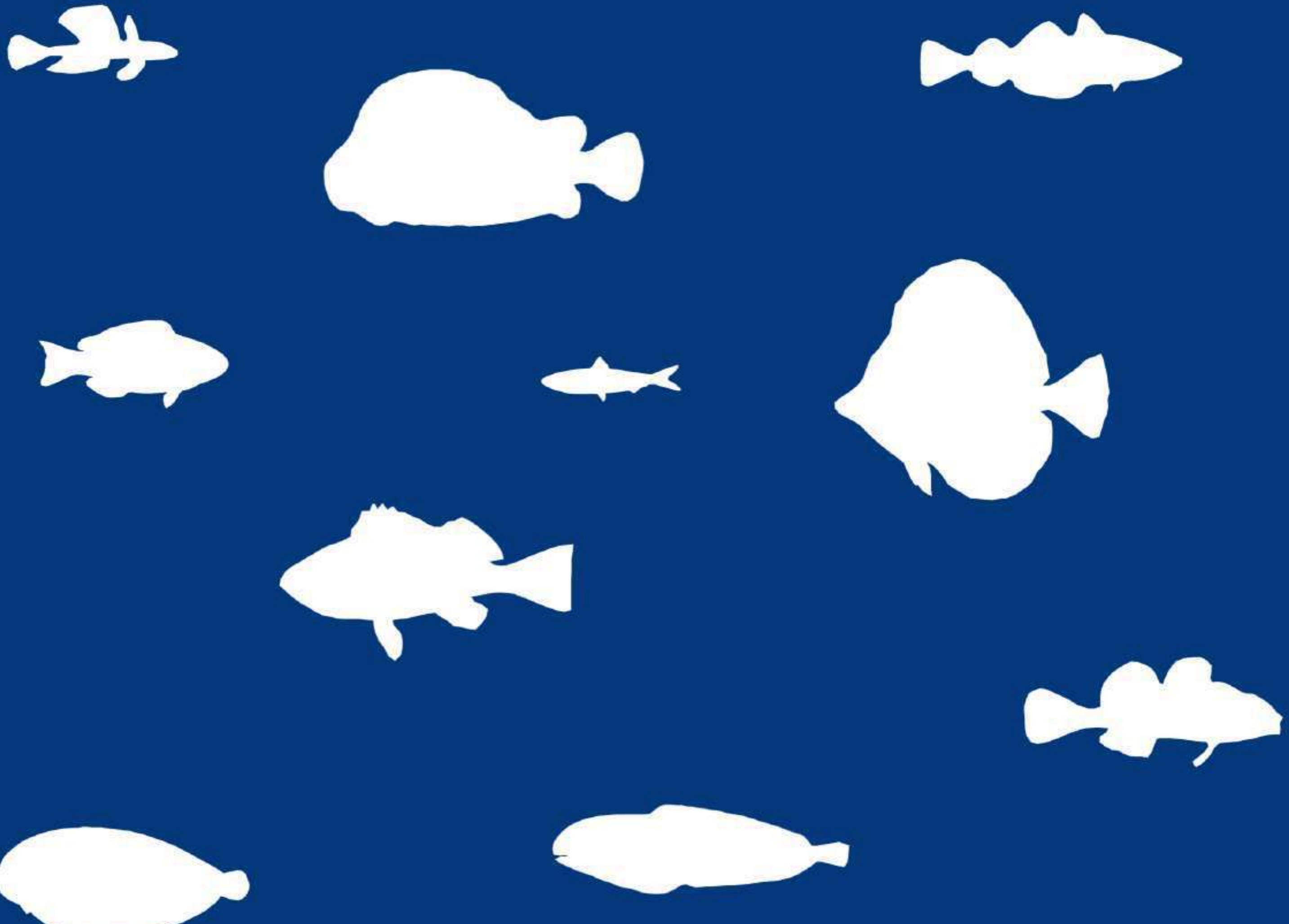
The multiple dimensions of fish diversity dynamics and community stability



Romain Frelat

The multiple dimensions of fish diversity dynamics and community stability

DISSERTATION

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Romain Frelat

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Examination committee:

Prof. Dr. Christian Möllmann (supervisor and examiner)
University of Hamburg
Institute of Marine Ecosystem and Fishery Science

Dr. Manuel Hidalgo (examiner)
Senior scientist at the Instituto Español de Oceanografia
Palma de Mallorca, Spain

Prof. Dr. Kai Jensen (chair)
Universität Hamburg
Institute of Plant Science and Microbiology

Dr. Martin Lindegren
Senior scientist at Technical University of Denmark, National Institute of Aquatic Resources
Lyngby, Denmark

Prof. PhD. Myron Peck
University of Hamburg
Institute of Marine Ecosystem and Fishery Science

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Summary

A decrease in global biodiversity has been recently recorded and is attributed to human activities, mainly caused by predation, modification of natural habitats and climate change. Biological diversity, defined as the variability among living organisms, is known to have a positive effect on productivity and stability of ecosystems. The loss of biodiversity can have a cascading effect and lead to drastic changes in the dynamics and functioning of ecosystems, and subsequently to the services they provide to humans. In marine ecosystems, fish are extremely valuable as a source of protein for more than 3 billion people, and a source of income for more than 40 million people. Yet, fish communities are threatened by high fishing pressure and fast changing habitat conditions. Using a collection of fisheries-independent bottom-trawl surveys and advanced statistical analysis, this thesis aims to understand the importance of biodiversity for the resilience of marine fish populations to climate change and fisheries exploitation. More specifically, this complex issue has been divided into three interconnected sub-questions: (i) how to characterize the spatio-temporal dynamics of fish assemblages and identify their external drivers? (ii) how does fish functional diversity respond to changing external pressures? and (iii) what is the importance of biodiversity for the stability of ecosystems?

This dissertation combines case studies demonstrating the benefits of using novel approaches to look at existing datasets and integrating information from multiple sources. Each chapter studies different aspects of the complexity of biodiversity dynamics. For instance, the interaction between spatial and temporal dynamics of fish communities was investigated using multiway multivariate analysis (chapters 2 and 3). Three-matrix multivariate approaches can integrate information about functional traits and disentangle the relation between traits and environmental changes (chapters 3, 4). Additionally, new morphological traits were derived from outline analysis and linked to environmental processes (chapter 5). Finally, the relationship between diversity and stability of communities was explored by combining abundance time series with ecological network analysis (chapter 6) and by considering the intra-specific trait variability (chapter 7). None of these approaches are better than another, but together they highlight the multiple dimensions of fish diversity dynamics and community stability.

A better understanding of the complexity and the multidimensionality of diversity is a first step toward an integrative ecosystem assessment. For example, understanding the link between traits and environment (chapters 3 and 4) is important to understand and predict the impact of changing environmental conditions on the functional diversity of communities. However, these predictions would be incomplete if one fails to consider the network of interactions between species and the possible cascading effects throughout the food web (chapter 6). Additionally, the intra-specific trait variability (chapter 7) might enhance the adaptation of communities to changing conditions. Combining these different approaches into a common framework can provide key information for the management and conservation of ecosystems, as well as relevant advices for marine ecosystem-based management.

Embracing the complexity of ecosystem dynamics is recognizing our limited scientific knowledge and the high unpredictability of community dynamics. Therefore, the safest and the most recommendable management option is the precautionary approach. It is urgent that society as a whole take actions to preserve biodiversity, in all its dimensions, which is the best management strategy to help biotic communities adapt to ongoing and future changes.

Zusammenfassung

Kürzlich wurde ein Rückgang der globalen Biodiversität verzeichnet, der auf Aktivitäten des Menschen wie Prädation, Modifikation natürlicher Lebensräume und den Klimawandel zurückzuführen ist. Die biologische Vielfalt, definiert als die Variabilität lebender Organismen, wirkt sich bekanntermaßen positiv auf die Produktivität und Stabilität von Ökosystemen aus. Eine Abnahme von Biodiversität kann kaskadenartig wirken und zu drastischen Veränderungen in der Dynamik und Funktionsweise von Ökosystemen führen, sowie zu Veränderungen in Ökosystem-Dienstleistungen, die sie für den Menschen bereitstellen. In marinen Ökosystemen sind Fische äußerst wertvoll, als Proteinquelle für mehr als 3 Milliarden Menschen und als Einkommensquelle für mehr als 40 Millionen Menschen. Fischgemeinschaften sind jedoch durch den hohen Fischereidruck und die sich schnell ändernden Lebensraumbedingungen bedroht. Anhand einer Sammlung von fischereiunabhängigen Untersuchungen der Grundschleppnetzfischerei und fortschrittlicher statistischer Analysen soll die Bedeutung der Biodiversität für die Widerstandsfähigkeit der Meeresfischbestände gegenüber dem Klimawandel und der Fischereibewirtschaftung verstanden werden. Im Einzelnen wurde dieses komplexe Thema in drei miteinander verbundene Unterfragen unterteilt: (i) wie lässt sich die räumlich-zeitliche Dynamik von Fischbeständen charakterisieren und deren externe Treiber identifizieren? (ii) wie reagiert die funktionale Fisch-Vielfalt auf sich ändernde äußere Einwirkungen? und (iii) welche Bedeutung hat Biodiversität für die Stabilität von Ökosystemen?

Diese Dissertation kombiniert Fallstudien, in denen die Vorteile der Verwendung neuer Ansätze zur Untersuchung vorhandener Datensätze und der Integration von Informationen aus mehreren Quellen demonstriert werden. In jedem Kapitel werden verschiedene Aspekte der Komplexität der Biodiversitätsdynamik untersucht. Zum Beispiel wurde die Wechselwirkung zwischen räumlicher und zeitlicher Dynamik von Fischgemeinschaften mithilfe einer multivariaten Mehrweg-Analyse untersucht (Kapitel 2 und 3). Multivariate Drei-Matrix-Ansätze können Informationen über funktionale Merkmale integrieren und die Beziehung zwischen Merkmalen und Umweltveränderungen aufdecken (Kapitel 3, 4). Darüber hinaus wurden neue morphologische Merkmale aus der Umrissanalyse abgeleitet und mit Umweltprozessen verknüpft (Kapitel 5). Schließlich wurde der Zusammenhang zwischen Diversität und Stabilität von Gemeinschaften untersucht, indem Abundanz-Zeitreihen mit einer ökologischen Netzwerkanalyse (Kapitel 6) kombiniert wurden und die intraspezifische Merkmalsvariabilität (Kapitel 7) betrachtet wurde. Keiner dieser Ansätze ist besser als der andere, aber gemeinsam betonen sie die vielfältigen Dimensionen der Dynamik der Fischvielfalt und der Stabilität der Gemeinschaft.

Ein besseres Verständnis der Komplexität und der Multidimensionalität von Diversität ist ein erster Schritt hin zu einer integrativen Ökosystembewertung. Das Verständnis der Verbindung zwischen Merkmalen und der Umgebung (Kapitel 3 und 4) ist wichtig, um die Auswirkungen sich ändernder Umweltbedingungen auf die funktionale Vielfalt von Gemeinschaften zu verstehen und vorherzusagen. Diese Vorhersagen wären jedoch unvollständig, wenn man das Netzwerk aus Interaktionen zwischen den Arten und die möglichen Kaskadeneffekte im gesamten Nahrungsnetz nicht berücksichtigt (Kapitel 6). Darüber hinaus kann die intraspezifische Merkmalsvariabilität (Kapitel 7) die Anpassung von Gemeinschaften an sich ändernde Bedingungen verstärken. Die Kombination dieser unterschiedlichen Ansätze in einem gemeinsamen Rahmen kann wichtige Informationen für das Management und die Erhaltung von Ökosystemen, sowie relevante Ratschläge für das Management von marinen Ökosystemen liefern.

Um die Komplexität der Ökosystemdynamik zu erfassen, müssen wir unser begrenztes wissenschaftliches Wissen und die hohe Unvorhersagbarkeit von Gemeinschaftsdynamik erkennen. Daher stellt ein vorsorglicher Ansatz die sicherste und empfehlenswerteste Managementoption dar. Es ist dringend geboten, dass die Gesellschaft als Ganzes Maßnahmen zum Erhalt der Biodiversität in all ihren Dimensionen ergreift. Dies ist die beste Managementstrategie, um Ökosysteme dabei zu unterstützen, sich an die fortlaufenden Veränderungen anzupassen.

Résumé

La perte actuelle de biodiversité dans le monde est attribuée aux activités humaines, telles que la prédation, la modification des habitats naturels et le changement climatique. La diversité biologique, définie comme la variabilité parmi les organismes vivants, a un effet positif sur la productivité et la stabilité des écosystèmes. La perte de biodiversité peut provoquer des changements radicaux dans la dynamique et le fonctionnement des écosystèmes, et ainsi affecter les services qu'ils fournissent aux Hommes. Dans les écosystèmes marins, les poissons sont une source importante de protéines pour plus de 3 milliards de personnes et une source de revenus pour plus de 40 millions de personnes. Cependant, les communautés de poissons sont menacées par la forte pression de pêche et par la modification rapide de leurs habitats. Cette thèse vise à comprendre l'importance de la biodiversité pour la résilience des populations de poissons au changement climatique et à l'effort de pêche. Plus précisément, cette question a été subdivisée en trois questions intermédiaires : (i) comment caractériser la dynamique spatio-temporelle des communautés de poissons et en identifier les causes ? (ii) comment la diversité fonctionnelle des poissons répond-elle aux changements environnementaux? et (iii) quelle est l'importance de la biodiversité pour la stabilité des écosystèmes ?

Chaque chapitre de cette thèse étudie des aspects différents des dynamiques de la biodiversité. Par exemple, l'interaction entre la dynamique spatiale et temporelle des communautés de poissons a été étudiée à l'aide d'une analyse multivariée multi-tableaux (chapitres 2 et 3). Les approches multivariées à trois matrices permettent d'intégrer les traits fonctionnels et d'indiquer la relation entre les traits et les changements environnementaux (chapitres 3, 4). De plus, une analyse de contour a été proposée pour caractériser la morphologie des poissons (chapitre 5). Enfin, le lien entre la diversité et la stabilité des communautés a été exploré en combinant des méthodes d'analyses de séries temporelles avec l'analyse de réseaux trophiques (chapitre 6) et en prenant en compte la variabilité intra-spécifique des traits (chapitre 7). Aucune de ces approches n'est meilleure que les autres mais, ensemble, elles mettent en évidence les multiples dimensions des dynamiques de la diversité des communautés de poissons et de leur stabilité.

Une meilleure compréhension de la complexité des communautés biologiques est un premier pas vers une gestion plus intégrale des écosystèmes. Par exemple, il est important de comprendre le lien entre les traits et l'environnement (chapitres 3 et 4) pour comprendre et prévoir l'impact des changements des conditions environnementales sur la diversité fonctionnelle des communautés. Cependant, ces prévisions seraient incomplètes si l'on ne tenait pas compte du réseau d'interactions entre les espèces et les possibles répercussions sur l'ensemble de la chaîne alimentaire (chapitre 6). De plus, la variabilité intra-spécifique des traits (chapitre 7) pourrait améliorer l'adaptation des communautés aux changements du milieu naturel. Combiner les résultats de ces différentes approches peut fournir des informations importantes pour la gestion et la conservation des écosystèmes marins.

Prendre en compte la complexité de la dynamique des écosystèmes, c'est reconnaître les limites des connaissances scientifiques et le caractère imprévisible des dynamiques des communautés biologiques. Par conséquent, le principe de précaution est l'option la plus recommandable pour la gestion des ressources marines. Il est urgent que la société dans son ensemble prenne des mesures pour préserver la biodiversité, dans toutes ses dimensions, ce qui est la meilleure stratégie pour aider les communautés biologiques à s'adapter aux changements de leur milieu naturel.

Chapter 1

General introduction

> "The real voyage of discovery consists not in seeking new landscapes,
> but in having new eyes."
>
> Marcel Proust

M.C. Escher, Fishes and scales (1959)
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A global decrease in biodiversity

A decrease in global biodiversity has been recently recorded (Young *et al.* 2016). The present extinction rate is comparable to the rate of the previous five mass extinction events, leading to claims that we may enter the sixth mass extinction (Barnosky *et al.* 2011; Ceballos *et al.* 2017). The **current loss of biodiversity is due to human activities**, mainly caused by predation, competition for resources, modification or fragmentation of natural habitats, spreading pathogens or non-native species, and changing global climate (Young *et al.* 2016). Due to the strong impact of human activities on ecosystems, scientists suggest that we have entered an era called “Anthropocene” (Crutzen 2002). In fact, humans have disturbed ecosystems since their origins, leading to losses of large predators and triggering strong defaunation (McCauley et al. 2015).

The negative impact of humans on ecosystems was first described over 150 years ago by George Perkins Marsh in his book *Man and Nature* (Marsh 1864). But it was only until the 1950’s, with the rise of the agricultural “Green revolution” that society started to question its role in ecosystems, and Ecology became a rising field of Science. For example, the concept of ecosystem gain prominence in mid-fifties (Odum 1953) and the multi-disciplinary field of conservation biology emerged in 1978 (Soule & Wilcox 1980). The research that followed evidenced the threats caused by the loss of biodiversity, thus, in 1992, governments and scientists met at the Earth Summit in Rio de Janeiro to create the Convention on Biological Diversity (CBD). The CBD is the first international treaty recognizing the importance of biodiversity and its conservation. Recently, the Parties of the CBD adopted the Aichi biodiversity targets for 2020, a ten-year framework to “take effective and urgent action to halt the loss of biodiversity in order to ensure that by 2020 ecosystems are resilient and continue to provide essential services, thereby securing the planet’s variety of life, and contributing to human well-being, and poverty eradication” (CBD 2010).

The **loss of biodiversity can have a cascading effect** leading to drastic changes in the dynamics and functioning of ecosystems, and subsequently to the services they provide to humans (Hooper *et al.* 2012). The relationship between biodiversity and ecosystem functioning (BEF) has been actively studied since the early 1990’s. A recent review of 25 years of BEF research based on more than 1,700 published papers concluded that i) ”there is now unequivocal evidence that biodiversity loss reduces the efficiency by which ecological communities capture biologically essential resources, produce biomass, decompose and recycle biologically essential nutrients.” and ii) “there is mounting evidence that biodiversity increases the stability of ecosystem functions through time” (Cardinale *et al.* 2012).

BEF research is mainly carried out with **theoretical models or experiments** (Tilman *et al.* 2014). Among others aspects, models have largely contributed to the debates about the impact of diversity on the stability of ecosystems (May 1971; Ives *et al.* 1999; Loreau & de Mazancourt 2013). While a simple prey-predator model extended to communities suggest the counter-intuitive idea that increase in diversity lead to a decrease in stability (May 1971), more complex models considering interaction strength and differences in environmental responses show the opposite (Ives *et al.* 1999; Loreau & de Mazancourt 2013). Whereas models are limited by their subjective assumptions, long term experiments carry out on small plots or microcosms provide a solution to test the relationship between diversity and ecosystem functioning (Tilman & Downing 1994; Gross *et al.* 2014). Metanalysis of the numerous experimental studies in terrestrial, freshwater and marine ecosystems concludes that biodiversity has a positive effect on productivity, stability and resistance to invasion (Tilman *et al.* 2014). Despite BEF experiments getting more complex (Soliveres *et al.*

2016) including multi-trophic levels (Duffy *et al.* 2007; Hillebrand *et al.* 2018b) and multiple stressors (Crain *et al.* 2008), these experiments are inherently limited to a confined area with restricted interactions. Natural ecosystems are complex systems that cannot be entirely re-created in laboratory conditions. In fact, ecosystems processes interact across spatial and temporal scales which may trigger unexpected changes (Holling 1973; Heffernan *et al.* 2014). Therefore, the study of the **past dynamics of real-world ecosystems** is an important source of information for macroecologists (Heffernan *et al.* 2014; Rose *et al.* 2017).

In recent years, species distributions has already been impacted by the changing climate (Burrows *et al.* 2011; Poloczanska *et al.* 2016). These observations can help us predict how the community will rearrange in the future and demonstrate the value of diversity for the resilience of ecosystems. However, given that in real-world observations everything is interlinked, it is difficult to show the effect of a single pressure on a single indicator (Cleland 2002; Ives & Carpenter 2007). Thanks to long-term monitoring program and to the recent improvement in data analysis, observational studies can bring valuable empirical evidence for disentangling long-lasting questions in ecology and environmental science (Edgar *et al.* 2016; LaDeau *et al.* 2017). However, observational studies on BEF are few and it remains to be demonstrated with observations **what is the role of biodiversity for the ecosystem functioning and especially for its resilience to increasing anthropogenic pressures?**

The multiple dimensions of diversity

Biological diversity is a multidimensional concept, defined by the CBD as "the variability among living organisms […] and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems."(United Nations 1992). Thus quantifying changes in biodiversity is not straightforward and diversity is often simplified into indicators that represent a level of diversity (Chao *et al.* 2014).

The most common indicator of biodiversity is **species richness**, defined as the number of species found in a location. It quantifies the obvious difference between a wheat field (low diversity) and a tropical rainforest (high diversity). Even if species richness is simple and quite easy to measure, the trends in species richness are highly debated (Dornelas *et al.* 2014; Vellend *et al.* 2017; Cardinale *et al.* 2018). The debates focus on local diversity (also called alpha diversity) which, depending on the study, can display an increasing or a decreasing trend. This debates stress the fact that diversity can be measured at different scales, spatially and temporally (Levin 1992; McGill *et al.* 2015). While the global diversity is decreasing (Young *et al.* 2016), local diversity in the past decades can be influenced by species invasions. Between local (called alpha diversity) and global (gamma diversity), another set of indicators focus on the turnover of species (beta diversity), comparing the dissimilarity of biomes across space or time (McGill *et al.* 2015). Beta diversity is rarely studied at large scales (McClain & Rex 2015; Hillebrand *et al.* 2018a) but is subject to rapid development of methodologies (Legendre *et al.* 2005; Jost 2007; Wang & Loreau 2014).

Furthermore, the relative species abundance in a community is important for its functioning (Hillebrand *et al.* 2008). For instance, if a diverse community is dominated by one species, interspecific interaction is reduced and the ecosystem processes will be mainly driven by this single species, not the myriad of other species. This intuitive reasoning led to the development of Shannon and Simpson indicators considering not only the number of species but also their relative abundance. These indicators were later grouped into a common framework of indicators called the Hill's numbers (Hill 1973; Chao *et al.* 2014).

Additionally, increasing evidence indicates that species characteristics, called traits, can better link the diversity to the functioning of ecosystems (Díaz & Cabido 2001; McGill *et al.* 2006; Violle *et al.* 2014). In fact, it is not the identity of species but their traits that determine which environments and habitats organism can inhabit and with which species they can interact (Verberk *et al.* 2013). A critical step towards better understanding and predicting future changes in species distributions is to identify the key attributes and adaptation by which species respond to the environment and to characterize the shape and nature of the **relationship between environmental variables and the response traits**. Trait-environment relationships have also been used to study changes in ecosystem functioning (Frainer *et al.* 2017) and to investigate the effect of management measures on ecosystem services (Wesuls *et al.* 2012; Lamarque *et al.* 2014).

Finally, organisms don't live in isolation, but interact with each other. In 1850's Alexander von Humboldt described **nature as a web of life and interactions**. Four primary types of interactions happen in nature: predatory (one eat the other), mutualistic (both species benefit from the interaction), commensalistic (one benefit, the other is neither helped or harmed) or parasitic (one benefit, the other is harmed). In all cases, a change in a single species abundance can impact species primarily interacting with it, and subsequently, the species interacting with these species, and so forth throughout the interaction network. Thanks to advances in graph theory and ecological network analysis, scientists can better predict the consequences of species loss (Berlow *et al.* 2009; Säterberg *et al.* 2013; Brose *et al.* 2016). Moreover, the structure of the interaction network is important for the stability of communities (Yodzis 1981; Rooney & McCann 2012).

As highlighted above, research on biodiversity is common but the efforts to integrate the multiple dimensions of diversity are rare. One of the remaining challenges is **how to characterize and integrate the multiple dimensions of biodiversity dynamics?**

Threats to valuable fish communities

Fish communities are extremely diverse and provide valuable services for human societies. Indeed, fish is the largest group of vertebrates on Earth, with 34,000 species known to science (Froese & Pauly 2017). Additionally, fish is an important source of protein for more than 3 billion people, with an annual production of 171 million tons, worth USD 362 billions and supporting the livelihood of more than 40 million people (FAO 2018). Therefore, it is important for management and conservation efforts to **understand the role of fish diversity for the functioning of ecosystems and the stability of services they provide to humans**. Yet, it is unclear how diversity helps the resilience of fish communities to changing environmental conditions and increasing human pressures. Fishing, habitat loss and degradation, and climate change are the three main anthropogenic pressures known to impact marine ecosystems.

Fishing is the only legally accepted (and sometimes subsidized) harvest of wild animals by humans (Young *et al.* 2016) and its impact on marine ecosystems has been the subject of many studies (Gordon *et al.* 2018). Numerous collapses of fish stocks have been witnessed since the 1960's and the spread of **industrial fishing** (Pinsky *et al.* 2011; McCauley *et al.* 2015), triggering drastic changes on ecosystem functioning (Hilborn *et al.* 2003). Currently 33% of commercially valuable fish are overexploited, 60% are fished to their maximum sustainable level and only 7% are within safe biological limits (FAO 2018). Fisheries are known to impact the trophic structure and the size distribution of fish population toward smaller and lower trophic level fish (Pauly *et al.* 1998; Jackson *et al.* 2001; Hilborn *et al.* 2003; Duarte *et al.* 2015; Gascuel *et al.* 2016). Fishing is also a selecting pressure responsible for changes in the genetic structure of fish populations (Jorgensen *et al.* 2007). Finally, fished communities are known to be less resilient than non-fished ones (Rochet & Benoit 2012).

Multiple human activities contribute to **habitat loss and degradation** such as contamination, extraction of marine resources and marine transport (Halpern *et al.* 2015). For instance, contamination through riverine run-off of agricultural fertilizers induce high eutrophication and primary production in the upper layer of the oceans, that can result in dead zone due to extremely low oxygen concentration in lower depth layers (Diaz & Rosenberg 2008). Another example of contamination are the plastic debris which accumulate in the oceans (Jambeck *et al.* 2015), and micro-plastics are known for their negative effects on organisms (Wright *et al.* 2013). Expansion of aquaculture, off-shore platforms, and sea floor mining disturb and may contaminate marine biota (McCauley *et al.* 2015; van Wesenbeeck *et al.* 2015). Additionally, global commercial shipping are vectors of invasive species that can have strong impact and disturb ecosystems (Seebens *et al.* 2013; Gallardo *et al.* 2016). Vessel traffic is also a source of noise disruption (Simpson *et al.* 2016), and an increased risk of contamination when transporting hazardous substances (Hjermann *et al.* 2007; Whitehead 2013).

Anthropogenic **climate change** is known to have multiple impact on marine ecosystems (Pörtner *et al.* 2014; Gattuso *et al.* 2015). Rising sea temperature can have dramatic effect on marine population if temperatures pass above their thermal tolerance, especially for species with low dispersal ability (Poloczanska *et al.* 2013; MacLean & Beissinger 2017). Increasing temperature can lead to deoxygenation of deeper waters due to increased stratification of the oceans (Pörtner *et al.* 2014). Ocean acidification will negatively impact organisms producing calcium carbonate shells and skeletons, and subsequently species interacting with them. Differences in species' environmental sensitivity and mobility lead to differences in the shift of species distribution that induce a reorganization of the biotic communities (Sorte *et al.* 2010; Burrows *et al.* 2014). Indeed, the impact of climate change on fish is cascading across levels of biological organization; from organisms, to population, to ecosystems. (Pörtner & Peck 2010).

Finally, all the pressures mentioned above are not simply cumulative but their impact on organisms can be amplified (Crain *et al.* 2008; Halpern *et al.* 2015). Yet it is unclear how the interaction between multiple stressors may affect biotic communities. This high scientific uncertainty brings challenges for the management of fish populations.

Management and monitoring of fish diversity

Managing dynamic fish populations under strong anthropogenic pressures is a difficult issue. Traditionally, single stock assessments are used to estimate the annual "maximum sustainable yield" per species given their reproduction rate and mortality. However, this approach is criticized for its over-simplification of biotic communities. **Ecosystem based management** (EBM) is an integrative framework that aim for the sustainable use of ecological resources (Pikitch *et al.* 2004; Leslie & McLeod 2007; Fogarty 2014). EBM advocates for the inclusion of the multiple uses of marine resources and their inherent trade-offs. Species stocks should be managed comprehensively, considering species interactions and environmental variability. EBM switches from the classic view of maximizing the catch of each single stock within its sustainable limit to the novel view of ensuring the health of ecosystems by setting coherent catch limits to multiple species.

To be effective, EBM needs integrative ecosystem assessment (Levin *et al.* 2009; Möllmann *et al.* 2014) that require **good estimation of population size** (i.e. fish stocks). However, estimating the abundance of fish living in the oceans is not a simple task. The best estimations of demersal fish abundance come from fisheries-independent scientific surveys. The sampling is performed by fishing with a bottom trawl net according to a standard protocol, and by counting, and identifying the species' names of all the catches. When the exact same procedure is repeated across a large area for decades it is then possible to estimate the distribution and the dynamics of fish species. However, our observations are only a tiny fraction of what occurs under water (Fig 1.1). This limited knowledge creates an even bigger challenge for marine ecologists: **how to understand marine complex ecosystems from scarce observations while integrating its multiple dimensions, multiple scales and large interaction networks?**

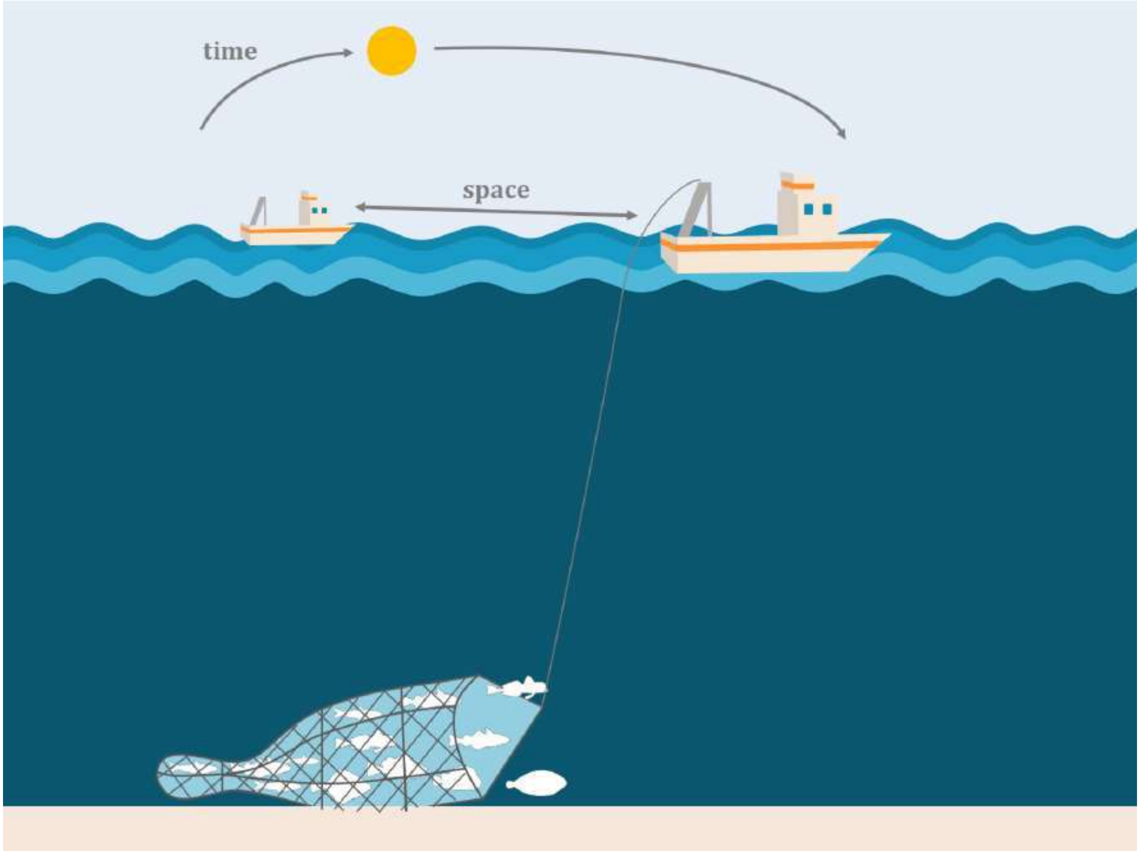

Figure 1.1: Scientific bottom trawl surveys sample the benthic fish community with a net trawled over the sea floor for a given period of time. It offers a snapshot of the communities in a given location. Repeated in different locations and over decades, the survey offers an estimation of the changes in abundance through time and space. The following chapters are all based on the analysis of such dataset using innovative methods and combining it with information from different data sources.

Objectives

The main goal of this dissertation is to understand the importance of biodiversity for the resilience of marine fish populations to climate change and fisheries exploitation. This complex issue is divided in three interconnected sub-questions (Fig. 1.2).

A. How to characterize the spatio-temporal dynamics of species assemblage and identify their external drivers?

Understanding the spatial and temporal dynamics of biotic communities containing large numbers of species represents a key challenge in ecology. Biotic communities are made of individuals from multiple species that are dynamic and their distribution can change in time and in space. However, the interaction between the spatial distribution and the temporal dynamics of species assemblages is difficult to grasp and requires specific methods that account for the multidimensional nature of community data.

In chapter 2, the multiple dimensions of diversity dynamics were studied with advanced multivariate statistical analysis called **tensor decomposition**. Tensor decomposition considers the 3D structure of the community data which can reveal the interplay between the spatial distribution and temporal dynamics in fish populations. Using the North Sea demersal fish community as a case study, we investigated how tensor decomposition can help (i) characterize the main **spatio-temporal patterns of species assemblages**, (ii) identify sub-communities that share similar spatial distribution and temporal dynamics, and (iii) **reveal external drivers of change** by applying additional correlation analyses and Monte-Carlo permutation tests.

In chapter 3, the multivariate methodology was refined into a comprehensive framework based on complementary multivariate statistical methodologies to **simultaneously investigate the effects of environmental conditions on the spatial, temporal and functional dynamics of species assemblages**. Using survey data collected in more than 4,000 stations over the Baltic Sea between 2001 and 2016, we investigated how the proposed framework can help (i) disentangle the effects of environmental changes on the structure of biotic communities, and (ii) identified sub-assemblages that co-exist and are susceptible to similar environmental conditions.

B. How does fish functional diversity respond to changing external pressures?

Chapter 4 originated from a collaborative work with Esther Beukhof, PhD student from DTU aqua in Denmark. Together, we investigated the **relationship between traits and environmental conditions across Large Marine Ecosystems**. We gathered a large dataset of bottom trawl surveys collected across the northeastern Pacific and northern Atlantic Ocean between 2005 and 2015. Based on more than 70,000 stations recording over 1,400 species, we investigated (i) which traits and which environmental variables best explain the distribution of marine fish? and (ii) what are the key trait-environment relationships for marine fish?

In chapter 5, **modern morphometrics** was used to quantify morphological traits of fish species. In fact, traits information is difficult to collect, especially for the rare and non-commercially important species that are less abundant in the scientific literature. Morphology is an integrative trait that combines functional and evolutionary information. However, the objective and quantitative description of the morphological diversity is quite challenging. In order to help with the data gathering and analysis, a master student, Florian Caillon from the University of Aix-Marseille, was recruited. Together, we described the shape of 85 fish species found in the North

Sea and demonstrated that outline analysis is a powerful tool to describe the morphology of fish species. We investigated how outline analysis can (i) provide a **new quantitative description of morphological variability**, and (ii) identify **environmental processes structuring the fish community** in a Large Marine Ecosystem.

C. What is the importance of biodiversity for the stability of ecosystems?

The structure of the interaction network between organisms is important for the stability of biotic communities. Due to environmental and anthropogenic pressures, ecological communities are constantly being reshaped. Yet, we do not know how the structure of food webs changes over time. In chapter 6, together with Pierre Olivier, PhD student from Abo Akademy in Finland, we developed a **new methodology to study the dynamics of the topological structure of food webs**. We studied the dynamics of fish and benthic macrofauna in the German Bight between 1998 and 2015 and investigated (i) whether the food web structural properties have changed and (ii) what is the origin of such change: is it primarily driven by changes in the species composition or in the trophic links composition?

Finally, chapter 7 investigates the **link between the diversity and the functioning of marine ecosystems**, revisiting a question that has puzzled ecologists for decades: why and under what conditions is the community more stable than the sum of its parts? Although most empirical studies used taxonomic classifications to define diversity, organisms undergo strong ontogenetic shifts during their lifetime, and intra-specific size variability might be an important stabilizing factor. Therefore, a size-based approach was developed to investigate the relative **influence of size asynchrony on the stability of communities**. This empirical study is based on time series of fish biomass from over 50,000 fisheries-independent stations spread across North-Atlantic Large Marine Ecosystems. The main questions of the study are: (i) what is the complementarity between size and taxonomic synchrony for the stability of communities? (ii) which factors could explain the differences between size and taxonomic synchrony and (iii) what are the regulatory mechanisms of stability?

Combining all the results together, the chapter 8 offers an overview of the multiple dimensions of fish diversity and community stability. The complementarity between chapters is discussed as well as their implication for marine ecosystem-based management.

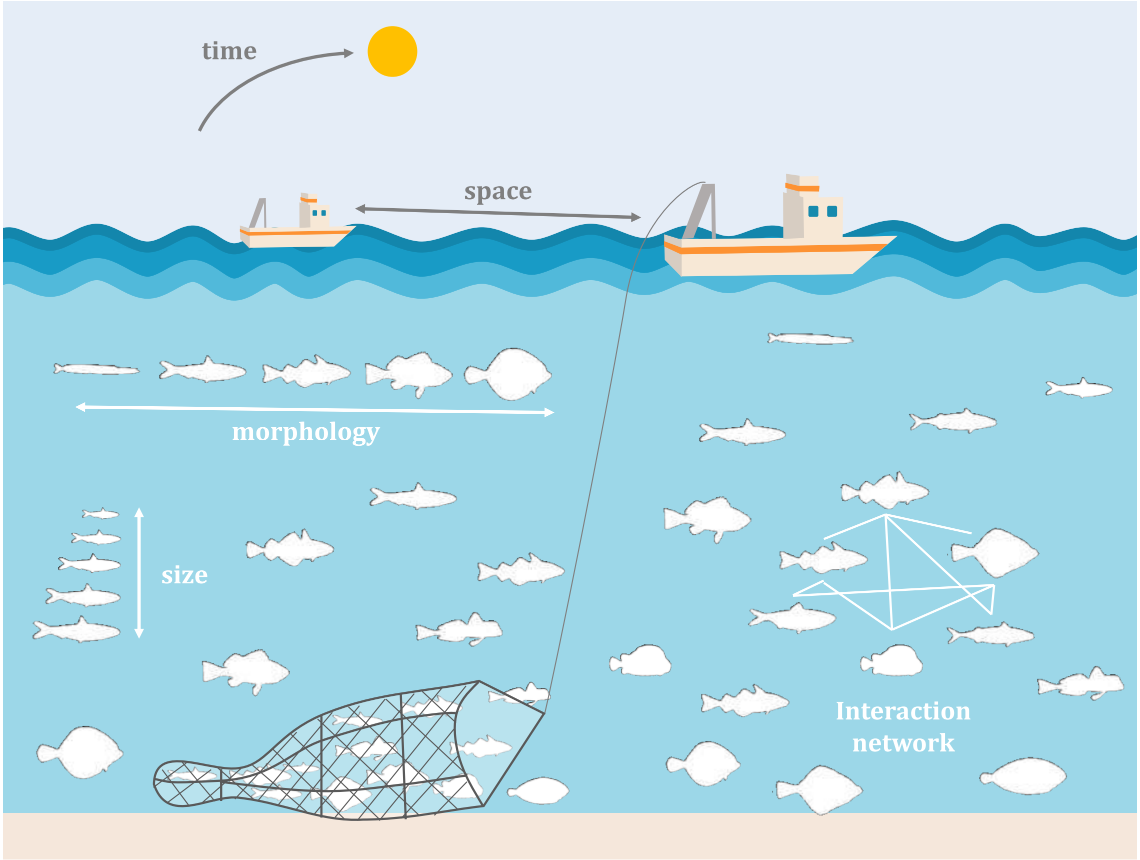

Figure 1.2: The multiple dimensions of fish diversity dynamics. The successive chapters of this dissertation integrate (i) the interaction between spatial and temporal dynamics (chapter 2 and 3), (ii) the link between traits and environmental changes (chapter 3, 4 and 5), (iii) the trophic interaction network between species (chapter 6), and (iv) the intra-specific size variability, important for the stability of communities (chapter 7).

Chapter 2

Tensor decomposition reveals spatio-temporal community dynamics

M.C. Escher, Man with cuboid (1958)
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Title: Community ecology in 3D: Tensor Decomposition reveals spatio-temporal dynamics of large ecological communities

Authors: Romain Frelat[1*], Martin Lindegren[2], Tim S. Dencker[2], Jens Floeter[1], Heino O. Fock[3], Camilla Sguotti[1], Moritz Stäbler[4], Saskia A. Otto[1] and Christian Möllmann[1]

[1] University of Hamburg, Institute for Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability (CEN), KlimaCampus Hamburg, Große Elbstraße 133, 22767 Hamburg, Germany

[2] Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet, Bygning 202, 2800 Kgs. Lyngby, Denmark

[3] Thünen-Institute of Sea Fisheries, Palmaille 9, 22767 Hamburg, Germany

[4] Leibniz-Centre for Tropical Marine Ecology, Fahrenheitstraße 6, 28359 Bremen, Germany

[*] **Corresponding author**: Romain Frelat, romain.frelat@uni-hamburg.de

Abstract

Understanding spatio-temporal dynamics of biotic communities containing large numbers of species is crucial to guide ecosystem management and conservation efforts. However, traditional approaches usually focus on studying community dynamics either in space or in time, often failing to fully account for interlinked spatio-temporal changes. In this study, we demonstrate and promote the use of tensor decomposition for disentangling spatio-temporal community dynamics in long-term monitoring data. Tensor decomposition builds on traditional multivariate statistics (e.g. Principal Component Analysis) but extends it to multiple dimensions. This extension allows for the synchronized study of multiple ecological variables measured repeatedly in time and space. We applied this comprehensive approach to explore the spatio-temporal dynamics of 65 demersal fish species in the North Sea, a marine ecosystem strongly altered by human activities and climate change. Our case study demonstrates how tensor decomposition can successfully (i) characterize the main spatio-temporal patterns and trends in species abundances, (ii) identify sub-communities of species that share similar spatial distribution and temporal dynamics, and (iii) reveal external drivers of change. Our results revealed a strong spatial structure in fish assemblages persistent over time and linked to differences in depth, primary production and seasonality. Furthermore, we simultaneously characterized important temporal distribution changes related to the low frequency temperature variability inherent in the Atlantic Multidecadal Oscillation. Finally, we identified six major sub-communities composed of species sharing similar spatial distribution patterns and temporal dynamics. Our case study demonstrates the application and benefits of using tensor decomposition for studying complex community datasets usually derived from large-scale monitoring programs.

Keywords: Species distribution, community assemblages, multiway multivariate analysis, beta diversity, demersal fish community, North Sea

Introduction

Understanding the spatial and temporal dynamics of biotic communities containing large numbers of species represents a key challenge in ecology and is crucial to guide ecosystem management and conservation efforts. However, the interaction between the spatial distribution and the temporal dynamics of species assemblages is difficult to grasp and requires specific methods that account for the multidimensional nature of community data. In fact, community data are intrinsically multidimensional, because each sample taken in a given location at a given time can be described by the abundances of multiple species. Hence, datasets from monitoring programs with repeated sampling at multiple locations can be organized as a 3-dimensional array (i.e., 3rd-order tensor) with species, space and time being its three dimensions.

Common approaches in community ecology use “two dimensional” multivariate analysis methods such as Principal Component Analysis (PCA) or Correspondence Analysis to analyze community data (Gauch 1982; Legendre & Legendre 2012). Because most of the statistical methods are developed to analyze matrices, one of the three dimensions of community data is often sacrificed to reduce the 3D array into a 2D matrix. Depending on the aim of the study, scientists have been simplifying either the species assemblages into diversity indicators (Daan 2006), the spatial distribution into barycentre coordinates (Perry *et al.* 2005), or the temporal dynamics by averaging over stable periods (Pecuchet *et al.* 2017). One way to keep the full information in 3D datasets is the extension of multivariate analysis to k-tables (such as STATIS (Thioulouse & Chessel 1987)) and the simultaneous analysis of a sequence of paired ecological tables (Thioulouse *et al.* 2004; Thioulouse 2011; Mendes *et al.* 2016). While the extension to k-tables is a clear improvement, which has found numerous applications among ecologists to study spatio-temporal patterns (Rossi *et al.* 2014; Kidé *et al.* 2015), the k-table approach considers one of the dimensions (often time or space) only as a repetition, restricting the results by the a-priori choice of the repetitive dimension and impeding the study of the interaction between time and space. Recently, other approaches have been developed to extend species distribution models to full communities, like the joint dynamic species distribution model (Thorson *et al.* 2016; Thorson & Barnett 2017) and the hierarchical modelling of species communities (Ovaskainen *et al.* 2017). Multispecies distribution models are promising approaches, but strongly limited in size by the rapidly increasing number of parameters to be estimated. In contrast, multivariate approaches are free from parameters and can analyze dataset with a large number of species in a high number of defined areas, for long-term time series. However, none of these multivariate methods can simultaneously study spatial and temporal dynamics, including the interaction between time and space across species assemblages which is needed for a comprehensive understanding of spatio-temporal changes of entire ecological communities (Cichocki *et al.* 2015).

Statistical tools able to investigate such multidimensional datasets were developed in the late 1960s within the fields of psychometrics (Tucker 1966). Tensor decomposition (TD) methods (also called multiway multivariate analysis, tensor factorization, or high order principal component analysis) are becoming an essential tool for data mining and have been successfully applied within chemistry (Bro 2006), neuroscience (Kauppi *et al.* 2015), bioinformatics (Omberg *et al.* 2007), geophysics (McNeice & Jones 2001) and geospatial science (Leibovici & Jackson 2011). The recent enthusiasm for TD fuelled by growing computing power and the emergence of big data (Mørup 2011), was followed by the development of new software (Leibovici 2010; Giordani *et al.* 2014). Currently, multiple introductions and tutorials are available (e.g. (Kolda & Bader 2009; Mørup

2011; Cichocki *et al.* 2015)) and provide the basis for new applications using TD. An increased adoption of TD methods among ecologists could be beneficial because community data collected from large-scale ecological monitoring programs are inherently multidimensional (i.e. have more than 2 dimensions).

Here we demonstrate and promote the use of TD for disentangling spatio-temporal ecological dynamics using the North Sea demersal fish community as an informative example. The North Sea marine ecosystem has suffered from strong anthropogenic pressures (Halpern *et al.* 2015), such as fisheries exploitation (Engelhard *et al.* 2015), and is already markedly impacted by climate change (Weinert *et al.* 2016). The need to manage the many commercially important fish populations providing highly valued ecosystem services (Emeis *et al.* 2015) has resulted in a rigorous and internationally coordinated monitoring scheme in the North Sea (ICES 2015). The *North Sea International Bottom Trawl Survey* created a unique long-term (>30 years) dataset covering multiple fish species abundance in time and space, which is openly available and provides an ideal basis for multiway analysis. Our study shows how TD can help (i) characterize the main spatio-temporal patterns of species assemblages, (ii) identify sub-communities that share similar spatial distribution and temporal dynamics, and (iii) reveal external drivers of change by applying additional correlation analyses and Monte-Carlo permutation tests.

Materials and methods

Tensor decomposition

A tensor is a multidimensional array; a generalization of a matrix (two-dimensional table) in more than 2 dimensions. For example, the observed abundance of a species is associated with a given location and a given time. Community data are made of observations of abundances of multiple species (also referred as species assemblages), repeated in multiple areas and at different times. The dataset can be seen as a three-dimensional (or third order) tensor with one dimension being the species taxa, a second dimension being the areas, and the third dimension being time (Fig. 2.1A). To get reliable and complete time series, stations (locations of individual haul) are often aggregated to areas sharing similar features.

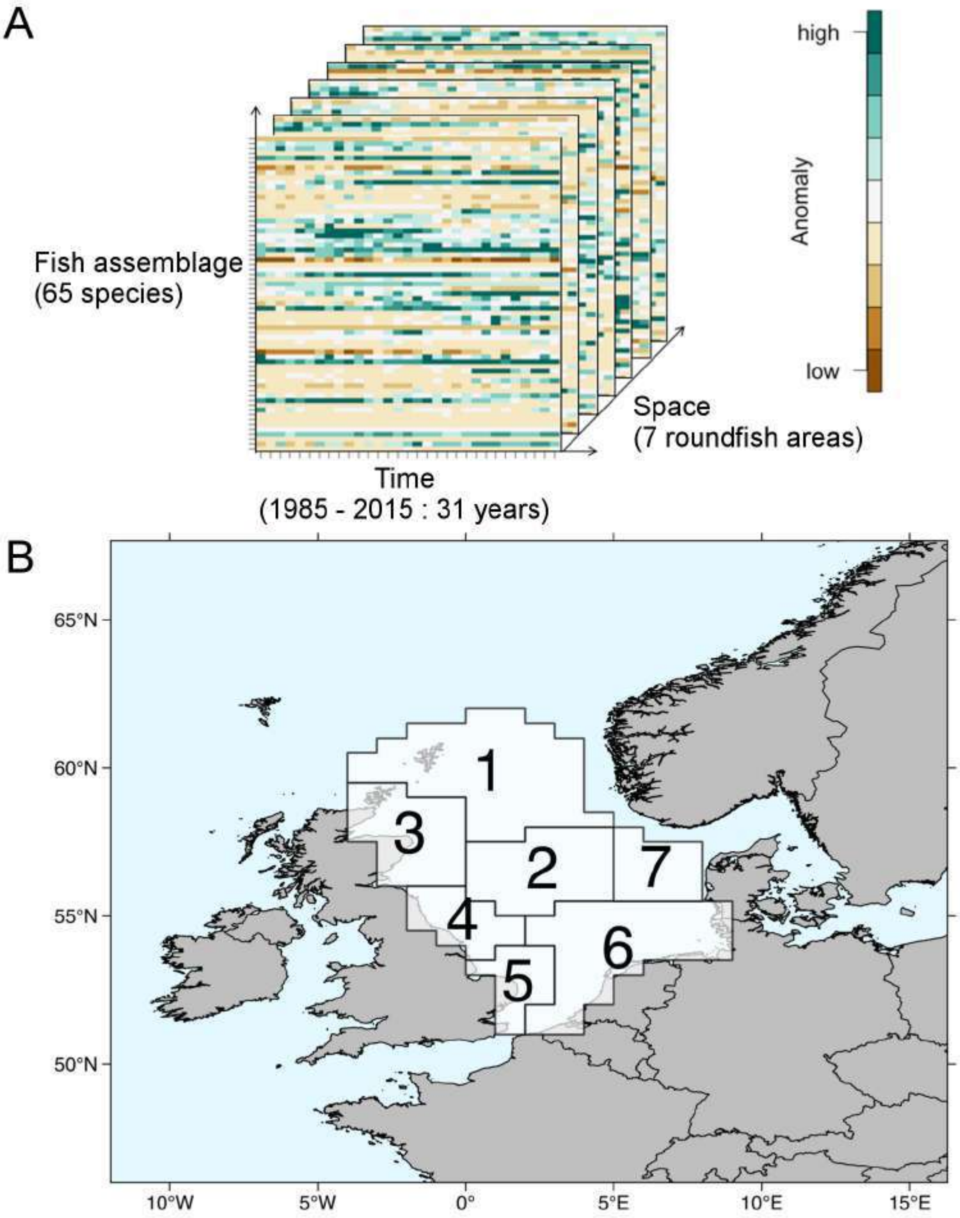


Figure 2.1: Presentation of the dataset and its multidimensional nature. (A) Community data represented as a three-dimensional tensor. Each pixel represents the abundance level (relative to the average abundance of each species in the survey) of the fish species in the North Sea in its 3 dimensions: species, time and space. (B) Map of the study area showing the 7 predefined areas (called roundfish areas) which serve as the spatial scale of our study.

Tensor decomposition (TD) shares the same objectives of multivariate analysis, simplifying the original dataset (here formatted as a tensor) and explaining the maximum proportion of the variance in the dataset with a minimum number of components of lower dimensions. With this trade-off, TD reveals the main pattern (or information) within the dataset and separates it from noise. Different methods of TD have been developed since the 1960s along with the development of multilinear algebra. Three methods are among the most popular: Tucker decomposition (Tucker 1966), canonical polyadic decomposition (also known by the acronyms CANDECOMP or PARAFAC, (Carroll & Chang 1970; Harshman 1970)) and Principal Tensor Analysis over k-modes (PTA) based on high order singular value decomposition (Leibovici & Sabatier 1998). Recent extensive reviews with detailed mathematical definitions and differences between these methods are available (Kolda & Bader 2009; Cichocki *et al.* 2015). From a practical point of view, PTA offers an easy-to-interpret and robust method to decompose a tensor. Compared to the Tucker decomposition, PTA has the advantage of being independent of the dimensions of the desired solution (or core tensor). Compared to canonical polyadic decomposition, PTA has better explanatory power (due to its flexibility of having non-diagonal core tensor). The definition and algebra of PTA can be found in Leibovici and Sabatier (Leibovici & Sabatier 1998). We believe that its high similarity with the properties of the well-known PCA may facilitate its adoption by ecologists.

A PTA is completed following the same three steps as a PCA: (1) scaling, (2) selecting relevant components and (3) visual interpretation of the components with a biplot. First, the scaling and transformation of the original data is an essential preliminary step for the analysis of community data (Legendre & Gallagher 2001). In the multidimensional context, the question is how to compute the distance between individuals and on which dimension(s) to center and/or scale the abundance values. The answer depends on the dataset and the focus of the study. In our case, the abundance values were highly right skewed so we log(x+1)-transformed the abundance values and choose to use Euclidean distances as a basis for the PTA (similar to a PCA). Then, we centred (mean of 0) and scaled (standard deviation of 1) the abundance of each species to consider the rare and abundant species equally. Second, the dominant modes of variability, summarized in principal tensors (PTs), are selected with a scree plot, showing the percentage of the variance explained by each successive PT (Fig. S2.1). Similar to successive eigenvalues from PCA, a visual inspection of the scree plot indicates the number of significant PTs, i.e. the best trade-off between minimum number of PTs and the maximum percentage of variance explained (Cattell 1966). Third, interpretation of PTs is made based on the projection of the dimensions on the selected PT (similar to a biplot in a PCA). PTA results in the simultaneous projection of the three dimensions (species, time and space) on simpler axis (PTs). The projection of time and space on the PT was plotted in a heatmap to represent the dominant spatio-temporal dynamics inherent in the dataset.

However, the large number of species analyzed in parallel renders the interpretation of the species projection derived by PTA difficult. Hence, we augmented the analysis by computing Euclidean distances between fish species from the projection of species scores on the PTs and subsequently conducted a Hierarchical Cluster Analysis (HCA) based on Ward's criterion. We selected the significant number of groups from the HCA based on a graphical interpretation of the dendrogram. The robustness of the selected number of clusters was tested by comparison with the alternative K-Means Cluster Analysis (Fig. S2.2). Using cluster analysis, we derived a simplification of the dynamics of the multitude of individual species into fewer sub-communities sharing similar spatio-temporal patterns. We also used information about species' traits, in terms of behaviour and life history, to characterize these sub-communities (data from (Engelhard *et al.* 2011); Table S2.1). We tested if sub-communities had significant differences in the distribution of traits with a Kruskal-Wallis test (for continuous traits) and Chi-square test (for qualitative traits).

Example dataset – the demersal fish assemblage of the North Sea

Abundance data of the North Sea demersal fish assemblage were compiled by the ICES (International Council for the Exploration of the Sea) Database for Trawl Surveys (DATRAS; http://datras.ices.dk/; data downloaded on the 16th of February 2016). Data were collected by the *North Sea International Bottom Trawl Survey* (ICES 2015), an international effort to monitor fish populations and communities. Each contributing research vessel applies a standard otter trawl as sampling gear. Individual hauls are standardized to catch per unit effort, which represents the average catch per unit of time of trawling. To assure representative sampling of the fish community, at least two hauls are regularly conducted in pre-specified spatial rectangles (ICES statistical rectangles) of one degree longitude and 0.5 degree latitude each (ICES 2015).

For our analysis, we only used data collected during the first quarter (January-March) of the year, in order to avoid seasonal bias and benefit from the longest time series available (31 year continuous period from 1985 to 2015). We investigated spatio-temporal changes of the fish community on the scale of the seven predefined areas (called roundfish areas by ICES, RAs; Fig. 2.1B) which sub-divide the North Sea based on ecological aspects of the fish fauna, including spawning, feeding and species composition (Daan *et al.* 1990; Daan 2006). Hence, our dataset represents reliable relative annual abundance estimates per RA based on the aggregation of at least 16 hauls. Our approach sacrifices spatial information collected on the smaller rectangle basis (ICES statistical rectangles) for a better estimation of the abundance on each spatial unit. Nevertheless, conducting the analysis on a higher spatial resolution resulted in similar outcomes (Fig. S2.3).

We conducted pre-processing checks for misnaming or misidentification of species, removal of non-fish organisms and pelagic fish species that are not representatively sampled by the gear (Fung *et al.* 2012). Furthermore, we excluded sporadic species that occurred less than once every year in at least one area. By this procedure, we removed 50% of the total number of species recorded. However, these species amounted to less than 1% of the total abundance. Our final dataset contained annual abundance expressed in catch per unit effort of 65 individual species for the period 1985 to 2015 averaged over the seven RAs. We log(x+1)-transformed and then standardized the data (zero mean and sd of 1) to reduce the skewness and to scale rare and abundant species equally. Finally, we organized the data for the statistical analysis in an array of three dimensions, i.e. species, space and time, which we refer to as a tensor in the following text (Fig. 2.1A).

Information about the biological characteristics of the species (maximum length, trophic level and biogeography) were extracted from Engelhard et al. (Engelhard *et al.* 2011). Boreal fishes are species that extend north to the Norwegian Sea and Icelandic waters. Lusitanian fishes tend to be abundant from the Iberian Peninsula to as far north as the British Isles and the central North Sea. Atlantic species are species widespread in the North Atlantic.

All data analyses were performed with the statistical software environment R (R Core team 2017). The PTA method is implemented in the R package PTA-k (Leibovici 2010) and a tutorial (containing script and data) explaining TD on fish assemblages is openly available on GitHub (https://github.com/rfrelat/Multivariate2D3D, DOI : 10.5281/zenodo.831739).

Environmental conditions and fishing pressure influences on spatio-temporal community patterns

We explored the effects of natural and anthropogenic drivers known to affect fish distribution patterns in the North Sea (Emeis *et al.* 2015), specifically depth, local hydrographic conditions, primary productivity, large-scale climate indices and fishing pressure. Depth was retrieved from the General Bathymetric Chart of the Oceans, (GEBCO 2014 grid, www.gebco.net) and averaged per subdivision. Local hydrographic conditions were represented by bottom and surface temperatures and salinities derived from optimally interpolated observations of the North

Sea (Núñez-Riboni & Akimova 2015). Chlorophyll *a* (Chl) concentration (as proxy for primary production) was estimated from GlobColour (http://globcolour.info), a product developed, validated, and distributed by ACRI-ST, France (Maritorena *et al.* 2010). The oceanographic dataset and GlobColour are provided with a monthly time step and at high spatial resolution (respectively 0.2° and 1km). We spatially averaged these values over the RAs and derived three temporal indices from the 12 monthly values: an annual index (averages over 12 months, labelled with the subscript $_{\mathrm{AN}}$), a first quarter index (average values over January-February-March, labelled with the subscript $_{\mathrm{Q1}}$) and a seasonality index (difference between the maximum and minimum monthly value, labelled with the subscript $_{\mathrm{var}}$). The annual and the seasonality indices were compared to the fish abundance estimated in the first quarter of the following year. We restricted the number of temporal indices by considering a maximum lag of 1 year between the possible drivers and responses in fish abundance, which represents recruitment success of most species in the North Sea.

Large-scale climate conditions were represented by the Atlantic Multidecadal Oscillation (AMO, (Enfield *et al.* 2001)), as well as the North Atlantic Oscillation (NAO, (Jones *et al.* 1997)) index. The two indices are known to affect the ecosystems of the North Atlantic and adjacent seas (Ottersen *et al.* 2001; Edwards *et al.* 2013). The NAO indicates high frequency (7-25 years) atmospheric variation, whereas AMO is a low frequency multidecadal (60 years) variation of the sea surface temperature. Time-series on both indices were derived from the climate indices platform of the Earth System Research Laboratory: http://www.esrl.noaa.gov/psd/data/climateindices/list/. Fishing effort as an index of exploitation pressure was estimated from a dataset provided by the Scientific, Technical and Economic Committee for Fisheries of the European Commission (https://datacollection.jrc.ec.europa.eu/data-dissemination). Annual fishing efforts (in hours per ICES rectangle per year and per gear type) are available from 2003 onwards. We followed the recommendation by Engelhard et al. (Engelhard *et al.* 2015) to consider beam and otter trawl effort separately.

Potential external drivers were identified through correlation analysis with the derived PTs, as well as with the spatio-temporal dynamics of the sub-communities (represented by the spatio-temporal distribution of species aggregated by cluster). For drivers that can be defined in time and space (e.g. hydrography and fishing effort), the relationships between the spatio-temporal matrices were tested using the RV coefficient, a generalization of the Pearson correlation coefficient for matrices, and applying a Monte-Carlo permutation test with 5,000 permutations (Heo & Gabriel 1998). For 1-dimensional drivers defined only in time (e.g. climatic indices) or space (i.e. depth), Pearson correlation coefficients were computed. To account for the autocorrelation inherent in the time-series affecting significance levels, p-values were calculated from 5,000 random time series with similar first order autocorrelation (AR1). Eventually, the p-values were adjusted for multiple testing to correct false discovery rates following a method suggested by Benjamini and Yekutieli (Benjamini & Yekutieli 2001).

Results

Spatio-temporal dynamics of fish assemblages in the North Sea

PTA decomposed the initial tensor, i.e. the array of fish abundance in the three dimensions – species, space and time - into the dominant modes of variability, summarized in PTs. Based on a visual interpretation of the scree plot, we identified four significant PTs, which in total explained 43.2 % of the variability in the North Sea demersal fish dataset (Fig. S2.1). We evaluated the significance of our results by performing a PTA on the same tensor, but with its values randomly shuffled. This analysis explained only 6% of the total variability, suggesting our decomposition to reliably capture the main patterns in our dataset. For simplicity and analogy with the more common PCA, we renamed the significant PTs with a number according to the decreasing order of variability explained, which differs from the labelling provided by the software used. The full results of the PTA (i.e., the output of the PTAk package) are provided in Fig. S2.1.

Our results showed that the spatial structure of the fish assemblage explained a larger proportion of the variability in the dataset compared to temporal variability. Spatial structure is represented by three PTs that together explained 38% of the total variability. The temporal pattern on the other hand is represented by only one PT and explained 5.2% of the total variability. We used heatmaps with time and space on the x- and y-axes respectively, to visualize the four main patterns found (Fig. 2.2). PT 1 – 3 (Fig. 2.2A-C) revealed strong differences between RAs displayed by homogeneity in the abundance levels over time (i.e. homogeneity in row colours). PT4 (Fig. 2.2D) represented a component of temporal variation that is homogeneous in space (i.e. homogeneity in column colours).

PT1 explained 23.7% of the variability in the dataset and discriminated the northern (RA 1, 2 and 3) and southern parts (RA 5 and 6) of the North Sea (Fig. 2.2A). Correlation analysis revealed significant relationships of PT1 with Chl (Chl_{Q1}, p-value = 0.03), the seasonality of sea bottom temperature (SBT_{var}, p-value = 0.03) and of sea bottom salinity ($SBS_{var,}$, p-value = 0.03) (Table 2.1 and Table S2.2). Moreover, PT1 was correlated with sea bottom salinity (SBS_{Q1}, p-value = 0.07) and depth (p-value = 0.07). Therefore, PT1 highlighted the differences of fish species living in the southern part of the North Sea, a shallow area with high primary production and pronounced seasonality in bottom temperature and salinity, compared to fish species living in the northern part, a deeper area with lower primary production and lower seasonal variations in temperature and salinity. In other words, the analysis revealed a strong north-south gradient in the composition of the North Sea fish community corresponding to a strong gradient in geography, hydrography and biological productivity.

PT2 and PT3 explained 8.7 and 5.6% of the variability in the dataset, respectively. PT2 showed the connectivity of fish communities to other seas and opposes the Atlantic entrance of the North Sea (toward the Norwegian Sea, RA 1, and the English Channel, RA 5) to the Baltic Sea entrance (RA 7) (Fig. 2.2B). PT3 discriminated the western (RA 3 and 4) and eastern NS (RA 1 and 7) (Fig. 2.2C). PTs 2 and 3 were tensors with a temporal mode associated to PT1, i.e. they shared the same temporal components. PTs 2 and 3 were uncorrelated with environmental conditions and fishing pressure (Table 2.1). PT4 displayed the main temporal trend in the fish community and discriminated parts of the community continuously decreasing in abundance compared to those continuously increasing over the last 30 years (Fig. 2.2D). The trend shown by PT4 was correlated with the AMO (p-value =0.07, Table 2.1).

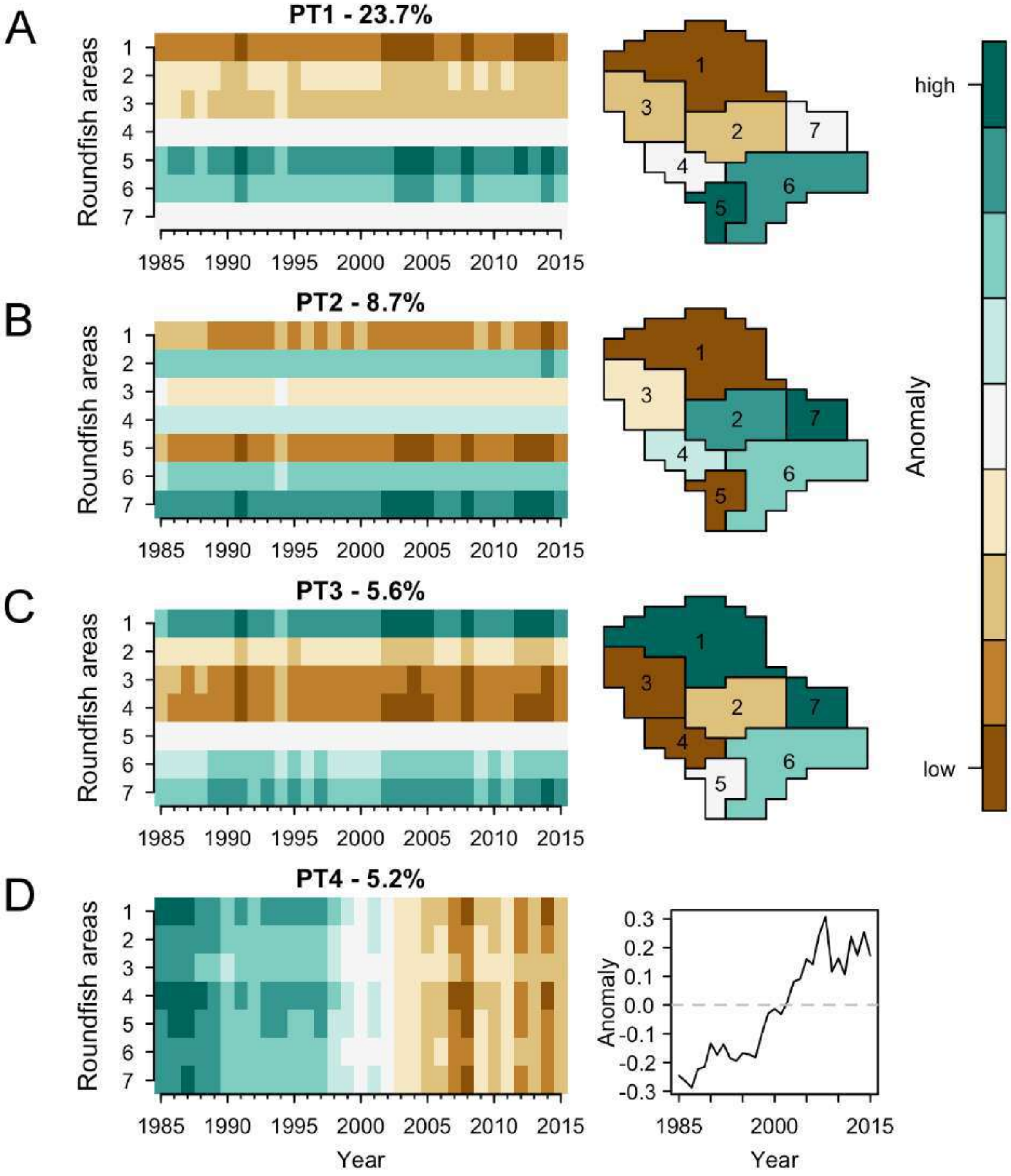


Figure 2.2: Results of the Principal Tensor Analysis with 4 principal tensors (PT) explaining together 43% of the total variability in the North Sea fish assemblage. (A) PT1 showed a spatial gradient in species abundance from North to South. (B) PT2 showed the difference in abundance between strongly localized species (either in the North or the South) and species living in the central part of the North Sea. (C) PT3 showed the abundance difference between species in the West and East of the North Sea. (D) PT4 showed a temporal trend in species abundance.

Table 2.1: Correlation analysis to identify environmental influences on spatio-temporal community patterns. Correlation coefficients between drivers (in rows) and spatio-temporal dynamics of the North Sea fish assemblages (in columns). Pearson correlation coefficients and RV coefficients were calculated for 1- dimensional (e.g. climatic indices, depth) and 2 dimensional (e.g. hydrography and fishing effort) drivers, respectively. The subscript 'Q1' represents the first quarter of the year, 'var' indicates the seasonality of the previous year, i.e. the difference between the minimum and the maximum monthly values. PTs are the principal tensors found by the Principal Tensor Analysis; the spatio-temporal dynamics of the clusters were represented by the projection of their barycentre on the PTs. Adjusted p-values to correct for false discovery rates in multiple testing were computed and correlation significance is indicated by '°' p<0.1 and '*'p <0.05.

	Tensor Decomposition				**Clusters**					
	PT1	PT2	PT3	PT4	Southern	Northern	NW Inc	SE Inc	Increasing	Decreasing
SST$_{Q1}$	0.47	0.24	0.4	0.03	0.25	0.21	0.73	0.93 *	0.44	0.07
SST$_{var}$	0.51	0.26	0.28	0.02	0.24	0.27	0.65	0.96 *	0.49	0.05
SBT$_{Q1}$	0.64	0.39	0.05	0.05	0.32	0.56	0.39	0.89 *	0.59	0.13
SBT$_{var}$	0.94 *	0.01	0.03	0.03	0.81 °	0.45	0.61	0.67	0.06	0.46
SSS$_{Q1}$	0.68	0.20	0.14	0.10	0.40	0.49	0.49	0.84 °	0.39	0.18
SSS$_{var}$	0.08	0.41	0.31	0.18	0.09	0.07	0.20	0.39	0.48	0.27
SBS$_{Q1}$	0.84 °	0.06	0.02	0.03	0.56	0.73 °	0.29	0.61	0.18	0.32
SBS$_{var}$	0.90 *	0.13	0.05	0.04	0.67	0.55	0.54	0.79 °	0.25	0.36
Chl$_{Q1}$	0.92 *	0.08	0.02	0.00	0.97 °	0.35	0.56	0.45	0.01	0.68
Chl$_{var}$	0.83 °	0.15	0.04	0.02	0.97 *	0.26	0.55	0.34	0.04	0.74
Otter	0.52	0.31	0.12	0.23	0.19	0.88	0.05	0.46	0.47	0.05
Beam	0.64	0.01	0.06	0.05	0.52	0.28	0.52	0.55	0.08	0.20
AMO	0.40	-	-	0.74 °	0.70	-0.72 °	0.74 °	0.74 °	0.74 °	-0.74 °
NAO	0.17	-	-	-0.06	-0.01	0.03	-0.06	-0.06	-0.06	0.06
Depth	0.88 °	0.36	-0.27	0.30	0.66	-0.96 *	-0.38	0.75	-0.52	-0.5

Characteristic sub-communities of North Sea fish species

The projection of the fish species on the four PTs was used to cluster species according to their spatio-temporal dynamics (Fig. 2.3A). The dendogram indicated six clusters of species confirmed by the scree-test (Fig. S2.2). The six clusters were projected separately on the four PTs (Fig. 2.3B-D). Two clusters (*Southern* and *Northern*) had strong spatial patterns and no temporal trend, while two clusters (*North-West Increasing* and *South-East Increasing*) had a strong spatial pattern and a weak temporal trend. The two remaining clusters (*Increasing* and *Decreasing*) were characterized by a temporal pattern (Fig. 2.4). In the following, clusters of species are referred to as sub-communities and we labelled them according to their spatio-temporal characteristics and characterized them through key species (identified by having the highest average abundance and represented by drawings in Fig. 2.4). The full species list and their assignments to the identified sub-communities is given in Table S2.1.

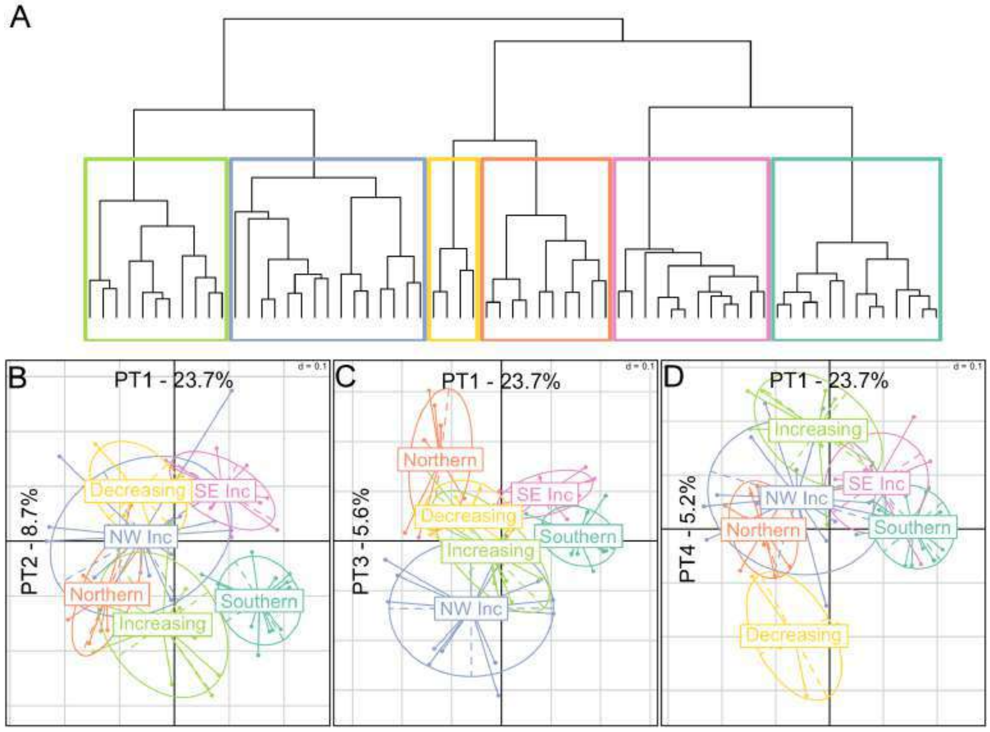


Figure 2.3: Classification of fish species based on their spatio-temporal dynamics. (A) Dendrogram of the Hierarchical Agglomerative Clustering and the separation of 6 clusters. (B-D) Clusters represented on the different principal tensors (PTs), with x-axis showing PT1 projections, and y-axis showing (B) PT2, (C) PT3 and (D) PT4 projections.

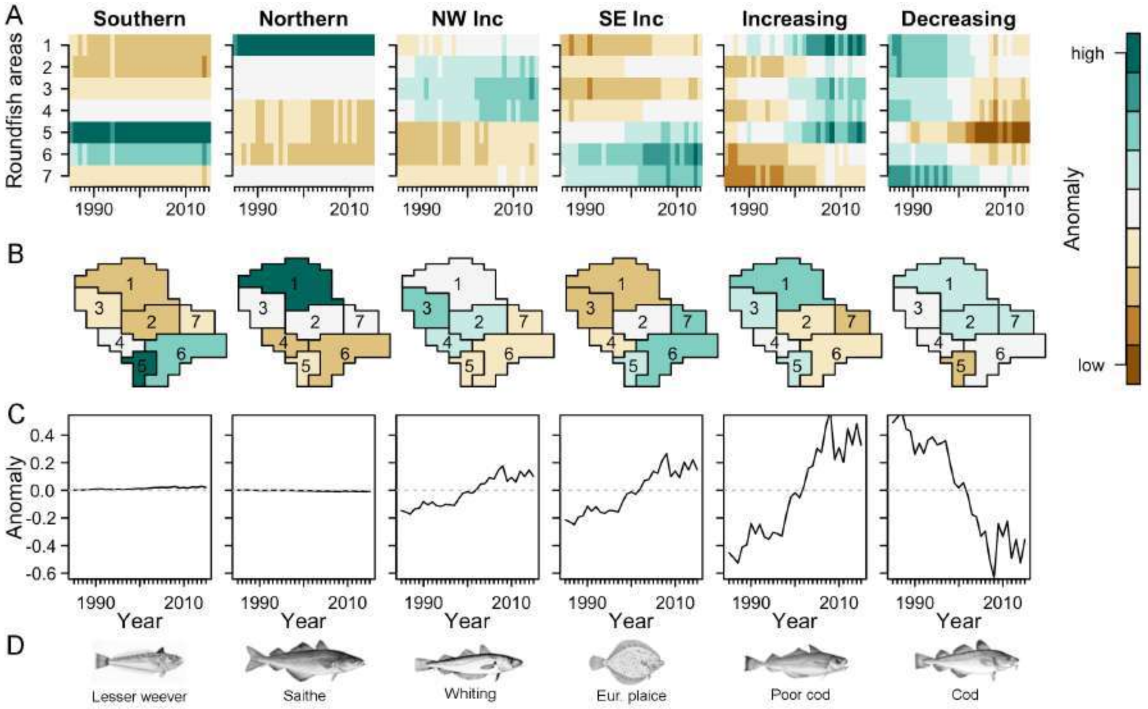


Figure 2.4: Main characterization of the sub-communities. (A) Spatio-temporal abundance, represented in a heatmap with time on the x-axis and space on the y-axis. (B) Spatially average abundance of the clusters in the roundfish areas. (C) Temporal average of the abundance per cluster. (D) Illustrations of fish species with the highest abundance in the respective cluster (images from FAO and Wikimedia).

The *Southern* sub-community consisted of 14 fish species, among them lesser weever (*Echiichthys vipera*) and sole (*Solea solea*) with a distribution concentrated in the southern NS (RAs 5 and 6) and very low abundance in the northern RAs 1 and 2 (Fig. 2.4). The *Southern* community was positively and significantly correlated with the Chl concentration and its seasonality (Chl_{Q1} and Chl_{var}; p-value = 0.07 and 0.03 respectively, Table 2.1) and mean annual sea bottom temperature of the previous year (SBT_{an}; p-value = 0.04, Table S2.2). The *Northern* community consisted of a cluster of 10 fish species, among them saithe (*Pollachius virens*), with high abundance in the North (RA 1) and very low occurrence in the southern RAs 4 and 6. The *Northern* community was negatively correlated with depth (p-value = 0.03) and had a weak positive relationship with sea bottom salinity (SBS_{Q1}, p-value = 0.07).

The *North-West increasing* sub-community was a very heterogeneous cluster composed of 15 fish species, including whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), dab (*Limanda limanda*) and Norway pout (*Trisopterus esmarkii*). The high heterogeneity of the sub-community resulted in weak temporal and spatial pattern, which appeared to be uncorrelated with environmental conditions and fishing pressure (Table 2.1). A positive temporal trend was observed for the *South-East increasing* sub-community, which consisted of 12 fish species, among them plaice (*Pleuronectes platessa*), concentrated in RAs 6 and 7. The *South-East increasing* sub-community was significantly correlated with sea bottom temperature (SBT_{Q1}, p-value = 0.03) and with sea surface temperature and its seasonality (SST_{Q1} and SST_{var},, p-value = 0.04 and 0.03 respectively).

The *Increasing* sub-community was a cluster composed of 11 species, among them poor cod (*Trisopterus minutus*) and hake (*Merluccius merluccius*) with a positive temporal trend and a weak spatial preference (Fig. 2.4) for the entrance of the Atlantic Ocean (RA 1 and 3) or the English Channel (RA 5). The *Decreasing* community was composed of a cluster of only 4 fish species, among them cod (*Gadus morhua*) and starry ray (*Amblyraja radiata*) characterized by a strong decreasing trend during the past 30 years. The two sub-communities *Increasing* and *Decreasing* were uncorrelated with environmental conditions and fishing pressure (Table 2.1).

Finally, we investigated the biological characteristics of the six sub-communities described above by comparing the traits of species classified into each sub-community. The distribution of biological traits significantly reflected the north-south division of the fish sub-communities (Fig. 2.5). Fish species were on average larger (significant difference, p-value = 0.001) in the *Northern* sub-community (median of 110 cm) and the *Decreasing* sub-community (107.5 cm), compared to fish in the *Southern* sub-community (41 cm) and *South-East increasing* sub-community (32.5 cm). The same separation was evident in the trophic level of the fish species (Fig. 2.5B, p-value = 0.04). The *Northern* and the *Decreasing* sub-community had a higher trophic level (on average 4.1 and 3.9, respectively) while the *Southern* sub-community and *South-East increasing* sub-community displayed lower average trophic levels (3.6 and 3.6, respectively). Furthermore, biogeography was a good indicator of the main temporal trends in the North Sea fish community (Fig. 2.5C, p-value = 0.002). The *Increasing* and *South-East increasing* sub-community were mainly composed of Lusitanian species, while the *Decreasing* cluster contained only boreal species. The latter division indicated the climatic influence on the temporal development of the North Sea fish community.

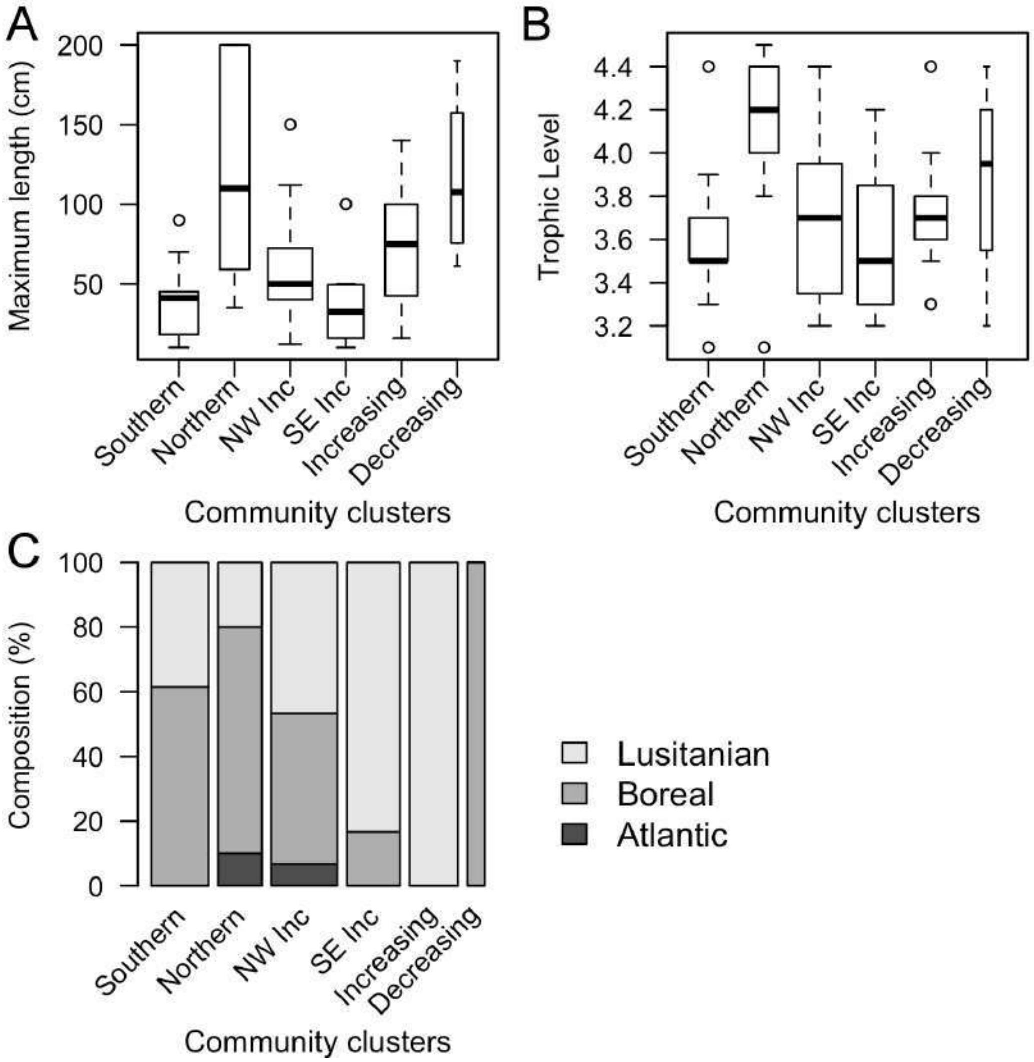


Figure 2.5: Biological characteristics of the spatio-temporal clusters (A: maximum length, B: trophic level and C: biogeography). Widths of the boxplot (A-B) and the bars (C) are proportional to the number of species per cluster.

Discussion

We demonstrated the use of TD, an integrative statistical analysis for studying multi-dimensional datasets, typically collected by large-scale ecological monitoring programs. Here we analyzed a multi-decadal dataset on the spatial distribution of 65 demersal North Sea fish species to better understand the spatial structure and recent temporal changes in the species assemblages. Our study shows that TD is able to identify strong and persistent spatial structure in the fish community while simultaneously identifying strong temporal changes in abundance.

The first main outcome of our study was the identification of a strong and stable spatial structure of the fish community into a *Northern* and a *Southern* sub-community. Correlation analysis explained this structure by differences in depth, primary production levels (represented by Chl concentrations), as well as the seasonality of temperature and salinity conditions. The demonstration of two very different sub-systems confirms earlier investigations in the area (Daan 2006; Dulvy *et al.* 2008). To a lesser degree, our analysis revealed a west to east gradient in community dynamics (PTs 2 and 3), which despite insignificant correlations with the explaining variables used, is likely related to the transition zones to the open Atlantic Ocean (PT2) and to the

Baltic Sea (PT3). The spatial structuring revealed by our TD approach is robust to using biomass instead of abundance and especially to the spatial scale applied (Fig. S2.3). A higher resolution, i.e. on a statistical rectangle basis and therefore sacrificing sample sizes and adding noise in the estimated abundance, revealed the same spatial community structure as shown with the relatively coarse spatial scale of the RAs.

A second main outcome of our study was that despite the strong and predominant spatial structure our method was able to identify strong temporal changes in the fish community. Although explaining only a comparatively small fraction of the overall variability in the dataset, this temporal trend indicates changes in community dynamics with a strong turning point around the late 1990s and the early 2000s. Correlation analysis indicated this change to be at least partly climate driven since it was correlated to the low frequency temperature variability of the AMO. The results confirm the importance of the recent positive anomaly phase of the AMO for ecosystem dynamics in the North-East Atlantic shown in earlier studies targeting single fish species or only small parts of the fish community alone (Beare *et al.* 2004; Sparrevohn *et al.* 2013), lower trophic level dynamics (Goberville *et al.* 2014) and multi-trophic ecosystem changes (Lindegren *et al.* 2012; Edwards *et al.* 2013). Our correlation analysis showed no significant correlation with fishing effort, although there is undoubtedly a high impact of fishing on many commercially important species [27]. We attribute this result to the length of the time-series of fishing effort beginning only in 2003. However, if the low and non-significant correlations with fishing effort are a result of data shortage or are a result of the TD methodology remains to be seen in future studies.

We used hierarchical cluster analysis on the PT projection to identify sub-communities that group species sharing similar spatio-temporal dynamics. We verified the internal consistency of these six sub-communities by investigating the distribution of biological traits within the identified clusters. This approach revealed meaningful results, showing that the *Northern* sub-community is composed of mainly boreal species with larger sizes and higher trophic levels compared to the smaller Lusitanian species residing primarily in the southern North Sea. Interestingly, the homogeneity in biological traits that we found for the clusters based on spatio-temporal dynamics supports the theory that organisms sharing similar traits exhibit similar dynamics (Engelhard *et al.* 2011; Pecuchet *et al.* 2017). However, future analyses would benefit from using additional biological characteristics.

As with any statistical approach, the ability of the method applied here is limited by the quality and amount of data available. For example, the dataset used covers the period 1985-2015, not including the stable period before the regime shift occurring in the North Sea during the late 1980s (Beaugrand 2004; Kenny *et al.* 2009). Including this period of change would likely increase the importance of the temporal component (represented by PT4) compared to the spatial components (PTs 1-3) by increasing the range of variability in species abundance fluctuations. Spatial limitations, however, mean that we cannot track fish species that move out of the study area. Moreover, limited sample sizes forced us to conduct the analysis on the scale of the seven RAs which may mask fine-scale spatial variability. However, as mentioned previously, we performed an additional analysis at the spatial scale of 168 statistical rectangles and found similar results (Fig. S2.3).

Overall, the results of our study have implications for the design of future modelling studies with respect to spatial structure and trophic group composition of fish assemblages, for example in food web models (Stäbler *et al.* 2016). Similarly, our results can readily inform future ecosystem-based management approaches that are multi-species or community-based compared to the prevailing single-species approaches (Lindegren *et al.* 2009; Möllmann *et al.* 2014). For example, PTA could be used to define species assemblages based on in-situ data or, with a finer spatial scale, to define areas for management based on ecology rather than current political boundaries. Furthermore, we argue and conclude that multiway statistical approaches accounting for multiple dimensions of community data are fruitful and ready for uptake in community ecology and macroecology. Ecosystems and the species they contain vary both in time and in space. Classical two-way analyses simplify this information, which is inherently three dimensional, and therefore cannot investigate the multiple interactions between these dimensions (Cichocki *et al.* 2015). Methods such as the one applied here reveal these multidimensional patterns and provide a promising tool for knowledge discovery in large-scale datasets derived from modern ecological monitoring programs.

Acknowledgment

The authors are grateful to all contributors of the North Sea International Bottom Trawl Survey, and to ICES DATRAS database who merged, cleaned and made the data open access. We thank Heather M. Patterson and the reviewers for their constructive and valuable comments made during the review process.

List of supplementary materials

Table S2.1: Biological characteristics of species, ordered by cluster. Information about the biogeography, the trophic level (TL), the maximum length (Lmax) are from Engelhard et al., 2011. Average Catch per Unit Effort (av CPUE) are calculated from the data itself.

Table S2.2: Full correlation coefficient table. Table of Pearson and RV correlation coefficient (c) with p-value (p) and adjusted p-value (ap).

Figure S2.1: Results of the Principal Tensor Analysis. Output of the PTA-k R-package (top) and selection of the four principal tensors (PTs) based on the scree-plot (bottom).

Figure S2.2: Clustering analysis of the fish species realised with K-means algorithm

Figure S2.3: Robustness analysis to data transformation and spatial scale. TD computed with (A) the method presented in the manuscript (abundance expressed in number/hour, at the scale of roundfish areas), (B) abundance expressed in biomass (catch per unit effort, expressed in kg/hour) and (C) a finer spatial resolution, at the scale of ICES rectangle (and abundance in number/hour). The three decompositions are similar, with 4 significant PT. The three first PTs show strong spatial patterns, while the PT4 shows a trend in time series.

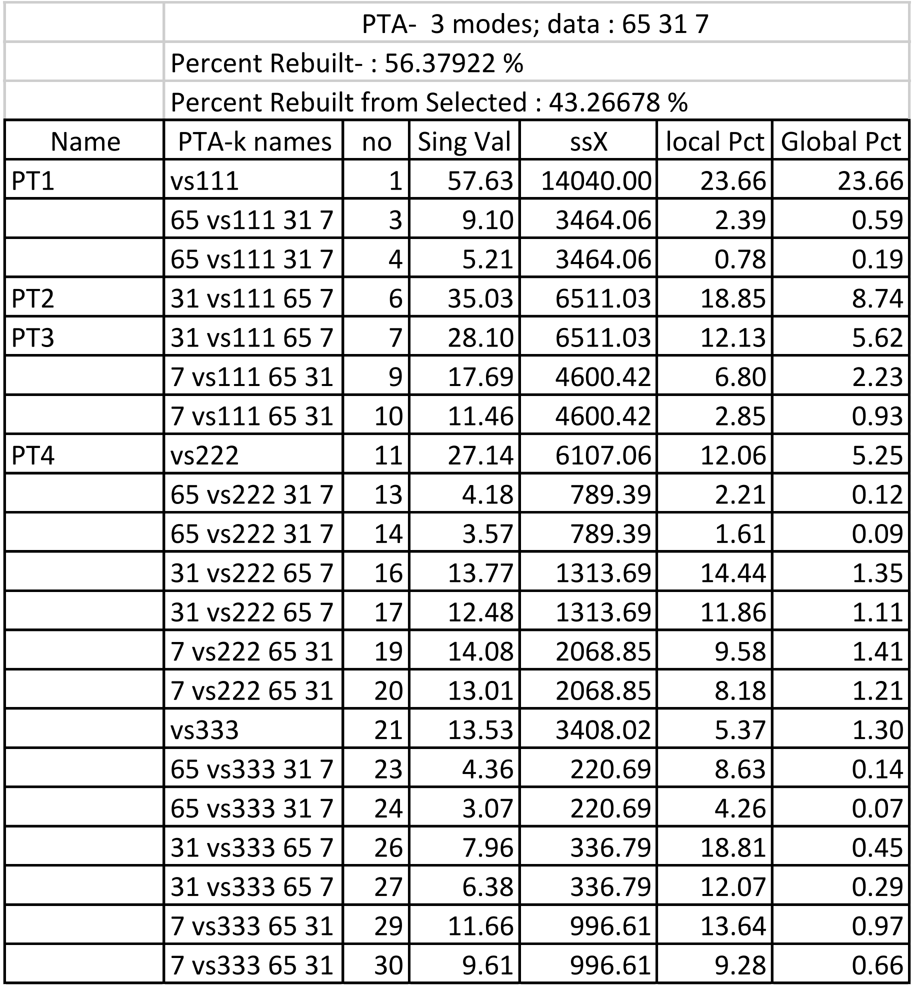
Table S2.1: Biological characteristics of species, ordered by cluster. Information about the biogeography, the trophic level (TL), the maximum length (Lmax) are from Engelhard *et al.*, 2011. Average Catch per Unit Effort (av CPUE) are calculated from the data itself.

	Species	Common name	Biogeography	TL	Lmax (cm)	av CPUE
Southern	*Agonus cataphractus*	Pogge (armed bullhead)	Boreal	3.4	21	5.0
	Ciliata mustela	Five-bearded rockling	Boreal	3.5	45	0.8
	Echiichthys vipera	Lesser weever fish	Lusitanian	4.4	15	15.2
	Enchelyopus cimbrius	Four-bearded rockling	Boreal	3.5	41	3.2
	Gaidropsarus vulgaris	Three-bearded rockling	Lusitanian	3.3	43	0.0
	Liparis liparis	Sea snail	Boreal	3.6	18	2.2
	Liparis montagui	Montagu's seasnail	Boreal	3.5	10	0.1
	Myoxocephalus scorpius	Bullrout (father lasher)	Boreal	3.9	60	2.9
	Pholis gunnellus	Butterfish (gunnel)	Boreal	3.5	25	1.0
	Raja clavata	Thornback ray	Lusitanian	3.8	90	2.5
	Solea solea	Sole	Lusitanian	3.1	70	2.9
	Taurulus bubalis	Sea scorpion	Boreal	3.6	18	0.7
	Trisopterus luscus	Bib	Lusitanian	3.7	45	3.8
Northern	*Brosme brosme*	Tusk	Boreal	4	100	0.0
	Glyptocephalus cynoglossus	Witch	Boreal	3.1	60	0.9
	Helicolenus dactylopterus	Bluemouth redfish	Atlantic	3.8	44	0.2
	Hippoglossus hippoglossus	Halibut	Boreal	4.5	200	0.0
	Lepidorhombus whiffiagonis	Megrim	Lusitanian	4.2	59	0.8
	Lophius piscatorius	Anglerfish	Lusitanian	4.4	200	0.6
	Molva molva	Common ling	Boreal	4.3	200	0.4
	Pollachius pollachius	Pollack	Boreal	4.2	130	0.3
	Pollachius virens	Saithe	Boreal	4.4	120	11.6
	Sebastes viviparus	Norway haddock	Boreal	4	35	0.2
NW Inc	*Callionymus lyra*	Common dragonet	Lusitanian	3.3	32	4.0
	Eutrigla gurnardus	Grey gurnard	Lusitanian	3.6	50	200.4
	Hippoglossoides platessoides	Long rough dab	Boreal	3.7	50	93.7
	Leucoraja naevus	Cuckoo ray	Lusitanian	3.9	70	1.0
	Limanda limanda	Dab	Boreal	3.3	40	619.4
	Melanogrammus aeglefinus	Haddock	Boreal	4.1	112	685.7
	Merlangius merlangus	Whiting	Lusitanian	4.4	70	1353.5
	Microstomus kitt	Lemon sole	Boreal	3.3	45	10.6
	Mullus surmuletus	Striped red mullet	Lusitanian	3.4	40	1.0
	Mustelus mustelus	Smoothhound	Lusitanian	3.8	150	0.1
	Myxine glutinosa	Hagfish	Atlantic	3.5	45	0.0
	Phrynorhombus norvegicus	Norwegian topknot	Boreal	4	12	0.3
	Scophthalmus rhombus	Brill	Lusitanian	3.8	75	0.1
	Squalus acanthias	Spurdog	Boreal	4.3	105	1.5
	Trisopterus esmarkii	Norway pout	Boreal	3.2	26	1828.5
SE Inc	*Arnoglossus laterna*	Scaldfish	Lusitanian	3.6	20	0.7
	Buglossidium luteum	Solenette	Lusitanian	3.3	15	7.2
	Callionymus reticulatus	Reticulate dragonet	Lusitanian	3.3	11	0.1
	Lumpenus lampretaeformis	Snake blenny	Boreal	3.6	49	0.4
	Platichthys flesus	Flounder	Lusitanian	3.2	50	1.1
	Pleuronectes platessa	European plaice	Boreal	3.3	100	44.9
	Pomatoschistus minutus	Sand goby	Lusitanian	3.2	10	0.8
	Scophthalmus maximus	Turbot	Lusitanian	4	100	0.4
	Syngnathus acus	Great pipefish	Lusitanian	3.4	46	0.5
	Syngnathus rostellatus	Nilsson's pipefish	Lusitanian	3.7	17	0.2
	Trachinus draco	Greater weever fish	Lusitanian	4.2	40	0.2
	Zeugopterus punctatus	Topknot	Lusitanian	4	25	0.1
Increasing	*Callionymus maculatus*	Spotted dragonet	Lusitanian	3.3	16	0.9
	Chelidonichthys cuculus	Red gurnard	Lusitanian	3.8	50	2.5
	Chelidonichthys lucerna	Tub gurnard	Lusitanian	3.7	75	0.1
	Entelurus aequoreus	Snake pipefish	Lusitanian	3.5	60	1.3
	Merluccius merluccius	European hake	Lusitanian	4.4	120	2.2
	Microchirus variegatus	Thickback sole	Lusitanian	3.3	35	0.1
	Mustelus asterias	Starry smoothhound	Lusitanian	3.7	140	0.4
	Raja brachyura	Blonde ray	Lusitanian	4	120	0.1
	Raja montagui	Spotted ray	Lusitanian	3.7	80	0.7
	Scyliorhinus canicula	Lesser spotted dogfish	Lusitanian	3.7	80	4.3
	Trisopterus minutus	Poor cod	Lusitanian	3.8	26	30.8
Decreasing	*Amblyraja radiata*	Starry ray	Boreal	4	90	8.5
	Anarhichas lupus	Wolffish (catfish)	Boreal	3.2	125	0.1
	Cyclopterus lumpus	Lumpsucker	Boreal	3.9	61	0.3
	Gadus morhua	Cod	Boreal	4.4	190	37.9

Table S2.2: Full correlation coefficient table. Table of Pearson and RV correlation coefficient (c) with p-value (p) and adjusted p-value (ap).

	Tensor Decomposition																Clusters																							
	PT1				PT2				PT3				PT4				Southern				Northern				NW Inc				SE Inc				Increasing				Decreasing			
	c	pv	apv		c	pv	apv		c	pv	apv		c	pv	apv		c	pv	apv		c	pv	apv		c	pv	apv		c	pv	apv		c	pv	apv		c	pv	apv	
SST_An	0.80	0.02	0.10	.	0.18	0.43	0.62		0.17	0.45	0.65		0.03	0.96	0.97		0.57	0.07	0.21		0.54	0.03	0.16		0.57	0.08	0.23		0.8	0.01	0.07	.	0.31	0.26	0.46		0.31	0.24	0.45	
SST_Q1	0.47	0.10	0.28		0.24	0.29	0.47		0.4	0.14	0.34		0.03	0.91	0.95		0.25	0.29	0.47		0.21	0.40	0.60		0.73	0.03	0.16		0.93	0.0016	0.038	*	0.44	0.13	0.32		0.07	0.76	0.87	
SST_var	0.51	0.08	0.23		0.26	0.27	0.46		0.28	0.23	0.44		0.02	0.87	0.92		0.24	0.28	0.47		0.27	0.26	0.46		0.65	0.05	0.17		0.96	0.0006	0.031	*	0.49	0.10	0.27		0.05	0.81	0.89	
SBT_An	0.73	0.02	0.13		0.13	0.41	0.60		0.02	0.76	0.87		0.02	0.82	0.89		0.86	0.0020	0.043	*	0.23	0.29	0.47		0.46	0.11	0.28		0.28	0.2308	0.44		0.03	0.72	0.86		0.68	0.006	0.071	.
SBT_Q1	0.64	0.04	0.16		0.39	0.15	0.35		0.05	0.78	0.88		0.05	0.74	0.87		0.32	0.18	0.40		0.56	0.03	0.16		0.39	0.17	0.37		0.89	0.0012	0.031	*	0.59	0.06	0.19		0.13	0.55	0.73	
SBT_var	0.94	0.0012	0.031	*	0.01	0.95	0.96		0.03	0.66	0.83		0.03	0.69	0.85		0.81	0.010	0.073	.	0.45	0.08	0.24		0.61	0.04	0.17		0.67	0.03	0.16		0.06	0.59	0.76		0.46	0.10	0.28	
SSS_An	0.45	0.10	0.28		0.31	0.20	0.41		0.14	0.40	0.60		0.04	0.70	0.85		0.18	0.36	0.57		0.3	0.20	0.41		0.46	0.11	0.28		0.86	0.01	0.07	.	0.53	0.08	0.23		0.03	0.84	0.90	
SSS_Q1	0.68	0.02	0.13		0.20	0.37	0.58		0.14	0.51	0.70		0.1	0.62	0.78		0.4	0.15	0.35		0.49	0.05	0.17		0.49	0.11	0.28		0.84	0.01	0.07	.	0.39	0.15	0.35		0.18	0.47	0.67	
SSS_var	0.08	0.76	0.87		0.41	0.14	0.34		0.31	0.27	0.46		0.18	0.54	0.73		0.09	0.73	0.87		0.07	0.76	0.87		0.2	0.51	0.70		0.39	0.14	0.34		0.48	0.04	0.17		0.27	0.25	0.45	
SBS_An	0.83	0.003	0.055	.	0.08	0.54	0.72		0.02	0.79	0.88		0.02	0.78	0.88		0.53	0.05	0.18		0.75	0.008	0.071	.	0.28	0.23	0.44		0.64	0.04	0.16		0.22	0.30	0.48		0.28	0.23	0.44	
SBS_Q1	0.84	0.005	0.071	.	0.06	0.60	0.76		0.02	0.78	0.88		0.03	0.73	0.87		0.56	0.05	0.17		0.73	0.009	0.071	.	0.29	0.22	0.44		0.61	0.04	0.16		0.18	0.34	0.54		0.32	0.19	0.41	
SBS_var	0.90	0.0008	0.031	*	0.13	0.52	0.71		0.05	0.90	0.94		0.04	0.94	0.96		0.67	0.02	0.14		0.55	0.05	0.17		0.54	0.07	0.21		0.79	0.010	0.073	.	0.25	0.29	0.47		0.36	0.18	0.40	
Chl_An	0.88	0.0024	0.048	*	0.10	0.48	0.67		0.02	0.80	0.89		0	1.00	1.00		0.98	0.0006	0.031	*	0.31	0.22	0.44		0.54	0.06	0.19		0.38	0.14	0.34		0.01	0.85	0.91		0.72	0.015	0.097	.
Chl_Q1	0.92	0.0004	0.031	*	0.08	0.59	0.76		0.02	0.87	0.92		0	1.00	1.00		0.97	0.0048	0.071	.	0.35	0.16	0.35		0.56	0.04	0.17		0.45	0.11	0.28		0.01	0.91	0.94		0.68	0.04	0.17	
Chl_var	0.83	0.006	0.071	.	0.15	0.41	0.60		0.04	0.77	0.88		0.02	0.96	0.97		0.97	0.0010	0.031	*	0.26	0.25	0.45		0.55	0.05	0.17		0.34	0.17	0.37		0.04	0.79	0.88		0.74	0.02	0.13	
Fishing Otter	0.52	0.04	0.16		0.31	0.20	0.41		0.12	0.59	0.76		0.23	0.31	0.50		0.19	0.23	0.44		0.88	0.03	0.16		0.05	0.81	0.89		0.46	0.04	0.17		0.47	0.03	0.16		0.05	0.55	0.73	
Fishing Beam	0.64	0.03	0.16		0.01	0.87	0.92		0.06	0.68	0.84		0.05	0.71	0.86		0.52	0.08	0.23		0.28	0.15	0.35		0.52	0.03	0.16		0.55	0.04	0.16		0.08	0.57	0.74		0.2	0.29	0.47	
Beam+Otter	0.02	0.81	0.89		0.24	0.27	0.46		0.31	0.20	0.41		0.07	0.56	0.73		0.09	0.59	0.76		0.17	0.40	0.60		0.24	0.29	0.47		0.02	0.82	0.89		0.17	0.36	0.56		0.06	0.63	0.79	
Climate AMO	0.40	0.03	0.16		0.40	0.04	0.16		0.4	0.04	0.16		0.74	0.009	0.071	.	0.7	0.009	0.071	.	-0.72	0.011	0.073	.	0.74	0.010	0.071	.	0.74	0.009	0.071	.	0.74	0.006	0.071	.	-0.74	0.006	0.071	.
Climate NAO	0.17	0.20	0.41		0.17	0.20	0.41		0.17	0.20	0.41		-0.06	0.40	0.60		-0.01	0.49	0.68		0.03	0.46	0.65		-0.06	0.39	0.60		-0.06	0.40	0.60		-0.06	0.39	0.60		0.06	0.41	0.60	
Depth	0.88	0.008	0.071	.	0.36	0.42	0.61		-0.27	0.56	0.73		-0.3	0.51	0.70		0.66	0.10	0.28		-0.96	0.0007	0.031	*	-0.38	0.41	0.60		0.75	0.05	0.17		-0.52	0.23	0.44		-0.5	0.25	0.45	

Figure S2.1: Results of the Principal Tensor Analysis. Output of the *PTA-k* R-package (top) and selection of the four principal tensors (PTs) based on the scree-plot (bottom).



	PTA- 3 modes; data : 65 31 7					
	Percent Rebuilt- : 56.37922 %					
	Percent Rebuilt from Selected : 43.26678 %					
Name	PTA-k names	no	Sing Val	ssX	local Pct	Global Pct
PT1	vs111	1	57.63	14040.00	23.66	23.66
	65 vs111 31 7	3	9.10	3464.06	2.39	0.59
	65 vs111 31 7	4	5.21	3464.06	0.78	0.19
PT2	31 vs111 65 7	6	35.03	6511.03	18.85	8.74
PT3	31 vs111 65 7	7	28.10	6511.03	12.13	5.62
	7 vs111 65 31	9	17.69	4600.42	6.80	2.23
	7 vs111 65 31	10	11.46	4600.42	2.85	0.93
PT4	vs222	11	27.14	6107.06	12.06	5.25
	65 vs222 31 7	13	4.18	789.39	2.21	0.12
	65 vs222 31 7	14	3.57	789.39	1.61	0.09
	31 vs222 65 7	16	13.77	1313.69	14.44	1.35
	31 vs222 65 7	17	12.48	1313.69	11.86	1.11
	7 vs222 65 31	19	14.08	2068.85	9.58	1.41
	7 vs222 65 31	20	13.01	2068.85	8.18	1.21
	vs333	21	13.53	3408.02	5.37	1.30
	65 vs333 31 7	23	4.36	220.69	8.63	0.14
	65 vs333 31 7	24	3.07	220.69	4.26	0.07
	31 vs333 65 7	26	7.96	336.79	18.81	0.45
	31 vs333 65 7	27	6.38	336.79	12.07	0.29
	7 vs333 65 31	29	11.66	996.61	13.64	0.97
	7 vs333 65 31	30	9.61	996.61	9.28	0.66

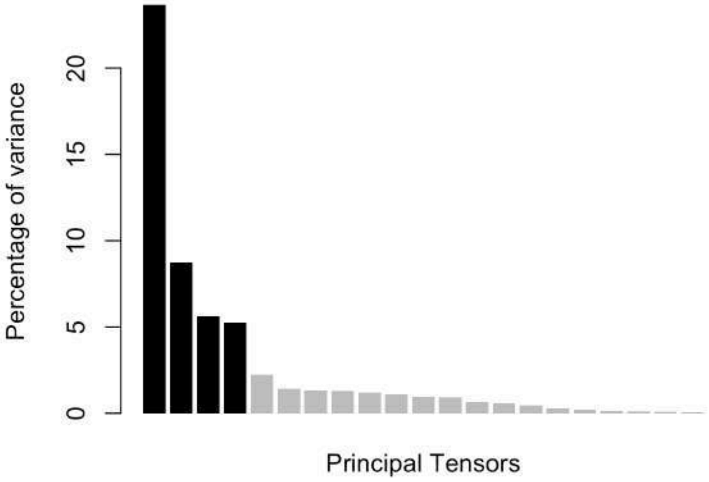


Figure S2.2: Clustering analysis of the fish species realised with K-means algorithm

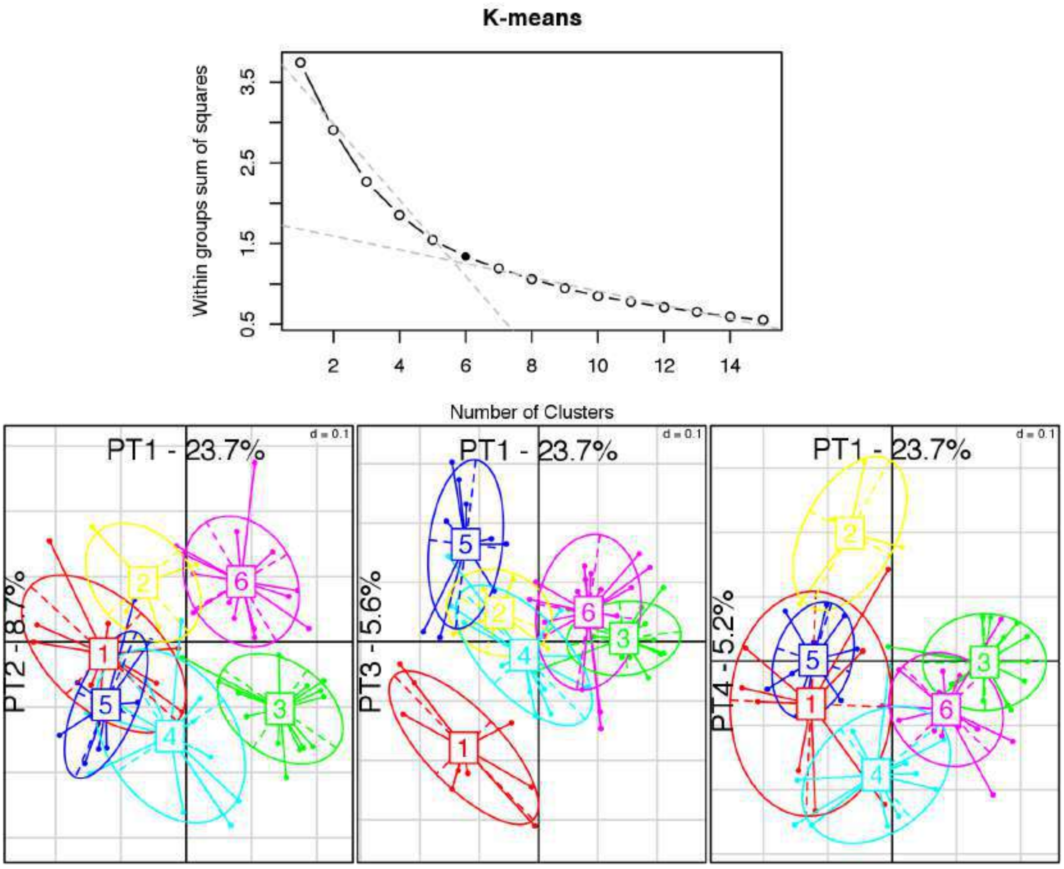
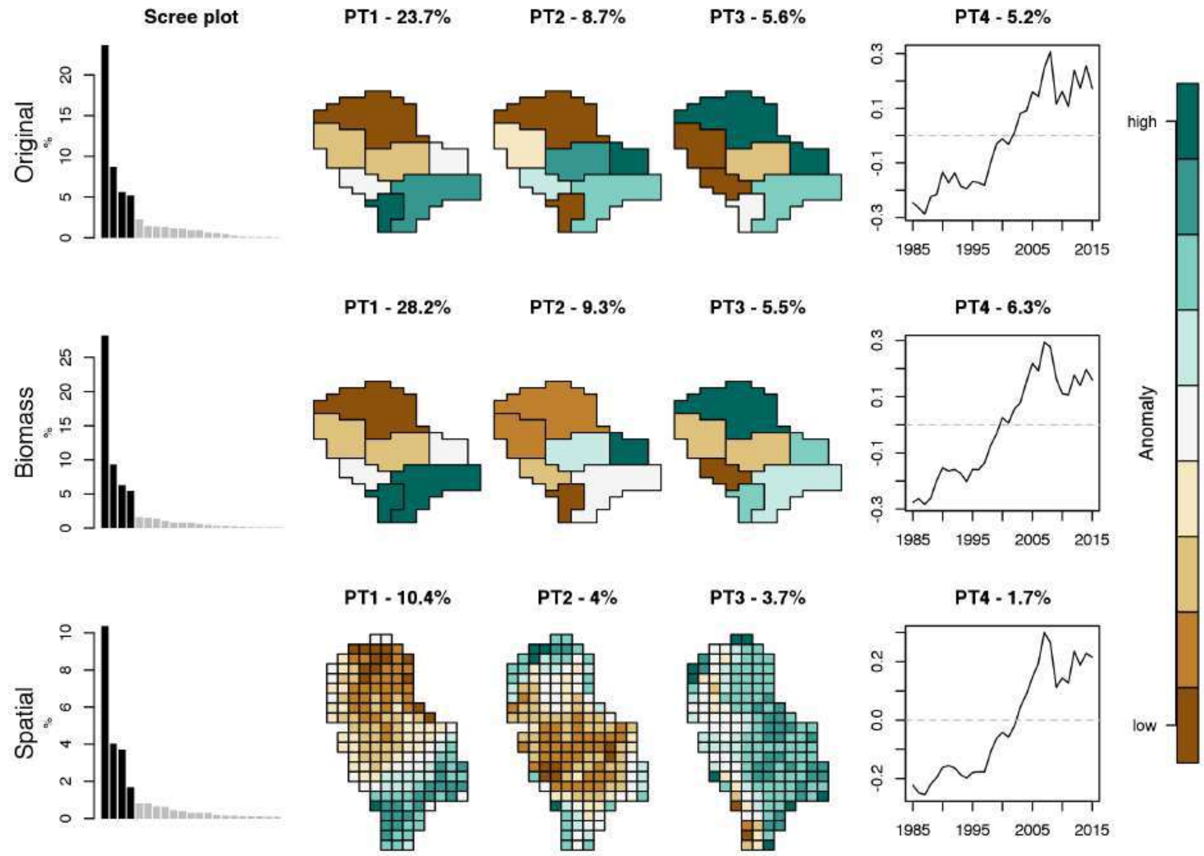


Figure S2.3: Robustness analysis to data transformation and spatial scale. TD computed with (A) the method presented in the manuscript (abundance expressed in number/hour, at the scale of roundfish areas), (B) abundance expressed in biomass (catch per unit effort, expressed in kg/hour) and (C) a finer spatial resolution, at the scale of ICES rectangle (and abundance in number/hour). The three decompositions are similar, with 4 significant PT. The three first PTs show strong spatial patterns, while the PT4 shows a trend in time series.



Chapter 3

3D view on biodiversity changes

Joerael Elliot, Collective computation (2016)
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Title: A three-dimensional view on biodiversity changes: spatial, temporal and functional perspectives on fish communities in the Baltic Sea

Authors: Romain Frelat[1]*, Alessandro Orio[2], Michele Casini[2], Andreas Lehmann[3], Bastien Mérigot[4], Saskia A. Otto[1], Camilla Sguotti[1] and Christian Möllmann[1]

[1] University of Hamburg, Institute for Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability (CEN), Hamburg, Germany.

[2] Swedish University of Agricultural Science, Department of Aquatic Resources, Institute of Marine Research, Lysekil, Sweden

[3] GEOMAR Helmholtz Centre for Ocean Research, Kiel, Germany

[4] University of Montpellier, UMR Marbec (CNRS, IFREMER, IRD, UM), Sète, France

* Corresponding author: Romain Frelat, romain.frelat@uni-hamburg.de

Abstract

Fisheries and marine ecosystem-based management requires a holistic understanding of the dynamics of fish communities and their responses to changes in environmental conditions. Environmental conditions can simultaneously shape the spatial distribution and the temporal dynamics of a population, which together can trigger changes in the functional structure of communities. Here, we developed a comprehensive framework based on complementary multivariate statistical methodologies to simultaneously investigate the effects of environmental conditions on the spatial, temporal and functional dynamics of species assemblages. The framework is tested using survey data collected during more than 4,000 fisheries hauls over the Baltic Sea between 2001 and 2016. The approach revealed the Baltic fish community to be structured into three sub-assemblages along a strong and temporally stable salinity gradient decreasing from West to the East. Additionally, we highlight a mismatch between species and functional richness associated with a lower functional redundancy in the Baltic Proper compared to other sub-areas, suggesting an ecosystem more susceptible to external pressures. Based on a large dataset of community data analyzed in an innovative and comprehensive way, we could disentangle the effects of environmental changes on the structure of biotic communities –key information for the management and conservation of ecosystems.

Keywords: Baltic Sea, demersal fish community, functional traits, multivariate analysis, spatio-temporal dynamics, species distribution.

Introduction

Understanding the impact of environmental conditions on the dynamics and diversity of fish communities is an essential preliminary step for a better prediction of their responses to future changes (Burrows *et al.* 2011) and for integrative ecosystem-based management (Pikitch *et al.* 2004; Levin *et al.* 2009; Möllmann *et al.* 2014). However, changing environmental conditions can impact biotic communities in multiple ways, and be responsible for changes in structure and function of ecosystems (McGill *et al.* 2006; Conversi *et al.* 2015). Environmental conditions are reported to shape the spatial distribution of species (Perry *et al.* 2005; Poloczanska *et al.* 2016; Smoliński & Radtke 2017), influence the temporal dynamics of communities (Rouyer *et al.* 2008; Möllmann *et al.* 2009; Hiddink & Coleby 2012), and select or favour some functional traits (Brind'Amour *et al.* 2011; Wesuls *et al.* 2012; Asefa *et al.* 2017). To the best of our knowledge, no holistic empirical study has investigated simultaneously the effects of environmental changes on (1) spatial distribution, (2) temporal dynamics and (3) functional structure of species assemblages likely due to a lack of appropriate statistical methodologies.

The development of multivariate statistical analyses during the past 20 years has provided ecologists with tools to comprehensively analyze community data and investigate the link between species assemblages, environmental conditions and functional traits (Dray *et al.* 2003; Dray & Dufour 2007; Legendre & Legendre 2012). Most notably, two frameworks were developed to extend the multivariate methods traditionally limited to the study of the common structure of a pair of data tables (e.g. matrices of species abundance and environmental data, Supplementary Table S3.1). First, the pair of data tables was extended to study a sequence of paired tables, sequence that could represent different times or spatial locations (Thioulouse *et al.* 2004; Thioulouse 2011). These approaches proved to bring new insights into the spatio-temporal structuring of ecological communities (Mazzocchi *et al.* 2012; Kidé *et al.* 2015; Chamaille-Jammes *et al.* 2016). Second, the pair of data tables was extended to a triplet of data tables (Dray & Legendre 2008; Pavoine *et al.* 2011; Dray *et al.* 2014) and allowed the analysis of additional information about traits to discern the traits selected by environmental conditions (Brind'Amour *et al.* 2011; Wesuls *et al.* 2012; Asefa *et al.* 2017). However, these two frameworks are often used separately, limiting studies to investigate the effect of the environment either on the spatio-temporal dynamics of communities or on the selection of traits.

Here, we developed a comprehensive framework based on complementary multivariate statistical methodologies to simultaneously investigate the effects of environmental conditions on the spatial, temporal and functional dynamics of species assemblages, using the Baltic Sea fish community as a case study. The Baltic Sea is a semi-enclosed sea strongly affected by anthropogenic pressures and climate change (Möllmann *et al.* 2009; Korpinen *et al.* 2012; Andersen *et al.* 2015). A strong west-east salinity gradient (Fig. 3.1A) allows the coexistence of approximatively 200 fish species (Ojaveer *et al.* 2010) ranging from marine to limnic species (Bonsdorff 2006). The species assemblages are dominated by clupeids, sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), that together with cod (*Gadus morhua*) and flounder (*Platichthys flesus*) account on average for 90% of the catches. Furthermore, regional climate change models predict an increase in temperature and a decrease in salinity but a high uncertainty remains about the impact of climate change on fish stocks (MacKenzie *et al.* 2007; Hiddink & Coleby 2012; Niiranen *et al.* 2013). The recent increase of anoxic and hypoxic areas in the central Baltic Sea also creates additional pressure on the demersal fish communities (Hinrichsen *et al.* 2011; Casini *et al.* 2016; Neumann *et al.* 2017). Therefore, it is urgent to investigate the role of environmental condition on the spatio-temporal dynamics and structures of fish assemblages in this area.

Here we provide a coherent and comprehensive analysis of spatial, temporal and functional dynamics of an entire fish community using modern multivariate statistical approaches. In our case study, we identified sub-assemblages of the Baltic Sea fish community that co-exist and are susceptible to similar environmental conditions. Comprehensive multivariate statistical analyses as suggested and demonstrated here provide crucial information needed for coherent ecosystem-based management of the oceans.

Material and Methods

Fish abundance data

Abundance data were collected during the *Baltic International Trawl Survey* (BITS) (ICES 2014). Since 2001, the survey has been carried out with a harmonized sampling scheme and a standard gear to sample the demersal fish community in the Baltic Sea. This sampling scheme consists of trawl hauls with a duration of 30 minutes on average, carried out at a speed of 3 knots with a demersal otter trawl gear best suited for sampling demersal fish such as gadoids and flatfish. Because of poor survey coverage in shallow areas, we excluded hauls carried out at depths shallower than 20 m. We only included valid hauls carried out during the first quarter of the year (15 February – 31 March). In total, our dataset included information from 4086 hauls carried out between 2001 and 2016. With around 250 hauls per year on average, the sampling has a good spatial coverage of the area defined from the Kattegat to the northern Baltic proper (no hauls were recorded at latitude higher than 59°N). The original dataset was downloaded from the ICES Database for Trawl Surveys (DATRAS; http://datras.ices.dk/ Home/Default.aspx; data downloaded on the 22nd of June 2017).

We conducted pre-processing checks to fix mis-identified species and removed non fish species following previous recommendations (Hiddink & Coleby 2012; Fung *et al.* 2012). We aggregated species to genus or family level when species were not consistently identified (only for *Gobiidae* and *Callionymus* spp.) as suggested by Fung *et al.* (2012). Among the pelagic species, only sprat and herring were retained in the analyses since they are the two species with the highest catches in the BITS and are consistently caught in almost all the hauls. Other pelagic fish species are not properly sampled by the otter trawl gear and were removed from the dataset. Details of data cleaning are given in Table S3.2. Furthermore, we excluded rare species that occurred in less than 1% of our dataset (i.e. recorded in less than 40 hauls). The procedure identified 60 rare species (61% of all recorded species), that in total correspond to less than 0.01% of the total abundance. The final community dataset consisted of abundance values (expressed in number per trawling hour) of 33 species from 4086 hauls.

Traits dataset

Information on the life history of Baltic fish species was retrieved from a previous study (Pecuchet *et al.* 2016) and the Fishbase database (Froese & Pauly 2017). Specifically, trophic level and maximum length (in cm) were extracted from Fishbase (Froese & Pauly 2017). Mean fecundity (in number of eggs spawned per adult female in one spawning season), the shape of the caudal fin (in 5 categories: rounded, truncated, emarginated, forked and continuous) and the body shape (in 4 categories: gadoid-like, flat, elongated and eel-like) were obtained from Pecuchet *et al.* (2016). In total, two qualitative and three quantitative traits were used to characterize the 33 fish species. These five different traits are complementary and describe the diet, habitat and reproduction for all species included in the study (Pecuchet *et al.* 2016). For graphical visualization, species were identified in accordance with their FAO 3-Alpha Species Codes provided in Table 3.1 (ASFIS, http://www.fao.org/fishery/collection/asfis/en, version Feb. 2017).

Table 3.1: Fish species found in the Baltic Sea, ordered per spatial cluster. Traits are derived from Pecuchet et al., 2016, 2017; Froese and Pauly, 2017.

	Species	FAO name	Trophic Level	Maximum length (cm)	Fecundity (# eggs)	Caudal shape	Body shape
Kattegat	*Arnoglossus laterna*	MSF	3.6	25	50,000	Rounded	Flat
	Callionymus	YVX	3.3	32	5,000	Rounded	Gadoid-like
	Eutrigla gurnardus	GUG	3.6	60	245,000	Emarginated	Gadoid-like
	Glyptocephalus cynoglossus	WIT	3.1	60	100,000	Rounded	Flat
	Hippoglossoides platessoides	PLA	3.5	83	380,000	Rounded	Flat
	Lepidorhombus whiffiagonis	MEG	4.2	60	500,000	Rounded	Flat
	Lumpenus lampretaeformis	LMJ	3.6	50	700	Rounded	Eel-like
	Melanogrammus aeglefinus	HAD	4	112	9,000,000	Emarginated	Gadoid-like
	Merluccius merluccius	HKE	4.4	140	1,000,000	Truncated	Elongated
	Microstomus kitt	LEM	3.2	65	200,000	Rounded	Flat
	Pholis gunnellus	FGN	3.5	25	100	Rounded	Eel-like
	Scophthalmus rhombus	BLL	3.8	75	5,000,000	Rounded	Flat
	Solea solea	SOL	3.1	70	300,000	Rounded	Flat
	Trachinus draco	WEG	4.2	53	57,600	Truncated	Gadoid-like
	Trisopterus esmarkii	NOP	3.2	35	220,000	Emarginated	Gadoid-like
	Trisopterus minutus	POD	3.7	40	10,000	Truncated	Gadoid-like
Western	*Agonus cataphractus*	AFT	3.4	21	3,000	Rounded	Elongated
	Gobiidae	FGX	3.2	10	3,000	Rounded	Elongated
	Limanda limanda	DAB	3.3	40	150,000	Rounded	Flat
	Merlangius merlangus	WHG	4.2	70	400,000	Truncated	Gadoid-like
	Pleuronectes platessa	PLE	3.3	100	552,000	Rounded	Flat
	Pollachius virens	POK	4.2	130	2,900,000	Emarginated	Gadoid-like
Eastern	*Clupea harengus*	HER	3.2	45	60,000	Forked	Gadoid-like
	Cyclopterus lumpus	LUM	3.8	61	100,000	Truncated	Gadoid-like
	Enchelyopus cimbrius	ENC	3.5	41	500,000	Rounded	Elongated
	Gadus morhua	COD	4.3	200	1,000,000	Truncated	Gadoid-like
	Gasterosteus aculeatus	GTA	3.4	11	350	Truncated	Gadoid-like
	Myoxocephalus quadricornis	TGQ	3.7	60	18,000	Truncated	Gadoid-like
	Myoxocephalus scorpius	MXV	3.6	60	10,000	Truncated	Gadoid-like
	Platichthys flesus	FLE	3.2	60	1,000,000	Rounded	Flat
	Scophthalmus maximus	TUR	4	100	5,000,000	Rounded	Flat
	Sprattus sprattus	SPR	3	16	10,000	Forked	Gadoid-like
	Zoarces viviparus	ELP	3.5	52	100	Continuous	Elongated

Environmental dataset

Based on the location and time of each of the 4086 hauls, we extracted nine environmental variables. We selected environmental variables based on their potential or known effect on the demersal fish community, specifically depth, local hydrographic conditions, primary productivity and large-scale climatic conditions. Additionally, we assured that the selected variables were not strongly cross-correlated (Pearson coefficient < 0.7).

Trawl depth was retrieved directly from the information provided in the BITS dataset. Five variables concerning local hydrographic conditions were derived from the Baltic Sea Ice-Ocean Model (BSIOM) (Lehmann & Hinrichsen 2000; Lehmann *et al.* 2002, 2014), a hydrodynamic model with an oxygen consumption calculation sub-module. BSIOM provided values of temperature, salinity and oxygen with a horizontal resolution of 2.5 km and 60 vertical levels. The temporal evolution of three-dimensional temperature, salinity and oxygen fields are in good agreement with hydrographic measurements of the ICES database (Lehmann *et al.* 2014). The five variables used in this study were annual bottom temperature, oxygen and salinity, surface temperature at the time of the survey and seasonality of bottom temperature. Annual bottom hydrographic conditions were selected as characteristic of the habitat (temperature: sbt_an, salinity: sbs_an, and oxygen: oxb_an). Average surface temperature during the first quarter (sst_q1) was selected as a snapshot of the hydrographic conditions at the time of the survey. The seasonality of bottom temperature (sbt_ra) was estimated as the range between average monthly temperatures and is an indicator of seasonal variation of the benthic habitat. Two variables concerning primary productivity were estimated from the Chlorophyll *a* concentration ($mg.m^{-3}$) of the GlobColour project (Maritorena *et al.* 2010), merging Ocean Colour products from different sensors. We used a monthly averaged dataset with a spatial resolution of 1 km, downloaded from http://hermes.acri.fr/ on 13th June 2017. The two variables selected as indicators of the primary production were Chlorophyll *a* concentrations averaged over the first quarter (chl_q1) and over the previous year (chl_an). Large-scale climate conditions were represented in our analysis by the North Atlantic Oscillation (NAO) index (Hurrell 1995), which indicates high frequency (7-25 years) atmospheric variations and is known to affect Baltic biotic communities (Hänninen *et al.* 2000; Möllmann *et al.* 2009). The NAO time series was downloaded from the climate indices platform of the Earth System Research Laboratory: http://www.esrl.noaa.gov/psd/data/climateindices/list/ on 2nd June 2017.

Multi-tables multivariate analyses

First, each dataset (i.e. species abundance, species traits and environmental data) was analyzed according to appropriate ordination methods corresponding to the nature of the variables (Fig. 3.1B, Table S3.1). Correspondence analysis (CA) was computed on the fish abundance dataset (a matrix of species by sample). CA is well suited for abundance data along large environmental gradient because species communities often show a unimodal distribution along a gradient and, using the chi-square distance, CA can highlight differences of species composition profiles (Legendre & Gallagher 2001; Greenacre 2017). Abundance was previously log-transformed (x+1) to reduce the influence of the dominant species in the analysis of community structure. Principal component analysis (PCA) was performed on the environmental dataset with 9 quantitative variables (a matrix of environment variables by sample) using the row weights (corresponding to the samples) from the previous CA on the fish abundance dataset in order to permit the comparison between species distribution and environmental conditions. The trait dataset (a matrix of species by trait) contained a mix of quantitative and qualitative variables and was analyzed using the Hill and Smith method (Hill & Smith 1976). This method combined a PCA on quantitative variables and a multiple correspondence analysis on qualitative variables. Species were weighted according to column weights in the previous CA on the fish abundance dataset, in order to permit the comparison between species distribution and species traits.

Secondly, we used within and between-group analysis to assess and separate spatial and temporal variabilities, with the year of sampling as grouping variable (Dolédec & Chessel 1987; Franquet *et al.* 1995). Between-group analysis is analogous to an ordination of the table of group means. In other words, it seeks to reveal the main temporal pattern by looking for the highest differences among years. Within-group analysis is the reverse of between-group analysis, i.e. it is the ordination of the residuals among initial data and group means. It removes the effect of the grouping variable and analyses the remaining variability, so in our case the spatial variability.

Thirdly, co-inertia analysis (COA) was used to link fish community composition with environmental conditions by coupling these two data tables (Dray *et al.* 2003, 2014). COA is an unconstrained symmetric analysis that searches for axes that maximize the covariance between the samples of both data tables. We applied COA on the results of the between and within-group analysis, resulting in the so called Between-group co-inertia analysis (BGCOA) and the Within-group co-inertia analysis (WGCOA) (Thioulouse 2011). BGCOA reveals the temporal co-dynamics between fish species and the environment. WGCOA shows the spatial structure of the fish community that could be explained by environmental conditions. Beforehand, the association between the two tables was tested using a Monte-Carlo permutation test and the RV coefficient (Heo & Gabriel 1998). The RV coefficient is a generalization of the Pearson's correlation coefficient for matrices (instead of vectors). A permutation test with 1,000 random permutations was performed to evaluate if the association between the two data tables was significantly stronger than expected by chance. In the cases that the p-value was higher than 0.05, the results of the COA were not analyzed and are not presented in the Results section.

Finally, fourth-corner and RLQ methods were used to assess the link between the species trait composition and environmental variation (Dolédec *et al.* 1996; Dray & Legendre 2008; Dray *et al.* 2014). The fourth-corner method is a permutation test to evaluate the pairwise association between traits and environmental variables, measured by a Pearson's correlation coefficient. We used a combination of permutations of samples and of species to correct for inflated type I error (Dray & Legendre 2008). RLQ is a multivariate method, that assess the trait-environment relationships (Dolédec *et al.* 1996). Partial RLQ takes into account the partition of environmental variation in within and between-groups analysis (Wesuls *et al.* 2012). In the case that none of the relationships between species traits and the environment was significant in the fourth-corner test, the results of the RLQ analysis are not presented in the Results section.

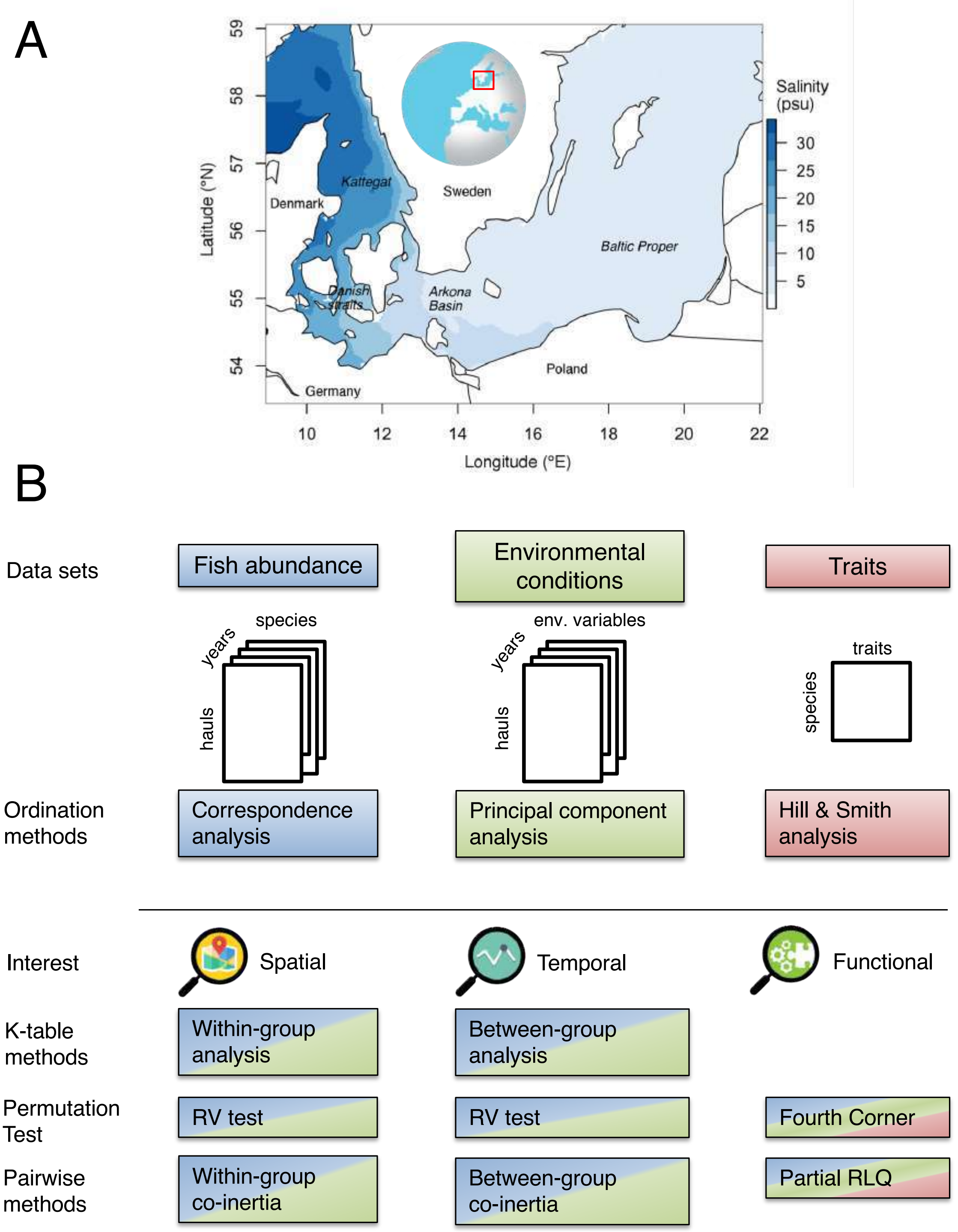


Figure 3.1: Overview of the study. (A) Map of the Baltic Sea with surface salinity of January 2015 represented in scales of blue. (B) Schematic representation of the different dataset and the multivariate methods used for their analysis. A description of the methods can be found in Table S3.2

Definition and characterization of spatial sub-assemblages

We defined sub-assemblages of Baltic Sea fish species that share similar spatial distributions and hence are favoured by similar environmental conditions. We computed Euclidean distances between fish species from the projection of species on the PCs of the WGCOA, and subsequently conducted a hierarchical cluster analysis based on Ward's criterion (Ward 1963). Based on a graphical interpretation of the dendrogram, we selected the number of clusters. The robustness of the selected number of clusters and of the clustering solution was tested by comparison with the alternative k-means cluster analysis. The clustering provided a simplification of the fish community into fewer sub-assemblages sharing similar spatial distributions. We characterize these sub-assemblages by looking at their temporal dynamics and functional richness. Functional richness was calculated as the area of the convex hull on the functional space, i.e. the volume of the functional space occupied by the community(Villéger *et al.* 2008). The functional space is defined from species projections on the principal components of the previous Hill and Smith analysis.

Software and sources

All statistical analyses were conducted in the programming environment R 3.3 (R Core team 2017). The ade4 package (Dray & Dufour 2007) was used to compute the multivariate analyses. The functional richness was calculated with the FD R package (Laliberté & Legendre 2010). Maps were created with the mapdata package (Becker *et al.* 2016). The cleaned datasets and the R-script are available in the Supplementary Material at *ICESJMS* online version of the article.

Results

Spatial distribution of the fish community linked with environment

The structure of the fish community in the Baltic Sea was strongly linked with salinity conditions and depth (Fig. 3.2). The first two principal components of the within-group co-inertia analysis (WGCOA) explained 95% of the covariance between fish abundance and environmental variables. The first principal component (PC1, 87% of the covariance) separated fish species favouring highly saline waters in the Kattegat, against fish species inhabiting less saline waters in the Baltic Proper (Fig. 3.2A&B). The salinity gradient was also associated with higher bottom temperatures (sbt_an), higher primary production (chl_q1) and shallower waters (Fig. 3.2F). Most of the fish species had a negative score on PC1 (Fig. 3.2E, left side on the x-axis), i.e. were located in highly saline waters. The second PC, explaining only 8% of the covariance, represented mainly the differences between shallow and deep waters (Fig. 3.2C&D). Deep basins were also associated with lower seasonal variation in bottom temperature and lower oxygen content (Fig. 3.2F). Some species strongly preferred shallow waters (*Scophtalmus maximus*, TUR), while others were caught mainly in deep basins (*Enchelyopus cimbrius*, ENC) (Fig. 3.2E).

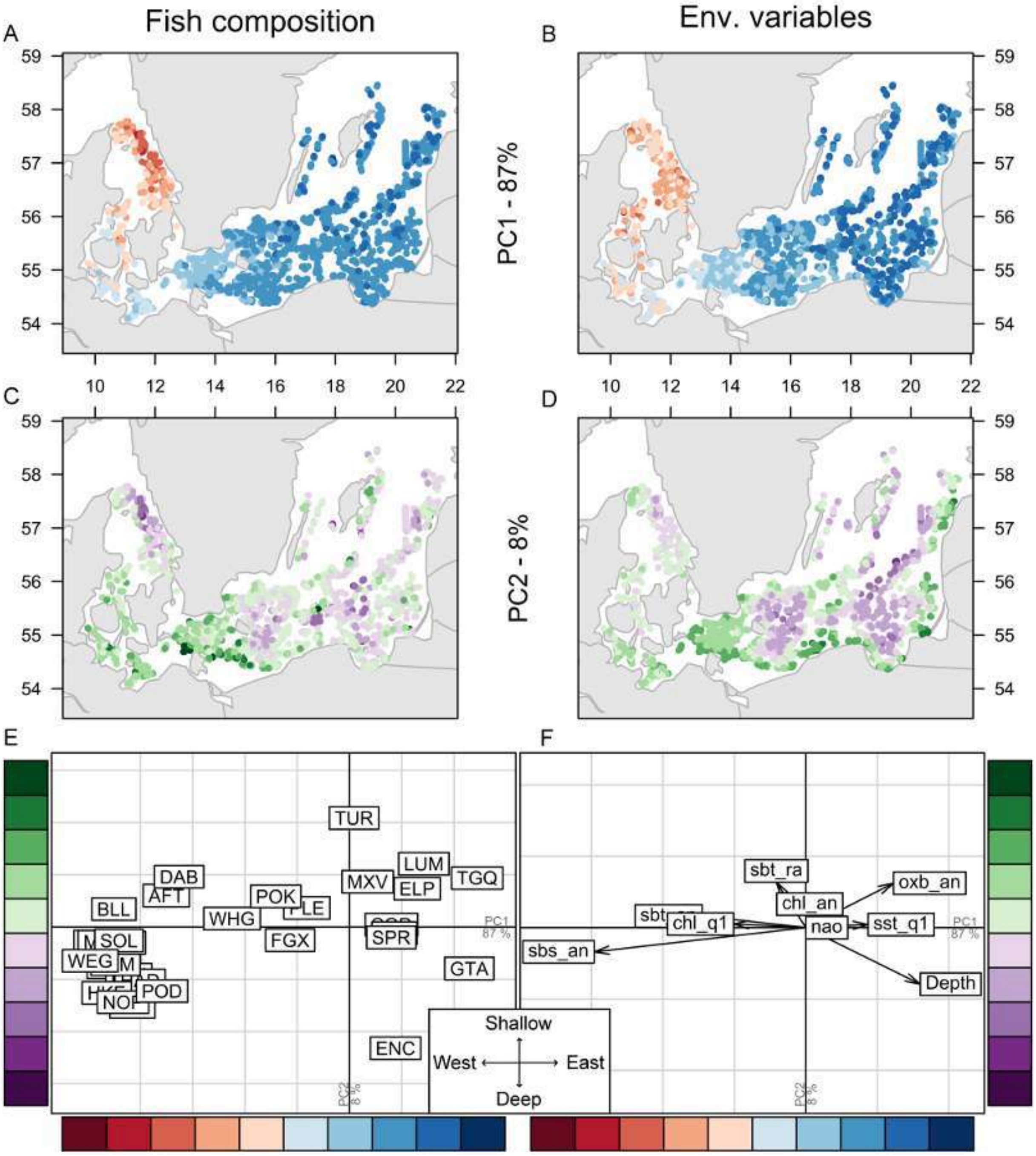


Figure 3.2: The within-group co-inertia analysis summarized the spatial links between community composition and environmental conditions in two Principal Components (PC). The red to blue colour gradient represents the hauls' score on the PC1 based on fish composition (A) or environmental variables (B). The purple to green gradient represents the hauls' score on PC2 based on fish composition (C) or environmental variables (D). The link between fish composition and environmental conditions can be visualized by the scores on the two first PCs of fish species (E) and environmental variables (F). Species are represented following the 3-letters code shown in Table 3.1. The names of the environmental variables showing low scores on the PCs were abbreviated: sbt_an is the annual bottom temperature, sst_q1 is the surface temperature during the first quarter, chl_q1 and chl_an are chlorophyll *a* concentrations averaged over the first quarter and over the previous year, respectively.

Three sub-assemblages of the Baltic Sea fish community were identified with hierarchical clustering analysis based on their PC scores derived by the WGCOA (Fig. 3.3A, as also confirmed by K-means, Supplementary Fig. S3.1). The sub-assemblages grouped species according to their spatial distribution and to whether they were sharing similar environmental conditions. The differences between sub-assemblages were mainly defined along PC1 (Fig. 3.3B, x-axis), in other words were strongly linked to the west-east salinity gradient. A sub-assemblage of 16 *Kattegat* fish species (Table 3.1) were favoured by high saline waters, therefore inhabiting only the Kattegat (latitude higher than 56°N and longitude lower than 13°E). The *Kattegat* sub-assemblage included among the most abundant species, American plaice (*Hippoglossoides platessoides*, PLA), norway pout (*Trisopterus esmarkii*, NOP), dragonets (*Callionymus spp.*, YVX) and greater weever (*Trachinus draco*, WEG). The cluster analysis identified another sub-assemblage of 6 *Western Baltic* fish species (Table 3.1), adapted to middle salinity conditions, with a distribution ranging from the Kattegat to the Arkona basin (longitude lower than 15°E). The *Western Baltic* fish species included dab (*Limanda limanda*, DAB), whiting (*Merlangius merlangus*, WHG) and European plaice (*Pleuronectes platessa*, PLE). The third sub-assemblage comprised 11 *Eastern Baltic* fish species (Table 3.1) that were favoured by low salinity conditions and could potentially inhabit the entire study area, from the Kattegat to the northern Baltic proper. The *Eastern Baltic* group included sprat (*Sprattus sprattus*, SPR), herring (*Clupea harengus*, HER), cod (*Gadus morhua*, COD) and flounder (*Platichthys flesus*, FLE).

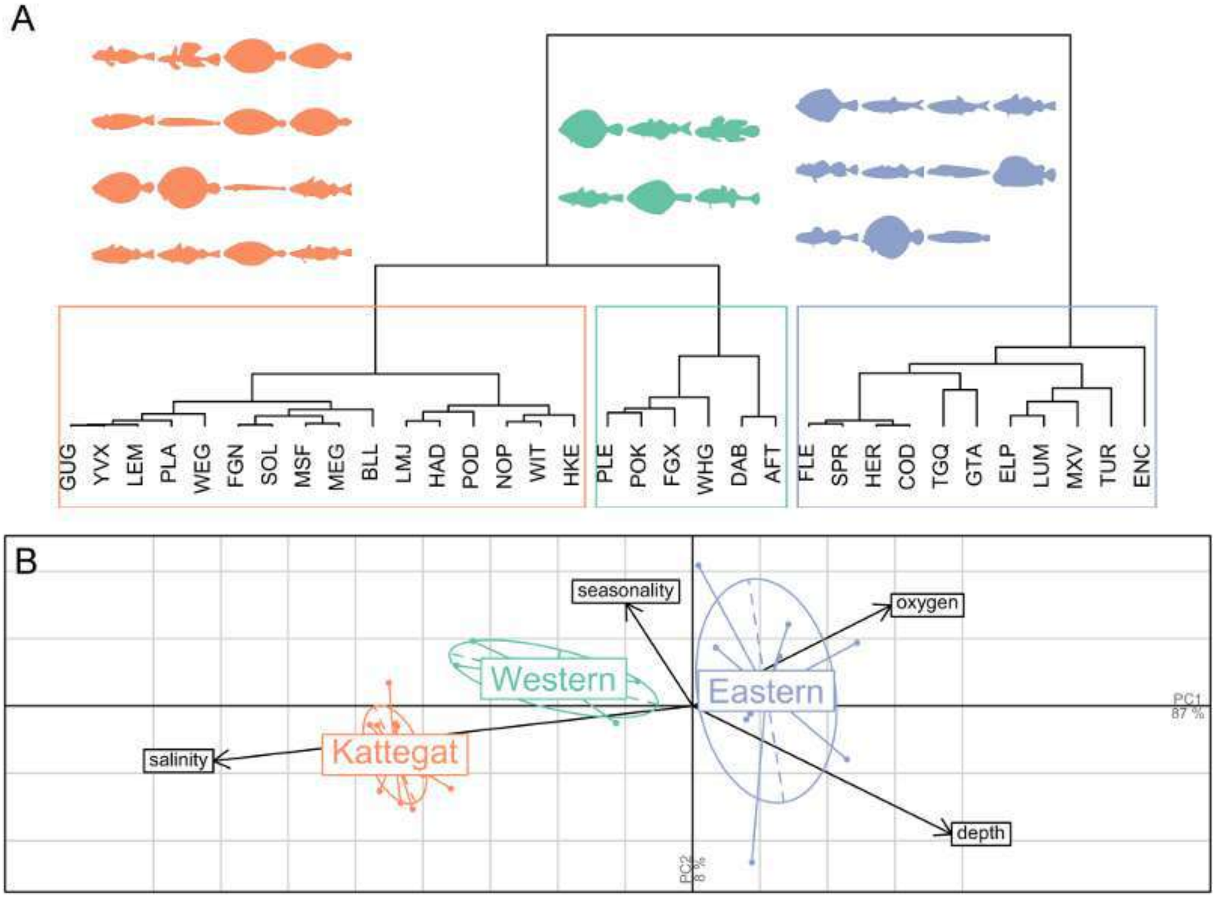


Figure 3.3: Three sub-assemblages were identified from a cluster analysis of Baltic Sea fish species according to their spatial distribution. (A) Dendrogram of the cluster analysis, suggesting three distinct groups. (B) Projection of the groups on the two first PC of the within-group co-inertia analysis. The key environmental drivers are shown on the PC.

Temporal and functional patterns of the fish community

According to the between-group analysis, the temporal dynamics of the Baltic Sea fish community accounted for only 2% of the variance of fish abundances, suggesting a relatively stable structure of fish assemblages during the period 2001-2016. The relationship with environmental dynamics, tested with a permutation test using the RV coefficient, was not significant (p-value = 0.1) (Fig. S3.2). Therefore, the results of the between-group co-inertia analysis linking fish dynamics and environment are not presented here, but rather the results of the between-group analysis of fish community dynamics (even if representing only 2% of total spatio-temporal variance). The main mode of variability in the fish community dynamics was associated with a general increase in species abundances between 2001 and 2016 (PC1, explaining 39% of the temporal variance) (Fig. 3.4A). The species with the highest relative increase were *Arnoglossus laterna* (MSF) and *Myoxocephalus quadricornis* (TGQ) (Fig. 3.4B). Some species also experienced a decrease, especially *Lepidorhombus whiffiagonis* (MEG) that was last recorded in the Baltic Sea in 2011. The second PC, explaining 19% of the temporal variance, highlighted the difference in abundances between the years 2001 and 2013 and the year 2016, which was mainly characterizing the dynamics of saithe (*Pollachius virens*, POK) (Fig. 3.4A&B).

The ordination of the five functional traits with the Hill and Smith analysis highlighted two main functional characteristics of fish species along the first two PCs, together explaining 55% of the traits variance (Fig. 3.4C). The first PC (32% of the total variance) summarized the small-large continuum. Large, high trophic level, and high fecundity species such as cod (*Gadus morhua*, COD) were separated from species that are small, with low trophic level and low fecundity such as rock gunnel (*Pholis gunnellus*, FGN) or sprat (*Sprattus sprattus*, SPR) (Fig. 3.4D). The second PC (23% of the total variance) revealed the difference between flat fish species with rounded caudal fin and the gadoid-like shaped species. The link between fish traits and environmental variables was tested with a fourth corner permutation test and no significant relation was found between individual traits and environmental variables (Fig S3.3).

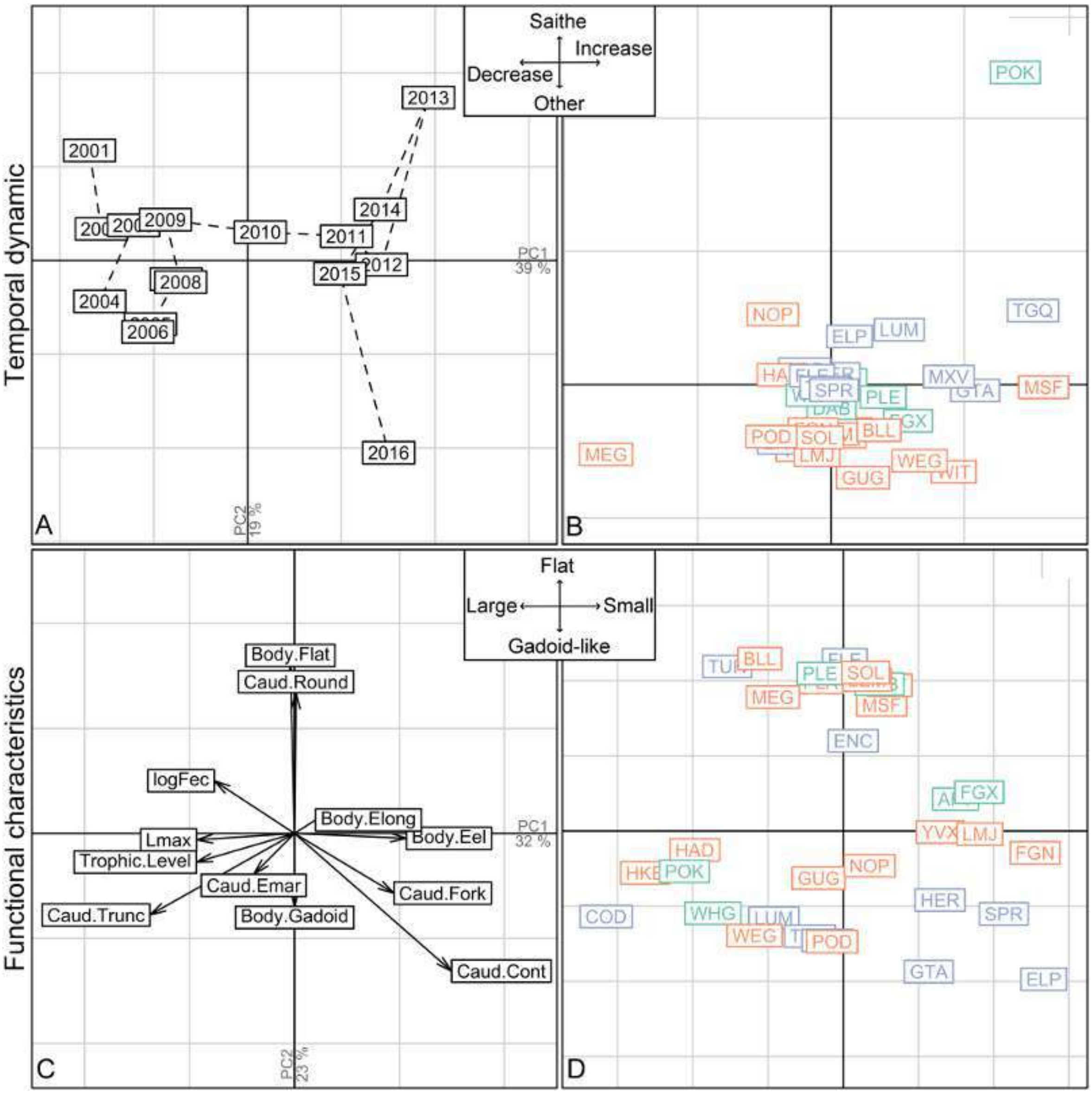


Figure 3.4: Temporal and functional characteristics of fish community. (A) The temporal dynamics revealed by between-group analysis and summarized in 2 PCs, explaining respectively 39 and 19% of the total variance. (B) Projection of fish species on these temporal PC is displayed with colour associated to their spatial sub-assemblage. (C) Functional space, revealed by Hill and Smith analysis, with 2 PCs explaining respectively 32% and 23% of the total variance. (D) Projection of fish species on these functional PC is displayed with colour associated to their spatial sub-assemblage.

Sub-assemblages characteristics and local biodiversity indices

The spatial distributions of the three sub-assemblages were nested, i.e. the *Western Baltic* sub-assemblage also inhabits the Kattegat, and the *Eastern Baltic* sub-community was present all over the surveyed area (Fig. 3.5A). The temporal dynamics were quite diverse but, on average, the abundance of fish species had increased in the observation period (grey shaded area in Fig. 3.5B). However, we observed differences between the sub-assemblages, the *Kattegat* displaying the lowest relative increase in abundances (apart of 2016) and the *Eastern Baltic* sub-assemblage the highest. Interestingly, the functional richness of the *Kattegat* and *Eastern Baltic* sub-assemblages was high (Fig. 3.5C).

The spatial overlap of the three sub-assemblages was confirmed by the community composition per haul (Fig. 3.6A&B). Hauls in the Kattegat (defined by latitude higher than 56°N and longitude lower than 13°E) were composed, on average, of 34% of *Kattegat* fish, 31% of *Western Baltic* fish and 35% of *Eastern Baltic* fish. Hauls carried out in the Baltic Proper (longitude >15°E) were nearly exclusively composed of species from the *Eastern Baltic* sub-assemblage (95% and 5% from the *Western Baltic* sub-assemblage). The spatial distribution of species richness per haul confirmed the increase of species richness along the salinity gradient (Fig. 3.6C). As expected from the nested sub-assemblages and the high functional richness of the *Eastern Baltic* sub-assemblage, functional richness had a relatively lower variation along the salinity gradient (Fig. 3.6D). The recent increase in abundance of some fish species of the *Eastern Baltic* assemblage could explain the recent increase of species richness among the less diverse hauls (the 9th decile showed an increase since 2009, while the median is more or less stable) (Fig. 3.6E).

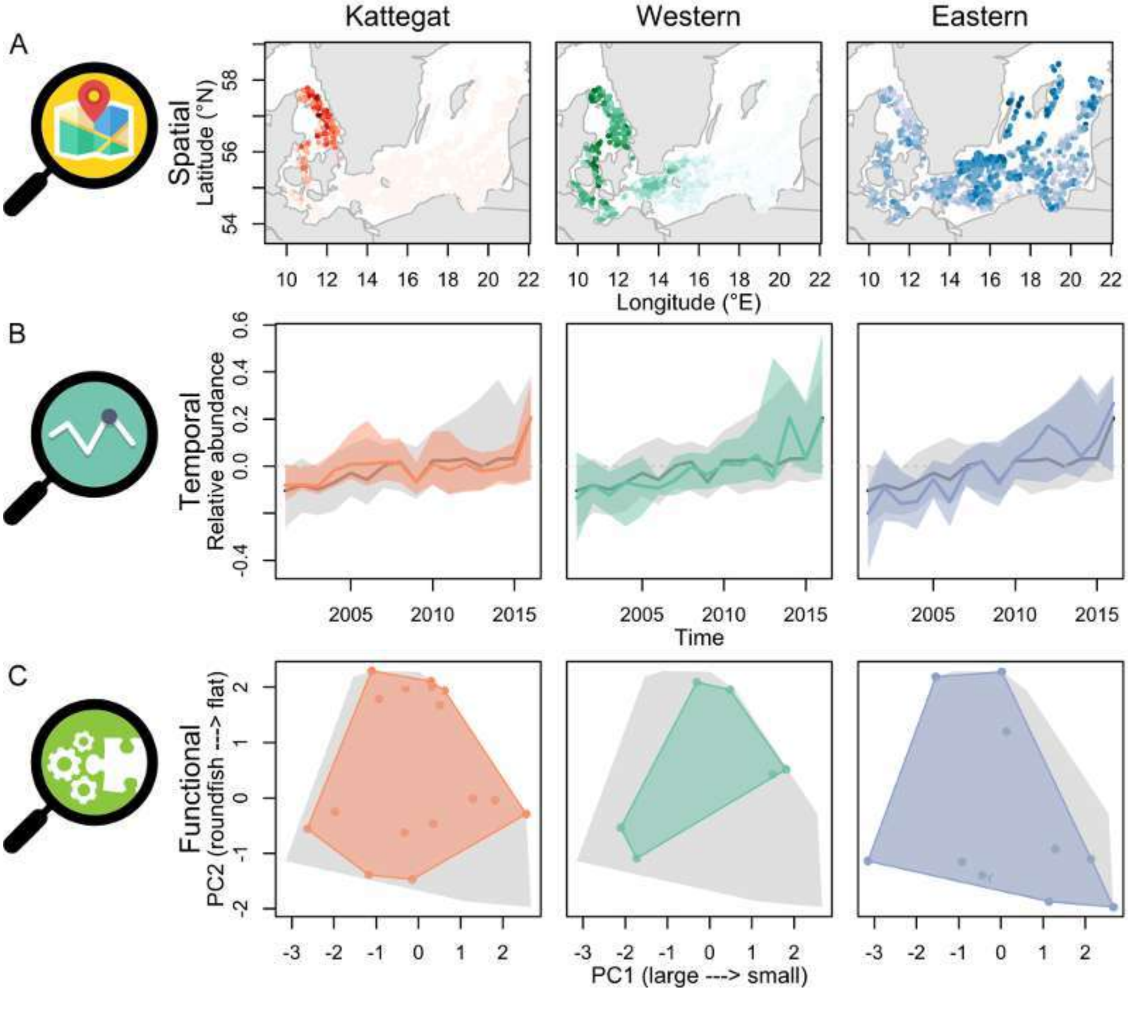


Figure 3.5: Spatial, temporal and functional characterization of the sub-assemblages. (A) Average spatial distribution, with the intensity of colours proportional to the spatial distribution. (B) Temporal dynamics from 2001 to 2016. The bold line represents the median relative abundance, the shaded area the inter-decile range. The whole fish assemblage is represented in grey, the sub-assemblages in their respective colours. (C) Functional richness of the sub-assemblages, compared with the whole community; PC1 in x-axis represents the difference between large (left) and small (right) fish species, PC2 in y-axis represent the difference between flat (up) and gadoid-like shaped (bottom) fish species.

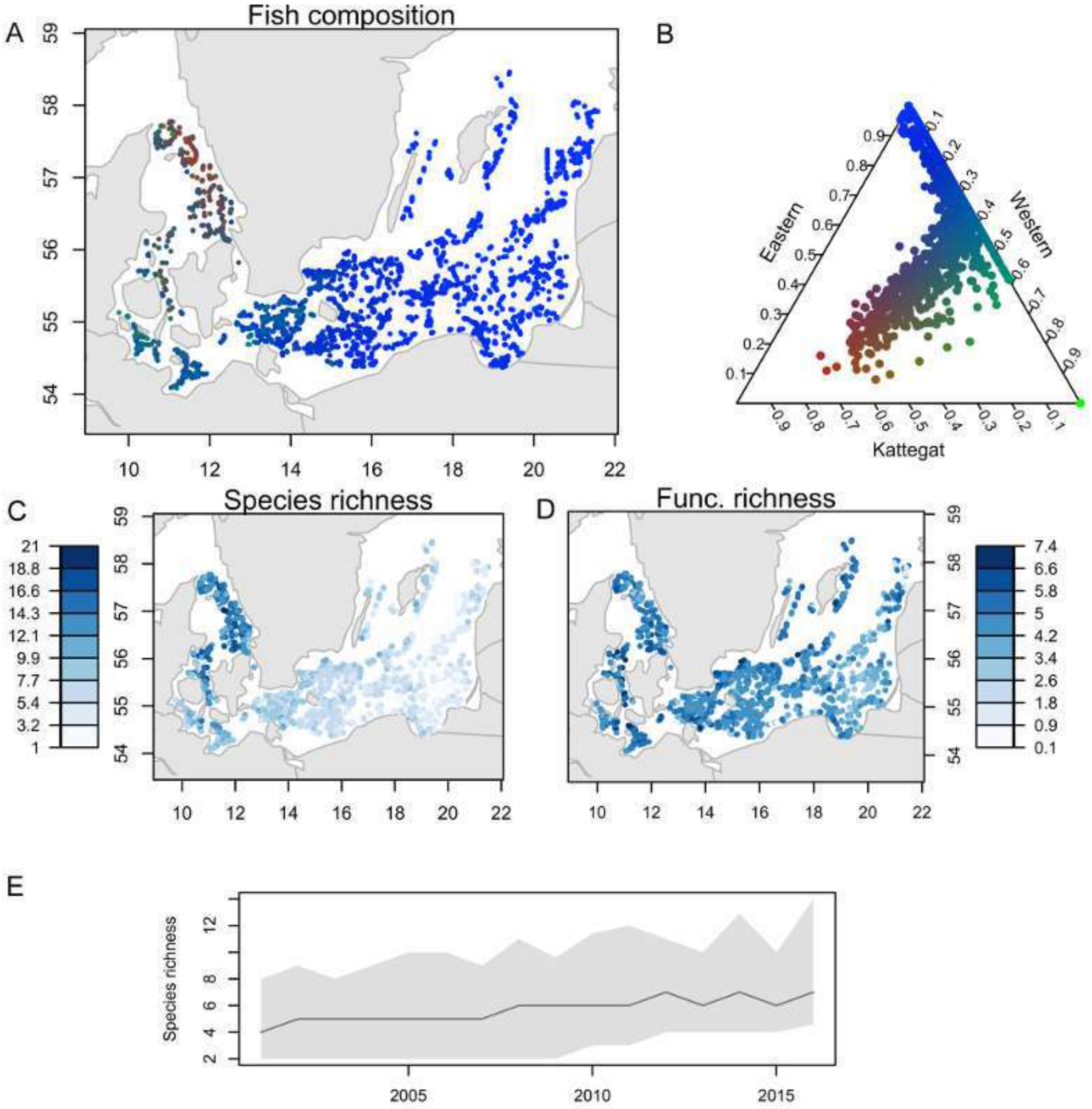


Figure 3.6: Fish biodiversity in the Baltic Sea from the information of more than 4,000 samplings. (A+B) Hauls composition of the three sub-assemblages are represented in RGB colour scale with red for the *Kattegat*, green for the *Western* and blue for the *Eastern* sub assemblages. (C+D) Spatial distribution of species and functional richness per haul. (E) Temporal evolution of species richness, the line represents the median, the shaded area represents the interdecile range.

Discussion

Environmental conditions drive fish community composition

Based on a large dataset of more than 4,000 samples and using complementary multivariate analyses and statistical tests, we investigate the links between fish communities and environmental conditions in the Baltic Sea. Salinity, decreasing from marine waters in the Kattegat to brackish waters in the Baltic Proper, is the main driver of fish community composition. Along this gradient, our statistical approach is able to identify three sub-assemblages within the overall Baltic fish community. The three sub-assemblages are nested, with most fish species inhabiting the Kattegat. This finding agrees with the predicted reduction of species richness from marine to brackish water

(Pecuchet *et al.* 2016; Smoliński & Radtke 2017), also found in the Baltic Sea zoobenthic community (Bonsdorff 2006). Additionally, our study disentangles the species composition and identifies 16 species strongly limited in their spatial distribution by salinity, preferring high-salinity conditions (the *Kattegat* sub-assemblage). Interestingly, the depth gradient is often reported as the most important environmental driver shaping the fish community in other Large Marine Ecosystem (Kidé *et al.* 2015; Dencker *et al.* 2017; Pecuchet *et al.* 2017). Here we find a weaker linkage of fish assemblages with depth, confirming the very unique conditions in the semi-enclosed brackish waters of the Baltic Sea. The salinity gradient is, by far, the main driver of fish assemblages, suggesting that the Baltic Sea could be more similar to a large estuary than open ocean. While this information is not novel, our study compares both drivers quantitatively and we find that salinity explain 87% of the covariance between fish and environmental conditions, while the depth gradient accounts only for 8%. If similar methodological framework would be applied to other ecosystems, we could compare the importance of different drivers across marine ecosystems. Our approach needs a large amount of collected data, which are already available for intensively monitored seas in Europe (Granger *et al.* 2015; Dencker *et al.* 2017; Frainer *et al.* 2017) or in North America (Batt *et al.* 2017).

Mismatch between taxonomic and functional diversity

Even though species distributions are highly linked with environmental gradients, we do not find any significant relationship between the functional characteristics of fish species and environmental conditions. If species would be selected randomly, the functional richness would tend to increase with the number of species (Mouillot *et al.* 2007). On the contrary, the spatial overlap of sub-assemblages and the high functional richness of *Kattegat* and *Eastern Baltic* sub-assemblages suggest that the number of species is reduced along the west-east gradient but without a decrease of functional richness (Fig. 3.5C&3.6C). This is especially surprising for the *Eastern Baltic* sub-assemblage, which includes the few species that can tolerate the low salinity conditions. These remaining species are able to occupy all the "niches" defined in the functional space, suggesting that the environmental conditions may limit similarities between the remaining species thus favouring the realisation of all the niches needed for the functioning of communities. This result agrees with Pecuchet *et al.* (2016) that proved a distinction between environmental filtering acting in the western Baltic Sea and neutral or limiting similarity acting in the Baltic Proper. However, Pecuchet *et al.* (2016) also found a link between functional richness and salinity when the diversity indicator was aggregated spatially into a regular grid. This link is not confirmed by our analysis made at the species level and considering each individual haul. The difference can be explained by some outlier hauls in the Baltic Proper with low catches, resulting in an abnormal low functional richness that can have a high influence on spatially averaged values. Moreover, the limited number of traits, although usual in functional studies of fish assemblages (Dencker *et al.* 2017; Pecuchet *et al.* 2017), covers only the life history strategies (survival, growth, reproduction) and do not take into account tolerance range of species (e.g. temperature or salinity preferences). Adding environmental tolerance traits would clearly increase the link between environment and traits, but our goal was to focus only on the life history strategies.

Limits of data driven approach

As with any statistical approach, the ability of the methods applied here is limited by the quality and amount of data available. For example, the dataset used covers the 16-year period from 2001 to 2016, i.e. after the regime shift occurring in the Baltic Sea during the late 1980s (Möllmann *et al.* 2009; Casini 2013). Including the period prior to the shift would likely increase the importance of the temporal dynamics and the capacity to detect a significant link with environmental variability. Even though the sampling started in 1991, we did not include data prior to 2001 because the sampling was performed using different gears and the sampling scheme of the surveys was different, potentially affecting the robustness of our analysis. The short length of the time series is the main limitation of our study, and it stresses the importance of rigorous and continuous data collection, a very valuable source of information in order to understand, preserve and manage marine ecosystems in a better way. In our analysis, the absence of a link between the temporal dynamics of fish species and the environmental conditions in the period 2001-2016 is informative. This finding is contrary to Hiddink and Coleby (2012) that linked the dynamics of species richness with temperature in Kattegat and salinity in Baltic Proper. The difference can be explained by a different time period (1990-2008) used by Hiddink and Coleby (2012) and the fact that our approach does not aggregate species into a diversity indicator and assume homogeneous dynamics over the whole study area. While looking at the dynamics of the sub-assemblages, we find that *Kattegat* and *Eastern Baltic* sub-assemblages have different dynamics, suggesting the use of methods that could study the interaction between spatial distribution and temporal dynamics, such as tensor decomposition (Frelat *et al.* 2017).

Moreover, we could not include fishing pressure or other direct anthropogenic pressures in our study because they are difficult to estimate and not available at the spatial resolution of our analysis. Yet, it is clear that human pressures have a strong impact on the fish community (Korpinen *et al.* 2012; Andersen *et al.* 2015) and their trait composition (Henriques *et al.* 2014; D'agata *et al.* 2014; Koutsidi *et al.* 2016). Another limit of our study remains in the fact that we study abundance at species level, which may hide information about different sub-populations of the same species. For example, cod is known to be divided in two populations: the Eastern and Western Baltic cod stocks (Aro 1989; Bagge *et al.* 1994), but here included as only one species, which may blur the temporal dynamics of these two stocks.

Management implications and concluding remarks

The mismatch between taxonomic and functional diversity, associated with the spatial overlap of sub-assemblages, suggests that the functional redundancy decreases from west to east in our study area. The low functional redundancy in the Baltic Proper implies that its ecosystem is susceptible to changes in external pressures such as hydrography, nutrient inputs and fisheries overexploitation that can provoke drastic reductions in fish abundances (Rice *et al.* 2013). Therefore, fisheries management in the Baltic Proper should be precautious by taking in consideration the specific local characteristics of the fish community. Our study demonstrates that based on a large dataset of community data, analyzed in an innovative and comprehensive way, we can provide a complete view of the effects of environment on the structuring of biotic communities in space, time and functions. Similar methodological framework can be used in other Large Marine Ecosystems to gain better understanding of the effect of environmental variations on biodiversity, key information for the management and conservation of ecosystems.

Acknowledgment

The authors are grateful to all contributors of the DATRAS database who collected and took part in the Baltic International Trawl Survey, and to ICES who merged, cleaned and made the data open access. We thank the two anonymous referees and Marta Coll for their useful comments that helped improve this manuscript.

List of supplementary materials

Table S3.1: Description of the different multivariate methods used in this study

Table S3.2: Pre-processing checks and corrections on BITS dataset

Figure S3.1: Clustering analysis of the fish species based on their spatial distribution realised with K-means algorithm.

Figure S3.2: RV-test for the between-group co-inertia between fish abundance and environmental variables.

Figure S3.3: Fourth-corner test between the traits of fish species and the environmental variables.

Table S3.1: Pre-processing checks and corrections on BITS dataset

Species removed from BITS dataset:

Species	Reason
Acanthascus (Rhabdocalyptus) mirabilis	Not a fish
Alosa fallax	Pelagic species
Cancer pagurus	Not a fish
Caranx rhonchus	Outside species range - probable missindentification
Cephalopoda	Not a fish
Engraulis encrasicolus	Pelagic species
Nephrops norvegicus	Not a fish
Osmerus eperlanus	Pelagic species
Scomber scombrus	Pelagic species
Trachurus trachurus	Pelagic species

Species mis-identified or aggregated to genus or family level:

Species name	Original name in Datras	Reason
Ammodytes	*Ammodytes marinus*	Often only identified to genus
Ammodytes	*Ammodytes tobianus*	Often only identified to genus
Callionymus	*Callionymus lyra*	Often only identified to genus
Callionymus	*Callionymus maculatus*	Often only identified to genus
Chelidonichthys lucerna	*Chelidonichthys lucernus*	Spelling variation
Gobiidae	*Gobius niger*	Many variations within family
Gymnocephalus cernua	*Gymnocephalus cernuus*	Spelling variation
Labridae	*Labrus bergylta*	Infrequent, with frequent identification at family level
Liparis liparis	*Liparis*	Spelling variation
Mullus surmuletus	*Mullus barbatus*	Spelling variation
Neogobius melanostomus	*Neogobius*	Spelling variation
Gymnocephalus cernua	*Perca cernua*	Spelling variation
Gobiidae	*Pomatoschistus*	Many variations within family
Gobiidae	*Pomatoschistus microps*	Many variations within family
Scophthalmus maximus	*Psetta maxima*	Spelling variation
Syngnathus	*Syngnathus acus*	Infrequent, with frequent identification at genus level
Syngnathus	*Syngnathus rostellatus*	Infrequent, with frequent identification at genus level
Syngnathus	*Syngnathus typhle*	Infrequent, with frequent identification at genus level
Myoxocephalus quadricornis	*Triglopsis quadricornis*	Spelling variation
Sprattus sprattus	*Sprattus sprattus balticus*	Spelling variation

Figure S3.1: Clustering analysis of the fish species based on their spatial distribution realised with K-means algorithm.

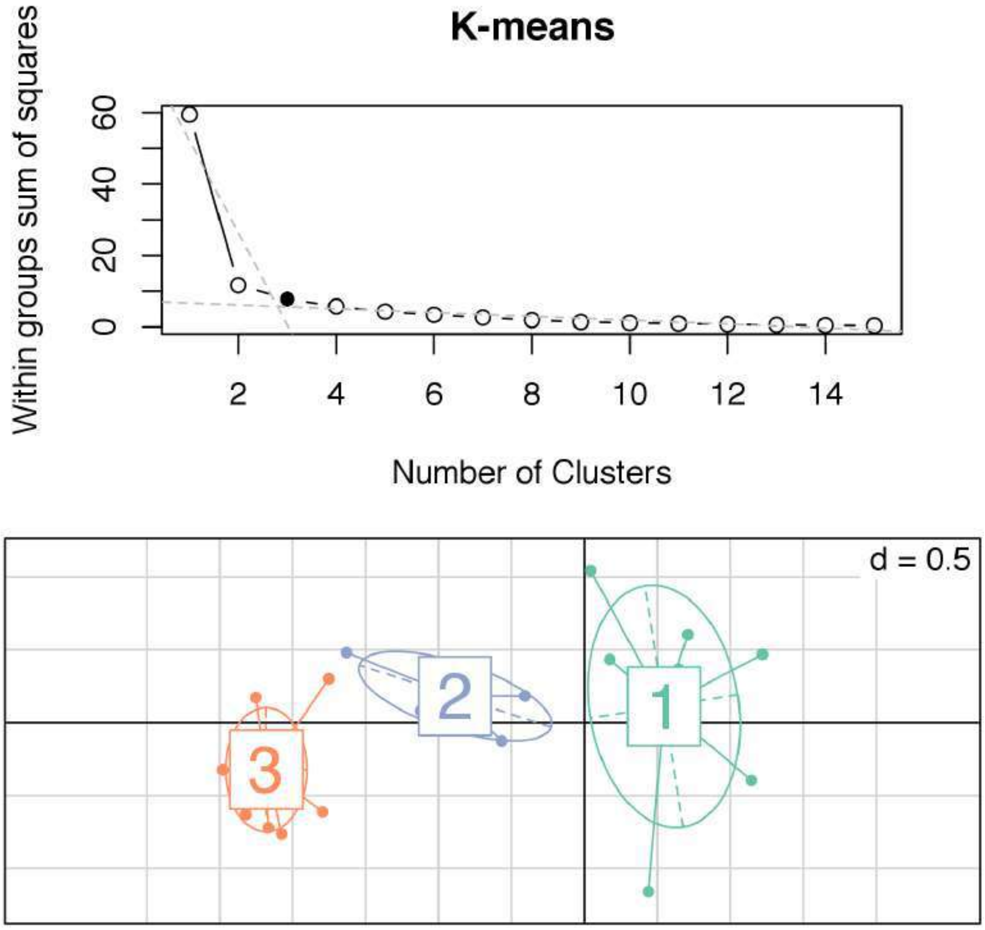


Figure S3.2: RV-test for the between group co-inertia between fish abundance and environmental variables.

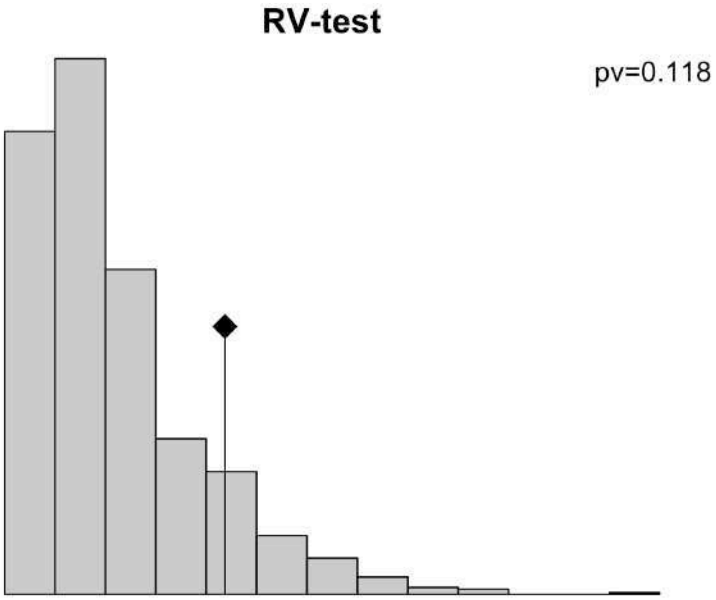
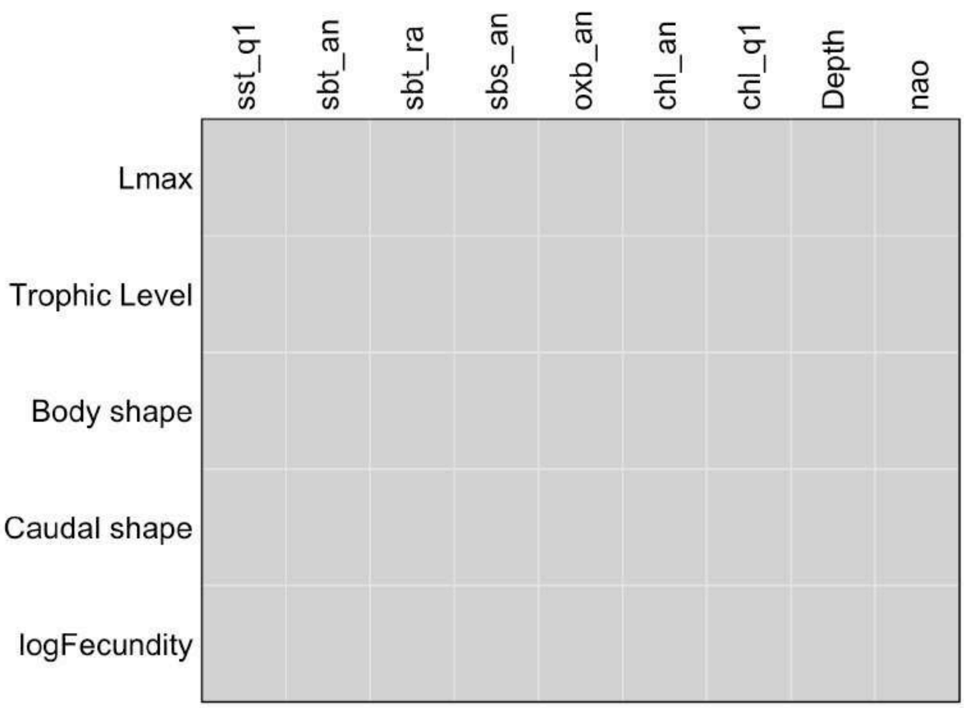


Figure S3.3: Fourth-corner test between the traits of fish species and the environmental variables. All the pairwise correlations are not significant (i.e represented in grey), meaning that adjusted p-values>0.05.



Chapter 4

Warm waters favour fast living fish

Clément Vuillier, Abysses (2016)
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Title: Warm waters favour fast living fish – evidence from big data across oceans

Authors: Esther Beukhof[1+*], Romain Frelat[2+], Laurène Pécuchet[1], Aurore Maureaud[1], Tim S. Dencker[1], Jón Sólmundsson[3], Heino Fock[4], Antonio Punzon[5], Raul Primicerio[6], Manuel Hidalgo[7], Christian Möllmann[2] and Martin Lindegren[1]

[1]Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet, Bygning 202, 2800 Kgs. Lyngby, Denmark

[2] University of Hamburg, Institute for Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability (CEN), Hamburg, Germany.

[3] Marine and Freshwater Research Institute, Skúlagata 4, 101 Reykjavík, Iceland

[4] Thünen-Institute of Sea Fisheries, Herwigstraße 31, 27572 Bremerhaven, Germany

[5] Instituto Español de Oceanografía, Centro Oceanográfico de Santander, Promontorio San Martín s/n, 39004 Santander-Cantabria, Spain

[6] Norwegian College of Fishery Science, UiT The Arctic University of Norway, 9037 Tromsø, Norway

[7] Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Ecosystem Oceanography Group (GRECO), Moll de Ponent s/n, 07015 Palma de Mallorca, Spain

[+] These authors contributed equally to this work

* Corresponding author: Esther Beukhof, estb@aqua.dtu.dk

Abstract

One of the most fundamental challenges in ecology is to understand why species occur where they are and where they are likely to be found in the future. Trait-based approaches has shown great promise in providing a mechanistic understanding of the underlying processes, since traits of species determine which environments and habitats a fish is capable to inhabit and additionally, with which species it may interacts. In this study, we used a unique dataset containing the spatial occurrence of over 1,400 marine fish species recorded in 70,000 stations in continental shelf seas across oceans – ranging from Northeastern Pacific Ocean to North Atlantic Ocean and the Mediterranean Sea. Three-matrix approaches (RLQ and fourth-corner analysis) were used to investigate the relationships between species traits and environmental variables through the information on species occurrences. Temperature was the strongest predictor driving latitudinal gradients in traits, particular those related to the fast-slow continuum (lifespan, age at maturity, growth coefficient K). The fast-slow continuum also followed a coastal-to-offshore gradient, that was characterized by depth and seasonality in temperature, in addition to temperature. When scaling up the species and trait information to the community level, the same trait-environment relationships were observed using random forests. Our results empirically confirm the accelerating effect of temperature on physiological rates by demonstrating a strong spatial association between bottom temperatures and the key response traits, namely growth, maturation and lifespan. Our study demonstrates the great benefit of collating datasets from multiple regions and, by using different approaches, to deliver robust results that have strong implications for our understanding and management of marine fish communities and for predicting how fish communities will adapt to a changing climate.

Keywords: biogeography, traits, fish, trait-environment relationships, big data, RLQ, fourth-corner, fast-slow continuum

Introduction

One of the most fundamental challenges in ecology is to understand why species occur where they are, and where they are likely to be found in the future. Traditionally, bio-geographers and macro-ecologists have tried to answer this question by analysing species distributions and their changes in space and time relative to the surrounding environment (Lomolino 2000; Keith *et al.* 2012). Such species-based approaches have successfully demonstrated the variety of species responses to environmental variables (e.g., temperature) (Walther *et al.* 2002; Poloczanska *et al.* 2016) and allowed us to forecast and explore species distributions in response to changes in these drivers (Maguire *et al.* 2015). However, they fail to provide a mechanistic understanding of the underlying processes whereby species respond to the environment (Kearney & Porter 2009) and as a consequence the predictive performance has shown to be quite poor (Brun *et al.* 2016a). Such a mechanistic understanding is therefore needed to more reliably predict future changes in species distributions and to inform policymakers and resource managers about the potential consequences of climate change on the biodiversity, functioning and services of ecosystems.

Trait-based approaches have shown great promise in providing this mechanistic understanding, since traits of species determine which environments and habitats an organism is capable to inhabit and additionally, with which species it may interacts (Verberk *et al.* 2013; Violle *et al.* 2014). Moreover, trait-based approaches enable us to search for fundamental principles by facilitating comparisons across ecosystems with entirely different species compositions. A critical step towards better understanding and predicting future changes in species distributions is to identify the key attributes and adaptation by which species respond to the environment and to characterize the shape and nature of the relationship between environmental variables and the response traits.

The recent increase in the availability of species occurrence data and trait information has inspired a growing number of large-scale studies on trait biogeography and its ties to the environment, primarily on land (Ordoñez et al. 2009, van Bodegom et al. 2014, Lawing et al. 2017), but also in fresh-water, estuarine and marine ecosystems (Mims *et al.* 2010; Brun *et al.* 2016b; Henriques *et al.* 2017; Pecuchet *et al.* 2017; Acevedo-Trejos *et al.* 2018; van Denderen *et al.* 2018). However, most studies express trait variation at an aggregated level of communities or functional groups, hence disregarding inter- and intra-specific trait variability, as well as spatial and temporal differences in species abundances and evenness across communities. Furthermore, trait distributions are primarily investigated in specific regions or across larger geographic areas, but at a single and often coarse spatial resolution. This limits the range of environmental conditions and trait expressions included and insufficiently accounts for fine-scaled variability and potential scale-dependence in trait expressions and trait-environment relationships. Fortunately, the rapid increase in computational power and the development of fast and efficient methods for analysis of large dataset offers a unique opportunity to make better use of available data to account for many of these issues and to expand the geographical scale and spatial resolution in macroecological and biogeographical studies (Peters *et al.* 2014; LaDeau *et al.* 2017).

In this study, we take advantage of these developments and compiled an extensive survey dataset of abundances and life-history traits for ~1,800 marine fish taxa across the North Atlantic and North-East Pacific. The data encompass >77,000 unique geo-referenced stations sampled along pronounced latitudinal- and environmental gradients over an 11-year time period (2005 to 2015). We then used a suit of complementary tools including machine learning, a three-matrix ordination approaches (RLQ analysis) and a permutation test (fourth corner analysis) (Dray *et al.* 2014), capable of summarizing station-specific information on species abundances, traits and environmental conditions. In order to understand marine trait-environment relationships and the degree to which these can explain and predict fish species distributions we formulated and pursued the following two research questions: (i) Which traits and which environmental variables best explain the distribution of marine fish species? and (ii) What are the key trait-environment relationships and how variable are these across regions and spatial scales?

Methods

Overview

To assess trait distributions and trait-environment relationships, we collated three datasets (Fig. 4.1): (i) survey data on fish species abundances (matrix L); (ii) species trait information (matrix Q); (iii) and environmental data (matrix R). The data were analyzed via different but complementary approaches (Kleyer *et al.* 2012). First, two species-based analyses summarized the structure among the three datasets using the distribution of fish species abundances to infer key traits and their trait-environment relationships. Second, a community-based approach used the fish abundance data and trait information to calculate community weighted mean (CWM) traits per sampling station. These CWM traits were then statistically modelled against the environmental data.

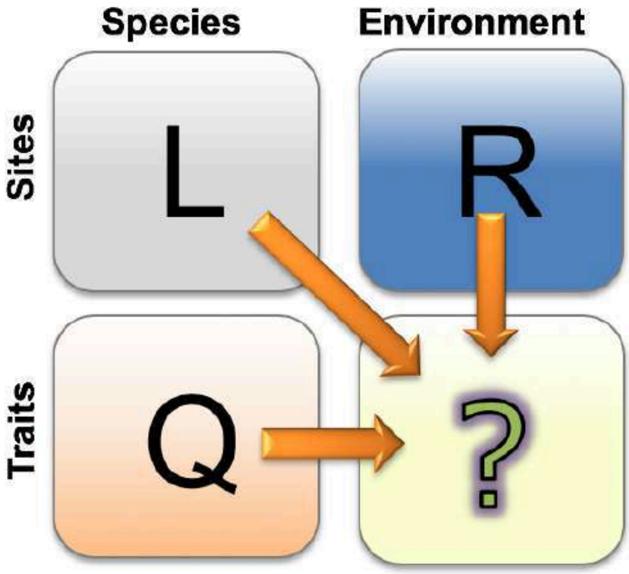


Figure 4.1: Presentation of the fourth corner problem. What is the link between the traits of fish species (matrix Q), and the characteristics of the environment (matrix R) that species inhabit (matrix L)?

Survey data

We collated data from 21 scientific bottom-trawl surveys in the North Atlantic and Northeast Pacific (Table S4.1). The aim of the surveys is to gather data on the stock size of commercially valuable species and to monitor the diversity and dynamics of species assemblages. Although gears and survey protocols vary between surveys, all surveys use otter trawls, and all catches are identified at species level whenever possible. We verified and updated the taxonomy of reported species with the World Register of Marine Species (WoRMS Editorial Board 2018).

Furthermore, we discarded all non-fish taxa by keeping only organisms from the following classes: Actinopterygii, Elasmobranchii, Holocephali, Myxini and Petromyzonti. We then selected only taxa that had been recorded at the family, genus or species level. Finally, we reduced the temporal extent to an 11-year period from 2005 to 2015 in order to reduce the influence of temporal variation and have a consistent sampling period across surveys. In total, we gathered data from 77824 stations, recording the abundance of 1889 different taxa (1583 taxa defined at species level, 203 at genus level and 103 at family level).

Trait data

We selected seven traits to represent the life history and ecology of fish, based on availability from literature, known trade-offs in life history strategies and the use in previous trait-based studies on fish (Winemiller & Rose 1992; Juan-Jordá *et al.* 2013). These traits are: maximum body length (cm), trophic level, fecundity (number of offspring produced by a female per year), offspring size (egg diameter, length of egg case or length of pup in mm), age at maturity (years), lifespan (years) and the Von Bertalanffy growth coefficient K (year^{-1}) as a proxy for growth rate. Trait information was extracted from a trait database of European and North American marine fish (Maureaud et al. in prep) that contains species trait values at the scale of Large Marine Ecosystems (LME), whenever such intraspecific trait information is present. The database's main source is Fishbase (Froese & Pauly 2017), and gaps were filled in by values from primary literature and genus- or family-averaged values. In order to account for intra-specific variability in species traits across the area, available trait values were averaged at the scale of Large Marine Ecosystems (LMEs). We additionally checked the pairwise correlation between traits, and all the Pearson correlations were below 0.7 (Figure S4.1).

Environmental data

We selected nine environmental variables representing hydrography, habitat, food availability and anthropogenic pressures, which are key factors known to affect the distribution of fish species. Sea bottom temperature (SBT in °C) and sea bottom salinity (SBS in psu) represented the hydrographical environment, and were obtained from the Global Ocean Physics Reanalysis with a spatial resolution of 1/4° (GLORYSs2v4, Ferry et al. 2012). Monthly SBT and SBS data from 2004 to 2015 were downloaded from the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu/). Chlorophyll *a* concentration (Chl, in mg·m^{-3}) served as a proxy for primary production and food availability. Aggregated monthly data from satellites optical sensors with a spatial resolution of 4 km were downloaded from the GlobColour database (Maritorena et al. 2010, http://hermes.acri.fr/).We extracted for each unique haul the corresponding monthly values of bottom salinity, bottom temperature and chlorophyll concentration. Additionally, we calculated the range of values of temperature and chlorophyll concentration within the past twelve months as indicators of seasonality. Depth was measured during the surveys and provided with the survey data. When not available or when measurements seemed incorrect (< 5% of the stations), we used the depth values from the General Bathymetric Chart of the Oceans, (GEBCO 2014 grid, www.gebco.net). As a measure of anthropogenic pressure, we used the cumulative demersal fishing pressure of 2013, which has been estimated globally at 1 km^2 spatial resolution (Halpern *et al.* 2015). We added up demersal fishing pressure estimates from both destructive and non-destructive trawling, as well as with high and low by-catches. We checked the pairwise correlation between environmental variables, and all Pearson correlations were below 0.7 (Fig. S4.2), although with a notable high correlation between bottom temperature and its seasonality.

Species-based analysis

The fourth corner and RLQ analysis are two complementary three-matrix approaches (Dray et al. 2014), that are based on a species occurrence or abundance matrix (L), a species-trait matrix (Q) and an environment-sites matrix (R) (Fig. 4.1). The fourth corner analysis tests pair-wise relationships between traits and environmental variables, while RLQ considers the inter-correlation of traits and environmental drivers. The RLQ analysis is a multivariate analysis that can be considered as an extension of a co-inertia analysis (ordination method exploring the link between two matrices). First, the three matrices R, L and Q are ordinated following the best suited method to their data type. In this study, we performed a correspondence analysis (CA) on the abundance matrix L, because the method uses the chi-square distance and is particularly well suited for abundance data along large environmental gradients (Legendre & Gallagher 2001; Greenacre 2017). Principal component analyses (PCA) on matrices Q and R were computed using the stations and species scores from the previous CA analysis on matrix L as weight of the rows. The RLQ analysis maximizes the cross-covariance between the environmental and trait ordinations. The result is a co-structure between the three matrices, which is quantified through so-called RLQ axes. The associations of species, traits and environmental variables with the RLQ axes represent the best compromise between traits and environmental variables through species abundances (Dray *et al.* 2014).

We tested the sensitivity of the RLQ analysis to different factors. First, we tested for potential scale-dependency between traits and the environment by spatially aggregating our station-based dataset into grid squares of 0.25°, 0.5°, 1° and 2.5°. Moreover, we divided our dataset into three different regions, following the coastlines of the Northeast Atlantic (NE Atlantic), Northwest Atlantic (NW Atlantic) and Northeast Pacific (NE Pacific), to test the validity of the RLQ analysis in the three main areas. We also divided our dataset into four different depth strata and seasons to test the influence of depth and season on our results.

The fourth corner method computes a trait-environment correlation matrix (so-called fourth corner matrix) based on the three matrices R, L and Q. Then, a permutation test on the abundance matrix L is performed with 5,000 permutations of rows and columns successively. The correlations between the traits and environmental variables are calculated with the randomly permuted L matrix. The actual correlation values were compared to these correlations with permutation to obtain the significance level of the correlations between traits and environment (Dray *et al.* 2014). The resulting p-values were adjusted for multiple testing, following the false discovery rate procedure (Benjamini & Hochberg 1995).

Community-based approach

Community weighted means (CWM) for all seven traits were computed as geometric mean trait values, based on species trait values and relative species abundances (Beukhof et al. in review, Garnier et al. 2004). Random Forests (RF, Breiman 2001) were applied to model the CWMs of each trait with the seven external pressure variables as predictors. RF does not make any assumptions on the distribution of the data, considers the interactions between variables and is known to have good predicting power (Cutler *et al.* 2007). To reduce the computational power required for modelling, stations were placed on a 0.25° by 0.25° grid, which was used to first calculate the relative species abundances and environmental variables per grid cell, followed by calculating the CWM traits per grid cell (8022 grid cells in total). We trained the RF for each trait on a training dataset containing 75% of the data (6016 sites), with 100 trees of 2 nodes. We selected the best RF over 10 RFs computed. To test the robustness of the models, we repeated 100 times the selection of the training dataset and the optimizations. This procedure yielded 100 optimized RFs per CWM trait, which were used to compute the average response of the CWM traits and the confidence interval of the response curves.

All data analyses were performed in the statistical software R (R Core team 2017). The RLQ and fourth corner method are implemented in the ade4 package (Dray & Dufour 2007), RFs were computed with the package randomForest (Liaw & Wiener 2002).

Results and discussion

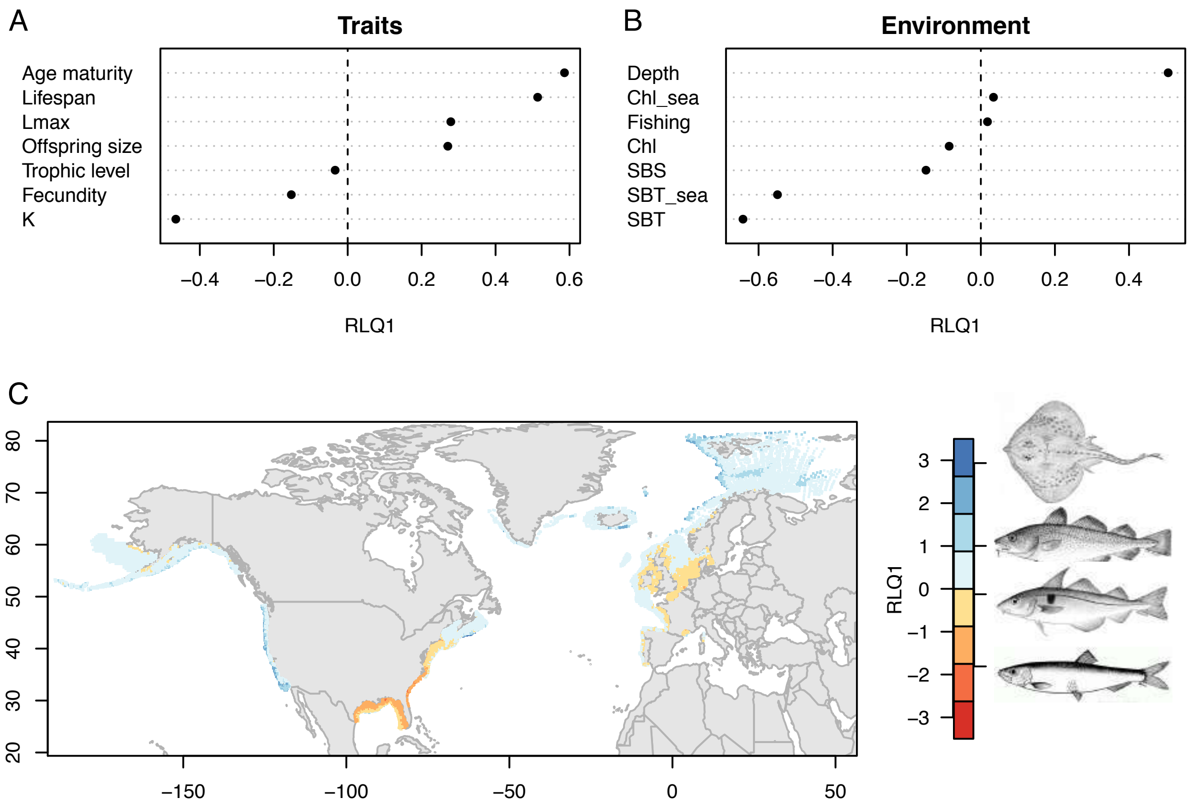
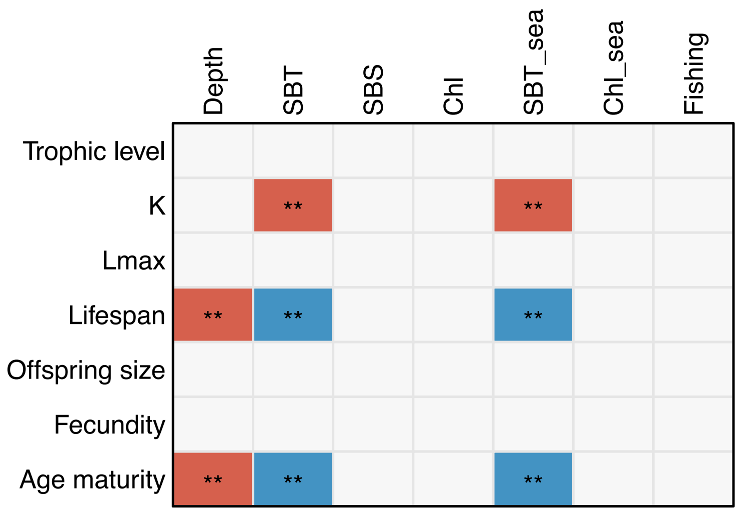


Figure 4.2. Results of the RLQ analysis summarizing the cross-covariance between traits and environmental variables across all species and sites. (A) Scores of the traits, (B) environmental variables, and (C) the scores of each individual stations and species on RLQ1. In order to illustrate the trait changes occurring along RLQ1, images of *Amblyraja radiata, Gadus morhua, Melanogrammus aeglefinus,* and *Sprattus sprattus* (from top to bottom) are shown as examples of species characterized by different growth rates, age at maturity and lifespan. (The images were derived from FAO website' and Wikimedia commons).

Trait environment relationship

The main relationships between the set of traits and environment variables are summarized by the first RLQ axis (RLQ1) which explained 96% of the cross-covariance between traits and environmental variables across all species and sites (Fig. 4.2). In other words, RLQ1 is the best compromise through which stations, species, traits and environment are projected on a single axis. The traits with the highest absolute score on RLQ1 were the growth coefficient K, age at maturity and lifespan, demonstrating highly positive or negative scores (Fig. 4.2a). Given by the high degree of explained variance of RLQ1, these traits can therefore be regarded as the key response traits of fish associated to the set of environmental variables included in our study. Maximum length, offspring size and fecundity were of intermediate importance, demonstrating only moderate scores on RLQ1, while trophic level had low importance, illustrated by scores close to zero. In terms of environmental variables, sea bottom temperature (SBT), seasonality in SBT (SBTsea) and depth were most strongly represented by RLQ1 (Fig. 4.2b). High negative RLQ1 scores were thus associated with high temperatures, strong seasonality and shallow waters, whereas highly positive scores reflect deep waters, lower temperatures and less seasonality in temperature. Consequently, these variables can be regarded as the dominant environmental drivers determining the distribution of species conditioned on their traits.

The station scores projected on RLQ1 reflected strong latitudinal gradients from negative scores in warm-temperate and sub-tropical waters (e.g., Gulf of Mexico) to positive scores in boreal and sub-polar seas around Greenland, Iceland, Norway, Newfoundland and Alaska (Fig. 4.2c). Because of the high score for SBT on RLQ1 (Fig. 4.2b), the gradient in station scores can largely be explained by a latitudinal gradient also in terms of SBT (Fig. S4.3). The absence of a strong latitudinal gradient in stations scores observed along the Northeast Pacific is likely due to the considerably weaker latitudinal gradient in SBT caused by the southward flowing California current, brining deep, cold and nutrient-rich water along the entire Pacific US coastline (Checkley & Barth 2009). In addition to the gradient in station scores from high to low temperatures, many areas along the three coastlines showed a marked transition from negative to positive scores from the coast to offshore waters (Fig. 4.2c). Since depth typically increases once moving offshore, the strong importance of depth on RLQ1 implies that differences in traits are also represented by a coastal-to-offshore depth gradient. The structuring effect of both temperature and depth on species traits was consistent based on the fourth corner analysis, demonstrating significant correlations between SBT, SBTsea and depth with growth coefficient K, age at maturity and lifespan (Fig. 4.3). The key drivers were also supported by the random forest (RF) approach where SBT and depth were found the best predictors of the spatial variability in community-weighted mean (CWM) traits (Fig 4.4). Furthermore, the resulting trait-environment relationships reflect the trade-offs between traits found in the RLQ and fourth corner analysis, illustrated by a positive relationship between growth (K) and SBT, but a negative relationship for maximum length (Lmax), lifespan and age at maturity. Interestingly, the response curves of the RFs revealed several non-linear trait-environment relationships that could not be detected by the RLQ or fourth corner analysis. For instance, the partial effect of SBT on growth shows a sigmoid relationship with a steep increase at intermediate temperatures (Fig. 4.4).



	Depth	SBT	SBS	Chl	SBT_sea	Chl_sea	Fishing
Trophic level							
K		🟥 **			🟥 **		
Lmax							
Lifespan	🟥 **	🟦 **			🟦 **		
Offspring size							
Fecundity							
Age maturity	🟥 **	🟦 **			🟦 **		

Figure 4.3: Fourth corner analysis demonstrating pair-wise correlations between traits and environmental variables. The p-values have been calculated from 5,000 permutation and corrected for multiple comparison using the false discovery rates. Cells in red show positive correlations, cells in blue show negative correlations. The significance level is given with the stars scale ('.' : p-value <0.1; '*' : <0.05; ; '**' : <0.01). Non-significant correlations are in light grey.

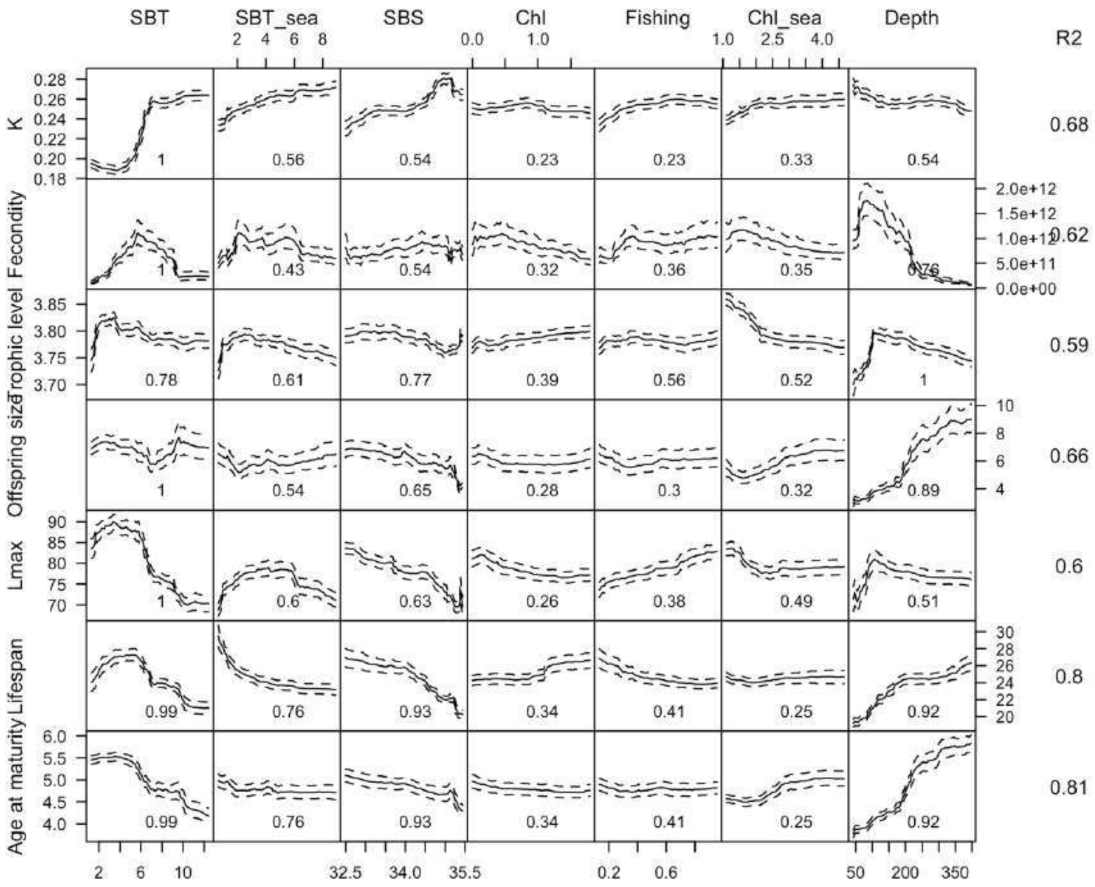


Figure 4.4: Response curves of the random forest models predicting the different traits (7 different models were computed, one for each trait, shown in rows). The relative importance (averaged over the 100 RFs) of explanatory variables (environmental variables and fishing pressure, in columns) is given below each curve. The R-squared of each model is shown on the right side of the plot. The confidence interval was computed from 100 different training sets.

Fast-slow continuum of fish follows warm-cold gradient

In summary, our suit of methods, including RLQ, fourth corner and RF consistently show that fish communities in warm areas at lower latitudes or at shallow depths are dominated by species characterized by rapid growth, early maturation and short lifespan. Conversely, fish communities in cold, deep and more seasonally stable environments are primarily composed of slow-growing, late-maturing and long-lived fish species. Our findings are consistent with the classification of organisms along a "fast-slow continuum" that ranks species according to their life-history traits from early-maturing, short-lived and fast-growing to late-maturing, long-lived and slow-growing (Read & Harvey 1989). The fast-slow continuum has been observed in plants (Franco & Silvertown 1996; Reich 2014), mammals (Stearns 1983; Oli 2004) and birds (Gaillard *et al.* 1989), but has also been reported for specific groups of fish (Rochet *et al.* 2000; Juan-Jordá *et al.* 2013; Wiedmann *et al.* 2014). The underlying mechanisms explaining the fast-slow continuum has primarily been related to a direct effect of temperature on physiology, particularly by regulating rates of metabolism, growth, feeding and mortality (Gillooly *et al.* 2001; Clarke 2006). Such direct temperature effects on growth and resting metabolism on individual fish species has been well documented by previous experimental and modelling studies (Gislason *et al.* 2010; Neuheimer *et al.* 2011). Our results empirically confirm the accelerating effect of temperature on physiological rates by demonstrating a strong spatial association between bottom temperatures and the key response traits, namely growth, maturation and lifespan. In addition to a direct physiological effect of temperature on traits, the degree of seasonality in terms of both temperature and resource availability (e.g., light, nutrients and primary production) has been shown to affect the distribution of traits and life-history strategies of fish (Winemiller and Rose 1992; Pecuchet et al. 2017).

These overall patterns consistent with a fast-slow continuum of fish species life-histories were consistent when repeating the analysis across a range of spatial resolutions (Fig. S4.4), as well as across seasons (Fig. S4.5). This indicates that the response traits and trait-environment relationships were robust and insensitive to spatial and temporal scales. However, some noticeable differences were observed if splitting the analysis into different depth strata or regions (Fig. S4.6). In the former case, the key response traits and drivers remained similar with increasing depth, except for the deepest depth strata (>300m), where fishing pressure and bottom salinity, as well as trophic level and lifespan showed relatively higher scores on RLQ1. Similarly, the analysis split by regions showed an increased importance of fishing pressure and bottom salinity in combination with maximum size and fecundity in the North-east Pacific, compared to the North-west and North-east Atlantic where the traits and trait-environment relationships remained similar. The lower importance of bottom temperature in structuring community composition in the North-east Pacific and below 300m is most likely due to the uniformly cold temperatures along the US Pacific coast (i.e., caused by the cold, southward flowing California Current) and at greater depth throughout the global ocean (Fig. S4.7). This highlights an important issue that while regional studies may identify more local drivers of traits (e.g., fishing), they may fail to recognize other drivers operating at significantly larger spatial scales (e.g., temperature). This clearly emphasizes the need for large-scale studies encompassing strong contrasts and pronounced gradients across a range of environmental variables to understand the underlying processes and drivers regulating species distributions, community composition and traits across regions and spatial scales (local, regional and global).

Implications and conclusion

Knowing the relationship between traits and the environment is of uttermost importance in order to better understand and predict the impact of changing environmental conditions on the future distribution and composition of organisms, including marine fish. For example, it is expected that global warming will result in an increase of temperature, as well as an increase in climate variability (Belkin 2009; Pörtner *et al.* 2014). Our results suggest that these new conditions will favour fast-living species, characterized by rapid growth, early maturation and short life-span, as it has already been shown in damselfly (Debecker & Stoks 2018). Additionally, warming waters may bring fast-living species to live at higher latitudes, as it has already been recorded in fish (Perry *et al.* 2005; Frainer *et al.* 2017). Furthermore, our study demonstrates the great benefit of collating datasets from multiple regions and, by using different approaches, to deliver robust results that have far-reaching implications for our understanding and management of marine fish communities and for predicting how fish communities will adapt to a changing climate.

Acknowledgements

The authors are grateful to all contributors of the bottom trawl surveys that sorted, identified, measured and reported the catch rigorously in databases, as well as institutions that supported them. We acknowledge the ICES Working Group on Comparative Analyses between European Atlantic and Mediterranean Marine Ecosystems to Move Towards an Ecosystem- based Approach to Fisheries (WGCOMEDA), during which the study was initiated, and are thankful to all the WGCOMEDA participants for their valuable comments.

List of supplementary materials

Table S4.1: Survey data overview

Figure S4.1: Pairwise correlation between species traits

Figure S4.2: Pairwise correlation between environmental variables

Figure S4.3: Spatial distribution of the seven external pressures

Figure S4.4: RLQ analysis per spatial scale

Figure S4.5: RLQ analysis per seasons

Figure S4.6: RLQ analysis per depth stratum

Figure S4.7: RLQ analysis per coastline

Table S4.1: Survey data overview

Survey	Area	Month	Number hauls	Depth min (m)	Depth max (m)
AI	Aleutian Islands	Jun.-Aug.	1,605	30	1,210
EBS	Eastern bergin Sea Shelf	Jun.-Aug.	3,756	20	210
EVHOE	Bay of Biscay & Celtic Sea	Oct.-Dec	1,535	20	560
FR-CGFS	English Channel	Sep.-Nov.	1,055	10	80
FR-MEDITS	French mediterranean coast	May-Jul.	945	20	870
GMEX	Gulf of Mexico	All	8,681	0	850
GOA	Gulf of Alaska	May-Aug.	3,700	10	980
Gre-GFS	Greenland	Oct.-Nov.	1,025	50	1,460
Ice-GFS	Iceland	Feb.-April	5,672	20	1,490
IE-IGFS	Ireland Shelf Sea	Sep.-Dec.	1,809	10	750
NEUS	North East US	Feb.-May; Sep-Dec.	7,334	10	920
NI-GFS	Irish Sea - Ireland	Oct.-Mar.	883	20	120
NorBTS	Norwegian coast and Barents Sea	All	12,423	20	2,100
NS-IBTS	North Sea	Jan.-Mar.; Jun.-Sep.	7,741	10	420
PT-IBTS	Portugal Shelf Sea	Sep.-Nov.	796	20	960
ROCKALL	Rockall plateau	Aug.-Sep.	385	130	460
SA	South East US	Apr.-Nov	6,338	0	10
SCS	Scotian Shelf	Feb-Aug.	3,084	20	1,940
SP-NORTH	North of Spain -Atlantic	Sep.-Oct	1,390	40	810
SWC-IBTS	Scotland Shelf Sea	Nov.-Mars	1,072	20	500
WCANN	West Coast US	May-Oct.	6,595	60	1,270
		TOTAL	77,824		

Figure S4.1: Pairwise correlation between species traits. The number represent the Pearson correlation r.

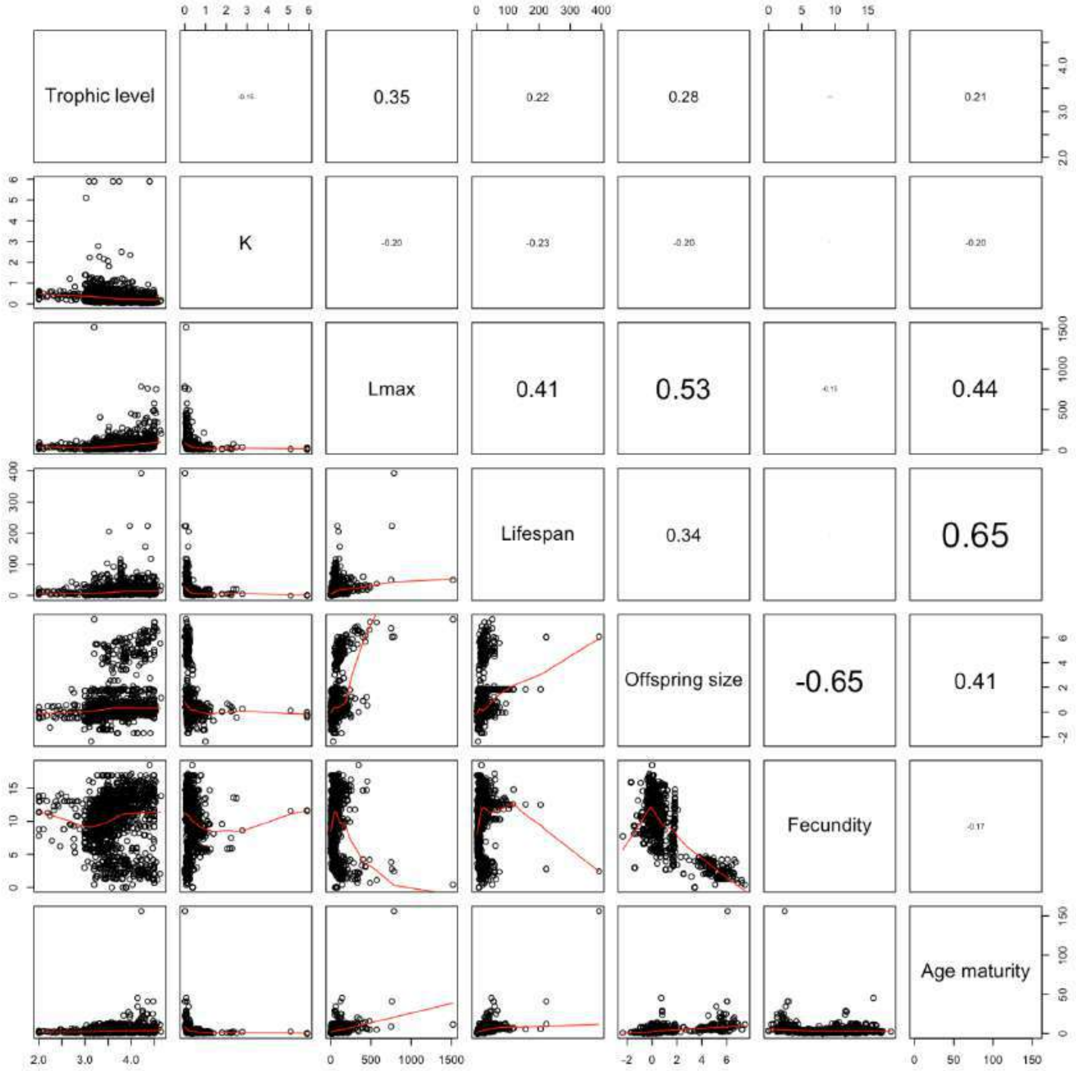


Figure S4.2: Pairwise correlation between environmental variables. The number on the upper right represent the Pearson correlation r.

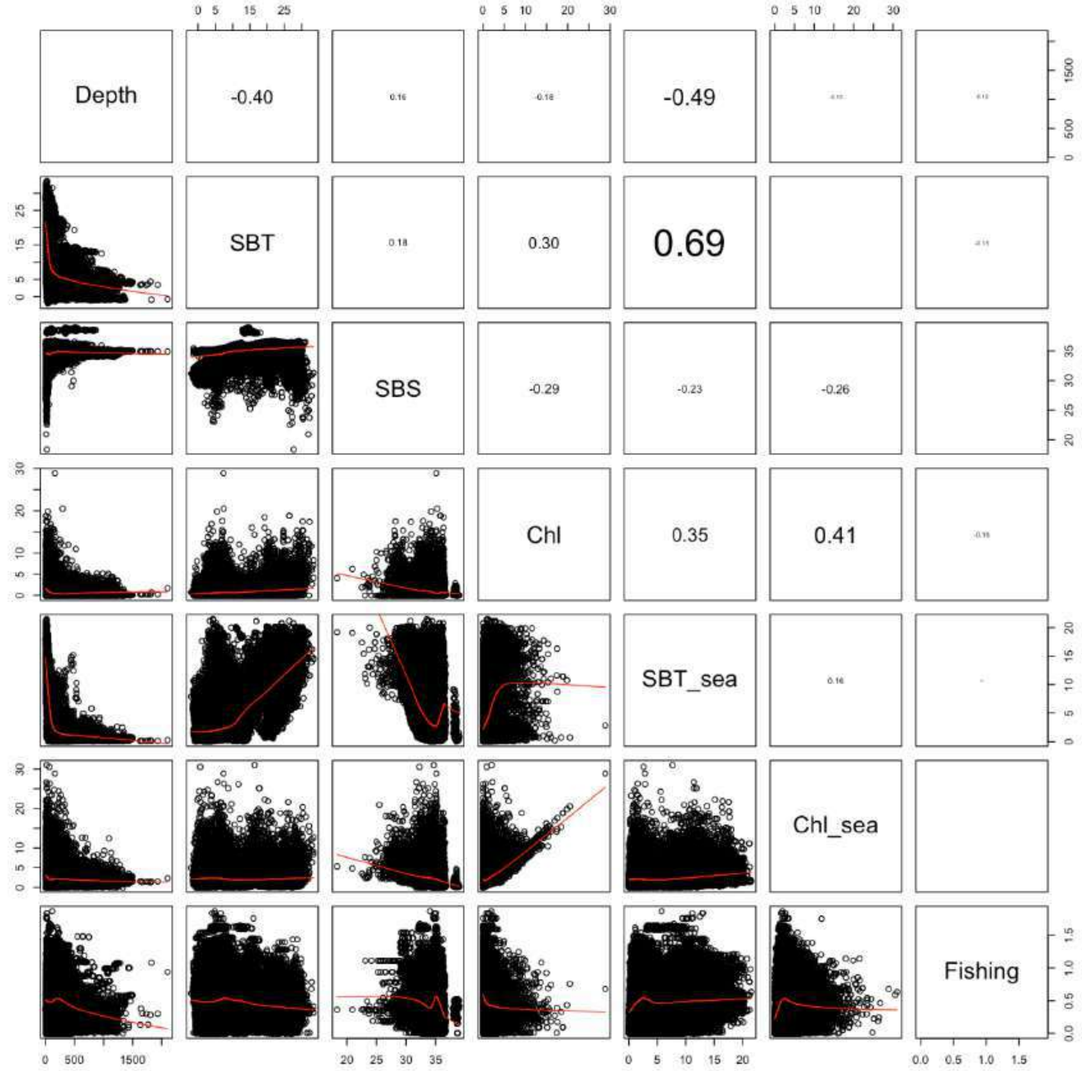


Figure S4.3: Spatial distribution of the seven external pressures, (A) depth in m; (B) sea bottom temperature in °C; (C) sea bottom salinity in °C; (D) Chlorophyll *a* concentration in mg·m^{-3}; (E) range of annual temperature; (F) range of annual chlorophyll *a* concentration; and (G) cumulative fishing pressure (Halpern *et al.* 2015).

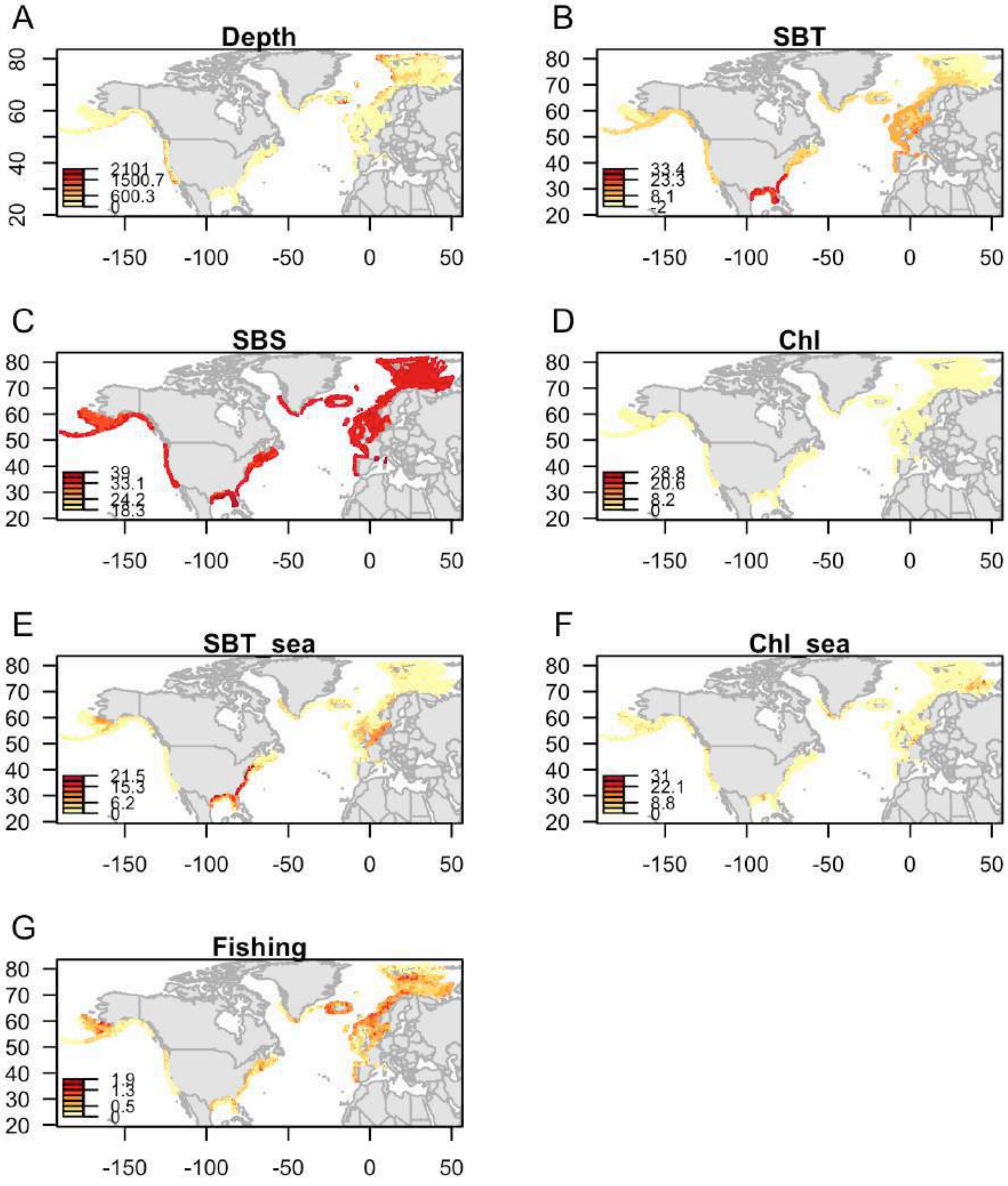


Figure S4.4: RLQ analysis per spatial scale, calculated by aggregating stations into (C) 0.25 degree, (D) 0.5 degree, (E) 1 degree and (F) 2.5 degree rectangle.

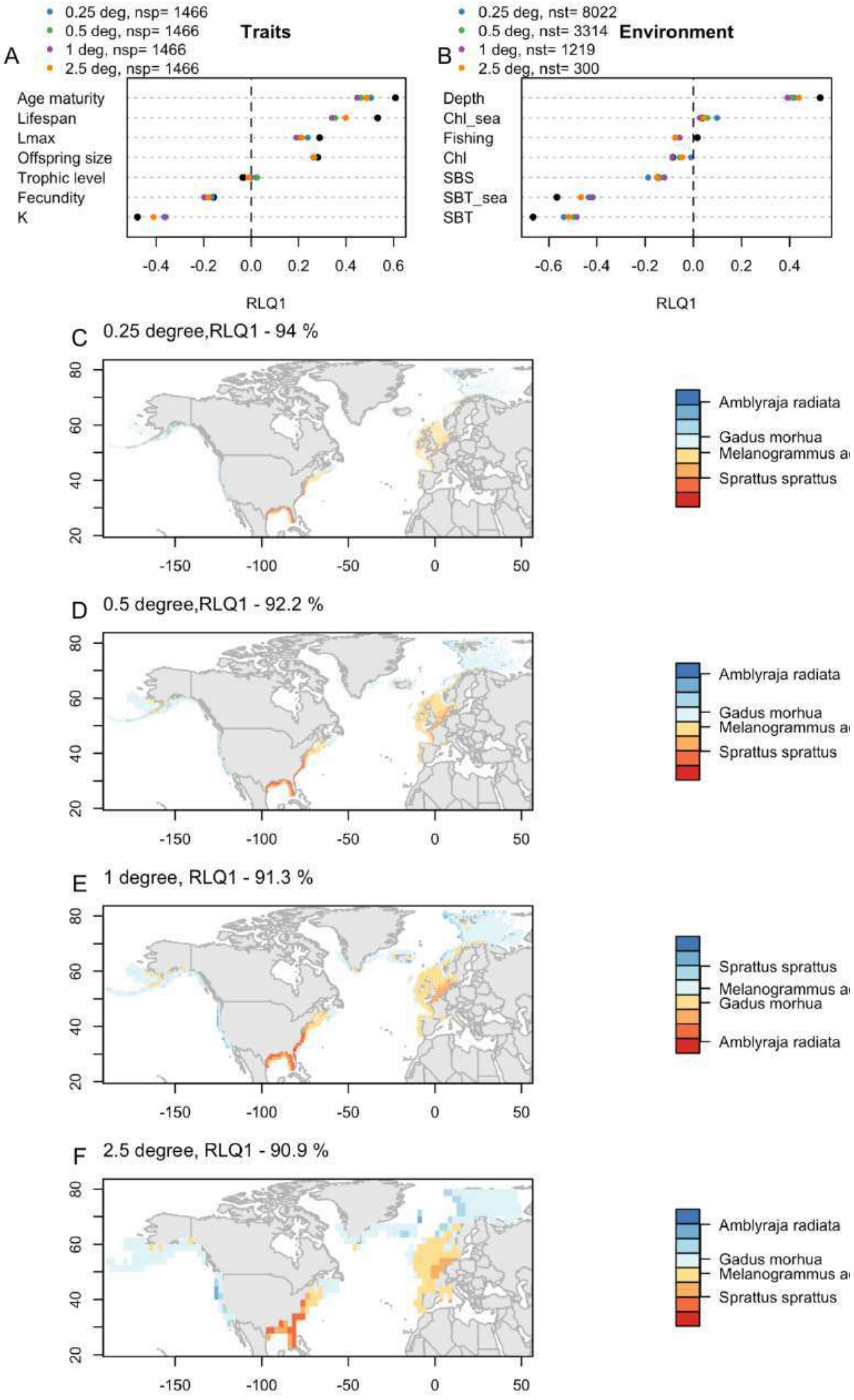


Figure S4.5: RLQ analysis per seasons calculated by dividing stations per season: (C) Q1, (D) Q2, (E) Q3 and (F) Q4.

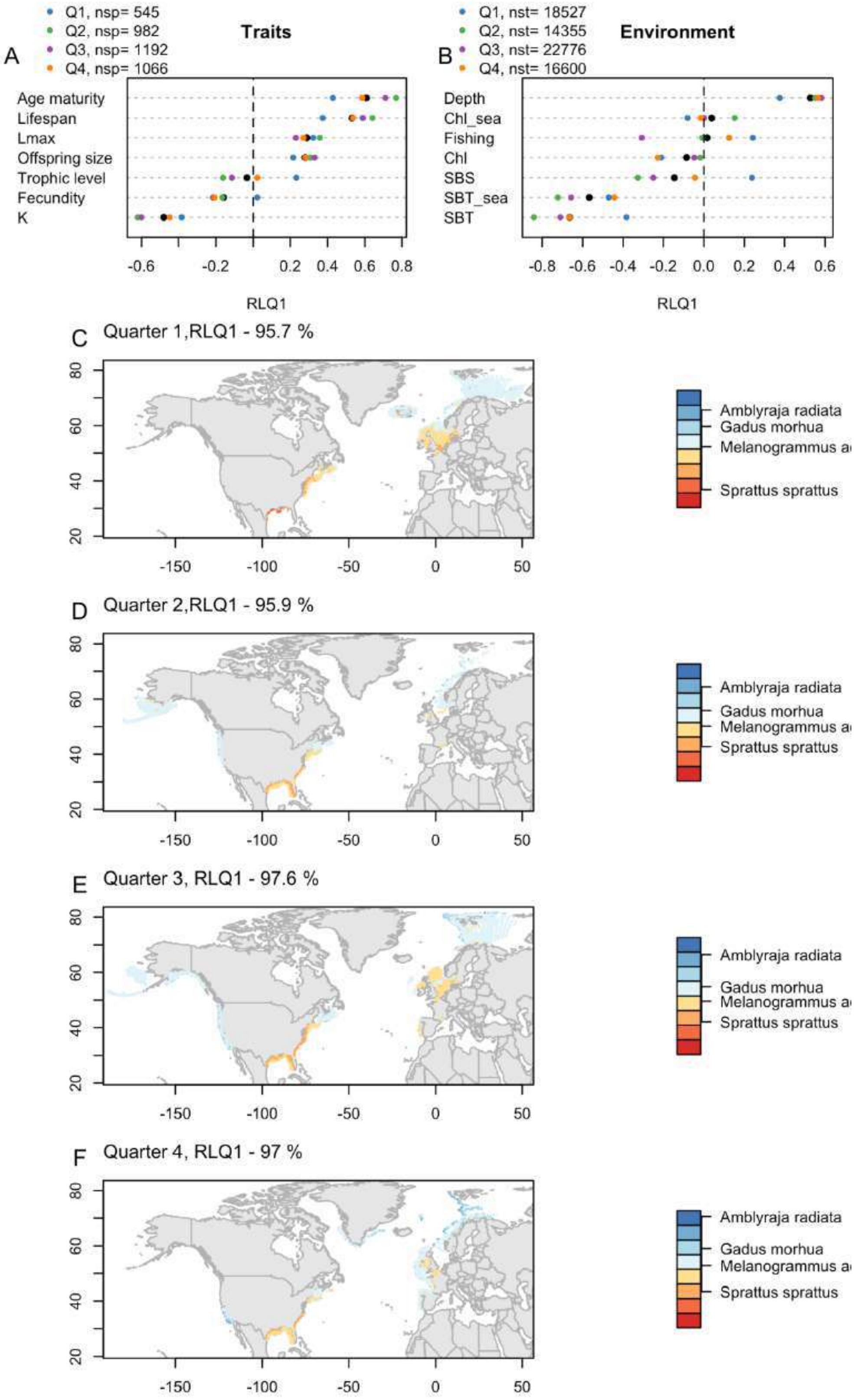


Figure S4.6: RLQ analysis per depth stratum, with stations divided into four depth layers. (A) scores of the traits on RLQ1, (B) scores of the environment variables on RLQ1. The colour of dots represents depth layer, with blue above 30m depth, green between 30 and 150m, purple between 150 and 300m, and orange below 300m depth. The black dot is the scores considering all the stations (as in Figure 2). (C-F) Scores of the stations and the species on RLQ1 divided per depth layer.

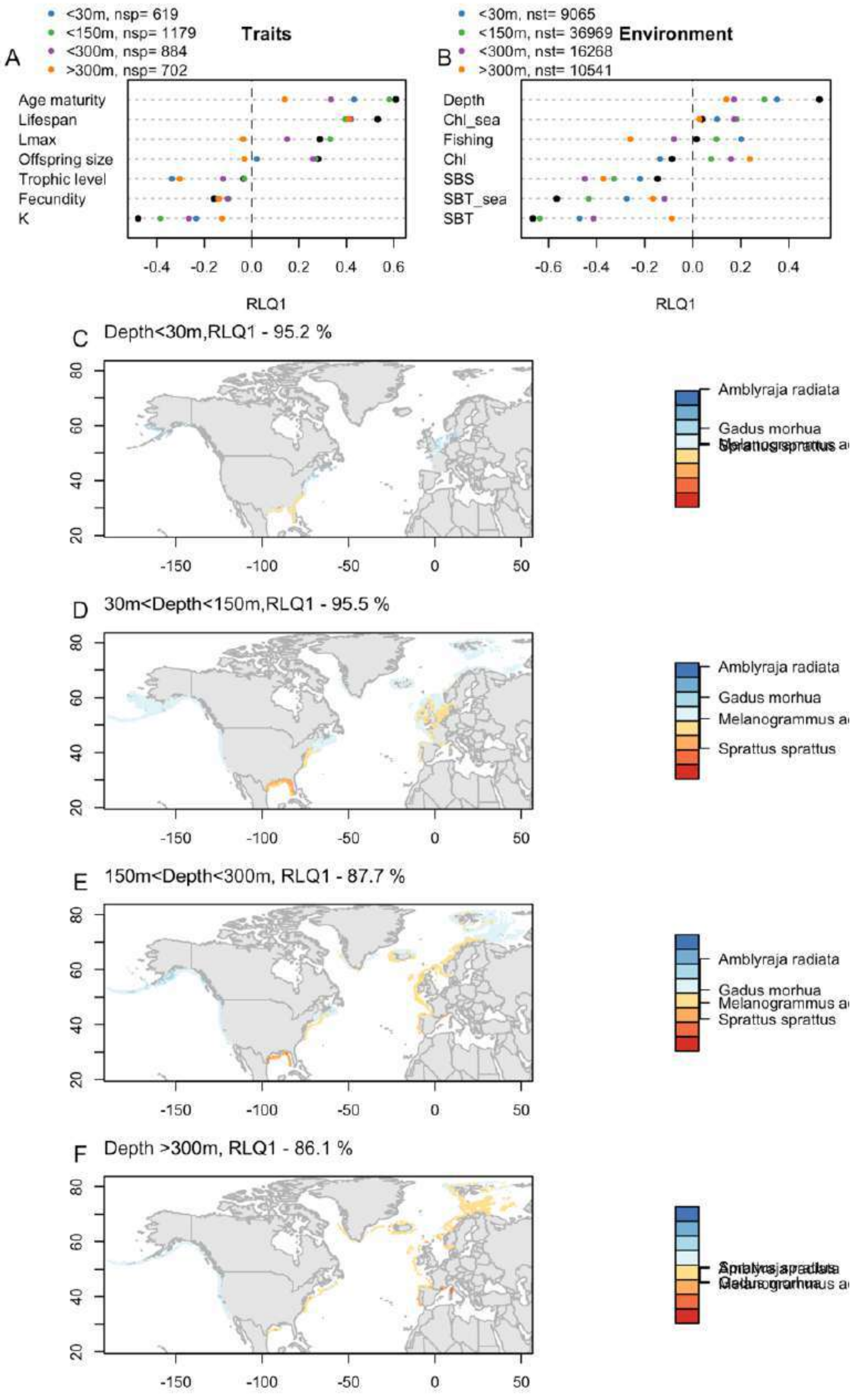
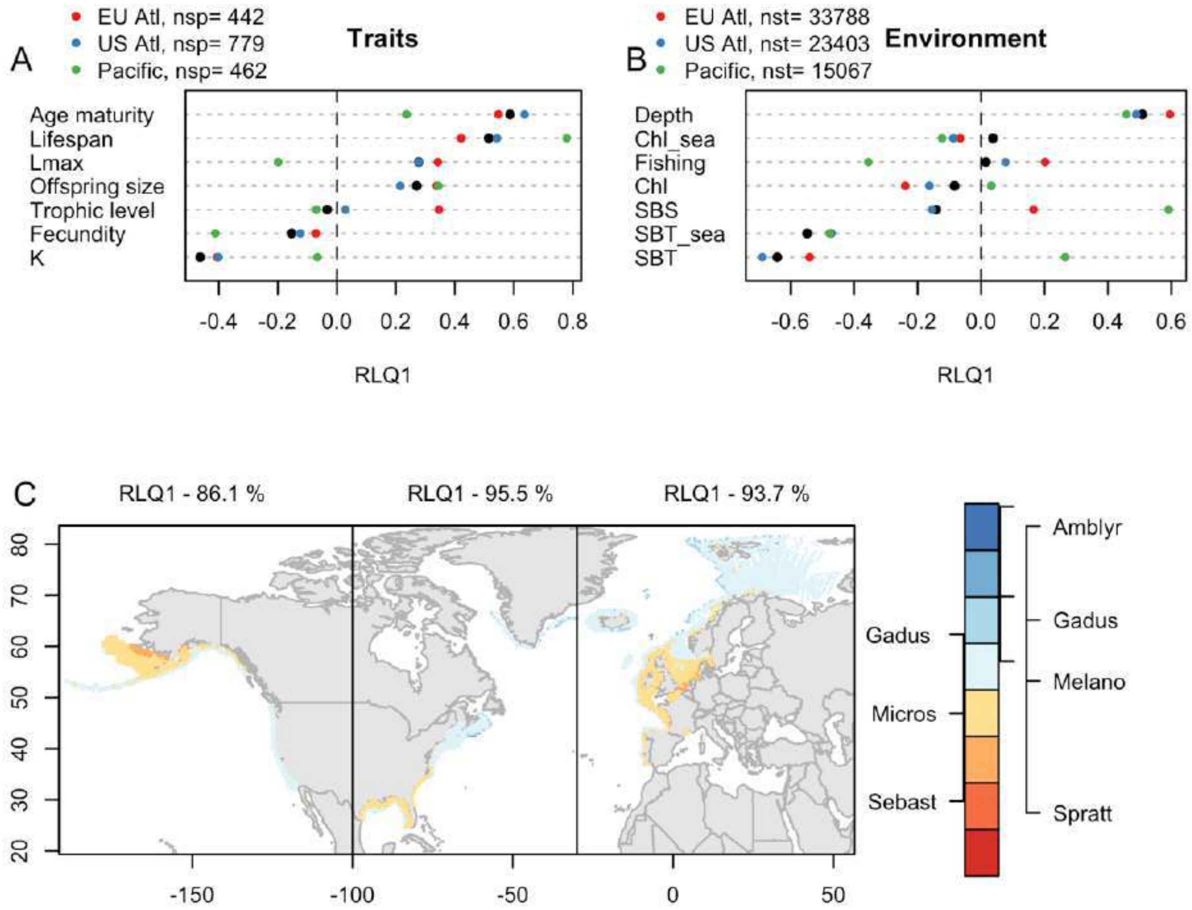
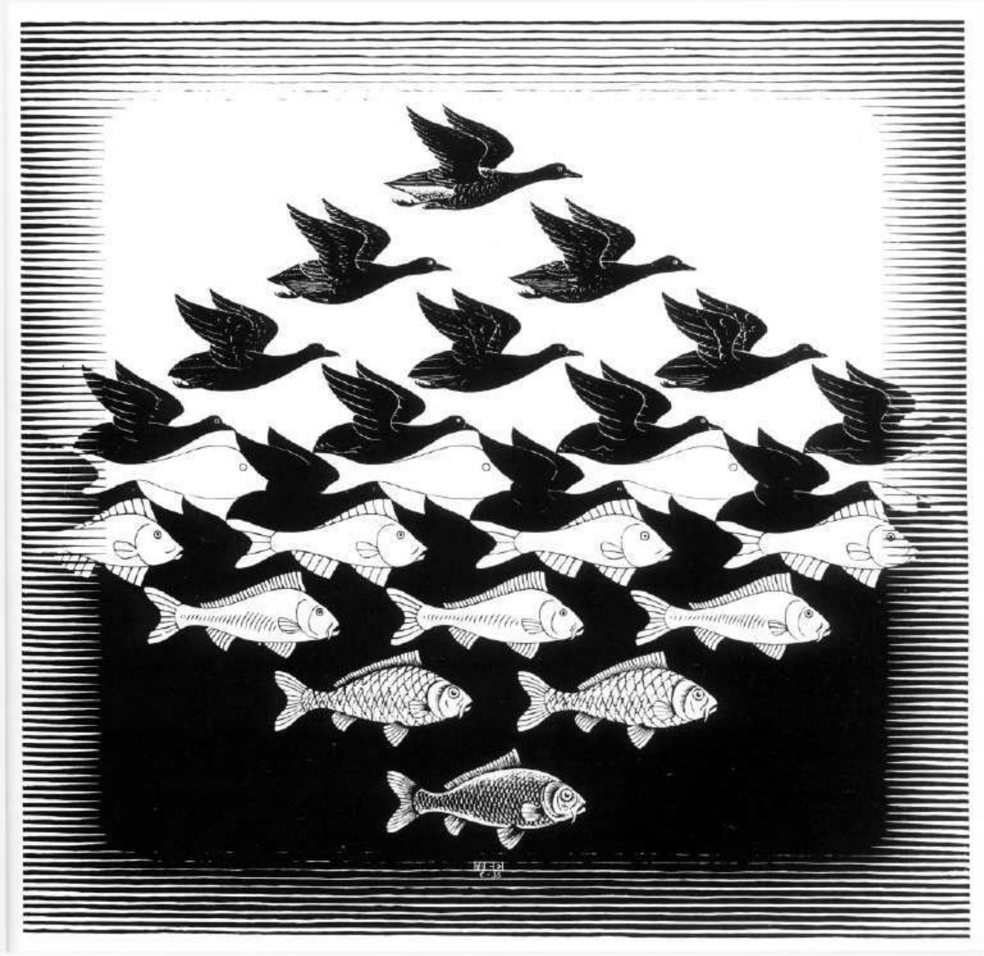


Figure S4.7: RLQ analysis per coastline with stations divided into three regions. (A) scores of the traits on RLQ1, (B) scores of the environment variables on RLQ1. The colour of dots represents the regions, with red for Northeast Atlantic, blue for Northwest Atlantic and green for Northeast Pacific. The black dot are the scores considering all the stations (as in Figure 4.2). (C) Scores of the stations and the species on RLQ1 divided per region.



Chapter 5

A morphometric dive into fish diversity



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Title: A morphometric dive into fish diversity

Authors: Florian Caillon[1], Vincent Bonhomme[2], Christian Möllmann[1], Romain Frelat[1*]

[1]University of Hamburg, Institute for Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability (CEN), University of Hamburg, Große Elbstraße 133, 22767 Hamburg, Germany

[2] UMR 5554 Institut des Sciences de l'Evolution, équipe Dynamique de la biodiversité, Anthropo-écologie Université de Montpellier, CNRS, IRD, EPHE Place Eugéne Bataillon, 34095 Montpellier Cedex 05, France

[*] Corresponding author: Romain Frelat, romain.frelat@uni-hamburg.de

Abstract

Trait-based approaches are increasingly popular in ecology to describe communities and their responses to natural or anthropogenic changes. Morphology is an integrative trait that combines functional and evolutionary information. However, the objective and quantitative description of the morphological diversity is quite challenging. Modern morphometrics encompass an array of mathematical approaches that turn shapes into quantitative variables. For models with no or only a few homologous points, outline analysis (e.g. elliptical Fourier transform) converts the outline geometry into quantitative variables, which can be used in the multivariate framework. The elliptical Fourier transform here describes the shape of 85 fish species found in the North Sea. This approach shows that the main component of morphological diversity is the elongation and development of dorsal, pelvic, and caudal fins. The spatial distribution of morphological diversity decreases along a latitudinal gradient, with higher diversity in the southern part. Compared to species diversity, our results indicate that environmental conditions filter morphological traits in the northern North Sea. Outline analysis is a powerful approach to provide an objective description of fish morphology and to improve our understanding of the diversity of Large Marine Ecosystems.

Keywords: fish diversity, morphological traits, outline analysis, elliptical Fourier transform, North Sea.

Introduction

Trait-based approaches are increasingly popular in ecology to describe communities and their responses to natural or anthropogenic changes (Keddy 1992; McGill *et al.* 2006; Mouillot *et al.* 2013). These approaches characterize species by key features, known as traits, which can be the morphological, biochemical, physiological, structural, phenological, or behavioural characteristics of an organism. Traits help researchers to understand species responses to the environment and the contribution of community biodiversity to the ecosystem functioning (Violle *et al.* 2007, 2014). Morphology is a highly integrative trait that combines functional and evolutionary information (Wainwright & Reilly 1994). The high inertial and viscous drag of water (e.g. compared to air) is a major selection pressure on the shape of marine organisms. However, the huge morphological diversity of fishes has often been described subjectively and qualitatively (Pecuchet *et al.* 2016; Froese & Pauly 2017). But trait-based approaches favour quantitative traits that are considered more practical, objective, and informative than their qualitative counterparts (McGill *et al.* 2006).

The quantitative description of shapes has long been challenging. Morphometrics, the statistical description of shapes, now distinguishes between *traditional* and *modern* morphometrics (Rohlf 1990). Traditional morphometrics rely upon the measurements of shape indicators such as lengths, areas, angles, and their ratios (Gatz 1979; Wainwright 1988; Wikramanayake 1990) hence focusing on selected aspects of shape only (subjectively chosen and/or technically constrained). Consequently, the original shape cannot be unequivocally reconstructed from the measured indicators. Modern morphometrics, in contrast, consider the entire shape and two main approaches are currently used: configuration of landmarks and outline analysis (Rohlf 1990; Claude 2008; Bonhomme *et al.* 2014). The first approach uses homologous points between shapes, known as landmarks, and studies their relative position. The technique has been used extensively in the last decades to study intra-species fish morphology (Loy *et al.* 2000; Klingenberg *et al.* 2003; Costa & Cataudella 2007; Elmer *et al.* 2010). However, homologous points are often hard to define between various shapes—e.g. between species from different families, and the number and position of homologous landmarks vary between studies and organisms (Farré *et al.* 2016). In contrast, outline analyses consider the whole outline. The most popular outline analysis approach is elliptical Fourier transform (EFT), and it has been used in marine biology to describe otolith shapes (Tracey *et al.* 2006; Mérigot *et al.* 2007), shells (Costa *et al.* 2008) and fish species morphologies (Loy *et al.* 2000; Ventura *et al.* 2017). To our knowledge, these studies considered very similar biological objects only and the technique was never extended to explore the diversity patterns in species assemblages.

Using the North Sea as a case study, this study demonstrates the use of EFT to quantitatively describe the morphological variability in a highly diverse marine fish species assemblage (Daan *et al.* 1990). The North Sea fish community is structured along a strong latitudinal gradient, mainly associated with differences in depth and primary production (Emeis *et al.* 2015; Frelat *et al.* 2017). The many commercially important fish populations provide highly valued ecosystem services. Our new quantitative description of morphological variability can improve our understanding of the community diversity and identify environmental processes structuring the fish community of this Large Marine Ecosystem.

Material and methods

Sample collection

Images of bony fishes from the North Sea were collected in January 2017 from nine online image databases (Table S5.1). Four criteria were used to only retain comparable images: (1) lateral views of (2) male individuals (to cope with any sexual dimorphism) (3) with all their fins well represented (i.e. spread and not eaten); (4) eel-shaped species were discarded because of their recurrent serpentine representation. We considered images of all species recorded regularly during bottom trawl survey in the North Sea and fitting the four criteria previously cited. When available, several images of the same species were included to evaluate the robustness of the approach. A total of 218 images (48 photos and 170 drawings) from 85 bony fish species of the North Sea were included in this study (Fig. S5.1).

Before performing the outline analysis, we transformed the images into black silhouettes (Fig. 5.1B). Numerous studies have defined landmarks on fish to study their morphology. We used five commonly used landmarks (Loy *et al.* 2000; Elmer *et al.* 2010; Farré *et al.* 2016) that are located on the outline, easily recognizable, and present on all species: (1) snout tip; (2) anterior insertion of the dorsal fin; (3) dorsal and (4) ventral insertion of the caudal fin; and (5) insertion of the pelvic fin (Fig. 5.1B). The silhouettes were then converted into (x; y) coordinates.

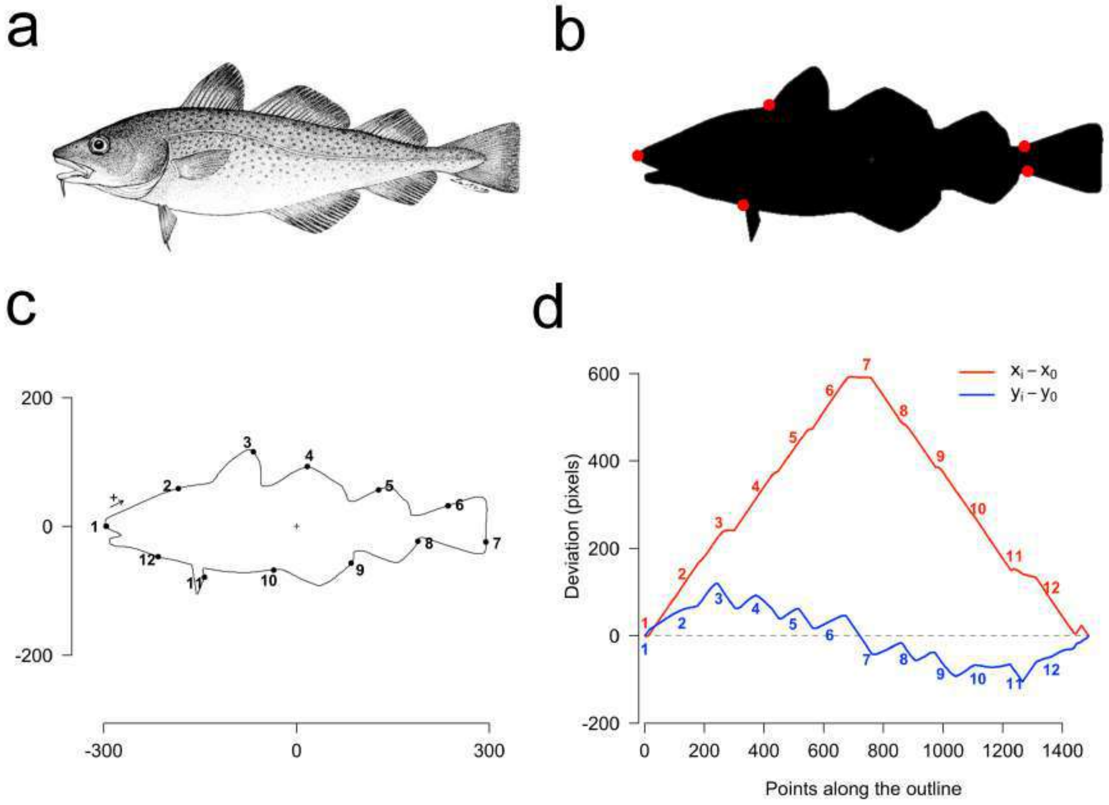


Figure 5.1: Illustration of outline analysis using elliptical Fourier transform. From original image (a), to black silhouette with five landmarks (b), on which the outline (c), can be described with elliptical Fourier transform (d). The species in the figure is *Gadus morhua*, image from FAO.

Elliptical Fourier transform

Elliptical Fourier transform (EFT) is a popular method of outline analysis, fitting separately the x and y coordinates of an outline projected on a plane (Rohlf 1990; Bonhomme *et al.* 2014). Before conducting such analysis, outlines must be aligned to remove differences in rotation, translation or size. We used five landmarks to align the outlines using a full Procrustes superimposition. This superimposition optimally rotates, translates and scales these five landmarks to minimize Procrustes distances between all landmark configuration. The first landmark (position of the mouth) was defined as the starting point of every outline. Outlines are closed curves than can be described as periodic functions. The elliptical Fourier transform (EFT) describes the outline geometry as two periodic functions—the difference between the abscissa/ordinate of the first and all successive points (Fig. 5.1C). The Fourier transform then decomposes them into a harmonic sum of trigonometric functions, weighted with coefficients known as harmonic coefficients. The original signal f can then be expressed as follows:

$$f(t) = \frac{a_0}{2} + \sum_{n=1}^{+\infty} \left[a_n \cos\left(n \frac{2\pi}{T} t\right) + b_n \sin\left(n \frac{2\pi}{T} t\right) \right]$$

with T as the perimeter of a given closed outline and t as the curvilinear abscissa that varies from 0 to T. The harmonic coefficients a_n and b_n can be expressed as follows:

$$a_n = \frac{2}{T} + \int_0^T f(t) \cos\left(n \frac{2\pi}{T} t\right) dt \qquad b_n = \frac{2}{T} + \int_0^T f(t) \sin\left(n \frac{2\pi}{T} t\right) dt$$

Four coefficients are obtained for each harmonic calculated. The number of harmonics was chosen to retain 99% of the cumulative harmonic power. The harmonic coefficients can be considered as quantitative variables and analyzed within a multivariate framework. More details can be found in Bonhomme et al. 2014. A principal component analysis (PCA) was calculated on the matrix of coefficients. Each principal component (PC) captured an independent and synthetic aspect of shape variability. Morphospaces, theoretical shapes regularly drawn on the factorial plane, helped to interpret the results. The first three PCs were compared to commonly used morphological traits by categorizing the caudal and body shapes (Pecuchet et al. 2016, Dencker et al. 2017; Fig. S5.2). Finally, we compared the morphological distance (Euclidean pairwise distances of images calculated from coordinates on the first three PCs) with the taxonomical distance calculated with five taxonomic levels (Fig. S5.3).

Morphological diversity in the North Sea

Abundance data of the North Sea fish community has been collected by the North Sea International Bottom Trawl Survey (ICES 2015), an international effort to monitor demersal fish populations. The sampling procedure monitored the North Sea on a regular grid of 1° longitude x 0.5° latitude, known as the ICES rectangles. Each contributing research vessel applies a standard otter trawl net which is hauled over the seabed for 30 minutes. The data for the first quarter of the period 2006 to 2015 was downloaded from http://datras.ices.dk/. To avoid any bias that may arise due to different sampling efforts (i.e. different number of hauls per ICES rectangles), 10 hauls per ICES rectangles were randomly selected, and we assessed their species and morphological richness. We repeated the random selection 100 times to estimate the variability of species occurrence (i.e. the presence or absence of species). ICES rectangles with less than 10 hauls in the 10-year period were removed from the analysis. In total, 172 ICES rectangles were included in the analysis.

Two indicators of morphological diversity were calculated for each ICES rectangle from occurrence data and the mean scores of species on the three PCs defining the morphospace (Villéger *et al.* 2008). Morphological richness is the volume of the morphospace occupied by the convex hull of the community. Morphological dispersion is the mean distance to the barycenter of each community (Laliberté & Legendre 2010). The morphological diversity was then compared to species (i.e. taxonomic) richness obtained from the occurrence data. We expected that the morphological richness increases with taxonomic richness. A null model for the relationship between species and morphological richness was estimated by randomly selecting a given number of species from the entire species pool (with specific probabilities in accordance with their occurrence in the North Sea) and by calculating the morphological diversity indicators with a random assemblage of species. We repeated the randomization process 1,000 times, and computed it for species richness ranging from 10 to 50.

Software and tutorial

All statistical analyses were conducted in the programming environment R 3.3 (R Core team 2017). Morphometric analyses were done with the package *Momocs* 1.2.3 (Bonhomme *et al.* 2014), while morphological diversity indicators were calculated with the *FD* package. The geographic distribution of species and morphological richness was visualized with the *mapdata* and *rgdal* packages. A tutorial explaining the elliptical Fourier transform on fish communities is available on GitHub: https://rfrelat.github.io/FishMorpho.html (DOI: 10.5281/zenodo.1108518).

Results

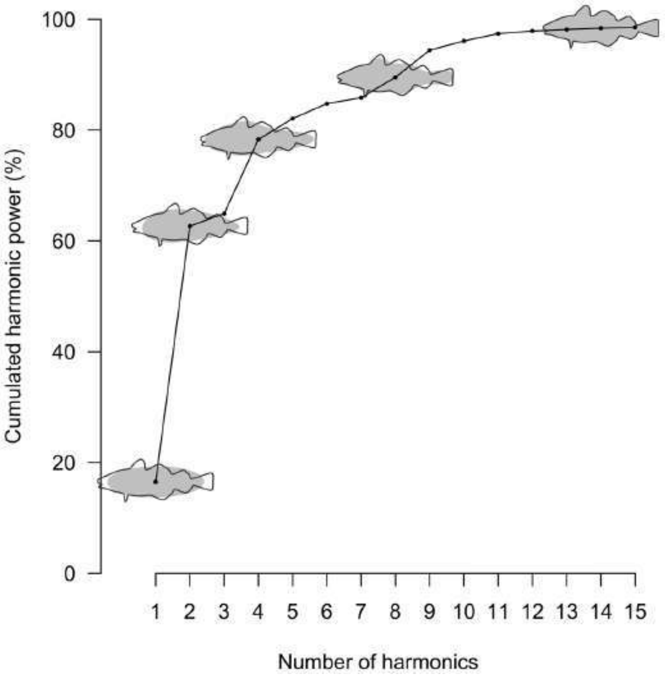


Figure 5.2: Progressive reconstruction of shapes. Fourteen harmonics gathered 99% of the total harmonic power.

Outline analysis and morphological space

Fourteen harmonics were enough to gather 99% of the total harmonic power (Fig. 5.2). The principal component analysis on the 56 resulting coefficients yielded three principal components, accounting for 78% of the variance (Fig. 5.3). The first principal component (PC1), accounting for 42% of the total variance, highlighted the general rounding or elongation of the shapes (Fig 5.3B). Shapes presenting the lowest scores on this PC belonged to elongated fish species like the smooth sandeel (*Gymnammodytes semisquamatus)* and the great sandeel *(Hyperoplus lanceolatus)*. On the other hand, shapes presenting the highest values on this component belonged to flat fish species like the turbot (*Scophthalmus maximus*) or the European plaice (*Pleuronectes platessa)*.

The second principal component (PC2), explaining 24% of the variability, highlighted the development of the pelvic fin and the underside. Shapes presenting the lowest values on this component belonged to species with strong and developed pelvic fins such as the tub gurnard (*Chelidonichthys lucerna*) and the golden redfish (*Sebastes norvegicus*). On the contrary, shapes presenting the highest values on this component belonged to species with smooth ventral sides and short pelvic fins like the Norway pout (*Trisopterus luscus*) and the sand sole (*Pegusa lascaris*).

Finally, the third principal component (PC3), explaining 12% of the variability, was related to the shape of the dorsal and caudal fins. Shapes that presented the lowest values on this component belonged to species with strong, short, and developed dorsal fins and fork-shaped caudal fins such as the Clupeidae family like the allis shad (*Alosa alosa*)*,* sardine (*Sardina pilchardus*), and herring (*Clupea harengus*). On the other hand, shapes presenting the highest values on this component belonged to species with a continuous body, long dorsal fins, and round-shaped caudal fins like the striped seasnail (*Liparis liparis*) and the checker eelpout (*Lycodes vahlii*). Body and caudal shape traits described by Pecuchet et al. (2016), were significantly linked with PC1 and PC3 respectively (Fig. S5.2). The morphological distance between individuals increased with the taxonomical distance (Fig. S5.3). We found no significant difference in the distances within species if calculated only with the same type of images, or with one drawings and one photo (p-value of the Student's t-test=0.26). This result indicated that the type of images does not influence our analysis. The average scores for each species on the three components is provided in Table S5.2.

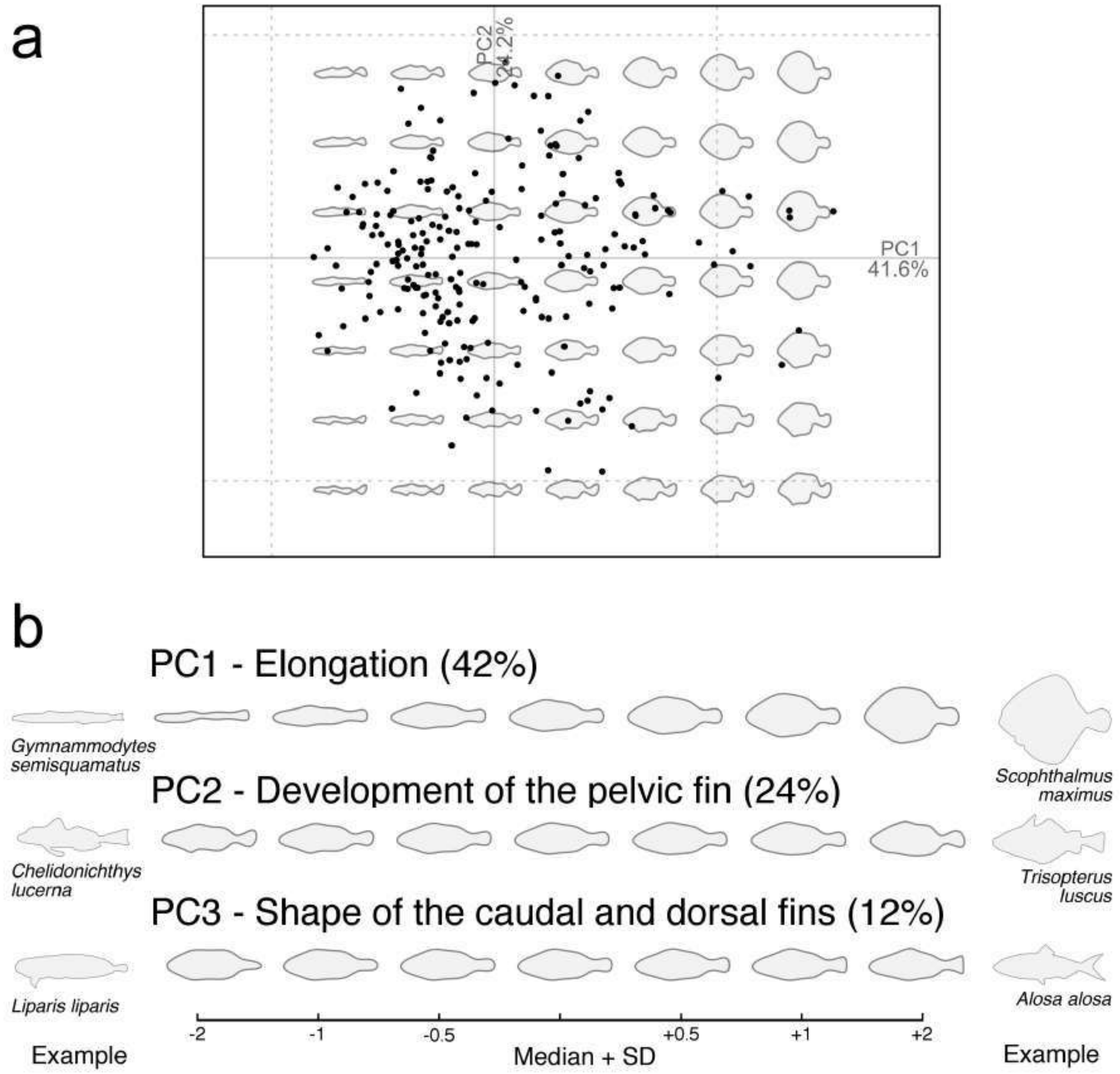


Figure 5.3: Principal component analysis calculated on the matrix of Fourier coefficients. (a) Scatterplot of the scores on the first two principal components (PC), accounting for 66% of the total variance; the morphospace in the background presents theoretical shapes reconstructed from the PCs. (b) Illustration of the synthetic components of shape captured by the first three PCs. Raw outlines of the species projected near PCs extrema are displayed as example.

Morphological diversity in the North Sea fish assemblages

Morphological diversity, expressed as richness or dispersion, decreased along a latitudinal gradient with highest values in the southern North Sea (Fig. 5.4AB). The maximum morphological diversity was observed in the Kattegat, at the Elbe river mouth, and at the connection to the English Channel. The Kattegat also presented the maximum species richness of all ICES rectangles (39 species recorded). As expected, a positive correlation was found between the species richness and the morphological richness in the null model (Fig. 5.4C). We compared the observed morphological diversity indicators of each ICES rectangle with their expected values in the null model (Fig. 5.4CD). As expected, the null model predicted that morphological richness increased with the number of species (Fig. 5.4C). Morphological dispersion was not linked with species richness, but the variance of the predictions of the null model decreased with the number of species (Fig. 5.4D). Most of the area in the northern North Sea had lower morphological richness than predicted by the null model, and nine ICES rectangles had significantly (P value < 0.05) lower morphological richness than expected by the 1,000 randomizations in the null model (Fig. 5.4E). In the southern North Sea, most of the rectangles had morphological richness falling within the range or slightly higher than the predicted level, but none was significantly different those in the null model. Similar patterns were found with morphological dispersion. Eight ICES rectangle in the southern North Sea had significantly higher morphological dispersion than expected, and twelve ICES rectangle located in the northern North Sea had significantly lower morphological dispersion than expected (Fig. 5.4F).

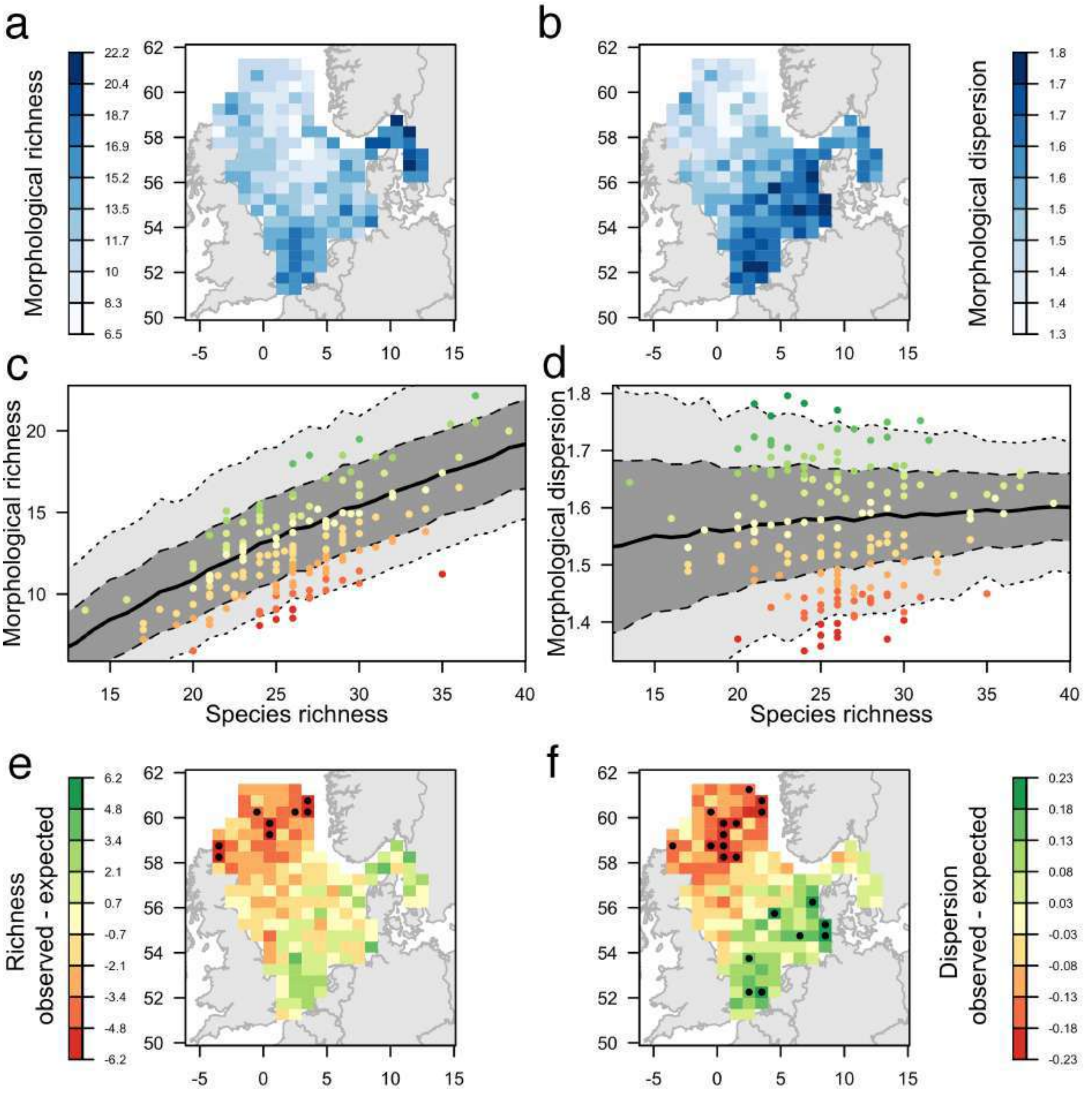


Figure 5.4: Spatial distribution of morphological diversity. (a-b) Spatial patterns of fish morphological diversity in the North Sea. (c-d) Relationship between the observed morphological diversity and species richness. The bold black line represents the mean morphological diversity of 1,000 random samplings for a given number of species; the shaded areas in dark and light grey represent the standard deviation and 95th percentile, respectively. (e-f) The map of the residuals between observed and predicted morphological diversity. Black dots indicate communities significantly different from the null model. The left column (a, c, e) represent morphological richness and the right column (b, d, f) represents morphological dispersion.

Discussion

Outline analysis appeared to be effective at describing the morphological diversity of fish species in the North Sea. Elliptical Fourier transform (EFT) revealed three main components of morphological diversity in marine fish species. The most important component was related to elongation of the main body; the second to the development of the pelvic fin; and the third to the shape of the dorsal and caudal fins. These three integrative and quantitative variables are good candidates for new morphological traits in accordance with the criteria stated by McGill et al. (2006): "To be useful to community ecology, traits should vary more between than within species and preferably be measured on continuous scales."

Morphological traits found in this study had already been described by previous subjective and qualitative descriptions (Pecuchet *et al.* 2016). Furthermore, we found elongation to be the major source of variability in shape, in accordance to numerous studies on fish morphology (Elmer *et al.* 2010; Claverie & Wainwright 2014; Ventura *et al.* 2017) and more generally, on vertebrates morphology (Collar *et al.* 2013). These similarities suggest that EFT can describe both quantitatively and objectively the known morphological features and reveal more subtle components of morphological diversity. Additional studies should link these morphological traits with specific functions of fish, like swimming performance and feeding behaviour (Norton *et al.* 1995; Bejarano *et al.* 2017).

Morphological diversity decreased along a latitudinal gradient with highest values in the southern North Sea. This shallow area is known to host a different species assemblage than the northern part due to different environmental pressures—for example, higher temperature and primary production (Daan *et al.* 1990; Frelat *et al.* 2017) and different epibenthic invertebrate community (Callaway *et al.* 2002). One of the main difference in species assemblages is the numerous small flatfish species that inhabits only the southern North Sea (Callaway *et al.* 2002). Adding quantitative morphological traits will help researchers to determine the community assembly rules, the relationship between taxonomic and functional diversity (Bellwood *et al.* 2002; Dencker *et al.* 2017). As expected, we observed that areas with high species richness were more likely to present a higher morphological richness. However, areas with low species richness in the northern North Sea presented significantly lower morphological diversity than expected, if the species were chosen randomly. This result suggests that the environmental conditions filter species lacking a specific combination of morphological traits (Keddy 1992; Mouillot *et al.* 2007). This observation was confirmed by morphological dispersion which showed a strong latitudinal gradient and suggests two opposing mechanisms: environmental filtering in the north and limiting similarity in the south. The border between the two mechanisms match the boundary between the thermally stratified waters of the northern North Sea and the permanently vertically mixed waters of the southern North Sea (Callaway *et al.* 2002). The high seasonal fluctuations in bottom water temperature in the south may be a factor limiting the morphological similarities between species, while the more stable conditions in the northern North Sea seems to filter morphologically similar species. This interpretation remains to be confirmed and tested in other Large Marine Ecosystems.

EFT is known to be sensitive to the choice of the alignment method but our analysis consistently found the same three main components (Fig. S5.4 and S5.5). Naturally, fishes are 3D objects whose morphological descriptions could be refined, for example, with EFT on 2D orthogonal views to characterize the cross-section body shape (Terral *et al.* 2004; Bonhomme *et al.* 2015; Bouby *et al.* 2016). It would require a collection of images of the cross-section data for numerous fish species that are not available online yet. Our study focused on only the shape, which is the form minus size, and the latter would probably be an informative covariate. Moreover, the outline analysis produced here only considers the information included in the outline, missing for example the shape and the position of the pectoral fin, the operculum and the eye, features known to have a functional role (Klingenberg *et al.* 2003; Mouillot *et al.* 2007; Farré *et al.* 2016). However, a comparison of landmark based approach and outline analysis showed no significant differences (Loy *et al.* 2000) and a recent study shows that most of the morphological variability in reef fishes was found in body elongation (Claverie & Wainwright 2014). The outline analysis of the shape of the single lateral view proved to bring important insights into the diversity of fish morphology. The outcome of the outline analysis can be of great interest for further morphological studies and trait-based approaches in ecology and biogeography. Extending such an approach to the species from other large marine or freshwater ecosystems would characterize the global spectrum of fish morphology.

List of supplementary materials

Table S5.1: Description of the online image databases used for the study

Table S5.2: Morphological characterization of 85 fish species in the North Sea

Figure S5.1: Outlines of the 218 images of fish.

Figure S5.2: Relationship between EFT results and commonly used morphological traits.

Figure S5.3: Comparison between the morphological and taxonomical distance

Figure S5.4: Shape alignment of the four different alignments tested

Figure S5.5: Robustness of the results from the alignment method

Table S5.1: Description of the online image databases used for the study with the number of images collected in each database and the nature of the image (drawing or picture).

ID	Name	Nature	Nb of images	Link
ADd	Animal Diversity Web	Drawing	1	http://animaldiversity.org/accounts/ Actinopterygii/pictures/
FAOd	FAO Fisheries and Aquaculture Department	Drawing	44	http://www.fao.org/fishery/species/ search/en
FAOp		Photo	2	
FBd	FishBase	Drawing	37	http://fishbase.mnhn.fr/photos/ BestPhotos.php
FBp		Photo	21	
GOBd	Gobidae	Drawing	1	http://gobiidae.com
IFd	Ittiofauna	Drawing	1	http://www.ittiofauna.org/
NPd	Naturporten	Drawing	1	http://naturporten.dk
NRMp	Swedish Museum of Natural History Ichthyology Database	Photo	10	http://artedi.nrm.se/nrmfish/ imgsearch.php
WIKd	Wikimedia Commons	Drawing	22	https://commons.wikimedia.org/ wiki/Accueil
WIKp		Photo	1	
WoRd	World Register of Marine Species	Drawing	63	http://marinespecies.org/
WoRp		Photo	14	

Table S5.2: Morphological characterization of 85 fish species in the North Sea

Species	PC1	PC2	PC3	Body	Caudal
Alosa alosa	-0.02	0.02	0.08	Normal	Forked
Alosa fallax	-0.04	-0.02	0.05	Normal	Forked
Ammodytes marinus	-0.10	0.00	-0.05	Elongated	Forked
Ammodytes tobianus	-0.10	-0.03	-0.06	Elongated	Forked
Anarhichas lupus	-0.05	0.02	-0.04	Elongated	Rounded
Aphia minuta	0.00	-0.08	-0.01	Normal	Rounded
Argentina silus	-0.06	0.00	0.03	Normal	Forked
Argentina sphyraena	-0.08	0.02	0.04	Normal	Forked
Arnoglossus imperialis	0.07	0.00	-0.04	Flat	Rounded
Arnoglossus laterna	0.06	0.03	-0.03	Flat	Rounded
Atherina presbyter	-0.06	0.00	0.02	Normal	Forked
Brosme brosme	-0.04	-0.04	-0.06	Elongated	Rounded
Buglossidium luteum	0.04	0.07	-0.04	Flat	Rounded
Callionymus maculatus	0.01	0.13	-0.01	Normal	Rounded
Chelidonichthys cuculus	-0.02	-0.04	0.00	Normal	Truncated
Chelidonichthys lucerna	-0.01	-0.09	-0.02	Normal	Truncated
Ciliata mustela	-0.06	0.00	-0.04	Elongated	Rounded
Clupea harengus	-0.05	-0.01	0.05	Normal	Forked
Crystallogobius linearis	-0.07	-0.10	-0.04	Elongated	Truncated
Ctenolabrus rupestris	0.04	-0.04	0.00	Normal	Rounded
Cyclopterus lumpus	0.05	0.09	-0.05	short_deep	Truncated
Dicentrarchus labrax	0.00	-0.05	0.01	Normal	Emarginated
Echiichthys vipera	-0.01	-0.09	-0.01	Normal	Truncated
Enchelyopus cimbrius	-0.08	0.03	-0.04	Elongated	Rounded
Engraulis encrasicolus	-0.09	0.03	0.05	Elongated	Forked
Eutrigla gurnardus	-0.03	-0.07	-0.03	Normal	Emarginated
Gadiculus argenteus	-0.05	-0.04	0.04	Normal	Truncated
Gadus morhua	-0.04	0.05	0.01	Normal	Truncated
Gaidropsarus vulgaris	-0.06	0.00	-0.02	Elongated	Rounded
Gasterosteus aculeatus	-0.06	0.04	0.03	Elongated	shark_like
Glyptocephalus cynoglossus	0.04	0.04	-0.03	Flat	Rounded
Gobius niger	0.04	-0.06	0.00	Normal	Rounded
Gymnammodytes semisquamatus	-0.12	0.00	-0.06	Elongated	Forked
Helicolenus dactylopterus	0.06	-0.04	0.03	short_deep	Truncated
Hippoglossoides platessoides	0.06	0.00	-0.01	Flat	Rounded
Hippoglossus hippoglossus	0.02	-0.02	-0.01	Flat	Rounded
Hyperoplus lanceolatus	-0.11	-0.05	-0.05	Elongated	Forked
Labrus bergylta	0.06	-0.04	0.01	Normal	Truncated
Labrus mixtus	0.02	-0.03	0.00	Normal	Rounded
Lepidorhombus whiffiagonis	0.06	0.02	-0.01	Flat	Rounded
Leptoclinus maculatus	-0.10	-0.02	-0.08	Elongated	Truncated
Lesueurigobius friesii	-0.03	0.01	0.03	Normal	Rounded
Limanda limanda	0.08	0.05	-0.01	Flat	Rounded

Liparis liparis	-0.02	-0.01	-0.04	Normal	Rounded
Liparis montagui	-0.03	0.03	-0.02	Normal	Rounded
Lycodes vahlii	-0.09	0.04	-0.11	Elongated	Continuous
Maurolicus muelleri	-0.02	-0.06	0.04	Normal	Forked
Melanogrammus aeglefinus	-0.03	0.04	0.03	Normal	Emarginated
Merlangius merlangus	-0.04	0.04	0.02	Normal	Truncated
Merluccius merluccius	-0.04	-0.04	-0.01	Elongated	Truncated
Microchirus variegatus	0.04	0.07	-0.04	Flat	Rounded
Micromesistius poutassou	-0.07	0.05	0.01	Normal	Emarginated
Microstomus kitt	0.10	0.03	-0.01	Flat	Rounded
Molva molva	-0.08	-0.02	-0.04	Elongated	Rounded
Mullus surmuletus	-0.01	0.02	0.03	Normal	Forked
Myoxocephalus scorpioides	0.01	-0.07	-0.04	Normal	Truncated
Myoxocephalus scorpius	-0.05	0.01	0.02	Normal	Truncated
Osmerus eperlanus	-0.05	-0.02	0.04	Normal	Forked
Phycis blennoides	-0.04	0.07	-0.01	Normal	Rounded
Platichthys flesus	0.09	0.01	0.01	Flat	Rounded
Pleuronectes platessa	0.12	0.00	0.00	Flat	Rounded
Pollachius pollachius	-0.04	0.02	0.05	Normal	Emarginated
Pollachius virens	-0.03	0.00	0.04	Normal	Emarginated
Pomatoschistus lozanoi	-0.06	0.11	0.04	Elongated	Rounded
Pomatoschistus minutus	-0.05	0.00	0.00	Elongated	Rounded
Pomatoschistus pictus	-0.03	-0.04	-0.03	Elongated	Rounded
Salmo trutta	-0.04	-0.01	0.03	Normal	Truncated
Sardina pilchardus	-0.06	-0.01	0.07	Normal	Forked
Scomber scombrus	-0.07	-0.02	0.02	Normal	Forked
Scophthalmus maximus	0.19	0.03	0.01	Flat	Rounded
Scophthalmus rhombus	0.15	0.03	0.00	Flat	Rounded
Sebastes norvegicus	0.05	-0.11	0.00	Normal	Truncated
Sebastes viviparus	0.06	-0.09	-0.01	Normal	Truncated
Solea solea	0.04	0.08	-0.05	Flat	Rounded
Spondyliosoma cantharus	0.07	-0.02	0.03	short_deep	Emarginated
Sprattus sprattus	-0.05	-0.01	0.05	Normal	Forked
Taurulus bubalis	0.03	-0.03	0.02	Normal	Rounded
Trachinus draco	-0.04	-0.01	-0.01	Normal	Truncated
Trachurus trachurus	-0.02	-0.04	0.03	Normal	Forked
Trigloporus lastoviza	-0.01	-0.05	0.00	Normal	Truncated
Triglops murrayi	-0.04	-0.05	0.01	Normal	Truncated
Trisopterus esmarkii	-0.05	0.04	0.01	Normal	Emarginated
Trisopterus luscus	0.00	0.09	0.02	Normal	Truncated
Trisopterus minutus	-0.03	0.08	0.01	Normal	Truncated
Zoarces viviparus	-0.08	0.01	-0.09	Elongated	Continuous

Figure S5.1: Outlines of the 218 images of fish.

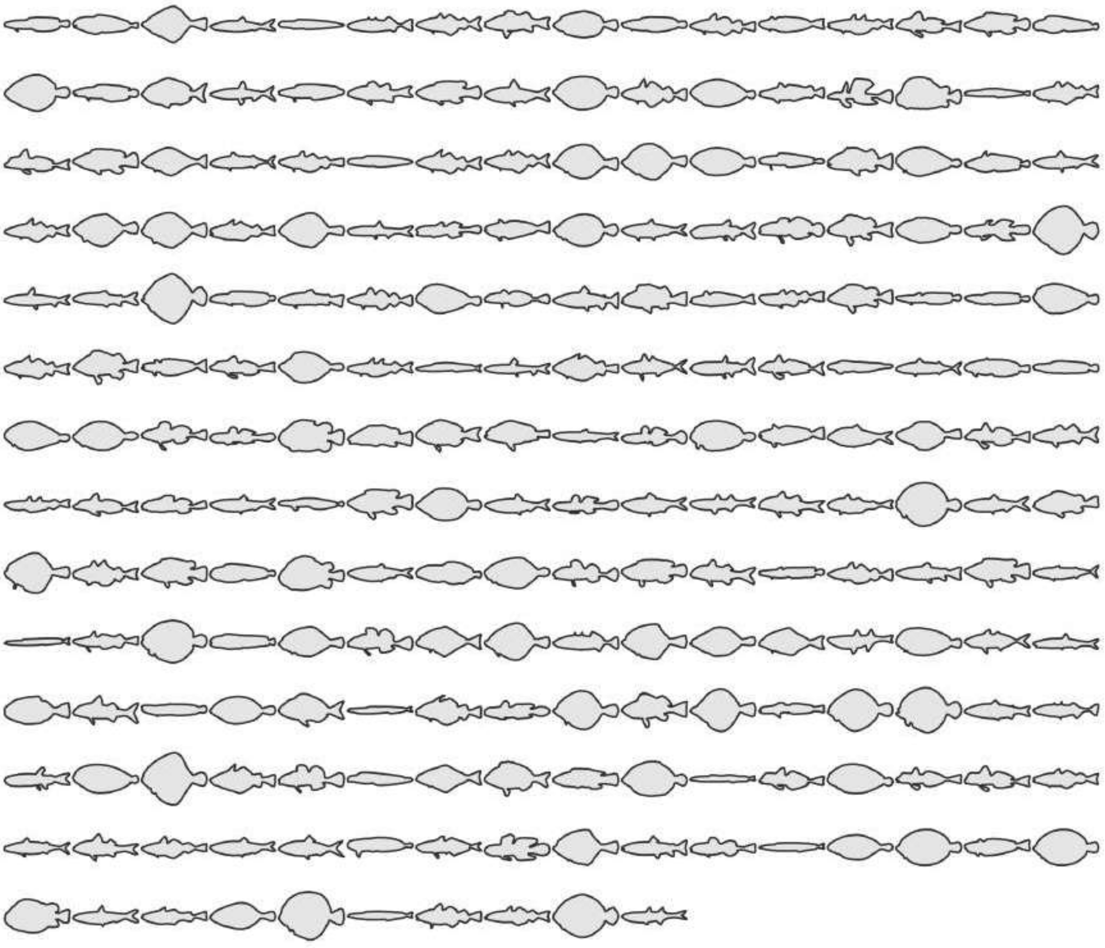
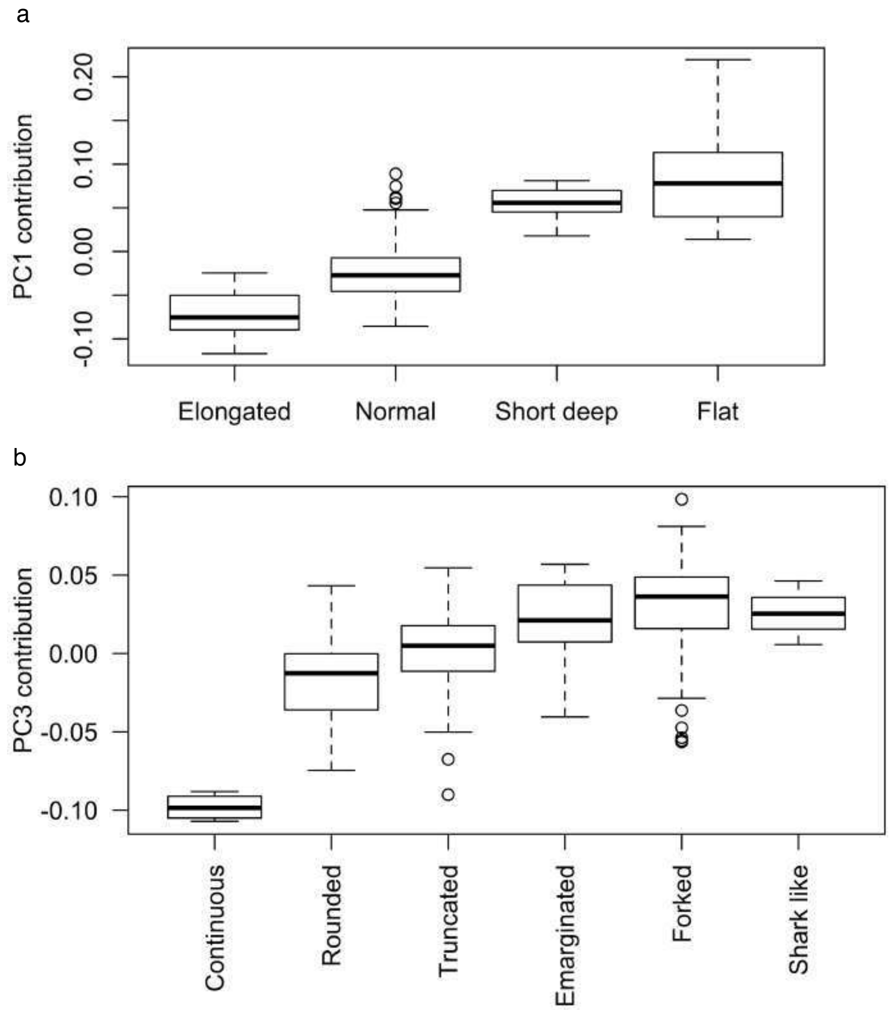


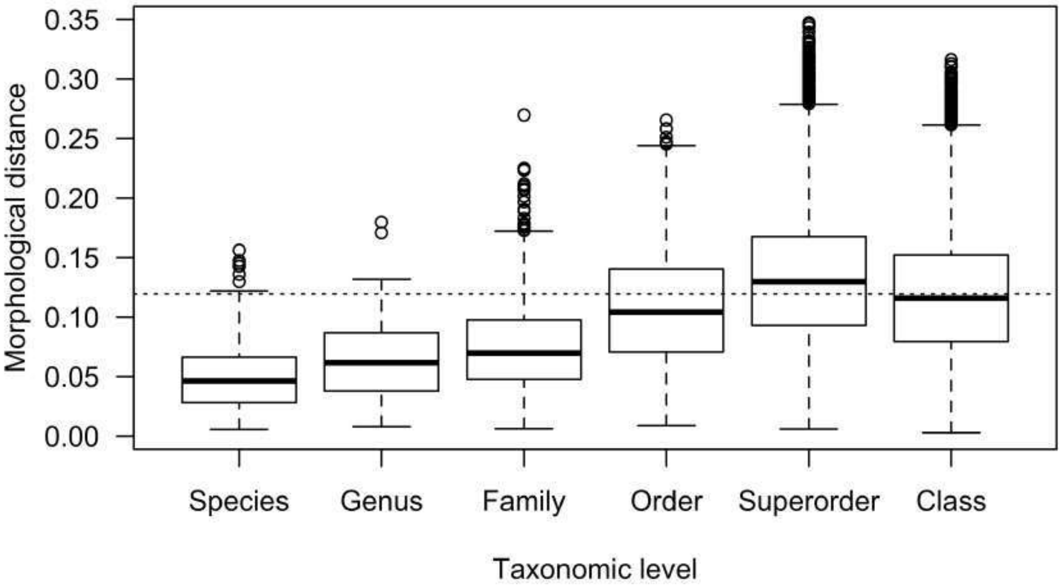
Figure S5.2: Relationship between EFT results and commonly used morphological traits. on (a) body and (b) caudal fin shape proposed by Pecuchet *et al.* (2016).



The first three PCs from EFT were compared with categorical morphological traits. We used the classification proposed by Pecuchet et al. (2016) that categorized the caudal fin shape into six classes (rounded, truncated, emarginated, forked, continuous, shark-like) and the body shape into four classes (gadoid-like, flat, elongated, eel-like). We compared the distribution of the component scores for every category using a boxplot and the non-parametric Kruskal–Wallis rank sum test.

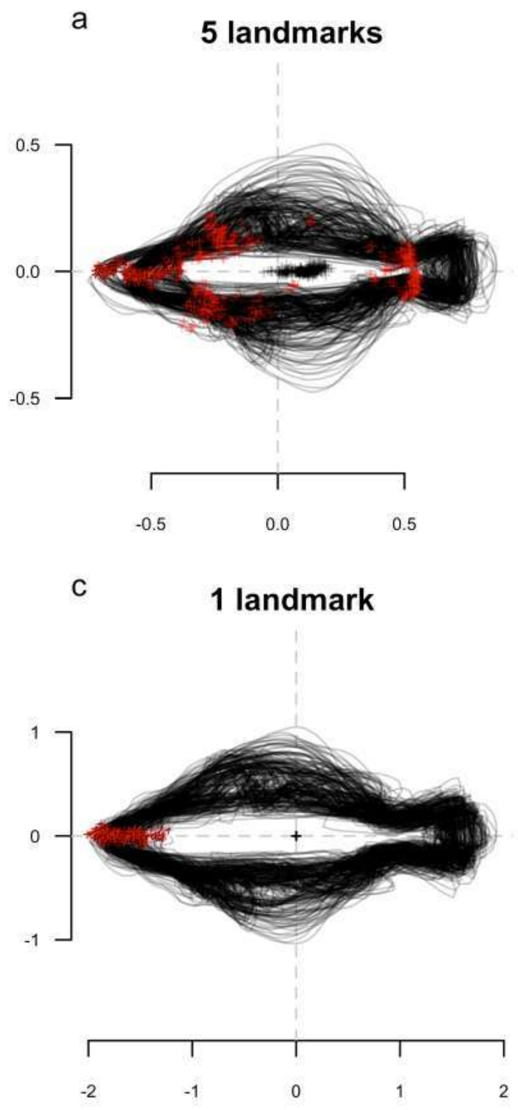
The first component, which was related to the elongation of the body, was linked to the categorical variable "body shape". Fish classified as "elongated" had negative scores on PC1, whereas flat fish had positive scores on PC1. The third component, which was related to the shape of the caudal and dorsal fins, was linked to the categorical variable "caudal shape". Fish classified as having a "shark-like" caudal fin had negative scores on PC3, whereas fish with a "continuous" caudal fin had the highest score on PC3. The two relationships described above were highly significant (P values < 0.001) with the Kruskal–Wallis rank sum test.

Figure S5.3: Comparison between the morphological and taxonomical distance. Boxplot of the relationship between morphological and taxonomical distances. The horizontal dotted line represents the mean pairwise morphological distance.



Taxonomically close species were expected to have similar morphology. To test this hypothesis, we compared the distance between the images computed with the scores on the morphospace (Euclidean distance) to the taxonomical distance. Five taxonomic levels were considered: genus, family, order, superorder, and class. The taxonomical distance was calculated using the *vegan* R package. The morphological distance increased with the taxonomical distance. A saturation was observed when the taxonomical distance was larger than the order and then the morphological distance fluctuated around its mean.

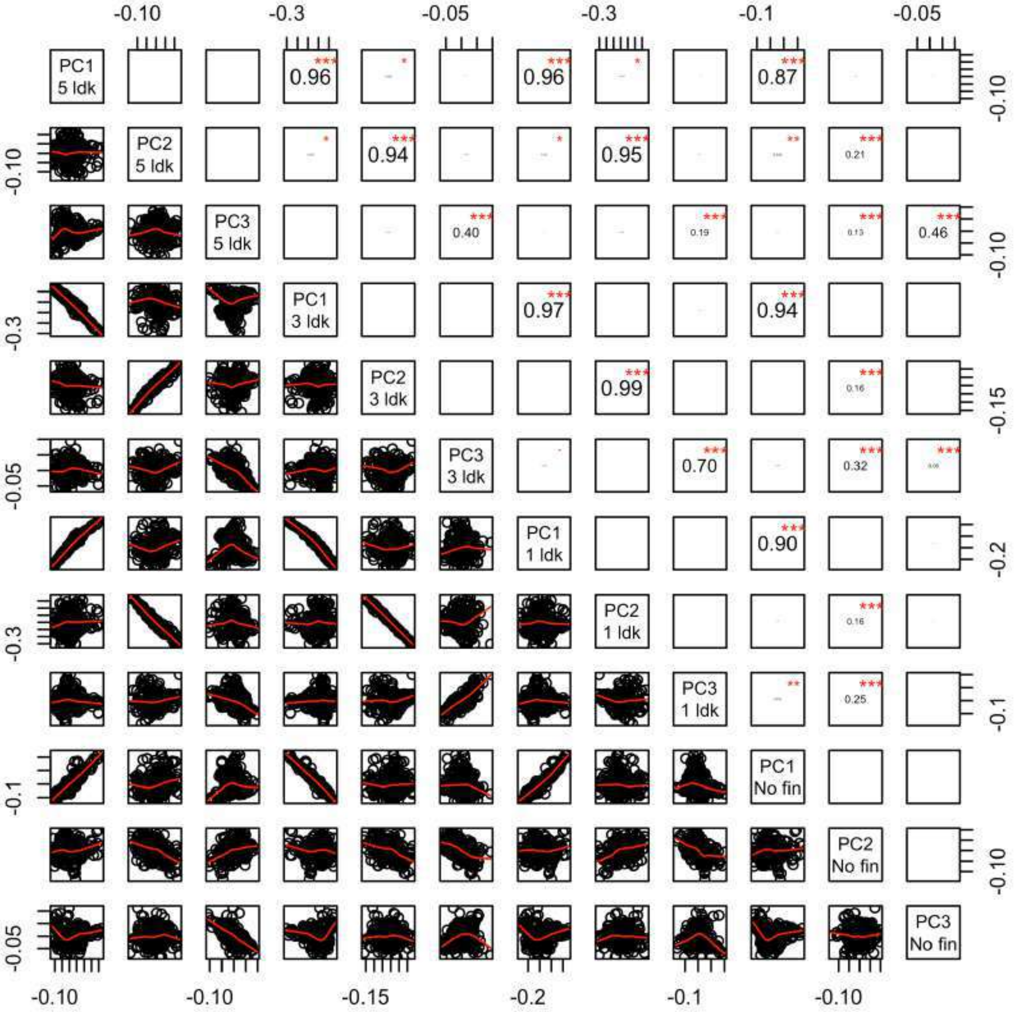
Figure S5.4: Shape alignment of the four different alignments tested: a) with 5 landmarks; b) with 3 landmarks; c) with 1 landmark; d) without fin and 3 landmarks. Red crosses represent landmarks and black crosses represent centroids.



Four different alignments were tested with different numbers of landmarks and with or without fins: (a) five landmarks (original study); (b) three landmarks: only the snout tip, and the ventral and dorsal insertion of the caudal fin; (c) one landmark: only the snout tip. The alignment was made by centering and scaling only (no Procrustes superimposition); (d) no fin: all fins apart of the caudal fin were removed from the outline, while three landmarks (snout tip and ventral and dorsal insertion of the caudal fin) were used for the Procrustes superimposition.

Depending on the number of landmarks considered, the resulting alignment differed visually. With three landmarks—with or without fins—all the species were scaled the same way to superimpose caudal fins and snout tips. For the alignment using only one landmark, the shapes were only centered using the centroid and scaled accordingly. When using five landmarks, the superimposition scaled the shapes in accordance with the position of the dorsal and pelvic fins.

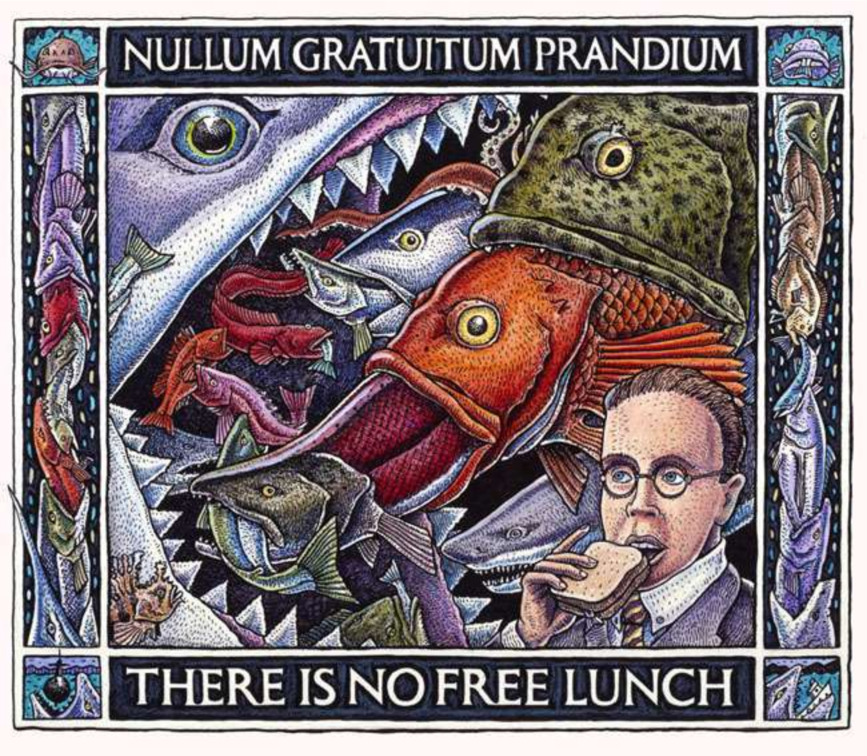
Figure S5.5: Robustness of the results from the alignment method. Pearson correlation (r^2) between the PC of the 4 different alignments.



PC scores from the EFT of the four different alignments were compared using Pearson's correlation coefficients. It was found that the first components of the four methods were correlated (Pearson correlation $r^2 > 0.87$, $P < 0.001$) as well as the second components of techniques considering fins ($r^2 > 0.9$, $P < 0.001$). The components of the "no fin" alignment were less correlated with the other components because they described shapes without the dorsal or pelvic fins. However, the third component of the "no fin" technique was correlated with the third component of the five landmarks' alignment used in this study ($r^2 = 0.46$, $P < 0.001$). The EFT method appeared to be robust when considering the alignment method. The first PC was always describing the elongation of fishes. The alignments considering fins had a similar PC2 and accordingly showed the development of the pelvic fins. The study without fins and the alignment with five landmarks characterized the shape of the caudal fin on PC3.

Chapter 6

Temporal variability of food web topology



Ray Troll, There is no free lunch (1989)
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Title: From community dynamics to temporal variability of food web topology: an empirical exploration of the structural dynamics of fish and benthic macrofauna in the German Bight

Authors: Pierre Olivier[1+*], Romain Frelat[2+], Erik Bonsdorff[1], Susanne Kortsch[1], Ingrid Kröncke[3], Christian Möllmann[2], Herman Neumann[3], Anne F. Sell[4], Marie C. Nordström[1]

[1] Åbo Akademi University, Environmental and Marine Biology, FI-20520 Åbo, Finland

[2] University of Hamburg, Institute of Marine Ecosystem and Fishery Science, 22767 Hamburg, Germany

[3] Senckenberg am Meer, Department for Marine Research, Südstrand 40, 26382 Wilhelmshaven, Germany

[4] Thünen-Institute of Sea Fisheries, Herwigstraße 31, 27572 Bremerhaven, Germany

[+] These authors contributed equally to this work

* Corresponding author: Pierre Olivier, pierre.olivier@abo.fi

Abstract

Ecological communities are constantly being reshaped in the face of environmental change and anthropogenic pressures. Yet, we do not know how food webs change over time. Food web science is characterized by a trade-off between complexity (in terms of the number of species and feeding links) and dynamics. Topological analysis uses complex, highly resolved food web models to explore the architecture of feeding interactions but is limited to a static view, whereas ecosystem models can be dynamic but use highly aggregated food webs. Here, we present a first attempt at reconciling this trade-off by exploring the temporal variability of a highly resolved empirical food web over a time period of 18 years, using the German Bight fish and benthic epifauna community as our case study. We relied on long-term monitoring ecosystem surveys (from 1998 to 2015) to build a metaweb, i.e. the meta food web containing all species and all possible trophic interactions recorded over the time span of our study. We then combined time series of species abundances with topological network analysis to construct annual food web snapshots. We developed food web metrics by including species abundances in order to represent the temporal dynamics of the food web structure. Our results suggest that structural food web properties change through time; however, food web structural properties may not be as temporally variable as the underlying changes in species composition and trophic interactions. Our results demonstrate how ecosystem surveys can be used to monitor temporal changes in food web structure, which are important ecosystem indicators for building marine management and conservation plans.

Keywords: food web structure, temporal variability, topology

Introduction

Ecological communities are constantly being reshaped with climate change and anthropogenic pressures either leading to losses (e.g. local extinctions) or gains (e.g. species invasions) in biodiversity (Pimm *et al.* 2014; Young *et al.* 2016). Additionally, species are connected through trophic interactions, and the presence or absence of a species may influence the dynamics of another through bottom-up or top-down control (Lynam *et al.* 2017). Food webs describe the 'who eats whom' in an ecosystem, i.e. the community composition and the trophic interactions among taxa. Understanding how changes in species composition and trophic interactions affect the structure and functioning of ecosystems is of vital importance to guide ecosystem management and conservation (Thompson *et al.* 2012; Cardinale *et al.* 2012). Yet, it remains unclear how the structure of food webs changes over time and the study of this temporal component remains neglected (Poisot *et al.* 2015).

The lack of temporal food web research arises from the difficulty in monitoring food webs through time, i.e. recording the occurrence of all species and all of their interactions at each time steps. Further, adding a layer of complexity to food webs such as the temporal dimension, has often resulted in aggregating taxa into functional groups, a procedure that will alter food web structure (Allesina & Bondavalli 2003; Pinnegar *et al.* 2005; Olivier & Planque 2017). For example, some food web studies have used poorly and/or unevenly resolved dynamical food webs to investigate stability of food webs or look at changes in their dynamic (McCann 2000; Heath 2005), or assess management scenarios or climatic projections (Christensen & Pauly 1992; Ulanowicz 2004; Mackinson & Daskalov 2007; Albouy *et al.* 2014). On the other hand, studies focusing on highly resolved food webs and their topology have only considered a limited number of time steps, e.g. before and after condition (Kaartinen & Roslin 2012; Yletyinen *et al.* 2016; Bodini *et al.* 2018).

Topological food webs portray the structure of food webs and can thereby encompass the large diversity in nature (Dunne 2009). Topological analyses are useful for summarizing structural properties of food webs and for comparing different ecosystems or regional food webs in space (Dunne *et al.* 2008; De Santana *et al.* 2013; Kortsch *et al.* 2018). However, topological food web analysis works under the assumption that food webs are static, and that species composition and species interactions do not vary over space or time (Pimm *et al.* 1991). This static view on food web structure not only neglects the spatio-temporal variability of species composition but also of realized trophic interactions (McCann & Rooney 2009; Poisot *et al.* 2012, 2015). Empirical spatio-temporal variability in food web structure can come from distributional shifts of species following changes in the environment, e.g. 'thermal niche tracking' (Beaugrand *et al.* 2014a; Hiddink *et al.* 2015) such as the northward migration of cod (Kortsch *et al.* 2015). The mechanism responsible for structural changes is a rewiring of the food web (Thierry *et al.* 2011). Considering food webs as static has major influence on how we understand their structure and functioning. Therefore, in order to understand how changes in communities affect the structure of food webs, a framework that operates at the nexus of food web topology and dynamical food web models should be developed and applied (Thompson *et al.* 2012; McMeans *et al.* 2015).

Although it is challenging to monitor food webs in space and time, large amounts of data have already been collected that could help building spatio-temporally resolved food webs (e.g. monitoring of species composition, abundances, gut content). From such data, it is possible to construct a metaweb that is a food web which include all the species occurrences and potential trophic interactions at any given time and site within an area, e.g. the 'Barents Sea food web'

(Planque *et al.* 2014). Subsampling a metaweb (i.e. creating food web snapshots) could represent spatio-temporal configurations of one food web solely based on which species co-occur (Dunne 2006). This technic was applied on spatially resolved empirical marine food webs to investigate the spatial variability of food webs (Kortsch *et al.* 2015, 2018). A similar approach could be used to study their temporal variability (Fig. 6.1).

In the present study, we use standard topological analysis on unweighted and weighted food web metrics (weighted by species abundance), to explore and document the temporal changes in the structure of a food web. We investigated temporal variability of a marine food web by combining food web topology and time series analysis of species abundances. We constructed a time series, spanning 18 years (1998-2015), of a food web for a small area in the German Bight (North Sea), which is monitored yearly. Using the monitoring data, we constructed a temporally resolved metaweb with limited aggregation of species. We hypothesized that the food web structure fluctuates over time, due to changes in the community likely as a response to large-scale changes in environmental conditions reported for the North Sea. For example, for the North Sea, changes both in the physics (e.g. warming, Belkin 2009) and ecology both of benthos and fish have largely been documented (e.g. climate-induced species migrations and distributional shifts, Perry et al. 2005, Neumann et al. 2013). Considering that both environmental conditions and ecological communities in the North Sea have changed, we should expect a temporal restructuring of the German Bight food web that follows changes in the occurrence of species and of their trophic interactions. Therefore, our aim is to understand (i) whether and how the food web structure has changed through time, and (ii) whether those potential changes are related to changes in the composition of species and links, or to the abundances of taxa?

Methods

Study area – Time series of taxa abundances

The North Sea makes a good case study to investigate community temporal changes for three main reasons. (i) It has been well sampled over decades (Ehrich *et al.* 2007). (ii) Numerous studies documented the ecology and dynamic of the system, e.g. community structure (Reiss et al. 2010); food web dynamic (Greenstreet et al. 1997). (iii) It is heavily impacted by diverse stressors (Emeis et al. 2015): high fishing pressure (Daan et al. 2005); climate change (Belkin 2009) that led to a modification of the community (Beaugrand 2004; Perry et al. 2005; Heath 2005; Simpson et al. 2011; Weinert et al. 2016). The North Sea has been reported to get warmer, with a recorded increase of 1.31°C between 1982 and 2006 (Belkin 2009). This warming caused a northward migration of fish (Perry *et al.* 2005), an increase in fish species richness (Hiddink & ter Hofstede 2008), and an increase of fish abundances (Simpson *et al.* 2011). It is potentially also the case for benthos (Weinert *et al.* 2016) with species expanding their distributional range in the German Bight (Neumann *et al.* 2013) or possibly leaving the German Bight (Kröncke *et al.* 2011). A biological shift was reported for the benthic macrofauna around 2000/2001 (Kröncke *et al.* 2013). Simultaneously, a biological shift in the plankton community have occurred between 1996 and 2003 in the North Sea and might have affected directly their predator populations and indirectly the predators of those predators (Beaugrand *et al.* 2014b). We expect changes in the food web structure due to changes in species occurrence.

We used data collected through the German Small-Scale Bottom Trawl Survey (GSBTS), a long term, high-intensity sampling in selected small areas of 10x10 nautical miles (Ehrich *et al.*

2007). This survey monitors benthic macrofauna and demersal fish. Three days of sampling every fall (quarter 3) are necessary to effectively sample benthic fish with an otter trawl in 21 stations and the macrofauna with a beam trawl in 9 stations. This protocol has been carried out continuously since 1998 (but no sampling was performed in 2013). In our study, we focus on the Box A, located in the German Bight (Fig. 6.1D). In the following text we use interchangeably the term macrofauna, invertebrates or macrofaunal invertebrates to refer to all invertebrates that live on sediment, or attached to hard substrates that were caught by a net with a 4mm mesh size of the cod end.

The taxa names were updated using the World Register of Marine Species (WoRMS Editorial Board 2018). To account for differences in sampling methodologies between fish and benthos, we standardized the abundances of fish and macrofauna separately by calculating their relative abundance (i.e. raw abundance divided by the average of abundance). Abundances were sometimes lacking (e.g. colonial organisms as bryozoa). Rather than removing taxa that may structure the community, we kept them but assigned them a constant abundance. Additionally, trawl survey does not sample correctly all taxa it captures. Pelagic fish were reported but would under-sampled with otter trawl gear. We tested the influence of the abundance of pelagic fish on our results (i.e. recorded abundances vs. constant abundance of one) and found no differences (Fig. S6.1). Therefore, we kept the recorded abundance because it is the more realistic estimate.

The GSBTS recorded 152 species. However, some “rare” taxa are only recorded occasionally, and their time series are too variable and does not represent their actual trends. We identified persistent taxa (i.e. taxa consistently reported) using the inflection points in the persistence plot, following Genner et al. (2004). The inflexion point was detected at 10 years (Fig. S6.2). Thus, we kept taxa that had been detected at least 10 years which, in total, represented 95% of the abundance.

Due to differences in sampling effort between years, we repeated 100 times a bootstrap to randomly select a constant number of sampling stations and evaluate the sensitivity of our results to the inherent variability of biological samplings. We selected randomly 14 fish stations and 7 macrofauna stations per year. Even if the sampling intensity was remarkably high for such a limited area (21 stations in total per year over 10 by 10 nautical miles), some rare species may not be detected properly. To test results' sensitivity to the sampling intensity, we considered a three-years moving window that would include 35 fish and 17 macrofauna stations. The results were coherent with the results from the annual sampling but would decrease the temporal resolution (Fig S6.3). We further worked with the annual sampling.

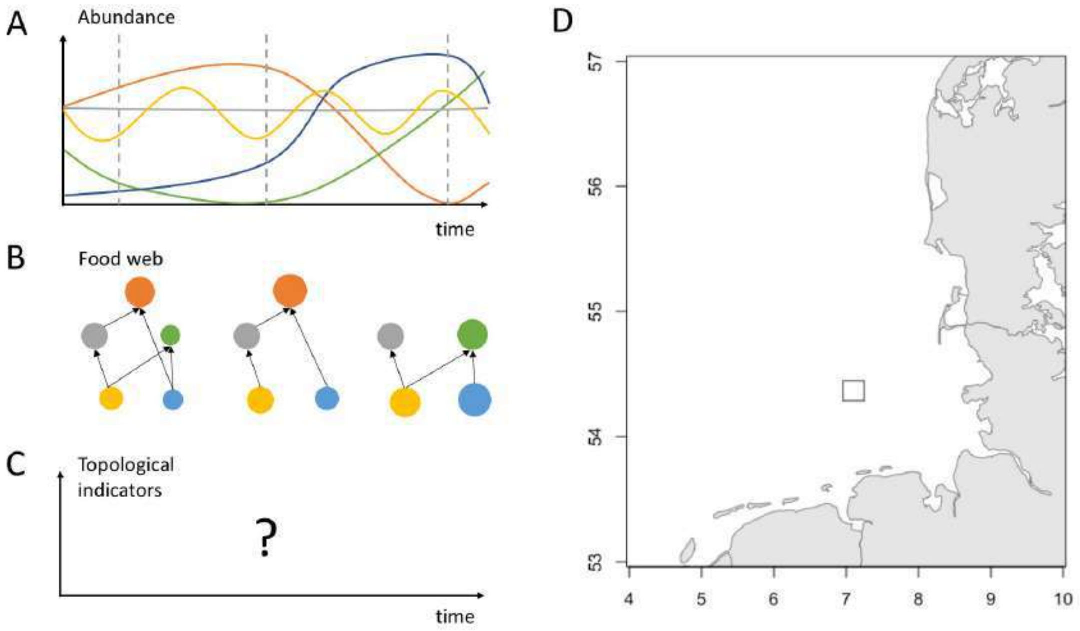

Figure 6.1: Schematic representation of the objectives of our study. (A) Temporal changes in abundance of species results in (B) changes in the topology of food webs that can be investigated with (C) time series of topological indicators. (D) Our case study is located in the German Bight, on a box of 10 by 10 nautical miles, where fish and benthic macrofauna have been sampled intensively for more than 17 years.

Trophic relationships

To build a food web, it is essential to know 'who is there' (i.e. the species composition) and 'who eats whom' (i.e. the trophic relationships also called 'trophic links'). We first built a metaweb which contained every taxa selected previously, together with their trophic interactions. This metaweb includes detailed information on macrofauna and demersal fish. We added seven compartments that were not sampled by the GSBTS survey but important for the food web structure: four primary producer compartments (phytoplankton, microalgae, macroalgae, macrophyta), bacteria, detritus, and one group 'zooplankton' as zooplankton may constitute the main resource for juveniles and pelagic fish. We considered the abundance of these seven compartments as constant.

The trophic interactions were established through an extensive literature review of diet and feeding studies. We first assumed that if trophic interactions happened in the past or in areas outside the North Sea, these were possible interactions also today or in our area of interest. Consequently, our metaweb represents a network of possible trophic interactions between taxa. Moreover, we did not consider ontogenic diet shifts (i.e. no distinction between a juvenile and an adult) and excluded any feeding on larvae or eggs because they are under-reported in the literature and such feeding may misrepresent the trophic positioning of taxa in the food web.

Information on trophic interactions are biased towards predators and commercial species (e.g. cod) which are better studied compared to rarer species or invertebrates. Indeed, most trophic interactions originate from observations of predator diet (e.g. stomach content analysis, feeding experiments), and the higher the trophic level, the more detailed the reported information. We tried to counter-balance this asymmetry by reviewing more intensively the diet of invertebrates. However, even after our long and careful review process, diet information for some taxon was still lacking. To solve this problem, we assumed that taxonomically related species may share the same predators or may have similar diets (i.e. predators target a morphology rather than an identity). We inferred links, which have been double-checked by experts. We had to remove three species for which trophic links were lacking or if their main prey were not selected (i.e. *Acteon tornatilis*, *Macropodia rostrata*, *Nymphon brevirostre*). The metaweb with the diet references and species list will be made available on publication of the manuscript.

Table 6.1: Selected food web metrics and their definition. '*L*' denotes the number of trophic links in the food web, S the number of species or species richness of the food web, w_i the abundance of trophospecies i, and l_i the number of links of trophospecies i, in_i is the number of prey of trophospecies i, n_j is the number of predators, sim_{ij} is the weighted mean of the Jaccard similarity of prey (weight of 0.4) and predators (weight of 0.6) between species i and j . The shaded part of the table contains community-level descriptors. The second part contains species- and population-level descriptors.

Metric and formula	Definition	Ecological implications
Linkage density $Z = \frac{L}{S}$	Average number of interactions per taxa (Dunne 2009).	Inform how connected species are within the network.
Weighted linkage density $wZ = \frac{\sum w_i \times l_i}{2\sum w_i}$	Abundance-weighted average number of interactions per taxa.	Inform how connected species are considering their respective abundances.
Directed connectance $C = \frac{L}{S^2}$	Proportion of all possible trophic links (S^2) that are realized (Dunne 2009)	One measure of network complexity which can be related to the robustness of food webs in the face of perturbation.
Weighted directed connectance $wC = \frac{\sum w_i \times l_i}{2 \times S \times \sum w_i}$	Abundance-weighted proportion of all possible trophic links that are realized.	Measures of food web complexity considering the abundance of species.
Generality $G = \frac{\sum_{j=1}^{n_j} l_{in}}{n_j}$	Mean number of prey per predators (Schoener 1989).	Indicates if the system contains more generalist or specialist species.
Weighted generality $wG = \frac{\sum_{j=1}^{n_j} w_i \times l_{in}}{\sum w_i}$	Abundance weighted mean of the number of prey per predators.	Idem as above but considering the relative abundance of species.
Normalized standard deviation in Generality $GenSD = \frac{1}{Z}\sqrt{\frac{1}{S-1}\sum (in_i - G_i)^2}$	Dispersion in the number of prey per taxa (Williams & Martinez 2000)	Reflects the variability in the number of prey per predators.
Short-weighted trophic level $TL = \frac{\sum TL_i}{S}$	Prey averaged trophic level calculated from the shortest path between a taxon and a basal species (Thompson *et al.* 2007; De Santana *et al.* 2013)	Lower TLs indicate a more energy efficient system with less steps between a taxon and a primary producer.
Mean maximum trophic similarity $MxSim = \frac{1}{S}\sum_{i=1}^{S} max\ sim_{ij}$ with $i \neq j$	Mean maximum similarity of shared predators and prey measured as the weighted Jaccard similarity index (Williams & Martinez 2000; Olivier & Planque 2017)	A low value shows that most consumers feed on the same resources which can indicate a low food partitioning and higher competition in the system.

Analysis and food web descriptors

We combined topology analysis with time series analysis to identify changes in the community structure. At each time step, we subsampled the metaweb according to the presence/absence data and applied structural analysis on the food web snapshot. When relevant, we adapted widely used food web descriptors to consider the effect of fluctuating abundances on the food web structure (Table 6.1). Community-level descriptors give an insight in how communities are structured while species-level descriptors inform on the species participation in the food web. We measured the species compositional and trophic interaction turnovers, i.e. the dissimilarity in species and trophic interactions between years (Poisot *et al.* 2012; Kortsch *et al.* 2018).

All data analyses were performed with the statistical software environment R (R Core team 2017) and the 'igraph' R package (Csárdi & Nepusz 2006).

Results

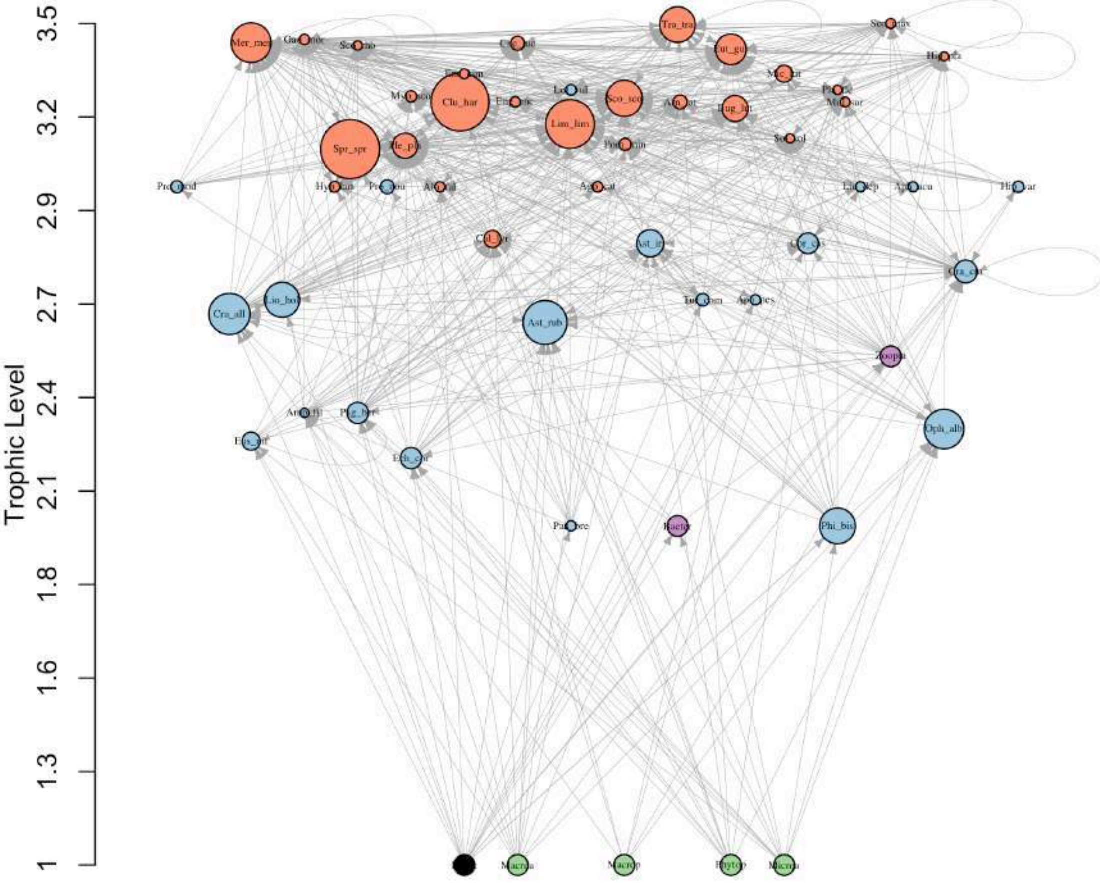

Figure 6.2: Metaweb of the fish and benthic macrofauna in the German Bight. The y-axis indicates the trophic levels of the species. Basal species are represented at the bottom and connected to higher trophic level by trophic links (i.e. arrows oriented from the prey to the predator). The size of the nodes is proportional to the mean abundance of species over the 17-years time-series. Name abbreviations are built from the first three letters of the genus and the names. Red, blue, purple, green and black nodes represent fish, invertebrates, grazers, primary producers and detritus, respectively.

The metaweb

After selection of the persistent species, we obtained a benthic metaweb that contained 55 trophospecies (S, out of originally 152 taxa). The food web contained 599 trophic links (L) between 21 macrofaunal invertebrates, 27 fish resolved to the species level, and 7 functional groups (Fig. 6.2). We kept food web aggregation to the minimum by not aggregating taxa with very similar, but often not equal diets. Of the 599 trophic links reported in our food web, 28% of them came from peer-reviewed literature, 40% from grey literature and diet databases, and 32% from inference and confirmed by expert. The link density (Z) was 10.9 links per nodes and the connectance (C) was of 0.20, i.e. the food web expresses 20% of all possible links. The annual snapshots subsampled from the metaweb (Fig. S6.4) were used to perform the food web topology analysis.

Temporal variability in the food web structure

The species richness increased in the early years from 45 in 1998 to above 50 species between 2005 and 2008, and decreased afterward to return to 45 species in 2015 (Fig. 6.3). The increase of species richness between 1998 and 2006 was accompanied with an increase in link density (Z) and generality (G), indicating that the new species had, in average more interactions, and specifically a larger number of prey. Weighted link density (wZ) showed similar fluctuations to its unweighted counterpart. Anomalies in abundance confirmed that more and more species with a high number of prey were becoming more frequent or became detectable in the beginning of the twenty-first century (Fig. 6.4). This was the case for a few flatfish species that were nearly absent in the early years of the time series (e.g. *Platichthys flesus*, *Scophthalmus rhombus*, with 28 to 24 prey taxa, respectively). In contrast, the taxa showing the largest increases in abundance over the time series were not generalist taxa but taxa with few prey and more predators than prey (i.e. between 3 to 9 prey and 10 to 22 predators; e.g. *Sprattus sprattus* and *Crangon allmanni*) at the exception of whiting (*Merlangius merlangus*, with 40 prey and 13 predators). Anomalies also revealed that generalist predators which were present at the beginning of the time series decreased in abundance, such as Atlantic mackerel (i.e. *Scomber scombrus* with 23 prey) and Atlantic horse mackerel (i.e. *Trachurus trachurus* with 23 prey). The mean short-weighted trophic level almost showed no fluctuations apart of the outlier year 2009.

The two metrics of connectance (C and wC) and the standard deviation of generality displayed a different pattern. Their trends changed direction in the early 2000s. The standard deviation of generality decreased constantly since 2000, suggesting a homogenisation of the number of prey per species. We additionally tested Pearson-correlations between the food web metrics (Fig. S6.5). The Pearson-correlation test revealed a strong positive relationship between connectance and generality (i.e. 0.65) but weak negative relationship with species richness. Weighted connectance (wC), however, showed a strong negative relationship with the standard deviation of generality (i.e. GenSD, -0.72).

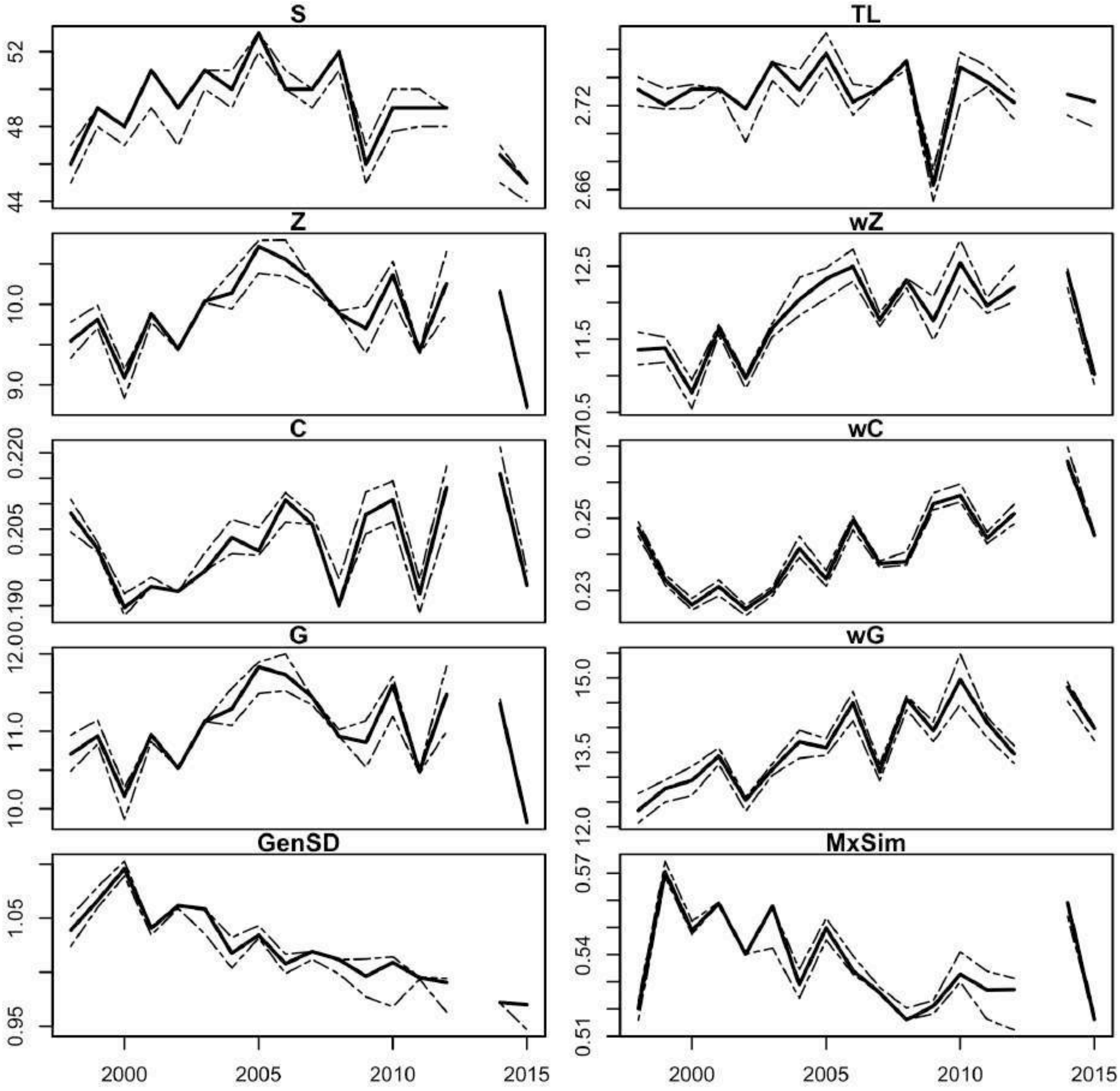

Figure 6.3: Time series of food web metrics. From left to right, top to bottom: species richness of the food web (S), mean trophic level (TL), link density (Z), weighted link density (wZ), connectance (C), weighted connectance (wC), generality (G), weighted generality (wG), standard deviation of generality (GenSD), mean maximum trophic similarity (MxSim). The bold black line indicates the median, the dotted lines are the first and third quartiles from the bootstrap of 100 repetitions.

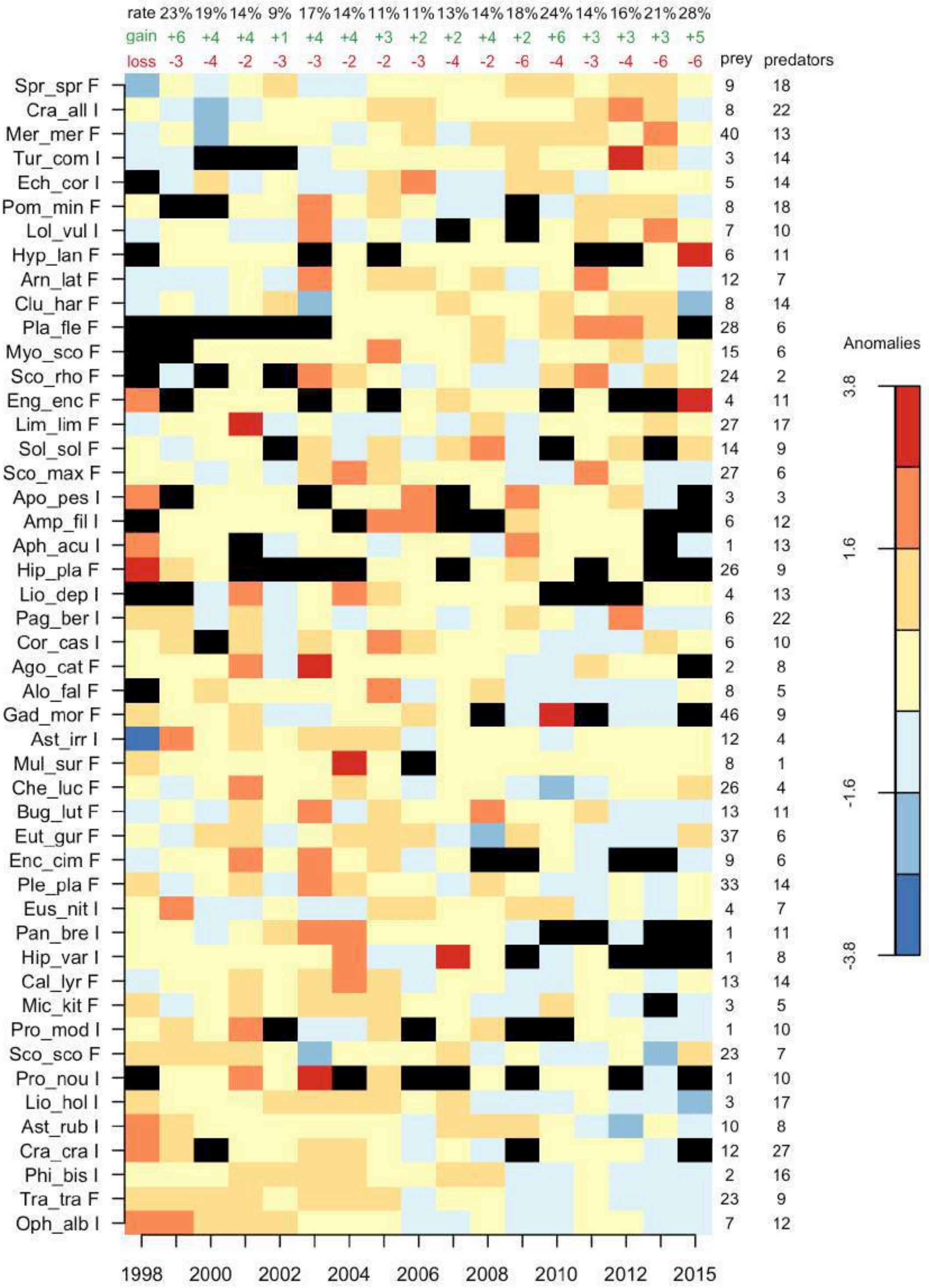

Figure 6.4: Time series of relative abundance anomalies. Red and blue colours indicate a difference between the median abundance of the year and the median over the time series. Black indicates a local extinction. Species are ranked in decreasing strength of their trend (approximated with the difference of their abundance in the first five years and the last five years) with the largest increase in abundance at the top and largest decrease in abundance at the bottom. The taxa names are abbreviated according to the species list, and a letter "F" or "I" indicates if the taxon is a fish or an invertebrate, respectively. At the top, black, green and red values indicate the rate of change in species composition, gains and losses of species from years to years. On the right of the heatmap are indicated the number of prey and predators of each trophospecies.

Turnovers in species composition vs. turnover in trophic interactions

The previous results highlighted that the community had changed over the time series. Prior to 2006, a decrease in both turnovers revealed that the changes in food web decreased, not only in terms of species composition, but also in terms of trophic interactions (Fig. 6.5). After 2006, the turnover in trophic interactions increased to higher values than before (i.e. ca. 0.15 in 1998 compared to ca. 0.20 in 2015) while the turnover in species composition went back to previous values (i.e. ca. 0.10). The dissimilarity in species composition is lower than the dissimilarity of trophic interactions, suggesting that the food web changed faster in terms of trophic interactions than in species composition (Fig. 6.5). This was also shown in the mean maximum trophic similarity (i.e. MxSim, Fig. 6.3) as taxa showed more redundancy in their sets of trophic interactions in the early 2000s than after 2006. However, if the food web diverged from its original counterpart, the change from years to years was not constant: the rate of change in species composition first slowed down to increase again after 2006 (Fig. 6.4).

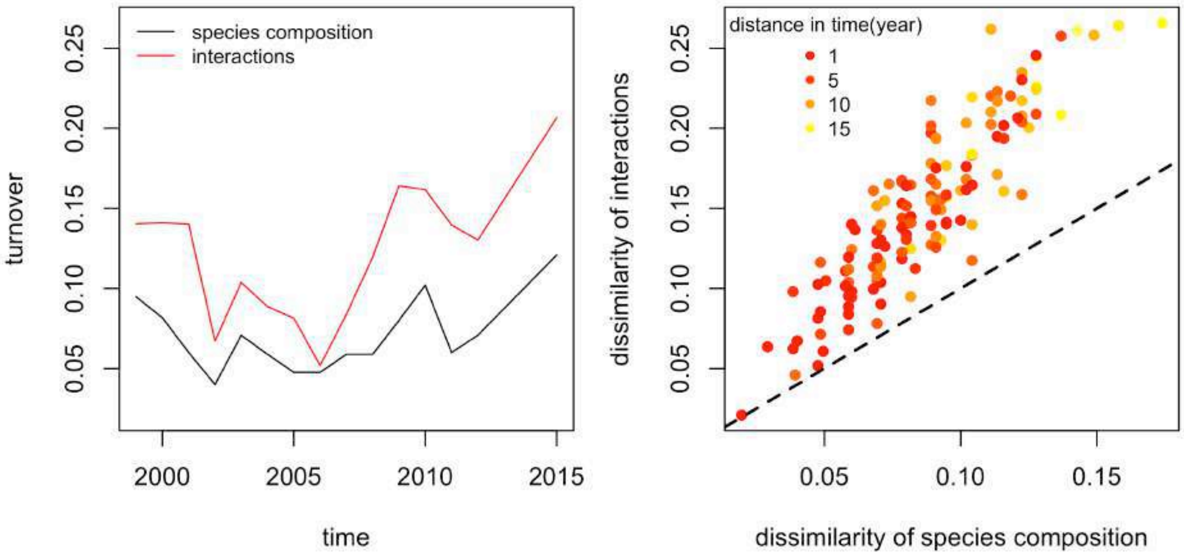

Figure 6.5: Species and interaction turnovers. Turnovers in species composition and interactions (left) and relationship between the two turnovers for all pairs of food web snapshots (right). The colour gradient indicates the time distance between food web snapshots. The dashed grey line indicates the 1:1 relationship.

Discussion

Food web structural response to a change

Our results demonstrate that population dynamic and food web structure revealed two complementary information. The food web has undergone a structural transition since the early 2000: the food web structure was following a trend that progressively reversed as the ecological community was changing. Our results revealed an opposite asynchronous response of species richness and complexity of the food web. Numerous studies argued as to how connectance should vary with species richness (Dunne 2006). We would expect connectance to decrease if the number of links increases linearly with the number of species (May 1972). If a decrease in connectance was observable in the first years of the time series, the food web structure underwent a structural inflation and complexification starting in the early 2000s (i.e. the food web became more complex as species richness of the food web increased). Connectance would increase only if the number of links would increase faster than the square of the number of taxa. The structural complexification that we observed could be explained by the introduction of taxa with a large number of links: either taxa with many prey, many predators or both. In our case, generalist taxa were introduced in the first phase posterior to the change (i.e. the rising of species richness). Our study revealed that the food web structure changed from a dominance of generalist consumers to a dominance of more specialist consumers. Our results are coherent with findings reported in the Baltic Sea, which reported a similar increase in generalism and no changes in other structural properties observed when comparing the structure of two food webs prior and following the Baltic Sea regime shift (Yletyinen *et al.* 2016). We suggest that food webs react to community changes by a progressive readjustment of the sets of trophic interactions, i.e. food web rewiring (Thierry *et al.* 2011), and a balancing of those interactions through fluctuating abundances of species and changes in dominance of species, i.e. asynchronization of resources (McMeans *et al.* 2015). Indeed, species abundance did not influence the fluctuations of structural properties at the food web level (i.e. link density and connectance) but influenced fluctuations at the taxa level (i.e. generality vs. weighted generality). This may suggest that each species contributions to the structure of the food web could be balanced by their own abundances.

High levels of turnover (both in species composition and species interactions), coupled with species density compensation, could be responsible for the rapid adaptability of community to changes. The constant reshuffling of species could allow for a progressive structural readjustment of the food web. An empirical study focusing on temporal variability in terrestrial food webs showed temporal consistency in quantitative food web metrics (i.e. such as weighted generality) at the local scale in the face of high compositional turnover (Kaartinen & Roslin 2012). They suggested that the stability of species composition in food webs may be partly resulting from a balancing between the abundance of species and their ecological specialisation. Our results would suggest that in the face of a disturbance, the food web structure could be transiting between phases of low and high ecological specialisation driven and compensated by variations in species abundance until it reaches an adequate balancing of those interactions (i.e. both structural presence and structural importance through abundance).

Limitations of our approach

Currently, our metaweb displays values similar to older generations of food webs that were criticized for overestimating food web structural properties (Dunne 2006). Building metawebs is time consuming and require a challenging data-quality check not to overestimate food web structural properties. An overestimation of food web metrics is indeed pathological of cumulative food webs which have been built upon accumulated data on species trophic interactions. Additionally, our food web does not consider the dynamic of trophic interactions and variability in trophic interactions only results from changes in the species composition. Our approach could be improved by integrating the dynamic of trophic interactions. It is likely that some trophic interactions that we included may no longer occur or not yearly. We have tried to partly overcome this weakness by assuming that trophic interactions with lower abundances should be less represented (and conversely). However, this assumption does not address consumers' preferences and behaviours. Consumers may have drastically different diet from years to years as some species may not occur yearly, or their preferred prey may become more abundant.

Annual time step may hide numerous seasonal patterns. For instance, it is likely that mobile organisms follow any periodicity (i) in the availability of their preferred prey or (ii) in the physics of their environment. Timing becomes critical and consumers will locally occur when it is most favourable for them (Durant *et al.* 2007). Variability in trophic interactions is believed to be responsible for the high adaptability of food webs in the face of a change and integrating spatial and temporal variability of trophic interactions will give better insight in the structure and functioning of food webs (Poisot *et al.* 2015; Ushio *et al.* 2018). We suggest that this weakness in our methodology could be overcome by combining our approach with trophic relationships inference technics that would allow for refining and improving both the metaweb and snapshots of food webs (Gravel *et al.* 2013; Poisot *et al.* 2015).

Implications for ecosystem management

Food webs constitutes an ideal tool to summarize changes occurring at the ecosystem level. Unfortunately, they become often too complex for management purposes and most management measures often focus on single species or group of species of commercial interest they interact with. The European Union required moving towards a more ecosystem-based management through the Marine Strategy Framework Directive (MSFD) which includes one specific descriptor for marine food webs (Rogers *et al.* 2010). Numerous food web indicators, including structural indicators, have been proposed to evaluate Good Environmental Status (Tam *et al.* 2017; Otto *et al.* 2018) but biomonitoring of food webs is still cruelly lacking (Gray *et al.* 2014). Combined with the right indicators, our coupled topology-time series analysis is an easy-to-use and practical tool to monitor ecological changes at the community scale and evaluate trends in the Good Environmental Status of ecosystems. This methodology only requires a metaweb and a way to assess changes in the community. It takes advantage of data that are already collected on a yearly basis. With the increase of monitoring effort and the proliferation of food webs, our proposed methodology is a promising approach to reveal changes in the ecological status of ecosystems.

Acknowledgement

The authors would like to thank Mira Grönblom, Marco Scotti and Anna Tornroos for helping in the literature review and Jens Floeter and Margarethe Nowicki for helpful comments and discussions. We acknowledge all the participants to the Ecological Network Analysis workshop 2018 in Bremen who gave valuable inputs in the interpretation of the results. Thanks to Jennifer Dunne for her discussion on some of the metrics.

List of Supplementary materials

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Figure S6.4: Snapshot of the food web at individual time step.

Figure S6.5: Matrix of correlations between food web structural properties

Figure S6.1: Time series of food web metrics but abundances of pelagic taxa were maintained constant to a value of one. From left to right, top to bottom: species richness of the food web (S), mean trophic level (TL), link density (Z), weighted link density (wZ), connectance (C), weighted connectance (wC), generality (G), weighted generality (wG), standard deviation of generality (GenSD), mean maximum trophic similarity (MxSim). The bold black line indicates the median, the dotted lines are the first and third quartiles from the bootstrap of 100 repetitions.

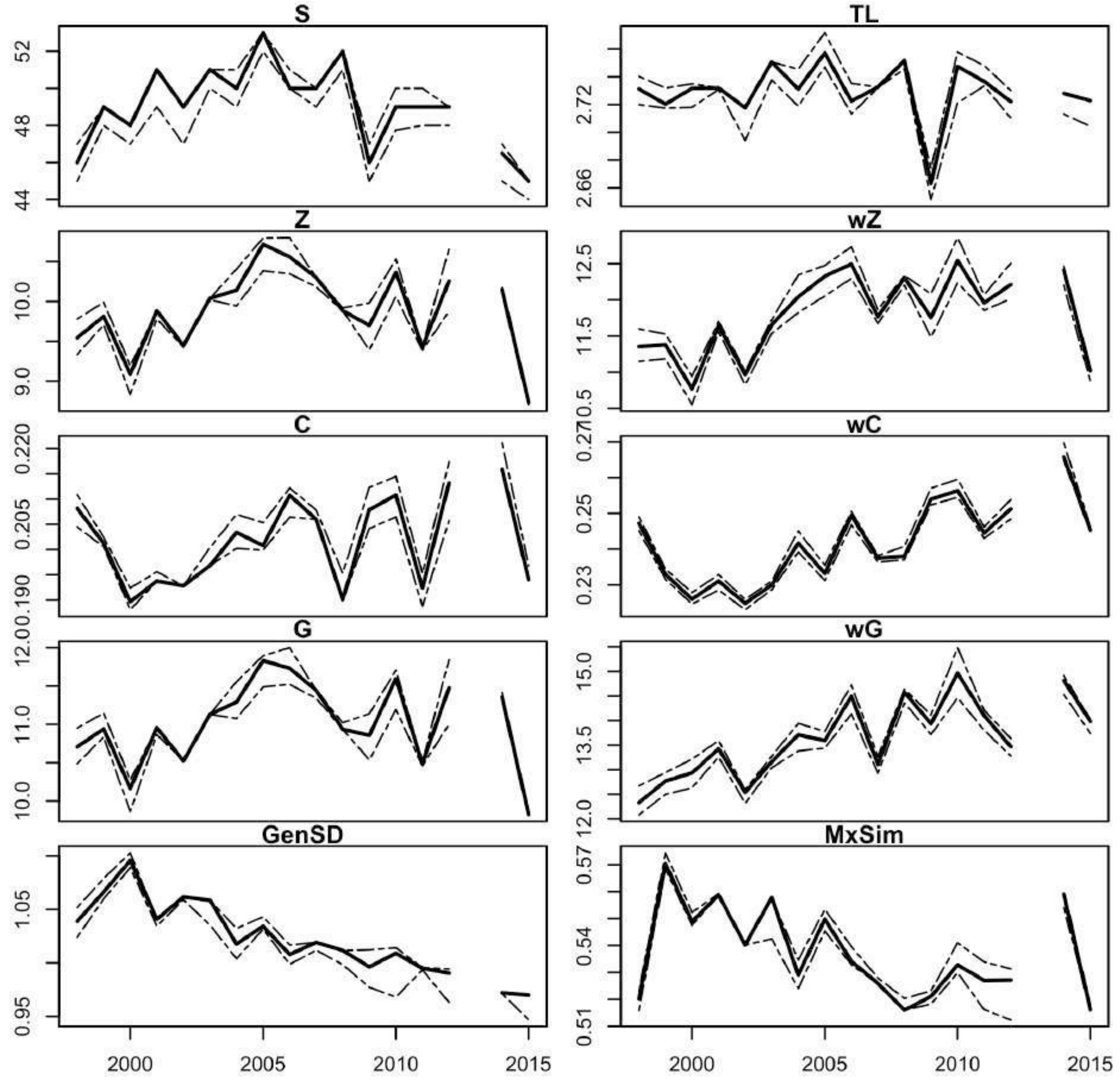


Figure S6.2: Plot of abundance against persistence for fish and invertebrate taxa in assemblages. The point of inflexion, identified around 10 years, represents the breakpoint between rare and common species.

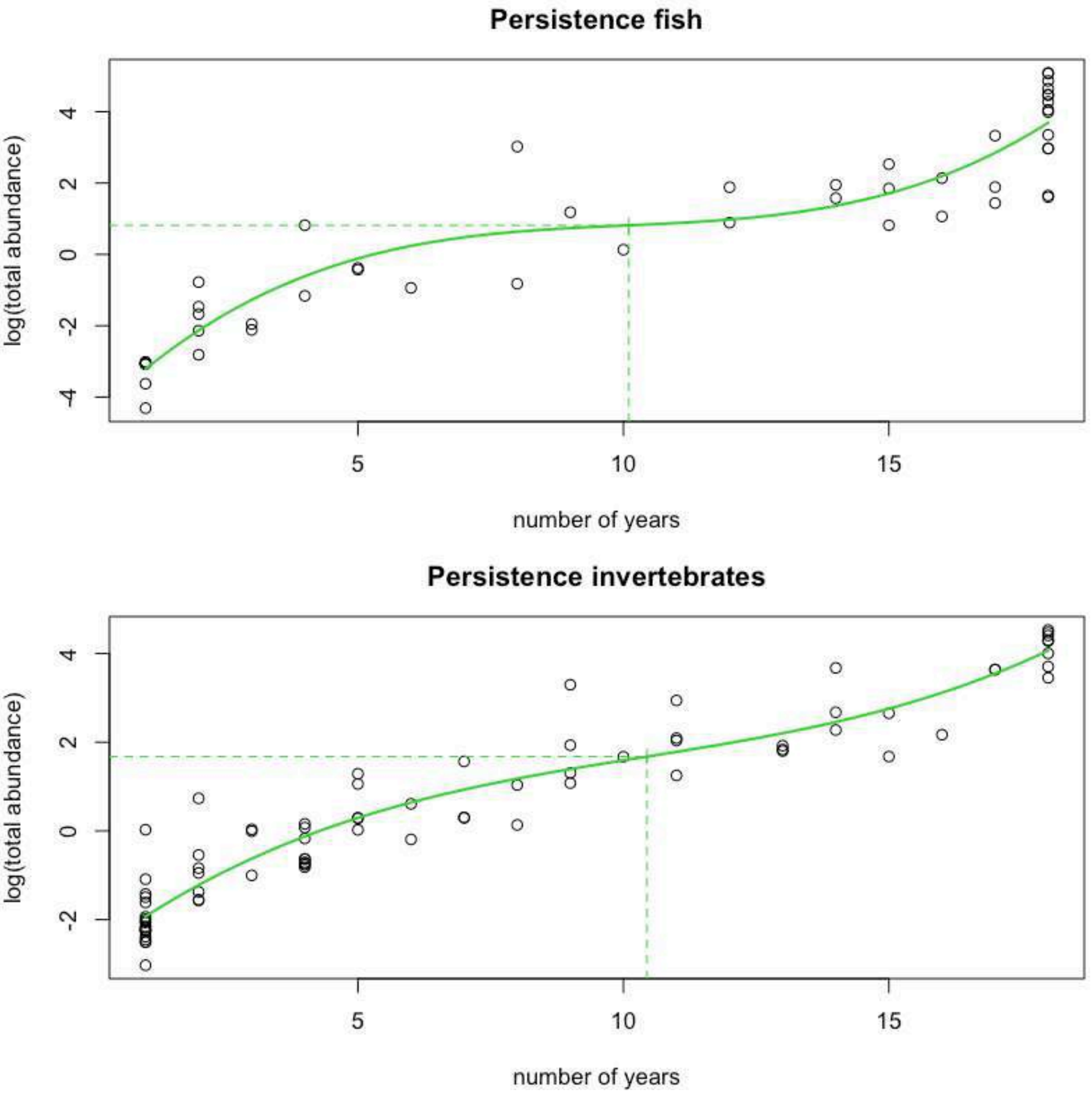


Figure S6.3: Time series of food web metrics considering a 3-years moving window on the abundance time series with information from 35 fish stations and 17 macrofauna stations. From left to right, top to bottom: species richness of the food web (S), mean trophic level (TL), link density (Z), weighted link density (wZ), connectance (C), weighted connectance (wC), generality (G), weighted generality (wG), standard deviation of generality (GenSD), mean maximum trophic similarity (MxSim). The bold black line indicates the median, the dotted lines are the first and third quartiles from the bootstrap of 100 repetitions.

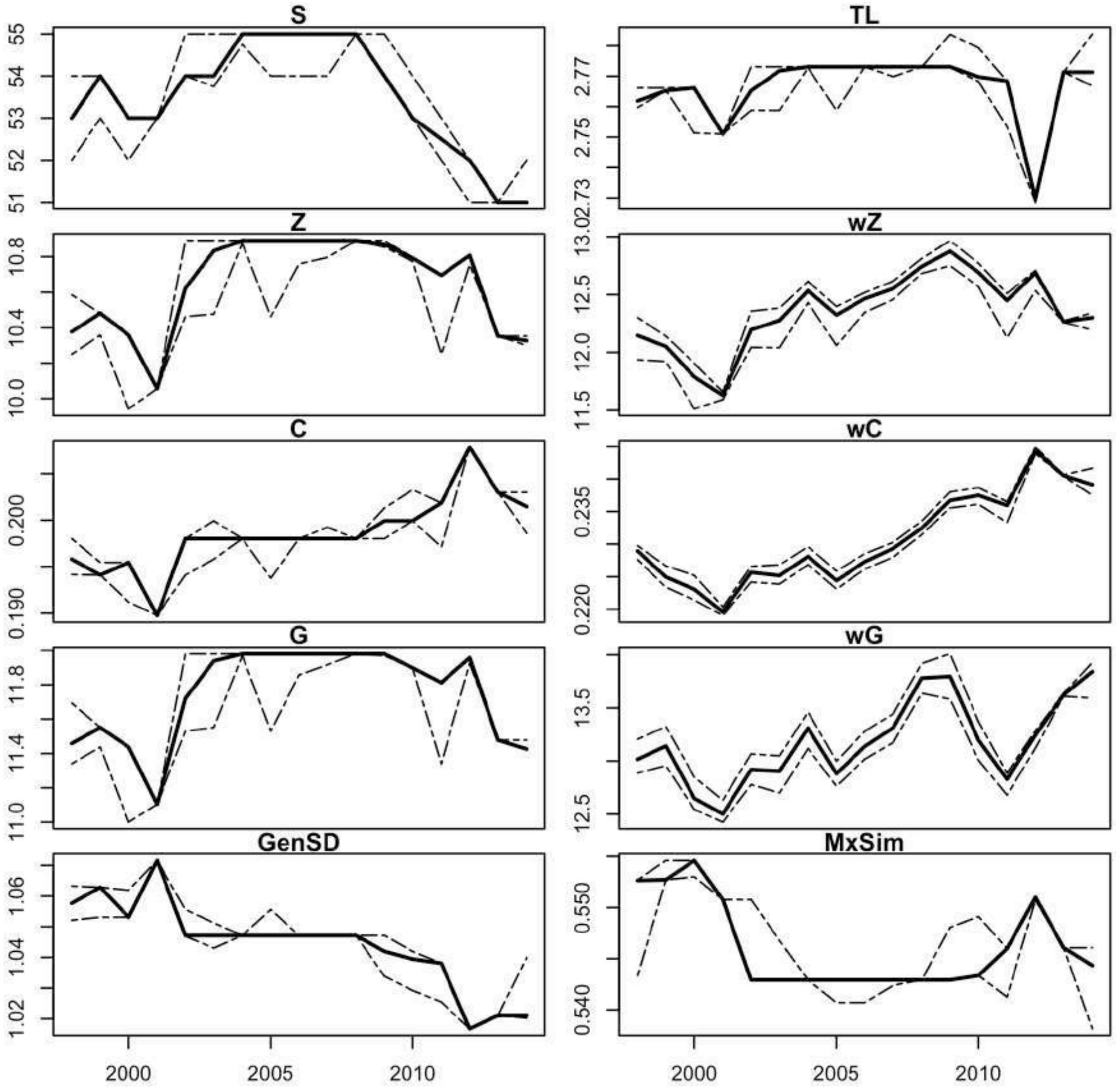


Figure S6.4: Snapshot of the food web at individual time step. The y-axis indicates the trophic levels of the species. Basal species are represented at the bottom and connected to higher trophic level by trophic links (i.e. arrows oriented from the prey to the predator). The size of the nodes is proportional to the abundance of species estimated by the median over 100 subsamplings. Red, blue, purple, green and black nodes represent fish, invertebrates, grazers with constant abundance, primary producers and detritus, respectively.

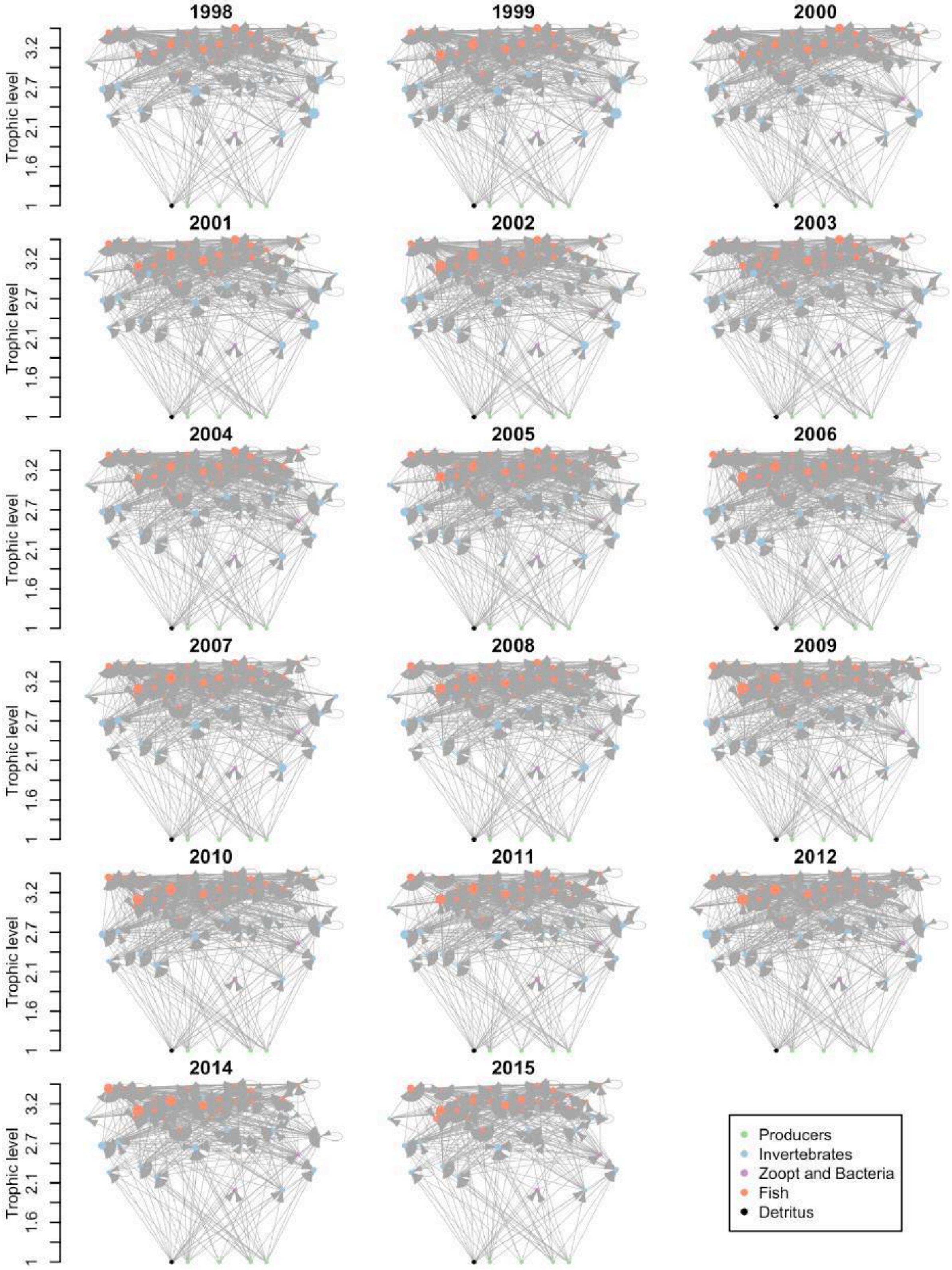
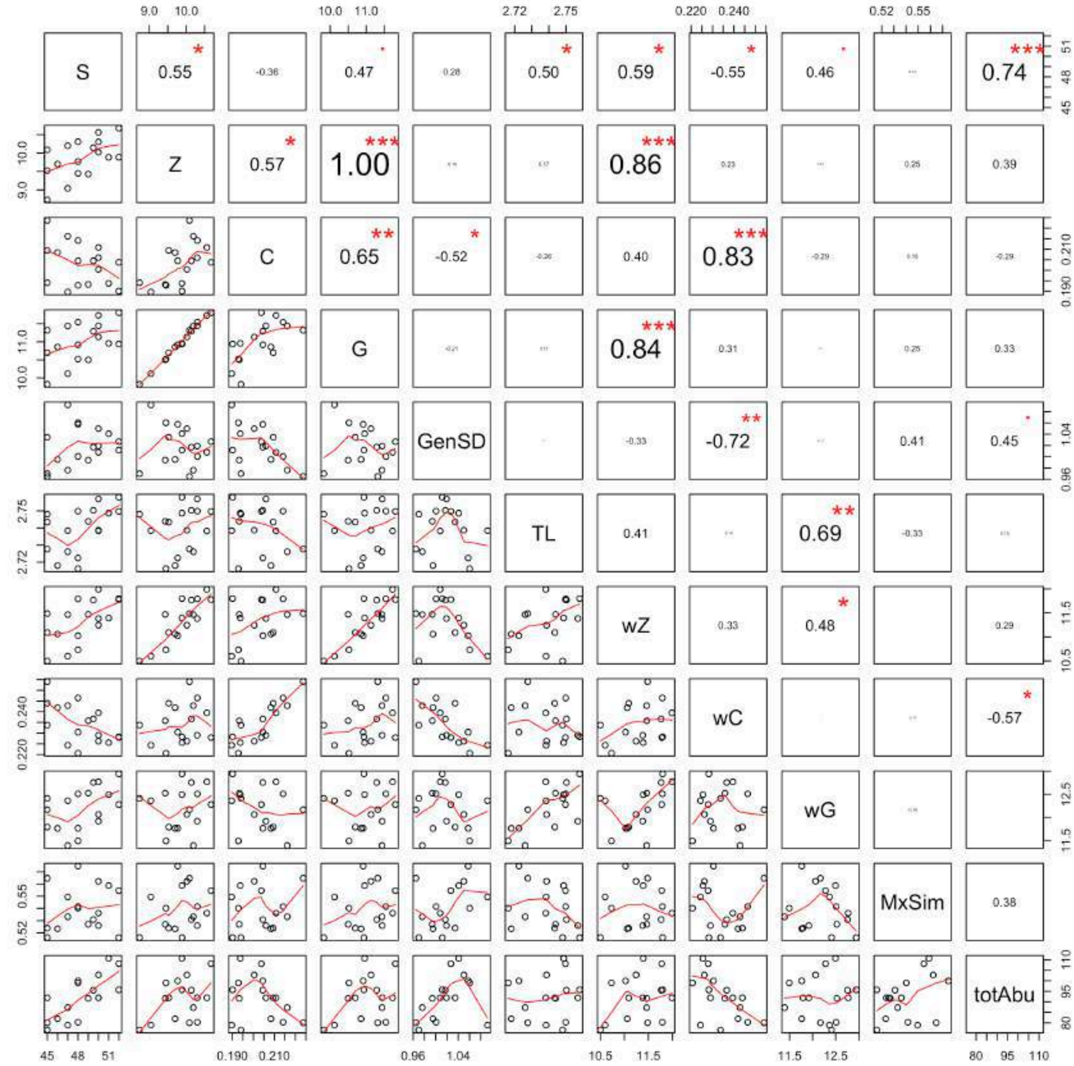


Figure S6.5: Matrix of correlations between food web structural properties. The size of the text as the asterisks indicates significance of a correlation. Significance is shown with stars : *** p-value <0.001, ** <0.01, * <0.05.



Chapter 7

Size asynchrony stabilizes uneven communities

Katsushika Hokusai, The great wave off Kanagawa (c. 1830)

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Title: Does community size structure influence the diversity-stability relationship? Empirical evidence from fish communities across large marine ecosystems.

Authors: Romain Frelat[1*], Manuel Hidalgo[2], Arnaud Auber[3], Heino O. Fock[4], Cristina Garcia[5], Sean M. Lucey[6], Matthew McLean[3], Katherine E. Mills[7], Antonio Punzón[8], Daniel Ricard[9], Nancy L. Shackell[10], Jón Sólmundsson[11], Christine Stortini[12], and Christian Möllmann[1]

[1] Institute for Marine Ecosystem and Fisheries Science, Center for Earth System Research and Sustainability (CEN), University of Hamburg, Große Elbstraße 133, 22767 Hamburg, Germany

[2] Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Ecosystem Oceanography Group (GRECO), Moll de Ponent s/n, 07015 Palma de Mallorca, Spain

[3] IFREMER, Laboratoire Ressources Halieutiques, Unité Halieutique de Manche Mer du Nord, 150 quai Gambetta, BP699, 62321 Boulogne-sur-Mer, France

[4] Thünen-Institute of Sea Fisheries, Herwigstraße 31, 27572 Bremerhaven, Germany

[5] Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Puerto Pesquero s/n, 29640 Fuengirola, Spain

[6] NOAA Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA

[7] Gulf of Maine Research Institute, 350 Commercial St., Portland, ME 04101 USA

[8] Instituto Español de Oceanografía, Centro Oceanográfico de Santander, Promontorio San Martín s/n, 39004 Santander-Cantabria, Spain

[9] Fisheries and Oceans Canada, Gulf Fisheries Centre, Moncton, Canada

[10] Ocean and Ecosystem Sciences Division, Bedford Institute of Oceanography, P.O. Box 1006, Fisheries and Oceans, Dartmouth, N.S. B2Y 4A2, Canada

[11] Marine and Freshwater Research Institute, Skúlagata 4, 101 Reykjavík, Iceland

[12] Department of Biology, Queen's University, 116 Barrie St., Kingston, Ont. K7L 3N6, Canada

[*] Corresponding author: Romain Frelat, romain.frelat@uni-hamburg.de

Abstract

The relationship between diversity and stability has challenged ecologists for decades. Most studies use taxonomic approaches to understand why and under what conditions a community is more stable than the sum of its parts. However, organisms undergo strong ontogenetic shifts during their lifetime, and intra-specific size variability might be an important stabilizing factor. Therefore, we developed a size-based approach to investigate the relative influence of size asynchrony on the stability of communities. Our empirical study is based on long time series (>20 years) of fish biomass from over 50,000 fisheries-independent stations spread across North-Atlantic Large Marine Ecosystems. We found that taxonomic and size asynchrony correctly predicted community stability. In particular, size asynchrony was a major stabilizing mechanism for communities dominated by few and large-bodied species. Our results challenge the current understanding of the regulation of stability and have far-reaching implications for integrative ecosystem-based management.

Keywords: diversity, evenness, stability, synchrony, insurance hypothesis, size spectra, intraspecific variations, traits, fish community, big data

Introduction

The long-lasting debate about the relationship between diversity and stability has fascinated generations of ecologists (Elton 1958; May 1971; McCann 2000; Loreau & de Mazancourt 2013). Currently, humanity's impact on ecosystems and their biodiversity is stronger than ever and expected to increase under population growth and changing climate conditions (Young *et al.* 2016). Given mankind's dependence on ecosystem services, unraveling the relationship between diversity and ecosystem stability is urgently needed and has strong implications for managing and conserving the biosphere.

The debate about the diversity-stability relationship (DSR) started with a relatively simple Lotka-Volterra model developed by Robert May in 1971 that contradicted the common understanding of the positive effect of diversity on ecosystem stability (Elton 1958). Since then, more complex models have been developed that account for interaction strengths between species (McCann *et al.* 1998), differential responses to environmental fluctuations (Yachi & Loreau 1999; Ives *et al.* 1999; Loreau & de Mazancourt 2013), and intra and inter-specific trait variability (Zhang *et al.* 2013). These models confirm the positive impact of diversity on ecosystem stability and suggest that community stability increases with differences in intrinsic environmental responses (in terms of effect and speed) and reduced strength of interspecific competition (Loreau & de Mazancourt 2013). Additionally, trait diversity, especially differences in growth rate, has been identified as an important factor stabilizing communities (Zhang *et al.* 2013). Finally, stability has been theoretically linked to the synchrony of species fluctuations and average species-level stability (Thibaut & Connolly 2013). Species evenness can be an important driver of stability, but it remains unclear whether its influence is positive or negative (Thibaut & Connolly 2013).

Numerous long-term biodiversity experiments have been conducted in terrestrial, freshwater and marine environments. Recent meta-analyses confirm that diversity increases both the productivity and stability of ecosystems at the community level, while destabilizing temporal dynamics of individual populations (Tilman *et al.* 2014; Gross *et al.* 2014). However, the large variability in the results of the experiments suggests that we have yet to fully grasp the mechanism of the connection between diversity and stability. Indeed, empirical studies examining natural communities have confirmed this large variability in DSR (Valone & Barber 2008; Schindler *et al.* 2010; Mikkelson *et al.* 2011; Thibaut *et al.* 2011; Anderson *et al.* 2013). For example, the insurance hypothesis (also called portfolio effect), which predicts that a community is more stable than the sum of its parts, has been rejected in terrestrial communities (Valone & Barber 2008), validated in salmon populations (Schindler *et al.* 2010) and coral fish (Thibaut *et al.* 2011), and was found to be either positive or negative depending on the system (Anderson *et al.* 2013; Cusson *et al.* 2015).

Trait-based approaches to diversity suggest that the characteristics of individuals might better inform the functioning of ecosystems and their responses to environmental variability than taxonomic approaches (Violle *et al.* 2007). Body size is generally recognized as a universally important trait influencing key organismal processes such as feeding, growth, and metabolism (Andersen *et al.* 2016). In vertebrates (e.g. mammals, birds, fish), body size is strongly correlated with prey size, motility, spatial range, reproductive output, physiology, and morphology. Some of these correlations have also been found for protozoa, algae, bacteria, and plants (Peters 1983). Moreover, fish are known for their strong ontogenetic shifts, i.e. there are strong differences in diet, predation risk, and environmental responses within species and between age classes (Cohen *et al.* 2003; Rudolf & Lafferty 2011; Zhang *et al.* 2013). In fact, similar size classes across species may have similar dynamics due to intra-size class competition for food, similar predators and similar environmental responses. Dynamical size-spectrum models have shown that community abundance can have self-induced oscillations, called waves, moving along the size spectrum from small to large body size (Law *et al.* 2009). Moreover, a dynamic trait-based size-spectrum model indicated that the diversity of growth rates stabilizes community dynamics through asynchrony in species waves (Zhang *et al.* 2013). However, these theoretical predictions have never been confirmed empirically in species assemblages, and it remains to be fully shown whether size categories (e.g. small, medium or large fish) are complementary to taxonomic descriptors for understanding the dynamics and stability of communities (Fig. 7.1A).

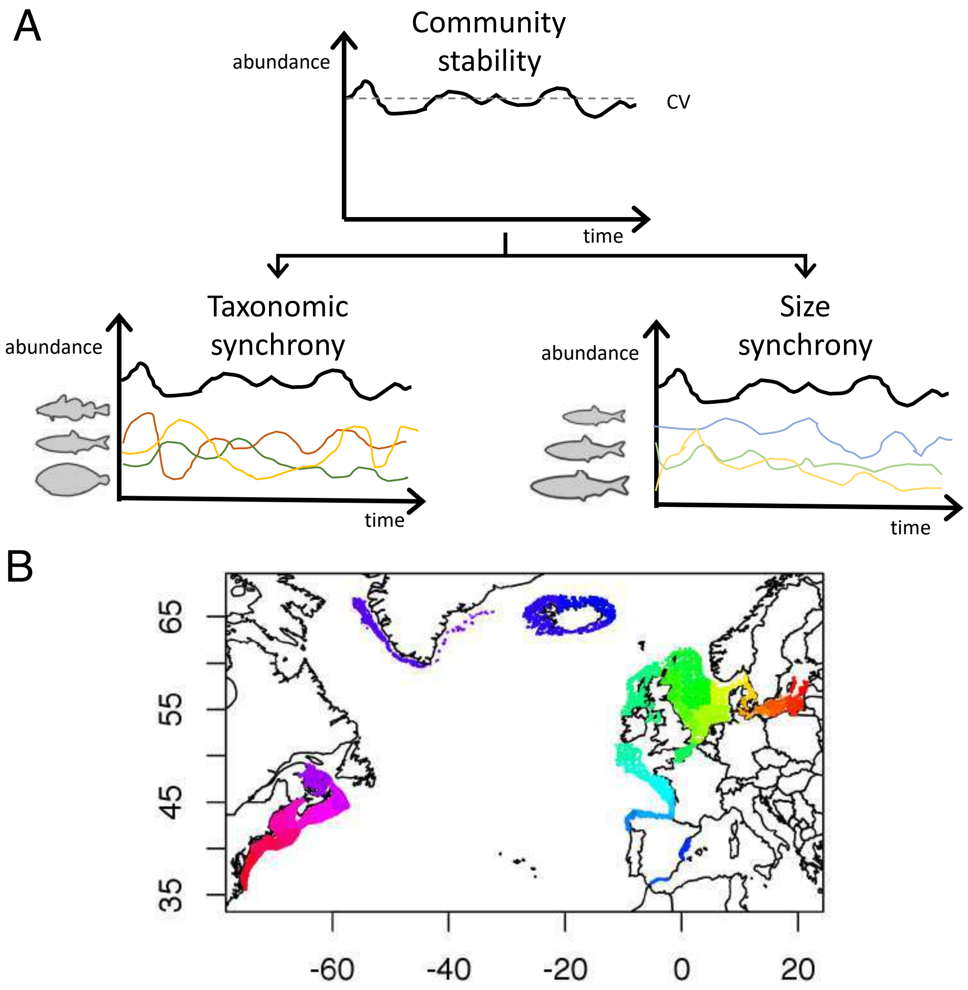

Figure 7.1: Conceptual approach and dataset. (A) Our goal is to understand community stability, as described by the coefficient of variation (CV) of the total biomass over time, by looking at synchrony between species (taxonomic synchrony) and between size classes (size synchrony). (B) Our study builds on empirical evidence from a large dataset (>50,000 stations) of fisheries-independent trawl surveys across the North Atlantic. Colours represent the 36 different areas, homogeneous in terms of species composition and habitat characteristics.

Our empirical study addresses the diversity-stability relationship using multiple datasets collected by large-scale and long-term fisheries-independent ecological monitoring programmes (Fig. 7.1B). By merging these national and regional surveys, we are able to test the robustness and variability of the DSR across ecosystems. As recently suggested, large datasets, such as ours, can bring valuable empirical evidence for disentangling long-lasting questions in ecology and environmental science (Edgar *et al.* 2016; LaDeau *et al.* 2017). Our analysis is based on more than 50,000 stations from twelve long-term fisheries-independent surveys spanning the northwestern and northeastern Atlantic shelves, the Baltic Sea, and the western Mediterranean Sea. We focus on the stability of productivity, measured here as the variability of biomass over time. The aim of our study is to understand the influence of size structure on the stability of fish communities and to explore the relative contribution of size asynchrony (i.e. asynchrony of biomass time series among size classes) on community-level stability in 36 different marine ecosystems. The main questions of our study are: i) what is the complementarity between size and taxonomic synchrony for the stability of communities? ii) which factors could explain the differences between size and taxonomic synchrony and iii) what are the regulatory mechanisms of stability?

Material and methods

Fisheries-independent bottom trawl surveys

We gathered data from twelve long-term monitoring surveys targeting groundfish populations across the North Atlantic coastlines, the Baltic Sea, and the western Mediterranean Sea (Fig. 7.1B and Table S7.1 in Supporting Information). The common goal of these surveys is to estimate the stock size of commercially-valuable species as well as to assess the diversity of species assemblages and their dynamics. Therefore, all catches were identified (mostly at species level), and the lengths of all individuals (or a representative subsample per species) were measured to monitor the size structure of species catches. The gears and protocols used vary between surveys (Table S7.1), but within each survey the protocol was kept constant and therefore the annual time series are consistent. We accounted for the seasonal migration pattern of fish species by considering only one season per year, identifying for each survey the season with the best sampling coverage and the longest time series (Table S7.1). In the case of surveys with 24-hour samplings, we removed the night stations to eliminate the effect of diurnal migration.

Our study investigated the multidecadal variation in demersal shelf fish assemblages. Therefore, we only kept hauls between 20 and 300 m depth, removing coastal and deep community samples (Pecuchet *et al.* 2017). The bottom trawls used in the surveys are efficient for estimating demersal fish populations, but may not consistently sample pelagic fishes. Consequently, we removed pelagic and mesopelagic fish species that spend most of their time in the upper water column, or that display variable catchability among years, such as European pilchard (*Sardina pilchardus*) and American shad (*Alosa sapidissima*). All taxa reported were checked to ensure consistency of taxonomic information reported throughout each survey and to prevent overestimating species richness and species turnover. Hereafter, we use "species" to refer to taxa, even if some taxa (only 2% of all records) correspond to the genus or family level.

From length to weight class

We transformed length measurements (in cm) to weight (in g) for all species, using length-weight relationships (Froese 2006). The coefficient of the arithmetic length-weight relationship a and the allometric growth parameter b were taken from local validated databases (Table S7.1). When the parameters were not available, we used data extracted from FishBase (Froese & Pauly 2017). If the parameters were not available in FishBase, we approximated a=0.01 and b=3, as these values are commonly accepted parameters and closely approximate the median of more than 3,500 fish species (Froese 2006).

We created classes of 0.5 log2 size bins following a commonly-used procedure in body size-spectra studies (Jennings & Dulvy 2005; Hidalgo *et al.* 2017). We evaluated the minimum and maximum size classes that were consistently sampled by visually detecting breaks in the slope of the size spectra (Fig. S7.1). The size classes were limited to the range between 23 g and 23 kg, because fish outside this range were rarely were rarely caught and not consistently sampled.

Community time series

The hauls (or stations) were grouped into "areas", which were subdivisions of the surveys defined as relatively homogeneous ecosystems in terms of fish species composition and habitat characteristics according to previous literature (Daan *et al.* 1990; Stefansdottir *et al.* 2010; Shackell *et al.* 2012). We restricted our dataset to areas that have been sampled at least 10 times annually, without interruption for at least 19 years. In total, we used information collected from 54,739 hauls in 36 different areas between 1963 and 2017, recording the abundance of 491 different species (Fig. 7.1B).

Not all demersal species are well-sampled by bottom trawl surveys. The "rare" taxa are only recorded occasionally, and thus their observed dynamics are highly variable and may not represent actual trends. Consequently, we limited species assemblages to persistent taxa, i.e. species that were consistently reported. We identified persistent taxa using inflexion points in a persistence plot, comparing the number of years of presence against the log of the biomass (Genner *et al.* 2004). The inflexion point was detected at 50% of the time series (Fig S7.2), therefore we only kept species that have been detected during more than 50% of the years in the time series.

Furthermore, the number of stations sampled was not constant over the time series or across areas, so we kept the same number of hauls per year for all surveys. This procedure assured that synchrony estimates are not influenced by the number of samples and the averaging effect. We randomly selected 10 hauls per year from each area and then repeated this random selection 100 times. This random selection procedure provided an estimation of the variability of our results.

Stability and diversity indicators

Stability was defined as the variability in community biomass over time, measured as the inverse of the coefficient of variation (McCann 2000). We used synchrony as the DSR indicator, defined as the ratio between community variance and species-level variance (Loreau & de Mazancourt 2008). The synchrony indicator varies between 0 (perfect asynchrony) and 1 (perfect synchrony) and has the advantage of being both mathematically robust and easy to interpret (Thibaut & Connolly 2013). For instance, if two species are perfectly synchronous, the sum of their biomasses will be highly unstable (similar to the sum of two waves with similar phases), while perfectly asynchronous species will counterbalance, and the sum of their biomasses will be constant.

We computed synchrony indicators for size classes and taxonomic classification (Fig. 7.1A) and referred to these as size synchrony and taxonomic synchrony. Moreover, to investigate the differences between the two synchrony indicators, we calculated their standardized difference ($dSyn$) divided by their mean:

$$dSyn = 2 \times \frac{syn_{size} - syn_{taxo}}{syn_{size} + syn_{taxo}}$$

Size and species richness were defined as the number of size classes and taxa, respectively, that were persistently recorded over the time series of 10 randomly selected hauls per year. Size richness was, by construction, limited to 20 size classes. Pielou's evenness, defined as the ratio between the Shannon index and the species richness, was used as an indicator of evenness in the species assemblages (Pielou 1966). Evenness is close to 0 if the community was dominated by few species, or close to 1 if most species had similar biomass. Diversity indicators (i.e. richness and evenness) were calculated for each time step, and then averaged over the entire time period.

We built a linear model predicting log-transformed CV with size and taxonomic synchrony including interactions. We tested pairwise relationships between different diversity indicators and $dSyn$ using linear models and Pearson correlation coefficients. For every linear model, we visually checked that all the assumptions of the linear model were verified, particularly the statistical independence, normality and homoscedasticity of the residuals.

All statistical analyses and data processing were conducted in the programming environment R3.3 (R Core team 2017). Maps were created with the *mapdata* package (Becker *et al.* 2016), 3D visualization with the *plot3D* package (Soetaert 2013) and diversity indicators were calculated using the *vegan* package (Oksanen *et al.* 2017).

Results

Spatial distribution of diversity and stability indicators

Species richness, measured as the number of species recorded persistently along the time series with 10 hauls per year, was highest (>30 species) in the Mediterranean Sea, the Celtic Sea and the Bay of Biscay, while lowest in the eastern Baltic Sea (< 10 species) (Fig. 7.2A). In the North Sea, we observed a strong latitudinal gradient from low species richness in the southeast to high values in the northwest. A similar gradient was observed along the east coast of North America, with lower diversity in the southwest. Species evenness was exceptionally high (0.7) where species richness was highest, i.e. in the Mediterranean Sea, the Celtic Sea and the Bay of Biscay (Fig 7.2B). Lowest evenness was found off the east coast of Greenland, dominated by Atlantic cod (*Gadus morhua*) and redfish (*Sebastes spp.*). In the North Sea, evenness followed an east-west gradient, with the western fish assemblages dominated by whiting (*Merlangius merlangus*) or haddock (*Melanogrammus aeglefinus*). Size richness reflects the maximum size class that was persistent in the time series. The size richness followed a latitudinal gradient (Fig. 7.2C) with lowest diversity in the Mediterranean Sea and the Mid-Atlantic Bight (12 size classes, corresponding to a maximum size of 1 kg), the largest diversity around Iceland and Greenland (20 size classes, maximum size 23 kg).

By definition, stability is inversely related to the coefficient of variation (CV). The most unstable communities (CV>1) were reported off the western coast of Greenland, the southwestern North Sea and the southern New England region along the US coast (Fig. 7.2D). The most stable communities (CV <0.5) reside in the Celtic Sea, the Bay of Biscay and the western Baltic Sea. Taxonomic and size synchrony displayed a similar spatial pattern, with strong synchrony in the assemblages off the western coast of Greenland, the southern North Sea and the eastern Baltic Sea (Fig. 7.2E&F).

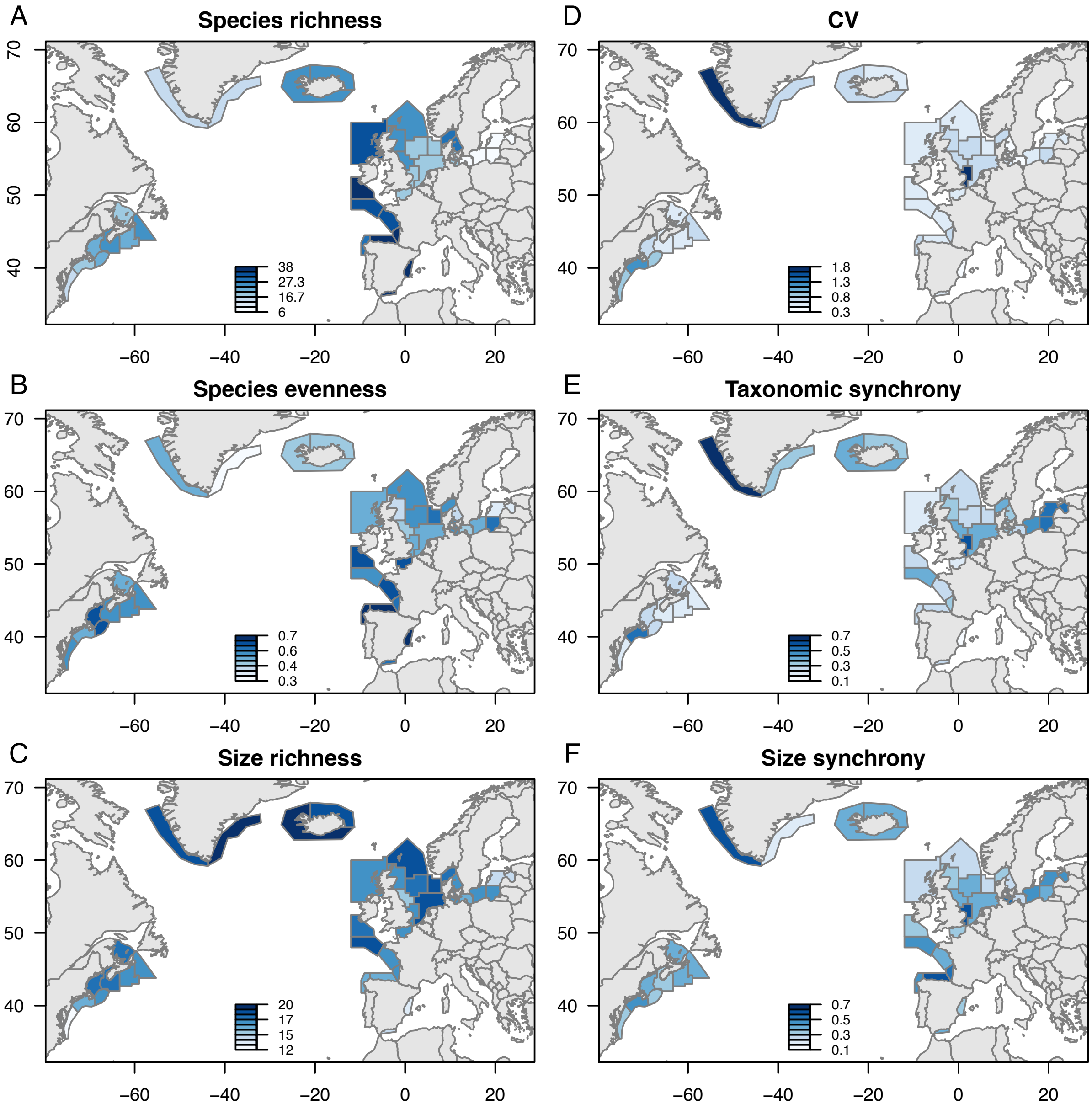

Figure 7.2: Spatial distribution of diversity and stability indicators. Diversity indicators are shown on the left side: species richness (A), species evenness (B) and size richness (C). Stability and synchrony indicators are shown on the right side: coefficient of variation of the community biomass (D), taxonomic synchrony (E) and size synchrony (F).

Asynchronous assemblages are more stable

We investigated the relation between stability and synchrony with a linear regression model predicting log-transformed CV from size and taxonomic synchrony including their interaction. The two synchrony indicators were positively and significantly associated with CV (Fig. 7.3A). In other words, low taxonomic or size synchrony was related to lower variability of biomass, i.e. higher stability. This observation confirmed the positive effect of asynchronous population dynamics on community stability. The partition of variance indicated that taxonomic and size synchrony explained together 34% of the variability of log-transformed CV (Fig. 7.3B). Taxonomic synchrony alone explained an additional 15% and size synchrony alone explained an additional 5%. Such a simple model with only two predictors was able to explain more than 53% of the variability of the coefficient of variation.

The majority of the points were situated on the left side of the 3D visualization (Fig. 7.3A), indicating than on average, size synchrony was higher than taxonomic synchrony. In fact, 27 areas out of 36 had, on average, a higher size synchrony than taxonomic synchrony. When considering the 95% confidence interval from random sampling, 17 areas (~50%) always had higher size synchrony than taxonomic synchrony; only 3 areas (~10%) demonstrated the opposite. In the remaining 16 areas, size and taxonomic synchrony were similar.

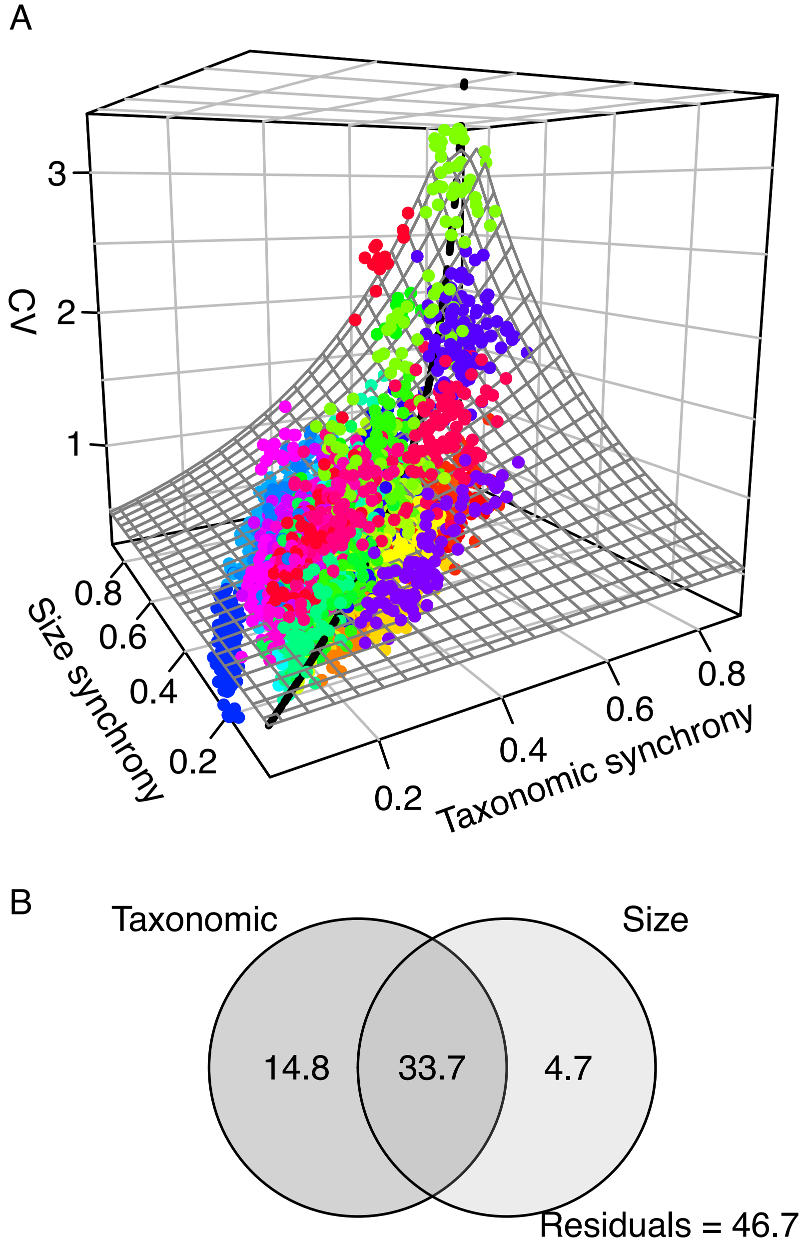

Figure 7.3: Relationship between size synchrony, taxonomic synchrony and stability (as indicated by CV). Points represent the 100 repetitions for each area and colours indicate areas (see Fig. 7.1B). The grey grid is a linear regression modeling the log-transformed CV from size and taxonomic synchrony including their interaction. The dark bold line is the predicted CV when size and taxonomic synchrony are equal. (B) Partition of the variance of log-transformed CV (in %), explained by taxonomic and size synchrony.

Relationship between evenness and synchrony

To investigate the factors that could explain the difference between size and taxonomic synchrony, we calculated the standardized difference between taxonomic synchrony and size synchrony (dSyn). Negative (or positive) differences denote stronger taxonomic (or size) synchrony. With high positive values, fish assemblages in the Ebro Delta in the Mediterranean Sea, the Cantabrian Sea, and the central Scotian Shelf had lower species synchrony, indicating that asynchrony among species dynamics had a stronger stabilizing effect than differences among size classes. In contrast, negative differences observed off east Greenland and in the Baltic Sea indicate assemblages with lower size synchrony than taxonomic synchrony, suggesting the opposite mechanism.

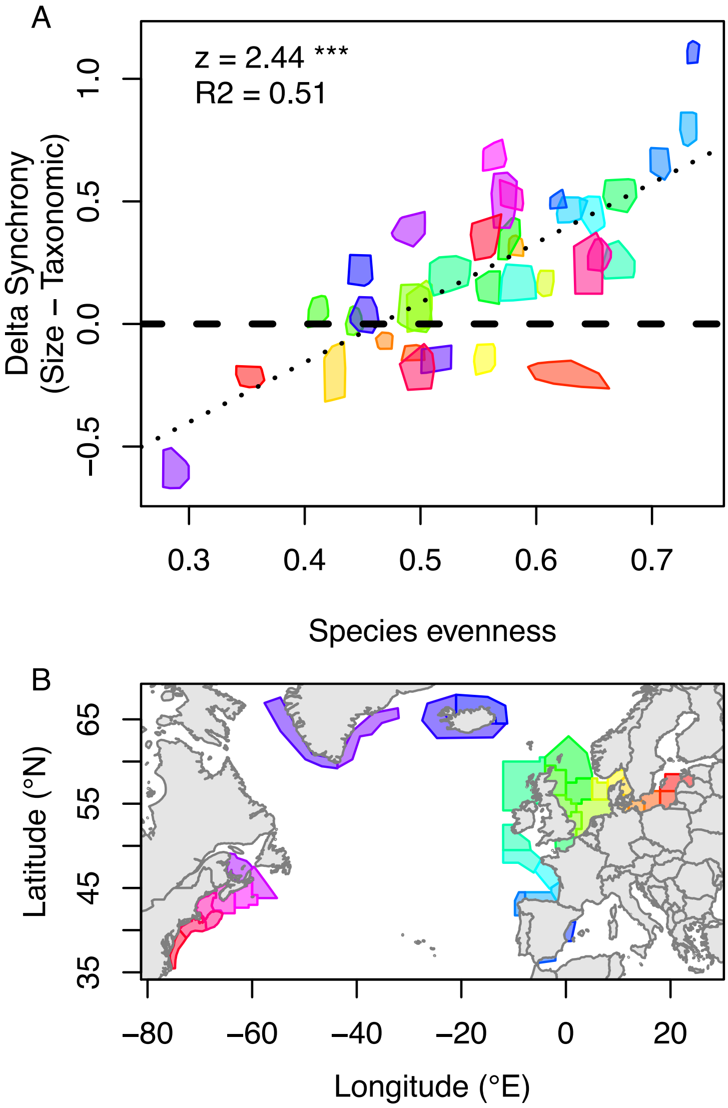

Figure 7.4: Relationship between species evenness and the difference between size synchrony and taxonomic synchrony. Polygons represent the variability of results, as indicated by the convex hull of the inter-quartile range of 100 repetitions for each area. The bold dashed line represents equality between taxonomic and size synchrony while the dotted line is the linear regression calculated from the 100 repetitions. Colours indicate areas, as mapped in (B).

The standardized difference in synchrony was positively correlated with species evenness (r=0.69, p-value<0.001, Fig 7.4A). Communities with a highly even assemblage (e.g. the Mediterranean Sea) displayed stronger taxonomic synchrony than size synchrony, while opposite for communities with low species evenness (e.g. off east Greenland). In fact, species evenness was the best explaining variable of dSyn among the 4 variables of richness and evenness tested (Fig. S7.3). Species richness and size evenness were also positively and significantly correlated with dSyn (Fig. S7.3A&C), but both variables were highly correlated with species evenness (Fig. S7.3D&F). Additionally, a negative correlation was found between dSyn and size richness (Fig. S7.3B). These results indicate that systems with high species diversity and high evenness maintain stability through between species asynchrony while systems with low species diversity and few large-bodied dominant species maintain stability through within-species size asynchrony.

Discussion

Size asynchrony stabilizes uneven communities

Our study offers a novel perspective on the link between synchrony, stability, species diversity and size structure, based on more than 50,000 samples from long-term fisheries-independent surveys. Across North Atlantic Large Marine Ecosystems, asynchrony was an important driver of stability in fish assemblages. In fact, the synchrony among taxa, and the synchrony among size classes could explained 53% of the variability of CV (Fig. 7.3). Our study empirically confirms the results of models about the "insurance hypothesis" or the "portfolio effect" (Yachi & Loreau 1999; Ives & Carpenter 2007; Thibaut & Connolly 2013). Additionally, our results indicate that taxonomic synchrony is important when species are even, while size synchrony is more important when assemblages are dominated by few species (Fig. 7.4). Evenness in community biomass seems to be a good indicator of the stability mechanism, corroborating the importance of evenness in ecosystem processes (Hillebrand *et al.* 2008). Indeed, when assemblages are dominated by few species, the difference in species' responses to environmental or anthropogenic perturbations does not stabilize the community, but rather asynchrony of different size classes of the dominant species. Lower evenness in the North Atlantic generally means that a system is dominated by a few large-bodied predatory species. Since these species have a wider range of sizes throughout their life-span, the asynchrony is mainly within species, not across species. In systems with high species evenness, which also means higher species richness, asynchrony is among species, not within species. In other words, the system seems to adjust to maintain stability and intra-specific trait variability, such as body size, which can be an important stabilizing mechanism in systems with strong dominance. Our results are in line with a recent meta-analysis on intra-specific variability which can have a higher or comparable effect on ecosystem functions (such as stability) than between species variability (Des Roches *et al.* 2018).

Limitations and robustness

Despite differences in sampling protocols between areas, we considered the time series of fish biomass within each area to represent the dynamics of that species assemblage. The level of stability of each area can be influenced by external drivers or different sampling protocols. However, the stabilizing mechanism identified here, either regulated by size or taxonomic asynchrony depending on community evenness, is independent of the level of stability. Our study did not consider possible drivers of synchrony or stability other than diversity. Environmental fluctuations and anthropogenic pressures have affected the areas differently, hence also influencing these indicators to variable degrees. For example, fishing pressure has been found to increase synchrony of populations, therefore ecosystems with lower fishing pressure are usually more stable (Bell *et al.* 2014). However, our study investigated the relationship between stability and synchrony, and external pressures impact both, therefore our results likely stand regardless of the level of environmental fluctuations or fishing pressure.

Our results were robust to multiple sensitivity tests on species inclusion, taxonomic resolution, size class resolution and spatial scale. Since the definition of "pelagic species" is subjective, we tested the sensitivity of our results to the deletion of pelagic species and our results stood even when we kept all pelagic species (Fig. S7.4). Because different surveys recorded taxa at varying taxonomic resolutions, we tested the effect of taxonomic resolution on our results. Running the same analysis aggregating species to genus or family confirmed our results (Fig. S7.5). To test whether our results were sensitive to the definition of size classes, we grouped size classes together, to keep only 10 or 7 size classes instead of 20. Again, the results and the relationship between synchrony and stability were consistent with the results presented here (Fig. S7.6). Finally, we tested for the effects of using different spatial scales in the analysis, but found similar results both at small (the size of one-degree longitude and 0.5-degree latitude rectangles, Fig. S7.7) and large (the extent of the surveys) scales (Fig. S7.8). Altogether, we are confident that our large dataset, although being a composite from many different sources, reliably demonstrates the relationship between stability and diversity, through two complementary mechanisms: asynchronous species fluctuations and within-species asynchronous size fluctuations.

Implications for ecology and conservation

Our study is, to the best of our knowledge, the first to provide empirical evidence for the role of species evenness in determining the mechanism by which marine populations maintain community-level stability. Our results indicate that, in species-poor ecosystems dominated by few large-bodied species, size diversity within species leads to asynchrony among size classes, which contributes to community-level stability. In species-rich ecosystems, the asynchrony among species, resulting from diverse responses to external pressure and growth rate, is the main factor of community-level stability. This result has far-reaching implications for our understanding of the regulation of stability in ecosystems and for integrative ecosystem-based management.

Communities evolve in an ever-changing environment, and conservation efforts should focus on preserving the diversity of environmental responses among species, rather than the species themselves (Schindler *et al.* 2015). Knowing that the dynamics of the size structure of communities can buffer ecosystems with few dominant species is highly relevant for management, particularly while there is ongoing debate about the benefits of balanced harvesting in fisheries management (Law *et al.* 2012; Jacobsen *et al.* 2014; Froese *et al.* 2016). Our study shows that the size structure in ecosystems dominated by few large-bodied species is important for their stability, hence maintaining size structure by lowering pressure on large individuals might improve the biomass stability of the community (and subsequently the stability of fisheries yield). Our study brings new evidence in favour of size-based and trait-based approaches for studying the role of diversity in ecological communities and for ecosystem functioning. In fact, size structure offers a complementary view to the taxonomic community description, which is important for understanding the complex and multidimensional relationship between diversity and stability (Donohue *et al.* 2016). For theorists and empiricists, our results suggest incorporating size distributions in future research on stability, and more generally to consider intra-specific trait variability for the study of ecosystem functioning.

Acknowledgments

The authors are grateful to all contributors of the bottom trawl surveys that sorted, identified, measured and reported the catch rigorously in databases as well as institutions that supported them. The authors would also like to acknowledge the data management personnel, especially Don Clark, Antonio Esteban, Sigfús Jóhannesson, Sigrún Jóhannsdóttir, Mike McMahon and Nicolas Rolland. We acknowledge the ICES Working Group on Comparative Analyses between European Atlantic and Mediterranean Marine Ecosystems to Move Towards an Ecosystem- based Approach to Fisheries (WGCOMEDA), during which the study was initiated, and are thankful to all the WGCOMEDA participants for their valuable comments.

List of supporting information:

Table S7.1: Description of the twelve scientific surveys

Figure S7.1: Size spectra

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Figure S7.5: Sensitivity to taxonomic level

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Figure S7.7. Sensitivity to spatial scale – high resolution

Figure S7.8. Sensitivity to spatial scale – low resolution

Table S7.1: Description of the twelve scientific surveys.

Survey	Region	Year start	Year end	Number hauls	Number areas	Number species	Contact	Local LW parameters
BITS	Baltic Sea	1991	2017	5,534	5	47	ICES DATRAS[1]	Fung et al. 2012[3]
CGFS	English Channel	1988	2014	1,846	1	54	IFREMER[2]	Fung et al. 2012[3]
EVHOE	Celtic Sea and Bay of Biscay	1997	2016	2,347	4	121	IFREMER[2]	Fung et al. 2012[3]
GBTS	Greenland	1981	2017	2,564	2	59	Heino Fock	private communication
GSL	Gulf of Saint Lawrence	1971	2002	2,489	1	52	Daniel Ricard	Wigley et al. 2003[4]
IGS	Iceland	1996	2017	4,747	2	77	Jón Sólmundsson	Use data from HF, Greenland
NEFSC	Northeastern coast of United States	1963	2009	10,646	4	198	Sean M. Lucey	Wigley et al. 2003[4]
NSIBTS	North Sea	1985	2017	11,292	9	109	ICES DATRAS	Fung et al. 2012[3]
SCS	Scotian Shelf	1970	2017	8,461	3	115	Nancy L. Shackell	Wigley et al. 2003[4]
SPATL	Spanish Atlantic coast	1991	2015	2,673	2	120	Manuel Hidalgo	private communication
SPMED	Spanish Mediterranean Sea	1994	2017	1,102	2	137	Manuel Hidalgo	private communication
SWCBTS	Scottish West Coast	1999	2017	1,038	1	77	ICES DATRAS	Fung et al. 2012[3]
	TOTAL	**1963**	**2017**	**54,739**	**36**	**491**		

[1] ICES DATRAS: http://datras.ices.dk/Data_products/

[2] IFREMER: http://www.ifremer.fr/SIH-indices-campagnes/

[3] Fung, T., Farnsworth, K. D., Reid, D. G., & Rossberg, A. G. (2012). Recent data suggest no further recovery in North Sea Large Fish Indicator. ICES Journal of Marine Science, 69(2), 235–239. doi:10.1093/icesjms/fsr206

[4] Wigley, S. E., McBride, H. M., & McHugh, N. J. (2003). Length-weight relationships for 74 fish species collected during NEFSC research vessel bottom trawl surveys, 1992-99. NOAA Technical Memorandum NMFS-NE-171

Figure S7.1: Size spectra calculated with log2 size bin from 1g to 131kg. Bin classes between 23g and 23kg were selected as correctly sampled by bottom trawl surveys.

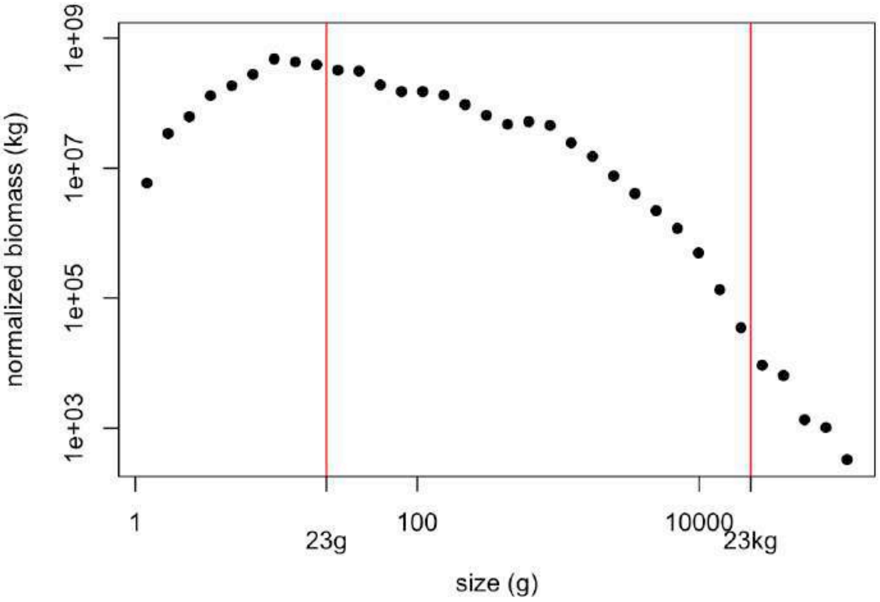


Figure S7.2: Persistence plot (length of time series vs log abundance) of all the species caught by demersal trawl survey. The points represent the different species while the colours represent the different areas. The lines are third-order polynomial regressions fitted to the different surveys, the vertical dotted lines are the inflexion points. The black line is the global model for the entire dataset, with an inflexion point at 53%.

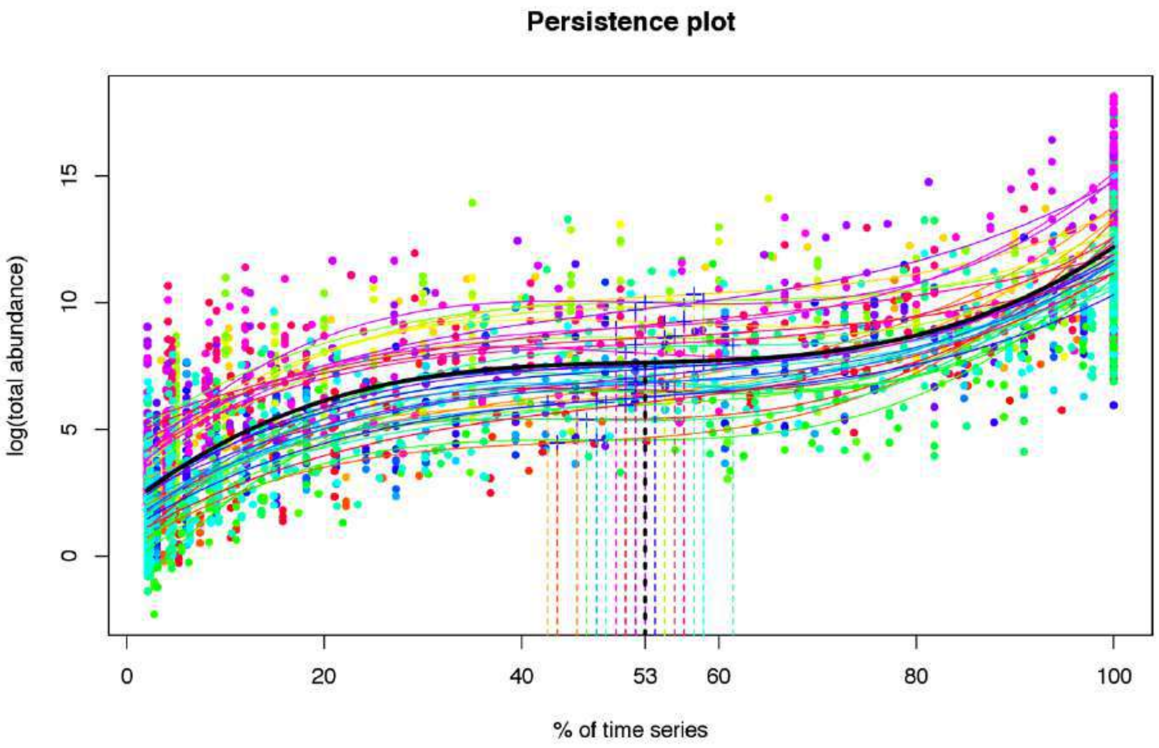


Figure S7.3: Pairwise correlation between diversity and synchrony. Relationship between the difference of synchrony (size-taxonomic) and (A) species richness, (B) size richness, and (C) size evenness. Relationship between species evenness and (D) species richness, (E) size richness and (F) size evenness.

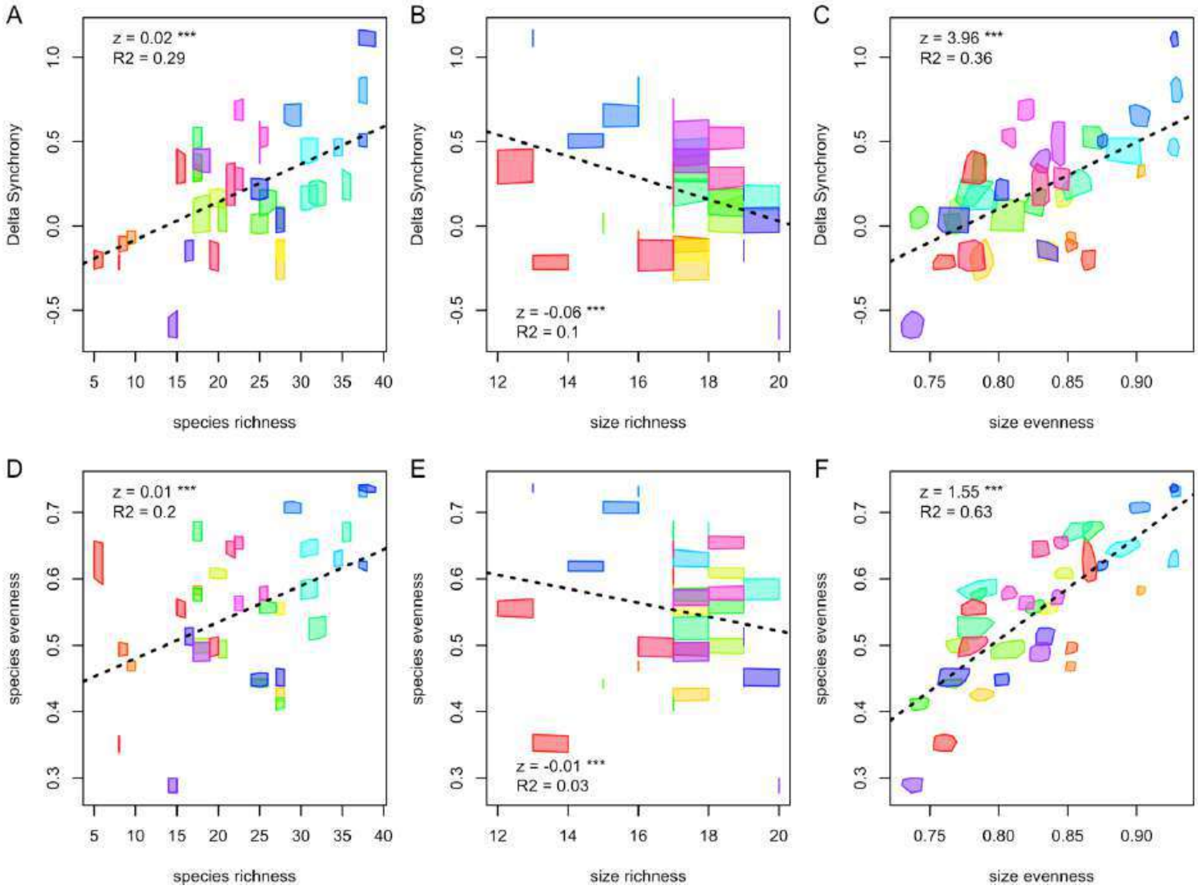


Figure S7.4: Sensitivity to pelagic species. Results using demersal and pelagic species. (A) Relationship between size synchrony, taxonomic synchrony and stability (as indicated by CV). Points represent the 100 repetitions for each area. The grey grid is a linear regression modeling the log-transformed CV from the size and taxonomic synchrony including interaction. The dark bold line is the predicted CV when size and taxonomic synchrony are equal. (B) Partition of the variance of log-transformed CV (in %), explained by taxonomic and size synchrony. (C) Relationship between species evenness and the difference between size and taxonomic synchrony. Polygons represent the variability of results, as indicated by the convex hull of the inter-quartile range of 100 repetitions for each area. The bold dashed line represents equality between taxonomic and size synchrony while the dotted line is the linear regression calculated from the 100 repetitions. Colours of the dots in (A) and of the polygons in (C) indicate areas, as mapped in (D).

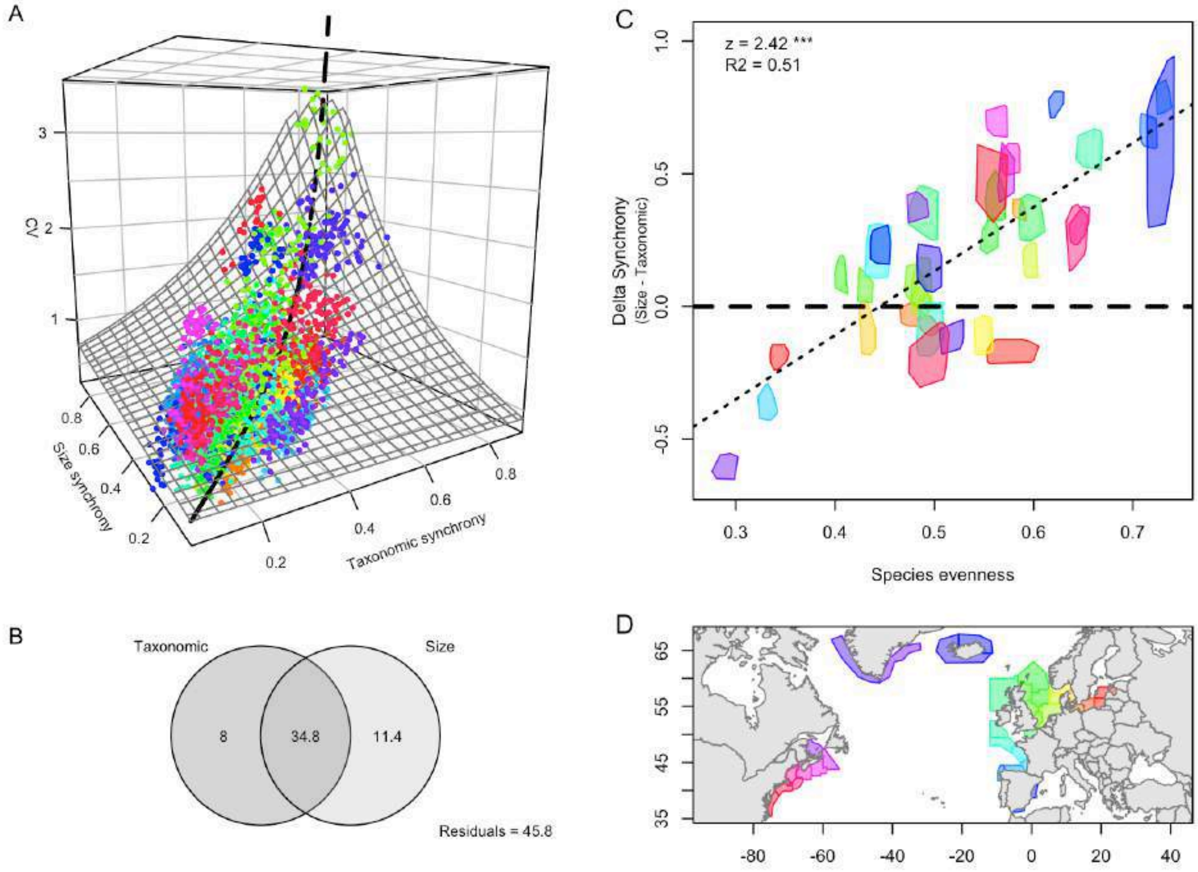


Figure S7.5: Sensitivity to taxonomic level. Results when taxa are all aggregated at family level. (A) Relationship between size synchrony, taxonomic synchrony and stability (as indicated by CV). Points represent the 100 repetitions for each area. The grey grid is a linear regression modeling the log-transformed CV from the size and taxonomic synchrony including interaction. The dark bold line is the predicted CV when size and taxonomic synchrony are equal. (B) Partition of the variance of log-transformed CV (in %), explained by taxonomic and size synchrony. (C) Relationship between species evenness and the difference between size and taxonomic synchrony. Polygons represent the variability of results, as indicated by the convex hull of the inter-quartile range of 100 repetitions for each area. The bold dashed line represents equality between taxonomic and size synchrony while the dotted line is the linear regression calculated from the 100 repetitions. Colours of the dots in (A) and of the polygons in (C) indicate areas, as mapped in (D).

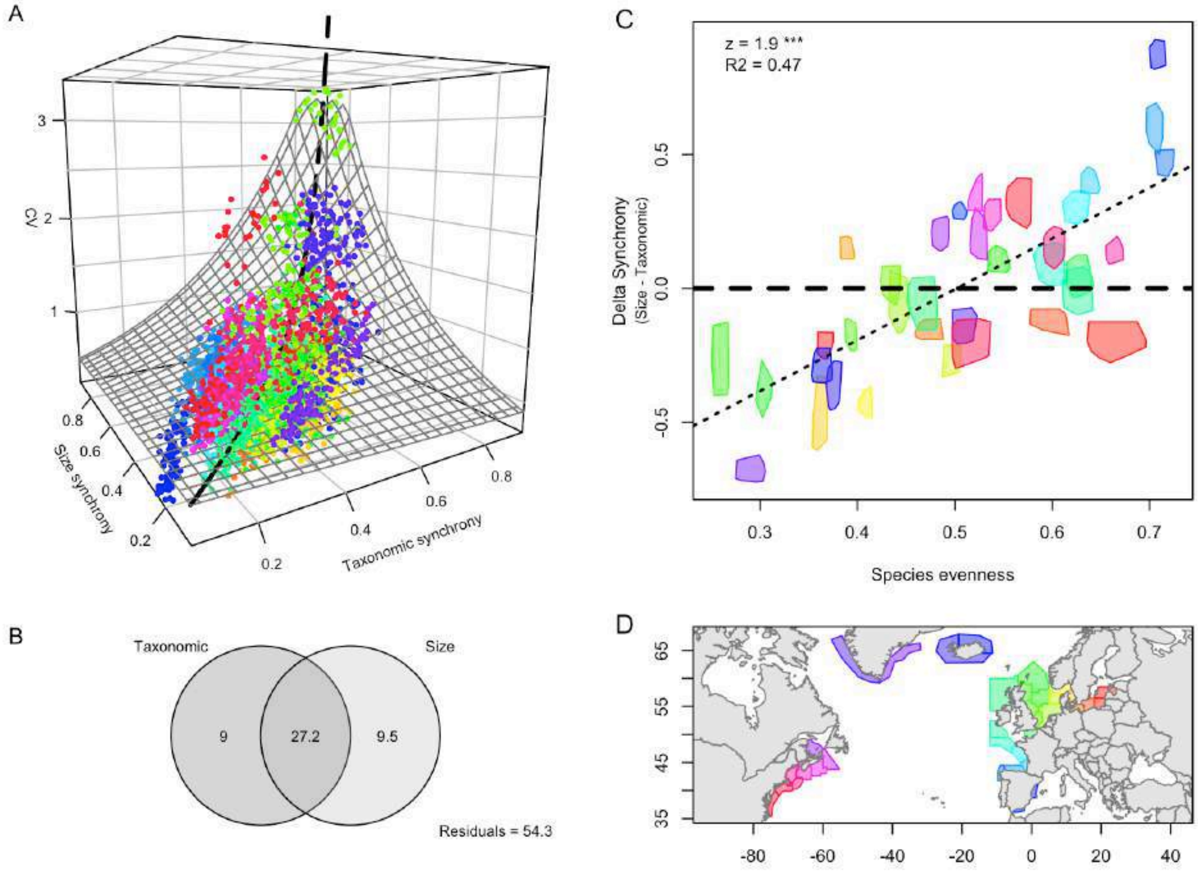


Figure S7.6: Sensitivity to size class width. Results when merging the size classes three by three (i.e. using 7 size classes instead of 20). (A) Relationship between size synchrony, taxonomic synchrony and stability (as indicated by CV). Points represent the 100 repetitions for each area. The grey grid is a linear regression modeling the log-transformed CV from the size and taxonomic synchrony including interaction. The dark bold line is the predicted CV when size and taxonomic synchrony are equal. (B) Partition of the variance of log-transformed CV (in %), explained by taxonomic and size synchrony. (C) Relationship between species evenness and the difference between size and taxonomic synchrony. Polygons represent the variability of results, as indicated by the convex hull of the inter-quartile range of 100 repetitions for each area. The bold dashed line represents equality between taxonomic and size synchrony while the dotted line is the linear regression calculated from the 100 repetitions. Colours of the dots in (A) and of the polygons in (C) indicate areas, as mapped in (D).

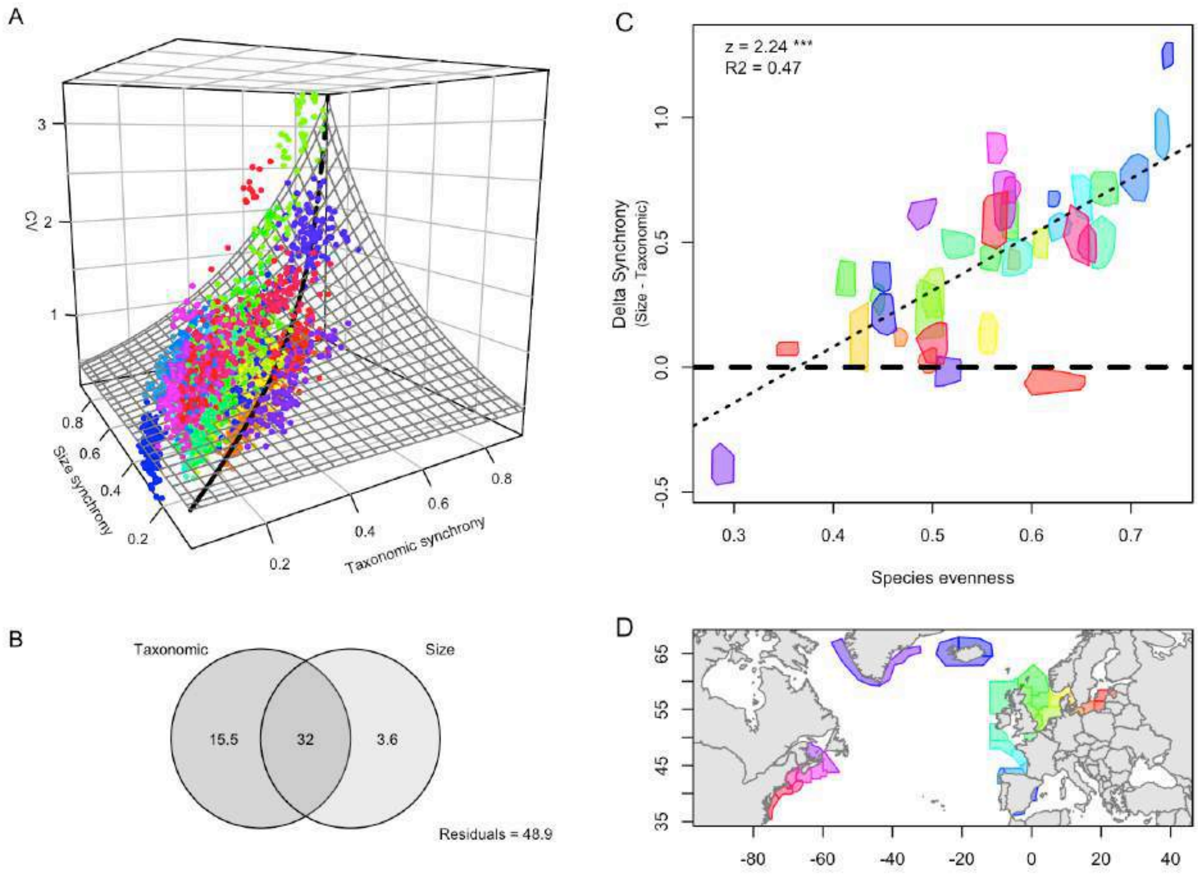


Figure S7.7: Sensitivity to spatial scale – high resolution. Results at fine spatial scales, using 330 rectangles of one-degree longitude and 0.5-degree latitude with at least one haul per year during 20 years. (A) Relationship between size synchrony, taxonomic synchrony and stability (as indicated by CV). Points represent each rectangle. The grey grid is a linear regression modeling the log-transformed CV from the size and taxonomic synchrony including interaction. The dark bold line is the predicted CV when size and taxonomic synchrony are equal. (B) Partition of the variance of log-transformed CV (in %), explained by taxonomic and size synchrony. (C) Relationship between species evenness and the difference between size and taxonomic synchrony. The bold dashed line represents equality between taxonomic and size synchrony while the dotted line is the linear regression calculated from the 100 repetitions. Colours of the dots in (A) and of the polygons in (C) indicate areas, as mapped in (D).

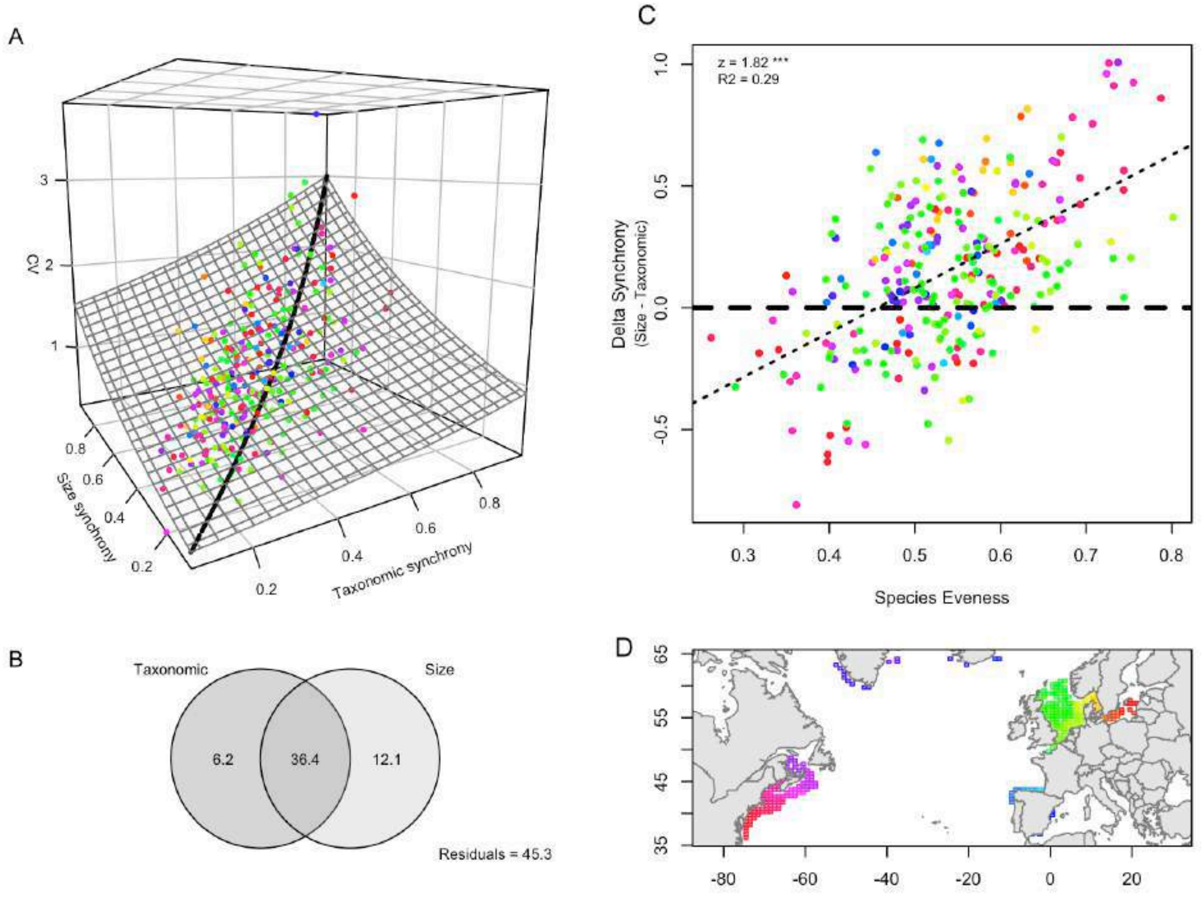
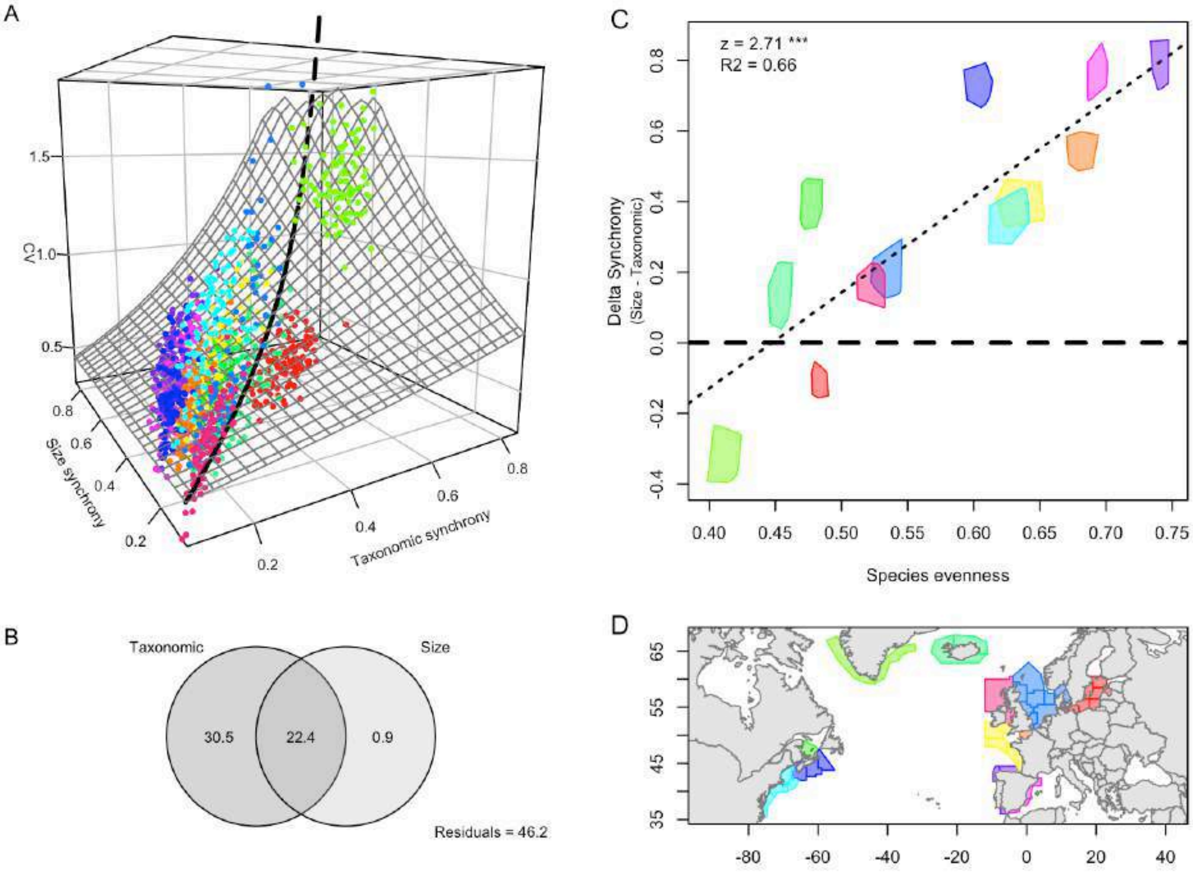


Figure S7.8: Sensitivity to spatial scale – low resolution. Results when merging the abundances per survey (i.e 12 surveys instead of 36 areas). (A) Relationship between size synchrony, taxonomic synchrony and stability (as indicated by CV). Points represent the 100 repetitions for each survey. The grey grid is a linear regression modeling the log-transformed CV from the size and taxonomic synchrony including interaction. The dark bold line is the predicted CV when size and taxonomic synchrony are equal. (B) Partition of the variance of log-transformed CV (in %), explained by taxonomic and size synchrony. (C) Relationship between species evenness and the difference between size and taxonomic synchrony. Polygons represent the variability of results, as indicated by the convex hull of the inter-quartile range of 100 repetitions for each survey. The bold dashed line represents equality between taxonomic and size synchrony while the dotted line is the linear regression calculated from the 100 repetitions. Colours of the dots in (A) and of the polygons in (C) indicate surveys, as mapped in (D).



Chapter 8

General discussion

Sharon Cummings, Under the Sea (2016)
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Summary of the 6 studies

A. How to characterize the spatio-temporal dynamics of species assemblage and identify their external drivers?

In chapter 2, the dynamics of North Sea fish community was analyzed using tensor decomposition. This case study demonstrated the application and benefits of **tensor decomposition for studying community datasets** derived from large-scale monitoring programs. Our results revealed a strong spatial structure persistent over time and linked to differences in depth, primary production and seasonality. Simultaneously, the temporal distribution changes were characterized and related to the low frequency temperature variability inherent in the Atlantic Multidecadal Oscillation. Finally, the fish community was divided in six major sub-communities composed of species sharing similar spatial distribution patterns and temporal dynamics.

In chapter 3, a comprehensive framework based on **complementary multivariate statistical methodologies** was developed to simultaneously investigate the effects of environmental conditions on the spatial, temporal and functional dynamics of species assemblages. The approach revealed the Baltic fish community to be structured into three sub-assemblages along a strong and temporally stable salinity gradient decreasing from West to the East. Additionally, a mismatch between species and functional richness highlighted a lower functional redundancy in the Baltic Proper compared to other sub-areas, suggesting an ecosystem more susceptible to external pressures. Based on a large dataset of community data analyzed in an innovative and comprehensive way, we could **disentangle the effects of environmental changes on the structure of biotic communities.**

B. How does fish functional diversity respond to changing external pressures?

Chapters 3 and 4 investigated the traits-environment relationship with three-matrices multivariate method; respectively at a local and global scale. While traits of fish communities in the Baltic Sea seem to be disconnected to environmental variations (Chapter 3), globally across the Atlantic and Pacific Oceans, the **fast-slow continuum of fish life history was strongly linked to the warm-cold temperature gradient** (Chapter 4). Our results empirically confirm the accelerating effect of temperature on physiological rates by demonstrating a strong spatial association between bottom temperatures and the key response traits, namely growth, maturation and lifespan. Our study demonstrates the benefit of collating datasets from multiple regions to deliver robust results that have strong implications for our understanding and management of marine fish communities and for predicting how fish communities will adapt to a changing climate.

In chapter 5, outline analysis was proposed to characterize fish morphology with quantitative and objective indicators. The elliptical Fourier transform described the shape of 85 fish species found in the North Sea. This approach shows that the main components of morphological diversity is the elongation and development of dorsal, pelvic, and caudal fins. The spatial distribution of morphological diversity decreases along a latitudinal gradient, with higher diversity in the southern part. Compared to species diversity, our results indicate that environmental conditions filter morphological traits in the northern North Sea. **Outline analysis is a powerful approach to provide an objective description of fish morphology** and to improve our understanding of the morphological diversity in marine ecosystems.

C. What is the importance of biodiversity for the stability of ecosystems?

In chapter 6, the **dynamics of the topological structure of the food web** was investigated using a novel methodology, combining time series analysis with ecological network analysis. The structural properties of the fish and macrofauna food web in the German Bight show differences in temporal variability. Our results suggest that food webs may be more stable than the underlying changes in the community composition. Our case study demonstrates the application and benefits of a coupled topology-time series analysis, which is a practical tool to **integrate food webs in management and conservation plans**.

Chapter 7 offers a novel perspective on the **link between stability, species diversity and size structure**, based on more than 50,000 samples from long-term fisheries-independent surveys. Across North Atlantic Large Marine Ecosystems, asynchrony was an important driver of stability in fish assemblages. Additionally, our results indicate that taxonomic synchrony is important when species are even, while size synchrony is more important when assemblages are dominated by few species. Our study provides empirical evidence for the role of species evenness in determining the mechanism by which marine populations maintain community-level stability. In species-poor ecosystems dominated by few large-bodied species, size diversity within species leads to asynchrony among size classes, which contributes to community-level stability. In species-rich ecosystems with evenly abundant species, the asynchrony among species, resulting from diverse responses to external pressure and growth rate, is the main factor of community-level stability.

Embracing complexity

The different chapters of this dissertation can be seen as **pieces of the diversity puzzle**. Biodiversity is a multidimensional concept and each chapter studies different aspects of the complexity of biodiversity dynamics. The successive chapters integrate (i) the interaction between spatial and temporal dynamics (chapter 2 and 3), (ii) the link between traits and environmental changes (chapter 3, 4 and 5), (iii) the trophic interactions between species (chapter 6), and (iv) the intra-specific trait variability, important for the stability of communities (chapter 7). Each chapter stands alone, but together, they convey a stronger message. The chapters are **complementary** and inform each-other. For instance, the absence of morphological traits in the study of traits-environment relationship (chapter 3 and 4) highlights the urgent need for new quantitative traits to characterize the variability of fish morphology (chapter 5). The study of the spatio-temporal dynamics of species assemblages reveals that the spatial variability is stronger than the temporal dynamics in large ecosystems with strong environmental gradient (chapter 2 and 3). This conclusion reinforced the choice of studying the spatial distribution of traits without considering the minor temporal dynamics across large spatial extent (chapter 4 and 5). The temporal dynamics was studied only when reduced to local environment (chapter 6), or by dividing the spatial extent to locally homogenous areas (chapter 7). None of these approaches is better than another, they are all equally important and answer different questions. Together, they **highlight the multiple dimensions of fish diversity dynamics and community stability**.

Ecological systems are complex and have processes interacting **across spatial and temporal scales** (Rose *et al.* 2017; Isbell *et al.* 2017). On one hand, large scale studies are important to provide context because large scale processes constrain and control lower level processes. On the other hand, small scale studies can reveal the details and the mechanisms of processes observed at larger scale (Heffernan *et al.* 2014). The six case studies presented here have **different spatial**

scales (Fig 8.1), from local (a box of 10 by 10 nautical miles in the German Bight, chapter 6) to one single Large Marine Ecosystem (the North Sea, chapters 2 and 5; the Baltic Sea, chapter 3) to multiple Large Marine Ecosystems across seas and oceans (chapters 4 and 7). At local scale, the ecology of each species and its interactions can be studied in great detail, but the results are hardly generalizable. On the contrary, studies across large spatial extent definitely neglect the specific local details but capture the large patterns emerging across ecosystems. Therefore, studies across spatial scales are complementary, and knowledge accumulated at one scale should inform studies at smaller and larger spatial scale.

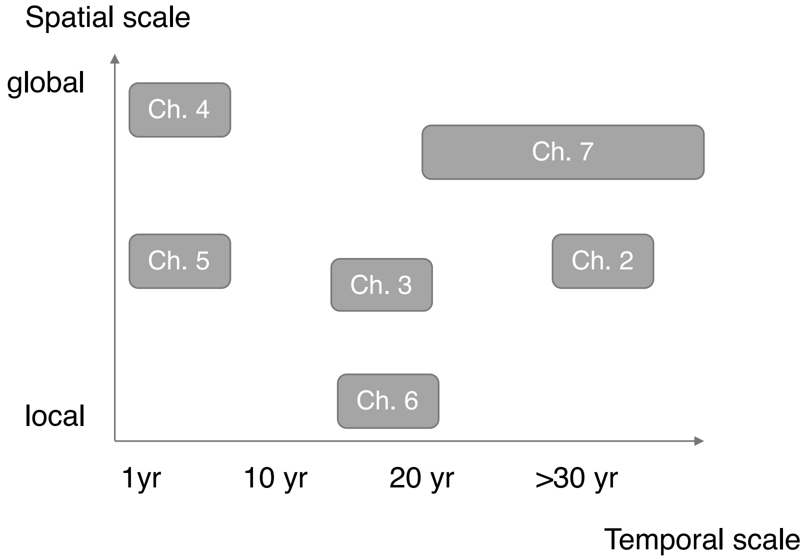

Figure 8.1: Spatial and temporal scales of the 6 case studies. Spatial scales vary from local (a box of 10 by 10 nautical miles in the German Bight, chapter 6 : "Temporal variability of food web topology"), to one single Large Marine Ecosystem (the North Sea, chapter 2 : "Tensor decomposition reveals spatio-temporal community dynamics" and chapter 5: "A morphometric dive into fish diversity"; the Baltic Sea, chapter 3: "3D view on biodiversity changes"), to multiple Large Marine Ecosystems across seas and oceans (chapter 4: "Warm waters favour fast living fish" and chapter 7 "Size asynchrony stabilizes uneven communities"). The temporal scales vary between one year and more than 50 years. Chapter 4 and 5 considers temporally constant communities from annual samplings; chapter 2, 3 and 6 use time series of 31, 16 and 17 years, respectively. Chapter 7 combines dataset across regions with time series of at least 20 years.

Similar cross-scale interactions happen across temporal scales. However, due to limitation of data availability, the temporal extent was limited between one year up to five decades (Fig 8.1). Two chapters considered temporally constant communities from annual samplings (chapters 4 and 5), whereas other chapters were limited to data availability, with less than 20 years in the Baltic Sea and the German Bight (chapters 3 and 6), and more than 20 years in the North Sea and across other Large Marine Ecosystems (chapters 2 and 7). The dynamics of fish was studied only with an annual time step, while seasonal migration are important for the resilience of communities through increase connectivity (Fisher *et al.* 2010; McMeans *et al.* 2015). Similarly, the dynamics of plankton was studied with annual or monthly time step while plankton have a fast and local dynamics. Cross-scale emergence of plankton small scale dynamics might play a major role in the productivity of ecosystems (Stock *et al.* 2017).

Understanding the complexity and the multidimensionality of diversity is a first step toward an integrative management of ecosystems. Thus, all the case studies presented here are relevant for an integrative ecosystem assessment that can provide relevant advices for marine ecosystem-based management (Levin *et al.* 2009).

Implications for the management of marine ecosystems

This dissertation is a modest contribution **towards an integrative understanding of ecosystem processes**, highlighting the importance of the multiple dimensions of fish community dynamics. For example, understanding the link between traits and environment (chapters 3 and 4) is important to understand and predict the impact of changing environmental conditions on the functional diversity of communities. However, these predictions would be incomplete if one doesn't consider the network of interactions between species and the possible cascading effects throughout the food web (chapter 6). Additionally, the intra-specific trait variability (chapter 7) might help communities to adapt to changing conditions. Therefore, integrating the multiple dimensions of diversity is crucial to reveal the interactions and trade-offs in ecosystems.

This thesis is a call to use **novel approaches to look at existing datasets and integrating information from multiple sources**. The six case studies focused on the dynamics of fish assemblages as measured from bottom trawl surveys. Advanced multivariate methods are effective to reduce the inherent complexity of community data and reveal the main spatio-temporal dynamics (chapters 2 and 3). Additionally, community dataset can be combined with information about the traits and life history of fish species from global databases (e.g. Fishbase in chapters 3 and 4) or diet information from literature review (chapter 6). Online images of fish were used to characterized the morphological diversity of fish communities (chapter 5). Moreover, spatio-temporal dynamics of fish communities were linked to external drivers using information from interpolated observations (e.g. Núñez-Riboni & Akimova 2015), reanalysis datasets (e.g. Ferry *et al.* 2012), large scale climate indicators (e.g. Jones *et al.* 1997) and remote sensing (e.g. GlobColour, Maritorena *et al.* 2010) Using novel approaches and combining different dataset into an integrative framework can **provide key information for the management and conservation of ecosystems**.

Communicating and **integrating complexity into management strategy** is challenging. In fact, more accurate but more complex answers to management issues might be too complicated to implement and therefore, less valuable for management (Cochrane 1999). Historically, scientists provided simple answers to simple questions (e.g. how much cod could be sustainably fished next year?); but often failed to predict correctly the ecological consequences of human actions combined with environmental variability (e.g. no scientists predicted accurately the simultaneous collapse of Northern Atlantic cod stocks). Understand the trade-offs between the exploitation of different of marine resources is crucial for a comprehensive marine management. Therefore, integrating more complexity, such as the prey-predatory interactions or the impact of environmental variability on biotic communities, is needed for ecosystem-based marine management and require experts from multiple fields.

Effective ecosystem-based management needs **multi-disciplinary collaboration** (Berkes 2012). One of the main factor omitted in this dissertation is the preponderant human and social dimension of marine socio-ecological systems (Holm *et al.* 2013; Ellis 2015). Human societies, similar to other biological communities, are organized in different hierarchical levels that interacts across spatial and temporal scales (Holling 2001). To give relevant advices for the management of marine resources, scientists need a better understanding of the trade-offs between users of marine resources and the cross-scale interaction between local, regional and international management strategies. Additionally, the fast and large scale changes in species distribution require a dynamic approaches to marine resource management (Lewison et al. 2015; Pinsky et al. 2018).

Multiple scientific approaches to study ecological systems should be encourage and especially the **collaboration between theoretical, experimental and observational sciences**. While this dissertation is only dedicated to observational evidences coming from real-world ecosystem datasets, the exploration and interpretations of empirical data is based on previous theoretical and experimental work. The joint development of theory, experiments and observational analysis is needed to provide strong evidence and inform society about the trade-offs between the ecosystem's health and its exploitation.

A call for open science

Ecosystems are complex, and if humans want to understand the multiple interactions within natural ecosystems, a **long-term global monitoring effort** is needed. The effect of multiple drivers can only be disentangled with long-term time series. Therefore, it is important that monitoring programs have continuous founding schemes and are extended to data-poor regions. Additionally, major scientific advances can only be done if monitoring data are **archived properly and shared openly** in order to combined different sources of information, such as modeled or remotely sensed datasets (Edgar *et al.* 2016). **Global scientific databases** (such as FishBase, the World Register of Marine Species, or the Global Biodiversity Information Facility) are a tremendous source of information for scientists and citizens alike (Costello *et al.* 2018). Such effort to centralize, clean and validate encyclopedic and cumulative knowledge should be encouraged and properly valued. In fact, the work presented here build on dataset shared openly and proves that **innovative statistical methods and open data can provide relevant information for ecology**.

This dissertation builds on the lives of millions of fish killed by scientists on monitoring cruises because it is, so far, the best way to estimate the abundance and diversity of benthic fish communities, as well as their diet and growth. However, innovative solutions could reduce the ecological and monetary costs of monitoring and therefore help increase its spatial and temporal coverage (Hampton *et al.* 2013; Borja *et al.* 2016). Among other solutions, monitoring could build on network of remote sensing devices (Laney *et al.* 2015; Pettorelli *et al.* 2018), autonomous surface or underwater vehicle (Ackleson *et al.* 2017) or citizen science (Dickinson *et al.* 2012; Stuart-Smith *et al.* 2017).

All case studies presented here use datasets that are publicly available online and free softwares to analyze them. The rapid development of machine learning and data mining tools in open source software such as R and Python have encouraged the **uptake of good statistical practices across scientific fields**. The processed dataset and the script used to run the analysis presented in the six previous chapters (2-7) are (or will be) provided as supplementary materials of the published articles. Sharing the scripts allow other scientists to reproduce and verify the analysis, but most importantly, it facilitates the uptake of novel methodologies by colleagues and contribute to the general improvement of statistical robustness in science. When possible, tutorials were developed to facilitate the uptake of the new methods (available online: https://rfrelat.github.io/). These tutorials were used for teaching at the University of Hamburg, at the Leibniz Center for

Tropical Marine Ecology (ZMT) in Bremen, and at the Integrated School of Ocean Sciences at the University of Kiel.

Future perspectives

Despite the important findings of this work, all the different chapters are but pieces of the diversity puzzle. Merging all the pieces together in an **integrative framework** can provide relevant information for the management and conservation of ecosystems. In fact, each chapter is a case study that could be extended to large continental or global scale, in order to provide relevant information for decision makers and management (Heffernan *et al.* 2014; Rose *et al.* 2017; Isbell *et al.* 2017). For example, extending the morphological description of fish using outline analysis (chapter 5) to a larger pool of species could provide a **global spectra of fish morphology across oceans**. Moreover, extending the collection of bottom trawls surveys across different oceans and combining this information with other sampling of fish abundance and diversity (e.g. Reef Life Survey, Stuart-Smith *et al.* 2017) would bring a better understanding of the global processes, and increase our ability to predict in data-poor regions. Additionally, increasing the spatial extent would favour research using the “space for time” approach (Blois *et al.* 2013). Indeed, the predicted future conditions of a given location may be the present conditions of another area, so scientists could use **Climate Analogues to comprehend upcoming changes and challenges of marine ecosystems** (Hallegatte 2009). Most importantly, the combination of these approaches together could bring new insights about the stability mechanism of fish communities. For example, new morphological traits would greatly improve the prediction of trophic interactions between organisms, that will help understanding the variability in the structure of interaction networks, valuable information for the sustainable management of ecosystems. Studying the dynamics of communities from a global perspective considering the multiple dimensions of diversity and the effect of scales on the spatial and temporal dynamics would lead to new exciting challenges and questions.

Embracing the complexity of ecosystem dynamics is **acknowledging the limited scientific knowledge and the high unpredictability of community dynamics**. Even with the best models and dataset, Science will not be able to forecast with precision the short- and long-term consequences of humans’ actions on its environment. Past experiences and models have proved that ecosystems dynamics can have drastic changes, such as regime shifts (Folke *et al.* 2004; Mollmann *et al.* 2014), or ecological surprises (Filbee-Dexter *et al.* 2017). These drastic changes are due to non-linear relationships, feedback loops, and hysteresis. Currently, we are on the verge of a global regime shift with unpredictable consequences (Barnosky *et al.* 2012). Therefore, the only safe and recommendable management option is to follow a precautionary approach (Schindler & Hilborn 2015; Selkoe *et al.* 2015). **Preserving biodiversity is the best management strategy to cope with increased environmental variability and changing climate** (Webster *et al.* 2017). Numerous studies (including this dissertation) show the importance of biodiversity for human well-being, and the current anthropogenic pressure on ecosystems might lead to drastic changes in diversity that would be difficult or impossible to reverse (Barnosky *et al.* 2012). It is urgent that society, as a whole, take actions to preserve the biodiversity, in all its dimension, which is the most effective way to help ecosystems adapt to ongoing and future changes.

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Outline of publications

Chapter 2:

Frelat R., Lindegren M., Dencker T.S., Floeter J., Fock H.O., Sguotti C., Stäbler M., Otto S.A. and Möllmann C. (2017) Community ecology in 3D: Tensor decomposition reveals spatio-temporal dynamics of large ecological communities. *PlosOne,* 12(11): e0188205. DOI 10.1371/journal.pone.0188205

RF, ML and CM designed the study, RF collated the data, made the statistical analysis and wrote the first draft of the manuscript, and all authors discussed results and contributed substantially to the manuscript.

Chapter 3:

Frelat R., Orio A., Casini M., Lehmann A., Mérigot B., Otto S.A., Sguotti C. and Möllmann C. (2018). "A three-dimensional view on biodiversity changes: spatial, temporal and functional perspectives on fish communities in the Baltic Sea", ICES Journal of Marine Science, *in press* DOI 10.1093/icesjms/fsy027

RF and CM conceived the ideas and designed methodology; AL provided the modeled environmental data, RF collated the data, analyzed the data and led the writing of the manuscript. All authors contributed ideas for the interpretation of the data and the critical revision of the manuscript. All authors gave final approval for publication.

Chapter 4:

Beukhof E., **Frelat R.**, Pécuchet L., Maureaud A., Dencker T.S., Sólmundsson J., Fock H., Punzon A., Primicerio R., Hidalgo M., Möllmann C. and Lindegren M. "Warm waters favour fast living fish – evidence from big data across oceans". *in prep.*

EB and RF contributed equally to this study. EB, RF and ML conceived the ideas and designed methodology, E.B., R.F., L.P., H.F., J.S., A.P., T.S.D and A.M. collated the data. E.B. and R.F. performed the analyses. E.B., R.F. and M.L. wrote the first draft of the manuscript, whereas all other authors contributed ideas for the interpretation of the analyses and revised the manuscript. All authors gave final approval for publication.

Chapter 5:

Caillon F., Bonhomme V., Möllmann C. and **Frelat R.** (2018). "A morphometric dive into fish diversity", Ecosphere, 9(5): e02220. DOI 10.1002/ecs2.2220

RF conceived the ideas and designed methodology; FC collected the data; FC, VB and RF analyzed the data; FC and RF led the writing of the manuscript. All authors contributed ideas for the interpretation of the data and the critical revision of the manuscript. All authors gave final approval for publication.

Chapter 6:

Olivier P., **Frelat R.**, Bonsdorff E., Kortsch S., Kröncke I., Möllmann C., Neumann H., Sell A.F., Nordström M.C., "From community dynamics to temporal variability of food web topology: an empirical exploration of the structural dynamics of fish and benthic macrofauna in the German Bight". *in prep.*

PO and RF contributed equally to this study. PO, RF and MCN conceived the original ideas and designed methodology; PO, IK, HN and AFS collected the data; PO and RF analyzed the data and prepared the figures; PO wrote the first draft of the manuscript. All authors contributed ideas for the interpretation of the data and the critical revision of the manuscript. All authors gave final approval for publication.

Chapter 7:

Frelat R., Hidalgo M. Auber A., Fock H.O., Garcia C., Lucey S.M., McLean M., Mills K.E., Punzón A., Ricard D., Shackell N.L., Sólmundsson J., Stortini C., and Möllmann C., "Does community size structure influence the diversity-stability relationship? Empirical evidence from fish communities across large marine ecosystems." *Submitted to Ecology Letters*

RF, MH and CM designed the study, MH, AA, HOF, CG, SML, MM, KEM, AP, DR, NLS, JS, CS provided the dataset and assisted on the proper handling and cleaning of the data, RF collated the data, made the statistical analysis and wrote the first draft of the manuscript, and all authors discussed results and contributed substantially to the manuscript.

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Eidesstattliche Versicherung / Declaration on oath

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hamburg, 5 November 2018

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cen
Center for Earth Systems Research
and Sustainability

Prof. PhD. Myron A. Peck
Institute of Hydrobiology and
Fisheries Science
Olbersweg 24 • D-22767 •
Hamburg
Tel +49 4042 838 6602
Fax +49 4042 838 6618
myron.peck@uni-hamburg.de

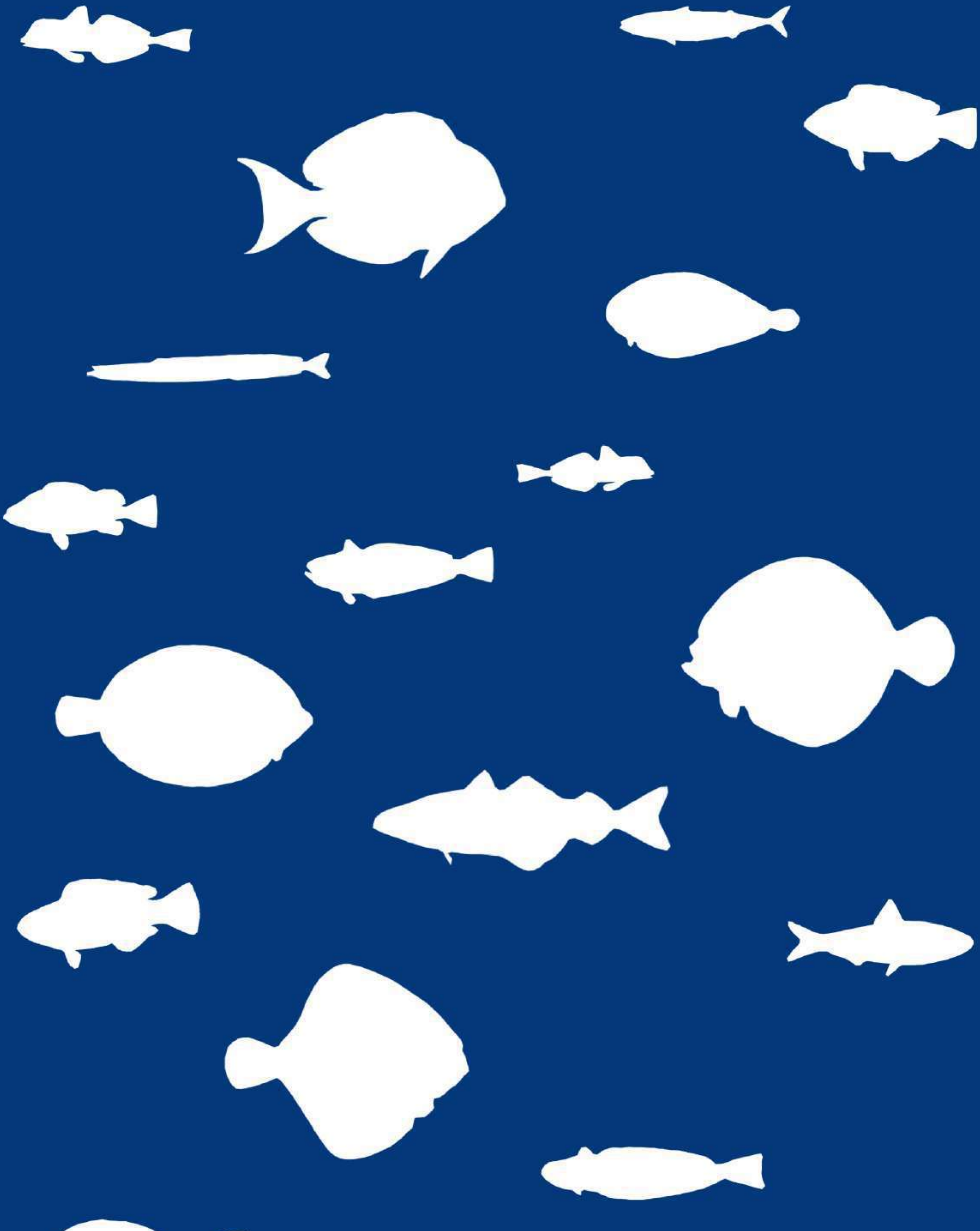
Universität Hamburg
Biozentrum Klein Flottbek
Studienbüro Biologie
z. H. Frau Sült-Wüpping
Ohnhorststr. 18
22609 Hamburg

Dear Frau Sült-Wüpping

I have briefly reviewed the thesis "The multiple dimensions of fish diversity dynamics and community stability" written by Romain Frelat. The thesis is written in English. As a native English speaker, I can attest that the writing (grammar and syntax) is acceptable. The English writing is of sufficient quality to move forward with the submission and review process.

Sincerely,

Prof. Myron A. Peck



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