fishing regulations notably decreased fishing pressure (Modica et al., 2014; Merillet et al., 2020). In our research, the study of this empirical natural system pointed to a gradual shift in years 1998-1999. Since the response to fishing pressure during those years is apparently linear, and concurs with a regime shift recently identified in NW Iberian coast plankton assemblages (Bode et al., 2020), a wider scale factor absent from this study's analyses might also be contributing to this shift. On top of that, and parallel to the community's complex process of recovery from a long history of high fishing effort (Modica et al., 2014; Arroyo et al., 2017; Punzón et al., 2021), global warming has provided a build-up in sea temperature, first limited to sea surface temperature, and later on also detectable at higher depths (González-Pola et al., 2005; Somavilla et al., 2016). These conditions have driven the demersal ecosystem into a process of meridionalization, i.e. a significant increase of abundance of temperate species with Lusitanian affinities, which accelerated around the late 90s, when most species increased their abundance as a result of an increasing temperature (Punzón et al., 2016, 2021).

The late 1990's shift reflects the fast change of a system in response to concurrent changes in its drivers (i.e. continuous response); while the early 2010's shift emerges as the typical fold bifurcation regime shift (Scheffer et al., 2001, 2009), i.e. a discontinuous response taking place after a threshold in a stressor (or a combination of stressors) is exceeded. The Cantabrian Sea demersal ecosystem did not abruptly collapse after succumbing to an accumulation of stressors, but shifted towards a new stable state responding to the retirement of a historically severe fishing pressure parallel to a marked increase of water temperature.

On one side, RDA results pointed to F_{com}, the community averaged fishing mortality, having an important effect on the system for the 1983-1998 period. F_{com} presents its peak in year 1988 and starts a decline that reaches its lowest values in the last years of the studied series. It is in the last two years, 2017 and 2018, that for the first time in the whole series, an $F_{com} \leq 1$ is reached (0.86 and 0.89, respectively), which corresponds to levels of exploitation consistent with MSY. In the period 1997-2003, improved management of fisheries achieved a 45% reduction in fishing pressure for the demersal Cantabrian community (Modica et al., 2014). This recovery is clearly reflected in our system variable, the PCsys. Initially, through the removal of biomass, fishing led to a near depletion of some targeted stocks, and had major impacts on the structure and functioning of the ecosystem (Arroyo et al., 2017, Hidalgo et al., 2017). Framed in the NE Atlantic rebuilding of previously overfished communities (Collie et al., 2013; Fernandes and Cook, 2013), management interventions achieved an increase in the biomass of the main predators and groups associated with demersal–benthic habitats. This was also observed as a homogenization of the Atlantic communities' size structure, which very likely facilitated a broader (less regionalized) impact of climate variations (Shackell et al., 2012, Hidalgo et al., 2017). However, this increase in abundance does not necessarily imply the achievement of other community indicators 'restoration end points', which would carry the full recovery of the functionality of the ecosystem (Collie et al., 2013; Arroyo et al., 2019). At low levels of trawling, the system's configuration abruptly changed, probably due to the effect of rapidly declining fishing in the previous period, followed by signs of hysteresis. The restoration trend of the bentho-demersal community regarding fishing impacts is undoubted and noticeable in the change of configuration of the community presented here. In fact, species that were favored in the recent period are mainly cartilaginous fish (rays and sharks), known to have a high sensitivity to trawling due to their equilibrium (K) life-history strategies (de Juan et al., 2020), and commercial species (such as hake, four spot megrim and conger eel), which corroborates our finding that fishing is indeed the key factor shaping the system. If global ecosystem stability is to be expected, however, the heavy decline in fishing needs to be interpreted along with an ongoing dynamic process of change captured by the decreasing values of resilience (see below). The probable shift of fishing activity to deeper grounds, an increasing pressure on pelagic species (Abad et al., 2010; Arroyo et al., 2019) and a systemic resilience breach enabled by climate conditions never experienced before (Punzón et al., 2016; Somavilla et al., 2016) are also an important part of the present's state of affairs.

During the second period of the time series, from the late 1990s to 2018, while moving towards an area of low resilience, an important change in tendency took place, located around years 2010 and 2012. A sharp increase in several fish species biomass around those years boosted the system into a new configuration. STARS and chronological clustering applied to our data detect it as a second shift, which would initiate a six-year period until the end of the series. Over those six years, the system was positively affected by temperature and salinity, and somehow detached from the influence of fishing (apparent as a smoothing of the slope in the PCsys-F_{com} relationship), while for the intermediate phase, years 1998-2012, the community's dynamics are apparently less subject to the interannual variation of SST and the impact of overfishing. We suggest wider environmental drivers, other than those included in our analyses, might have been at play over this period. The regional hydroclimatic conditions then, coincide with a period of La Niña like-conditions in the tropical Pacific (cold phase of ENSO), a positive phase of AMO and low absolute values of the NAO index in the North Atlantic (a 'non-NAO' period). Independently of the index used to approach climatic forcing, this period between 1997 and 2012 is marked by a reorganization of heat budget and circulation in all ocean basins. In particular, in the North Atlantic these years were characterized by cooling conditions at the ocean surface which favoured a large transfer of heat and salt from upper to deeper ocean layers (Somavilla et al., 2016). Community Weighted Mean Temperature (CWMT) calculated for the area reflects this warming and salting of mid-layers, which could have affected recruitment processes and bathymetric and geographical displacement of species (Auber et al., 2015; Punzón et al., 2016, 2021). In 2011, months after an extreme NAO annual mean value, the system experienced a striking intake of fresher waters, which reversed the previous salting trend that had been going on since the 2005 strong winter mixing. From year 2012 onwards, the increasing trend of abundances in the studied community continues, while CWMT coherently decreases along the drop-off in temperature and salinity at mid-depths (Punzón et al., 2021).

Of all these expressions of external forcing, fishing pressure stands out in our statistical analyses as the most critical feature for the system. Nevertheless, by taking account of previous research in which climate has been associated with the general boost in biomass, frequency of occurrence and CWMT (Punzón et al., 2016; Punzón et al., 2021) altogether with the opposed trends warming and fishing display at long-term scale (Ter Hofstede et al., 2010; Ter Hofstede and Rijnsdorp, 2011; Hidalgo et al., 2017), we consider the definite inducer of both state shifts on the bentho-demersal realm was a combination of environmental and anthropogenic factors. It has thoroughly been discussed how surface oceanic features are strong drivers for demersal resources, (e.g., Alemany et al., 2013; Druon et al., 2015; Sion et al., 2020). For instance, changes in air-sea heat exchanges linked to the water column vertical structure and occurrence of ecological hotspots are often primary drivers of marine resources (e.g. Behrenfeld and Boss, 2014; Druon et al., 2021), becoming also triggers of regional scale shifts in highly impacted ecosystems (Hidalgo et al., 2022c). In terms of the system's response to warming, the inertia driving the main system trends at the present moment is also uncertain and it is fair to assume the system finds itself inside an ongoing process of change. Its resilience in response to fishing has been eroding in reference to the 1990's decade, and at present, Cantabrian demersal ecosystem moves along a faint attractor, fluctuating even without clear stochasticity driving it. In this transition scenario, further studies at smaller spatial (i.e. local) and ecological (i.e. food web or species-level) scales need to be conducted to suggest appropriate management strategies aimed at foreseeing anomalies in response to warming as well as regulating fisheries expansions (Arroyo et al., 2019). Even when systemic changes have not yet been observed, many marine ecosystems whose resilience was slowly compromised got to a situation of collapse that could have been predicted and reversed (Choi et al., 2005; Hamazaki et al., 2005; Carpenter et al., 2011). In the case of the Cantabrian Sea, current values of resilience are also associated to a pronounced sensitivity to environmental variability and low predictability of the type and direction of it response. This calls for implementation of adaptive management (Hidalgo et al., 2022a).

This is the first application of an IRA in a marine community of the NE Atlantic. There are two main novelties in this study compared to previous IRA applications on empirical marine communities (Vasilakopoulos et al. 2017; Tsimara et al. 2021; Damalas et al. 2021; Ma et al., 2021; Hidalgo et al. 2022c). First, the system dynamics in 1988-2018 form a stability landscape with three system states but two system-stressor couplings (basins of attraction), due to the regime shift of the late 1990s taking place at a point of rapidly declining fishing. This scheme is theoretically possible (Scheffer et al., 2001), but has not been previously observed in an empirical setting. Second, the inclusion of F_{com} as a stressor and its eventual manifestation as the key stressor shaping a system are unique, in the sense that previous studies had not examined any proxy of fishing as candidate stressor, but environmental variables alone.

The shifts we report here lie within a history of mostly climate-driven shifts identified in NE Atlantic and Mediterranean Sea at different ecological levels. Particularly, the late 90s transition taking place in Cantabrian Sea bentho-demersal community coincides with thelate 1990s shift detected by other authors in the area (Hemery et al., 2008; Luczak et al., 2011; Auber et al., 2015; Bode et al., 2020, to name a few). In the Mediterranean Sea, where climate change and fishing have also been defined to act as a tandem in deteriorating the ecosystem structure and function (Albuoy et al., 2015), multiple climate-induced regime shifts were associated to the global acceleration in the rise of SST after the 1997/1998 El Niño event (Vasilakopoulos et al., 2017). Climate variability in the Northern Hemisphere has been postulated as the dominant factor inducing regime shifts in North Atlantic ecosystems (Möllmann and Diekmann, 2012), but in many studies fishing pressure was accounted responsible for debilitating resilience and triggering trophic cascades, both significant contributors to the occurrence of regime shifts (Alheit et al., 2005; Choi et al., 2005; Auber et al., 2015).

The disentangling of the opposed long-term trends of past fishing impacts and present warming is still a critical challenge. The identification of the driver/s to which a natural system responds to at a given time is a cornerstone of the design of plausible adaptive measures to cope with climate change impacts (Hidalgo et al., 2022a). Our results provide new insights to face this challenge, by looking into a process associated to these interacting drivers over time, and the way they have shaped the system in the most recent period. Either abrupt or smoothly, Cantabrian Sea ecosystem is currently reflecting the consequences of its vulnerability to fishing and climate change. We corroborate that marine communities have complex, distinctive adaption mechanisms to changes in their environment, inextricably dependent on their resilience dynamics. When aiming for environmental sustainability and human welfare, it is imperative to carry a careful monitoring of the ecosystem's resilience dynamics, with a specific study of their implications on the configuration of the ecosystem, so as to enable an integrative assessment of current and future marine ecosystems.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are openly available in OSF at http://doi.org/10.17605/OSF.IO/W4EH3, reference number DOI 10.17605/OSF.IO/W4EH3.

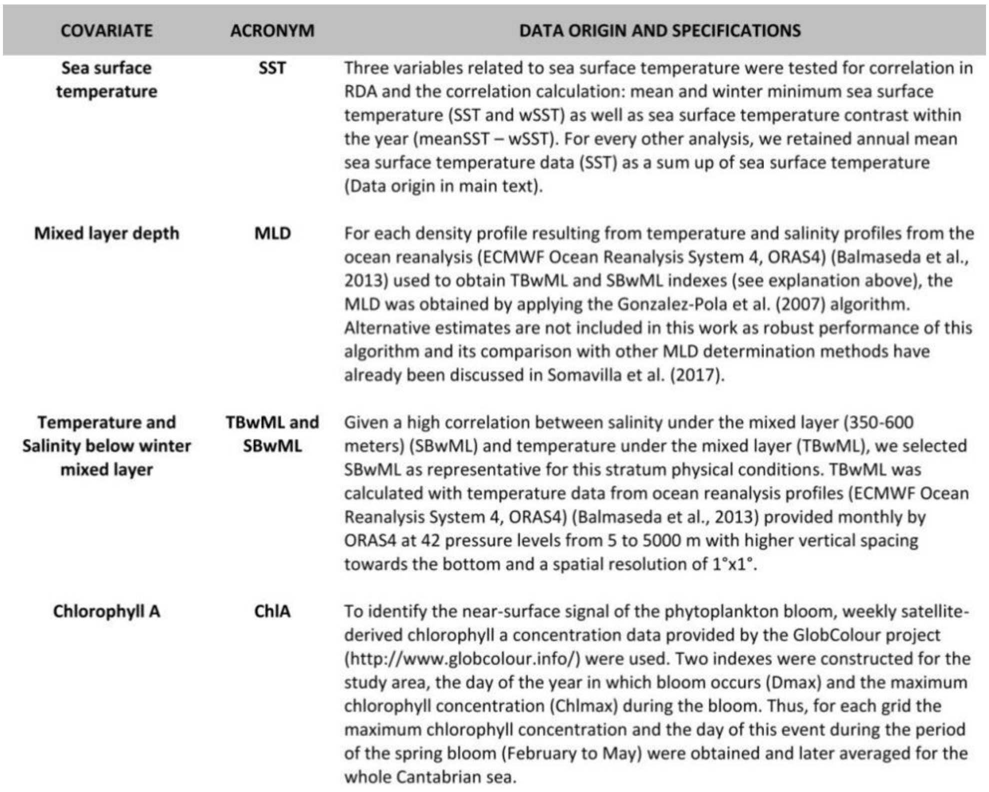
4.5 SUPPORTING INFORMATION

APPENDIX 1: SUPPORTING METHODS

Redundancy Analysis (RDA): in this study RDA served a double purpose: contributing to the final selection of abiotic variables (RDA I) as well as graphically associating the systematic pattern revealed by the PCA to the abiotic dataset (RDA II). As a constrained version of PCA, RDA models response variables as a function of explanatory variables and quantifies its associations (Zuur et al., 2007). It was selected as the proper constrained multivariate analysis after carrying a Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980; Leps and Smilauer, 1999). The function for DCA is included in R package vegan (Oksanen et al., 2019). RDA was performed on the species data set and an initial abiotic dataset, consisting of 13 explanatory variables (Table Supp. 1). Together with a correlation plot (Figure Supp. 2), RDA I triplot was used for the selection of the explanatory variables included in further analyses. To study the goodness of fit of RDA I, adjusted R-squared (adj-R^2) was calculated.

APPENDIX 2: SUPPORTING TABLES

Table Supp. 1. Initial selection of abiotic covariates names, acronyms, basic descriptions and source of data.



COVARIATE	ACRONYM	DATA ORIGIN AND SPECIFICATIONS
Sea surface temperature	**SST**	Three variables related to sea surface temperature were tested for correlation in RDA and the correlation calculation: mean and winter minimum sea surface temperature (SST and wSST) as well as sea surface temperature contrast within the year (meanSST – wSST). For every other analysis, we retained annual mean sea surface temperature data (SST) as a sum up of sea surface temperature (Data origin in main text).
Mixed layer depth	**MLD**	For each density profile resulting from temperature and salinity profiles from the ocean reanalysis (ECMWF Ocean Reanalysis System 4, ORAS4) (Balmaseda et al., 2013) used to obtain TBwML and SBwML indexes (see explanation above), the MLD was obtained by applying the Gonzalez-Pola et al. (2007) algorithm. Alternative estimates are not included in this work as robust performance of this algorithm and its comparison with other MLD determination methods have already been discussed in Somavilla et al. (2017).
Temperature and Salinity below winter mixed layer	**TBwML and SBwML**	Given a high correlation between salinity under the mixed layer (350-600 meters) (SBwML) and temperature under the mixed layer (TBwML), we selected SBwML as representative for this stratum physical conditions. TBwML was calculated with temperature data from ocean reanalysis profiles (ECMWF Ocean Reanalysis System 4, ORAS4) (Balmaseda et al., 2013) provided monthly by ORAS4 at 42 pressure levels from 5 to 5000 m with higher vertical spacing towards the bottom and a spatial resolution of 1°x1°.
Chlorophyll A	**ChlA**	To identify the near-surface signal of the phytoplankton bloom, weekly satellite-derived chlorophyll a concentration data provided by the GlobColour project (http://www.globcolour.info/) were used. Two indexes were constructed for the study area, the day of the year in which bloom occurs (Dmax) and the maximum chlorophyll concentration (Chlmax) during the bloom. Thus, for each grid the maximum chlorophyll concentration and the day of this event during the period of the spring bloom (February to May) were obtained and later averaged for the whole Cantabrian sea.

Table Supp. 1. (cont.)

Upwelling index	**Uw**	The annual mean upwelling index was extracted from NOAA's FNMOC model from the series provided by Spanish Oceanography Institute (IEO) (www.indicedeafloramiento.ieo.es). They use the sea level pressure data from WRF atmospheric model of Meteogalicia. We considered the data corresponding to 'Banco de Galicia' (43N, 11W) as the regional index for the whole area.
North Atlantic Oscillation index	**NAO and wNAO**	NAO is characterized by a meridional dipole in the pressure field between the Azores high and Icelandic low (the North Atlantic action centers). Along with the Eastern Atlantic pattern, NAO highly influences European land CO_2 sink and has been related to major changes in a number of environmental and planktonic variables in this region (Beaugrand, 2000; Bode et al., 2009; Mellado-Cano et al., 2019). We kept NAO index annual mean (NAO in the paper's figures) instead of the winter NAO since it correlated less with winter EA index (wEA) (Pearson coefficient -0.1) and appeared to explain a higher variance in RDA I. This way the two main climatic variability patterns in the East North Atlantic area were included in our preliminary analysis. (Data origin in main text)
Winter EA index	**wEA**	The second pattern of climate variability in the region is the Eastern Atlantic pattern. Data for the whole period was downloaded from the Climate Prediction Center of the NOAA (https://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml). Recent studies refer to it as a well-defined sea level pressure monopole south of Iceland and west of Ireland. It has been indicated to interact with NAO to the point of modulating the location of the North Atlantic action centers and shaping the surface responses to the NAO. For example, the EA played a key role in determining the climate anomalies during the outstanding negative NAO episodes associated with the extremely cold European events of December 2010 and winter 2006/07 (Mellado-Cano, 2019 and references therein).
ENSO index	**ENSO**	The Multivariate ENSO Index represents a holistic overview of the atmospheric and oceanic anomalies during ENSO events. The index we used is based on five variables from the tropical Pacific. These five variables are: sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, and outgoing longwave radiation (Wolter et al., 2011 and references therein). Data were extracted from the National Center for Atmospheric Research Staff (Eds). Last modified 15 Jul 2019. "The Climate Data Guide: Multivariate ENSO Index." Retrieved from https://climatedataguide.ucar.edu/climate-data/multivariate-enso-index.

APPENDIX 3: SUPPORTING FIGURES

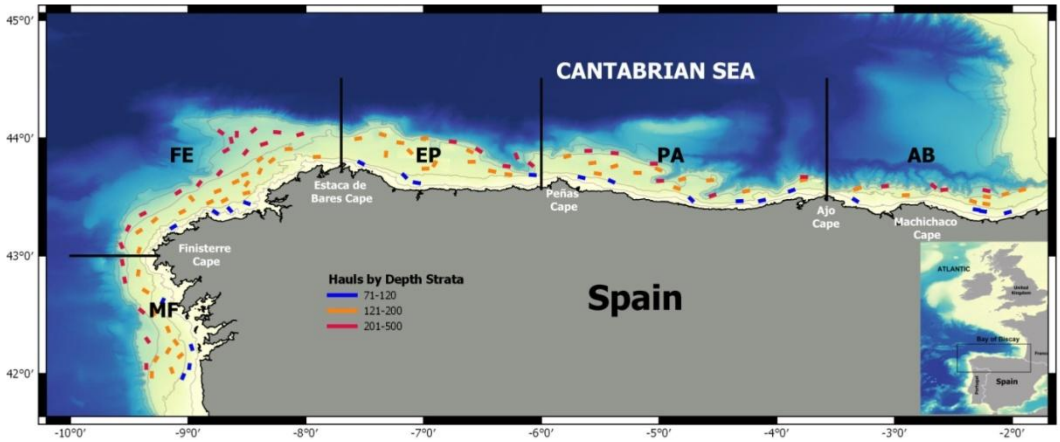


Figure Supp. 1 Samples in the study area by depth strata and year (1983–2017). Colors refer to depth strata (blue to shallowest, between 71 and 120 meters deep, orange to the intermediate strata, between 121 and 200 m, and red to the deepest, between 201 and 500 meters deep. The survey sampling scheme is arranged along five geographical sectors: Miño River- Cape Finisterre (MF), C. Finisterre- C. Estaca (FE), C. Estaca-C. Peñas (EP); C. Peñas-C. Ajo (PA); and C. Ajo-Bidasoa River (AB).

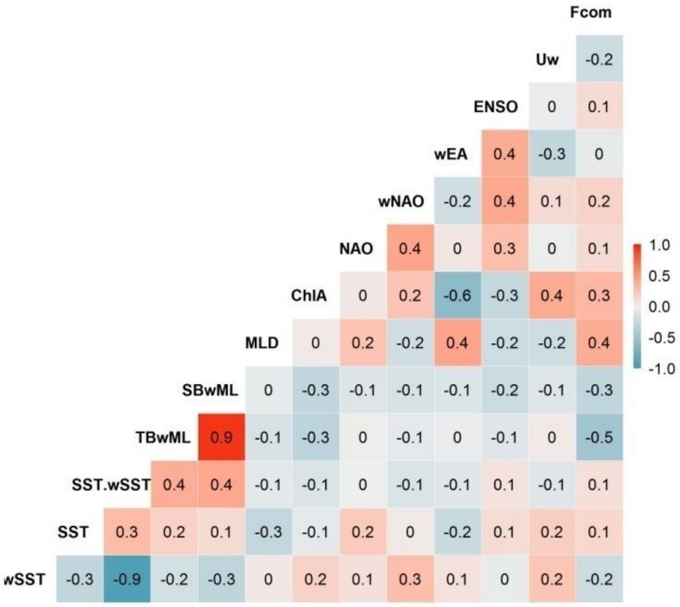


Figure Supp. 2. Correlation plot of every stressor. Pearson coefficients were computed for every variable combination: winter sea surface temperature (wSST), annual mean sea surface temperature (SST), sea surface temperature contrast within the year (meanSST.wSST), temperature and salinity below winter mixed layer (TBwML and SBwML), mixel layer depth (MLD), start of the Chlorophyll bloom (ChlA), North Atlantic Oscillation index (NAO and wNAO), winter Eastern Atlantic pattern index, El Niño-Southern Oscillation index (ENSO), upwelling index (Uw) and fishing mortality (Fcom).

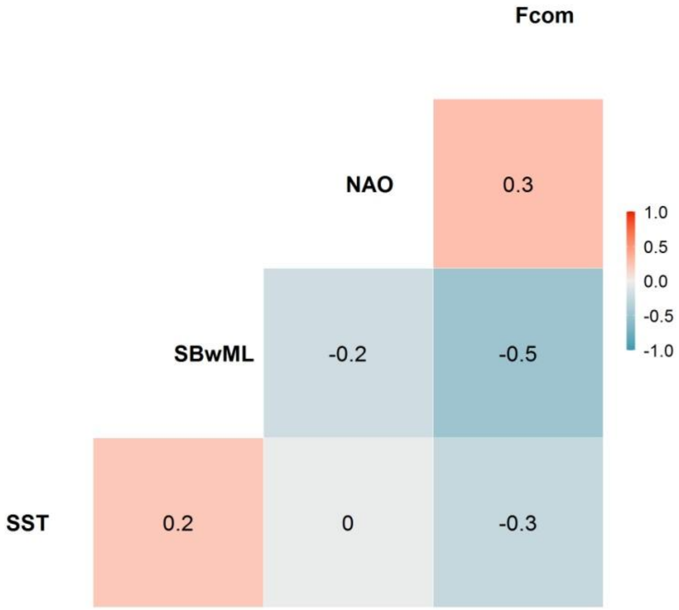


Figure Supp. 3. Matrix of four final stressors' Pearson coefficients: annual mean sea surface temperature (SST), salinity below winter mixed layer (SBwML), North Atlantic Oscillation index (NAO) and fishing mortality (F_{com}).

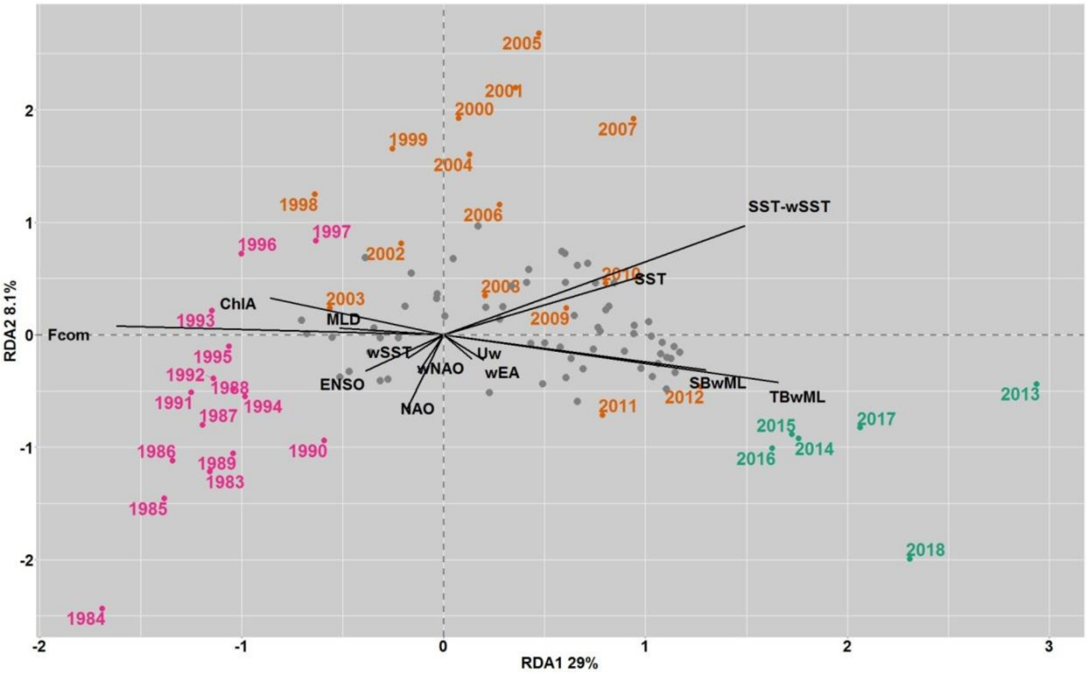


Figure Supp. 4. Explanatory variable selection RDA I triplot, based on the correlation matrix and species conditional scaling. The length and direction of black lines correspond to the variance explained by the variable. The angle between lines reflects the correlations between explanatory variables. The narrower the angle, the stronger the correlation. The explained variance of RDA1 and RDA2, i.e. the sum of canonical eigenvalues for the constrained axes divided by total variance (inertia), is 36.5% and RDA I adjusted R-squared is 35.12%. SST and meanSST - wSST have a high correlation value, so only SST appears in the triplot since they would overlap. Years are colored in accordance to the clusters of the chronological clustering (see Fig. 5 in main text). Find acronyms used for variables in Suppl. Table 1.

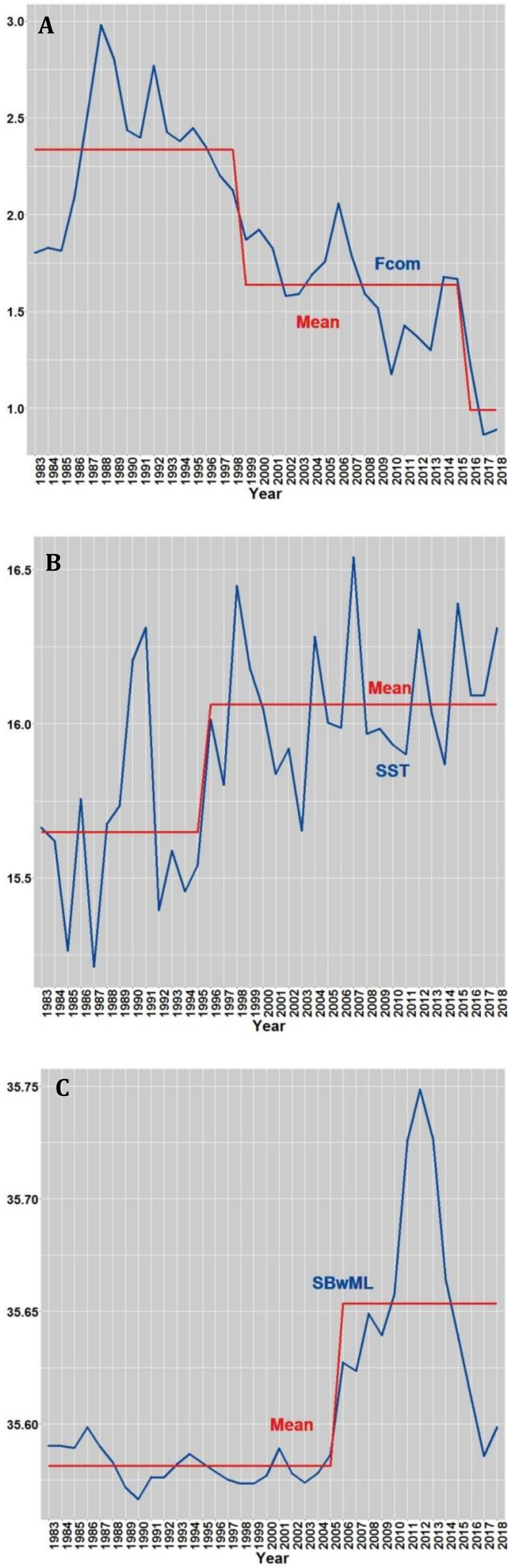


Figure Supp. 5. Plots of STARS applied on F_{com} (A), SST (B) and salinity below winter mixed layer (SBwML) (C). Red line shows the stepwise trend containing the regime shift in the mean detected by STARS method. Blue lines represent the stressors raw data.

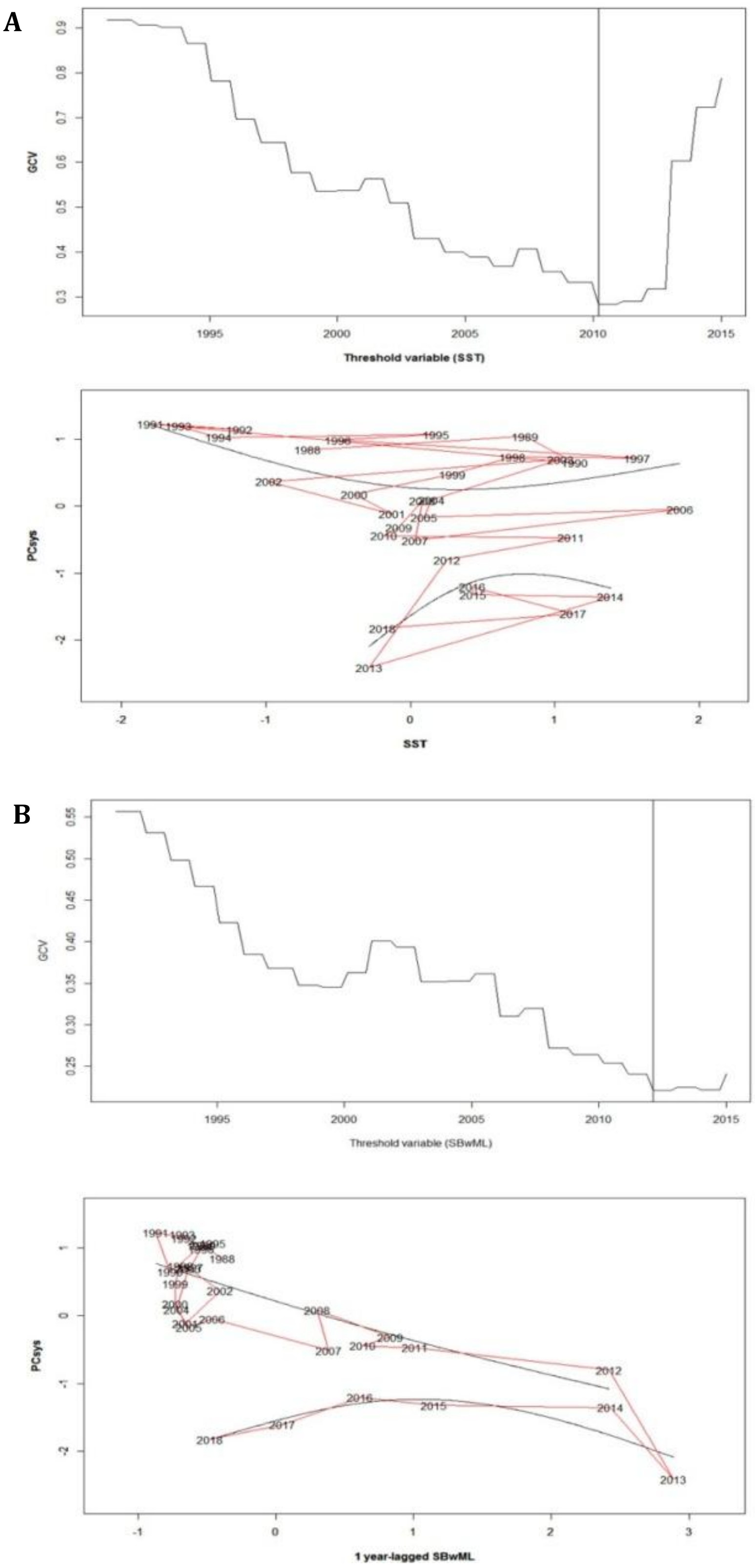


Figure Supp. 6 Plots of GCV values of TGAMS with threshold years (top) of optimal fits for each system variable (PCsys) – stressors relationship for 1988-2018 series. Table with the gCV values used for model selection are in Table 1 in the main text. A) TGAM of PCsys-no-lagged SST (R^2adj. = 78.1%) showing a threshold in 2010. B) TGAM of PCsys-1-year lagged salinity (SBwML) (R^2adj. =81.9%) showing a threshold in 2012.

C

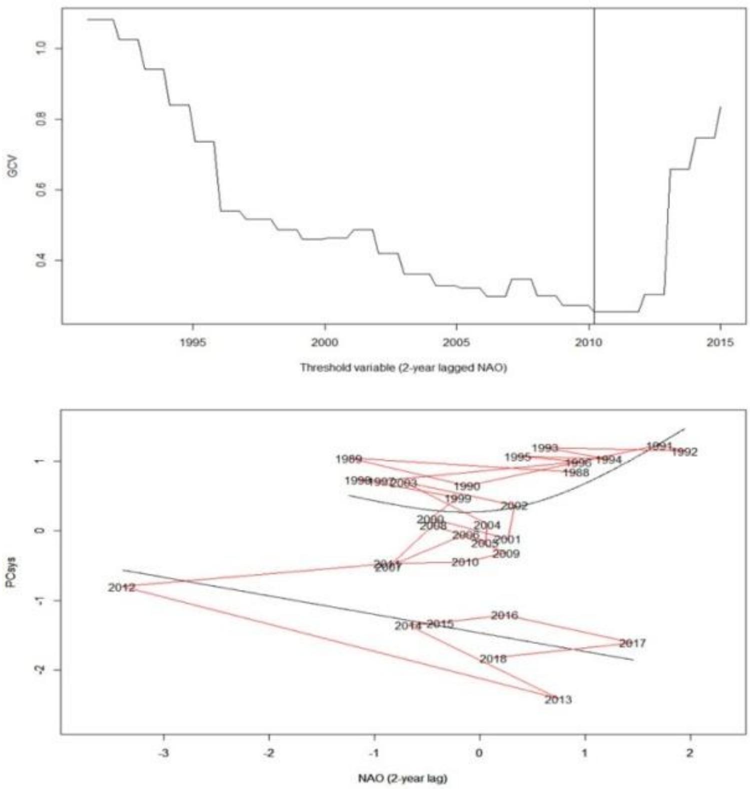


Figure Supp. 6. (cont.) Plot of GCV values of TGAMS with threshold years (top) of optimal fits for each system variable (PCsys) – stressors relationship for 1988-2018 series. Table with the gCV values used for model selection are in Table 1 in the main text. C) TGAM of PCsys- 2-year lagged NAO (R^2adj. = 72.1%) showing a threshold in 2011.

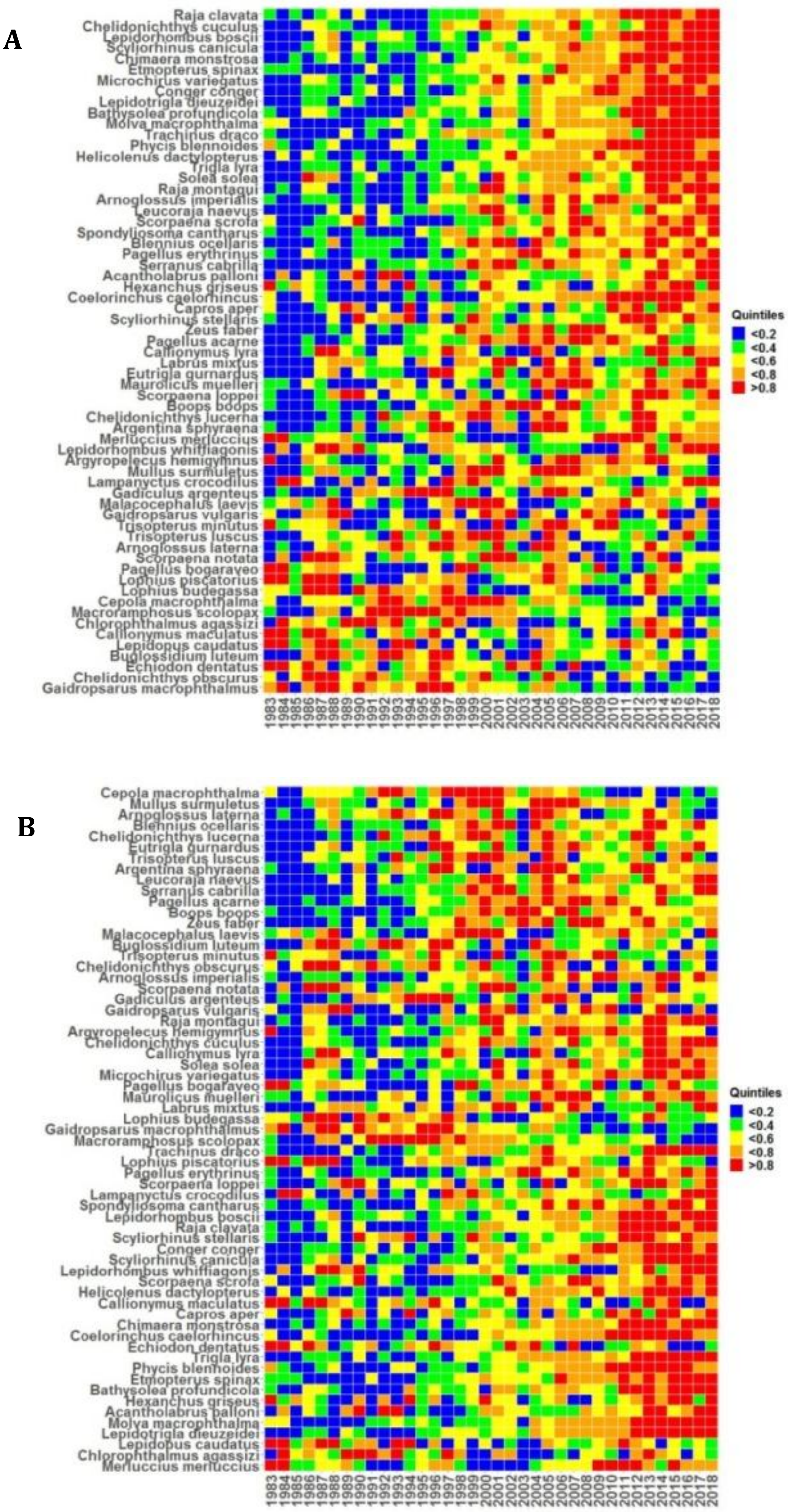


Figure Supp. 7. Relative contribution to PC1 (A) and PC2 (B) of the biomass of the 63 fish species selected as representative of Cantabrian Sea's bentho-demersal community. Species are sorted by their contribution to the principal components. Top species contribute higher and bottom species contribute less.

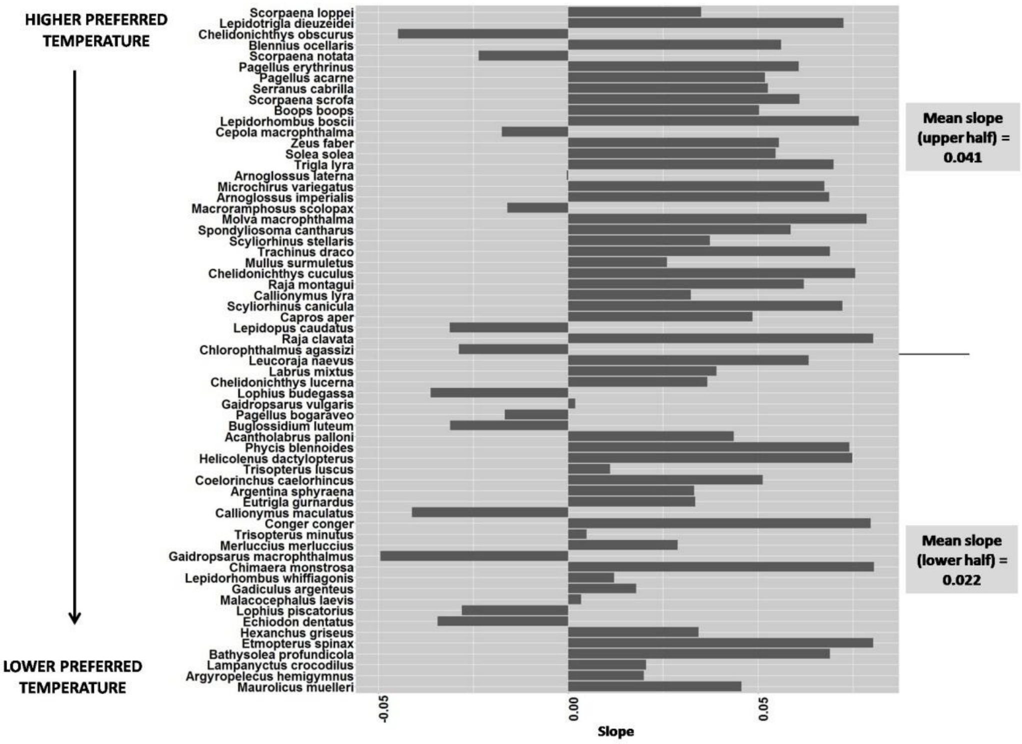


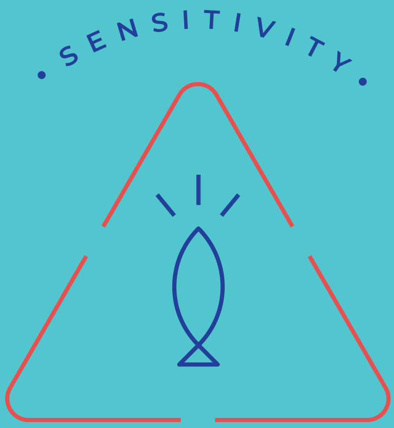
Figure Supp. 8 Slopes of the linear models for the biomass of the 63 bentho-demersal species in the period 1983-2018. Species are ordered in line with Figure 1 in the main text, those with higher thermal affinities on the top and the 'colder' ones on the bottom. There has been a general increase in most species' biomass, but there are higher slopes in the more thermophilic section of the selection. The mean slope calculated for the 32 species in the upper half is 1.9 times higher than the mean slope for the 32 species in the lower half. Black line in the right margin of the plot points to the mid-point of the species selection, species number 32.

APPENDIX 4: SUPPORTING RESULTS

The correlation matrix of abiotic variables jointly with RDA I results, indicated the presence of variables with extremely high correlated values representing similar ecological signals. In the RDA I triplot, angles between lines of quantitative explanatory variables represent the correlations between them as accurately as a PCA applied only on the explanatory variables would (Figure Supp. 4). We omitted those with highest Pearson coefficients and limited the final dataset of possible drivers to a set of 4 variables (F_{com}, SST, NAO and SBwML).

EFFECTS OF CLIMATE CHANGE AND FISHING ON DEMERSAL ECOSYSTEMS

AN APPROACH TO HUMAN IMPACTS ON
NORTH EAST ATLANTIC AND SPANISH
MEDITERRANEAN COMMUNITIES



CHAPTER

05

DEVELOPMENT OF INDICATORS OF THE COMMUNITIES’ SENSITIVITY TO CLIMATE CHANGE AND FISHING

CHAPTER 5. DEVELOPMENT OF INDICATORS OF THE COMMUNITIES' SENSITIVITY TO CLIMATE CHANGE AND FISHING

To thoroughly characterize spatio-temporal dynamics of communities' vulnerability, a growing number of studies analyzes high quality data on communities' exposure to climate change and other anthropogenic stressors in conjunction with semi-qualitative, trait-based Vulnerability Assessments (VAs), which investigate the sensitivity and adaptive capacity of marine communities. VAs have proved useful tools for the application of efficient management strategies that allow realistic adaptations to climate change effects.

This chapter sums up an ongoing research aimed at characterizing the spatial and temporal sensitivity patterns to fishing and climate change of bentho-demersal communities (fish and megabenthos) in the Cantabrian and Spanish Mediterranean seas using a semi-qualitative, expert-based VA. For this purpose, a dataset of species traits expected to be responsive to warming and trawling was compiled, with the aim of combining the trait information of the communities' most representative species inside indicators of the system's sensitivity. We expected the indicators would shed light on the ecosystem status and its cumulative response to two major pressures, climate change and fishing. A co-authored data publication on the compilation of the trait database and selection of representative species has been included as an annex (Annex I) to this thesis. Said data paper and this unpublished chapter, which is expected to be continued in the foreseeable future and framed as a second scientific publication, are two main outcomes of this research.

5.1 INTRODUCTION

In the last decades, the Cantabrian Sea fisheries have undergone dramatic shifts in effort. Fishing pressure in Cantabrian Sea peaked in the 1980s and has decreased during the last decades. After the enforcement of strict fishing regulations in the 1990s many stocks have recovered (Modica et al., 2014). Concurrently, sea temperature in this region has increased, and climate change impacts have increasingly become noticeable at various ecological levels in the last two decades (Punzón et al., 2016; Bode et al., 2020; Punzón et al., 2021; Chust et al., 2022; Polo et al., 2022). The Spanish Mediterranean Sea has experienced a similar decrease in fishing pressure, but contrastingly, it still endures overexploitation of many stocks (Farriols et al., 2019) and is more severely exposed to climate change effects than other regions. In fact, the Mediterranean's warming rate is two to three times that of global oceans' (Vargas-Yáñez et al., 2008; D'Amen et al., 2022). Between and within regions, communities might be very diverse in their response to sustained levels of external stress (Ter Hofstede and Rijnsdorp, 2011). In these two regions, this is partly due to distinct levels of exposure, but also depends on the cumulative, possibly often interactive effects of fishing pressure and anthropogenic warming (Punzón et al., 2016; Hidalgo et al., 2017; Polo et al., 2022), as well as the ecological assemblages' structure and functioning. Since these aspects ultimately define the communities' vulnerability to shifting conditions, approaches to fully acknowledge communities' response mechanisms are key for the design of effective adaptation and mitigation actions.

The trait-based approach is often used to characterize communities' vulnerability to stressors. This functional (non-taxonomic) approach to vulnerability focuses on how certain biological traits and ecological features shape the sensitivity of assemblages, and is a methodology considered to highly reduce the complexity of the community assessment (De Juan et al., 2020). Although trait-based assessments of sensitivity have been widely applied, few studies have focused on the sensitivity of whole assemblages to more than one pressure (Butt et al., 2022), and still fewer have integrated the potential interaction between pressures, which, when synergistic, can act as an additional force (Perry et al., 2010; Möllmann and Diekmann, 2012).

The VA framework allows a straightforward assessment of the three components of vulnerability (i.e., exposure, sensitivity and adaptive capacity) at various ecological levels, from population (i.e., assemblages of a single species) to community (i.e., various populations) and ecosystem (i.e., the communities and their habitats) (De Lange et al., 2010; Hare et al., 2016). In general, a typical VA framework starts by determining the sensitivity of traits through a pre-defined scoring system established on expert judgment. The expert-based sensitivity ratings have been used for assessing the vulnerability of species, as did Pecl et al. (2014), whom individually measured the relative sensitivity of commercial species to climate change, or Stortini et al. (2015) and Bueno-Pardo et al. (2021) whom evaluated the vulnerability of a selection of marine species to different warming scenarios. Following a similar approach, regarding the assignment of sensitivity degrees to trait categories which were later weighted by the species abundance, De Juan and Demestre (2012) and González-Irusta et al. (2018) built invertebrate trait-based sensitivity indices to trawling disturbance. However, most commonly, the study of sensitivity scores is conducted at an assemblage level, by weighting the ranked traits by the population or community biomass data (Spencer et al., 2019; Allyn et al., 2020). Beyond the species-based studies, VAs have also been applied to assess the vulnerability of entire ecosystems dependent on habitat-forming species, such as mangroves, (Ellison, 2015) or to assess the vulnerability of fishing communities to climate change (Pinnegar et al., 2019).

Building on these previous studies, and with the aim of understanding at a regional and sub-regional level how marine communities in Cantabrian and Spanish Mediterranean seas have responded to the combined effects of climate change and fishing, we explored two indicators of communities' sensitivity, separately and combined. For this purpose, (i) we determined and compiled a list of traits and ecological preferences relevant for the species' sensitivity to each pressure, for a selection of 246 species representative of the two communities, (ii) the trait values were converted to a score according to their sensitivity to increasing trawling and warming (from 1, low sensitivity, to 3 or 4, high or very high sensitivity, respectively), (iii) the species' sensitivity scores dataset and species biomass information from bottom trawl surveys were used for the computation of community weighted mean (CWM) sensitivity indicators to trawling, to warming, and to their combination. We calculated annual time series of CWM sensitivity at the level of the entire regions, and studied potential spatial patterns in the time series of the indicators by calculating their rate of change (slope) per sub-region.

The indicators are expected to reflect the community's response to sea temperature and fishing pressure, with possible spatial differences among communities. For example, the indicator of community sensitivity to fishing is expected to be negatively correlated to fishing pressure, as a high fishing effort would cause a decreased abundance of the most sensitive species in the community (e.g., due to increasing mortality). Similarly, we would expect the indicator of community sensitivity to climate change to be negatively correlated to sea temperature, as increasing temperature would cause a decreased abundance, in the community of the most sensitive species to warming (e.g., due to increasing mortality or range-shifts). If the response of the indicators turned out to be incoherent with the dynamics of sea temperature and fishing effort, it could either mean that the indicators are somehow flawed and the rationale for their development should be reconsidered, or it could be due to a confounding effect that owes to, for example, other non-accounted for pressure impacting the ecosystem or spatial variation in the pressure-indicator relation. To assess the latter, we also investigated temporal changes of the indicators at sub-regional scale and discussed them based on the known spatial dynamics of the stressors.

5.2 MATERIAL AND METHODS

5.2.1 SELECTION OF SPECIES

The number of unique species sampled in each demersal survey (DEMERSALES, in the Bay of Biscay, and MEDITS, in the Spanish Mediterranean) was high, with over 680 species in the southern Bay of Biscay and 620 in the Spanish Mediterranean during the study period. While it is often assumed that the most accurate understanding of a biological system's dynamics is met with the inclusion of as many species as possible; a representative selection of species from a community depends also on the research questions and the communities' nature, structure and functional diversity. For this study we excluded species of sporadic occurrence so as to minimize constraints in the achievement of trait information. To obtain a set of species representative of the communities' composition we analyzed changes in communities' richness using yield-effort curves. These allowed assessing how the accumulated richness changes across time (when increasing the number of years), across space (increasing the number of hauls in each annual survey) and with abundance patterns (with an increasing abundance threshold, in each haul and year) (analyses to support the representativeness of this selection are included in the Annex I). Following those three criteria, we selected a set of species representative of the communities, provided that they accounted for over 95% of the community biomass in any of the two study regions, in any given year of the series. The visual inspection of the accumulation curves (included in the Annex 1) yielded the following three filters for each survey database: by annual occurrence (only keeping species that appeared at least 12 years), by abundance (in number of individuals per km2) within the year (only keeping species that occurred at least in 12 hauls a year) and by abundance per haul (only keeping species with abundance values over the first abundance decile). The filtering resulted in a subset of 246 species that constituted the basis for subsequent analyses.

5.2.2 TRAITS DATABASE

In order to characterize the species according to their sensitivity to fishing and climate change, we assembled a trait dataset with 12 traits related to life-history and 6 ecological features related to thermal and depth preferences. The collection of traits included information about preference of habitat conditions (these features were expected to be responsive to environmental changes), morphology and position in the water column (expected to be more responsive to trawling), and the life-history of the species (often used in literature as responsive to either stressor) (Poloczanska et al, 2013; Beukhof et al, 2019; McLean et al, 2021). The traits were compiled for the most recurrent 246 species at the lowest possible taxonomic level. The information was gathered from online databases, namely WoRMS, BIOTIC (MarLIN, 2006), FishBase (Froese and Pauly, 2014) and SeaLifeBase, and diverse sources ranging from general handbooks to specialized papers. In total, more than 200 scientific publications were reviewed to this aim (see Annex I).

In the database, each trait value was accompanied by the taxonomic rank for which it was retrieved, its reference and the available information on revised literature (Annex 1). Due to a lack of information on many traits for a large set of species (data do not exist or are not published), it was difficult to limit the gathering of information to the species level. To minimize gaps when information of a particular trait for a species was missing, the mean value (or most frequent category, for categorical traits) of that trait for the genus was assigned, if available, or else for the most immediate taxonomic category with information for the trait, limiting the search to the database itself.

Additionally, a set of 6 ecological traits was obtained from the bioclimatic envelope models developed by AQUAMAPS (Kaschner et al., 2019) and presence data from the Ocean Biogeographic Information System database (OBIS, 2019). The mean depth and the depth range of species distribution was estimated based on the global species presence records (OBIS, 2019) and the digital bathymetry provided by EMODNET (http://www.emodnet-bathymetry.eu). This approach was preferred over the depth data provided by AQUAMAPS, as EMODNET provided a better resolution of the depth for each sampling station, which is essential in regions with steep depth gradients such as our study regions. The computation of the mean values and ranges followed the process described in the Material and Methods section of the Chapter 3 of this thesis.

After the bibliographical review and the estimation of the missing features, a total of 3634 traits were gathered with their correspondent taxonomic rank and only 71 ranks could not be assigned. Within the database, 73.5% of the traits were associated at the species level (see Annex 1).

5.2.3 STRESSORS' DYNAMICS

We analyzed the communities' exposure to external stressors by studying the spatio-temporal variation of bottom trawling effort and warming. Data on pair and otter trawling effort came from Vessel Monitoring System (VMS) and logbooks, provided by the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA). Data covered the period 2009-2020 and the entire North Atlantic Iberian Coast. VMS is a satellite-based monitoring system that provides information related to the position of fishing vessels, which when crossed with information from logbooks allows the estimation of the area swept by the trawling gear, as a function of the hours spent actively fishing, the average fishing speed and the gear width (Punzón et al., 2016). As a proxy for warming, we analyzed temporal and spatial dynamics of Sea Surface Temperature (SST) data from the oceanic physics re-analysis product 'Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis', generated by CMEMS IBI-MFC (find a detailed description in Sotillo et al., 2016). The model produced daily mean surface temperature for the period 1994-2020 with a 0.05° spatial resolution, which we re-scaled at 0.2° and then averaged to annual values per latitude/longitude of the 4464 sampling stations of the Cantabrian region and the 2177 of the Spanish Mediterranean region. To visually assess the temporal trends of the stressors we fitted General Additive Models (GAMs; Hastie and Tibshirani, 1990) on SST and VMS data, using the gam function in R package mgcv (Wood, 2011), assuming a gaussian distribution and limiting the degrees of freedom to a k=5.

5.2.4 SENSITIVITY ASSESSMENT

After going through a wide literature review, trait categories were scored according to the sensitivity to the pressures they conferred the species. The categories and their corresponding sensitivity scores to fishing (trawling) and climate change (warming) are summarized in Table 1 and Table 2, respectively. We categorized the continuous variables by dividing them in quantiles to create groups with similar number of observations, a technique well supported by literature (Foden et al., 2013; Carr et al., 2014; Bohm et al., 2016; González-Irusta et al., 2018).

Table 1. Degree of sensitivity to fishing (trawling) associated to each trait's category. The first seven traits are numerical and were categorized by dividing the continuous variables in quantiles.

SENSITIVITY TO FISHING

Trait	Low sensitivity (Score = 1)	Moderate sensitivity (Score = 2)	High sensitivity (Score = 3)	Very high sensitivity (Score = 4)
LONGEVITY	<5 years	5-10 years	>11 years	
BODY SIZE	Small <20 cm	Medium 20-50 cm	Large >50 cm	
FECUNDITY	>200000 eggs	12000-200000 eggs	<12000 eggs	
OFFSPRING SIZE	>1.5 mm	0.8-1.5 mm	<0.8 mm	
GROWTH COEFFICIENT	K > 0.60	K = 0.20-0.60	K < 0.20	
TL	Low trophic levels (<3)	Intermediate trophic levels (3-4)	High trophic levels (>4)	
AGE AT MATURITY	<2 years	2-3 years	>3 years	
PARENTAL CARE	Non-guarder planktonic lay, Non-guarder	Non-guarder demersal lay	Guarder brooder (external care)	Guarder bearer (internal care)
HABITAT	Pelagic, Bathypelagic	Demersal, Bathydemersal	Benthic, Suprabenthic	
MOTILITY	Swimmer	Burrower, Crawler	Sessile	
BODY SHAPE	Fusiform	Eel-like, Elongated, Bullet-like	Flat, Lenticular	Globular, Compressiform Hook-shaped
FEEDING MODE	Scavenger, Generalist, Detritivorous	Planktivorous	Surface deposit feeders, Benthivorous, Suprabenthic feeder	Suspensivorous, Suspension feeders

Table 2. Degree of sensitivity to climate change (warming) associated to each trait's category. The last six traits are numerical and were categorized by dividing the continuous variables in quantiles

SENSITIVITY TO CLIMATE CHANGE

Trait /eco-preference	Low sensitivity (Score = 1)	Moderate sensitivity (Score = 2)	High sensitivity (Score = 3)	Very high sensitivity (Score = 4)
SPAWNING CATEGORY	Non-seasonal (>=9)	Wide spawning season (3-8)	Narrow spawning season (=<3)	
PARENTAL CARE	Guarder brooder, guarder bearer	Non-guarder planktonic lay	Non-guarder	Non-guarder benthic lay
HABITAT	Pelagic, Bathypelagic	Demersal, Bathydemersal	Benthic, Suprabenthic	
SURFACE THERMAL AFFINITY (SST)	>20°C	15-20 °C	<=15 °C	
BOTTOM THERMAL AFFINITY (SBT)	>13°C	10-13 °C	<=10 °C	
SURFACE THERMAL RANGE (STT)	>16 °C	12-16 °C	<12 °C	
BOTTOM THERMAL RANGE (BTT)	>23 °C	19-23 °C	<19 °C	
MEAN DEPTH	>200 m	95-200 m	<95 m	
DEPTH RANGE	<=750 m	750-1300 m	>=1300 m	

While some vulnerability assessments separate the adaptive capacity attributes from those related to sensitivity, we considered both components together, following Hare et al. (2016). In general terms, scientific literature associates an increase in the pressure, whether this is warming or fishing pressure, to decreases in longevity, body size, age at first maturity and trophic level, and an increase of growth rates and fecundity, which correspond to faster life strategies linked to faster metabolisms as well as the selective extraction of the biggest organisms in the population, if not both (e.g., Beukhof et al., 2019c; Wang et al., 2020). Some of these sensitivity traits were categorized differently in previous studies, so here, we decided to avoid the use of uncertainly categorized traits as much possible, and excluded them from the development of the indicator of the pressure to which they showed conflict. Find below a brief explanation of the rationale and references by which each trait category was scored:

- Longevity: higher longevity has been related to a slow growth and development, and therefore to higher sensitivity to disturbances, due to larger generation times and lower overall reproductive outputs (Mace et al., 2008; González-Irusta et al., 2018; Bueno-Pardo et al., 2021; Butt et al., 2022). In most publications longer living organisms were associated with higher vulnerabilities, but since in certain studies high longevity and large size were considered as strong resistance traits to environmental impacts (Van Treek et al., 2020; Wang et al., 2020), to avoid disagreement on this trait's sensitivity to climate change, it was only used as a proxy for sensitivity to fishing. This continuous trait (measured in 'years') was categorized in three groups, from less to more sensitive: ≤5 years; 5-10 years; ≥11 years.

- Body size: this trait is considered an indicator for species sensitivity to both trawling or climate change (Simpson et al., 2011; Cheung et al., 2013; Pörtner et al., 2014; Jørgensen et al., 2016; González-Irusta et al., 2018; Hewitt et al., 2019; de Juan et al., 2020). Fishing is a strongly size-selective activity and larger organisms are expected to display a greater temperature-size response, due to their reduced surface area to body mass ratio, and the associated challenge of maintaining metabolic rates (e.g., Petrik et al., 2020; Lavin et al., 2022). In general, smaller organisms were considered to be less sensitive than bigger ones. However, exceptions in which a small body was related to higher environmentally-driven mortality rates (Jaric et al., 2018; Van Treek et al., 2020) led us to exclude this trait from the indicator of sensitivity to climate change. We categorized the trait, which was originally a continuous variable, in three groups: ≤20 cm; 20-50 cm; ≥50 cm.
- Fecundity: external perturbations may affect the reproductive potential of the community. More fecund species, those producing higher number of eggs per spawning event, are expected to be less sensitive to perturbations than those producing less eggs (Planque et al., 2010; Drinkwater et al., 2010; Ottersen et al., 2010; Van Treek et al., 2020; Bueno-Pardo et al., 2021). This trait was excluded from the calculation of sensitivity to climate, as there was certain controversy on the direction of its response to warming (Barneche et al., 2018). The categories used for scoring the species sensitivity to fishing were, from less to more sensitive: ≥200000 eggs; 12000-200000 eggs; ≤12000eggs.
- Offspring size: The size of the eggs is inversely proportional to mortality rates at sea (Ware, 1975, 1977; Ottersen et al., 2004). In this research, the size of the individual eggs was categorized, from less to more sensitive to perturbations as follows: ≥1.5 mm, 0.8-1.5 mm, ≤0.8mm.
- Growth coefficient: Fast growing species are often expected to be favored by warming (Hare et al., 2016; Bueno-Pardo et al., 2021), but there is some level of disagreement in this respect (Wang et al., 2020; Huang et al., 2021), so this trait was not used as proxy for sensitivity to climate change. As for sensitivity to fishing, K-strategists, characterized by a slow growth, late age at maturity, long life spans, low fecundity are considered to be especially vulnerable to high levels of exploitation (Stevens et al., 2000). We determined the following sensitivity categories: K≥0.60; K=0.20-0.60; K≤0.20, from lowest to highest sensitivity.
- Trophic level (TL): Previous studies have shown higher trophic levels' longer generation times and higher commercial interest are related to higher rates of mortality (Pauly et al., 1998; McLean et al., 2018; de Juan et al., 2020). The tolerance of the highest trophic levels to climate changes has been recently argued (Hu et al., 2022) so we avoided this trait when computing climate change sensitivity. Low

trophic levels (≤3) were scored with the minimum sensitivity, intermediate levels, between 3 and 4, as moderate sensitivity, and high trophic levels (≥4) as very sensitive.

- Age at maturity: A species first reproduction, or generation length, is considered an important trait for predicting reproductive turnover. Species with shorter generation lengths (time to maturity) are expected to have a faster population turnover and therefore are considered to have more opportunities for evolutionary or epigenetic changes in response to stressors (Bush et al., 2016; González-Irusta et al., 2018; Beukhof et al., 2019c; de Juan et al., 2020; Bueno-Pardo et al., 2021; Butt et al., 2022). As there was some disagreement on the response of this trait to warming (Free et al., 2019), it was excluded from the assessment of sensitivity to climate change. The age at maturity was categorized, from lowest to highest sensitivity, as follows: age of maturity under 2 years, between 2-3 years, over 3 years.
- Spawning season duration: this trait was categorized in three classes, which are here ordered from lowest to highest sensitivity to environmental changes: i) Non seasonal (spawning season ≥9 months): species that spawn continuously throughout the year without a defined spawning season are expected to suffer less from adverse effects of climate change. ii) Wide spawning season (3-9 months): species that go through several spawning events throughout the year are expected to have a moderate risk. iii) Narrow spawning season (≤3 months): species that may spawn several times per year but concentrate all spawning events in one season have a high risk of being affected by climate change (Hare et al., 2016; Biggs et al., 2021). This trait was only used as proxy for sensitivity to climate change, due to a lack of information on its response to fishing pressure.
- Parental care: following Ocaña et al. (2019), in which a species type of parental care is used as proxy for ability to recover from a stressful event, we scored the categories oppositely for sensitivity to environmental change and trawling. As argued by Bueno-Pardo et al. (2021) and Butt et al. (2022), individual juveniles under parental care would expectedly be less sensitive to environmental changes than organisms without parental care, in this respect, the most sensitive would be non-guarder species with benthic lay. Conversely, species providing either internal or external care (bearer and brooder organisms, respectively) would be more sensitive to the effects of trawling, due to low reproductive capacity.
- Habitat: pelagic species are considered to be less sensitive to either warming or trawling, as they can inhabit the whole water column, while benthic organisms are associated to higher sensitivity (McLean et al., 2018; de Juan et al., 2020; Le Marchand et al., 2020; Bueno-Pardo et al., 2021; Butt et al., 2022). We mixed two habitat-related traits, 'Zone' and 'Depth' from the trait vulnerability scoring carried by Butt et al. (2022). Pelagic and bathypelagic were scored as less sensitive, with a

score of 1, demersal and bathydemersal a score of 2 and benthic and suprabenthic a score of 3.

- Motility: species with limited movement capacity are expected to be more sensitive to local stressors as they will not easily move to avoid the stressor (González-Irusta et al., 2018; Hewitt et al., 2019; de Juan et al., 2020; Bueno-Pardo et al., 2021; Butt et al., 2022). As there was some discrepancy in literature according to this trait's sensitivity to warming, it was only included in the estimation of communities' sensitivity to trawling pressure (Chaudhary et al., 2021).
- Body shape: We used categories established by Beukhof et al. (2019a) and considered fusiform species the least sensitive (sensitivity score of 1), followed by those eel-like, elongated and bullet-like (score of 2). Highest sensitivity scores to trawling were assigned to species with flat or lenticular shapes (score of 3) and those globular, compressiform and hook-shaped (sensitivity score of 4), given their volumes would more easily entangle in fishing nets.
- Feeding mode: Even if changes in trophic networks due to climate change would surely affect differently the species in reference to their feeding strategies, we only found information on this trait as a proxy to vulnerability to fishing. Therefore, it was only included in the sensitivity to trawling community indicator. Scavengers, generalists and detritivorous were scored as the least sensitive, while planktivorous were assigned a moderate sensitivity, surface deposit feeders, benthivorous and suprabenthic feeders would have a high sensitivity and suspensivorous and suspension feeders a very high sensitivity, due to turbidity in highly overfished areas (González-Irusta et al., 2018).
- Ecological traits: We used data on mean surface and bottom thermal affinity (SST and SBT, respectively), surface and bottom thermal range of tolerance (STT and BTT, respectively), as well as the mean depth of distribution and depth range (Hare et al., 2016). We categorized them and associated the more thermophilic species (with higher SST and SBT of affinity) to lower sensitivity to warming, as well as species showing wider thermal tolerances (STT and BTT) and wider distribution in depth. Species that distribute in the shallowest waters (lower mean depth) were categorized as less sensitive, as deeper species (higher mean depth) in a warming environment are expected to meet their distributional limit earlier.

After the literature revision and the exclusion of potentially conflictive and overlapping attributes in the two indicators, the final selection of traits and niche properties included for the study of sensitivity to climate change was: spawning category, habitat, motility and the six eco-traits. Traits included for the study of sensitivity to trawling were longevity, body size, fecundity, offspring size, growth coefficient, trophic level, age at maturity, parental care, habitat, motility, body shape and feeding mode.

Using histograms, we visually inspected the distribution of these traits categories along different levels of the stressors. Then, we computed the sensitivity of each species by calculating the mean sensitivity value across the different traits that characterized the species functional niche. The mean sensitivities to trawling and climate change (separately) were computed for each species following the equation:

$$Sensitivity_s = \frac{\sum Sensitivity_{TRAITn}}{N}$$

Where *Sensitivity* would be the sensitivity score of the species *s* to either climate change or trawling, and $Sensitivity_{TRAITn}$ is the sensitivity value of each (n) trait responding to that stressor for a given species (s), and N is the total number of traits responding to the stressor.

To have a general overview of how species distribute in the 'sensitivity space' (S_{CC} as x-axis and S_{FP} as y-axis) and identify species particularly sensitive or resistant to climate change and fishing pressure according to our criteria, the species were plotted according to their sensitivity scores rescaled between 0 and 1.

After this, the sensitivity obtained for each species was weighted by the abundance of each species in each sampling station, therefore estimating a sensitivity value for each sampling station, following the formula:

$$Sensitivity_{PRESSURE} = \frac{\sum Sensitivity_s \ x \ Density_s}{Density_{TOTAL}}$$

Where $Sensitivity_{PRESSURE}$ to either 'Fishing Pressure', 'S_{FP}', or to 'Climate Change', 'S_{CC}', is the community's weighted mean sensitivity at a given sampling station (located in a particular longitude/latitude and year), and $Dens_s$ is a species density in number/km^2 at that sampling station. $Dens_{TOT}$ would be the sum of the individual densities of every species at that given sampling station. This way, each species' sensitivity would be weighted by its relative abundance, therefore making the final sensitivity values comparable in space and time.

Then, the sensitivity values of the community, obtained independently for climate change and fishing, were combined inside a unique indicator of sensitivity to climate and fishing, S_{GLOBAL}, which combined both sensitivities additively.

We calculated annual mean sensitivity at the region-level by averaging the station-level sensitivity scores per year.

To explore temporal trends, we fitted General Additive Models (GAMs; Hastie and Tibshirani, 1990) using the gam function in R package mgcv (Wood, 2011), to the values of sensitivity of the community for each region, S_{CC}, S_{FP} and S_{GLOBAL}. We limited the degrees of freedom of the smoothers to 4 to avoid overfitting. Then, we analyzed spatio-temporal patterns in S_{CC} and S_{FP}. To do so, we separated sub-regions using a CLARA, a non-hierarchical clustering technique (Kaufman & Rousseeuw, 1986) on the sampling stations and their coordinates, with *k* set on 20 groups, to group neighbor samples. For each group, the sensitivity scores were averaged per year and a linear model was performed to obtain the annual rate of change (i.e., the slope of the linear model) of the community's sensitivity.

5.3 RESULTS

5.3.1 STRESSORS' EVOLUTION

Sea surface temperature in both study areas has progressively increased (Figure 1), with mean annual SST values between 15.3 and 16.4°C in Cantabrian Sea and between 18.4 and 20°C in the Mediterranean region. The areas that have experienced steepest increases are located along the Mediterranean (Figure 2), the Gulf of Valencia showing slightly higher warming, while Cantabrian Sea shows a generalized warming, smoother towards the outer Galician margin.

Pair and otter trawling effort have overall decreased in both areas in the period 2010-2018 (Figure 1), except at the inner Bay of Biscay (Figure 2) and from the Gulf of Valencia towards the south of the Mediterranean region, where fishing pressure has remained at similar levels for the whole period.

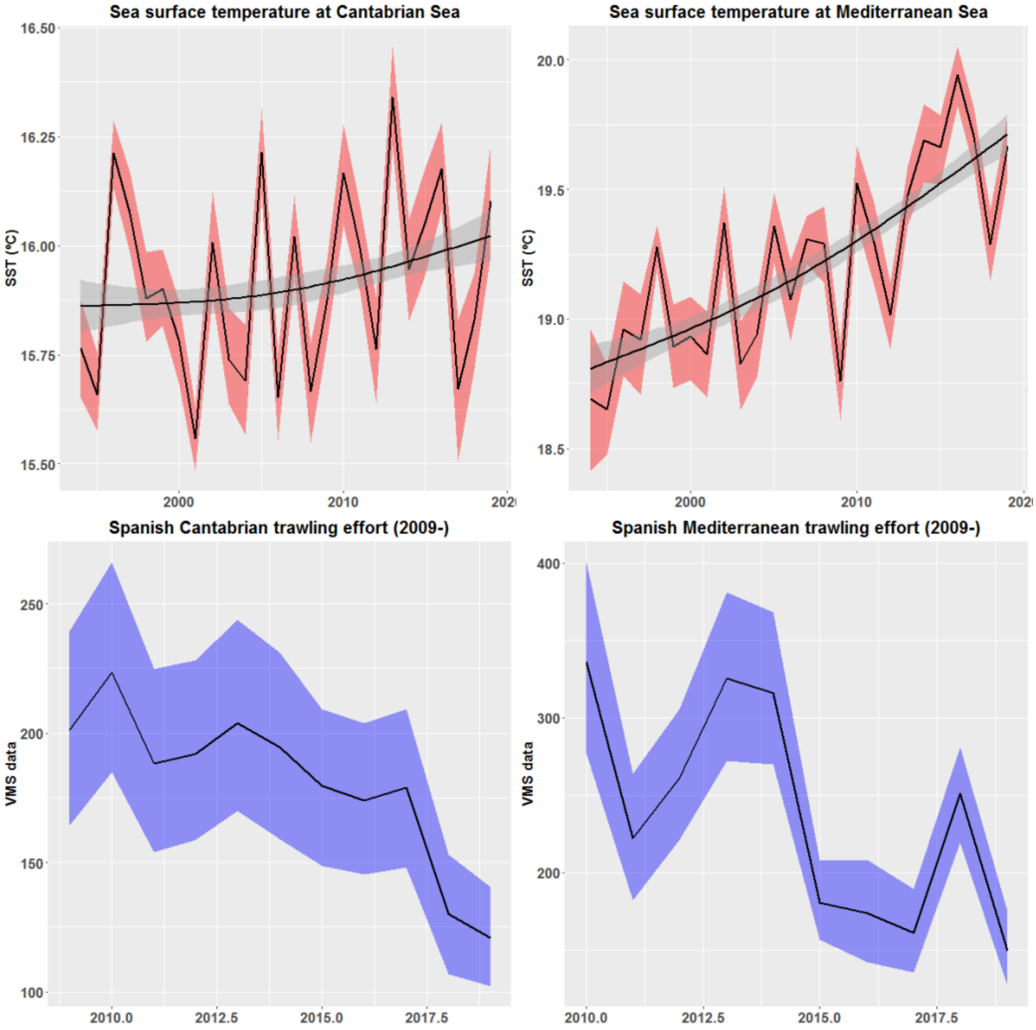


Figure 1. Evolution of the two main systems' stressors, temperature (SST) (top) and fishing pressure (FP) (bottom). Black lines represent mean temporal tendencies and red (in the case of temperature) and blue (for fishing pressure) shaded areas represent the 95% confidence intervals. Smoothed lines (black with a grey shaded confidence interval) were added to better visualize general trends.

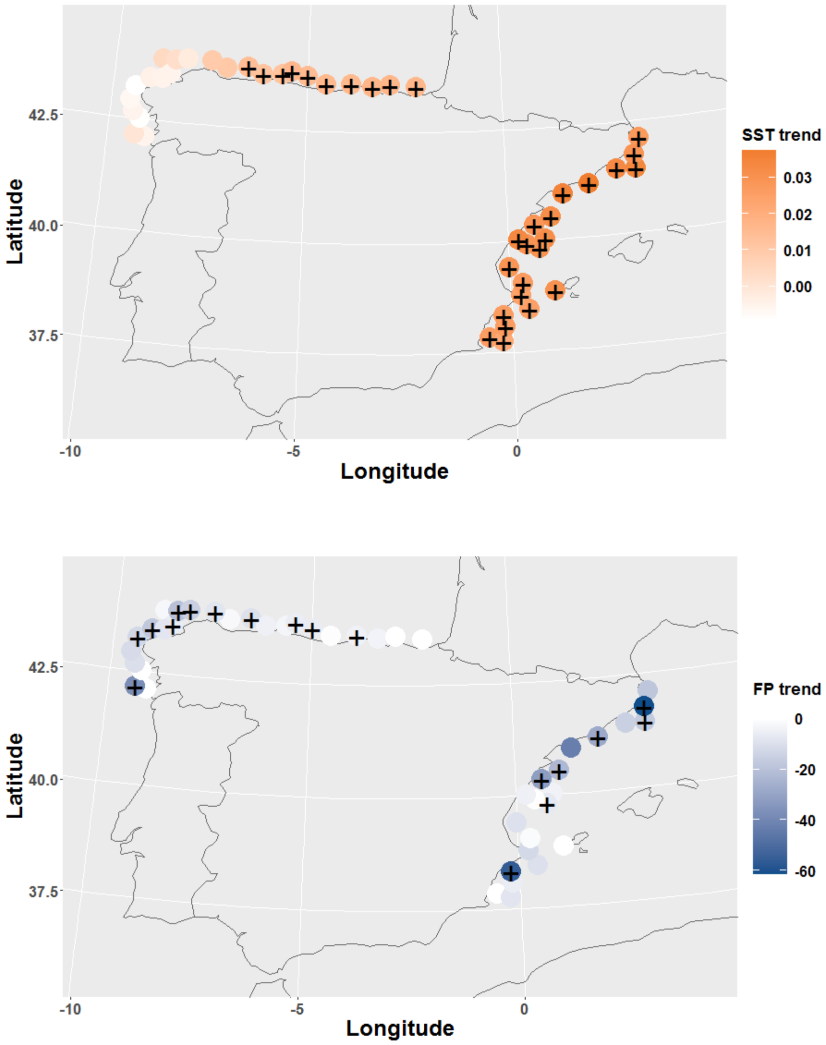


Figure 2. Spatio-temporal plots. In these stressors' trends are summarized. In general, the Spanish Mediterranean region has undergone higher warming (dark orange points) while the Cantabrian region shows milder increases (light orange and white). In the spatio-temporal representation of fishing pressure, darker blue points correspond to areas with pronounced decreases of otter and pair trawling effort, and light blue and white points are sub-regions in which tendencies are close to 0 or even slightly positive. Black crosses indicate areas with significative trends.

5.3.2 SENSITIVITY ASSESSMENT

The study of the species sensitivity to both climate change and fishing (Figure 3) did not reveal a clear pattern between the sensitivities to the different stressors. Species of different Phyla were well distributed in the 'sensitivity space'. According to the classification in sensitivity scores followed in this research, certain species emerged as particularly sensitive or resistant to climate change and fishing pressure. In particular, species 232 (*Tetronarce nobiliana*) and 236 (*Trachinus draco*) showed the highest values of sensitivity to fishing (S_{FP}=1), although remaining below an S_{CC} of 0.5. Few species were categorized as 'resistant' to either pressure, i.e., only 71 (*Engraulis encrasicolus*), 97 (*Illex coindetii*), 1 (*Abralia veranyi*), 93 (*Histioteuthis reversa*), 151 (*Octopus vulgaris*), 124 (*Maurolicus muelleri*) remained below an S_{CC} and an S_{FP} of 0.3. The most 'sensitive' species to both pressures was

58 (*Corella parallelogramma*), with an S_{CC} of 1 followed by 14 (*Aporrhais pespelecani*) and 52 (*Chimaera monstrosa*). Then species 15 (*Aporrhais serresiana*) and 103 (*Lepidorhombus whiffiagonis*) had also high values of sensitivity to climate change.

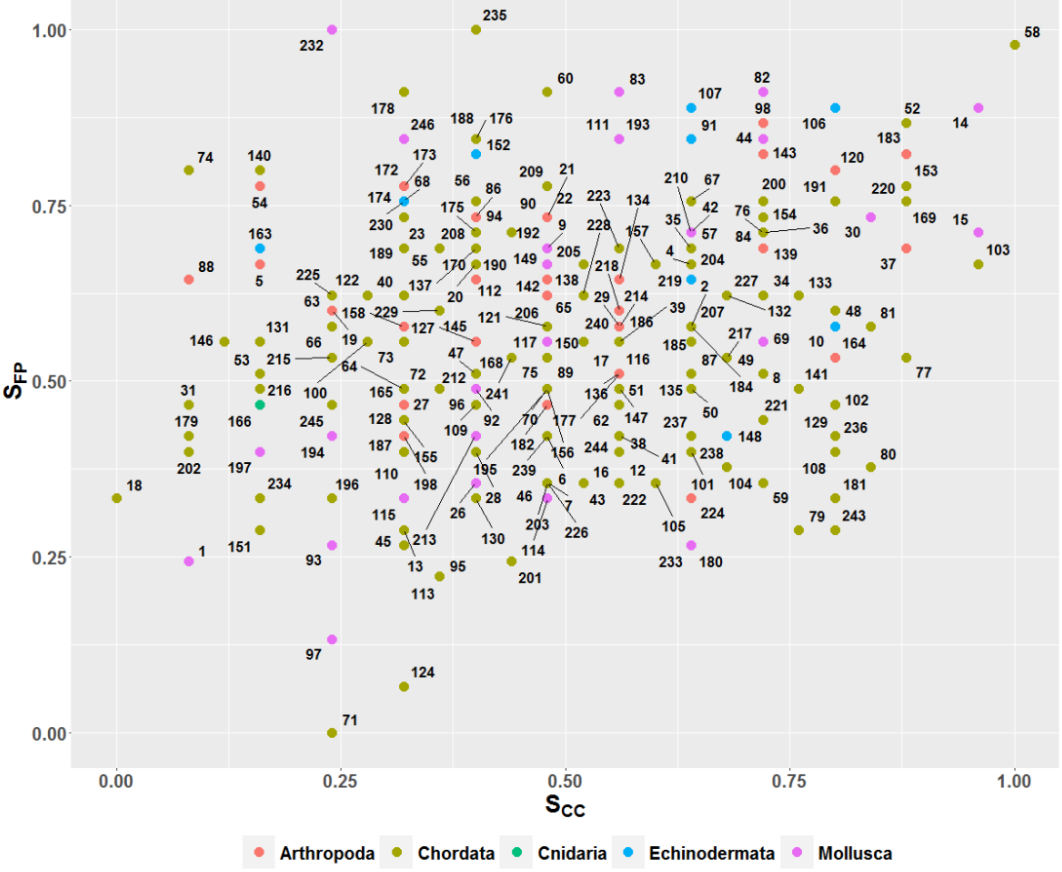


Figure 3. Species position in the 'sensitivity space'. Correspondence between numbers and species is detailed in Table Supp. 1. X-axis and y-axis represent sensitivity to climate change (S_{CC}) and Fishing Pressure (S_{FP}), respectively. The different Phyla are colored following the bottom legend.

At the community level, the two indicators, S_{CC} and S_{FP}, displayed high inter-annual variability in both areas (Figure 4). In the Cantabrian Sea, communities' sensitivity to climate change, S_{CC}, and fishing pressure, S_{FP}, showed contrasting patterns, almost opposite. S_{CC} declined until 2002, whereas S_{FP} increased, peaking around 2005. Then S_{CC} increased, reaching a peak at the beginning of the 2010s, trend reversely mirrored by S_{FP}. The combined sensitivity indicator S_{GLOBAL} increased linearly in the 2000s decade, after which it decreased.

In the Spanish Mediterranean Sea, the communities' sensitivity to both stressors shows a similar decline until the beginning of 2000s. Then, after year 2000 S_{CC} stabilized and S_{FP} kept declining albeit at a lower rate. The combined sensitivity indicator S_{GLOBAL} decreased sharply from the beginning of the time series to the first 2000s, after which the decrease continued at a lower rate.

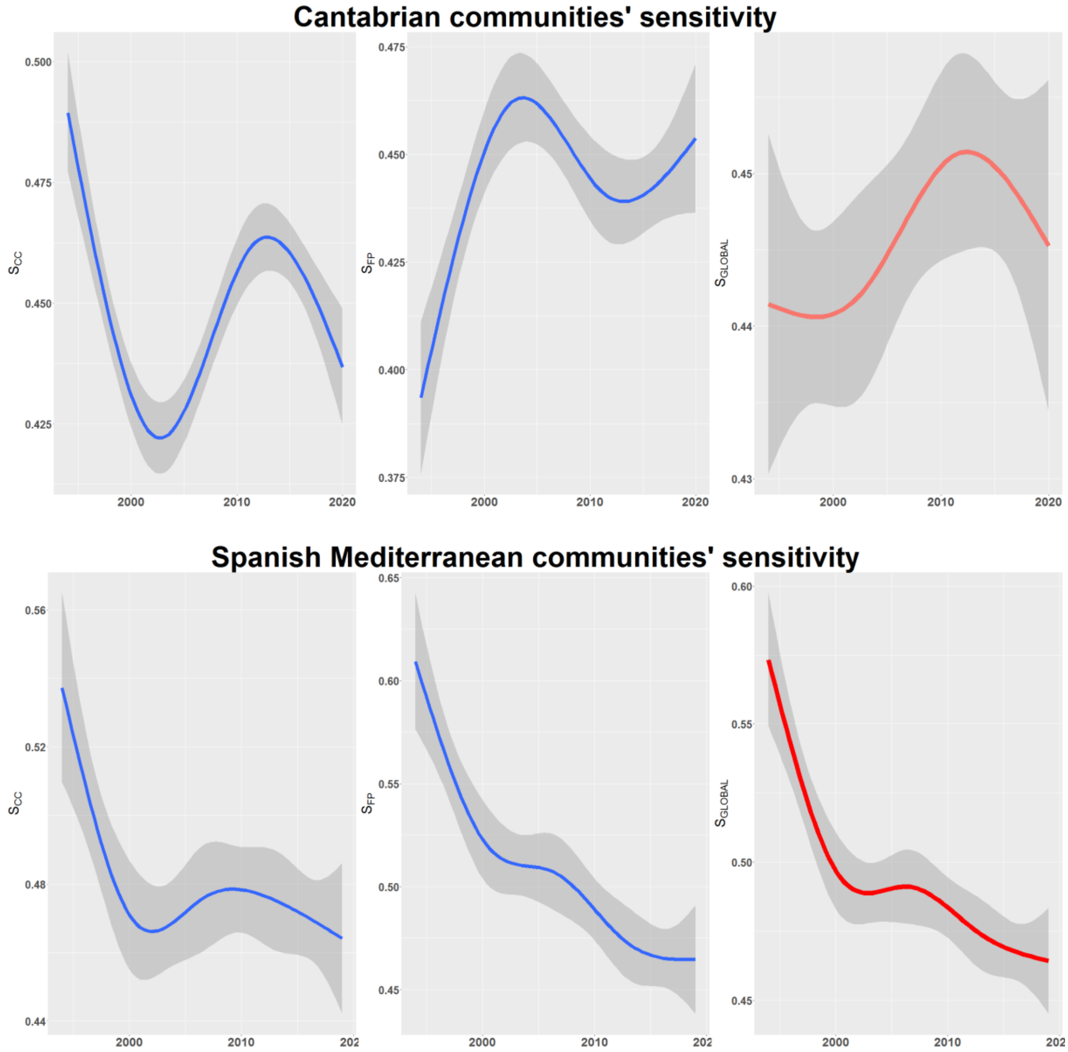


Figure 4. Annual changes in the relative abundance of species sensitive to warming, S_{CC} (left), species sensitive to trawling, S_{FP} (central) and the combined sensitivity indicators, S_{GLOBAL} (right plot), in Cantabrian (top row) and Mediterranean communities (lower row). The shaded areas represent the 95% confidence intervals.

When studying potential spatial variation in the rate of change of communities' sensitivity, we found that the communities that have experienced the largest decreases in community weighted mean sensitivity, either in terms of warming or fishing, are located along the Spanish Mediterranean coast (Figure 5). S_{CC} showed the largest decreases around the Gulf of Valencia, in the centre of the Mediterranean study area. The rate of change of the sensitivity to fishing pressure in the Mediterranean region was more spatially homogeneous, generally showing steep decreases in S_{FP} along the coast, with the exception of communities associated to the eastern Balearic Sea, for which S_{FP} did not change significantly.

Cantabrian communities displayed an increase of the indicator of sensitivity to fishing at certain communities in the western and northern sub-areas, although mixed with communities with no clear trend, or even a slight increase of the sensitivity to trawling towards the inner Bay of Biscay and in the middle of the Cantabrian region. The bentho-demersal communities of the Cantabrian Sea have heterogeneously shifted their community weighted mean sensitivity to climate change (S_{CC}), decreases are found in the westernmost Galician sub-region and towards the inner Bay of Biscay.

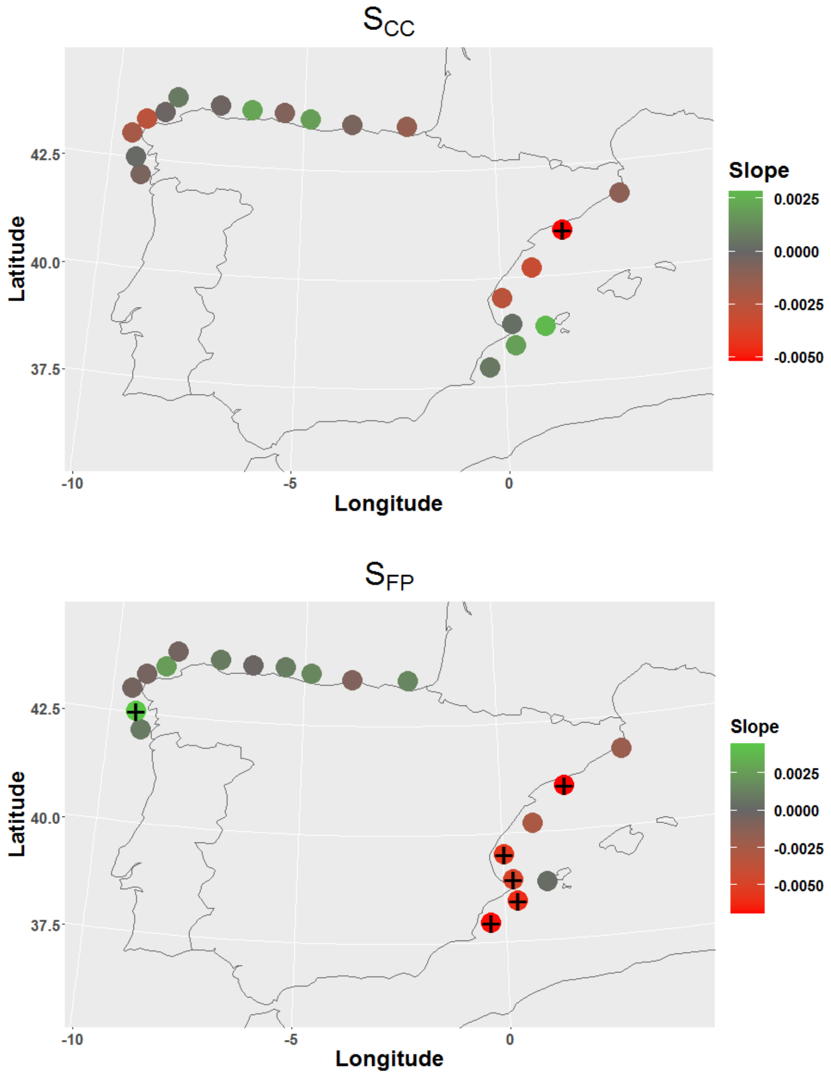


Figure 5. Spatio-temporal variation of sensitivity to warming (upper map) and trawling (lower map). The communities with negative trends of sensitivity scores, in red, have undergone a decrease in the relative abundance of sensitive traits, while in communities with positive trends, represented as green dots, sensitive traits' contribution has increased. Black crosses indicate the communities with significative trends.

5.4 DISCUSSION

This research is a first attempt to assess the spatio-temporal patterns of sensitivity of the bentho-demersal communities in the northern and western margins of Iberian Peninsula, two areas with distinct histories of exposure to fishing and climate change. We have carried a trait-based evaluation of sensitivity that allowed the identification of a clear turnover in terms of the relative contribution of sensitive species to said communities, closely following the systems' two main stressors dynamics. Our results illustrate how communities have changed in terms of their most sensitive species to trawling and warming and revealed particular inflection points around ecological regime shifts previously detected in both areas, related to both environmental changes and shifts in fishing effort (Hidalgo et al., 2022; Polo et al., 2022). The methodology and results provided by this study portray the potential of trait-based approaches for assessing communities' vulnerability. We argue the interpretation of these indicators should take into account how traits respond to stressors in each region, in order to avoid possible biases in the assignment of sensitivity scores to trait categories.

As expected, our results reflected a tight link between the communities' sensitivity and the evolution of temperature and fishing effort in both regions. The relative contribution to the community of the species classified as highly sensitive to both warming and trawling has changed since the beginning of the time series. For example, in Cantabrian Sea, the indicators of sensitivity to climate and fishing showed contrasting patterns with maxima and minima that matched in time. From the beginning of the time series until the 2000s, these communities experienced a relative increase in the contribution of species sensitive to fishing, paralleled by a decrease in those more sensitive to warming. The Cantabrian marine ecosystem in this period is characterized by the recovery from the overexploitation some populations experienced in the 1980s (Guénette and Gascuel, 2012; Arroyo et al., 2017). High trawling effort usually implies the removal of mostly species with slow life histories (big sized, long living and with lower reproductive rates) (De Juan et al., 2007; Planque et al., 2010; Pecuchet et al., 2017) and so has been demonstrated for Cantabrian communities (Modica et al., 2014; Hidalgo et al., 2017). During this first period, from year 1994 until the first years of the 2000s decade, in Cantabrian Sea, communities experienced a large recovery in sensitivity towards fishing impacts, matching the implementation of restrictive national and international fishing regulations (Modica et al., 2014; Arroyo et al., 2017). This increase in the relative contribution of sensitive species was followed by some fluctuations around 2010 but the community has generally maintained high sensitivity values until present.

Over the time series, Cantabrian communities register a decrease in the relative abundance of species sensitive to warming. It reaches its lowest level right after year 2000 after which S_{CC} rises again until the first years of the 2010s decade, when it drops again until present. Alongside the continuously increasing temperatures, species less resistant to warming (cold affinity species with narrow spawning seasons, no parental care and narrow distributional ranges in depth and temperature) had difficulties to thrive. This situation is less accentuated in the Cantabrian communities than in the Mediterranean ones, maybe due to differences in the dynamics of the main stressors in the two regions. A sound interpretation of the communities' sensitivity patterns needs to account for the similar response of many life-history traits to both warming and fishing. Even if the traits we selected for this study were carefully chosen to avoid overlaps in the two indicators, the relaxation of one of the stressors (the decrease in fishing effort in the Cantabrian communities' case) could indirectly affect the sensitivity indicator for the other stressor. Also, the effect of fishing is expected to reflect quite directly on the communities' composition (Planque et al., 2010; Guénette and Gascuel, 2012) and thus, in community weighted mean traits, while some properties of the communities such as inertia, hysteresis or a lagged response might be masking the extent of other impacts (Friberg et al., 2011). Given the effect of temperature at a community level is often non-linear (Hsieh et al., 2005; Burkett et al., 2005; Vasilakopoulos et al., 2017) and interactive with other pressures (Hewitt et al., 2016), the increase in the relative contribution of sensitive species might be better understood if both stressors are considered together (in an additive manner as in this research's S_{GLOBAL}, or accounting for possible interactions).

The communities associated to Spanish Mediterranean, however, have experienced steep decreases in the relative abundance of sensitive species to either stressor, a trend that stabilized right after year 2000 respecting sensitivity to warming, but not to fishing. The stabilization of the sensitivity to climate change (S_{CC}) values reached after year 2000 in this region can be interpreted as a manifestation of a community that has progressively adapted to climate change impacts through changes in a species composition which would become dominated by more resistant species, in opposition to those more specialist, stenotherm and with narrower niche breadth. The loss of the most vulnerable species and the 'flexibilitation' of communities have been identified as coping mechanisms in situations of environmental instability (Sexton et al., 2017) and have been previously associated to communities in this region (Farriols et al., 2017; Polo et al., *under revision*). The ongoing decrease in sensitivity to fishing aligns with the studies and reports that alert of a still heavy fishing impact on this area's assemblages (Farriols et al., 2017; FAO. 2018).

The spatial distribution of the most sensitive communities to climate change in Cantabrian and Spanish Mediterranean seas is coherent with local hotspots of warming towards the inner Bay of Biscay (Chust et al., 2022) and the Gulf of Valencia, in the middle of the Mediterranean study area. In fact, the Gulf of Valencia has been associated to a local maximum of warming, where climate trajectories originate and diverge to the North and the South (Sanz-Martín et al., *under revision*). Also, this sub-region has been identified in a different study (Polo et al., *under revision*) as occupied by communities with high bottom thermal affinities. The Northwestern Mediterranean (i.e., the Gulf of Lion), however, was depicted in our study as a sub-region occupied by communities with a moderate level of sensitivity to climate change and fishing, despite this area having been defined as a 'cul de sac' for climate migrants (Ben Rais Lasram et al., 2010; Burrows et al., 2014). This unexpected outcome could be due to the Gulf of Lion's acting as a climatic refuge for cold species (Sabatés et al., 2006) or the fact that this projection of species reaching their distributional limit has not become noticeable yet, at least in an indicator such as the ones developed here. The communities in the westernmost sub-area of Cantabrian Sea are subdued to upwelling, which smoothes the annual warmest extremes (Lavín et al., 2006; Santos et al., 2012), and therefore would be expected to act as a shelter for the less tolerant species to environmental changes. However, in the middle of this sub-area, there is a local decrease in the indicator of sensitivity to climate change. This result needs to be interpreted along a reduction in the upwelling intensity and duration in this sub-area in the last decades (Álvarez-Salgado et al., 2008; Bode et al., 2009; Garza-Gil et al., 2015) which has eventually been related to a reduction in the productivity of the system (e.g., a reduction in diatom abundance and even in sardine landings; Cabrero et al., 2018 and references therein). Also, the spatio-temporal heterogeneity in the indicator of sensitivity to warming in the Cantabrian region reinforces the idea that the demersal assemblages of the Southern Bay of Biscay are subject to complex interactions between hydroclimatic features (Borja et al., 2019), which results in a high uncertainty when approaching this system's inertia (Polo et al., 2022). On another note, the communities in the Galician margin and westernmost Cantabrian Sea have experienced significant increases in the relative contribution of species sensitive to fishing, which is consistent with the generalized recovery of the communities from fishing (Modica et al., 2014; Arroyo et al., 2017).

In the studied communities, our scoring system identified as highly sensitive species the tunicate *Corella parallelogramma*, the sea snails *Aporrhais pespelicani* and *A. serresiana* (the latter classified as more sensitive to climate change) and the deep chondryctian *Chimaera monstrosa*, a species inhabitant of deep and cold waters and considered as highly vulnerable (De Juan et al., 2020) and classified as 'Near Threatened' by the IUCN Red List (Dulvy et al., 2021; Jac et al., 2022 and references therein). The species of flatfish Lepidorhombus *whiffiagonis,* showed high values of sensitivity to climate change. This cold-affinity species of megrim is expected to decrease its abundance in future warming scenarios (Maltby et al., 2020) and has already shown decreases in biomass in the Cantabrian region (Punzón et al., 2016). The highest values of sensitivity to fishing (S_{FP}=1) were held by *Tetronarce nobiliana*, a top-predator and the largest species of the family of Atlantic rays Torpedinidae (Mulas et al., 2021), and the fish species *Trachinus draco*, which, however, have S_{CC} values below 0.5 (the latter showed low vulnerability to climate change in Bueno-Pardo et al., 2021). On the other side of the sensitivity spectrum, the widely distributed (geographically and in depth) squids *Abralia veranyi*, *Illex coindetii* and *Histioteuthis reversa*, had low sensitivity scores, so they could be considered resistant species together with the mollusk *Octopus vulgaris*, classified as a tolerant species to fishing and environmental impacts in previous researches (González-Irusta et al., 2018; Bueno-Pardo et al., 2021), and the fish species *Maurolicus muelleri* (cold affinity) and *Engraulis encrasicolus* (which in Bueno-Pardo et al., 2021 proved to be a species of low vulnerability to climate change impacts, mostly related to its high adaptive capacity).

The selection of traits used for the design of the indicators intended to capture different features of the species that are directly related to the vulnerability of the species to climate change and fishing. However, as seen in our results (Figure Supp. 1 And Figure Supp. 2), in the studied communities some traits do not seem to be substantially structured in regard to temperature or trawling effort. Following previous trait-based species and community assessments (such as Hare et al., 2016; González-Irusta et al., 2018; Bueno-Pardo et al., 2021), this certain degree of variability in the relationship between traits and stressors has not prevented us from including the traits in the indicators of sensitivity. Approximately half of the trait categories did respond to the different levels of the pressures as expected (e.g., almost every trait category in the life-history traits responded as expected to the different levels of fishing pressure, such as the life-history traits 'Feeding mode' and 'Motility'; or the 'Body shape' category 'sessile, compressiform, globular or hook shaped', which was less abundant in areas with high trawling effort, etc). However, the other half of the trait categories did not follow our literature-based expectations, mainly those of the ecological traits (e.g., species with narrower thermal ranges were more abundant in warm areas or species with higher mean sea surface temperature of affinity appeared more in low temperature hauls, etc). A plausible explanation for the apparently contradictory direction in the response of some of these traits is that we might not be anticipating (neither identifying) non-linearities in the response to the stressor. For that matter, previous studies have revealed a dome shaped relation between one or more traits and certain stressors. In these cases, trait values peaked at intermediate levels of the pressure. So was the case of the trait 'Recruitment' when exposed to wind turbulence (Ottersen et al., 2010) and 'Growth', 'Body length' and 'Lifespan' in response to temperature (Beukhof et al, 2019). In addition, if a threshold in the relationship between the trait and the stressor has not been reached, or in the case of already degraded ecosystems, if the threshold is located at much lower levels of the pressure than the ones we are studying in our time series, with the methods applied in our study we will not observe the expected direction of the pressure's effect on the trait categories.

Furthermore, we have attempted a rigorous segregation at categorizing the traits, through which categories contain a similar number of observations. However, it is possible that a categorization in levels of sensitivity might be more adequate for certain traits if accounting for the different ecological levels intrinsic to said trait. For example, instead of the sensitivity categories for the trait 'Depth Range' suggested by our scoring system (under 750 meters, between 750 and 1300 meters, over 1300 meters), a scoring that consistently accounted for the ecology of the species could be a categorization of the species depending on whether their habitat is restricted to the continental shelf, or if they can reach the slope, or even occupy the deep ocean (Sanz-Martín et al., *under revision*). Another example could be a classification of the communities according to their thermal affinities through a clustering technique, such as the k-means algorithm (Punzón et al., 2021). Likewise might happen with other traits such as 'Fecundity', in which the category the most sensitive to fishing included species producing an already big amount of eggs, less than 12000. Although Pecl et al. (2014) used for their most sensitive category species producing less than 100 eggs annually, Bueno-Pardo et al. (2021) adjusted the category to the biology of their selection of species and set the most sensitive category to <1000. In this respect, a region-specific study of the traits response to climate change and fishing could allow a better understanding of each systems' sensitivity dynamics, by accounting for possible differences in the response of a trait to a stressor related to the communities' structure.

This trait-based approach to the sensitivity of two communities with different levels of exposure to climate change and fishing (associated to Cantabrian and Spanish Mediterranean seas) has served as a first attempt to tackle the challenging study of the biological communities' response to their two most important external drivers. While it is known long histories of exploitation interact with warming in influencing populations' vulnerability (Möllmann and Diekmann, 2012; Free et al., 2019), in this approach we have only accounted for additive impacts and did not delve in the interacting effects of the drivers on traits' responses. However, ignoring the potential interactive effects of warming and fishing pressure on exploited ecosystems can be inaccurate and ultimately lead to inefficient conservation strategies (Kath et al., 2018). Hence, further efforts in understanding traits' response to their environment will be valuable for any trait-based study of the status of biotic assemblages and can even resolve situations in which contradictory scorings were found in literature. E.g., species location in the water column was inconsistently regarded in terms of its sensitivity to climate change effects; while some authors considered pelagic species to be more sensitive than benthic ones, due to the access to thermal refugia of the latter (Burrows et al., 2019; Chaudhary et al., 2021), others considered pelagic motility to be advantageous, given the associated ability to exploit the entire water column and avoid extreme events (Le Marchand et al., 2020; Bueno-Pardo et al., 2021). In this particular case, a preliminary study of the direction of the trait 'Habitat position' response, specific to the community under study, could provide additional confidence on the scoring system.

In spite of its limitations, the VA framework has allowed us a preliminary, straightforward assessment, which can set the basis for further research in this direction. An efficient adaptation to and mitigation of climate change effects requires that ecosystem-based management accounts for the areas at most risk from different stressors (Hare et al., 2016; Hewitt et al., 2019). For its simplicity and functionality and the growing availability of trait datasets, trait-based VAs can provide robust metrics and replicable systematic methods of assessing sensitivity that ultimately assist management in properly coping with anthropogenic global change.

5.5 SUPPORTING INFORMATION

APPENDIX 1: SUPPORTING TABLES

Table Supp. 1. Species representative of Cantabrian and Spanish Mediterranean bentho-demersal communities.

1	Abralia veranyi	**36**	Calliostoma granulatum	**71**	Engraulis encrasicolus
2	Acanthocardia echinata	**37**	Calocaris macandreae	**72**	Epigonus denticulatus
3	Actinauge richardi	**38**	Capros aper	**73**	Epigonus telescopus
4	Aegaeon cataphractus	**39**	Carapus acus	**74**	Etmopterus spinax
5	Aegaeon lacazei	**40**	Cataetyx alleni	**75**	Eusergestes arcticus
6	Alloteuthis media	**41**	Centracanthus cirrus	**76**	Euspira fusca
7	Alloteuthis subulata	**42**	Cepola macrophthalma	**77**	Eutrigla gurnardus
8	Alosa fallax	**43**	Ceratoscopelus maderensis	**78**	Funiculina quadrangularis
9	Alpheus glaber	**44**	Charonia lampas	**79**	Gadiculus argenteus
10	Anseropoda placenta	**45**	Chauliodus sloani	**80**	Gaidropsarus biscayensis
11	Antedon mediterranea	**46**	Chelidonichthys cuculus	**81**	Gaidropsarus macrophthalmus
12	Anthias anthias	**47**	Chelidonichthys lastoviza	**82**	Galeodea echinophora
13	Aphia minuta	**48**	Chelidonichthys lucerna	**83**	Galeodea rugosa
14	Aporrhais pespelecani	**49**	Chelidonichthys obscurus	**84**	Galeus melastomus
15	Aporrhais serresiana	**50**	Chelon auratus	**85**	Gennadas elegans
16	Arctozenus risso	**51**	Chelon ramada	**86**	Geryon longipes
17	Argentina sphyraena	**52**	Chimaera monstrosa	**87**	Glossanodon leioglossus
18	Argyropelecus hemigymnus	**53**	Chlorophthalmus agassizi	**88**	Gnathophausia zoea
19	Aristeus antennatus	**54**	Chlorotocus crassicornis	**89**	Gobius niger
20	Arnoglossus imperialis	**55**	Citharus linguatula	**90**	Goneplax rhomboides
21	Arnoglossus laterna	**56**	Coelorinchus caelorhincus	**91**	Gracilechinus acutus
22	Arnoglossus rueppelii	**57**	Conger conger	**92**	Helicolenus dactylopterus
23	Arnoglossus thori	**58**	Corella parallelogramma	**93**	Histioteuthis reversa
24	Asteronyx loveni	**59**	Crystallogobius linearis	**94**	Hoplostethus mediterraneus
25	Astropecten irregularis	**60**	Dalatias licha	**95**	Hygophum benoiti
26	Bathypolypus sponsalis	**61**	Dardanus arrosor	**96**	Hymenocephalus italicus
27	Bathysolea profundicola	**62**	Deltentosteus quadrimaculatus	**97**	Illex coindetii
28	Benthosema glaciale	**63**	Deosergestes henseni	**98**	Inachus dorsettensis
29	Blennius ocellaris	**64**	Dicentrarchus labrax	**99**	Labrus mixtus
30	Bolinus brandaris	**65**	Diplodus annularis	**100**	Lampanyctus crocodilus
31	Boops boops	**66**	Diplodus vulgaris	**101**	Lepidopus caudatus
32	Brissopsis lyrifera	**67**	Dipturus oxyrinchus	**102**	Lepidorhombus boscii
33	Calliactis parasitica	**68**	Echelus myrus	**103**	Lepidorhombus whiffiagonis
34	Callionymus lyra	**69**	Eledone cirrhosa	**104**	Lepidotrigla cavillone
35	Callionymus maculatus	**70**	Eledone moschata	**105**	Lepidotrigla dieuzeidei

Table Supp. 1 (cont.). Species representative of Cantabrian and Spanish Mediterranean bentho-demersal communities.

106	Leptometra celtica	**153**	Ophiothrix fragilis	**200**	Scaphander lignarius
107	Leptometra phalangium	**154**	Ophiura ophiura	**201**	Scomber colias
108	Lesueurigobius friesii	**155**	Pagellus acarne	**202**	Scomber japonicus
109	Lesueurigobius sanzi	**156**	Pagellus bogaraveo	**203**	Scomber scombrus
110	Lesueurigobius suerii	**157**	Pagellus erythrinus	**204**	Scophthalmus rhombus
111	Leucoraja naevus	**158**	Pagrus pagrus	**205**	Scorpaena elongata
112	Liocarcinus depurator	**159**	Pagurus alatus	**206**	Scorpaena notata
113	Lobianchia dofleini	**160**	Pagurus cuanensis	**207**	Scorpaena porcus
114	Loligo forbesii	**161**	Pagurus excavatus	**208**	Scorpaena scrofa
115	Loligo vulgaris	**162**	Pagurus prideaux	**209**	Scyliorhinus canicula
116	Lophius budegassa	**163**	Parapenaeus longirostris	**210**	Scyliorhinus stellaris
117	Lophius piscatorius	**164**	Parastichopus regalis	**211**	Sepia elegans
118	Luidia ciliaris	**165**	Pasiphaea multidentata	**212**	Sepia officinalis
119	Macropipus tuberculatus	**166**	Pasiphaea sivado	**213**	Sepia orbignyana
120	Macropodia tenuirostris	**167**	Pelagia noctiluca	**214**	Sepietta oweniana
121	Macroramphosus scolopax	**168**	Peristedion cataphractum	**215**	Sergia robusta
122	Malacocephalus laevis	**169**	Philocheras echinulatus	**216**	Serranus cabrilla
123	Marthasterias glacialis	**170**	Phycis blennoides	**217**	Serranus hepatus
124	Maurolicus muelleri	**171**	Pilumnus spinifer	**218**	Solea solea
125	Medorippe lanata	**172**	Plesionika acanthonotus	**219**	Solenocera membranacea
126	Meganyctiphanes norvegica	**173**	Plesionika gigliolii	**220**	Spatangus purpureus
127	Merluccius merluccius	**174**	Plesionika heterocarpus	**221**	Spicara maena
128	Microchirus ocellatus	**175**	Plesionika martia	**222**	Spicara smaris
129	Microchirus variegatus	**176**	Plesionika narval	**223**	Spondyliosoma cantharus
130	Micromesistius poutassou	**177**	Polybius henslowii	**224**	Sprattus sprattus
131	Mola mola	**178**	Polycheles typhlops	**225**	Squilla mantis
132	Molva dypterygia	**179**	Pomatomus saltatrix	**226**	Stomias boa
133	Molva macrophthalma	**180**	Pomatoschistus marmoratus	**227**	Symphurus ligulatus
134	Monodaeus couchii	**181**	Pomatoschistus minutus	**228**	Symphurus nigrescens
135	Mullus barbatus	**182**	Pomatoschistus pictus	**229**	Synchiropus phaeton
136	Mullus surmuletus	**183**	Pontophilus spinosus	**230**	Syngnathus acus
137	Munida intermedia	**184**	Processa canaliculata	**231**	Tethyaster subinermis
138	Munida speciosa	**185**	Processa nouveli	**232**	Tetronarce nobiliana
139	Munida tenuimana	**186**	Pteria hirundo	**233**	Todarodes sagittatus
140	Mustelus mustelus	**187**	Pteroctopus tetracirrhus	**234**	Todaropsis eblanae
141	Myctophum punctatum	**188**	Raja asterias	**235**	Torpedo marmorata
142	Natatolana borealis	**189**	Raja clavata	**236**	Trachinus draco
143	Nephrops norvegicus	**190**	Raja miraletus	**237**	Trachurus mediterraneus
144	Neptunea contraria	**191**	Raja montagui	**238**	Trachurus picturatus
145	Nettastoma melanurum	**192**	Raja polystigma	**239**	Trachurus trachurus
146	Nezumia aequalis	**193**	Ranella olearium	**240**	Trachyrincus scabrus
147	Notacanthus bonaparte	**194**	Rondeletiola minor	**241**	Trigla lyra
148	Notoscopelus elongatus	**195**	Rossia macrosoma	**242**	Trisopterus luscus
149	Nymphaster arenatus	**196**	Sardina pilchardus	**243**	Trisopterus minutus
150	Octopus salutii	**197**	Sardinella aurita	**244**	Uranoscopus scaber
151	Octopus vulgaris	**198**	Scaeurgus unicirrhus	**245**	Xenodermichthys copei
152	Ophichthus rufus	**199**	Scalpellum scalpellum	**246**	Zeus faber

APPENDIX 2: SUPPORTING FIGURES

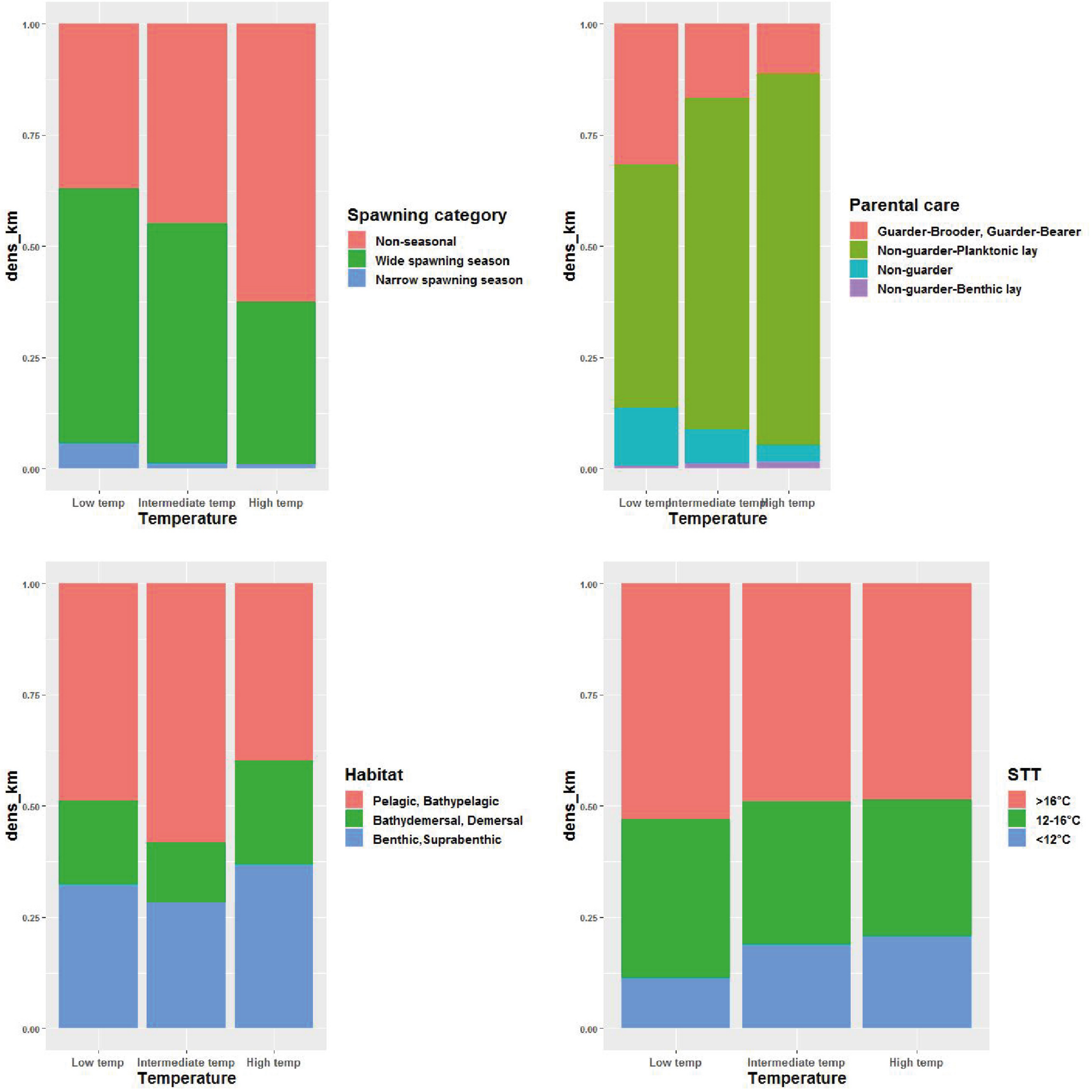


Figure Supp. 1. Variation in the relative abundance (number of individuals per km^2, *dens_km*) of each trait's category at each level of temperature, from low (left column) and intermediate (central) to sampling stations with higher temperatures (right). Categories are ordered from bottom to top from the category related to higher sensitivity to climate change to the category related to a lower sensitivity. Coded ecological traits are the following: surface thermal range of tolerance (STT), bottom thermal range of tolerance (BTT), Sea Surface thermal affinity (SST), Sea Bottom thermal affinity (SBT).

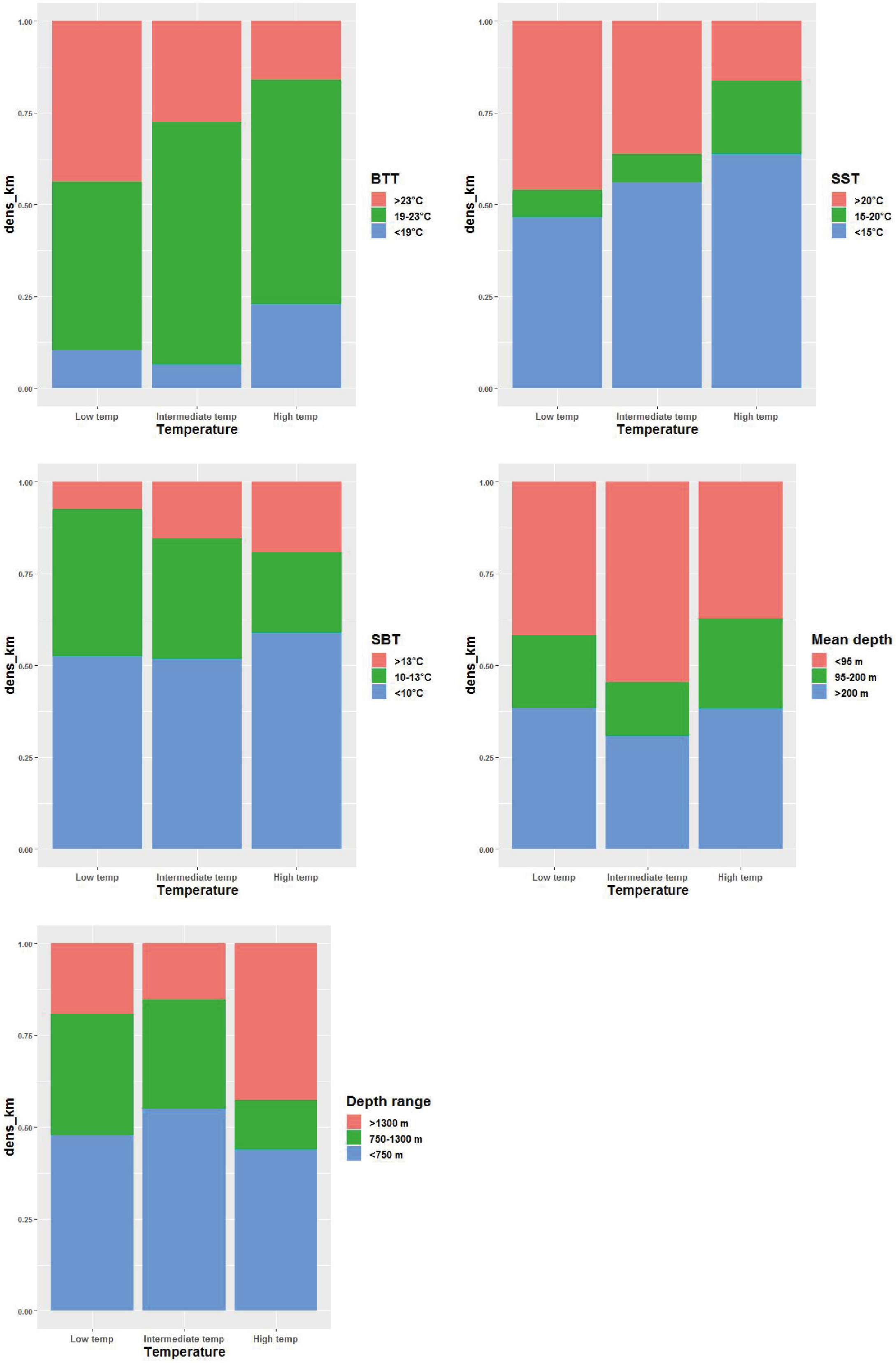


Figure Supp. 1. (cont.)

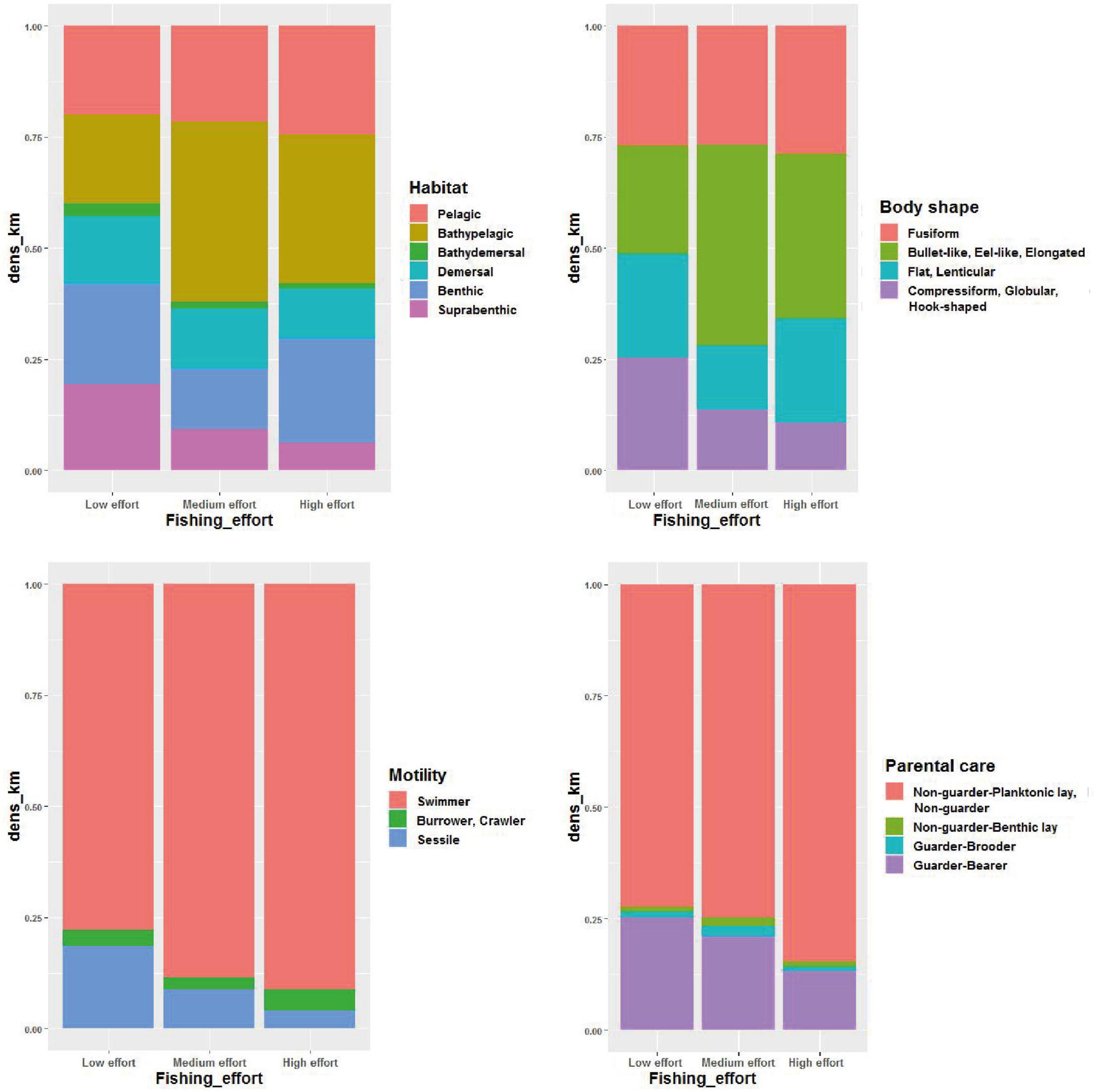


Figure Supp. 2. Variation in the relative abundance (number of individuals per km², *dens_km*) of each trait's category at each level of fishing pressure, from sampling stations with low effort (left column) and medium effort (central) to sampling stations with higher fishing effort (right column). Categories are ordered from bottom to top from the category related to higher sensitivity to trawling to the category related to a lower sensitivity.

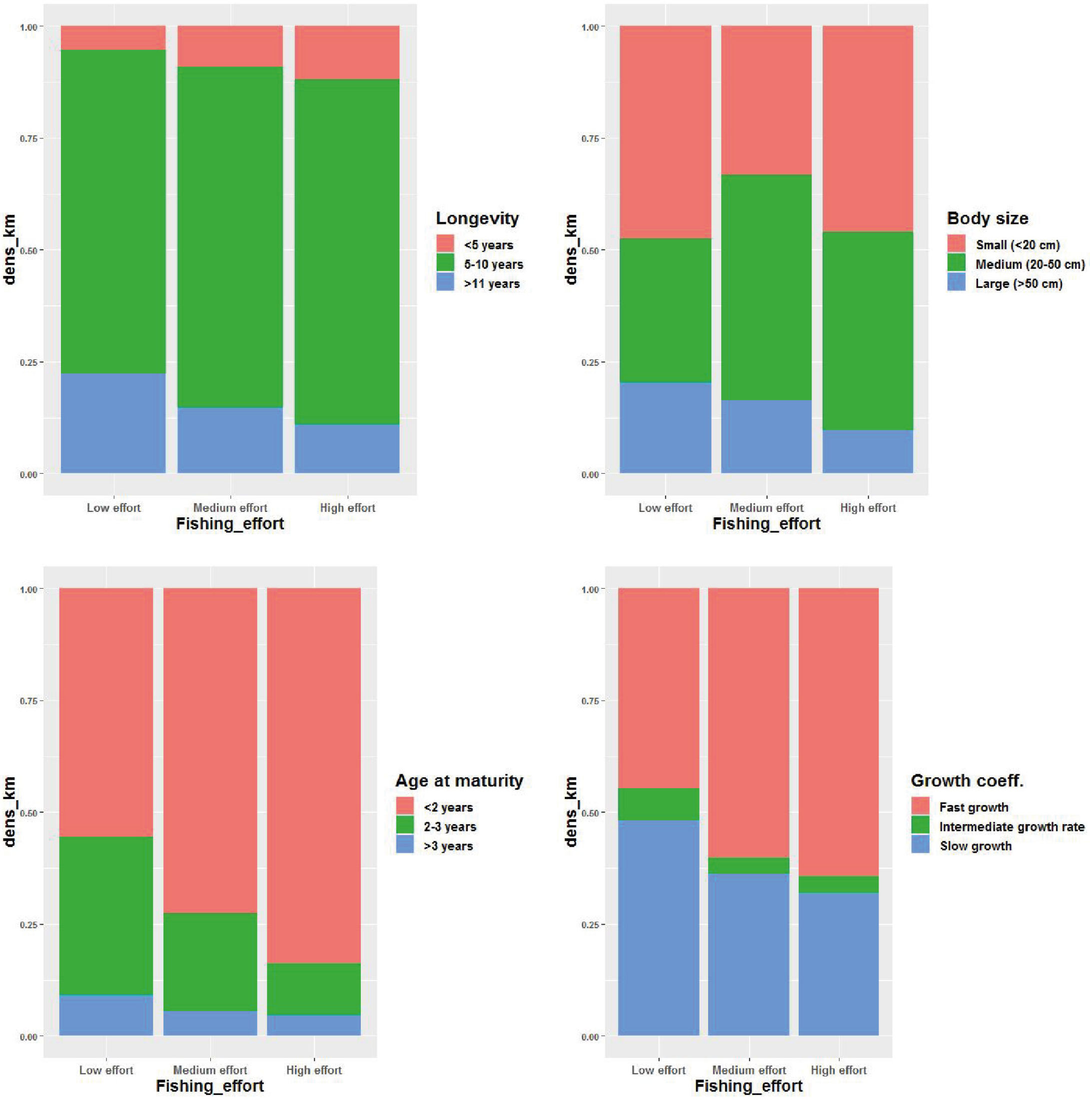


Figure Supp. 3. (cont.)

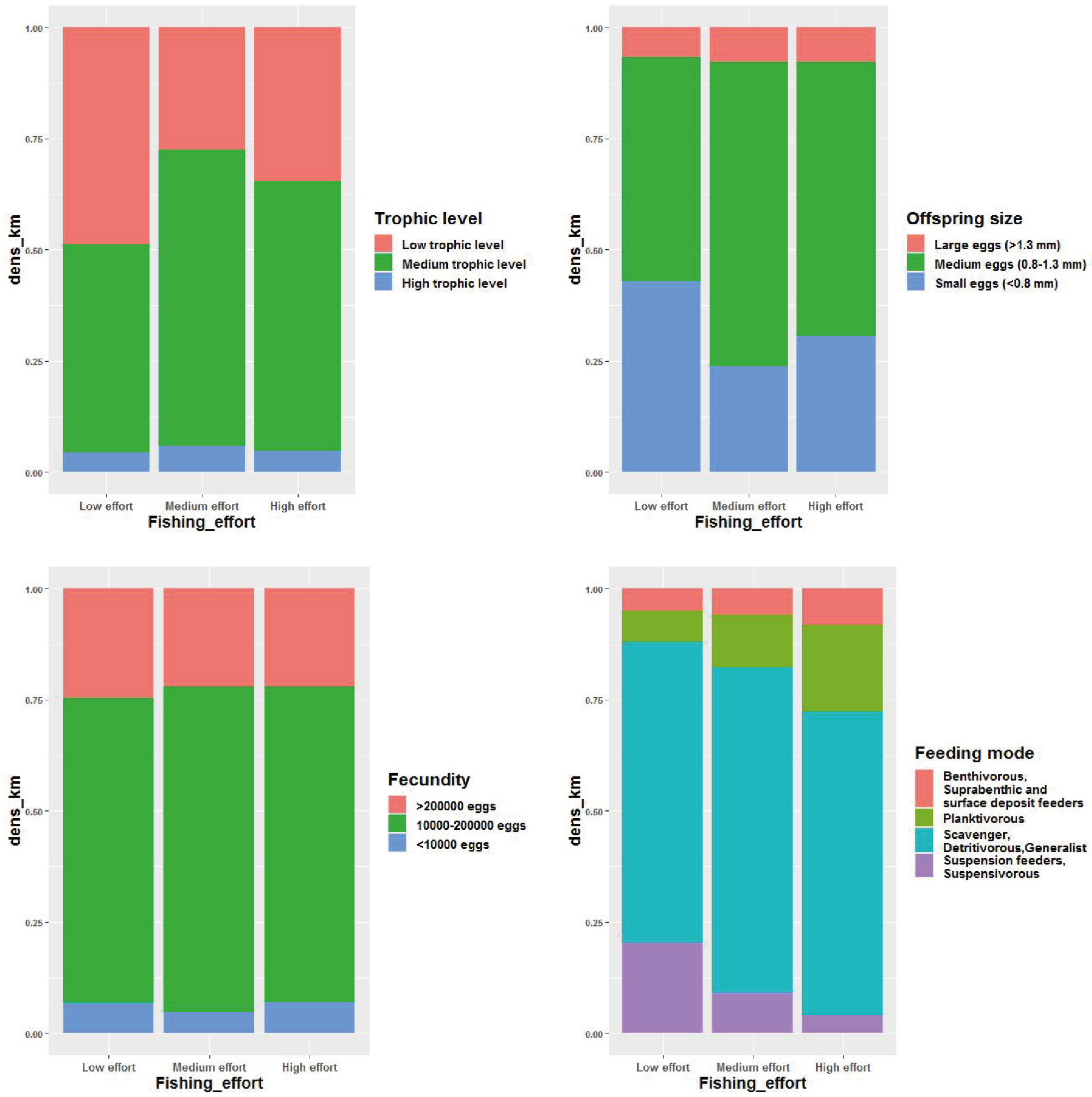
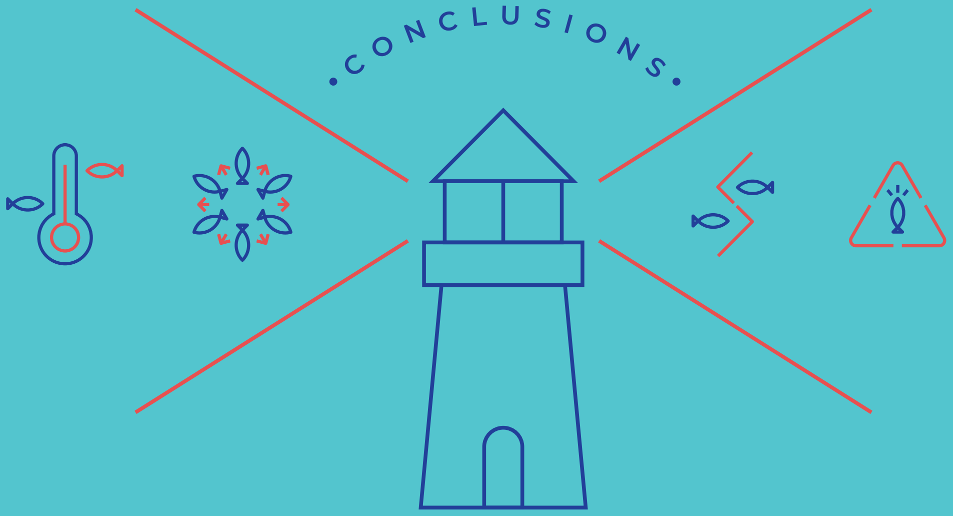


Figure Supp. 4. (cont.)

EFFECTS OF CLIMATE CHANGE AND FISHING ON DEMERSAL ECOSYSTEMS

AN APPROACH TO HUMAN IMPACTS ON
NORTH EAST ATLANTIC AND SPANISH
MEDITERRANEAN COMMUNITIES



CHAPTER

06

CONCLUSIONS

CHAPTER 6. CONCLUSIONS

The effect of climate change on the demersal communities of Cantabrian and Spanish Mediterranean seas is entangled with other pressures, among which fishing stands out. Both effects are difficult to understand separately and the study of their interaction has become and should continue to be considered a priority. The identification of the drivers of natural systems at a given time is a cornerstone of the design of plausible adaptive measures to cope with climate change impacts. This is especially relevant when prevailing conditions, such as climate change, have an influence on the status indicators of the ecosystem components.

Long standardized monitoring programs make it possible to analyze the evolution of communities or habitats over time and space, and are an essential tool for medium- and long-term predictions and the development of management and adaptation strategies. Therefore, the establishment of new monitoring programmes that allow the analysis of ecological components not monitored at present (e.g.,benthic biogenic habitats) would be convenient.

Due to intrinsic and extrinsic factors, such as the internal structure of a community or its level of exposure to external pressures, the response to their stressors of similar marine communities in terms of a taxonomic composition can highly differ.

Cantabrian and Spanish Mediterranean seas show regional differences in terms of their exposure to warming and fishing. Our research has confirmed these differences mainly concern the rate of change of their stressors, which linked to different communities' structures and ecosystems' connectivity, ultimately reflects in how the associated biological communities accommodate external changes, such as progressive warming or fluctuating fishing efforts.

6.1 SHIFTING SPATIAL DISTRIBUTIONS

Our results show that the CWMT responds to the actual temperature of the water column reproducing its space-time trends in the Cantabrian Sea: (i) an increase from SW to NE, towards the inner Bay of Biscay, (ii) a decrease with depth, except in the SW area characterized by an intense upwelling, (iii) a general increase along the time series. These increases affected also bottom thermal ranges, indicating not only that communities in this area are increasing its mean preferred temperatures, but also increasing and diversifying its thermal tolerance.

Applying a k-means classification to the CWMT data we identified warm-, temperate- and cold- communities over the shelf and slope and their spatial changes in the last decades. The distribution pattern of these three 'thermal affinity communities', places the warm communities to the coastal interior of the Bay of Biscay, the temperate communities to the continental shelves and the Galician coastal zone under the influence of upwelling, and the cold communities to the shelf break and deep water. In this region, the area occupied by warm communities has expanded 268.4 km2 /yr since the 80s, while cold communities have retracted at a speed of -155.4 km2 /yr.

Although not capturing information on species replacements or migration of new species into the Bay of Biscay the CWM eco-traits studied here captured major aspects of the communities' dynamics. Tropicalization beyond the thermal realm reflects in the niche's multivariate nature. Also in Cantabrian Sea, communities' weighted mean latitude is decreasing, reflecting the community's hosting of species from lower mean latitudes.

A flexibilitation of ecological ranges paired the expected poleward, deep-ward shift, significant in the communities of the Spanish Mediterranean. In this region, the communities' composition was not entirely the expected, as warmer communities were not clearly defined by lower mean depth and latitude, but the main difference between cold and warm communities was the width of their distributions in latitude and depth, wider for cold communities.

6.2 REGIME SHIFTS AND RESILIENCE DYNAMICS

The Cantabrian bentho-demersal fish community has undergone two regime shifts in the period 1983–2018, results of continuous and discontinuous responses to environmental changes and fishing pressure.

In the period from 1988 to 2011, the community changed linearly in response to a declining fishing effort, after which it exited its previous strong coupling with fishing (as seen in the change towards a less steep slope of the system–F_{com}'s interaction) and it reached a low resilience state, which we argue was mostly climate-driven, that led to the occurrence of a second discontinuous regime shift.

The study of Cantabrian Sea's demersal fish biomass confirmed a global increase in temperate species abundances already recognized in the region by previous authors.

Among all the studied expressions of external forcing (Sea Temperature, position of the mixed layer depth, chlorophyll A, the upwelling index, NAO, ENSO and EA indices and a proxy for fishing mortality), fishing pressure stood out in our analyses as the most critical feature for the system. However, we took account of previous research in which climate was associated with the general boost in biomass, in the frequency of occurrence and the thermal affinities of the communities, and we considered the definite inducer of both state shifts on the bentho-demersal realm a combination of environmental and anthropogenic factors.

In the period 1997–2003, the improved management of fisheries achieved a 45% reduction in fishing pressure for the demersal Cantabrian community. In the last two years of the studied time series, 2017 and 2018, for the first time in the entire period, an $F_{com} \leq 1$ was reached, which corresponds to levels of exploitation consistent with MSY.

The inertia driving this system's main trends at present is uncertain and it would be fair to assume the system finds itself inside an ongoing process of change. Its resilience in response to fishing has been eroding in reference to the 1990s decade, and at present, Cantabrian demersal fish communities move along a faint attractor, in what we have considered a transition scenario.

6.3 COMMUNITIES' SENSITIVITY TO CLIMATE CHANGE AND FISHING

A trait-based evaluation of the sensitivity towards climate change and fishing effects of bentho-demersal communities in Cantabrian and Spanish Mediterranean seas has revealed relevant spatio-temporal variability in terms of the relative contribution of sensitive species to said communities, which closely follows the systems' two main stressors dynamics (fluctuations in sea temperature and trawling effort).

Although the degree of exposure to warming and fishing differens among Spanish Mediterranean and Cantabrian seas. In both regions sea temperature at surface has significantly increased since the mid 1980s and pair and otter trawling effort has decreased in the period 2009-2020.

The Cantabrian communities have undergone a general increase in the relative abundance of sensitive species to trawling, coherent with a generalized recovery of exploited populations after the implementation of fishing regulations. Spanish Mediterranean communities, by contrast, have experienced steep decreases in the relative abundance of sensitive species to trawling, hand in hand with the ongoing heavy fishing activities taking place in this region.

In the Spanish Mediterranean Sea, parallel to the increasing temperatures, communities sensitivity to climate change has decreased, overlapping a 'flexibilitation' of the communities, which have become more dominated by resistant species.

The coherence between the spatio-temporal dynamics of the most sensitive communities to warming and trawling and these two drivers of marine communities' variability allowed us to conclude that the trait-based Vulnerability Assessment framework is an effective tool in assessing communities' sensitivity. However, if aiming for a reliable estimation of the communities present status, and even if aiming at projecting future scenarios, the use of species life-history traits and niche related features (ecological traits) for these type of assessments should take into account that traits' response to external pressures can be context-dependent, as well as possible interactions between the studied drivers. Therefore, a previous analysis of the direction of the species traits response to stressors in the studied community can help avoid possible biases in the assignment of sensitivity or vulnerability scores to trait categories.

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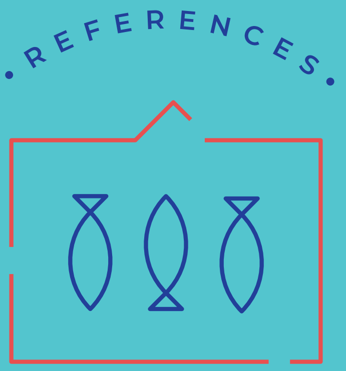

CHAPTER

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REFERENCES

CHAPTER 7. REFERENCES

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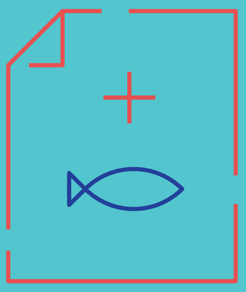
EFFECTS OF CLIMATE CHANGE AND FISHING ON DEMERSAL ECOSYSTEMS

AN APPROACH TO HUMAN IMPACTS ON NORTH EAST ATLANTIC AND SPANISH MEDITERRANEAN COMMUNITIES

• ANNEX 1 •



ANNEX

1

ANNEX 1: *SENSITIVITY TO SPECIES SELECTION OF COMMUNITIES' TRAIT-BASED INDICES*

This annex is a modified version of the research article in preparation 'Sensitivity to species selection of communities' trait-based indices' by Sainz Bariáin, M., Polo, J., Punzón, A., Hidalgo, M., García, E., González-Irusta, J.M., Esteban, A., Vivas, M., Gil de Sola, L. and López-López, L.

1.INTRODUCTION

Trait-based approaches focus on individual trait information rather than specific taxonomic information and are based on the expectation that organisms with similar characteristics have similar responses to environmental and anthropogenic stressors (Gitay et al., 1999, Gladstone-Gallagher et al., 2019; Martini et al. 2020; De Juan et al., 2022). Moreover, organism-groupings based on characteristics such as feeding type, reproductive strategy, locomotion type or habitat preference can provide valuable information about ecosystem functions and processes (Usseglio-Polatera et al., 2000; Mouillot et al., 2005; Siefert, 2012; Mueller et al., 2013). These studies are of vital importance for applied ecology, as they enable a functional approach to the monitoring of the effects of global change and can help planning effective management strategies for marine ecosystems. Specifically, biological traits, morphological, behavioural or related to any other aspect of a species life-history, are often considered jointly, as they determine the role of organisms on ecosystem functioning. The so called 'functional multidimensional niche' ultimately shapes the organisms' response to environmental variation and therefore, its effect on the ecosystem functioning (Keddy, 1992; Bremner et al., 2003; Violle et al., 2007; Hewitt et al., 2008; Törnroos et al., 2015). Thus, Biological Trait Analysis (BTA) uses a series of life-history characteristics of species present in assemblages to indicate aspects of their ecological functioning (Jennings et al., 1999; Usseglio-Polatera et al., 2000; Bremner, 2008). Since these traits can be shared by organisms that differ widely in their taxonomic identity (Usseglio-Polatera et al., 2000), BTA can be applied to very different taxonomic groups (Doledec and Statzner, 1994).

Traditionally, taxonomic approaches, mostly based on species level analyses, have prevailed in climate change studies by focusing on the identification of changes in community or species distributions related with external factors such as warming (Punzón et al., 2016; Quinzán et al., 2019; Polo et al., 2022). Similarly, the response of communities to other human pressures such as trawling has been commonly evaluated by studying the effects of fishing pressure on individual species biomass, on size spectra or on trophic networks (Pauly et al., 1998; Daan et al., 2005; Piet and Jennings, 2005; Greenstreet and Rogers, 2006; Agnetta et al., 2019). However, in recent years, a vast body of literature has focused on the use of trait-based ecological indicators for the detection of long-term changes on the benthic communities. The taxa selection in community studies in which species are the analytical unit usually aims at the inclusion of as many species as possible while avoiding rare and occasional species as well as wrongly identified organisms; additional filters to the selection of the species representing the community are often aggregated depending on the research question (Punzón et al., 2016; Pecuchet et al., 2017; González-Irusta et al., 2018). However, when analyses are trait-based, the criteria for the selection of taxa needs to attend different concerns, e.g., if the study aims at assessing a community's functional spatio-temporal dynamics or at checking its functional redundancy or dispersion (Levin and Lubchenko, 2008; Wiedmann et al., 2014), the optimum criteria might be the same than in a species-based study, while if it pursues the understanding of a community's vulnerability to a particular stressor, the best selection might be the one where the most sensitive species are accounted for (Rijnsdorp, et al., 2009; González-Irusta et al., 2018). Trait-based indicators have proven a useful tool to characterize the vulnerability status of marine ecosystems and ultimately design well-informed mitigation strategies for human originated impacts, such as fishing or pollution (De Juan and Demestre, 2012; Sampaio et al., 2012; De la Torriente et al., 2019; Serrano et al., 2022).

Despite the significant advancements in recent decades, the limited knowledge of some species behavioural and life-history characteristics continues to be a hurdle to undertake BTA in large biological communities. This is particularly challenging in rich and diverse temperate- and warm-water ecosystems, despite the numerous databases that have recently arose to standardise the information scattered in the scientific literature (MarLIN, 2006; Beukhof et al., 2019; Gallagher et al., 2020; Quimbayo et al., 2021). Additional hurdles to the consolidation of BTA in marine ecology on a global scale are the heterogeneity of trait nomenclature, the consideration of species traits as non-varying in space and time (Bastias et al., 2017), and the heterogeneous assignment of traits to different populations in certain studies (Fitzsimmons, 2013). Although the selections of traits and species are mostly driven by research questions, some common definitions and guidelines are essential to allow for cross-study comparisons and meta-analysis identifying commonalities and drawing sound conclusions (De Juan et al., 2022). This study explores the implications of using different criteria for selecting a representative community in BTA analyses. We have completed a dataset of reproductive, behavioural and morphological traits for the most representative species of two bentho-demersal communities in the Atlantic and the Spanish Mediterranean. The dataset will be published to support studies on the ecological response of exploited communities, i.e., the characterization of vulnerability of the communities to the combined impact of global warming and fishing. Also, and central to this annex, based on the analysis at the community level of this large set of biological and ecological traits, in two differently exposed temperate ecosystems, the implications of the use of different species selection criteria on the resulting ecological indicators are assessed and discussed.

2. MATERIAL AND METHODS

2.1 SURVEY DATA AND STUDY AREA

Species data (richness and abundance) were gathered from two annual bottom trawl surveys conducted in the Atlantic and the Mediterranean shelf seas of the Iberian Peninsula, DEMERSALES and MEDITS respectively. The aim of both scientific surveys is to collect and provide data for assessment on the distribution of the benthic-demersal community. The DEMERSALES survey covers an approximate area of 20000 km^2 of the southern Bay of Biscay from the mouth of the Miño River to that of the Bidasoa River (Punzón et al., 2021) (Figure 1). This area has been sampled every autumn (September-November) since 1983 (except for 1987) to 2019 by the Instituto Español de Oceanografía (IEO) and following the ICES standardized methodology for International Bottom Trawl Surveys (IBTS) (ICES, 2017). It consists in a random stratified sampling by three bathymetric depth strata (71–120, 121–200 and 201–500 meters) along five geographical sectors (two in Galician waters and three in the Cantabrian Sea). On the other hand, the MEDITS survey is set on the eastern Iberian Peninsula, to the West of the Balearic Sea, known as the Mediterranean geographical subarea 6 (GSA6) covering an approximate area of 32500 km^2 (Spedicato et al., 2019). This area has been sampled every early summer since 1994 to 2019 following a similar protocol than in DEMERSALES but standardized by the General Fisheries Commission for the Mediterranean (GFCM). In both surveys, the sampling unit consists of 30-minute hauls at a speed of 3.0 knots, using a Baca 44/60 otter trawl gear. All species caught were identified, counted, and weighed in each haul. To ensure consistency in the identification of invertebrates across the surveys in the Cantabrian region, we only used hauls for the period 1994-2019. Therefore, both surveys cover the periods 1994-2020 (25 years).

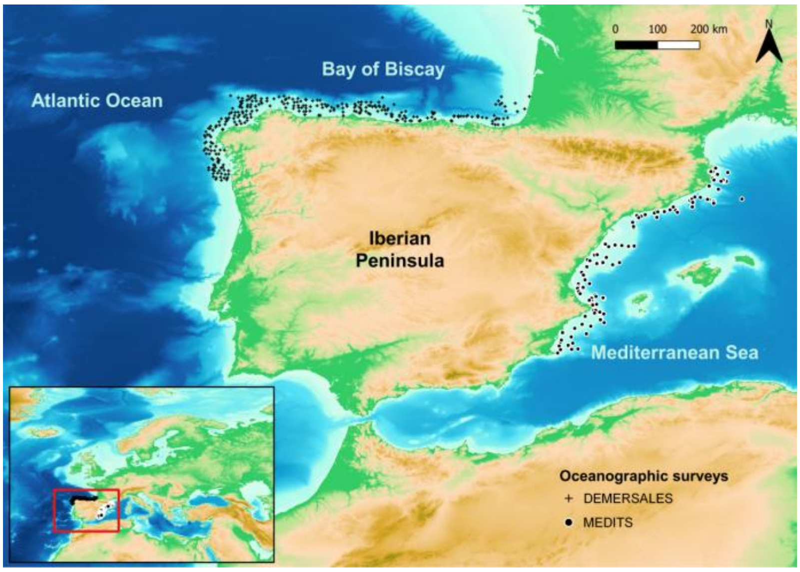


Figure 1. Study areas and geographical position of the hauls for the DEMERSALES survey (coast of the North-East Atlantic Ocean) and the MEDITS (Mediterranean). Map was created by using QGIS® software.

2.2 SELECTION OF SPECIES

The community time series resulting from both demersal surveys showed a high species richness, with over 680 species in the southern Bay of Biscay and 620 in the Spanish Mediterranean during the study period. To obtain representative communities we analysed changes in community richness using yield-effort curves, to assess how the accumulated richness changes across time (increasing the number of years), across space (increasing the number of hauls in each annual survey) and with abundance patterns (with an increasing abundance threshold, in each haul and year). Based on the visual inspection of these accumulation curves, we selected our primary subset of species (F0) after filtering each survey database by annual occurrence (we kept species that appeared at least 12 years), abundance within the year (we only kept those species that occurred at least in 12 hauls a year) and abundance per haul (by getting rid of rare species, with abundance under the first decile), which consisted on 246 species, which constitute the basis for subsequent analyses (Table Supp. 1).

To compare how the number and occurrence of selected species affects in traits studies, two alternative filtering combinations were applied to obtain two more constrained community subsets. On the one hand, we obtained F1 subset by filtering those species that appeared in 19 years and occurred in 12 hauls a year with abundance under the first decile. On the other hand, F2 subset compiles the species that appeared in at least 19 years, 19 hauls a year and with abundances under the fifth decile.

2.3 BIOLOGICAL TRAITS DATABASE

A set of 15 biological traits were selected based on the general knowledge of the effect of trawling impacts on the biology and ecology of the selected species as well as their response to climate change impacts (Table 1). We compiled information regarding these 15 biological features (traits) for the most recurrent 246 species at the lowest possible taxonomic level, by consulting online databases: WoRMS; BIOTIC (Marshall et al., 2006); FishBase (Froese and Pauly, 2014) and SeaLifeBase; and diverse sources ranging from general handbooks to specialized papers. In total, more than 200 scientific publications were reviewed to this end. Thus, compiled traits included information about preference of habitat, morphology and life-history.

Table 1. Biological traits (life-history, morphology, and behaviour) and categories defined in this study.

Subject area	Traits	Code	Variable nature	Factor	Categories: Units (Numerical) and modes (Categorical)
Life-history	**Maximal age**	**MA**	Numerical	/	Maximum recorded age of species
Life-history	**Body size**	**BS**	Numerical	/	Maximum recorded lenght of species (in mm)
Life-history	**Fecundity**	**FE**	Numerical	/	Number of eggs produced per female per year
Life-history	**Offspring size**	**OS**	Numerical	/	Size (in mm) of the released eggs or young (bearer)
Life-history	**Growth coefficient**	**GC**	Numerical	/	Speed at which an organism increases its mass/size (mm/year)
Life-history	**Trophic level**	**TL**	Numerical	/	Position in the food web based on diet composition and mean trophic level of food items (Nondimensional)
Life-history	**Age maturity**	**AM**	Numerical	/	Age at first maturity
Life-history	**Size maturity**	**SM**	Numerical	/	Length at first maturity (in cm)
Life-history	**Spawning period**	**SP**	Numerical	/	Central month of the spawning period
Life-history	**Egg development position**	**EP**	Categorical	**1**	Planktonic
				2	Benthic
				3	Other (attached to external organism)
				4	Attached to parental body /Ovoviviparous/viviparous
Life-history	**Parental care**	**PC**	Categorical	**1**	Non Guarder - Planktonic (Eggs are released in the water column)
				1	Non Guarder (limited information)
				2	Non Guarder - Benthic (Eggs are released/attached at the seabed)
				3	Guarder - Brooder
				4	Guarder - Bearer (Eggs are carried by a parent or develop inside the parent, give birth)

Table 1. (cont.)

Morphology	**Body shape**	**SH**	Categorical	**1**	Fusiform
				2	Elongated
				2	Bullet-like
				2	Eel-like
				3	Lenticular
				3	Flat
				4	Hook-shaped
				4	Compressiform
				4	Globular
Behaviour	**Mobility/movement**	**MO**	Categorical	**1**	Swimmer
				2	Burrower
				2	Crawler
				3	Sessile
Behaviour	**Habitat preference**	**HP**	Categorical	**1**	Pelagic
				1	Bathypelagic
				2	Demersal
				2	Bathydemersal
				3	Benthic
				3	Suprabenthic
Behaviour	**Feeding mode**	**FM**	Categorical	**1**	Scavenger
				1	Generalist
				1	Detritivorous
				2	Planktivorous
				3	Benthivorous
				3	Surface deposit feeders
				3	Suprabenthic feeder
				4	Suspensivorous

To complete the database, each trait value was accompanied by the taxonomic rank at which it was retrieved, the reference and available information on revised literature. Because of the lack of specific information on many traits for a large set of species (data do not exist or are not published), it was difficult to limit the gathering of information to the species level. Therefore, to minimize gaps, missing information was estimated using coarser taxonomic levels (the most immediate one available) of the database itself. For example, if no information for the fecundity of the fish *Gobius niger* (Fam. Gobiidae) was found, we tried to retrieve the mean fecundity of the genus, based on the Gobius spp. in the database. If fecundity of no other Gobius spp. was available, we calculated the mean fecundity of the Gobiidae family based on other Gobiidae from the community, and so on.

2.4 SENSITIVITY TO SPECIES SELECTION:

COMMUNITY-WEIGHTED MEAN BIOLOGICAL PREFERENCES

Community Weighted Mean (CWM) trait analyses were performed to characterize both communities by combining information on species traits and distribution (by haul and year) for each subset of species in each long-term series, based on previous work by Punzón et al. (2021), where these authors used the index Community Weighted Mean Temperature (CWMT) to link the thermal preference of demersal fish communities and temperature. The CWM trait index is calculated in each haul as,

$$CWMT_i = \Sigma T_s * W_{si} / \Sigma\, W_{si}$$

where CWMTi is the Community Weighted Mean Trait in haul i, the T is the trait value characteristic of the species and Wsi is the biomass in weight of species s in the haul i (Punzón et al., 2021).

For the final analyses in this paper, a set of five variables (traits) was selected; maximal age (MA), body size (BS), body shape (BH), feeding mode (FM) and mobility (MO). Thus, we ensured the inclusion of traits related to life-history, morphology, and behaviour in the analyses and therefore traits linked with both fishing and climate change impacts. In addition, two of them are numerical variables and three categorical, covering thus the different nature of the variables. The categorical variables were factorized by assigning a number to each category as depicted in Table 1. The rationale to factorize categorical traits follows Polo et al. (*in prep)*, in which trait categories are given a number according to the sensitivity to trawling they are expected to confer the species, as taken from previous research. The factors go from 1-3 or from 1-4, depending on the trait. Community Weighted Means were calculated for the five selected traits in each haul and year of the two time series for the three filter combinations (F0, F1, F2), as well as for three additional subsets of species, these being: a subset only including taxa with traits assigned at a species level, another subset with only chordates and a last one including chordates with traits assigned at species level.

COMPARISON OF DIFFERENT SPECIES SELECTIONS

To determine how the selection of species influences the results obtained after a Biological Trait Analysis to characterize each community, the mean value for each selected trait was compared between different subsets of species (F0, F1, and F2) by means of one-way ANOVAs. In addition, to identify the influence of the nature of the species included, the analyses were repeated for each of the filters (F0, F1, and F2) comparing the different aggregations of species (whole community, only taxa with trait assigned at species level, only chordates, and chordates with trait assigned at species level) for the selected trait (MA, BS, SH, MO, and FM). Comparisons of means were based on Tukey's honestly significant difference (T) method (Sokal and Rohlf, 1981).

To visually assess the temporal trends of the community weighted mean (CWM) traits and the differences between the filtered subsets and taxa selections, a locally weighted scatterplot smoothing regression technique (LOESS, Cleveland, 1979) was applied on the CWM traits data. For this same purpose, boxplots of the different selections and subsets allowed an additional visual representation of their similarities.

All numerical analyses were performed on R statistical software version 4.2.1. (R Core Team, 2022). We accessed the FishBase database (Froese and Pauly, 2022: www.fishbase.org) and the SeaLifeBase database (Palomares and Pauly, 2022: www.sealifebase.se) using ‘rfishbase’ R package (Boettiger et al., 2022). Additionally, we accessed the World Register of Marine Species database (WoRMS, 2021: www.marinespecies.org) using ‘worrms‘ R package (Chamberlain, 2018).

3. RESULTS

3.1 AVAILABILITY AND QUALITY OF BIOLOGICAL TRAITS DATA FOR DEMERSAL SPECIES

After applying the first combination of species filtering (F0), we obtained a subset of 246 taxa comprised of 143 chordates (57.9 %); and 104 invertebrates (42.1 %, including Arthropoda, 48 species; Mollusca, 35; Echinodermata, 16; Cnidaria, 4; Annelida; 1) (Figure 2 and Table Supp. 1). The application of different filters to both communities’ dataset produced 4 subsets; F1 contained 133 and 177 species in the Atlantic and the Mediterranean, respectively, and F2 110 and 102 (Figure 2a). The percentage of taxa on phylum distribution also varied with respect to the 246 list of species (Figure 2b). Hence, some phyla such as Echinodermata, Cnidaria or Annelida are no longer represented in the most constrained selections (Figure 2).

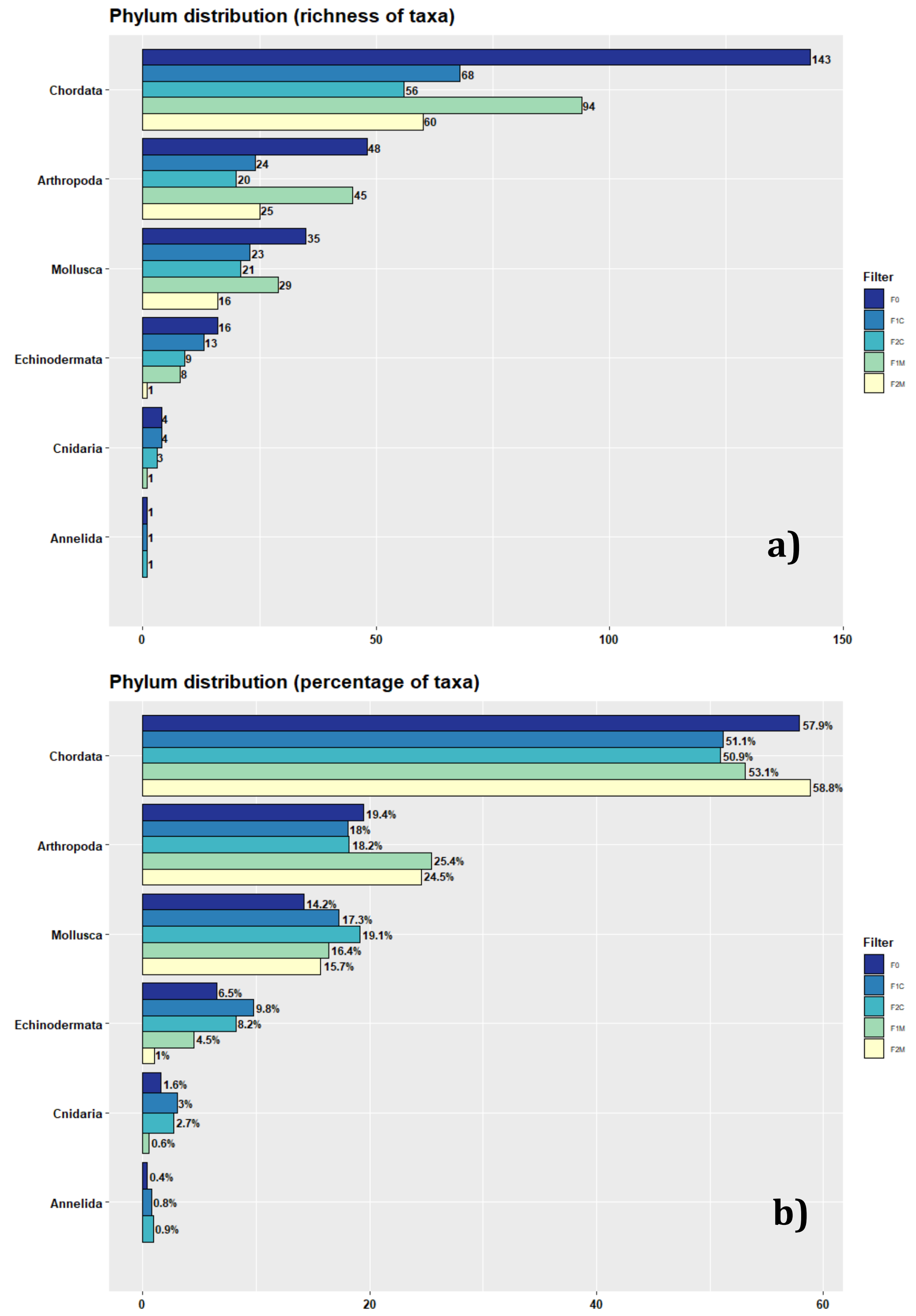


Figure 2. Composition of eachsubset of taxa according to filter selection in a) number of species and b) percentage of species for different Phylum.

Taking the first subset of 246 species (F0 aggregation) as the basis of the studio, we compiled data on 15 traits related to life-history, morphology and behaviour information. As a result, we obtained an array of 246 species with 15 variables (traits) and 45 categories for these traits (Table 1). At the end of the bibliographical review, most of the data retrieved from the literature corresponded to fish species (around 2000 data). In addition, more than 90% of them were assigned at the species level and the remaining at genus (around 5%) and family (around 4%). However, for the invertebrate community, some traits were obtained at class and order level (0.2 and 0.7% respectively), and around 86% were obtained at species level, 7% at genus level and 5% at the family level (Table Supp.). At this stage 664 gaps remained in the database, so we followed the routine described in the methods section, estimating these traits based on data of coarser taxonomic levels. Thereafter only 71 gaps remained (Figure 3). As a result, of the 15 categories of traits, 9 (maximal age, MA; body size, BS; fecundity, FE; growth coefficient, GC; age of maturity, AM; size of maturity, SM; egg development position, EP; parental care, PC; habitat preference; HP) were completed for all species at any of the taxonomic ranks. The other 6 (offspring size, OS; trophic level, TL; spawning period, SP; body shape, SH; mobility, MO; feeding mode, FM), were completed above 95% except for spawning season, for which 22.3% of the species had missing data. Notably, most of the traits were allocated at species level (73.5%). Between 5.7 and 6.7% were determined at the levels of Genus, Family and Order. And finally, between 2.7 and 3% were assigned to the higher levels, Class and Phylum. Comparing the information assigned to the species level for the different traits we found that age at maturity, although being completed for the 246 species, only had 46.6% assigned at a species level. However, other traits such as body shape and mobility, did not have information available for every species in our dataset, but a 95.5% were assigned at the species level.

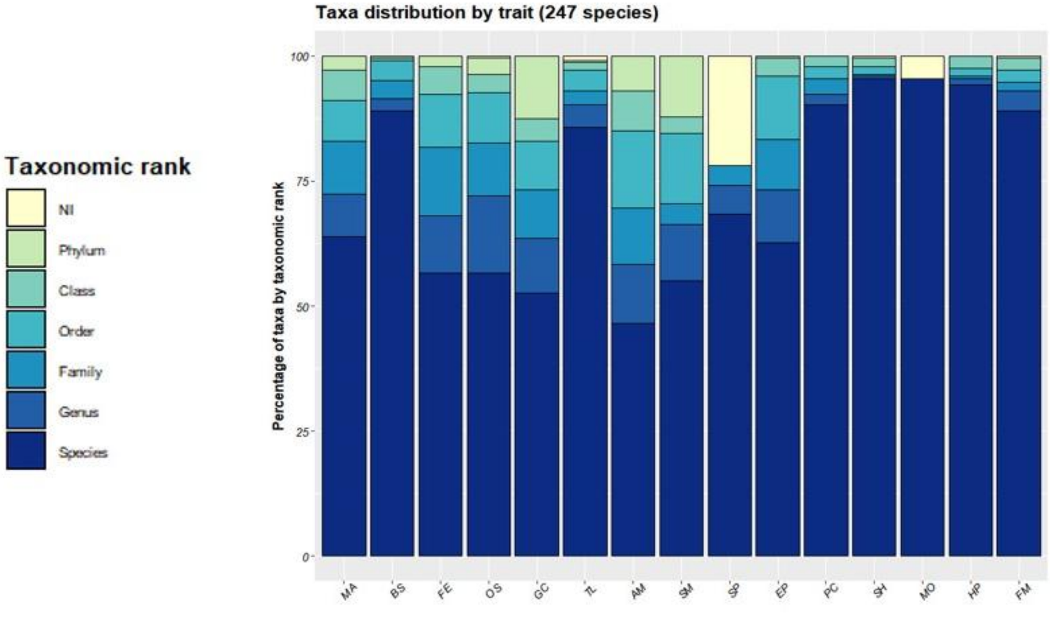


Figure 3. Percentage of coverage of traits assigned at each taxonomic rank for the F0 subset of taxa (246 species) after the literature review and gaps estimation for each trait; maximal age (MA), body size (BS), fecundity (FE), offspring size (OS), growth coefficient (GC), trophic level (TL), age maturity (AM), size maturity (SM), spawning period (SP), egg development position (EP), parental care (PC), body shape (SH), mobility (MO), habitat preference (HP), and feeding mode (FM).

3.2 COMMUNITY WEIGHTED MEAN BIOLOGICAL TRAITS

In the North-East Atlantic community, almost every trait showed no differences among the different filtered subsets (Figure 4 and Table 2). Differences were only apparent between two subsets, F0 and F2, for body size (Tukey HSD, p-value <0.05), when the community weighted mean trait was computed only for chordate species, indicating that the three filters, despite resulting in three subsets of species with large differences in species richness, gave similar community weighted mean traits. On the other hand, subselecting the community based on their taxonomy or the availability of data at the species level (whole community, only taxa with traits found at species level, only chordates, chordateswith traits assigned at species level) for each of the filters, resulted in significant differences between the community weighted mean traits' values (Figure 4c and Table 3). Notably, the CWM traits were always significantly different when considering the full community (all taxa) instead of only considering the chordates in the community. The CWM traits of the full community also differed to the values obtained if considering only the data originally retrieved at the species level, but for CWM body shape (Table 3). However, for chordates, only restricting the analysis to the data originally retrieved at the species level had no significant effect on any of the CWM traits.

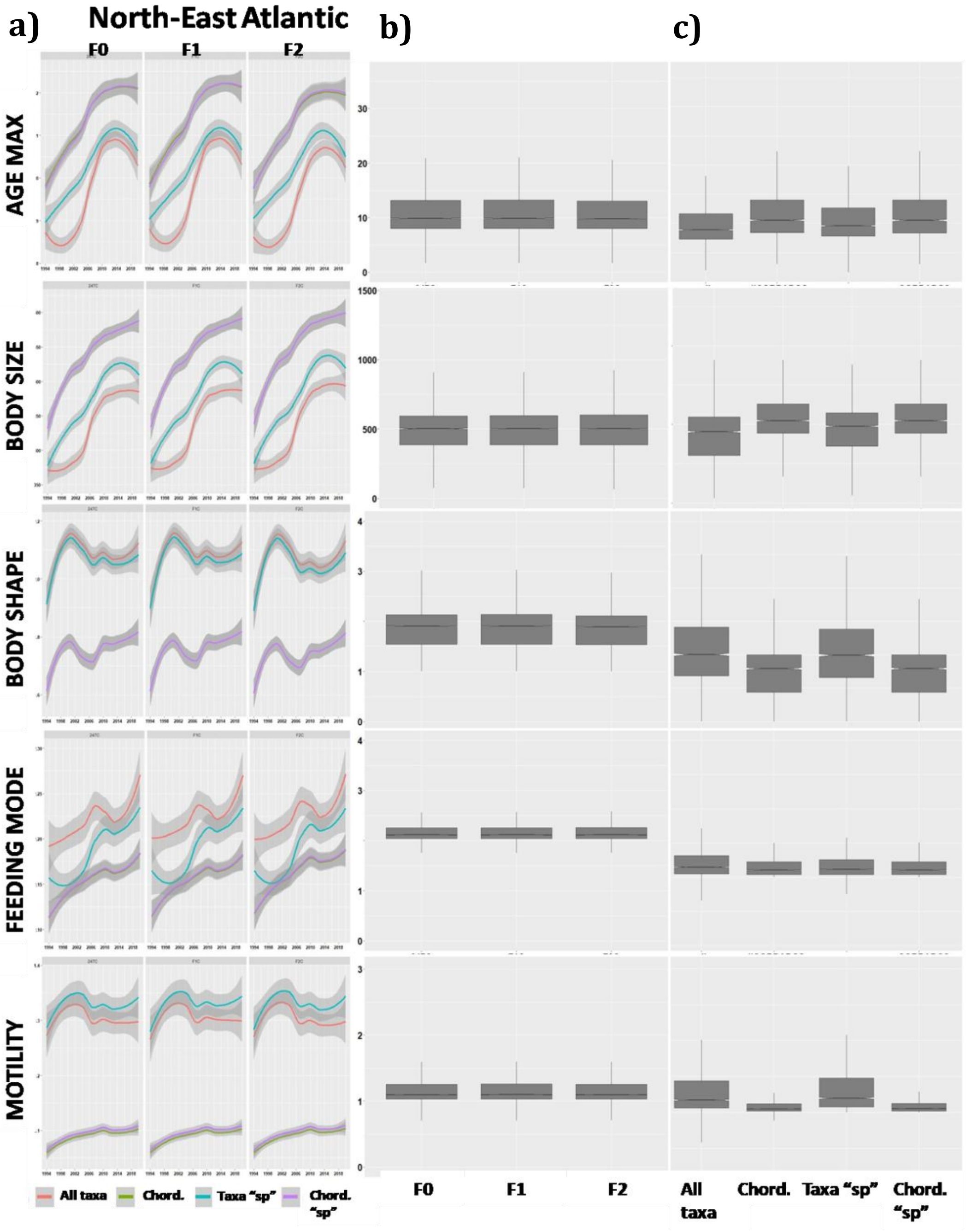


Figure 4. North-East Atlantic Ocean. a) Trends in Community Weighted Mean (CWM) over a 25-year period (from 1994 to 2019) for five biological traits: maximal age (MA), body size (BS), body shape (SH), mobility (MO), and feeding mode (FM) for the different combinations of filters and taxa subsets. Points are fit with a nonparametric regression function using locally weighted scatter plot smoothing (LOESS). b) Box plots representing the CWM across different filtering combinations (F0, F1, F2) for each trait (MA, BS, BH, MO, FM). c) Box plots representing the CWM across different species aggregations (whole community, only taxa with trait assigned at species level, only Chordata taxa, and Chordata with trait assigned at species level) applied on the F0 filtered community (246 species) for each trait.

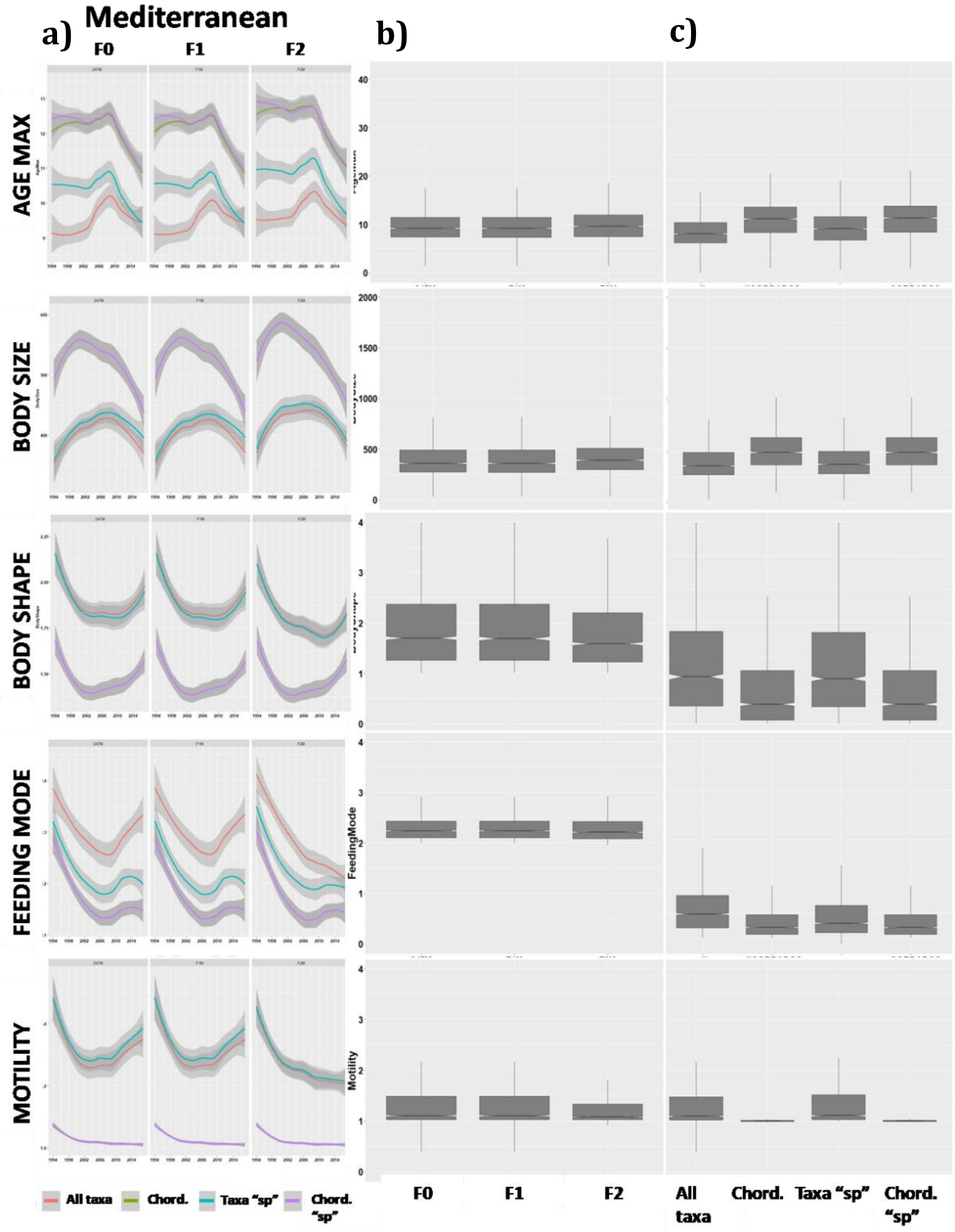


Figure 5. Mediterranean Sea. a) Trends in Community Weighted Mean (CWM) over a 25-year period (from 1994 to 2019) for five biological traits: maximal age (MA), body size (BS), body shape (SH), mobility (MO), and feeding mode (FM) for different combinations of filters for community selection and taxa subsets. Points are fit with a nonparametric regression function using locally weighted scatter plot smoothing (LOESS). B) Box plots representing the CWM across different filtering combinations (F0, F1, F2) for each trait (MA, BS, BH, MO, FM). C) Box plots representing the CWM across different species aggregations (whole community, only taxa with trait assigned at species level, only Chordata taxa, and Chordata with trait assigned at species level) applied on the F0 community (246 species) for each trait.

Table 2. Results from one-way ANOVA tests for the five studied traits; Maximal age (MA), Body size (BS), Body shape (SH), Mobility (MO), and Feeding mode (FM) comparing different subsets of species (F0, F1, F2) for each taxa aggregation (All taxa, Taxa assigned at species level, Chordates, Chordates assigned at species level) in the North-East Atlantic Ocean. Comparisons of means were based on Tukey's method.

NORTH-EAST ATLANTIC

All taxa

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**
Maximal age	2	50	25.21	2.128	0.119
Body size	2	63122	31561	0.907	0.404
Body shape	2	1	0.2831	0.821	0.44
Mobility	2	0	0.00662	0.055	0.947
Feeding mode	2	0	0.01197	0.191	0.827
Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
F0-F1	0.9228854	0.9446308	0.9832915	0.9618024	0.9126026
F0-F2	0.2608780	0.3987057	0.5693667	0.9991804	0.8172177
F1-F2	0.1257898	0.5944379	0.4611435	0.9502169	0.9786288

Taxa assigned at species level

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**
Maximal age	2	4	2.147	0.177	0.838
Body size	2	95228	47614	1.592	0.204
Body shape	2	1	0.3240	0.947	0.388
Mobility	2	0	0.0067	0.055	0.946
Feeding mode	2	0	0.00655	0.118	0.889
Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
F0-F1	0.9329463	0.8842696	0.9848052	0.9426761	0.9300970
F0-F2	0.9696532	0.1953482	0.5141895	0.9928621	0.8892239
F1-F2	0.8247980	0.4214663	0.4142482	0.9752376	0.9946138

Table 2. (cont.)

All chordates

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	2	30	15.19	1.214	0.297	
Body size	2	309377	154689	4.5.07	0.0063	**
Body shape	2	0.6	0.2967	1.563	0.209	
Mobility	2	0	0.000914	0.072	0.931	
Feeding mode	2	0.12	0.06247	2.611	0.0735	
Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**	
F0-F1	0.7396685	0.5856075	0.9545762	0.9676358	0.9646431	
F0-F2	0.6919607	0.0052392	0.3592425	0.9262195	0.0910133	
F1-F2	0.2641689	0.0841032	0.2224944	0.9909226	0.1570429	

Chordates assigned at species level

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	2	13	6.395	0.507	0.603	
Body size	2	309377	154689	5.07	0.0063	**
Body shape	2	0.6	0.2981	1.57	0.208	
Mobility	2	0	0.000976	0.075	0.928	
Feeding mode	2	0.13	0.06298	2.111	0.0754	
Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**	
F0-F1	0.7985249	0.5856075	0.9545784	0.9664258	0.9658285	
F0-F2	0.9332927	0.0052392	0.3573984	0.9233187	0.9658285	
F1-F2	0.5812951	0.0841032	0.2211181	0.9905029	0.1592664	

In contrast, for the Mediterranean community, when the five CWM traits were computed, significant differences were observed between the filtered subsets (Figure 5b and Table 4). Thus, if every taxon was included in our analyses (full community), Tukey HSD for every trait showed that F2 significantly differs of F0 and F1 (Table 4). While the filtered subsets did not differ for all CWM traits when selecting data retrieved exclusively at the species level or only chordates, CWM body size between F0, F1 and F2 remained signidicantly different regardless of the selection of data. The CWM traits were significantly different in all instances of the ‘all taxa’ and ‘only chordates’selections. On the other hand, the ‘full chordates’ communityweighted mean traits were not different from those of chordates retrieved at the species level (Figure 5c and Table 5).

Table 3. Results from one-way ANOVA tests for the five studied traits; maximal age (MA), body size (BS), body shape (SH), mobility (MO), and feeding mode (FM) comparing different aggregations of species (All taxa, Taxa’sp’, Chordates, Chordates ‘sp’) for each subset (F0, F1, F2) in the North-East Atlantic Ocean. Comparisons of means were based on Tukey's method.

NORTH-EAST ATLANTIC

F0

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	3	7088	2362.6	194.7	<2e-16	***
Body size	3	26940731	8980244	309.1	<2e-16	***
Body shape	3	350	116.55	435.5	<2e-16	***
Mobility	3	172.8	57.61	870.8	<2e-16	***
Feeding mode	3	9.9	3.310	81.23	<2e-16	***

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
All taxa-Chordates	0	0	0	0	0
All taxa-Taxa’sp’	0	0	0.42927	0.0005442	0
All taxa-Chord.’sp’	0	0	0	0	0
Taxa’sp’-Chordates	0	0	0	0	0
Chordates- Chord.’sp’	0.9943236	1	1	0.8021015	0.995469
Taxa’sp’- Chord.’sp’	0	0	0	0	0

Table 3. (cont.)

F1

	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
Maximal age	3	7354	2451.3	193.6	<2e-16	***
Body size	3	28445854	9481951	313.2	<2e-16	***
Body shape	3	348	116.09	426	<2e-16	***
Mobility	3	175.7	58.56	872.5	<2e-16	***
Feeding mode	3	10.4	3.473	84.43	<2e-16	***

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
All taxa-Chordates	0	0	0	0	0
All taxa-Taxa’sp’	0	0	0.4314112	0.0004324	0
All taxa-Chord.’sp’	0	0	0	0	0
Taxa’sp’-Chordates	0	0	0	0	0
Chordates- Chord.’sp’	0.9858873	1	1	0.8037170	0.9956227
Taxa’sp’- Chord.’sp’	0	0	0	0	0

F2

	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
Maximal age	3	7569	2523	209.8	<2e-16	***
Body size	3	31101371	10367124	296.5	<2e-16	***
Body shape	3	349	116.17	447.1	<2e-16	***
Mobility	3	171.8	57.28	848.2	<2e-16	***
Feeding mode	3	8.6	2.861	66.49	<2e-16	***

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
All taxa-Chordates	0	0	0	0	0
All taxa-Taxa’sp’	0	0	0.3603573	0.0002744	0
All taxa-Chord.’sp’	0	0	0	0	0
Taxa’sp’-Chordates	0	0	0	0	0.0000009
Chordates- Chord.’sp’	0.996377	1	1	0.8040945	0.9955245
Taxa’sp’- Chord.’sp’	0	0	0	0	0.0000030

Table 4. Results from one-way ANOVA tests for five traits; Maximal age (MA), body size (BS), Body shape (SH), Mobility (MO), and Feeding mode (FM) comparing different subsets of species (F0, F1, F2) afor each taxa aggregation (All taxa, Taxa assigned at species level, Chordates, Chordates assigned at species level)in the Mediterranean Sea. Comparisons of means were based on Tukey's method.

MEDITERRANEAN SEA

All taxa

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	2	75	37.3	3.122	0.0441	*
Body size	2	486083	243041	6.294	0.00186	**
Body shape	2	10.9	5.437	10.48	2.86E-05	***
Mobility	2	3.7	1.8252	10.38	3.17E-05	***
Feeding mode	2	0.9	0.4517	6.552	0.00144	**

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
F0-F1	0.9629028	0.9999951	0.9931754	0.9955052	0.9880362
F0-F2	0.1071949	0.0060675	0.0001743	0.0002872	0.0063246
F1-F2	0.0582547	0.0060083	0.0002769	0.0001976	0.0038656

Taxa assigned at species level

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	2	186	93.25	7.52	0.000548	***
Body size	2	334887	167443	4.355	0.0129	*
Body shape	2	8.4	4.221	8.257	0.000262	***
Mobility	2	6.1	3.0712	17.4	2.91E-08	***
Feeding mode	2	0.04	0.01808	0.376	0.687	

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
F0-F1	0.9994001	0.9999983	0.9920301	0.9977613	0.9970604
F0-F2	0.0021457	0.0285403	0.0010167	0.0000012	0.7126629
F1-F2	0.0024129	0.0286797	0.0015908	0.0000008	0.7568143

Table 4.. (cont.)

All chordates

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	2	104	52.11	3.84	0.0215	*
Body size	2	485848	242924	5.6	0.00372	**
Body shape	2	0.1	0.03447	0.134	0.874	
Mobility	2	0.003	0.001726	0.592	0.553	
Feeding mode	2	0	0.00028	0.008	0.992	

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
F0-F1	0.9988892	0.9576373	0.9205081	0.9959889	0.9999547
F0-F2	0.0459721	0.0069741	0.8751377	0.5881505	0.9936464
F1-F2	0.0409323	0.0165592	0.9940192	0.6423260	0.9925337

Chordates assigned at species level

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	2	66	33.06	2.468	0.0848	.
Body size	2	485848	242924	5.6	0.00372	**
Body shape	2	0.1	0.03447	0.134	0.874	
Mobility	2	0.004	0.002046	0.704	0.495	
Feeding mode	2	0	0.00015	0.005	0.995	

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
F0-F1	0.9954808	0.9576373	0.9205081	0.9730861	0.9999863
F0-F2	0.1453732	0.0069741	0.8751377	0.5014312	0.9964992
F1-F2	0.1203098	0.0165592	0.9940192	0.6415791	0.9960488

Table 5. Results from one-way ANOVA tests for five traits; Maximal age (MA), Body size (BS), Body shape (SH), Mobility (MO), and Feeding mode (FM) comparing different aggregation of species (All taxa, Taxa'sp', Chordates, Chordates'sp') for each subset (F0, F1, F2) in the Mediterranean Sea. Comparisons of means were based on Tukey's method.

MEDITERRANEAN SEA

F0

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr (>F)**	
Maximal age	3	9724	3241	255.7	<2e-16	***
Body size	3	24411253	8137084	199.5	<2e-16	***
Body shape	3	338.4	112.8	283.8	<2e-16	***
Mobility	3	175.7	58.57	589.7	<2e-16	***
Feeding mode	3	23.6	7.88	167.7	<2e-16	***

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
All taxa-Chordates	0	0	0	0	0
All taxa-Taxa'sp'	0	0.1609033	0.7669336	0.1083922	0
All taxa-Chord.'sp'	0	0	0	0	0
Taxa'sp'-Chordates	0	0	0	0	0
Chordates- Chord.'sp'	0.7556352	1	1	0.9999954	0.9999953
Taxa'sp'- Chord.'sp'	0	0	0	0	0

Table 5. (cont.)

F1

	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
Maximal age	3	9815	3272	259	<2e-16	***
Body size	3	25233206	8411069	204.4	<2e-16	***
Body shape	3	344.3	114.8	289.9	<2e-16	***
Mobility	3	177.2	59.08	589.2	<2e-16	***
Feeding mode	3	24.1	8.021	169.2	<2e-16	***

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
All taxa-Chordates	0	0	0	0	0
All taxa-Taxa'sp'	0	0.1623446	0.7604961	0.1202603	0
All taxa-Chord.'sp'	0	0	0	0	0
Taxa'sp'-Chordates	0	0	0	0	0
Chordates- Chord.'sp'	0.7809811	1	1	1	0.9999931
Taxa'sp'- Chord.'sp'	0	0	0	0	0

F2

	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
Maximal age	3	9556	3185	241.8	<2e-16	***
Body size	3	25438376	8479459	207.2	<2e-16	***
Body shape	3	221.5	73.83	202.9	<2e-16	***
Mobility	3	113.5	37.84	548.1	<2e-16	***
Feeding mode	3	16.1	5.368	122.3	<2e-16	***

Tukey HSD (p adj)	**Maximal age**	**Body size**	**Body shape**	**Mobility**	**Feeding mode**
All taxa-Chordates	0	0	0	0	0
All taxa-Taxa'sp'	0	0.396996	0.9687042	0.8479944	0
All taxa-Chord.'sp'	0	0	0	0	0
Taxa'sp'-Chordates	0	0	0	0	0
Chordates- Chord.'sp'	0.9695196	1	1	1	1
Taxa'sp'- Chord.'sp'	0	0	0	0	0

4. DISCUSSION

Our analyses indicate that selecting a subset of species representative of a community is a crucial step in any BTA analysis and, as such, the criteria used for the selection should be explicitly incorporated in the methods. While the number of studies focusing on functional properties of organisms instead of the taxonomy-based approach has increased as an alternative method to study biological communities and their functioning (Cadotte et al., 2015; González-Suárez & Revilla, 2013; Laughlin & Messier, 2015; Moles, 2018; Schneider et al., 2019), most of them do not provide the criteria baking up the selection of species they deemed representative of their community. This study aimed to fill this gap, adding up to other studies that critically evaluate the assumptions and biases of trait-based research.

The importance of clearly acknowledging the communities' data filtering methodologies is not often highlighted, even though it can have a major influence in any research conclusions. A good example of this is how three different studies on the 'tropicalization' and 'meridionalization' processes (increase in warm-affinity native and non-native species, respectively) of the community associated to Spanish Mediterranean communities with different species selection criteria shed light on different processes taking place within the community. In line with Moullec et al.'s (2019) expectations of a global increase of small pelagic and thermophilic species, Hidalgo et al (2022) found an increase in the community weighted mean temperature for 75 fish and invertebrate species in our study area, while two studies of the same community, Sanz-Martín et al. (*under revision*) and Polo et al. (*under revision*) did not found the expected rise in mean thermal affinities from meridionalization processes. The three studies used the same ecological indicator, the community weighted mean thermal affinity, but filtered the community differently and reached different conclusions. In Hidalgo et al. (2022), the optimum selection of species was set by applying a Principal Component Analysis on different datasets, each dataset containing species caught in a one-year shorter time series, and then examining the difference between the PCA's characterization of the community dynamics (Hidalgo et al., 2022). In Sanz-Martin et al. (*under revision*), the community was represented by the 102 most frequent species, a number reached by filtering the dataset to only include species occurring in 10 years or more, while Polo et al. (*under revision*) used 220 species (the same selection and datasets used in the present study). While this case alerted us on the leverage of the filters by which a community is defined, our results revealed the taxa accounted for in the subsetting of the complete dataset might be more influential than the inclusion of more or less species in what is by nature a multitaxon community.

The three subsets of species used in our study (F0, F1, F2) were reached by filtering the total sample of the two scientific surveys by means of three aspects of community structure often used for the definition of the community unit in spatio-temporal studies, these being: annual occurrence, abundance per year and numerical abundance within sampling stations. By restricting the analyses to the most frequent species in the time series and the most abundant within sampling stations, researchers do not only reduce the likelihood of mistaken identifications and remove rare species (Punzón et al., 2016; González-Irusta et al., 2018; Beukhof et al., 2019). The filtering by occurrence across the time series serves as a temporal filtering, and depending on the scale of the study, whether it aims at the characterization of more or less regional or local ecological mechanisms, accounting for the proportion of surveyed cells in which the selected species are present can serve as a spatial filtering, as well as a way to avoid species with low catchability (Sánchez and Serrano, 2003; Preciado et al., 2019). In terms of the abundance patterns within sampling stations, the exclusion of non-dominant species, those under a certain abundance percentile serves also the constitution of a final dataset that represents correctly sampled, resident rather than occasional taxa (Merillet et al., 2021).

The sensitivity analyses we have undertaken in this work indicate that restricting the biological trait analysis to a single phylum results in values that strongly differ from the full communities. In fact, analyses on fish communities are common in the literature (Punzón et al., 2021; Polo et al., 2022) as these are mostly large species of commercial value and thus information on their behaviour and life cycle is readily available. In fact, this was the case in the database compiled in this study, in which chordate information could be retrieved over 99% of the cases at the species level, making any differences between the full chordate database and the chordate database only retrieved at the species level negligible. On the other hand, differences between the full community and the ‘only-chordates’ community stood up in every occasion, highlighting that only chordates cannot represent the full community patterns and dynamics while pointing to the fundamental role of invertebrates in the communities. This bias of knowledge towards some faunistic groups is well known in the scientific literature: fish are much better known than invertebrates, and studies mostly focus on large bodied species or those of commercial interest, and with large abundances or wide distributions (Tyler et. al, 2012). This non-randomness in missing data needs to be carefully assessed in modelling studies, as conventional approaches to fill data gaps might be not valid or present important challenges (González-Suárez et al., 2013). In fact, our analyses identify differences in the CMW traits when comparing the trait information retrieved at the species level with the full database after filling the gaps, particularly for continuous traits as lifespan and body size, but also for feeding mode. While the phylogenetic approach we used to fill the database gaps is well supported in the literature, as sister species are supposed to show less interspecific variation than phylogenetic distant groups, almost 15% of the data had to be filled based on taxa distantly related with the species (Order or Class), increasing the uncertainty of the estimations. Our results suggest that binning continuous trait data into categories could be a strategy to reduce this uncertainty, at the cost of coarsening the underlying trait information.

By using species trait data researchers assume that intraspecific variability is small compared to variations among species, however, within-species variation often neglects seasonal fluctuations, differences among populations and the small sample size on which some estimates are based, which compromise confidence of trait measurements (Garamszegi and Møller, 2010). In fact, environmental filtering seems to be a major driver of intraspecific variability with species traits most likely varying in the space-time continuum (e.g., Cassidy et al., 2020; Luiz et al., 2022). In this context, accessing and integrating trait data from different sources remains a challenge in BTA research. The large availability of trait information on some species does not necessarily mean more robust and solid estimates. In fact, there are large inconsistencies among databases that could be reflecting intraspecific variability at different spatial scales, temporal variability in the estimates, or different scoring for similar trait descriptions, commonly causing larger inconsistencies in traits subject to researchers' interpretations (Fitzsimmons, 2013). In this sense, open data initiatives offer a solution to overcome these challenges of functional traits science, advocating for open data, open source and open methods and thus standardising and integrating data across organisms, geographical regions and time, while securing access to the data and accelerating global synthesis (Galhager et al., 2020).

The two continental shelf systems analysed here shared the majority of species (75 %) but have endured contrasting degrees and types of impact during the last decades (Aragão et al, 2021), fact that could explain the different trends observed for community weighted mean traits among systems. On one side, the communities associated to the Atlantic shelf of Iberian Peninsula, while recovering from long term overfishing (Modica et al., 2014; Hidalgo et al., 2017; Arroyo et al., 2019; Punzón et al., 2021; Polo et al., 2022) are also accommodating the impacts of a sea surface warming rate of 0.23 °C per decade (Chust et al., 2022). These impacts' effect has been identified in complex ecological regime shifts at various levels (Bode et al., 2021; Polo et al., 2022), including evidences of 'meridionalization', i.e. increase in the abundance of native fauna with southern affinities (Punzón et al., 2016 and references therein; Punzón et al., 2021). In contrast to the Atlantic communities, fishing impacts on Mediterranean fish stocks and communities are heavy and ongoing (Farriols et al., 2019; SOMFI, 2021). Over the whole Mediterranean basin, climate change is fostering the meridionalization and tropicalization of the communities and ecosystems (Fogarty et al., 2017 and references therein; Vasilakopoulos et al, 2017; Hidalgo et al., 2022), which are coping with a higher warming rate of 0.35°C per decade (Pastor et al., 2020). As these two bentho-demersal systems are differently exposed to anthropogenic impacts, they were deemed appropriate case studies for the comparison between different subsets of a community. Our expectation was that the temporal trends of communities' traits would differ among systems, as did in fact happen, given the two systems inherent differences, but that the comparison of different filters and subsets of the largest species' pool would ultimately produce relatively similar results among systems, which did also happen, somehow endorsing the consistence of setting a filtering methodology based on the different aspects of a species' presence in a wider species pool and its relative contribution to the community under study.

Through the study of the sensitivity of ecological indicators, such as the communities' weighted life-history traits, to the species selection, our findings have highlighted the heavier influence of the number of the phyla represented in the community rather than being slightly more or less restrictive in the filtering of the complete datasets. Studies focused on traits are essential to understand the changes occurring in communities in response to external changes (e.g. McLean et al., 2018; Beukhof et al., 2019; Punzón et al., 2021), complementing taxonomic approaches that study species richness or diversity. Trait-based studies allow the identification of the characteristics that give species an advantage when it comes to dealing with or adapting to environmental changes. The biological traits we selected have been used in the literature associated with species' vulnerability in different ways, e.g., species with shorter life cycles or with greater reproductive capacity (multivoltine species or with greater number of offspring per year) are expected to adapt easier to changes in environmental conditions or in the fishing activity within their ecological niche (Juan-Jordá et al., 2013; Merillet et al., 2021). Reproductive traits such as fecundity and age to first reproduction are expected to partly determine the capacity of populations to adapt to or recover from anthropogenic stressors and pressures at their location (Juan-Jordá et al., 2013). Moreover, morphological features as body size or maximum length are frequently used in assessments of vulnerability (King and McFarlane, 2003; Ormseth and Spencer, 2011; Bender et al., 2013; Chessman, 2013; González-Suárez et al., 2013; Juan-Jordá et al., 2013; Sunday et al., 2015; Jørgensen et al., 2016). Large-bodied species are generally more vulnerable to many stressors (Bender et al., 2013; Davidson et al., 2012), although depending on the stressor and the species. Finally, species with narrow ecological niches or low capacity of movement to migrate will be more vulnerable than species with large distributions.

The compilation and analysis of biological trait information can improve the knowledge of how communities adapt to environmental changes related not only to climate warming but also to fishing, and in this sense, taking into account as many phyla as the quality of the data allow, might give a more accurate idea of the adaptive capacity and sensitivity inherent to studied communities, while limiting studies to the most familiar species will ignore a big dimension of a communities' structure, ultimately leading to inaccurate results that inform biased management actions. If a well informed ecosystem-based management is intended, the selection of species that shape the studied community needs to be acknowledged and suit the study's research question. Also, if aiming for the development of a thorough BTA framework, more efforts for the development of trait datasets that integrate information on the complexities of multitaxon biological assemblages should be encouraged, and the possible biases related to the use of traits instead of that of taxonomical units should be addressed.

5. SUPPORTING INFORMATION

APPENDIX 1: SUPPORTING TABLES

Table Supp. 1. Taxonomic information for taxa included in the biological trait database

Phylum	**Class**	**Order**	**Family**	**Species**	**Common name**
Mollusca	Cephalopoda	Teuthida	Enoploteuthidae	***Abralia veranyi*** **(Rüppell, 1844)**	Verany's enope squid
Mollusca	Bivalvia	Veneroida	Cardiidae	***Acanthocardia echinata*** **(Linnaeus, 1758)**	European prickly cockle
Cnidaria	Anthozoa	Actiniaria	Hormathiidae	***Actinauge richardi*** **(Marion, 1882)**	
Arthropoda	Malacostraca	Decapoda	Crangonidae	***Aegaeon cataphractus*** **(Olivi, 1792)**	
Arthropoda	Malacostraca	Decapoda	Crangonidae	***Aegaeon lacazei*** **(Gourret, 1887)**	Hardshell shrimp
Mollusca	Cephalopoda	Teuthida	Loliginidae	***Alloteuthis media*** **(Linnaeus, 1758)**	Midsize squid
Mollusca	Cephalopoda	Teuthida	Loliginidae	***Alloteuthis subulata*** **(Lamarck, 1798)**	European common squid
Chordata	Actinopteri	Clupeiformes	Clupeidae	***Alosa fallax*** **(Lacepède, 1803)**	Twaite shad
Arthropoda	Malacostraca	Decapoda	Alpheidae	***Alpheus glaber*** **(Olivi, 1792)**	Red snapping shrimp
Echinodermata	Asteroidea	Valvatida	Asterinidae	***Anseropoda placenta*** **(Pennant, 1777)**	Goose-pied starfish
Echinodermata	Crinoidea	Comatulida	Antedonidae	***Antedon mediterranea*** **(Lamarck, 1816)**	Feather star
Chordata	Actinopteri	Perciformes	Serranidae	***Anthias anthias*** **(Linnaeus, 1758)**	Sea perch
Chordata	Actinopteri	Gobiiformes	Gobiidae	***Aphia minuta*** **(Risso, 1810)**	Transparent goby
Mollusca	Gastropoda	Littorinimorpha	Aporrhaidae	***Aporrhais pespelecani*** **(Linnaeus, 1758)**	Common pelican's foot shell
Mollusca	Gastropoda	Littorinimorpha	Aporrhaidae	***Aporrhais serresiana*** **(Michaud, 1828)**	Serre's pelican-foot
Chordata	Actinopteri	Aulopiformes	Paralepididae	***Arctozenus risso*** **(Bonaparte, 1840)**	Spotted barracudina
Chordata	Actinopteri	Argentiniformes	Argentinidae	***Argentina sphyraena*** **Linnaeus, 1758**	Lesser silver smelt
Chordata	Actinopteri	Stomiiformes	Sternoptychidae	***Argyropelecus hemigymnus*** **Cocco, 1829**	Hatchet fish
Arthropoda	Malacostraca	Decapoda	Aristeidae	***Aristeus antennatus*** **(Risso, 1816)**	Blue and red shrimp
Chordata	Actinopteri	Pleuronectiformes	Bothidae	***Arnoglossus imperialis*** **(Rafinesque, 1810)**	Imperial scaldfish
Chordata	Actinopteri	Pleuronectiformes	Bothidae	***Arnoglossus laterna*** **(Walbaum, 1792)**	Scald fish
Chordata	Actinopteri	Pleuronectiformes	Bothidae	***Arnoglossus rueppelii*** **(Cocco, 1844)**	Rüppell's scaldback
Chordata	Actinopteri	Pleuronectiformes	Bothidae	***Arnoglossus thori*** **Kyle, 1913**	Spotted scaldfish
Echinodermata	Ophiuroidea	Euryalida	Asteronychidae	***Asteronyx loveni*** **Müller & Troschel, 1842**	Pipe-cleaner brittlestar

Table Supp. 1. (cont.)

Echinodermata	Asteroidea	Paxillosida	Astropectinidae	***Astropecten irregularis* (Pennant, 1777)**	Sand star
Mollusca	Cephalopoda	Octopoda	Octopodidae	***Bathypolypus sponsalis* (P. Fischer & H. Fischer, 1892)**	Globose octopus
Chordata	Actinopteri	Pleuronectiformes	Soleidae	***Bathysolea profundicola* (Vaillant, 1888)**	Deepwater sole
Chordata	Actinopteri	Myctophiformes	Myctophidae	***Benthosema glaciale* (Reinhardt, 1837)**	Glacier lantern fish
Chordata	Actinopteri	Blenniiformes	Blenniidae	***Blennius ocellaris* Linnaeus, 1758**	Butterfly blenny
Mollusca	Gastropoda	Neogastropoda	Muricidae	***Bolinus brandaris* (Linnaeus, 1758)**	Purple dye murex
Chordata	Actinopteri	Spariformes	Sparidae	***Boops boops* (Linnaeus, 1758)**	Bogue
Echinodermata	Echinoidea	Spatangoida	Brissidae	***Brissopsis lyrifera* (Forbes, 1841)**	Heart urchin
Cnidaria	Anthozoa	Actiniaria	Hormathiidae	***Calliactis parasitica* (Couch, 1842)**	Hermit anemone
Chordata	Actinopteri	Syngnathiformes	Callionymidae	***Callionymus lyra* Linnaeus, 1758**	Common dragonet
Chordata	Actinopteri	Syngnathiformes	Callionymidae	***Callionymus maculatus* Rafinesque, 1810**	Spotted dragonet
Mollusca	Gastropoda	Trochida	Calliostomatidae	***Calliostoma granulatum* (Born, 1778)**	Shining top-shell
Arthropoda	Malacostraca	Decapoda	Axiidae	***Calocaris macandreae* Bell, 1846**	
Chordata	Actinopteri	Caproiformes	Caproidae	***Capros aper* (Linnaeus, 1758)**	Boar fish
Chordata	Actinopteri	Ophidiiformes	Carapidae	***Carapus acus* (Brünnich, 1768)**	Pearl fish
Chordata	Actinopteri	Ophidiiformes	Bythitidae	***Cataetyx alleni* (Byrne, 1906)**	
Chordata	Actinopteri	Spariformes	Centracanthidae	***Centracanthus cirrus* Rafinesque, 1810**	Curled picarel
Chordata	Actinopteri	Priacanthiformes	Cepolidae	***Cepola macrophthalma* (Linnaeus, 1758)**	Red bandfish
Chordata	Actinopteri	Myctophiformes	Myctophidae	***Ceratoscopelus maderensis* (Lowe, 1839)**	Horned lantern fish
Mollusca	Gastropoda	Littorinimorpha	Ranellidae	***Charonia lampas* (Linnaeus, 1758)**	Trumpet shell
Chordata	Actinopteri	Stomiiformes	Stomiidae	***Chauliodus sloani* Bloch & Schneider, 1801**	Sloan's viperfish
Chordata	Actinopteri	Perciformes	Triglidae	***Chelidonichthys cuculus* (Linnaeus, 1758)**	Red gurnard
Chordata	Actinopteri	Perciformes	Triglidae	***Chelidonichthys lastoviza* (Bonnaterre, 1788)**	Streaked gurnard
Chordata	Actinopteri	Perciformes	Triglidae	***Chelidonichthys lucerna* (Linnaeus, 1758)**	Tub gurnard
Chordata	Actinopteri	Perciformes	Triglidae	***Chelidonichthys obscurus* (Walbaum, 1792)**	Long-finned gurnard
Chordata	Actinopteri	Mugiliformes	Mugilidae	***Chelon auratus* (Risso, 1810)**	Golden grey mullet
Chordata	Actinopteri	Mugiliformes	Mugilidae	***Chelon ramada* (Risso, 1827)**	Thinlip mullet

Table Supp. 1. (cont.)

Chordata	Chondrichthyes	Chimaeriformes	Chimaeridae	**_Chimaera monstrosa_ Linnaeus, 1758**	Rabbit fish
Chordata	Actinopteri	Aulopiformes	Chlorophthalmidae	**_Chlorophthalmus agassizi_ Bonaparte, 1840**	Shortnose greeneye
Arthropoda	Malacostraca	Decapoda	Pandalidae	**_Chlorotocus crassicornis_ (Costa, 1871)**	Green shrimp
Chordata	Actinopteri	Pleuronectiformes	Citharidae	**_Citharus linguatula_ (Linnaeus, 1758)**	Spotted flounder
Chordata	Actinopteri	Gadiformes	Macrouridae	**_Coelorinchus caelorhincus_ (Risso, 1810)**	Hollow-nosed rattail
Chordata	Actinopteri	Anguilliformes	Congridae	**_Conger conger_ (Linnaeus, 1758)**	European conger eel
Chordata	Ascidiacea	Phlebobranchia	Corellidae	**_Corella parallelogramma_ (Müller, 1776)**	Gas mantle ascidian
Chordata	Actinopteri	Gobiiformes	Gobiidae	**_Crystallogobius linearis_ (Düben, 1845)**	Cristal goby
Chordata	Chondrichthyes	Squaliformes	Dalatiidae	**_Dalatias licha_ (Bonnaterre, 1788)**	Darkie charlie
Arthropoda	Malacostraca	Decapoda	Diogenidae	**_Dardanus arrosor_ (Herbst, 1796)**	Striated hermit crab
Chordata	Actinopteri	Gobiiformes	Gobiidae	**_Deltentosteus quadrimaculatus_ (Valenciennes, 1837)**	Toothed goby
Arthropoda	Malacostraca	Decapoda	Sergestidae	**_Deosergestes henseni_ (Ortmann, 1893)**	
Chordata	Actinopteri	Perciformes	Moronidae	**_Dicentrarchus labrax_ (Linnaeus, 1758)**	European seabass
Chordata	Actinopteri	Spariformes	Sparidae	**_Diplodus annularis_ (Linnaeus, 1758)**	Annular sea bream
Chordata	Actinopteri	Spariformes	Sparidae	**_Diplodus vulgaris_ (Geoffroy Saint-Hilaire, 1817)**	Common two-banded sb
Chordata	Chondrichthyes	Rajiformes	Rajidae	**_Dipturus oxyrinchus_ (Linnaeus, 1758)**	Longnosed skate
Chordata	Actinopteri	Anguilliformes	Ophichthidae	**_Echelus myrus_ (Linnaeus, 1758)**	Painted eel
Mollusca	Cephalopoda	Octopoda	Octopodidae	**_Eledone cirrhosa_ (Lamarck, 1798)**	Horned octopus
Mollusca	Cephalopoda	Octopoda	Octopodidae	**_Eledone moschata_ (Lamarck, 1798)**	Musky octopus
Chordata	Actinopteri	Clupeiformes	Engraulidae	**_Engraulis encrasicolus_ (Linnaeus, 1758)**	European anchovy
Chordata	Actinopteri	Pempheriformes	Epigonidae	**_Epigonus denticulatus_ Dieuzeide, 1950**	Pencil cardinal
Chordata	Actinopteri	Pempheriformes	Epigonidae	**_Epigonus telescopus_ (Risso, 1810)**	Black cardinal fish
Chordata	Chondrichthyes	Squaliformes	Etmopteridae	**_Etmopterus spinax_ (Linnaeus, 1758)**	Velvet belly
Arthropoda	Malacostraca	Decapoda	Sergestidae	**_Eusergestes arcticus_ (Krøyer, 1855)**	Arctic red prawn
Mollusca	Gastropoda	Littorinimorpha	Naticidae	**_Euspira fusca_ (Blainville, 1825)**	Brown moon-shell
Chordata	Actinopteri	Perciformes	Triglidae	**_Eutrigla gurnardus_ (Linnaeus, 1758)**	Grey gurnard

Table Supp. 1. (cont.)

Cnidaria	Anthozoa	Pennatulacea	Funiculinidae	***Funiculina quadrangularis* (Pallas, 1766)**	Tall sea pen
Chordata	Actinopteri	Gadiformes	Gadidae	***Gadiculus argenteus* Guichenot, 1850**	Silvery pout
Chordata	Actinopteri	Gadiformes	Gaidropsaridae	***Gaidropsarus biscayensis* (Collett, 1890)**	Mediterranean bigeye rockling
Chordata	Actinopteri	Gadiformes	Gaidropsaridae	***Gaidropsarus macrophthalmus* (Günther, 1867)**	Rockling
Mollusca	Gastropoda	Littorinimorpha	Cassidae	***Galeodea echinophora* (Linnaeus, 1758)**	Spiny bonnet
Mollusca	Gastropoda	Littorinimorpha	Cassidae	***Galeodea rugosa* (Linnaeus, 1771)**	Rugose bonnet
Chordata	Chondrichthyes	Carcharhiniformes	Scyliorhinidae	***Galeus melastomus* Rafinesque, 1810**	Blackmouthed dogfish
Arthropoda	Malacostraca	Decapoda	Benthesicymidae	***Gennadas elegans* (Smith, 1882)**	Shrimp
Arthropoda	Malacostraca	Decapoda	Geryonidae	***Geryon longipes* A. Milne-Edwards, 1882**	Mediterranean geryon
Chordata	Actinopteri	Argentiniformes	Argentinidae	***Glossanodon leioglossus* (Valenciennes, 1848)**	Greater silver smelt
Arthropoda	Malacostraca	Lophogastrida	Lophogastridae	***Gnathophausia zoea* Willemoës-Suhm, 1873**	Mysid
Chordata	Actinopteri	Gobiiformes	Gobiidae	***Gobius niger* Linnaeus, 1758**	Black goby
Arthropoda	Malacostraca	Decapoda	Goneplacidae	***Goneplax rhomboides* (Linnaeus, 1758)**	Square crab
Echinodermata	Echinoidea	Echinoida	Echinidae	***Gracilechinus acutus* (Lamarck, 1816)**	White sea urchin
Chordata	Actinopteri	Perciformes	Sebastidae	***Helicolenus dactylopterus* (Delaroche, 1809)**	Blue-mouth redfish
Mollusca	Cephalopoda	Teuthida	Histioteuthidae	***Histioteuthis reversa* (Verrill, 1880)**	Reverse fewell squid
Chordata	Actinopteri	Trachichthyiformes	Trachichthyidae	***Hoplostethus mediterraneus* Cuvier, 1829**	Pink
Chordata	Actinopteri	Myctophiformes	Myctophidae	***Hygophum benoiti* (Cocco, 1838)**	Benoit's lantern fish
Chordata	Actinopteri	Gadiformes	Macrouridae	***Hymenocephalus italicus* Giglioli, 1884**	Italian grenader
Mollusca	Cephalopoda	Teuthida	Ommastrephidae	***Illex coindetii* (Vérany, 1839)**	Broadtail squid
Arthropoda	Malacostraca	Decapoda	Inachidae	***Inachus dorsettensis* (Pennant, 1777)**	Longlegged spider cr
Chordata	Actinopteri	Labriformes	Labridae	***Labrus mixtus* Linnaeus, 1758**	Cuckoo wrasse
Chordata	Actinopteri	Myctophiformes	Myctophidae	***Lampanyctus crocodilus* (Risso, 1810)**	Lantern fish
Chordata	Actinopteri	Scombriformes	Trichiuridae	***Lepidopus caudatus (Euphrasen, 1788)***	Cutlass fish
Chordata	Actinopteri	Pleuronectiformes	Scophthalmidae	***Lepidorhombus boscii (Risso, 1810)***	Megrim
Chordata	Actinopteri	Pleuronectiformes	Scophthalmidae	***Lepidorhombus whiffiagonis* (Walbaum, 1792)**	Megrim

Table Supp. 1. (cont.)

Chordata	Actinopteri	Perciformes	Triglidae	**_Lepidotrigla cavillone_ (Lacepède, 1801)**	Large-scaled gurnard
Chordata	Actinopteri	Perciformes	Triglidae	**_Lepidotrigla dieuzeidei_ Blanc & Hureau, 1973**	Spiny gurnard
Echinodermata	Crinoidea	Comatulida	Antedonidae	**_Leptometra celtica_ (M'Andrew & Barrett, 1858)**	
Echinodermata	Crinoidea	Comatulida	Antedonidae	**_Leptometra phalangium_ (Müller, 1841)**	
Chordata	Actinopteri	Gobiiformes	Gobiidae	**_Lesueurigobius friesii_ (Malm, 1874)**	Frie's goby
Chordata	Actinopteri	Gobiiformes	Gobiidae	**_Lesueurigobius sanzi_ (de Buen, 1918)**	Sanzo's goby
Chordata	Actinopteri	Gobiiformes	Gobiidae	**_Lesueurigobius suerii_ (Risso, 1810)**	Lesueur's goby
Chordata	Chondrichthyes	Rajiformes	Rajidae	**_Leucoraja naevus_ (Müller & Henle, 1841)**	Cuckoo ray
Arthropoda	Malacostraca	Decapoda	Polybiidae	**_Liocarcinus depurator_ (Linnaeus, 1758)**	Blue-leg swimcrab
Chordata	Actinopteri	Myctophiformes	Myctophidae	**_Lobianchia dofleini_ (Zugmayer, 1911)**	Dofleini's lantern fish
Mollusca	Cephalopoda	Teuthida	Loliginidae	**_Loligo forbesii_ Steenstrup, 1856**	Veined squid
Mollusca	Cephalopoda	Teuthida	Loliginidae	**_Loligo vulgaris_ Lamarck, 1798**	European squid
Chordata	Actinopteri	Lophiiformes	Lophiidae	**_Lophius budegassa_ Spinola, 1807**	White angler fish
Chordata	Actinopteri	Lophiiformes	Lophiidae	**_Lophius piscatorius_ Linnaeus, 1758**	Angler fish
Echinodermata	Asteroidea	Paxillosida	Luidiidae	**_Luidia ciliaris_ (Philippi, 1837)**	Seven-armed starfish
Arthropoda	Malacostraca	Decapoda	Portunidae	**_Macropipus tuberculatus_ (Roux, 1830)**	Knobby swimcrab
Arthropoda	Malacostraca	Decapoda	Inachidae	**_Macropodia tenuirostris_ (Leach, 1814)**	Slender spider crab
Chordata	Actinopteri	Syngnathiformes	Centriscidae	**_Macroramphosus scolopax_ (Linnaeus, 1758)**	Snipe-fish
Chordata	Actinopteri	Gadiformes	Macrouridae	**_Malacocephalus laevis_ (Lowe, 1843)**	Soft-headed rattail
Echinodermata	Asteroidea	Forcipulatida	Asteriidae	**_Marthasterias glacialis_ (Linnaeus, 1758)**	Common starfish
Chordata	Actinopteri	Stomiiformes	Sternoptychidae	**_Maurolicus muelleri_ (Gmelin, 1789)**	Pearlside
Arthropoda	Malacostraca	Decapoda	Dorippidae	**_Medorippe lanata_ (Linnaeus, 1767)**	Demon-faced porter crab
Arthropoda	Malacostraca	Euphausiacea	Euphausiidae	**_Meganyctiphanes norvegica_ (M. Sars, 1857)**	Norwegian krill
Chordata	Actinopteri	Gadiformes	Merlucciidae	**_Merluccius merluccius_ (Linnaeus, 1758)**	European hake
Chordata	Actinopteri	Pleuronectiformes	Soleidae	**_Microchirus ocellatus_ (Linnaeus, 1758)**	Foureyed sole
Chordata	Actinopteri	Pleuronectiformes	Soleidae	**_Microchirus variegatus_ (Donovan, 1808)**	Thickback sole

Table Supp. 1. (cont.)

Chordata	Actinopteri	Gadiformes	Gadidae	***Micromesistius poutassou*** **(Risso, 1827)**	Blue whiting
Chordata	Actinopteri	Tetraodontiformes	Molidae	***Mola mola*** **(Linnaeus, 1758)**	Ocean sunfish
Chordata	Actinopteri	Gadiformes	Lotidae	***Molva dypterygia*** **(Pennant, 1784)**	Blue ling
Chordata	Actinopteri	Gadiformes	Lotidae	***Molva macrophthalma*** **(Rafinesque, 1810)**	Spanish ling
Arthropoda	Malacostraca	Decapoda	Xanthidae	***Monodaeus couchii*** **(Couch, 1851)**	True crab
Chordata	Actinopteri	Syngnathiformes	Mullidae	***Mullus barbatus*** **Linnaeus, 1758**	Red mullet
Chordata	Actinopteri	Syngnathiformes	Mullidae	***Mullus surmuletus*** **Linnaeus, 1758**	Surmullet
Arthropoda	Malacostraca	Decapoda	Munididae	***Munida intermedia*** **A. Milne-Edwards & Bouvier, 1899**	Squat lobster
Arthropoda	Malacostraca	Decapoda	Munididae	***Munida speciosa*** **von Martens, 1878**	
Arthropoda	Malacostraca	Decapoda	Munididae	***Munida tenuimana*** **Sars, 1872**	Narrow-legged squat lobster
Chordata	Chondrichthyes	Carcharhiniformes	Triakidae	***Mustelus mustelus*** **(Linnaeus, 1758)**	Smoothhound
Chordata	Actinopteri	Myctophiformes	Myctophidae	***Myctophum punctatum*** **Rafinesque, 1810**	Spotted lanternfish
Arthropoda	Malacostraca	Isopoda	Cirolanidae	***Natatolana borealis*** **(Lilljeborg, 1851)**	
Arthropoda	Malacostraca	Decapoda	Nephropidae	***Nephrops norvegicus*** **(Linnaeus, 1758)**	Norway lobster
Mollusca	Gastropoda	Neogastropoda	Buccinidae	***Neptunea contraria*** **(Linnaeus, 1771)**	Left-handed neptune whelk
Chordata	Actinopteri	Anguilliformes	Nettastomatidae	***Nettastoma melanura*** **Rafinesque, 1810**	Blackfin sorcerer
Chordata	Actinopteri	Gadiformes	Macrouridae	***Nezumia aequalis*** **(Günther, 1878)**	Smooth rattail
Chordata	Actinopteri	Notacanthiformes	Notacanthidae	***Notacanthus bonaparte*** **Risso, 1840**	Bonapart's spiny eel
Chordata	Actinopteri	Myctophiformes	Myctophidae	***Notoscopelus elongatus*** **(Costa, 1844)**	Lanternfish
Echinodermata	Asteroidea	Valvatida	Goniasteridae	***Nymphaster arenatus*** **(Perrier, 1881)**	
Mollusca	Cephalopoda	Octopoda	Octopodidae	***Octopus salutii*** **Vérany, 1836**	Spider octopus
Mollusca	Cephalopoda	Octopoda	Octopodidae	***Octopus vulgaris*** **Cuvier, 1797**	Common octopus
Chordata	Actinopteri	Anguilliformes	Ophichthidae	***Ophichthus rufus*** **(Rafinesque, 1810)**	Rufus snake-eel
Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	***Ophiothrix fragilis*** **(Abildgaard in O.F. Müller, 1789)**	Spiny brittle-star
Echinodermata	Ophiuroidea	Ophiurida	Ophiuridae	***Ophiura ophiura*** **(Linnaeus, 1758)**	Serpent star
Chordata	Actinopteri	Spariformes	Sparidae	***Pagellus acarne*** **(Risso, 1827)**	Auxillary seabream
Chordata	Actinopteri	Spariformes	Sparidae	***Pagellus bogaraveo*** **(Brünnich, 1768)**	Red sea-bream

Table Supp. 1. (cont.)

Chordata	Actinopteri	Spariformes	Sparidae	***Pagellus erythrinus* (Linnaeus, 1758)**	Pandora
Chordata	Actinopteri	Spariformes	Sparidae	***Pagrus pagrus* (Linnaeus, 1758)**	Redtail porgy
Arthropoda	Malacostraca	Decapoda	Paguridae	***Pagurus alatus* Fabricius, 1775**	Smooth flounder
Arthropoda	Malacostraca	Decapoda	Paguridae	***Pagurus cuanensis* Bell, 1845**	Hairy hermit crab
Arthropoda	Malacostraca	Decapoda	Paguridae	***Pagurus excavatus* (Herbst, 1791)**	Hermit crab
Arthropoda	Malacostraca	Decapoda	Paguridae	***Pagurus prideaux* Leach, 1815**	Deeper hermit crab
Arthropoda	Malacostraca	Decapoda	Penaeidae	***Parapenaeus longirostris* (Lucas, 1846)**	Deep water pink shri
Echinodermata	Holothuroidea	Aspidochirotida	Stichopodidae	***Parastichopus regalis* (Cuvier, 1817)**	Gilding sea cucumber
Arthropoda	Malacostraca	Decapoda	Pasiphaeidae	***Pasiphaea multidentata* Esmark, 1866**	Pink glass shrimp
Arthropoda	Malacostraca	Decapoda	Pasiphaeidae	***Pasiphaea sivado* (Risso, 1816)**	White glass shrimp
Cnidaria	Scyphozoa	Semaeostomeae	Pelagiidae	***Pelagia noctiluca* (Forsskål, 1775)**	Purple-striped jelly
Chordata	Actinopteri	Perciformes	Peristediidae	***Peristedion cataphractum* (Linnaeus, 1758)**	African armoured searobin
Arthropoda	Malacostraca	Decapoda	Crangonidae	***Philocheras echinulatus* (Sars, 1861)**	
Chordata	Actinopteri	Gadiformes	Phycidae	***Phycis blennoides* (Brünnich, 1768)**	Beard
Arthropoda	Malacostraca	Decapoda	Pilumnidae	***Pilumnus spinifer* H. Milne Edwards, 1834**	Red hairy crab
Arthropoda	Malacostraca	Decapoda	Pandalidae	***Plesionika acanthonotus* (Smith, 1882)**	Lesser striped shrimp
Arthropoda	Malacostraca	Decapoda	Pandalidae	***Plesionika gigliolii* (Senna, 1902)**	Italian deepsea shrimp
Arthropoda	Malacostraca	Decapoda	Pandalidae	***Plesionika heterocarpus* (Costa, 1871)**	Arrow shrimp
Arthropoda	Malacostraca	Decapoda	Pandalidae	***Plesionika martia* (A. Milne-Edwards, 1883)**	Golden shrimp
Arthropoda	Malacostraca	Decapoda	Pandalidae	***Plesionika narval* (Fabricius, 1787)**	Narwal shrimp
Arthropoda	Malacostraca	Decapoda	Polybiidae	***Polybius henslowii* Leach, 1820**	Nipper crab
Arthropoda	Malacostraca	Decapoda	Polychelidae	***Polycheles typhlops* Heller, 1862**	Blind lobster
Chordata	Actinopteri	Scombriformes	Pomatomidae	***Pomatomus saltatrix* (Linnaeus, 1766)**	Bluefish
Chordata	Actinopteri	Gobiiformes	Gobiidae	***Pomatoschistus marmoratus* (Risso, 1810)**	Marbled goby
Chordata	Actinopteri	Gobiiformes	Gobiidae	***Pomatoschistus minutus* (Pallas, 1770)**	Sand goby
Chordata	Actinopteri	Gobiiformes	Gobiidae	***Pomatoschistus pictus* (Malm, 1865)**	Painted goby
Arthropoda	Malacostraca	Decapoda	Crangonidae	***Pontophilus spinosus* (Leach, 1815)**	Spiny shrimp

Table Supp. 1. (cont.)

Arthropoda	Malacostraca	Decapoda	Processidae	***Processa canaliculata*** **Leach, 1815**	Processa shrimp
Arthropoda	Malacostraca	Decapoda	Processidae	***Processa nouveli*** **Al-Adhub & Williamson, 1975**	
Mollusca	Bivalvia	Pterioida	Pteriidae	***Pteria hirundo*** **(Linnaeus, 1758)**	European wing oyster
Mollusca	Cephalopoda	Octopoda	Octopodidae	***Pteroctopus tetracirrhus*** **(Delle Chiaje, 1830)**	Fourhorn octopus
Chordata	Chondrichthyes	Rajiformes	Rajidae	***Raja asterias*** **Delaroche, 1809**	Starry ray
Chordata	Chondrichthyes	Rajiformes	Rajidae	***Raja clavata*** **Linnaeus, 1758**	Thornback ray (Roker)
Chordata	Chondrichthyes	Rajiformes	Rajidae	***Raja miraletus*** **Linnaeus, 1758**	Brown ray
Chordata	Chondrichthyes	Rajiformes	Rajidae	***Raja montagui*** **Fowler, 1910**	Spotted ray
Chordata	Chondrichthyes	Rajiformes	Rajidae	***Raja polystigma*** **Regan, 1923**	Speckled ray
Mollusca	Gastropoda	Littorinimorpha	Ranellidae	***Ranella olearium*** **(Linnaeus, 1758)**	Horse conch
Mollusca	Cephalopoda	Sepiolida	Sepiolidae	***Rondeletiola minor*** **(Naef, 1912)**	Lentil bobtail
Mollusca	Cephalopoda	Sepiolida	Sepiolidae	***Rossia macrosoma*** **(Delle Chiaje, 1830)**	Stout bobtail
Chordata	Actinopteri	Clupeiformes	Clupeidae	***Sardina pilchardus*** **(Walbaum, 1792)**	Pilchard
Chordata	Actinopteri	Clupeiformes	Clupeidae	***Sardinella aurita*** **Valenciennes, 1847**	Round sardinella
Mollusca	Cephalopoda	Octopoda	Octopodidae	***Scaeurgus unicirrhus*** **(Delle Chiaje [in Férussac & d'Orbigny], 1841)**	Unihorn octopus
Arthropoda	Hexanauplia	Pedunculata	Scalpellidae	***Scalpellum scalpellum*** **Linnaeus, 1767**	
Mollusca	Gastropoda	Cephalaspidea	Scaphandridae	***Scaphander lignarius*** **(Linnaeus, 1758)**	Woody canoe-bubble
Chordata	Actinopteri	Scombriformes	Scombridae	***Scomber colias*** **Gmelin, 1789**	Spanish mackerel
Chordata	Actinopteri	Scombriformes	Scombridae	***Scomber japonicus*** **Houttuyn, 1782**	Chub mackerel
Chordata	Actinopteri	Scombriformes	Scombridae	***Scomber scombrus*** **Linnaeus, 1758**	Mackerel
Chordata	Actinopteri	Pleuronectiformes	Scophthalmidae	***Scophthalmus rhombus*** **(Linnaeus, 1758)**	Brill
Chordata	Actinopteri	Perciformes	Scorpaenidae	***Scorpaena elongata*** **Cadenat, 1943**	Slender rockfish
Chordata	Actinopteri	Perciformes	Scorpaenidae	***Scorpaena notata*** **Rafinesque, 1810**	Small red scorpionfi
Chordata	Actinopteri	Perciformes	Scorpaenidae	***Scorpaena porcus*** **Linnaeus, 1758**	Black scorpionfish
Chordata	Actinopteri	Perciformes	Scorpaenidae	***Scorpaena scrofa*** **Linnaeus, 1758**	Red scorpionfish
Chordata	Chondrichthyes	Carcharhiniformes	Scyliorhinidae	***Scyliorhinus canicula*** **(Linnaeus, 1758)**	Lesser spotted dogfi
Chordata	Chondrichthyes	Carcharhiniformes	Scyliorhinidae	***Scyliorhinus stellaris*** **(Linnaeus, 1758)**	Nurse hound
Mollusca	Cephalopoda	Sepiida	Sepiidae	***Sepia elegans*** **Blainville, 1827**	Elegant cuttlefish

Table Supp. 1. (cont.)

Mollusca	Cephalopoda	Sepiida	Sepiidae	***Sepia officinalis* Linnaeus, 1758**	Common cuttlefish
Mollusca	Cephalopoda	Sepiida	Sepiidae	***Sepia orbignyana* Férussac, 1826**	Pink cuttlefish
Mollusca	Cephalopoda	Sepiolida	Sepiolidae	***Sepietta oweniana* (d'Orbigny, 1841)**	Common bobtail
Arthropoda	Malacostraca	Decapoda	Sergestidae	***Sergia robusta* (Smith, 1882)**	Strong prawn
Chordata	Actinopteri	Perciformes	Serranidae	***Serranus cabrilla* (Linnaeus, 1758)**	Comber
Chordata	Actinopteri	Perciformes	Serranidae	***Serranus hepatus* (Linnaeus, 1758)**	Brown comber
Chordata	Actinopteri	Pleuronectiformes	Soleidae	***Solea solea* (Linnaeus, 1758)**	Sole (Dover sole)
Arthropoda	Malacostraca	Decapoda	Solenoceridae	***Solenocera membranacea* (Risso, 1816)**	Atlantic mud shrimp
Echinodermata	Echinoidea	Spatangoida	Spatangidae	***Spatangus purpureus* O.F. Müller, 1776**	Purple heart urchin
Chordata	Actinopteri	Spariformes	Centracanthidae	***Spicara maena* (Linnaeus, 1758)**	Blotched picarel
Chordata	Actinopteri	Spariformes	Centracanthidae	***Spicara smaris* (Linnaeus, 1758)**	Picarel
Chordata	Actinopteri	Spariformes	Sparidae	***Spondyliosoma cantharus* (Linnaeus, 1758)**	Black seabream
Chordata	Actinopteri	Clupeiformes	Clupeidae	***Sprattus sprattus* (Linnaeus, 1758)**	Sprat
Arthropoda	Malacostraca	Stomatopoda	Squillidae	***Squilla mantis* (Linnaeus,1758)**	Mantis shrimp
Chordata	Actinopteri	Stomiiformes	Stomiidae	***Stomias boa* (Risso, 1810)**	Boa dragonfish
Chordata	Actinopteri	Pleuronectiformes	Cynoglossidae	***Symphurus ligulatus* (Cocco, 1844)**	Elongate tonguesole
Chordata	Actinopteri	Pleuronectiformes	Cynoglossidae	***Symphurus nigrescens* Rafinesque, 1810**	Tonguesole
Chordata	Actinopteri	Syngnathiformes	Callionymidae	***Synchiropus phaeton* (Günther, 1861)**	Phaeton dragonet
Chordata	Actinopteri	Syngnathiformes	Syngnathidae	***Syngnathus acus* Linnaeus, 1758**	Great pipefish
Echinodermata	Asteroidea	Paxillosida	Astropectinidae	***Tethyaster subinermis* (Philippi, 1837)**	
Chordata	Chondrichthyes	Torpediniformes	Torpedinidae	***Tetronarce nobiliana* (Bonaparte, 1835)**	Electric ray
Mollusca	Cephalopoda	Teuthida	Ommastrephidae	***Todarodes sagittatus* (Lamarck, 1798)**	European flying squid
Mollusca	Cephalopoda	Teuthida	Ommastrephidae	***Todaropsis eblanae* (Ball, 1841)**	Lesser flying squid
Chordata	Chondrichthyes	Torpediniformes	Torpedinidae	***Torpedo marmorata* Risso, 1810**	Marbled electric ray
Chordata	Actinopteri	Perciformes	Trachinidae	***Trachinus draco* Linnaeus, 1758**	Greater weever fish
Chordata	Actinopteri	Carangiformes	Carangidae	***Trachurus mediterraneus* (Steindachner, 1868)**	Mediterranean scad
Chordata	Actinopteri	Carangiformes	Carangidae	***Trachurus picturatus* (Bowdich, 1825)**	Blue jack mackerel

Table Supp. 1. (cont.)

Chordata	Actinopteri	Carangiformes	Carangidae	***Trachurus trachurus*** **(Linnaeus, 1758)**	Horse mackerel
Chordata	Actinopteri	Gadiformes	Macrouridae	***Trachyrincus scabrus*** **(Rafinesque, 1810)**	Roughnosed rattail
Chordata	Actinopteri	Perciformes	Triglidae	***Trigla lyra*** **Linnaeus, 1758**	Piper
Chordata	Actinopteri	Gadiformes	Gadidae	***Trisopterus luscus*** **(Linnaeus, 1758)**	Whiting pout
Chordata	Actinopteri	Gadiformes	Gadidae	***Trisopterus minutus*** **(Linnaeus, 1758)**	Poor cod
Chordata	Actinopteri	Uranoscopiformes	Uranoscopidae	***Uranoscopus scaber*** **Linnaeus, 1758**	Stargazer
Chordata	Actinopteri	Alepocephaliformes	Alepocephalidae	***Xenodermichthys copei*** **(Gill, 1884)**	Bluntsnout smooth-he
Chordata	Actinopteri	Zeiformes	Zeidae	***Zeus faber*** **Linnaeus, 1758**	John dory

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