Do traits follow taxonomy? Biodiversity and community assembly in marine ecosystems

Dencker, Tim Spaanheden

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Do traits follow taxonomy? Biodiversity and community assembly in marine ecosystems

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Tim Spaanheden Dencker
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Supervisors:

Martin Lindegren
Mark R. Payne
Peter Grønkjær
Preface

This thesis was submitted as part of the requirements to fulfil the Doctor of Philosophy Degree (PhD) at the Technical University of Denmark (DTU). The research presented in the thesis was carried out at the Centre for Ocean Life under the National Institute for Aquatic Resources (DTU Aqua) between September 2015 and February 2019 under supervision by Dr. Martin Lindegren (DTU Aqua), Dr. Mark R. Payne (DTU Aqua) and Dr. Peter Grønkjær (Aarhus University). In addition, two external research stays were carried out at Rutgers University, USA, in collaboration with Dr. Malin Pinsky and his research group, and at Oldenburg University, Germany, in collaboration with Dr. Helmut Hillebrand and Dr. Dorothee Hodapp.

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Kongens Lyngby, February 27

Tim Spaanheden Dencker

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Acknowledgements

"To cope alone and unaided with a subject so vast, so complex, and so infinitely mysterious as the sea would be a task not only cheerless but impossible, and I have not attempted it."
Rachel L. Carson, The Sea Around Us, 1951.

Even though a single name appears on the front cover of this thesis, I owe gratitude and thanks to several people who have contributed their time and energy in one way or another over the last three years to help me arrive at this point. First, Martin Lindegren for supporting me in every possible way throughout my time at DTU Aqua. Your enthusiasm and passion have been contagious, and you have shown me not only how to conduct science, but also how to balance a life in science. A great deal of appreciation for Mark R. Payne as well. Your knowledge and clear analytical mind have helped me when I have struggled with statistical analyses or coding. A thanks goes out to Peter Grønkjær as well.

Throughout my time at the Centre for Ocean Life and DTU Aqua, I have been fortunate to work with a fantastic group of people. I will especially look back with fondness on the times spent with friends and colleagues in Martin Lindegren’s group, including Aurore, Esther, Neil, Anna, Laurene, Daniel and Jeremy. Our constant discussing and chatting, peaking over computer screens to share code, trait references and bounce ideas off each other will forever be an academic highlight of mine. It has been a privilege working with all of you on multiple collaborations and projects. To Mridul for being a kindred spirit when it came to having discussions outside our little bubble of trait-based sciences. To Lillian and Chris, two wonderful colleagues and people, who have helped me with countless tiny, yet challenging problems.

A PhD has a way of seeping into every crevice of one’s life, and I owe my friends and family a great deal. To Sannyas, the best place to call home; to Ross, Peter, Ole, and Martin, I have a deep gratitude for your friendships; to Theis and Signe, your relationship, friendship and love is inspirational, and you have been solid anchors for the last three years. Bjørn and Frode, one day I will explain everything in this thesis to you. For now, it will have to be a boring bedtime story. Last, but not least, my mother and father for supporting me whenever I have faltered. I could not have done this without you!
Abstract

More than 2/3 of the Earth’s surface is covered by oceans, encompassing vast environmental gradients and variability in habitats. Thousands of species inhabit this seemingly endless space, yet we know surprisingly little about its stunning diversity, how it is shaped, assembled and structured. Consequently, understanding these mechanisms and how they vary in space and time is a key objective in ecology. These questions have traditionally been approached with a species-centric focus. However, this taxonomic approach is inherently limited, as the mere presence of a species reveals little to nothing about why the species is present and able to persist. Instead, species can be characterized by their traits, describing phenotypical characteristics that determine the species’ response to environmental conditions, its interactions in a food web and ultimately its effect on ecosystem functioning. This trait-based approach has emerged as a promising field of research allowing for a more causal and mechanistic understanding of marine biodiversity and ecosystems. In this thesis, I have explored marine demersal (bottom-living) fish communities across spatial and temporal scales in the North Atlantic and Northeast Pacific with regard to patterns and trends in biodiversity, community assembly processes, and environmental and anthropogenic drivers.

Structuring of communities has been suggested to follow deterministic processes associated with responses to abiotic factors (environmental filtering) and interactions with other species (limiting similarity). An interplay between these two assembly processes shape and maintain community compositions. We used spatially and temporally resolved survey data on species abundances and traits to investigate temporal spatial patterns of species and trait diversity and the underlying community assembly mechanisms in the North Sea. Our results show that overall temporal trends in species richness and trait richness were highly correlated but varied considerably in space, indicating different degrees of either environmental filtering and limiting similarity acting on community assembly at local scales in the North Sea.

In addition to deterministic assembly processes, communities can be structured by neutral, stochastic processes, such as dispersal, speciation, ecological drift and local extinctions. Deterministic and neutral theories have been considered antithetic to each other, despite a common historical origin. To study the effect and relative importance of these assembly processes acting on community composition across spatial scales we compiled a unique high-resolution dataset of scientific bottom-
trawl surveys from the North Atlantic and North-east Pacific, encompassing geo-referenced occurrences and abundances of >1000 species along with information on six life-history traits. Total taxonomic and trait beta-diversity, demonstrating the degree of similarity in species and trait composition between communities was calculated and compared at multiple spatial scales. Overall, our results show that both taxonomic and trait beta-diversity were mainly driven by deterministic assembly processes, primarily channeled through environmental filtering along gradients relating to temperature, depth and available energy.

Human activities have left a considerable footprint on marine ecosystems worldwide with ensuing biodiversity loss at global scales. Halting further loss require quality assessment of biodiversity changes and consensus on how to measure such change. We tracked multiple components of biodiversity across time in seven marine ecosystems from both Atlantic and Pacific oceans, incorporating species, abundance and trait information for ~600 species. Despite no systematic trend in species richness over time, we observed significant directional changes in species identities and abundance structures over both short and long time-scales, while trait compositions remained relatively stable. These changes were linked to biotic homogenization, suggesting biotic impoverishment at local scales over time.

The research presented in this thesis emphasizes the need to incorporate multiple components of biodiversity in spatial and temporal assessments of community changes and community assembly processes. The results are not only relevant for ecology research. The trait-based approach applied in this thesis provides important information furthering our mechanistic understanding and predictive capabilities; for use in research-based conservation and ecosystem-based management; and ultimately increasing our chances of halting further loss of biodiversity.

Struktureringen af de biotiske dele af økosystemer er blevet foreslået at følge deterministiske processer, hvor artssammensætning er afgjort af miljøet og interaktionen med andre arter. Vi undersøgte graden, hvormed disse deterministiske processer påvirker biodiversiteten i Nordsøen. Både arts- og karakterrigdommen steg i Nordsøen over den undersøgte årrække og havde spatiale mønstre, der indikerede, at graden mellem miljøpåvirkning og interaktion mellem arter varierede på lokal-spatial skala.

Som kontrast til disse deterministiske processer, bliver økologiske samfund også struktureret i forhold til neutrale, stokastiske mekanismer, hvor arters tilstedeværelse i et økosystem er defineret af processer som spredning af æg og larver, artsdannelse og uddøen. Disse processer udgør fundamentet i en mere neutral forklaringsmodel for økosystemers sammensætning. Ud fra et datasæt med mere end 1000 fiskearter og deres karaktertræk i Nordatlanten og Stillehavet undersøgte vi hvorledes fiskesamfund varierede på tværs og på langs af de Nordamerikanske og Nordeuropæiske økosystemer, både i arter og karaktertræk. Karaktertræk varierede mindre langs disse spatiale
gradienter, hvilket tyder på, at miljøvariabler, der selekterer for visse karaktertræk i økosystemer har høj grad af kongruens på tværs af økosystemer, mens artssammensætningen samtidig kan variere. Endvidere konkluderer vi, at fiskesamfundene i høj grad er struktureret efter deterministiske processer med stor påvirkning af temperaturgradienter, habitatdiversitet og tilgængelig energi.

Menneskelige aktiviteter har påvirket samtlige marine økosystemer, hvilket har ført til tab af biodiversitet på globalt plan. Internationale og regionale politiske tiltag byder lande, at stoppe nedgangen i biodiversitet. Dog beror disse indsatser på målemetoder, der ikke nødvendigvis afspejler samtlige underlæggende ændringer i økosystemerne. Det mest anvendte mål for biodiversitet, artsrigdommen, er blevet kritiseret for at være utilstrækkeligt, og man burde i højere grad monitorere andre former for biodiversitet for at få en dybere forståelse af, hvilke dele af økosystemerne, der er påvirket og går tabt. I det tredje studie i denne PhD-afhandling afdækkede jeg de temporale skift i økosystemer gennem fire årter ud fra arters tilstedeværelse, abundans og karaktertræk. Til trods for ingen systematiske ændringer i artsrigdommen var samtlige økosystemer forandret over tidsperioden, når vi tog højde for sammensætningen af arter, deres abundans. Endvidere var lokale økosystemer blevet mere ens i forhold til hinanden, hvilket tydede på et fald i den lokale biotiske unikhed over tid.

Forskningen præsenteret i denne PhD-afhandling underbygger argumentet om at anvende både arter og deres karaktertræk for at opnå en dybere forståelse for de mekanismer, der strukturerer de marine økosystemer gennem tid og rum. Sådan en viden er uundværlig for at øge kvaliteten og effektiviteten af politiske tiltag, der har til mål at stoppe nedgangen i biodiversitet.
List of included research manuscripts and dissemination at conferences

Appended first-author and equal-authorship manuscripts


2. **Tim Spaanheden Dencker**, Aurore Maureaud, Malin Pinsky, Martin Lindegren. *Large-scale patterns and drivers of marine beta-diversity shed light on the underlying processes of community assembly across latitudes*

3. **Tim Spaanheden Dencker**, Helmut Hillebrand, Dorothee Hodapp, Martin Lindegren. *Beyond species richness - turnover, traits and abundances reveal important temporal community changes*


Appended abstracts of co-authored papers

1. Esther Beukhof, **Tim Spaanheden Dencker**, Laurene Pecuchet and Martin Lindegren. *Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change.* (Published in MEPS https://doi.org/10.3354/meps12826)


3. Aurore Maureaud, Dorothee Hodapp, Pieter Daniël van Denderen, Helmut Hillebrand, Henrik Gislason ,**Tim Spaanheden Dencker**, Esther Beukhof, Martin Lindegren. *Testing the biodiversity-ecosystem functioning concept in the ocean: fish biomass is driven by evenness, not by species richness.* In review


6. Matthew McLean, David Mouillot, Eric Goberville, Martin Lindegren, Georg Engelhard, **Tim Spaanheden Dencker**, Tarek Hattab, Arnaud Auber *Unraveling the underlying processes of community thermal shifts*. *In prep*

Conference dissemination


## Contents

1 General Introduction ................................................................................................................. 1
   1.1 Biological diversity ............................................................................................................ 1
      1.1.1 History and definitions ............................................................................................. 1
      1.1.2 Standardization ......................................................................................................... 3
      1.1.3 Measuring biological diversity .................................................................................... 5
      1.1.4 What to apply where? ............................................................................................... 9
   1.2 Traits in biodiversity and ecology ..................................................................................... 10
      1.2.1 Applications ............................................................................................................. 10
      1.2.2 Selecting key traits ..................................................................................................... 12
      1.2.3 Intraspecific variability ............................................................................................. 14
   1.3 Community assembly rules ............................................................................................... 15
   1.4 Marine ecosystems .......................................................................................................... 17
      1.4.1 Data availability ......................................................................................................... 17
      1.4.2 Anthropogenic pressures ........................................................................................... 18
   1.5 Aim of the thesis .............................................................................................................. 21

2 Synopsis .................................................................................................................................. 32
   2.1 Alpha-diversity and community assembly rules in the North Sea .................................. 32
   2.2 Beta-diversity and community assembly rules along latitudinal gradients ..................... 33
   2.3 Community changes beyond species richness ................................................................. 35
   2.4 Trait information for demersal fish .................................................................................. 36

3 General discussion .................................................................................................................. 40
   3.1 Traits in diversity – diversity in traits ............................................................................... 40
   3.2 Trait-based biogeography .................................................................................................. 43
   3.3 Community changes and conservation ............................................................................ 44

4 Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: Causes and consequences ................................................................................. 49
   4.1 Introduction ....................................................................................................................... 51
   4.2 Materials & Methods ....................................................................................................... 54
   4.3 Results ............................................................................................................................... 60
   4.4 Discussion ......................................................................................................................... 64

5 Large-scale patterns and drivers of marine beta-diversity shed light on the underlying processes of community assembly across latitudes ........................................................................... 87
   5.1 Introduction ....................................................................................................................... 89
   5.2 Materials & Methods ....................................................................................................... 92
   5.3 Results ............................................................................................................................... 99
   5.4 Discussion ......................................................................................................................... 105
6 Beyond species richness - turnover, traits and abundances reveal important temporal community changes ................................................................. 130
   6.1 Introduction ................................................................................................. 132
   6.2 Material & methods ..................................................................................... 134
   6.3 Results ......................................................................................................... 138
   6.4 Discussion .................................................................................................... 145

7 A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas .............................................................. 168
   7.1 Background and summary ............................................................................ 169
   7.2 Spatial coverage .......................................................................................... 169
   7.3 Taxonomic coverage .................................................................................... 169
   7.4 Traits ............................................................................................................ 169
   7.5 Trait extraction procedure .......................................................................... 178
   7.6 Missing trait values ...................................................................................... 179

Appendix ................................................................................................................ 181
   8.1 Appendix A Beukhof et al. 2018 (accepted) .................................................... 181
   8.2 Appendix B Beukhof et al. (in prep) .............................................................. 182
   8.3 Appendix C Maureaud et al. (in review) ....................................................... 183
   8.4 Appendix D Frelat et al. 2017 (accepted) ....................................................... 184
   8.5 Appendix E Visser et al. (in prep) ................................................................. 185
   8.6 Appendix F McClean et al. (in prep) ............................................................. 186
1.1 Biological diversity

1.1.1 History and definitions

Life on Earth is heterogeneously distributed and is characterized by a striking variation in the
number of species, abundances of individuals, traits and evolutionary history in both space and
time. This variation has intrigued and puzzled researchers for centuries (von Humboldt &
Bonpland 1805, Von Humboldt 1849). Undoubtedly, this fascination goes beyond modern
history and is today encapsulated by the concept of “biological diversity”, forming the focal
point for entire research fields such as biogeography and macroecology. As noted in Magurran
(2004), the use of the term “biological diversity” dates back to papers, such as Gerbilskii &
Petrunkevitch (1955) and Whiteside & Harmsworth (1967). However, the first mentions of the
term were used to describe specific research topics and not as an attempt to describe the broader
concept of biological diversity. This description first appeared in Norse et al. (1986), where the
concept of biological diversity was dissected into its individual components describing
variation within and between species and between communities.

While the term “biological diversity” is used widely within the scientific literature, the
abbreviated version “biodiversity” has gained widespread popularity both within research,
media and the general public (Magurran 2004). Both terms are now used almost entirely
interchangeably. The shorter term, biodiversity, was coined in 1985 at the planning of the 1986
National Forum on BioDiversity and in the following book by E. O. Wilson (Wilson 1988,
Magurran 2004). However, already by 1992, Knopf (1992) noted that the definitions of
biodiversity are "…as diverse as the biological resource", and DeLong (1996) reviewed more
than 85 different definitions in 1996.
Biological diversity is most often defined as proposed by The United Nations Environment Programme (UNEP) (Heywood et al. 1995):

"Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species between species and of ecosystems”

The UNEP definition was later adapted into the Convention of Biological Diversity in 1992 (CBD 2014), yet many researchers have suggested more simple and rigorous definitions before and since, with perhaps the simplest being related simply to the number of species and potentially also their relative abundances (Magurran 2004).

Figure 1: Graphical presentation of the hierarchical organization of ecosystems. Individuals of a species form populations; populations of different species make up the units of communities, and different communities together with abiotic components form ecosystems. The UNEP definition of biological diversity encapsulates all these different levels.

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1 However, some confusion may arise when including ecosystems, which inherently have an abiotic component to them, in a definition of the variation of strictly biotic components.
For this thesis, the definition suggested by Magurran (2004), “the variety and abundance of species in a defined unit of study” is used as a starting point. However, as will hopefully become evident throughout this thesis, despite species being the most common currency in studies of biological diversity, additional ecological insights may be gained from examining information on species’ morphological, physiological and life-history traits.

1.1.2 Standardization

Studies of biological diversity often constitute comparative research, where some measure of diversity is calculated and compared between two or more spatially or temporally segregated sites. While this may seem like an intuitive exercise, the quality, and ultimately the usefulness, of such a comparison hinges on several criteria. Two of these criteria are the standardization of scale and sampling effort. The dynamics of both of these criteria are captured by the relationship between the area sampled and the estimated species richness, known as the species-area relationship (Connor & McCoy 2001). This relationship predicts that as the size of area of investigation \( A \) increases, so does species richness \( S \) and is considered one of the fundamental “laws” in ecology (Schoener 1976, Lomolino 2000). This relationship may be caused by multiple mechanisms, such as indirect effects from habitat diversity or more direct effects such as edge effects or decreased risk of extinction in larger areas (Connor & McCoy 2001). The practical consequence of this relationship means that sampling units of comparison should have roughly equal area as to investigate dynamics at similar scale.

The next relationship between area sampled and biodiversity is described by the scaling of species richness as a function of sampling effort within defined sampling units. As sampling effort (e.g., area covered or time spent sampling) increases, an increasing proportion of the true underlying species pool is sampled. This means that the number of species observed in a single sample is likely not representative of the true underlying species richness of the sampled community (Magurran 2004). Visualization of sampling effort and estimation of the true number of species are achieved through species-accumulation curves (SACs), where number of species is a function of sampling effort. The curve will increase monotonically, approaching a limiting asymptote as sufficient sampling is undertaken (Gotelli & Colwell 2011). However, even in smaller areas or areas of extensive sampling, complete sampling of the biological diversity is often not achieved (Chao et al. 2009) and complete sampling can be prohibitively
laborious (Lawton et al. 1998). In order to estimate the total number of species in an area, asymptotic mathematical functions (e.g., a Michaelis-Menten function; (Keating & Quinn 1998)) can be fitted to an existing SAC, after which extrapolation to the asymptote of the function (Figure 2) can be achieved. As an extension of this method, knowing the estimated richness of an area allows one to gauge whether the performed sampling effort has been sufficient and to standardize sampling effort between sampling units. In situations where a high degree of sampling effort heterogeneity exists, simply counting the number of species present in the samples may provide incomparable values of species richness. While it may seem intuitive to then standardize the number of samples between sampling areas, rather, standardization of sampling effort should rely on fixing “completeness”, expressed as a percentage of the estimated species richness (Chao & Jost 2012).

Figure 2: Species accumulation curve for a site: Black solid line indicates the observed increase in identified species as a function of increased number of samples. Teal dashed line is the estimated increase in species richness from extrapolation. The asymptotic species richness is denoted as $S_{\text{max (estimated)}}$.

In addition to the abovementioned uses of standardization via species-area relationships, Gotelli and Colwell (Gotelli & Colwell 2011) note that a set of assumptions is inherent to the use of SACs in order to compare species richness or sampling effort completeness between sample units. These assumptions include sufficient sampling to achieve statistical power; standardization of sampling gear and protocols across samples and sampling units as to avoid biases; taxonomic similarity in assemblages sampled; and independent and random samples.
1.1.3 Measuring biological diversity

So far, the focus has been on assessing and standardizing the sampling as to make measures of biodiversity comparable. Through the species-area relationship it becomes evident that species richness will increase as more area is sampled until an entire region, continent or the total biosphere has been covered. However, the acceleration of increase in species richness will depend on the differentiation in species identities between the areas sampled and as such, it becomes important to measure similarity/dissimilarity between sampling areas. R. H. Whitaker recognized how the scaling relationship between area-specific biodiversity and differentiation between areas determine the overall regional species richness in 1960 (Whittaker 1960) and coined the three levels of organization $\alpha$-, $\beta$- and $\gamma$-diversity, with $\alpha$- and $\gamma$-diversity being point-specific diversity at local and regional scale respectively, while $\beta$-diversity expresses the level of differentiation between areas. The scaling relationship is most simply captured by a multiplicative approach where $\beta$-diversity is defined as the ration between $\gamma$ and $\alpha$ (Figure 3).

![Figure 3: Graphical representation on the relationship between $\alpha$-diversity, $\gamma$-diversity and $\beta$-diversity.](image)

The shape of the species-area relationship depends on the differentiation ($\beta$-diversity) between communities, and as such, $\beta$-diversity links the two different scales of $\alpha$-diversity and $\gamma$-diversity. In A, no differentiation in species identity (low $\beta$-diversity) exists between communities 1-3 and no increase in $\alpha$-diversity is observed as increasing area is sampled. In B, communities 1-3 all contain 5 unique species (high $\beta$-diversity). Consequently the species-area relationship exhibits a positive trend.

While Whittaker introduced a more extensive hierarchy of scales at which biodiversity can be assessed (Whittaker 1972), $\alpha$-diversity and $\beta$-diversity have become the most widely used (Jurasinski et al. 2009) and both levels of biodiversity are the focus of chapters included in this thesis.
1.1 Biological diversity

**α-diversity**

α-diversity is most often synonymous with biodiversity, and biodiversity is in turn regularly equated with species richness. However, the biodiversity of an area is characterized not only by its number of species, but also by the frequency with which the species can be found. As such, α-diversity becomes a two-dimensional concept, describing both species richness and the abundance distribution. Indices have been developed to capture each dimension separately and jointly.

Species richness indices focus solely on capturing a measure of the number of species present in an area. While seemingly the most easily quantifiable metric, species richness is highly sampling sensitive as outlined in the previous chapters on standardization. Several methods have been developed to correct for this sensitivity in order to derive comparable measures of estimated species richness (see Walther & Martin 2001, Magurran 2004, Walther & Moore 2005) for extensive reviews). Species richness is also highly sensitive to the detection of rare species thereby increasing variability in observed species numbers when samples are repeated from the same ecosystem (Gotelli & Colwell 2011). More importantly, species richness provides no information about species identity nor relative abundance. For these reasons species richness measures have been criticized for being ecologically uninformative and treating abundant and rare species equally (Gotelli & Chao 2013).

Indices describing the relative abundances of species in sampling units convey information on the evenness or dominance structures within communities. Thus, a community in which species are equally abundant is characterized by a high degree of evenness, while communities dominated by one or a few species with relatively high abundance are deemed to have low evenness (i.e., high dominance) (Pielou 1977). The degree of evenness (or dominance) in a system can be used as an additional dimension to separate areas of interest and ecological dynamics, and has repeatedly been shown to complement measures of species richness with new information (Stirling & Wilsey 2001, Wilsey et al. 2005). Some of the most often used indices of evenness include Pielou’s evenness (Pielou 1966) or Simpson’s evenness (Simpson 1949). The estimation of biodiversity can also rely on joint metrics, where species richness and evenness effects are combined into a single measure. Some of the most widely used joint
1.1 Biological diversity

metrics are the Shannon and the Simpson’s Index (Magurran 2004). Such metrics are not the focus of this thesis, and extensive reviews are presented in (Jost 2007, Magurran & McGill 2011, Morris et al. 2014).

Figure 4: $\alpha$-diversity is a two-dimensional concept, encapsulating both the number of species present (species richness) and the relative abundance distribution of those species (species evenness). Communities can be characterized by these two dimensions. Community 1 and 2 both have five species (equal species richness), but differ in the relative abundance distribution (different species evenness). Community 1 is characterized by relatively low evenness/high dominance of a single species, while Community 2 is characterized by high evenness/low dominance as all species have equal abundance. Redrawn from bioninja.com.au.

$\beta$-diversity

Assessing the degree of heterogeneity between samples as a measure of biodiversity has been suggested numerous times (Peirce 1884, Jaccard 1901), but $\beta$-diversity was conceptualized within a framework and defined by Whittaker in his seminal work as “the extent of change in community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments” (Whittaker 1960, 1972). In the last decades, studies on $\beta$-diversity have increased drastically (Anderson et al. 2011) and the concept is now widely used in a variety of studies, ranging from community assembly rules (Jones et al. 2008, Moura et al. 2017, Mori et al. 2018), biogeography (Smit et al. 2017, Holt et al. 2018) and conservation (Socolar et al. 2016).
β-diversity has been described as “… a key concept for understanding the functioning of ecosystems, for the conservation of biodiversity, and for ecosystem management.” (Legendre et al. 2005) and may be important in explaining local biodiversity changes (Cardinale et al. 2018, Primack et al. 2018, Hillebrand et al. 2018). Just as with α-diversity, β-diversity can be partitioned into two components as heterogeneity between samples can be contributed to differences in species identity or the number of species (Baselga 2010) (Figure 5). It has long been recognized that β-diversity is composed of these two antithetic components, coined turnover and nestedness (Baselga 2010). Despite recent disputes over the interpretation of the framework (Schmera & Podani 2011, Legendre 2014, Baselga & Leprieur 2015), it is still crucial to distinguish between the two components of β-diversity as they may inform about different ecological processes (Soininen et al. 2017). Turnover between communities is related to mechanisms of endemism at various spatial scales (Baselga 2010), such as habitat heterogeneity, dispersal mechanisms and rates of speciation (Condit 2002, Baselga et al. 2012). Nestedness, on the other hand, may be more related to ordered nested habitats, environmental filtering, and selective extinction-recolonization events along gradients (Ulrich & Gotelli 2009).

Figure 5: Schematic representation of turnover and nestedness components of β-diversity. β-diversity can be driven by changes in species identity (turnover) and differences in species richness (nestedness) between two communities if one or more species identities are shared between communities. A→B: β-diversity driven entirely by nestedness. A→C: β-diversity driven by both nestedness and turnover. A→D: β-diversity driven entirely by turnover, as there is no species richness difference. A→E: β-diversity driven entirely by turnover. The species richness difference will not contribute to nestedness, as no species identities are shared. Redrawn from Baselga (2010).
1.1.4 What to apply where?
As is evident, assessing biodiversity is both a question of what and how to measure. Indices of $\alpha$-diversity and $\beta$-diversity can be applied to several tiers within a hierarchical framework going from individuals to communities, from sampling units to biogeographical regions. Several authors have attempted to link concepts of $\alpha$-diversity and $\beta$-diversity to specific ecological or geographical, delineated units. Pielou (1967) and Loreau (2000) tied $\alpha$-diversity inherently to communities, while Whittaker (Whittaker 1972) and Gray (2000) set up tiered frameworks, linking different facets of biodiversity to ever-increasing geographical scales. It has been argued that such a link is problematic due to challenges in delineating ecological units, such as populations and communities or clear geographical boundaries of habitats and ecosystems (Strayer et al. 2003). As argued in Magurran (2004), while it may be problematic to link measures of biodiversity to specific ecological or geographical boundaries, it bids researchers to consider and define the scale at which the research is being conducted. The work of this thesis is focused on comparing biodiversity within and between marine demersal fish communities across both space and time at multiple scales, going from hemisphere to local dynamics.

A consensus on how to define a community has not yet been reached, but typically a community is defined as an assemblage consisting of populations of different species within a given area, where its constituents are linked by biotic interactions (Magurran 2004, Levin et al. 2009). Describing the biodiversity within and between communities has been done at great length, ranging from investigations of small scale dynamics (Teagle et al. 2018), global biogeographical patterns (Tittensor et al. 2010), community responses to disturbances (van Denderen et al. 2014), and community assembly rules (Pecuchet et al. 2016) to the effects of community composition on ecosystem functioning (Gamfeldt et al. 2015). However, up until recently, most investigations have used only taxonomic information, and even then, most often, biodiversity has been equated with species richness (Balvanera et al. 2006). Taxonomic measures assume that all species contribute equally to the measure, and that species biomass is the only differentiating characteristic between species (Magurran 2004). Yet, the ecological impact of a species is not always correlated to its numerical presence in a community, as evident from the concept of keystone species (Power et al. 1996). Furthermore, species differ in their
importance for specific ecosystem processes and functioning (Lefcheck & Duffy 2015) or their strategies under different abiotic conditions (Grime 1974, Pecuchet et al. 2017). In recognition of these properties, communities are now often characterized by their composition of traits in addition to taxonomic composition.

1.2 Traits in biodiversity and ecology
Classification of species into groups based on their characteristics dates back centuries (Weiher et al. 1999, Wilkins 2009), and ecology as a research field is inherently about describing structure of and interactions within communities mediated through traits (Mlambo 2014). In order to gain ecological insights about species’ roles and importance for ecosystem processes and functions, researchers have increasingly started incorporating information on species traits as an alternative or complement to taxonomy-based measures of biodiversity (Swenson et al. 2011, Cheng et al. 2014, Törnroos et al. 2014, Toussaint et al. 2016). A trait is often defined as morphological, physiological or phenological characteristics of an individual (McGill, Enquist, et al. 2006, Violle et al. 2007, Reiss et al. 2009). Traits of an organism influence its environmental tolerances and habitat requirements, and thus determine under which environmental conditions the organism can live (Violle & Jiang 2009); how it interacts with other individuals within the community (Werner & Peacor 2003); and its contributions to ecosystem processes and functions, such as nutrient use (Tilman 1997, Reiss et al. 2009, Flöder & Hillebrand 2012).

1.2.1 Applications
Quantification of trait variation and the use of multi-trait biodiversity metrics have become more prominent as awareness of the influence species’ traits have on community structuring and functions increases (Cadotte et al. 2011). The so-called “trait-based approach” to community ecology and biodiversity has been adopted into several fields of research (Kiørboe et al. 2018). Trait structures, rather than taxonomy, have been shown to predict trophic interactions and food web topology (Laigle et al. 2018), and Pécuchet et al. (2018) and Törnroos et al. (2018) showed that trait variation varied predictably between different trophic levels in marine ecosystems. A trait-based approach has allowed researchers to investigate niche satisfaction and redundancy within communities and linking these properties to increased
1.2 Traits in biodiversity and ecology

resilience of ecosystems to invasions (Arenas et al. 2006, Vaz-Pinto et al. 2013) and perturbations (Martins et al. 2012, Mori et al. 2013). Lefcheck and Duffy (2015) and Duffy et al. (2016) found that trait biodiversity measures were better predictors of community biomass, linking properties of the community to ecosystem services. In general, investigations of trait-biodiversity have shown that this dimension of communities may reveal more mechanistic and causal relationships between environmental change, biodiversity and ecosystem functioning (McGill, Enquist, et al. 2006).

The field of biogeography has traditionally been grounded in the species concept (Davies et al. 2011, Holt et al. 2013, Violle et al. 2014) and has indeed treated each species as a qualitative entity. However, Violle et al. (2014) have called for the “... analysis of the patterns, causes, and consequences of the geographic distribution of the diversity of form and function—namely, trait diversity”. So far, studies have shown that the taxonomic and trait biodiversity may however be decoupled across spatial scales (Devictor et al. 2010, Villéger et al. 2012, Stuart-Smith et al. 2013, Wiedmann et al. 2014, Brun et al. 2016, Pécuchet et al. 2016, Dencker et al. 2017, Holt et al. 2018) and investigations of both single traits (Brun et al. 2016, Beukhof et al. 2019) and multivariate trait-indices (Stuart-Smith et al. 2013) have revealed new biogeographical patterns. Understanding patterns of trait diversity in relation to environmental gradients may shed light on the processes that shape ecological communities and allow for detection and quantification of the underlying assembly rules (Lamanna et al. 2014, Holt et al. 2018) (covered in section 1.3). Conservation research and efforts have also increasingly started to use trait-based approaches in order to inform protection efforts (Bremner 2008) or elucidate mismatches between placement of protected areas and intended protection purposes (Lindegrén et al. 2018).

Adaptation of a trait-based approach into many different fields has prompted the development of multiple conceptual and methodological frameworks in order to accommodate the aims of the specific research in question (Botta-Dukat 2005, Mason et al. 2005, Petchey & Gaston 2006, Laliberte & Legendre 2010, Mouchet et al. 2010, Schleuter et al. 2010, Villéger et al. 2012, Podani et al. 2013, Mouillot et al. 2014). As is the case with species diversity, it has been argued that trait diversity can be dissected into independent components of richness and properties of the abundance distribution (Mason et al. 2005). Mason et al. (2005) presented this framework
based on a single axis of variation (i.e., a single trait), while Villéger et al. (2008) expanded the concept to allow for incorporation of multiple axes (i.e., multiple traits) into a $n$-dimensional trait-space, where $n$ is equal to the number of traits included. Trait richness is then expressed as the range of trait values present in the community, either along a single trait axis (Mason et al. 2005) or as the degree of trait space (i.e., hypervolume) occupied by the community. This index is the equivalent to species richness (Villéger et al. 2008). Describing the abundance distribution of species amongst considered traits can be achieved by considering trait evenness (Mason et al. 2005). Trait evenness, as with species evenness, describes the degree of skewness in abundance distributions towards either even or uneven tendencies across traits (Villéger et al. 2008).

### 1.2.2 Selecting key traits

Despite disagreements surrounding the concept of a species (Agapow et al. 2004), species are routinely used as the operational/discrete units of analyses in ecology. In trait-based biodiversity studies the species is defined by a single or numerous traits, and as such, it becomes important to not only define what constitutes a trait, but also which traits to be included in an analysis.

According to Violle et al. (2007) a trait is defined as “…any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level”. Litchman et al. (2013) put this concept into a Darwinian framework, positing that a trait should be viewed through the key “missions of life”, namely surviving, feeding and reproducing. Success within anyone of these missions affects the fitness of the individual and so the definition of a trait can be expanded and defined as the phenotypic characteristics of an organism that affect its performance and fitness (Litchman et al. 2013). This definition opens up for a seemingly endless number of traits, and it is important to define key traits in relation to both the research focus in question and its taxonomic scope (Lavorel & Garnier 2002). Traits relating to predator-prey interactions and food web topology (Gravel et al. 2016) may be different from traits used to describe life history strategies (Winemiller et al. 2015), or ecological roles and niches of species (Mouillot et al. 2005, Winemiller et al. 2015). Likewise, traits which directly influences a species’ response to environmental gradients or changes
(Ferreira et al. 2007) are different from those used to describe the contribution of species to specific ecosystem functions (Granberg et al. 2008).

The usefulness of trait-based biodiversity metrics is dependent on not only the trait selection, but also on the number of traits included. Certain trait-based measures are sensitive to the number of traits included, making interpretation difficult if too few or too many are included (Schleuter et al. 2010). The number of traits to be included is often viewed as a balance between capturing a sufficient degree of differentiation between species, while also not including so many traits as to effectively simply mirror species diversity (Schleuter et al. 2010, Lefcheck et al. 2015). Recently, Laughlin (2014) and Eklöf (2013) showed that between 3-5 traits were sufficient to characterize plant communities and species interaction networks, while Pecuchet et al. (2017) used six traits to adequately capture variation of life history strategies in demersal fish communities across European shelf seas. Certain traits co-vary naturally in ecosystems (Beukhof et al. 2019), however, correlations between traits used in a given study pose another challenge for analytical approaches and may further encumber interpretations of results (Villéger et al. 2008). Trait correlations can be reduced by using techniques such as like principal coordinates analysis (Villéger et al. 2008, 2013, Laliberte & Legendre 2010).

A priori selection of traits depends on several criteria (Petchey & Gaston 2006, Lefcheck et al. 2015). A critical first step is to select only traits relevant to the task at hand. Such a selection is influenced by a clearly defined research question, the taxonomic scope of the study, and understanding the links between traits, and between traits and environmental drivers. Investigations of trait-based diversity in marine fish communities often rely on an assumed relationship between the set of traits selected and ecosystem functioning (Stuart-Smith et al. 2013, Wiedmann et al. 2014, Duffy et al. 2016). This assumed relationship forms the justification for incorporation of traits into indices of biodiversity (McGill, Enquist, et al. 2006) and has led to the coining of the terms “functional trait” and “functional diversity”. While the importance of traits in relation to ecosystem functioning has been thoroughly established (Tilman 2001), this mechanistic relationship is seldom stated nor tested specifically in multi-trait studies of biodiversity, and with the increased popularity of incorporating traits into biodiversity, the definitions of functional traits and functional diversity have become ambiguous and have received criticism (Violle et al. 2007, Mlambo 2014, Fontana et al. 2016).
While the term ‘functional diversity’ has gained widespread use and is accepted in the scientific literature, we prefer the use of the term ‘trait diversity’, when no direct link between the selected traits and a specific ecosystem function or processes is established. This consideration is resonated in Fontana et al. (2016).

The focus of this thesis was not to capture dynamics between biodiversity and ecosystem functioning, but rather to investigate taxonomic and trait biogeographical patterns and community changes over temporal and spatial scales. Such patterns and changes are potentially strongly linked to environmental conditions, and the selection of traits in chapters 5 and 6 is reflected in this consideration. This trait composition-environment link has been established for fish through life history strategies models, where suites of traits are modelled and understood as responses to constraining abiotic environmental gradients (Winemiller & Rose 1992, Winemiller et al. 2015). The strategies emerge from a theoretical model aggregating variation of traits into three overall ecological modes: equilibrium, periodic and opportunistic. Equilibrium species are characterized by long life-spans, few offspring with high survival rate; opportunistic species are characterized by short generation time, low offspring survival and batch spawning, while, lastly, periodic species are characterized by small eggs, low offspring survival and high fecundity (Winemiller & Rose 1992, Pecuchet et al. 2017). The emergent life history strategies have been shown to be closely linked to variation in environmental conditions, and their prevalence shifts along environmental gradients in both freshwater (Mims et al. 2010) and marine ecosystems across Northwest and Northeast Atlantic shelf seas (Fisher et al. 2011, Pecuchet et al. 2017), making them a suitable framework for the selection of traits to be used in studies of community changes and community assembly rules (Winemiller & Rose 1992).

1.2.3 Intraspecific variability

Variability in traits is not only expressed between species but also within species. In most studies of trait-variation in communities mean values of traits are assigned to species (McGill, Enquist, et al. 2006). Such averaging occurs in spite of research showing that intraspecific trait variation is an important factor in elucidating community assembly dynamics (Hoffmann et al. 2010, Jung et al. 2010), stabilizing community fluctuations (Wood et al. 2017) and play an important role in coexistence (MacArthur & Levins 1967). The incorporation of intraspecific variability is however debated. Albert et al. (2012) showed that the statistical effects of
1.3 Community assembly rules

Understanding which mechanisms govern the assembly processes of communities is a fundamental challenge in ecology. Disentangling these different mechanisms is not only important for ecology alone, but may also provide insight into how communities might respond to future environmental change. Central to the development of assembly rules theory is Robert H. MacArthur’s theories on limiting similarity, competition and coexistence (MacArthur & Levins 1967) and on island biogeography (MacArthur & Wilson 1963). The former theory explains species diversity patterns from species trait-environment relationships for predicting species niches (Chase & Myers 2011), while the latter predicts communities on islands as an interaction between processes, such as colonization and extinction, and properties, such as island size and distance from more regional species pools (Chase & Myers 2011). The development of these two theories is tied to the two contemporary perspectives on how communities assemble: niche theory and neutral theory (Hubbell 2001, Chase & Myers 2011, Kraft et al. 2015).

Niche theory is centered around a “filtering” concept (Weiher et al. 2011), where community structure is a result of filtering steps through an interplay of species interactions with their environment and each other (Kraft et al. 2015) (Figure 6). The strength of these “filters” will ultimately predict the composition of the community. The first filter relates to the selection of species from a regional species pool that can survive under prevailing abiotic (i.e., environmental filtering). This filter is suggested to lead to convergence of trait values amongst species due to common adaptations to the abiotic conditions. The second filter is suggested to cause trait dispersion between coexisting species by minimizing niche overlap due to resource competition (MacArthur & Levins 1967). The strength of such assembly processes on
community assemble can then be assessed by analyzing the trait composition among observed species (Mouillot et al. 2007, Lebrija-Trejos et al. 2010, Spasojevic & Suding 2012, Kraft et al. 2015). Deterministic community assembly rules are considered in the first and second study of this thesis (chapter 4 and 5).

![Conceptual schematic of two assembly theories: neutral theory and niche theory. Community structure under neutral theory is governed by processes, such as colonization through dispersal and immigration, random extinctions and speciation. Niche theory predicts community structure based on filtering mechanisms, where species are filtered by environmental conditions via niche-requirements (environmental filtering) and by species-interactions, where niche-overlaps are diminished (limiting similarity). Redrawn from (Mouillot et al. 2007)](image)

Niche-based theories are linked to the differentiation of niches between species via their traits. Antithetic to niche theory, Hubbell’s neutral theory (Hubbell 2001) posits that communities can be structured according to processes such as dispersal limitation, random ecological drift, extinction and speciation (Chase & Myers 2011) (Figure 6). The emphasis of dispersal, and a balance between extinction and speciation tie Hubbell’s neutral theory to the concept of island biogeography of MacArthur, where species are not differentiated by traits and niche preferences (Chase & Myers 2011). Despite a common historical ancestry (i.e., Robert H. MacArthur and colleagues), the theories of niche-based and neutral assembly have been considered antithetic to each other for decades (Dornelas et al. 2006, McGill, Maurer, et al. 2006, Chase & Myers 2011). This division is now lessening, and it is increasingly recognized that the two assembly...
1.4 Marine ecosystems

More than 2/3 of the Earth’s surface is covered by oceans, encompassing vast environmental gradients and variability in habitats. Estimates of total species richness in marine ecosystems range from 300,000 (Costello et al. 2011) to >10,000,000 (Grassle & Maciolek 1992). While most studies from the last decade estimate global marine species richness to be below 2,000,000 species, estimates are not converging (Caley et al. 2014). This apparent lack of agreement partly stems from estimation methods, yet even similar methods may diverge in estimates (Appeltans et al. 2012, table 1). Overall, Appeltans et al. (2012) conclude that 1/3 to 2/3 of marine species remain to be described.

Despite uncertainties in the total number of species in the oceans, specific taxonomic groups have been well-sampled. Fish represent one of the most sampled groups with around 75% to 80% of the estimated species richness already known (Mora et al. 2008, 2011, Appeltans et al. 2012). More than 16,000 species of fish are described globally (Appeltans et al. 2012), making it the most speciose vertebrate group. In addition, fish are present in every marine habitat. These factors make fish a well-suited taxonomic group for use in studies of biogeographical patterns and community assembly processes.

1.4.1 Data availability

Any kind of assessment, either quantitative or qualitative, of biodiversity relies on “…knowing what, where, and when species are present” (Costello, Basher, et al. 2017). Sampling of marine ecosystems are more laborious, logistically difficult and more costly compared to sampling of terrestrial ecosystems, making marine data on species, traits and environmental variables less accessible. Despite such challenges, long-term data sets with standardized sampling schemes are increasingly made publicly available (ICES 2015, trawlData package, OBIS, REEF Life surveys). Especially standardized bottom trawl survey data are often used in studies of marine
1.4 Marine ecosystems

ecosystems. While initially focusing on commercially important fish species, these trawl surveys now target a wider fraction of demersal and pelagic fish communities, allowing for analyses of temporal and spatial trends in community composition (Perry et al. 2005, Pécuchet et al. 2016, Batt et al. 2017). Important datasets are however still publically unavailable and can only be utilized after contact with national fisheries research institutes (Costello, Basher, et al. 2017). Studies in this thesis contain distribution and abundance data from both publically available and access-restricted datasets from multiple sources.

With the upsurge of trait-based approaches in community ecology studies from local to global scale, utilization of traits also becomes a question of availability. Obtaining complete information across the desired traits in multi-trait analyses and for the taxonomic scope of the study may not always be possible (Stuart-Smith et al. 2013, Wiedmann et al. 2014, Pécuchet et al. 2016, Dencker et al. 2017). The final trait coverage in studies is therefore often a compromise between desired and available trait information, and a subset of the initial taxonomic scope. It remains unclear what consequences such data gaps and compromises may have for the ecological conclusions drawn in trait-based studies of biodiversity, though measures of trait-based biodiversity have been shown to be sensitive to missing trait information and changes in taxonomic scope (Schleuter et al. 2010, Pakeman 2014, Májeková et al. 2016). Just as it is with trawl survey data, trait data is increasingly coalesced from primary literature of smaller scale into large-scale databases (e.g. Fishbase (Froese & Pauly 2015)) or regional-scale reports covering the full taxonomy of a region accompanied by extensive records of morphological, physiological and life-history trait information (e.g. The Barents Sea Fish Atlas and The North Sea Fish Atlas (Wienerroither et al. 2011, Heessen et al. 2015)).

1.4.2 Anthropogenic pressures

Marine ecosystems exhibit natural variation in biotic and abiotic components, such as prey availability, temperature and salinity. Species have adapted to this variability and community compositions reflect past and present biotic and abiotic gradients and connectivity (Clarke & Crame 2010). In addition to this natural variability, marine communities experience a multitude of stressors of anthropogenic origin. All marine ecosystems are affected by multiple anthropogenic stressors (Halpern et al. 2008) and very little untouched marine nature remains (Halpern et al. 2008, Jones et al. 2018). Individually and cumulatively, these anthropogenic
stressors affect the different levels of organization in ecosystems, ranging from individual and genetic changes to ecosystem functioning.

**Climate change**

Marine communities experience variation in temperature regimes on seasonal (Sims et al. 2004) to multi-decadal (Kerr 2000) and evolutionary time scales (Clarke 1990), affecting phenologies (Kuczynski et al. 2017), migration patterns (Sims et al. 2004), fish stock-recruitment relationships (Akimova et al. 2016) and ultimately community compositions and biogeographical patterns of marine species (Tittensor et al. 2010, Pinsky et al. 2013, Costello, Tsai, et al. 2017). Indeed, changes in community structure is increasingly understood by investigating the effects of temperature variability in space and time (Garcia et al. 2018, Waldock et al. 2018).

Global anthropogenic emissions of greenhouse gases have increased steadily since the beginning of the industrial revolution (Pachauri et al. 2014), exceeding atmospheric CO$_2$-concentrations of 400 ppm (Bala 2013). The increased levels of greenhouse gases have significantly contributed to excessive heat trapping. A large fraction (~84%) of the total extra heating of the Earth system over the last 40 years has been trapped by the oceans (Levitus et al. 2005), contributing to significant long-term increases in mean temperatures in both surface and deep-sea water masses (Kaplan et al. 1998, Purkey & Johnson 2010, Wijffels et al. 2016). In addition to widespread ocean warming, physical changes as a result of climate change include increasing frequencies of extreme events (Stott 2016), changes in sea level (Nerem et al. 2018), decreased sea ice extent (Gagné et al. 2015), and increased thermal stratification (Roxy et al. 2016). The effects of these temperature-related changes are already observed across marine communities in shelf seas, with changes to trophic structures (Rijnsdorp et al. 2009, Goberville et al. 2014), shifts in warm-water and cold-water species abundances (Engelhard et al. 2011, Frainer et al. 2017), changes in predator-prey interactions (Langbehn & Varpe 2017), reshuffling (Poloczanska et al. 2013, Cheung et al. 2013) and homogenization (Magurran et al. 2015) of taxonomic and trait composition in coastal ecosystems. Expected increases in atmospheric content of greenhouse gases are predicted to further change marine ecosystems dynamics and community compositions at local and global scales (Cheung et al. 2009).
Fishing

The effects of climate change are part of a complex system of multiple stressors that have already compounded marine ecosystems and altered marine biodiversity (Planque et al. 2010, Harvey et al. 2013, Engelhard et al. 2014, Worm & Lotze 2016). A significant component of this multi-stressor systems is fishing (Jackson 2001). Globally, 90% of fish stocks are fished at their biologically sustainable level or beyond, while ~33% are fished unsustainably (FAO 2018). Such fishing pressures not only have consequences for stock health and potential landings, but also affect marine ecosystems from genetic to community levels. All fishing is non-random in what individuals are removed from the populations (Heino et al. 2015) and fishing pressure may induce changes in life-history traits such as maturation, reproduction and growth, and shifts in the size spectrum of communities (Enberg et al. 2012, Heino et al. 2015).

Community-level responses to fishing are well-documented (Thurstan et al. 2010, Cardinale et al. 2015). Historically, fishing pressure has decreased abundance levels of large consumer species globally (Jackson 2001), and historical records document marine communities characterized by significantly larger species and individuals compared to present-day communities (Wolff 2000, Bennema & Rijnsdorp 2015). Elasmobranchs, characterized by slow growth, late maturation and low fecundity, are especially susceptible to fishing pressure (Quetglas et al. 2016) and populations sizes have indeed declined in coastal regions (Ward-Paige et al. 2012, Sguotti et al. 2016). The removal and depletion of large-bodied species and individuals have cascading consequences for marine systems (Myers et al. 2007). Shifting fisheries to lower trophic levels and subsequent declines in forage fish abundances reduces food-availability for higher-trophic level animals, affecting population dynamics in seabirds and marine mammals (Cury et al. 2011, Smith et al. 2011, Koehn et al. 2017). While, globally, fish stocks are still under immense pressure from fishing, regional stocks are recovering in certain areas, such as the European shelf, where EU fisheries regulations have led to more sustainable fishing (Fernandes & Cook 2013), with following increases in large-bodied individuals (Engelhard et al. 2015). Yet, what we perceive as “recovered” may be far from historical levels (i.e., shifting baseline syndrome) (Pauly 1995, Pinnegar & Engelhard 2008, Soga & Gaston 2018).
1.5 Aim of the thesis

The overarching aim of this thesis is to identify biogeographical patterns of biodiversity and understand the key drivers and underlying assembly processes explaining the pronounced variability in multiple dimensions of marine fish diversity in both space and time. To follow this aim, we compiled scientific bottom trawl data from multiple survey campaigns with considerable temporal and spatial resolution from the Northern Hemisphere. Additionally, we collected trait data for more than 1700 fish species, covering important life history traits.

In the first paper (chapter 4), we investigate spatial and temporal trends in four widely used $\alpha$-diversity indices using both taxonomy and traits for the North Sea fish fauna. The observed trends are then linked to community assembly rules with the use of null-models and correlated to environmental and anthropogenic drivers.

The second paper (chapter 5) focuses on longitudinal and latitudinal differences in taxonomic and trait $\beta$-diversity along Pacific and Atlantic coastlines. $\beta$-diversity is partitioned into its turnover and nestedness component, and overall $\beta$-diversity is related to neutral and deterministic assembly rules.

Temporal trends of species richness at local scales have shown no clear signal of biodiversity loss. Rather, many studies have reported no significant trends or significant increasing trends in local richness. Our third study (chapter 6) investigates temporal trends in community biodiversity across the northern hemisphere, focusing on species richness and turnover metrics of both taxonomy and traits, emphasizing considerable structural changes in communities in addition to biotic homogenization.

The last paper of the thesis (chapter 7) involves the trait data collected and used in the various studies presented. Summary figures are presented and briefly discussed.
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2.1 Alpha-diversity and community assembly rules in the North Sea

Biodiversity is not limited to the variation of species, and ecological traits are increasingly being incorporated into studies as a complement to taxonomy (Villéger et al. 2008, Mouchet et al. 2010, Mindel et al. 2016, Oliveira et al. 2016). However, the two biodiversity components may be decoupled in time and space (Devictor et al. 2010, Parravicini et al. 2014, Törnroos et al. 2014). Temporal and spatial mismatches indicate that different components of biodiversity may respond differently to perturbations, and that changes in one component might happen independently of the other. The relationship between taxonomic and trait diversity may also be used to infer the strength of different community assembly processes (Mouillot et al. 2007). Under considerable environmental strain, the abiotic conditions of an ecosystem may act as filter, allowing only a subset of species with similar traits to persist, while strong biotic effects, such as competition, will drive differentiation in traits to prevent niche overlaps between species (MacArthur & Levins 1967, Mouillot et al. 2007). Furthermore, ecosystems defined by low redundancy of traits across the species pool may be more impacted by environmental change, as species contributing disproportionally more to the trait diversity may be lost.

The North Sea represents one of the most well-studied large marine ecosystems, but also one of the most heavily impacted by anthropogenic pressures, such as climate change and fishing (Halpern et al. 2008). We used distribution and CPUE data for demersal fish species from the North Sea International Bottom Trawl Survey (NS-IBTS) from 1983 to 2014. 77 species with complete trait information across eight traits were found across 9401 unique hauls in 119 ICES rectangles.

We examined the tempo-spatial patterns of multiple marine biodiversity metrics and related these to environmental drivers. Species and trait richness increased significantly during the temporal span of the study. These increases were linked to increases in Lusitanian ‘warm-water’ species immigrating into the North Sea, contributing with new traits formerly not present. Northern increases in species richness did however not contribute with new traits to the same
degree as species immigrating into the North Sea via the English Channel and the Southern Bight. Species and trait richness partly overlapped spatially in the western and northern North Sea, though not in the central and eastern areas near the Norwegian Trench. The spatial incongruences between the distributions of taxonomic and trait richness were compared with a null model constructed from randomization of the species pool per ICES rectangle. This allowed us to disentangle the contributions of underlying deterministic community assembly processes relating to environmental filtering and limiting similarity. The central North Sea was characterized by overdispersion of traits, potentially linked to limiting similarity, while the southeastern and northern North Sea were mainly driven by environmental filtering. The observed spatial patterns of biodiversity metrics were closely linked to abiotic drivers, with depth, temperature, habitat heterogeneity and fishing effort being of high importance. Our findings show that tempo-spatial dynamics of multiple dimensions of biodiversity can be decoupled from each other, and that investigating such differences may further our understanding of community assembly processes in the North Sea, but also inform conservation and ecosystem-based management purposes.

2.2 Beta-diversity and community assembly rules along latitudinal gradients

Consistent biogeographical patterns in biodiversity exist across altitudes, depths and latitudes in terrestrial and marine realms (Hillebrand 2004, Gaston & Blackburn 2008, Tittensor et al. 2010). Underlying these patterns is the continuous addition and loss of species, forming a mosaic of communities which all differ in composition. Shedding light on the differences between these communities may help elucidate which mechanisms structure biological communities (Svenning et al. 2011, Mori et al. 2018).

We compiled data from 18 scientific bottom trawl surveys covering subtropical to arctic shelf seas from both the Pacific and Atlantic oceans with a temporal span of more than 40 years. By including ~1000 demersal fish species and six life history traits, we investigated spatial patterns of $\beta$-diversity and underlying drivers and community assembly rules. Both taxonomic and trait $\beta$-diversity were separated into its nestedness and turnover components at hemisphere, regional and local scales allowing to tease apart the contribution of species richness differences (nestedness) and replacement of species (turnover). These two antithetic components of $\beta$-
diversity are driven by different processes and may indicate important structuring mechanisms of biodiversity. Our results show that traits were significantly more nested between communities than taxonomy both between and along coastlines, suggesting trait convergence, potentially linked to environmental constrains selecting for similar life history strategies despite taxonomic differences. We used a modified version of traditional distance-based redundancy analysis in combination with variation partitioning in order to evaluate contributions of spatial and environmental gradients to β-diversity. Redundancy analysis allows for an assessment of how much of observed differences between communities may be due to spatial distances, hinting at neutral theory assembly mechanisms, and environmental gradients, suggesting niche-base theory. Both taxonomic and trait β-diversity were mainly driven by environmental gradients, signifying that species and traits follow the predictions of niche-theory more than neutral theory. However, a proportion of both taxonomic and trait β-diversity were linked to pure spatial distances between sites, suggesting that mechanisms from both neutral and niche theory may be acting on communities simultaneously.

Finally, variation partitioning on environmental gradients showed that community differences were influenced by variation in temperature, bathymetry and available energy at coarse biogeographical scales. The major environmental determinants were consistent between coastlines and taxonomic and trait β-diversity. The contribution of thermal-related gradients to β-diversity was in accordance with previous studies expressing the significance of temperature for community composition. A considerable degree of variation in β-diversity was explained jointly by bathymetry and available energy suggesting that biomass reaching the seabed where it enters demersal and benthic energy pathways may be important for structuring demersal communities.

In summary, our study provide evidence for the role of environmental filtering in structuring communities along latitudinal gradients and sheds light on the mechanisms underlying the large-scale biogeographical patterns, such as the latitudinal diversity gradient. The incorporation of traits and separation of total β-diversity into its nestedness and turnover components added new information on biogeographical patterns and their drivers, important for a more mechanistic understanding of biodiversity.
2.3 Community changes beyond species richness

Marine communities have adapted to the natural fluctuations in abiotic and biotic conditions in ecosystems over time and space. However, multiple stressors in the form of overfishing, pollution, climate change and habitat destruction (Halpern et al. 2008, Jones et al. 2018) are now pushing ecosystems beyond this natural variability, affecting community structures (Lotze et al. 2006, Engelhard et al. 2014). The magnitude of change in ecosystems and biodiversity has led to the coining of the term “global biodiversity crisis” (Driscoll et al. 2018). This crisis is often equated with declines in species numbers, and it is estimated that species are lost at rates 10-1000 times higher than the background rate of extinction (Pimm et al. 2014, Ceballos et al. 2015). Recently, however, studies have found increasing or neutral trends in species richness at regional or local scales, arguing that species richness is a poor metric of community change, and that the biodiversity crisis goes beyond net species richness changes. Instead, the focus should be shifted towards underlying gross changes in communities (Dornelas et al. 2014, Vellend et al. 2017, Hillebrand et al. 2018). Correct assessment of biodiversity changes over time and space is paramount to conservation and management.

In this study, we investigate temporal changes in community structure in seven marine ecosystems focusing on occurrence, abundance and traits of demersal fish species. We use long-term temporal bottom trawl survey data of marine fish from both the North-East Pacific and the North Atlantic. Additionally, an extensive trait data set is utilized to incorporate information on important life history traits of fish. Species accumulation curves are used to standardize sampling effort across grid cells to ensure comparable representations of the underlying communities. Net change in species richness at regional and local scale is investigated, and we calculate gross changes, tracking immigrations and local extinctions between years in order to calculate turnover metrics of the community. In addition to occurrence-based turnover, we incorporate abundances and traits of species, allowing us to assess changes in both taxonomic and trait structure of the communities. These changes are tracked on an annual basis, and over time, as change might accumulate over the survey period. Last, we investigate the degree of biotic homogenization across spatial scales for each year for each survey region.
We found predominantly increasing long-term temporal trends in species richness, at regional and local scales. Annual gross changes in immigrations and local extinctions in community structure varied considerable, even at low or no net change in the number of species. These gross changes were evident both in species composition, species abundance structures and traits. Short-term turnover changes in either component of biodiversity were uncorrelated, showing that changes in one component can happen without being detectable in other. Changes in community composition and abundance structure accumulated with increasing temporal distance between years, yet trait composition remained relatively stable. We found pronounced biotic homogenization for four out of seven survey regions, signifying that community are losing their “uniqueness”.

Our results indicate that community change is not restricted to net changes in species richness, but also evident in multiple components of biodiversity, including abundance structures and traits. We argue that species richness as a metric falls short of capturing community dynamics, and as such, should be complemented by assessments of other biodiversity components to gain a more realistic gauge of community change. In this regard, utilizing both abundance and trait data may provide important, and otherwise undetected, information of turnover in communities.

2.4 Trait information for demersal fish

As the trait-based approach to biodiversity and community analysis becomes more prevalent, the need for available and extensive trait data increases. While trait information has been collected for numerous marine species, the information is spread across individual papers or gathered in online repositories, such as Fishbase (Froese & Pauly 2015), which may be difficult to compile for use in multi-trait studies. In chapter 7 we collected information for 14 morphological, physiological and life-history traits for 1702 unique species of marine fish covering 801 genera and 236 families in the Northeast Pacific, Northwest Atlantic and Northeast Atlantic shelf seas and made it available in an easy to read and ready to use format.

The trait dataset is based on fish taxa observed during international bottom trawl surveys. While these scientific surveys mainly targets demersal (bottom-dwelling) fish species, pelagic species are regularly caught and sampled as well. The goal of this dataset was to collect information on ecological traits for as many fish taxa as possible and to find area-specific trait values in order
to account for intraspecific variation in traits, especially for widely distributed species. The majority of trait values come from Fishbase (Froese & Pauly 2015) and have been supplemented with values from primary literature.


Chapter 3

General discussion

The research presented in this thesis is centered around the use of a trait-based approach to study patterns of biodiversity and the mechanisms shaping and maintaining the structure of biological communities. I have applied this approach across multiple components of biodiversity and in multiple marine ecosystems across oceans basins and latitudes. In order to further the integration of traits into biodiversity research, I will discuss recent advancements, limitations and future directions of a trait-based approach. In particular regarding the selection of traits, approaches for moving towards a more mechanistic understanding of biogeography and ecosystem structuring, and implications for conservation and management.

3.1 Traits in diversity – diversity in traits

As the trait-based approach is increasingly applied in community ecology and studies of biodiversity its advantages have become clear, yet certain pitfalls and challenges remain. As an ecological trait is defined as any phenotypic (i.e., morphological, physiological, behavioral) characteristic that is related to the fitness and performance of an organism (McGill et al. 2006, Violle et al. 2007), it becomes evident that any measurable characteristic of an organism can be defined as a trait. Thus an organism can be described by a near-infinite number of characteristics, which ultimately risks failing one of the main motifs of incorporating traits in ecology: to reach a simpler, yet thorough understanding of the processes underpinning communities and ecosystems by the use of a few key traits (Kiørboe et al. 2018). This emphasizes the critical importance of trait selection in ecological analyses. Certain traits, such as size, have been identified to be taxa-transcending due to their significant and consistent impact on the ecology of an organism (Andersen et al. 2016) and indeed are often used in studies of trait biodiversity and community structure. Yet many traits find relevance only in certain scenarios, making the selection of traits question and context dependent (Violle et al. 2007, Lefcheck et al. 2015).
A useful distinction to make initially is the difference between key traits used in studies of the effects of biodiversity on ecosystem functioning, and those traits used to elucidate community assembly processes and community change under environmental perturbations. This distinction was also at the forefront as trait diversity emerged as a concept (Laureto et al. 2015), and is indeed captured by the concept of effect and response traits (Suding et al. 2008).

A most pressing question in the Anthropocene is how the degradation and loss of biodiversity will affect the goods and services we derive from ecosystems (Cardinale et al. 2012, Mace et al. 2014). This motivation is indeed behind much of the reason for incorporating traits into studies of biodiversity (Laureto et al. 2015). It has been established that traits form a useful link between species diversity and ecosystem functioning (Tilman 1997, Tilman et al. 2014). Consequently, changes in trait composition due to invasive species (Maximov et al. 2015), loss of species after habitat degradation (Villéger et al. 2010), or overfishing (Taylor et al. 2006) may alter ecosystem functioning. A mechanistic link between traits and ecosystem functioning exists for certain taxonomic groups, such as plants, where traits relating to stem, leaf and seed structures are identified as key effect traits, yet for many groups, such causal relationships have not been set forth. For many marine groups, in particular, we are lacking a mechanistic understanding of the influence of trait composition on ecosystem functioning. A promising way forward for marine ecology and a trait-based approach to marine ecosystem functioning is to integrate experimental ecology and theoretical modelling with observational data to make predictions about functions or services. A recent example is Brun et al. (2019), where experimental data on copepod fecal pellet production, mechanistic modelling on diel vertical migration, observational data on copepod occurrences and trait data were used to infer rates of carbon sequestration from surface waters to depth in the North Atlantic. The identification of key traits from experiments thus provides a suitable framework for selection of traits to collect and survey, but also gives a quantitative foundation for making predictions about the effects of changing biodiversity on ecosystem functioning. However, experimental and quantitative data on the contribution of fish to many ecosystem functions are scarce, especially for multi-species setups. Instead, mathematical modelling of marine fish communities could be used to test specific ideas, that can then be tested and compared to observational survey data, for example the connection between biodiversity indicators and ecosystem functions, such as productivity (Maureaud et al. in review, (Appendix C)).
If community structure is governed by deterministic processes as suggested by niche theory (Pecuchet et al. 2017), then a trait-based approach, rather than a species-centric approach, may provide valuable understanding communities respond to environmental perturbations. Such advancements not only hold interest for ecology, but also for conservation and management. Certain traits and certain trait combinations change more rapidly in response to environmental perturbations or along environmental gradients (Beukhof et al. 2019), making species more or less vulnerable to change. Small pelagic fish species with rapid life history cycles are sensitive to changes in temperature and are often observed to respond fast compared to species characterized by slower life histories, such as elasmobranchs (Perry et al. 2005). Different functional groups of a community may also exhibit vastly different and opposite responses to environmental change depending on their trait composition (McLean et al. 2018). Current research is focusing on both multi-trait setups and investigating the response of community weighted means trait (CWM, the mean trait value of the species present in a community or grid cell weighted by their abundances) for individual traits revealing trait-environment relationship on local and near-global scales (McLean et al. 2018, Beukhof et al. in prep (Appendix B)). The generality of the trait-environment relationships observed in these studies can form part of a more predictive research framework (Beukhof et al. in prep (Appendix B)). Nonetheless, certain challenges present themselves in studies of trait-environment relationships. Testing these relationships is often done by comparing the CWMs along a gradient (Beukhof et al. 2019), however, this may pose a statistical challenge. The environmental value imposed on the grid cell or community is site-specific, whereas the trait values are often species level values, which may represent an aggregated value from multiple and spatially-separate areas (Miller et al. 2018). Consequently, the CWM trait value may not represent the locally most optimal trait under the given environmental conditions (Muscarella & Uriarte 2016), while also ignoring both inter- and intraspecific trait variability, which may be important to consider in studies of community assembly (Blanck & Lamouroux 2007, Bu et al. 2011, Violle et al. 2012), and community response under environmental stress (Dijkstra & Simkanin 2016, Wood et al. 2017). This challenge could be met by investigating and integrating intraspecific trait variability in order to reach CWM values aggregated at spatial scales similar to those of used for aggregating environmental values.
3.2 Trait-based biogeography

Biogeography is traditionally concerned with the distributions of plants and animals over time and space (Ebach 2015), and historically, biogeography is rooted in the species-concept (Violle et al. 2014). There has been a call to have biogeography and macroecology move from describing patterns to understanding underlying processes and make predictions (Keith et al. 2012). With the emergence of trait-based approaches to community ecology and a better understanding of species’ responses to environmental gradients new avenues open up for a better macroecological understanding of biogeographical patterns and drivers (Holt et al. 2018). Establishing a solid foundation for how species are affected by environmental gradients through traits would move biogeography from a correlative to a more mechanistic and predictive science (Violle et al. 2014). Novel biogeographical patterns emerge as traits are mapped across spatial scales: confirming established theories, such as Bergman’s rule in copepods (Brun et al. 2016); suggesting decoupling between phylogenetic and trait structures due to strong environmental filtering in mammals (Holt et al. 2018), diatoms (Soininen et al. 2016) and fish (Villéger et al. 2013); revealing new hot spots of biodiversity (Stuart-Smith et al. 2013); and unraveling the effects of historical factors, such as glaciations and past climate-oscillations (Svenning et al. 2011, Ordonez & Svenning 2017). Additionally, biogeographical trait distributions are incorporated into predictive frameworks (Sukumaran & Knowles 2018), allowing for predictions of macroecological processes, such as diversification and geographical range evolution (Sukumaran et al. 2015).

Trait-based biogeography is still, however, an emerging field of research with several challenges (Violle et al. 2014). Firstly, biogeography relies on available data on large-scale distributions of traits and species. Such data sets are emerging at ever-increasingly finer grain, but marine ecosystems remain disproportionally underrepresented (Costello et al. 2017). Furthermore these data sets should be coupled with high-quality environmental layers to allow for fine-scale analyses. However, as biogeography (and ecology in general) transitions into big data, certain challenges arise in computational power, statistical modelling and statistical training (Farley et al. 2018). Secondly, as our understanding of species and trait responses along spatial and environmental gradients increases, increased attention should be given to integration of theories of community assembly across a variety of spatial scales, combining multiple theories (Tittensor & Worm 2016, Viana & Chase 2018, Worm & Tittensor 2018). Lastly,
investigations of multi-trophic interactions and food-web structures may provide insights on how local to regional scale biogeographical patterns emerge (Piatt et al. 2018) and how trait variability cascades across trophic levels in marine ecosystems (Pecuchet et al. 2018). These advancements will further ecological insights and forecasting abilities, ultimately allowing us to reconstruct biogeographical patterns and test underlying causes.

### 3.3 Community changes and conservation

The integration of the abovementioned avenues of research will aid in understanding community changes due to anthropogenic pressures and provide conservation effort with a better foundation for protecting biodiversity, whether the incentives to do so are based on inherent ecological values of life (Hungate & Cardinale 2017) or anthropocentric interests such as goods and services (Mace et al. 2012). As with biogeography, conservation has traditionally been species-centric. However, there is a pressing need to encompass several components of biodiversity in assessments, since stressors, such as climate change and habitat degradation, affect taxonomic, trait and phylogenetic structures simultaneously and differently (Villéger et al. 2010, Knapp et al. 2017).

A major challenge in conservation is the placement and regulation of protected areas (Agardy et al. 2011). Placement of protection rests upon prioritization of which components should be protected. There is increasing evidence that hot spots of different biodiversity components, ecosystem processes and aesthetic values do not overlap in any significant manner, and placement of protection thus represents a trade-off between these components. Indeed, already existing protection, such as marine protected areas, often fails at maximizing protection of several hot spots of different biodiversity components globally (Klein et al. 2015, Lindegren et al. 2018), neglecting phylogenetic and trait biodiversity, and at times still allowing for fishing in areas of high endemism (Mouillot et al. 2011). Conservation efforts should be informed by ecological research on how communities respond to environmental change and to what degree biodiversity in all its components affect ecosystem functioning. As human pressures continuously and increasingly impact natural systems, conservation faces the challenge of constantly having to evaluate a moving target (Bull et al. 2013). Effective and sufficient monitoring is a requirement for assessing change, as changes may happen in individual components of biodiversity and certain ecosystem functions may be altered disproportionately.
depending on a given community change (Mouillot et al. 2013). Due to the close link between traits, environmental change and ecosystem functions, long-term monitoring of trait variation and change may give indications of ecosystem change otherwise not captured by traditional species-centric biodiversity metrics (Törnroos et al. 2018). Trait-based marine indicator development is however lacking (Beauchard et al. 2017) and conservation efforts rest not solely on ecological advice, but also on societal concerns and political will (Brister 2016). Just as managing fisheries is about managing people (Hilborn 2007), there is also a clear need to integrate other research disciplines in order to understand the links between biological systems and social processes in the Anthropocene (Corlett 2015).
Bibliography


Hilborn R (2007) Managing fisheries is managing people: what has been learned? Fish Fish 8:285–296


Chapter 4

Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: Causes and consequences

Tim Spaanheden Dencker¹, Lauréne Pécuchet¹, Esther Beukhof¹, Katherine Richardson², Mark R. Payne¹, Martin Lindegren¹

¹Centre for Ocean Life, National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, Kgs. Lyngby, Denmark
²Centre for Macroecology, Evolution and Climate, Danish Natural History Museum, University of Copenhagen, Copenhagen, Denmark

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Abstract

Biodiversity is a multifaceted concept, yet most biodiversity studies have taken a taxonomic approach, implying that all species are equally important. However, species do not contribute equally to ecosystem processes and differ markedly in their responses to changing environments. This recognition has led to the exploration of other components of biodiversity, notably the diversity of ecologically important traits. Recent studies taking into account both taxonomic and trait diversity have revealed that the two biodiversity components may exhibit pronounced temporal and spatial differences. These apparent incongruences indicate that the two components may respond differently to environmental drivers and that changes in one component might not affect the other. Such incongruences may provide insight into the structuring of communities through community assembly processes, and the resilience of ecosystems to change. Here we examine temporal and spatial patterns and drivers of multiple marine biodiversity indicators using the North Sea fish community as a case study. Based on long-term spatially resolved survey data on fish species occurrences and biomasses from 1983 to 2014 and an extensive trait dataset we: (i) investigate temporal and spatial incongruences between taxonomy and trait-based indicators of both richness and evenness; (ii) examine the underlying environmental drivers and, (iii) interpret the results in the context of assembly rules acting on community composition. Our study shows that taxonomy and trait-based biodiversity indicators differ in time and space, and that spatial patterns are correlated to natural and anthropogenic drivers, notably temperature, depth and substrate richness. Our findings show that trait-based biodiversity indicators add information regarding community composition and ecosystem structure compared to and in conjunction with taxonomy-based indicators. These results emphasize the importance of examining and monitoring multiple indicators of biodiversity in ecological studies as well as for conservation and ecosystem-based management purposes.
4.1 Introduction

Understanding patterns of biodiversity and their underlying drivers has challenged scientists for centuries (von Humboldt & Bonpland 1805, Tittensor et al. 2010), and it remains a fundamental and strongly debated field in ecology (Sutherland et al. 2013). Biodiversity is a multifaceted concept comprising several components, as recognized by the Convention of Biological Diversity (CBD 2014), and yet biodiversity studies have traditionally focused on taxonomic units to describe patterns and drivers of biodiversity (species richness and abundance distribution) at various spatial scales (Pianka 1966, Chaudhary et al. 2016). These biodiversity indicators include no other information than the taxonomic identity of the species and imply that all species are equally important (Magurran 2004). However, it is well known that species differ in their contribution to ecosystem processes (Luck et al. 2009), and that they exhibit marked differences in their responses to changing environments. This recognition has led to the exploration of components of biodiversity other than taxonomic diversity in ecosystems and species assemblages.

One such component is the diversity of ecologically important traits, often referred to as “functional diversity” (Petchey & Gaston 2002, Mason et al. 2005). Traits are defined as measurable attributes affecting the fitness of organisms through the processes of feeding, reproduction and survival (Violle et al. 2007, Litchman et al. 2013). These attributes can be morphological (e.g. size and body shape), physiological (e.g. metabolic pathways or growth related) or behavioral (e.g. diurnal migration, feeding patterns). Together, combinations of traits can describe the ecological niche of species (Violle & Jiang 2009, Cadotte et al. 2015). Furthermore, traits determine the response of species to environmental gradients and perturbations (Mouillot et al. 2013) and provide insight into the functional role of species in ecosystems (Duffy et al. 2016). Recently, terrestrial and marine studies taking into account multiple components of biodiversity using both taxonomic and trait information have revealed that the two components of biodiversity may exhibit temporal and spatial differences (Devictor et al. 2010, Stuart-Smith et al. 2013, Törmöros et al. 2014, Mindel et al. 2016). These apparent discrepancies indicate that the two components of biodiversity may respond differently to environmental drivers and perturbations (Mayfield et al. 2010, Villéger et al. 2010).
Furthermore, these differences between species and trait diversity can provide insight into the key mechanisms and processes structuring biological communities (Mouillot et al. 2007, Pécuchet et al. 2016). Local communities may display greater, or lesser, trait diversity than expected from a random selection of species from a regional species pool. The resulting patterns of so-called over- or underdispersion of traits may be indicative of the effects of abiotic or biotic forces acting on community assembly, through the processes of environmental filtering or limiting similarity, respectively (MacArthur & Levins 1967). Environmental filtering is hypothesized to lead to trait homogenization in communities as only species with a specific set of traits might survive and thrive under certain abiotic conditions. Limiting similarity, on the other hand, acts mainly through biotic processes, as competition over limiting resources leads to separation of niches and increased trait heterogeneity (Grime 2006).

In addition to the structuring mechanisms of environmental filtering and limiting similarity marine fish communities have been and are heavily altered by fishing at global and regional scales (Jennings, Greenstreet, et al. 1999, Halpern et al. 2008, Sharpe & Hendry 2009). The composition of fish communities might be affected by changes in the biomass of targeted and bycatch species and especially by the strong structuring effect of size-selective harvesting (e.g. trawling), which typically targets large individuals, thereby reducing trait variability and shifting the abundance distribution of the community towards smaller individuals, while not necessarily affecting the number of species, i.e. species richness (Fisher et al. 2010). The potential resilience of ecosystems to such anthropogenic and natural stressors may also depend on the ratios between different components of biodiversity (Mouillot et al. 2014). The loss of species with unique functional traits may have more severe consequences on ecosystem functioning compared to the loss of species with traits that are more commonly expressed within the community (Bremner et al. 2003). This redundancy is however highly variable across ecosystems. For instance, certain Argentinean plant communities could lose 75% of their species before any unique functional group would disappear (Fonseca & Ganade 2001), while some coastal fish and avian assemblages exhibit low degrees of functional redundancy, thus revealing high vulnerability to species loss (Micheli & Halpern 2005, Micheli et al. 2014, Mouillot et al. 2014).
Disentangling and decoupling the temporal and spatial dynamics of species diversity and trait diversity is therefore critical for elucidating the drivers and processes of community assembly (Mouchet et al. 2010, Pécuchet et al. 2016), and for developing an understanding of the effect of biodiversity loss on ecosystem functioning (Cadotte et al. 2011). In addition, such an understanding can provide valuable input for informing and planning broad-scale conservation and ecosystem-based management strategies. Here, we examine spatial and temporal patterns and compare drivers of multiple marine biodiversity indicators using the North Sea demersal fish community as a case study. The North Sea (Figure 1) is a heavily impacted large marine ecosystem (Halpern et al. 2008) that has experienced rapid changes in environmental conditions (Hiddink & ter Hofstede 2008) and shifting community compositions (Dulvy et al. 2008, Hiddink & ter Hofstede 2008). Using an extensive trait dataset and standardized long-term spatially resolved survey data on fish species occurrences and abundances, we: (i) investigate the temporal and spatial differences between taxonomy and trait-based biodiversity indicators, (ii) assess the importance of environmental drivers on the observed biodiversity patterns, and (iii) interpret the results in the context of assembly rules acting on community composition and ecosystem resilience.

Figure 1 Map of the North Sea and its geographical position. Labels correspond to the names of specific localities in terms of areas and geographic features including banks, bights and islands mentioned in the study.
4.2 Materials & Methods

Fish survey data

Distribution and abundance data for demersal fish species were obtained from the North Sea International Bottom Trawl Survey (NS-IBTS), publicly available from the ICES trawl surveys database (ICES 2015). As survey methods have been standardized among all participating countries since 1983, data on Catch per Unit Effort (CPUE; catch in numbers of individuals of the same species adjusted to one hour of trawling) per length class were extracted from 1983 to 2014 for the months of January to March (hereafter referred to as quarter one). To avoid potential bias related to changes in the sampled survey area over time, only ICES statistical rectangles (1° longitude × 0.5° latitude; hereafter ICES rectangle) that were sampled in at least 26 out of 32 years (80%) were used in the analysis. In order to standardize haul duration, only hauls with duration lengths of between 27 and 33 minutes (median haul duration of 30 minutes ± 10%) were retained. All invertebrate and pelagic fish species were removed from the dataset, limiting the analysis to demersal fish species. In addition, a minimum hauling depth of 20 meters was selected to exclude samples which might represent coastal or estuarine areas, as these areas are not prioritized in the survey. To minimize the effect of misidentifications or sporadically occurring species due to the effects of inadequate sampling, only species that were present in at least 7 out of 32 years (20%) were kept for further analyses. This selection criterion excluded 27 species. We acknowledge that the criterion might have an effect on the number of rare species reported but not on the species that show consistent recurrence or increase over time. Furthermore, a few ecologically similar species of the same genus were aggregated due to identification problems in the reporting scheme (Heessen et al. 2015) and the lack of trait information (Appendix S1). For consistency, we refer to all species and species aggregates as species. Using length-weight parameters for each species, CPUEs per length classes were converted into biomass caught per hour following (Fung et al. 2012). Conversion parameters and relative biomass of species are outlined in Appendix S2 and Appendix S3. The data corrections resulted in a dataset containing 9401 unique hauls in 119 ICES rectangles and biomass catch per hour for 77 demersal fish species.
**Fish trait data**

Eight ecological trait categories were used to summarize community biodiversity. The selected trait categories are related to the morphological, life history, reproductive or dietary aspects of marine fish species, and have been shown to determine structure and function in marine fish communities (Table 1). Morphology of the fish species was described using body size, body shape and caudal fin shape. Life history was covered by age at maturity, while reproductive and dietary aspects were captured by, respectively, offspring size, fecundity and spawning behavior, and diet. The set of traits was selected to reflect different and complementary aspects of the ecological niche of the species, and this trait set has a high degree of resemblance to sets used in similar multi-trait studies (Stuart-Smith et al. 2013, Wiedmann et al. 2014, Duffy et al. 2016, Pécuchet et al. 2016). Trait information was extracted from the primary literature and Fishbase (Froese & Pauly 2015) (Appendix S4). Since trait data were not available from the North Sea for all species, some trait data were also derived from neighboring areas (such as the Baltic Sea) or from the larger North Atlantic regions.
Table 1. Overview of the eight selected trait categories sorted according to traits, description and ecological relevance.

<table>
<thead>
<tr>
<th>Trait category</th>
<th>Trait</th>
<th>Description</th>
<th>Relevance</th>
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<tbody>
<tr>
<td>Body size</td>
<td>Asymptotic length</td>
<td>length the fish would attain if they were to grow for an infinitely long period</td>
<td>Information on food web structure and ecological niche occupation</td>
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<tr>
<td>Age at maturity</td>
<td>Continuous</td>
<td>Age at which 50% of the individuals are sexually mature</td>
<td>Relates to lifespan and generation time</td>
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<tr>
<td>Fecundity</td>
<td>Continuous</td>
<td>Average number of eggs per adult female during a spawning season</td>
<td>Relates to energy output, allocation and production</td>
</tr>
<tr>
<td>Egg size</td>
<td>Continuous</td>
<td>Size of oocyte at spawning</td>
<td>Relates to spawning behavior and offspring investment</td>
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<tr>
<td>Body shape</td>
<td>Gadoid-like</td>
<td>The shape of the body</td>
<td>Insights into predation behavior, mobility and habitat selection</td>
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<td>Plankto-piscivore</td>
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<tr>
<td>Spawning behavior</td>
<td>Ob - Oviparous with benthic eggs</td>
<td>Main spawning behavior, divided between oviparity and viviparity, and further between the degree of parental care, mode of release and egg characteristics</td>
<td>Relates to ecological constraint on habitat selection(Ciannelli et al. 2015)</td>
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<td>Og - Oviparous guarders</td>
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<td>Op - Oviparous with pelagic eggs</td>
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<td>Os - Oviparous shelterers</td>
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<td>Ov - Oviparous with adhesive eggs</td>
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<td>V - Viviparous</td>
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<td>Caudal fin shape</td>
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<td>The shape of the caudal fin</td>
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</table>
Biodiversity indicators

Four commonly used indicators of biodiversity were calculated: species richness (SRic), species evenness (SEve), trait richness (TRic) and trait evenness (TEve). SRic was calculated as the number of unique species, while SEve was calculated as Pielou’s evenness (Pielou 1966). The value of Pielou’s evenness ranges from 0 to 1, with larger values indicating a more even distribution in relative biomass among species in a sample. The trait-based biodiversity indices follow the proposed mathematical formulas suggested by (Cornwell et al. 2006, Laliberté et al. 2015), allowing for standardizing of trait values, and are calculated based on all eight traits. Both TRic and TEve are represented by a multidimensional trait space. TRic represents the multidimensional trait space occupied by the community calculated as the minimum convex hull volume which includes the trait values of all species considered (Cornwell et al. 2006). TRic was standardized between 0 and 1, with larger values indicating a larger convex hull volume, hence a higher richness of traits in a sample. TEve was defined as the evenness of the distribution of relative biomass of species in the trait space (Mason et al. 2005), and ranges, as in the case of SEve, from 0 to 1, depending on the degree of evenness in the distribution of biomass among traits in a sample. TRic and TEve were chosen to be comparable to their taxonomy-based equivalents, respectively SRic and SEve. The taxonomy and trait-based indicators were calculated following standard approaches implemented in the R packages “vegan” (Oksanen et al. 2017) and “FD” (Laliberté et al. 2015). All biodiversity indicators were calculated per ICES rectangle per year and then averaged across either ICES rectangles or years to investigate temporal trends and spatial patterns, respectively. Temporal trends were assessed with generalized additive models (GAMs) (Hastie & Tibshirani 1986) with a smoother function of year as the single predictor. No temporal autocorrelation was detected in the residuals. As the number of hauls conducted in each ICES rectangle per year varied from 1 to 11 (mean: 2.0, median: 2.9), all biodiversity indicators were standardized for differences in sampling effort by using GAMs which effectively accounts for potential non-linear relationships (Hastie & Tibshirani 1986).

Natural and anthropogenic environmental drivers of biodiversity

To investigate potential drivers of species and trait diversity, ten natural and anthropogenic environmental drivers were selected as covariates. The drivers were selected based on their demonstrated importance in shaping patterns of fish biodiversity in marine ecosystems (Reiss et al. 2010, Pécuchet et al. 2016). Only spatial patterns of biodiversity were investigated due to two reasons: the highest variability was found across spatial scales, and not all drivers were fully available across
the full temporal scale of the study. Depth was calculated by averaging the depth of sampled hauls per ICES rectangle from the NS-IBTS data. Sea bottom temperature (°C) and sea bottom salinity data were obtained from Núñez-Riboni & Akimova (2015) on a monthly basis with a resolution of 0.2° × 0.2°. Mean winter (Dec-Feb) sea bottom temperature and salinity were derived per ICES rectangle per year. Temperature seasonality was expressed as the difference between winter and summer (Jun-Aug) temperatures for each ICES rectangle. Salinity variability was expressed as the difference between minimum and maximum salinity within each ICES rectangle per year and then averaged across years. Phytoplankton biomass was estimated by proxy using the Phytoplankton Colour Index (PCI) (SAFHOS) during quarter one and retrieved from the Continuous Plankton Recorder program provided by the Sir Alister Hardy Foundation for Ocean Science (SAFHOS). PCI is a semi-quantitative index that provides an estimate of phytoplankton biomass based on the greenness of water samples (Reid et al. 2003). PCI data were available for the entire study period, but not for the whole study area in every year, hence spatial interpolation of this data source was performed using a GAM with a two-dimensional (latitude, longitude) tensor product smoother. Phytoplankton biomass was represented by mean quarter one PCI per ICES rectangle across all years. Seabed substrate richness and evenness were calculated based on seabed substrate classifications from The European Marine Observation and Data Network (EMODnet 2015). Six different substrate categories were used and substrate richness was defined as the number of categories present in each ICES rectangle. Substrate evenness was calculated as Pielou’s evenness, based on the relative coverage of substrate categories within each ICES rectangle. Anthropogenic pressure from fishing was estimated from data on the spatial distribution of international bottom trawling effort in the North Sea for two separate periods: 1990-1995 (Jennings, Alvsvåg, et al. 1999) and 2003-2012 (STECF 2014, Engelhard et al. 2015). Beam and otter trawl effort were considered separately as recommended by Engelhard et al. (Engelhard et al. 2015). Data, summary statistics and sources of environmental covariates can be found in the supplementary material (Appendix S5).

**Modelling**

To investigate the relative importance of natural and anthropogenic drivers in explaining the spatial patterns of biodiversity, we fitted a series of GAMs to each indicator of biodiversity. GAMs are non-parametric modelling methods that allow a high degree of flexibility in the form of the response (Hastie & Tibshirani 1986). The relationship between biodiversity indicators and drivers was only investigated for spatial patterns, as complete temporal coverage was not available for the entire study.
period. Two sets of GAMs were performed: one using the mean values of all natural drivers over the entire study period; and one using a reduced data set containing mean values of all natural and anthropogenic drivers for the two periods in which fishing effort data were available. All GAMs were performed with a Gaussian error term and restricted to a three degrees of freedom smoother (k = 3), equivalent to a second degree polynomial. Instead of a traditional model reduction procedure, each covariate was considered for inclusion and could reasonably be considered as having an effect, despite failing to meet an *a priori* determined significance level of *p* < 0.05 (Gelman et al. 1995, Burnham & Anderson 2002, Cinner et al. 2016). Instead, the importance of each covariate was assessed using relative variable importance (RVI) from the R package ‘MuMIn’ (Bartoń 2016) based on weighted Akaike’s Information Criterion (AIC) (Anderson 2008). The higher the RVI for an explanatory variable, the more important it is for explaining the spatial patterns of the biodiversity indicators (Burnham & Anderson 2002). No spatial autocorrelation was detected in the residuals of the spatial GAMs.

**Null model - detecting assembly processes**

To investigate potential assembly processes impacting the community composition we compared observed spatial values of TRic with simulated TRic values obtained from a null model, based on 999 randomized species assemblages taken from the observed species pool. Randomizations were obtained by controlling for both row sums (sites; i.e. ICES rectangles) and column sums (species) using the ‘permatswap()’ function in the ‘vegan’ package in R (Oksanen et al. 2017). If assemblages have higher TRic than expected from a null model at a given level of SRic, these assemblages will be influenced mainly by limiting similarity, while assemblages with lower TRic than expected from a null model will be influenced mainly by environmental filtering. The deviance of the observed TRic from the simulated TRic was considered as an indication of the relative importance of the two suggested assembly rules. Values within the interquartile range corresponded to assemblages where neither of the assembly rules dominate, while values below or above the 25% and 75% quartiles, respectively, indicate assemblages predominantly structured through either environmental filtering or limiting similarity. Assemblages with values outside the 95% range were considered to be significantly different from the null-model and to be strongly structured through either environmental filtering or limiting similarity. All statistical analyses were performed in R (version 3.3.2) (R Core Team 2016).
4.3 Results

Tempo-spatial patterns of biodiversity

The average SRic per ICES rectangle showed a significant long-term increase with a recent stagnation from 2005 onwards (Figure 2A). This trend is reflected also in TRic, albeit with a more moderate increase (Figure 2D). TRic was significantly positively correlated to SRic (GAM: F = 92.28, e.d.f. = 1, $R^2 = 0.75$, p < 0.05), although a significant decrease in the ratio between TRic and SRic was observed during the study period (GAM: F = 87.3, e.d.f. = 1.85 $R^2 = 0.75$, p < 0.05), indicating that TRic did not increase at the same rate as SRic (Appendix S6). The increase in SRic was reflected by a significantly increasing trend in 51% of the ICES rectangles (Figure 2B), mainly found in rectangles located in the northwestern and southwestern North Sea. TRic increased primarily in the southwestern and western central North Sea, coinciding with areas of increases in SRic. However, only 26% of the ICES rectangles showed a significant increase in TRic, indicating a more localized extent of increase compared to SRic (Figure 2E). With respect to the evenness indicators, SEve showed pronounced fluctuations, but no significant temporal trend was detected throughout the study period (Figure 2G), while TEve showed a significant long-term decrease (Figure 2J). SEve was generally characterized by low values, ranging from 0.3 to 0.4, in contrast to TEve, where observed values ranged from 0.78 to 0.83. SEve decreased significantly in 16% of the ICES rectangles, primarily in the southern North Sea, with a distinct band across the central North Sea following the northern border of Dogger Bank. The northern North Sea was characterized by significant increases in SEve, although over a more restricted area than the observed decreases in the southern North Sea (Figure 2H). TEve decreased significantly in the southeastern, central and western regions of the North Sea, whereas little temporal change was detected in the northern parts (Figure 2K).
4.3 Results

Figure 2: Temporal trends and spatial patterns of multiple biodiversity indicators in the North Sea. (A, D, G, J) Time-series and temporal trends of fish species richness (SRic), trait richness (TRic), species evenness (SEve), and trait evenness (TEve) as annual averages across all ICES rectangles. Significant temporal trends were observed for SRic (GAM: F = 37.45, e.d.f. = 1.92, R² = 0.64, p < 0.001), TRic (GAM: F = 5.6, e.d.f. = 1.78, R² = 0.33, p < 0.01) and TEve (GAM: F = 39.84, e.d.f. = 1.75, R² = 0.71, p < 0.001). Shaded grey represent 95% confidence intervals. (B, E, H, K) Tempo-spatial patterns of biodiversity indicators represented by the slope and significance of a linear regression model fitted to each ICES rectangle across years. Green colors indicate a positive trend, while purple colors indicate a negative trend. Significant trends are indicated by black crosses (p<0.05). (C, F, I, L) Spatial patterns of biodiversity indicators shown as average value for each ICES rectangle across all years.
In terms of spatial patterns, the highest values of SRic were observed in the northern North Sea from the coast of Scotland to the Shetland Islands, whereas the areas with lowest SRic were found in the central and southeastern North Sea (Figure 2C). Areas with medium to high values of SRic were observed along the British coast, coinciding with the highest values of TRic, and in the eastern parts along the Danish coast (Figure 1F). TRic was observed to be consistently high along the British coast with intermediate-values in the northern and central-eastern North Sea. Low values of TRic were found in the southeastern North Sea, with the lowest values in coastal areas. Several transition zones were identified, marking steep changes in biodiversity values between adjacent areas. SRic was observed to decrease markedly towards the central and southeastern North Sea, while two distinct transition zones were found for TRic. A first transition zone was found at Dogger Bank with high values to the west and north, while low values were observed south and east of the bank. Secondly, the Southern Bight was clearly split between a western and eastern component with high values of TRic on the British coast and low values on the Dutch and Belgian coast. SRic and TRic show a high degree of overlap with two exceptions: the area with maximum values of TRic is situated farther south than the area for SRic. Moreover, the northern central North Sea is characterized by low SRic, but by mid to high levels of TRic. No strong spatial pattern was observed in the average values of SEve, though it showed a marked peak in values in the central North Sea (Figure 2I). The spatial pattern of TEve, on the other hand, was marked by a clear transition over Dogger Bank, with lower values in the southern and southeastern part and higher values towards the British coast and into the central and northern North Sea (Figure 2L).

**Drivers of biodiversity**

The spatial GAMs explained 76% and 36% of the spatial variability of SRic and SEve, while 55% and 69% of the spatial variability was explained for TRic and TEve, respectively. The most influential drivers across the four diversity indicators were depth, sea bottom temperature and substrate richness, followed by beam trawl effort, temperature seasonality and salinity variability. The relative importance of the drivers varied, however, between biodiversity indicators (Figure 3). Drivers of SRic and TRic showed a high degree of agreement with respect to the importance of drivers, and their relationship to the biodiversity indicators. Both richness indicators were positively related to sea bottom temperature and substrate richness, and negatively related to beam trawl effort and temperature seasonality. For depth, SRic was observed to follow a positive relationship, while TRic peaked at intermediate depths of around 80-100 meters. A low degree of congruence was observed
between the importance of drivers on the evenness indicators. Only salinity variability was found to be important for these and a negative relationship was found for evenness indicators. Additionally, beam effort, temperature seasonality and PCI were important for SEve, where a negative relationship was found for the first two drivers, and a unimodal relation for PCI. Depth, sea bottom temperature, and substrate richness were the most important drivers for TEve, in addition to salinity variability, with unimodal, negative and positive relationships, respectively.

Figure 3: Relative variable importance (RVI) of environmental and anthropogenic drivers and their relationship to the biodiversity indicators. Drivers are sorted according to their cumulative importance across the four investigated biodiversity indicators. RVI>0.9 signifies high importance of a driver, RVI>0.6 signifies moderate importance, while RVI<0.6 is considered low or no importance. Relationships between drivers and biodiversity indicators based on GAMs are indicated by symbols: + indicate a positive relationship, ÷ indicate a negative relationship, ▷ indicate a unimodal relationship. If no symbol is assigned, the RVI of the driver is below 0.6.

**Observed TRic against null model**

TRic and SRic showed a positive relationship, which was reflected also in the simulated null-model relationship (Figure 4A). For low levels of SRic (<11 species), the observed TRic values were primarily distributed outside the 95% range, thus being significantly different from the null-model distribution. For higher levels of SRic (≥11 species), the observed TRic occupied both areas outside and inside the 95% interval. The spatial distribution of residuals of observed TRic from the null-model was characterized by a clear northern and southern component of significantly lower values than expected from the null model, notably in the German Bight and in the northern North Sea between the Shetland Islands and Norway. Areas characterized by higher than expected TRic were
observed primarily in the central North Sea following a west-to-east band cutting across from the British coast to Skagerrak (Figure 4B)

4.4 Discussion

Our study documents pronounced differences in temporal trends and spatial patterns between multiple components of demersal fish biodiversity in the North Sea, including taxonomic identity and ecological traits. Below we elaborate on these incongruences, discuss their underlying causes and drivers, and discuss the associated ecological consequences.

Differences in time and space

Despite similar increasing temporal trends, the close match between SRic and TRic starts to break down when the spatial dimension is taken into account. While similar increases in both SRic and TRic were observed throughout the Southern Bight, a limited degree of spatial overlap was found in the northern North Sea. This suggests that species gains in the southern Bight have contributed with novel trait values, while the widespread increase in SRic noted in the northern North Sea has contributed only locally to novel trait values. The observed spatial differences can be driven by the introduction of new species and range shifts of already existing species. Interestingly, the distribution
range of species with different biogeographic affinities has shifted unevenly within the North Sea (Engelhard et al. 2011) with small-sized Lusitanian species expanding their distribution ranges compared to large-bodied Boreal (northerly) species (Hiddink & ter Hofstede 2008). Thus, their expansion into the North Sea can likely explain the contribution of new trait values, particularly along the “entry point” in the southern North Sea (i.e., the Southern Bight). The high degree of spatial differentiation in the contribution of new species and traits into existing local assemblages highlights that immigration from adjacent regions into the North Sea is an important factor in structuring fish diversity and community composition.

As in the case of the temporal dynamics described above, the spatial patterns of the biodiversity indicators displayed both similarities and differences. The similarities are illustrated by a pronounced north-south gradient in both SRic and TRic. This supports earlier studies showing a clear separation in community composition between the northern and southern North Sea (Callaway et al. 2002, Daan 2006, Dulvy et al. 2008). Despite these similarities, the two indicators demonstrate pronounced local differences, particularly in the central North Sea - an area characterized by considerably higher TRic compared to its corresponding level of SRic. This indicates a high degree of trait heterogeneity between assemblages across levels of species richness. This is in accordance with findings from the Barents and Baltic Seas demonstrating similar spatial differentiation between species richness and trait richness, albeit at lower levels of species richness (Wiedmann et al. 2014, Pécuchet et al. 2016).

It is recognized that the ecological effect of a species on ecosystem processes is generally proportional to its relative biomass in the community (Grime 1998), with the notable exception of keystone species showing a disproportionally large effect compared to their biomass (Paine 1966, 1969). Furthermore, biodiversity patterns depend not only on the presence and absence of the species and their traits, but also on their relative abundance and biomass (Stuart-Smith et al. 2013). In order to account for species biomasses, we therefore included indicators of species and trait evenness. The North Sea was generally characterized by low SEve during the study period which suggests a community with a few dominating species (e.g. whiting (Merlangius merlangus), common dab (Limanda limanda), and Atlantic cod (Gadus morhua)). This is in contrast to TEve which despite showing a significant decrease over the study period, remained relatively high over time and throughout space. These contrasts may indicate a community characterized by a few dominant species, but also with high regularity in the distribution of biomass across traits. Similar differences in evenness indicators have
previously been found for tropical fish across several lagoon systems (Villéger et al. 2010). Many marine ecosystems have been impacted by marked environmental changes (Halpern et al. 2008), and the North Sea fish community has undergone major distributional shifts during the last four decades due to increasing sea bottom temperatures (Perry et al. 2005). These shifts, in addition to the effect of fishing and the appearance of novel species potentially affected the relative biomass distribution across species and traits. Shifts in evenness patterns can lead to changes in interspecific interactions, ecosystem processes and ecosystem stability (Hillebrand et al. 2008). More importantly, evenness indicators might respond more rapidly to changes in communities than species or trait richness, as changes in abundances or biomass often precede local species extinctions (Chapin et al. 2000).

**Natural and anthropogenic drivers**

The observed similarities and differences between biodiversity indicators suggest that the investigated components of the North Sea demersal fish biodiversity may respond differently to environmental and anthropogenic drivers. One of the most influential drivers in this study, sea bottom temperature had a positive effect on both SRic and TRic. This suggests that temperature is an important driver for structuring of communities by determining patterns of species occurrences. This is in concordance with previous studies linking temperature increases to changes in community composition (Beare et al. 2004, Ehrich et al. 2009, Simpson et al. 2011). In addition to temperature, depth was found one of the most influential explanatory variables. Although depth has shown to be a suitable predictor for community structure (Callaway et al. 2002, Ehrich et al. 2009, Reiss et al. 2010) it is unlikely the actual driving force behind the observed patterns, but rather a proxy for factors of more direct influence, such as water column mixing or geographical proximity to the highly diverse species pool of the Northeast Atlantic. In addition to temperature and depth, substrate richness demonstrated a strong positive relationship with all biodiversity indicators, except SEve. This supports the *habitat heterogeneity hypothesis* (Tews et al. 2004), stating that structurally more complex habitats provide more niches thereby increasing species and trait richness. The higher trait evenness may also be linked to the higher number of niches available in environments with high habitat heterogeneity. More niches may support a more diverse community at relatively even abundances compared to niche poor environments, where single or few species might dominate. This opposite end of the spectrum may be evident in the southeastern North Sea, which was characterized by both low species and trait richness, as well as by low species evenness and low substrate richness.
In addition to the natural drivers, three out of the four biodiversity indicators were negatively correlated to beam trawl effort, but uncorrelated to otter trawl effort. Although fishing can significantly impact marine communities (Martins et al. 2012), particularly in terms of evenness (i.e. by affecting the underlying population abundances of target and non-target species), the negative correlation may not necessarily reflect a true effect on the biodiversity indicators, but rather may be a result of the clear spatial preference of the beam trawl fisheries for the southern North Sea. This preference has previously been explained by external environmental factors such as primary productivity, depth and sediment grain size, largely favoring the main targeted flatfish species (van Denderen et al. 2014). However, the potential effects of trawling have been investigated in other studies (Engelhard et al. 2015) and historical records show that the southern North Sea used to have a much higher proportion of large-bodied elasmobranchs and diadromous fishes (Wolff 2000, Bennema & Rijnsdorp 2015) than is the case today. This suggests that fishing has had a clear effect on community composition in the southern North Sea. In addition, fishing pressure affects fish communities non-randomly, often targeting large, predatory species and individuals (Myers & Worm 2003, Fisher et al. 2010, Genner et al. 2010), leading to changes in both the presence and abundance of certain key traits, such as body length, which may lead to a loss of trait heterogeneity and potentially affecting the trophic structures of marine communities (Hildrew et al. 2007). The historical records and the non-random effects of fishing pressure highlight the need to adopt trait-based approaches in long-term perspectives to understand fishing impacts on community composition and marine ecosystems. One such example is the Large Fish Indicator (Greenstreet et al. 2011), indicating the proportion of large fish (>40 cm) in the North Sea demersal fish community. The indicator has been used to detect the positive effects of recent effort reductions in the North Sea fishing fleet (Engelhard et al. 2015).

**Causes and consequences of differences between biodiversity indicators**

Assessing differences between biodiversity components can provide information on the underlying abiotic or biotic processes shaping community assembly (Mouillot et al. 2007). The null model results revealed areas where local assemblages are either more or less diverse in traits than if assembled at random and illustrated a clear spatial separation between deterministic assembly processes in the North Sea. The significant underdispersion of the southeastern North Sea indicate a strong effect of environmental filtering acting on community composition through a stressful habitat characterized by pronounced seasonal fluctuations in temperature and salinity, low substrate richness and shallow
depths. These environmental conditions, along with pronounced bed stress via waves and tides, as well as bottom trawling, make the southern North Sea a relatively stressful environment, where only species with a limited set of traits enabling them to cope with these conditions can exist. In contrast, the central North Sea is characterized by pronounced overdispersion, wherein biotic interaction and resource competition likely serve to increase trait dissimilarity through the process of limiting similarity. Some communities may also exhibit overdispersion due to external factors or phenological events. For example, the pronounced overdispersion around the Thames estuary may be linked to a contraction of the distribution range of several elasmobranch species into the coastal estuarine areas (Sguotti et al. 2016), or because these areas serve as spawning and nursing grounds for some shark and skate species (Ellis et al. 2012). Both of these mechanisms would lead to a disproportionate expansion of the existing trait space through unique traits, such as large body size, low fecundity, large offspring size, and high age at maturity; characteristics of elasmobranch species.

Areas of over- or underdispersion potentially reveal not only mechanisms of community assembly, but also information on the potential ecological consequences of biodiversity loss in ecosystems. Whether the loss of an individual species may lead to a functional degradation depend on whether this species carries a unique trait (or combination of traits) or not. In the former case, degradation is likely to occur, especially if the actual trait also supports a particular ecosystem function. In the latter case, functionally similar species (sharing the same traits and ecological niche) may show a compensatory increase, hence buffering for the lost species and ensuring a continued support for any associated ecosystem function. High redundancy within communities may indicate that ecosystem processes and functions are less likely to be altered than in ecosystems exhibiting low redundancy, as each species will account for a disproportionately large amount of the trait diversity in the latter case. Temporal studies of trait redundancy in the North Sea demersal fish communities have shown that trait-wise similar groups with a larger number of species showed higher stability in terms of biomass than groups with fewer species (Rice et al. 2013). The degree of trait redundancy in species-rich ecosystems may therefore act as an insurance promoting stability of ecosystem processes and functions against species loss (Naeem & Li 1997, Yachi & Loreau 1999, Bellwood et al. 2003, Boyer & Jetz 2014).
Conclusions

Protection and conservation efforts are often based on the spatial distribution of biodiversity hotspots, focusing on a single or a few parameters (Mouillot et al. 2011). Differences between biodiversity indicators and trait redundancy are presently receiving increasing attention in the support of management and biodiversity conservation (Micheli & Halpern 2005, Stelzenmüller et al. 2009) as marine and freshwater ecosystems remain vulnerable to loss of species (Mouillot et al. 2014, Toussaint et al. 2016). However, trait diversity may still be significantly underrepresented in protected areas (Devictor et al. 2010, Guilhaumon et al. 2015). This study shows that using trait-based approaches can provide information relevant to conservation and management which could not be obtained through the use of taxonomy-based biodiversity indicators alone. The results emphasize the importance of investigating multiple components of biodiversity (e.g. taxonomy, traits and abundances) to reveal temporal and spatial incongruences, and community assembly rules, but also to inform conservation efforts to protect a broader scope of biodiversity components in general.

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Table S1-1: Overview of species aggregations into multi-species groups.

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<th>Reported species</th>
<th>Multi-species group</th>
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<td>Mustelus spp.</td>
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<td>Mustelus asterias</td>
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<tr>
<td>Callionymus maculatus</td>
<td>Callionymus spp.</td>
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<td>Callionymus reticulates</td>
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<tr>
<td>Callionymidae</td>
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<td>Translucent gobies</td>
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<tr>
<td>Crystallogobius linearis</td>
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<td>Liparis spp.</td>
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Appendix S2

Table S2-1: List of all taxa in the study, together with their corresponding length-weight regression parameters $a$ and $b$. Length to weight conversion was done using the equation $W = aL^b$, where $L$ represents the length class (cm) indicated in the DATRAS NS-IBTS data. Parameters were obtained from Fung et al. (2012) unless stated otherwise.

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<th>Taxa</th>
<th>$a$</th>
<th>$b$</th>
<th>Reference</th>
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Appendix S3

Figure S5-1: Barplot of relative biomass of all taxa.
## Appendix S4

Table S3-1: Trait information for all species. List of species with trait information and references. (*L*∞ (cm) (von Bertalanffy length at infinity); Age at 50% maturity (years) (age at which 50% of the population become mature for the first time); Fecundity (Average number of eggs per adult female for one spawning season); Offspring size (mm) (Size of the released eggs or young (in case of live birth)); Body shape (shape of body); Diet (main dietary group(s)); Spawning behavior (reproductive mode); Fin shape (the shape of the caudal fin). * inferred from *A. silus; ** inferred from *L. naevus; *** inferred from *P. pollachius

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<th>Offspring size</th>
<th>Body shape</th>
<th>Diet</th>
<th>Spawning strategy</th>
<th>Fin shape</th>
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<td>17</td>
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<td>Benth-o-piscivore</td>
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Supplementary Material
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<td>Offspring size</td>
<td>Body shape</td>
<td>Diet</td>
<td>Spawning strategy</td>
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<td>Reference</td>
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<td>Os</td>
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<td>Op</td>
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<td>Benthivore</td>
<td>V</td>
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Appendix S5

Table S4-1: Summary statistics of natural and anthropogenic environmental covariates used in the Relative Variable Importance analysis

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<th>Maximum</th>
<th>Mean</th>
<th>Median</th>
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<td>3568.6</td>
<td>1930.8</td>
<td>7260.4</td>
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</table>


Data Availability Statement

Data available on request:

**Phytoplankton Colour Index (PCI):** The specific PCI dataset used in the study is not allowed to be shared. However, individual requests can be made to the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). Information on PCI dataset used in the analysis (DOI: 10.7487/2016.109.1.969) can be found at http://doi.sahfos.ac.uk/doi-library/tim-dencker.aspx. Data request form can be found at https://www.sahfos.ac.uk/data/our-data/ or directly contact djoh@sahfos.ac.uk for dataset requests.

**Beam effort:** Beam effort data for the period 1990 to 1995 were obtained from simon.jennings@uea.ac.uk and is available at https://www.researchgate.net/publication/314242635_North_Sea_fishing_effort_data_from_Fisheries_Research_40_125-134_1999.

Beam effort data for the period 2003 to 2012 were obtained from georg.engelhard@cefas.co.uk and originated from [49].

**Otter effort:** Otter effort data for the period 1990 to 1995 were obtained from simon.jennings@uea.ac.uk and is available at https://www.researchgate.net/publication/314242635_North_Sea_fishing_effort_data_from_Fisheries_Research_40_125-134_1999.
Otter effort data for the period 2003 to 2012 were obtained from [49].

Appendix S6

Figure S6-1: Temporal trends of ratios between TRic and SRic (A), and TEve and SEve (B). Blue curves represent fitted generalized additive models. Grey shaded areas represent 95% confident intervals.
Bibliography


Chapter 5

Large-scale patterns and drivers of marine beta-diversity shed light on the underlying processes of community assembly across latitudes

Tim Spaanheden Dencker¹, Aurore Maureaud¹, Malin Pinsky², Martin Lindegren¹

¹ Centre for Ocean Life, National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, Kgs. Lyngby, Denmark
² Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, New Jersey, United States of America
Abstract

Studies of changes in community compositions, also known as beta-diversity, have often been focused on taxonomic shifts, ignoring important ecological trait-differences between species. Integrating species trait information in studies of biodiversity may reveal new biogeographical patterns and provide insight into community assembly processes. We investigated the latitudinal patterns of taxonomic and trait beta-diversity in marine demersal fish, partitioning total beta-diversity into its turnover and nestedness-components, and determining the degree to which niche-based and neutral processes structure spatial community patterns. By standardizing sampling effort across 18 combined demersal trawl surveys, we showed distinct patterns of both taxonomic and trait beta-diversity and nestedness across spatial scales. Variation partitioning revealed that both taxonomic and trait beta-diversity were spatially structured and mainly driven by niche-based processes related to variation in temperature, bathymetry and available energy at coarse biogeographical scales.
5.1 Introduction

Life on Earth is heterogeneously distributed, and consistent broad-scale patterns, such as the latitudinal diversity gradient, are observed across spatial scales in both terrestrial and marine realms (Gaston 2000, Hillebrand 2004, Tittensor et al. 2010, Worm & Tittensor 2018). Despite a long history of research demonstrating the generality of these patterns, the drivers and processes giving rise and maintaining them still remain debated (Rohde 1992, Hillebrand 2004, Kinlock et al. 2018, Sutherland et al. 2013). Underlying these spatial patterns in biodiversity is the continuous addition and loss of species, and as such, studying compositional changes in biological communities along gradients may provide key insights into the factors structuring the distribution of life (Svenning et al. 2011, Myers & LaManna 2016, Mori et al. 2018).

In his seminal work R. H. Whittaker laid the foundation for quantifying the ‘extent of change in community composition’ between sites by introducing the term beta-diversity (Whittaker 1960, 1972). Beta-diversity forms the link between site-specific diversity (alpha-diversity) and region-specific diversity (gamma-diversity). It therefore provides a suitable framework for investigating mechanisms of community assembly and biodiversity patterns at large (Svenning et al. 2011, Swenson et al. 2012, Yang et al. 2015, Smit et al. 2017, Zellweger et al. 2017), as well as providing valuable information for conservation and management (Socolar et al. 2016). Studies addressing beta-diversity have increased markedly over the last two decades (Anderson et al. 2011) and the concept has been extended with an array of new methodological approaches (Tuomisto 2010, Anderson et al. 2011) since its original conception (Jaccard 1912, Simpson 1943, Whittaker 1960). One such extension is a general framework to distinguish the ecological processes acting on community assembly by partitioning total beta-diversity into its two antithetic components, turnover and nestedness (Baselga 2010). Turnover signifies replacement of species between communities (Baselga 2010), typically caused by habitat heterogeneity, dispersal barriers and local speciation (Condit 2002, Gaston, Evans, et al. 2007, Fitzpatrick et al. 2013, Soininen et al. 2017). Nestedness, on the other hand, refers to species loss or gains leading to richness difference between nested communities and may be more related to environmental filtering, and selective extinction-recolonization along gradients (Ulrich & Gotelli 2009). In addition to new methodological approaches, studies of beta-diversity are increasingly incorporating information on the ecological traits of organisms (e.g. morphological, physiological and behavioral characteristics affecting individual fitness
(Violle et al. 2007, Litchman et al. 2013) as an alternative, or complement to taxonomy-based measures (Swenson et al. 2012, Villéger et al. 2012, 2013, 2014, Bishop et al. 2015, Loiseau et al. 2017, Holt et al. 2018). This shift comes from the recognition that taxonomy alone does not provide information on the species’ niches and functional role in the ecosystem (McGill et al. 2006) and that by incorporating ecological traits, we can better identify the structuring processes of community composition and its changes in space and time (Bellwood et al. 2002, Swenson et al. 2011). Together, these two additions may enable insights into the underlying processes that have shaped and maintain patterns of biodiversity across latitudes and along environmental gradients (Baselga 2010, Swenson et al. 2011, Soininen et al. 2017).

These processes, suggested to determine the distributions and composition of biodiversity, fall within two broad categories: the \textit{niche-based deterministic processes} (MacArthur & Levins 1967, Chase & Myers 2011) and the \textit{spatial-based neutral processes} (Hubbell 2001, MacArthur & Wilson 2009, Chase & Myers 2011). The former proposes that environmental filtering determines species distributions and community composition by the match of a species’ fundamental niche requirements with prevailing environmental conditions (Hutchinson 1957, MacArthur & Levins 1967). Structures within environmental gradients should thus be reflected in a sorting of species based on their ecological traits and adaptations to contemporary environmental conditions (Hutchinson 1957, Chase & Leibold 2003, Qiao et al. 2015). The latter process proposes that species do not differ in their affinities for particular environments, and rather that distribution patterns observed in natural communities may be explained by spatial processes, such as dispersal limitations and stochastic events, without the need to infer the species’ fundamental niche and environmental preferences (Hubbell 2001). This should thus be reflected in a spatial (i.e., distance) gradient over which communities differ. Contemporary understanding of community assembly mechanisms suggests that niche and neutral processes are not antithetic to each other, and that both processes may interact and act upon communities at the same time (Chase & Myers 2011). Partitioning the contribution of niche-based and neutral processes in explaining patterns of beta-diversity hence enables ecologists to tease apart the underlying mechanisms of community assembly and provide a more mechanistic framework for macroecological studies (Rodríguez-Zaragoza et al. 2011, De Cáceres et al. 2012, Smit et al. 2017, Zellweger et al. 2017, Chiantore et al. 2018).
In order to shed light on the biogeographical patterns and underlying mechanisms of community assembly, high-resolution data on species occurrences and traits sampled across large spatial scales and ranges in environmental conditions are needed but often lacking, especially in the ocean. As a result, our understanding of macroecological patterns and drivers of marine biodiversity lags behind that of terrestrial realms. However, fisheries-independent scientific surveys, as well as extensive repositories of trait information are increasingly becoming publically available (Batt et al. 2015; Froese & Pauly 2015; Edgar & Stuart-Smith 2016), hence enabling marine ecologists to study macroecological patterns at a high spatial and temporal resolution on a near global scale. In this study, we compiled an extensive dataset of species occurrences and life-history traits for ~1000 demersal (bottom-living) fish species sampled across ~173,000 individual geo-referenced hauls across the continental shelves of the North Atlantic and Northeast Pacific. Based on this unique, high-resolution data set, we formulated and tested a set of hypotheses with the overall aim of understanding the patterns, drivers and underlying processes of marine taxonomic and trait beta-diversity across and along three latitudinal gradients spanning from subtropical to polar waters in the North Atlantic and North Pacific.

In accordance with niche-based theory, traits define a species’ fundamental niche (Hutchinson 1957, Violle & Jiang 2009) and thus the type of habitats and environmental conditions under which it can exist and thrive (Southwood 1977, Lamouroux et al. 2002, Weinstein et al. 2014, Pécuchet et al. 2016, Penone et al. 2016). Consequently, if areas share similar environmental conditions, but are otherwise currently or historically isolated, community compositions should differ in terms of taxonomy, but share similar traits. Previous studies conducted across a range of organism groups suggest that while species identity may shift markedly between areas, similarities in environmental conditions can lead to convergence in trait compositions along spatial gradients (Qian & Ricklefs 2000, Lamouroux et al. 2002, Siefert et al. 2013, Villéger et al. 2013, Dolbeth et al. 2016). If environmental conditions across spatial gradients exhibit a degree of homogeneity, we hypothesize that trait beta-diversity is lower than taxonomic beta-diversity between and within coastlines ($H_1$) and that the nestedness-component of beta-diversity will be consistently higher for traits than for taxonomy ($H_2$). Finally, previous studies on beta-diversity across environmental and spatial suggests that both niche-based and neutral assembly processes can act across a variation of scales (Legendre et al. 2009, Rodríguez-
Materials & Methods

Trawl survey data

Georeferenced data on the occurrences of marine demersal fish species were collected from 18 fisheries-independent scientific bottom trawl surveys operating on the continental shelves of the Northeast Pacific, Northwest Atlantic, and Northeast Atlantic. The combined surveys covered 173,949 individual geo-referenced hauls sampled across latitudes (i.e., range from 24°-81°N) and seasons over a total of 50 years from 1968 to 2017 (Appendix S1) with 2603 registered marine taxa. To reduce the influence of local-scale dynamics and variation, and to emphasize regional-scale patterns, hauls were aggregated within 1.5° by 1.5° grid cells. For each of the 722 created grid cells, sampling across years were aggregated so as to only investigate spatial patterns. To enable a comparison of patterns, drivers and processes of community composition along multiple latitudinal gradients we divided the combined dataset into three coastlines corresponding to the Northeast Pacific, Northwest Atlantic, and Northeast Atlantic. The trawl survey data from Southern Greenland was included in the Northwest Atlantic cluster. In order to use data consistently across surveys, several standardizations were performed to correct for differences in sampling within and between surveys. First, all invertebrate and mammalian species were removed, leaving only species in a paraphyletic group consisting of Elasmobranchii, Actinopterygii, Holocephali, Myxini, and Petromyzonti, henceforth referred to as “fish”. Due to inconsistencies in the classification of species across surveys, each species name was checked against the World Register of Marine Species (Horton et al. 2018), and updated to the accepted scientific name when appropriate. Then, only entries reported to species level were retained. Secondly, hauls with a depth above 20 meters and below 380 meters (i.e., corresponding to the 95% percentile of sampling depths across all surveys) were excluded to avoid including coastal and deep-water species that were not targeted or well-sampled by the surveys. Thirdly, pelagic species not accurately sampled by bottom-trawling
gears were excluded according to the habitat trait listed in Beukhof et al. *in prep* (chapter 7), hence restricting the analysis to demersal (bottom-living) fish species.

**Trait data**

To broadly represent the life history and ecology of fish in terms of their feeding, growth, survival and reproduction (Winemiller & Rose 1992) we selected species specific information on six traits including: maximum length, life span, trophic level, fecundity, offspring size and parental care. These traits, either separately or in combination, have been shown to vary markedly along environmental gradients in both freshwater and marine ecosystems (Mims et al. 2010; Fisher et al. 2011, Pecuchet et al. 2017), making them a suitable selection of traits to be used in studies of community composition and its changes in space and time. Trait information for each of the six traits was sourced from Beukhof et al. *in prep* (chapter 7). Only species for which we found complete trait information for all traits were kept for further analysis (mean trait cover for species: 91% (Appendix S2)). To incorporate information on intraspecific trait variability, we collected available area-specific trait values for each species, averaged at the spatial scale of Large Marine Ecosystem (LME) or the official areas used by the Food & Agriculture Organization (FAO). Taking into account intraspecific variation in traits resulted in 2438 unique combinations of species and trait values.

**Sampling heterogeneity and standardization of sampling effort**

The number of available hauls within each grid cell varied from 1 to 1841 (Appendix S3). This apparent heterogeneity in sampling effort is important to standardize for, since differences in effort can bias results and potentially lead to faulty comparisons (Chao & Jost 2012). A commonly used method to assess the level of completeness of sampling is to construct species accumulation curves (SACs), where the species richness sampled is a function of the sampled area or of the number of samples. In order to standardize sampling effort across grid cells, we constructed SACs and fitted Michaelis-Menten functions to estimate the asymptotic species richness for each grid cell based on all available hauls (using the “vegan” package in R; Oksanen et al. 2017) (Appendix S3). We decided to standardize according to completeness of sampling (Chao & Jost 2012), not equal sampling effort across grid cells, to satisfy the replication principle (Hill 1973, Chao & Jost 2012). Since three samples is the minimum number of samples needed to construct a SAC, all grid cells with less than three hauls were
5.2 Materials & Methods

removed prior to constructing SACs. To represent various levels of taxonomic completeness the number of samples needed to achieve 80, 65 or 50% of the estimated asymptotic species richness in each grid cell was calculated. All grid cells that did not meet the required number of samples for the desired level of completeness were removed from the analysis. As the number of discarded grid cells across the different thresholds of completeness was small, we selected the highest threshold (80% completeness) to maximize community information for each grid cell (Appendix S3). After standardization of taxonomy and trait information, and sampling coverage, a total of 1006 species from 164,397 unique hauls within 675 grid cells were included in the analysis.

**Calculation of biodiversity metrics**

In order to avoid sampling bias in the calculation of biodiversity metrics, each grid cell was randomly resampled through 999 permutations for the required number of hauls to reach the desired 80% level of taxonomic completeness. All biodiversity metrics were calculated for each permutation and afterwards averaged. Taxonomic and trait beta-diversity were calculated at three spatial scales: i) across all three coastlines (Figure 1A), ii) per coastline (Figure 1B), and iii) per grid cell (Figure 1C), representing hemisphere, regional and local scale spatial resolution respectively. The three scales were chosen to reflect hypotheses H1 and H2 regarding spatial patterns of total beta-diversity and its nestedness component for taxonomy and traits. For the comparisons across coastlines at hemisphere scale and within coastlines at regional scale, we calculated beta-diversity metrics as multiple-site dissimilarity for total beta-diversity and its turnover and nestedness components following Baselga (2012) and Villéger et al. (2011). Per grid cell beta-diversity at local scale was derived from pairwise dissimilarities between each grid cell and its neighboring cells. This was done by using a “sliding window” approach, where a focal cell along with its adjacent grid cells within a 2.5° radius was considered. Pairwise dissimilarities were then calculated and the average value was attributed to the focal cell. This window of focus was then shifted along latitudes until all grid cells along a coastline were compared to its respective adjacent grid cells within the given radius. This method allowed us to express the “uniqueness” of each grid cell in relation to smaller scale latitudinal changes along coastlines (Williams et al. 1999, Gaston, Davies, et al. 2007, Kallimanis et al. 2007, Melo et al. 2009, Leprieur et al. 2011, Maestri & Patterson 2016). For near-edge grid cells close to survey boundaries or coastlines fewer comparisons were available. For the sliding window
approach, nestedness was standardized by total beta-diversity to reflect latitudinal changes in its importance despite changing total beta-diversity. Pairwise calculations of taxonomic beta-diversity and its turnover and nestedness components followed the methods outlined in Baselga (2010) and (2012), and pairwise calculations of trait beta-diversity and its nestedness component followed the methods outlined in Villéger et al. (2013). For our third hypothesis (H₃) and investigation of the importance of niche and neutral theory assembly rules for beta-diversity along coastlines, we calculated a full pairwise distance matrix between grid cells for each coastline for both total taxonomic and total trait beta-diversity (Figure 1D). These six distance matrices allowed us to investigate the degree to which the different assembly rules acted on the two types of beta-diversity (i.e., taxonomy and traits) and how this varied between coastlines.

Gower’s distance (Gower 1971) was used to calculate trait-based distances between pairs of species. Gower’s distance was chosen as it allows for standardization of mixed-type trait data, including both continuous and categorical variables. We then performed a principle coordinate analysis (PCoA) on the resulting distance matrix (Villéger et al. 2008, Laliberte & Legendre 2010). The first three axes of the PCoA were retained as they cumulatively explained 82% of the variation in traits, following a trade-off between variation explained and computation time. Trait-based beta-diversity can then be expressed as the trait space not shared between two communities divided by the total trait space of both communities. This makes the measure analogous to the Jaccard dissimilarity index (Jaccard 1912) used for taxonomic beta-diversity in this study. Consequently, it can be further divided into its turnover and nestedness components. Calculations of beta-diversity were performed with the “betapart” R package (Baselga & Orme 2012, Baselga et al. 2017). Details of calculations of beta-diversity and its turnover and nestedness components are outlined in Appendix S4.
5.2 Materials & Methods

Figure 1: Graphical representation of the input data, data processing and subsequent set of analyses performed within this study. Matrices and arrows indicate data and direction of processing and analysis. Blue: species occurrence and biodiversity data analyses; teal: trait data and trait beta-diversity matrices; green: environmental predictor variables; brown: 96ortionin distance between grid cells within each coastline. Analyses are marked with references to either tables or figures within this study. Capital letters in red corresponds to the three different scales at which beta-diversity was calculated at for testing hypotheses H1 and H2 and full beta-diversity distance matrices used for testing H3: A: Multiple-site hemisphere total taxonomic and trait beta-diversity and its turnover and nestedness components (largest dotted square); B: Multiple-site coastline total taxonomic and trait beta-diversity and its turnover and nestedness components (smallest dotted square); C refers to a graphical presentation of the pairwise-comparisons used in the sliding window approach with the focal cell marked with a red dot and the adjacent cells within the selected radius (green dotted circle); D refers to the six full distance matrices for total taxonomic and trait beta-diversity for all coastlines used to investigate community assembly rules.

Environmental and spatial predictor variables

In order to identify key drivers explaining the derived patterns of taxonomic and trait beta-diversity, six candidate environmental predictor variables were obtained for each grid cell to
represent the effects of temperature, availability of energy, and bathymetry. Temperature is commonly regarded as a major determinant of biodiversity patterns across taxa in both terrestrial and marine realms (Roy et al. 1998, Gaston 2000, Willig et al. 2003, Fuhrman et al. 2008, Tittensor et al. 2010, Stuart-Smith et al. 2017). Another suggested driver is the availability of energy (e.g., in terms of light and nutrients), largely resulting in spatial differences in primary production and the way it is channeled through food-webs (Evans et al. 2005, van Denderen et al. 2017). Last, differences in depth may affect regional patterns of richness and community composition (Anderson et al. 2013, Mindel et al. 2016, Zintzen et al. 2017). Three different temperature variables were included: annual average SST (SST\textsubscript{ann}), annual minimum SST (SST\textsubscript{min}), and annual variation in SST (SST\textsubscript{var}). All temperature variables were obtained from The Hadley Centre Global Sea Ice and Sea Surface Temperature (HadISST) dataset (Rayner et al. 2003). As a measure of energy or basal resource availability, net primary production (NPP) (mg chlorophyll \(a\) \(m^{-3}\) \(d^{-1}\)) was calculated as the annual mean of each grid cell and was obtained from the vertically generalized production model using MODIS data from between 2003 and 2008 (http://www.science.oregonstate.edu/ocean.productivity) (Behrenfeld & Falkowski 1997). Average depth of each grid cell was calculated from the trawl survey data. In addition, a metric of seabed rugosity was calculated as the mean of the absolute difference between a given grid cell and the depths of the eight surrounding cells. Rugosity was calculated using the “raster” package in R (Hijmans 2016). To account for potential non-linear relationships between beta-diversity metrics and variables we added quadratic terms to all candidate variables. To avoid co-linearity between variables Variance Inflation Factor (VIF) was computed for all 12 variables. Given a threshold of VIF>5 (Kutner et al. 2004) SST\textsubscript{min} was excluded from the analysis (Appendix S5).

In addition to the environmental predictors, we derived spatial predictor variables. These were based on distance-based Moran’s eigenvector maps (dbMEMs) (Dray, Legendre, and Peres-Neto 2006). dbMEMs express the spatial autocorrelation structures between samples, ranging from fine to coarse spatial scales (Borcard et al. 2018). A PcoA was performed on a geographic distance matrix created from the Euclidean distances between grid cell centroids within each coastline (Figure 1). Principal coordinates for each positive eigenvalue were retained as Moran’s eigenvector maps. Coarse-scale variation is captured by the first eigenvectors, while medium and fine-scale variation is represented by progressively smaller eigenvectors. A total
of 61, 82 and 151 positive dbMEMs were constructed for Northeast Pacific, Northwest Atlantic, and Northeast Atlantic, respectively, out of which 13, 29 and 34 were retained after checking for significant positive autocorrelations using Moran’s I ($p \leq .05$ in Moran’s I test). The retained dbMEMs were visually checked to see if they still captured a variety of scales ranging from coarse to fine. The dbMEMs are henceforth referred to as spatial structures and allowed for a description of the spatial autocorrelation structures among grid cells.

**Investigating key drivers of beta-diversity**

Distance-based redundancy analysis (dbRDA; Legendre & Andersson 1999) was used to test the relationship between taxonomic and trait-based beta-diversity and the sets of environmental and spatial predictor variables for each coastline (Figure 1). dbRDA is a multivariate multiple linear regression method followed by a PCoA analysis technique (Borcard et al. 2018). It allows for extracting and summarizing variation explained in a set of response variables (e.g., beta-diversity distance matrices) by a set of explanatory variables (e.g., environmental and spatial distance matrices, such as spatial structures derived from dbMEM analysis) (Borcard et al. 2018). Traditional dbRDA relies on Euclidean distances (Legendre & Legendre, 2012), but as described in McArdle & Anderson (2001), using non-Euclidean distances (such as Jaccard dissimilarities) can inflate the total sum of squares of the non-Euclidean response matrix, hence affecting the model’s explanatory power. McArdle & Anderson (2001) incorporated a multi-response permutation test accounting for the inflated total sum of squares when using non-Euclidean distances. This permutation test was integrated into the modified dbRDA by Legendre (2014), here referred to as dbRDA.D. This method was applied to full distance matrices of total taxonomic and trait beta-diversity for each coastline (Figure 1D).

First, we ran a full dbRDA.D with the taxonomic and trait beta-diversity distance matrices for each coastline against all the retained environmental predictors. Then, a backward-selection procedure as described by (Blanchet et al. 2008) was used to reduce the risk of type I errors and arrive at a more parsimonious set of predictors, after which the individual and cumulative importance of the selected predictors was assessed for each metric of beta-diversity for each coastline (Appendix S9).

Second, we calculated the relative contribution of the environmental and spatial predictor variables (Legendre et al. 2005) through variation partitioning. Variation partitioning separates how much the variation in beta-diversity is explained by the spatially-unstructured
and structured environmental predictor variables alone (i.e., niche-based environmental filtering), how much is purely spatially structured (i.e., neutral theory), and how much remains unexplained (Legendre et al. 2005). The unexplained variation may be due to missing important environmental or spatial structures, lack of integration of biotic interactions or stochastic events, which could not be modelled (Borcard et al. 2004). In order to disentangle the relative importance of niche-based and neutral theory processes, the predictor variables were clustered into two groups corresponding to the environmental or spatial structures. Only environmental predictor variables from the backward-selection were used.

Third, we assessed the importance of each of the spatial structures found across the set of retained dbMEMS following Ollier, Couteron, and Chessel (2006) and Moura et al. (2017). A stepwise dbRDA.D was computed on each distance matrix of taxonomy and trait beta-diversity along the coastlines. The initial step of the dbRDA.D contained only the coarsest spatial structure (i.e., the 1st dbMEM) as a predictor variable. Each step then added the subsequent spatial structure until all structures (going from coarsest to finest scale) had been included. For each added spatial structure, the adjusted-$R^2$ of variation explained by the included spatial structure was computed. The output was used to construct orthogram plots with cumulative adjusted-$R^2$ plotted against the spatial structures (Ollier, Couteron, and Chessel 2006). Finally, to assess the individual contributions of different types of environmental predictor variables, we grouped them into three clusters relating to temperature, availability of energy and bathymetry (Figure 4). The contribution of each cluster and the shared contribution between them were computed using the adjusted-$R^2$ from multiple dbRDA.D tests done on all possible combinations of clusters. All calculations and statistical analysis were performed in R version 3.4.0 (R Core Team 2016).

5.3 Results

Spatial patterns of taxonomic and trait beta-diversity

Hemisphere-scale multiple-site total taxonomic beta-diversity was high and driven by turnover, signifying a near complete taxonomic replacement between the Atlantic and Pacific coastlines. Total trait beta-diversity was lower than its taxonomic counterpart, and was marked by a higher proportion of nestedness (Table 1). Multiple-site calculations of beta-diversity at regional scale within coastlines revealed similar pronounced taxonomic replacement. While total taxonomic beta-diversity remained high (e.g. close to 1) for each coastline and was dominated by a high
5.3 Results

dergree of turnover, total trait beta-diversity was lower (between 0.64 and 0.73) and the
nestedness-component constituted a greater proportion (Table 1). The multiple-site beta-
diversity values at hemisphere and regional scales indicate that the trait composition of
communities was more nested within each other than taxonomic composition across and along
coastlines. The sliding window approach, aiming to represent latitudinal changes in community
and trait composition at local scales within coastlines, revealed that mean trait beta-diversity
across latitudinal bands was significantly and consistently lower than taxonomic beta-diversity
(Appendix S6). This significant difference between the two beta-diversity metrics was
consistent across coastlines (Figure 2C). Furthermore, the mean nestedness-component of total
beta-diversity across latitudinal bands was significantly higher for traits than taxonomy for both
the Pacific and Atlantic coastlines (Appendix S6, Figure 2F), indicating lower replacement of
traits compared to species along coastlines. In addition, the proportion of taxonomic nestedness
generally increased from low to higher latitudes, especially along the Northwest Atlantic
coastline where a clear linear increasing trend was observed. However, in the Northeast Pacific
and Northeast Atlantic the proportion of nestedness decreased again at high latitudes (i.e., at
~45°N and 65°C, respectively). Albeit being significantly different from each other along all
coastlines, taxonomic beta-diversity and trait beta-diversity exhibited a high degree of variation
in overlap and divergence within coastlines. Both measures of beta-diversity followed a similar
trajectory across latitudinal steps on the Pacific US coastline (Figure 2C). A similar parallel
latitudinal trajectory was not observed along neither coastlines in the Atlantic Ocean (Figure
2C). Several areas of overlap between the measures of beta-diversity were observed along the
Northwest Atlantic and Northeast Atlantic coastlines (Figure 2C). Not only did both taxonomic
and trait beta-diversity reach high values in the North Sea around the 58th degree latitude, but
there was also a clear overlap between the two measures, suggesting a boundary between two
distinct biogeographic regions, with similarly low species and trait convergence within the
boundary zone.
Table 1: Values of mean taxonomic and trait beta-diversity from multiple-site and pairwise calculations across and within coastlines.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Component</th>
<th>Taxonomy</th>
<th>Trait</th>
</tr>
</thead>
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<tr>
<td></td>
<td>Between coastlines</td>
<td></td>
<td></td>
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<tr>
<td>Multiple-site</td>
<td>Total beta-diversity</td>
<td>0.99 ± 0.001</td>
<td>0.82 ± 0.002</td>
</tr>
<tr>
<td></td>
<td>Turnover</td>
<td>0.98 ± 0.0001</td>
<td>0.67 ± 0.01</td>
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<td></td>
<td>Nestedness</td>
<td>0.01 ± 0.001</td>
<td>0.15 ± 0.003</td>
</tr>
<tr>
<td></td>
<td>Within coastlines</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Multiple-site</td>
<td>Total beta-diversity</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>North Pacifc</td>
<td>0.99 ± 0.001</td>
<td>0.72 ± 0.003</td>
</tr>
<tr>
<td></td>
<td>Trait</td>
<td>0.73 ± 0.002</td>
<td>0.99 ± 0.001</td>
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<tr>
<td></td>
<td>Northwest Atlantic</td>
<td>0.98 ± 0.001</td>
<td>0.60 ± 0.007</td>
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<td></td>
<td>Trait</td>
<td>0.51 ± 0.001</td>
<td>0.98 ± 0.01</td>
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<td>Northeast Atlantic</td>
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<td>0.02 ± 0.001</td>
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<tr>
<td></td>
<td>Trait</td>
<td>0.22 ± 0.001</td>
<td>0.12 ± 0.006</td>
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<tr>
<td></td>
<td>Sliding window*</td>
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<td></td>
<td>Total beta-diversity</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Northeast Pacific</td>
<td>0.53 ± 0.08</td>
<td>0.48 ± 0.09</td>
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<td></td>
<td>Trait</td>
<td>0.24 ± 0.13</td>
<td>0.32 ± 0.14</td>
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<td></td>
<td>Northwest Atlantic</td>
<td>0.48 ± 0.09</td>
<td>0.32 ± 0.14</td>
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<tr>
<td></td>
<td>Trait</td>
<td>0.48 ± 0.07</td>
<td>0.39 ± 0.19</td>
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<tr>
<td></td>
<td>Northeast Atlantic</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trait</td>
<td>28.0 ± 11.0</td>
<td>32.2 ± 13.2</td>
</tr>
</tbody>
</table>

* mean of sliding window values per coastline
◊ Percentage nestedness of total beta-diversity
5.3 Results

Figure 2: Spatial patterns of taxonomic and trait beta-diversity and its nestedness component along coastlines. The taxonomic (A) and trait (B) beta-diversity reflect the mean pair-wise dissimilarity between each grid cell and its neighbouring cells within in 2.5° radius. The taxonomic (D) and trait nestedness (E) reflect the corresponding contribution of nestedness to the total beta-diversity. The box-plots summarizes and compares the taxonomic and trait beta-diversity (C) and nestedness (F) values in bins of 2.5° latitude for each coastline. For visualization a trend line was derived for each set of boxplots using a LOESS smoother.

Environmental and spatial drivers of taxonomic and trait beta-diversity

The variation of beta-diversity along coastlines was explained jointly by both environmental and spatial variables selected by the preceding dbRDA.Ds (Figure 3, Appendix S7). The total variation explained by the set of environmental and spatial predictors was high (55.1 to 71.6%) except for trait beta-diversity along the European coastline, where only 31.4% of the variation was explained. Environmental drivers (either spatially structured or spatially unstructured) were of high importance for both taxonomic and trait beta-diversity, with broad consistency in variation explained across
coastlines (47.1 to 64%), except for trait beta-diversity along the European coastline (variation explained by the environmental drivers: 27.3%).

Taxonomic beta-diversity was to a larger degree explained by the unique contribution of environmental predictors, whereas the contribution of unique spatial structures were higher for trait beta-diversity, albeit still being markedly low compared to the contribution of environmental variables. The observed spatial structures were also investigated across different scales to assess any scale-dependent contributions. Patterns of beta-diversity were mainly driven by processes operating at broad to medium-scales as evident from the orthogram plots (Appendix S8), with little added contribution of explained variation from fine-scale spatial structures.

The contribution to variation explained by environmental gradients was further investigated in detail. Environmental predictors explained a moderate (~25%) to high (~76%) degree of variability in taxonomic and trait beta-diversity along the three coastlines (Appendix S9). Differences in the mean or minimum SST were the most important environmental drivers for all metrics of beta-diversity across coastlines. In addition to temperature-related variables, differences in the mean depth was found to be an important predictor for both taxonomic and trait beta-diversity along coastlines.
5.3 Results

Differences in NPP explained only a minor degree of variability, indicating that availability of energy was a poor predictor of taxonomic or trait beta-diversity. To assess the unique and joint contribution of temperature, energy and bathymetry-related predictor variables, three distinct clusters were used. Temperature predictors formed the most important individual cluster for all coastlines and metrics (Figure 4). Energy in the form of available energy from NPP was the least important cluster, yet had a relative large joint contribution with bathymetry for taxonomic beta-diversity along all three coastlines, and trait beta-diversity along the Pacific US. The highest variation explained was for taxonomic beta-diversity along the Northwest Atlantic coastline, while the residual unexplained variation varied between 23.3% and 47.1%, except for trait beta-diversity along the European coastline, where only 27% of the variation was explained.

Figure 4: Variation partitioning of taxonomic (A, B and C) and trait (D, E and F) beta-diversity along the three coastlines according to temperature-, energy- and bathymetry-related predictor variable clusters. Different letters are assigned to each unique or joint contribution: [a] temperature unique, [b] energy unique, [c] bathymetry unique, [d] temperature+energy, [e] temperature+bathymetry, [f] energy+bathymetry, [g] temperature+energy+bathymetry. Values are reported in percentages of total variation.


5.4 Discussion

Uncovering the community assembly processes that have shaped and maintain the distribution of life on Earth is paramount to predict the consequences of environmental change on community structure. Incorporating several facets of biodiversity into ecological research is therefore an important step. Our study investigated the compositional change in species and their ecological traits along latitudinal gradients in the Pacific and Atlantic Oceans covering subtropical to polar climates. Distinct patterns of beta-diversity and its nestedness component were evident between and along coastlines, revealing consistent latitudinal gradients and potential convergence of ecological traits across spatial distances. Changes in both community and trait composition were mainly driven by niche-based environmental filtering linked to abiotic drivers relating to temperature variation and shared contributions between depth and available energy.

To shed light on the patterns, drivers and mechanisms underlying changes in species and trait composition along the latitudinal biodiversity gradient a set of hypotheses pertaining to the expected relationship between taxonomic and trait beta-diversity and their latitudinal changes along coastlines were proposed. Studies of global or regional patterns of beta-diversity have shown that compositional change is often characterized by turnover of species, caused by differences in environmental conditions or historical and contemporary physical barriers for dispersal and colonization (Svenning et al. 2011, Villéger et al. 2013, Viana et al. 2016, Alahuhta et al. 2017). The effect of physical barriers is clearly evidenced by the marked taxonomic turnover between the Northeast Pacific and the North Atlantic, which have been virtually separated for millions of years (Briggs 1970). However, despite the large differences in species composition we found similar trends of taxonomic turnover along all coastlines. In previous studies investigating geographical patterns of both taxonomic and trait beta-diversity, high taxonomic turnover between assemblages have been shown to be contrasted by considerably lower trait turnover and a larger contribution of nestedness, indicating that traits are more converged across spatial gradients. Such convergence of traits across gradients of taxonomic turnover has been found in multiple taxa, ecosystems and scales, including North American trees, global terrestrial mammals and birds (Siefert et al. 2013, Penone et al. 2016, Ricklefs 2012), as well as freshwater, reef and estuarine fish across continental scales (Lamouroux et al. 2002, Villéger et al. 2013, Bender et al. 2017; Dolbeth et al. 2016). This convergent evolution may be explained by the habitat template concept (Southwood 1977, Winemiller et al. 2015), which predicts that species inhabiting similar environments exhibit similar traits. We found that trait beta-diversity in marine
demersal fish was significantly lower than its taxonomic counterpart and was characterized by a higher degree of nestedness than taxonomic beta-diversity across several scales, going from hemisphere to local scale within all three coastlines, hence confirming our $H_1$ and $H_2$ hypotheses. These results suggest that the environmental conditions characterizing the demersal habitats in this study is nested between and along the coastlines, while certain barriers or dispersal limits may hinder species from spreading, leading to assemblages with high taxonomic turnover, but nested trait compositions. For marine demersal communities several barriers of dispersal may limit distributions of certain species, creating taxonomically distinct biotas. At large scales, a lack of ocean current connectivity and unsuitable deep sea basins may limit dispersal (Muss et al. 2001, Luiz et al. 2012), while locale scale features such as steep environmental gradients around transitional zones or physical barriers, such as submerged canyons or land masses may lead to high taxonomic turnover (Muss et al. 2001, Shaw et al. 2004, Luiz et al. 2012, Anderson et al. 2013, Navarrete et al. 2014). While our study does not explicitly investigate trait convergence, the partitioning of beta-diversity into its turnover and nestedness-components and the use of traits allowed us to identify the spatial patterns which may stem from such underlying processes. Our results emphasize the importance of these new methodological approaches in studies of beta-diversity.

The proportion of nestedness in taxonomic beta-diversity increased along both Atlantic coastlines, suggesting a potential macroecological pattern in marine demersal fish. A latitudinal gradient in nestedness has previously been documented in studies of dung beetles (Baselga 2010), amphibians (Baselga et al. 2012), birds, mammals (Dobrovolski et al. 2012) and freshwater fish (Leprieur et al. 2011). A recent cross-realm and cross-taxa meta-analysis (Soininen et al. 2017) specifically attributed these patterns to historical events, such as glaciations and to environmental filtering under contemporary climatic conditions (Leprieur et al. 2011, Baselga et al. 2012, Dobrovolski et al. 2012). Furthermore, these studies found that higher degrees of nestedness of taxonomic beta-diversity was correlated to the amount of time an area had been ice-free since the last maximum glaciation event, with a higher degree of nestedness for areas with more recent glaciation. Glaciations in the Northern Hemisphere during the Quaternary period would have affected small-range species (Pianka 1966, Davies et al. 2011), while post-glaciation recolonization from adjacent areas could lead to nested communities, as only a subset of a species-rich community would be able to establish itself into a new environment (Baselga 2010, Davies et al. 2011, Soininen et al. 2017). However, we observed a decrease in nestedness in the Northeast Atlantic above 65° N a coincides with the biogeographical
transition zone in the Barents Sea, where more southern Boreal species assemblages meet northern Arctic assemblages (Johannesen et al. 2012). Across this boundary zone, related to the flow and currents of converging Atlantic and Arctic waters (Loeng 1991), the demersal fish communities change taxonomically towards more Arctic species (Wiedmann, Aschan, et al. 2014, Wiedmann, Primicerio, et al. 2014), which would decrease the proportion of nestedness.

By partitioning the explained variation in beta-diversity between environmental gradients and pure spatial structures, we assessed the strength of community assembly processes suggested to shape and maintain patterns of variation in biodiversity, namely environmental niche-based deterministic processes and the spatial-based neutral processes (Borcard et al. 1992, Legendre et al. 2005, 2009). It is recognized that the processes are not antithetic (Thompson & Townsend 2006, Chase & Myers 2011), and the degree to which either process acts on shaping communities varies between taxonomic groups, ecosystems and spatial scale (Jones et al. 2008, Smith & Lundholm 2010, Myers et al. 2013, Yang et al. 2015, Soininen et al. 2016, Smit et al. 2017). Beta-diversity of both taxonomy and traits in marine demersal fish was mainly explained by environmental drivers, both spatially unstructured and structured, suggesting that deterministic niche-assembly processes relating to environmental filtering, were the main processes structuring communities, thereby confirming our third hypothesis.

The contribution of environmental gradients was largely consistent across the Northeast Pacific and North Atlantic, signifying that fish communities across all coastlines are mainly structured by similar deterministic niche-based processes. While niche-based processes were of highest importance overall, our study detected spatial structures in the species and trait composition between communities that were not related to environmental gradients, indicating that the two facets of biodiversity do not respond in similar ways to the structuring processes. The importance of these purely spatial gradients are often linked to neutral processes, such as dispersal limitation (Gilbert & Lechowicz 2004, Legendre et al. 2009, Smit et al. 2017). While the selected life-history traits used in the study have been shown to be closely linked to environmental gradients, they may also indicate variation in dispersal capabilities between the three overall life-history strategies (i.e. opportunistic, equilibrium and periodic species). This link has not been tested specifically for marine fish, but studies from freshwater systems indicate that dispersal modes are linked to life-history traits (Comte & Olden 2018). The spatial signal observed for trait beta-diversity in our study may indicate that differences in trait composition between communities are driven by variability in dispersal capabilities inherent to the selected life-history trait strategies.
However, pure spatial structures may not necessarily be linked directly to neutral theory processes, but could also represent abiotic gradients not accounted for in our study (Legendre et al. 2005), or anthropogenic impacts from habitat destruction and fishing (Lotze et al. 2006), as well historical climatic variation (Svenning et al. 2011, Leprieur et al. 2011, Dobrovolski et al. 2012). If such unaccounted variables have a spatial structure, the resulting spatial organization would be evident in the present study, but inaccurately be attributed to the contribution of neutral theory processes. Furthermore, it is important to recognize that our analysis covers mostly temperate to subpolar waters and, that the strength and relative importance of different assembly processes may vary with latitude, as shown by Myers et al. (2013), where temperate and tropical forest communities were structured according to different mechanisms of community assembly. Additionally, spatial and temporal patterns of beta-diversity are scale dependent (Mac Nally et al. 2004, De Cáceres et al. 2012, Barton et al. 2013), and little conceptual synthesis of potential scale dependence of beta-diversity exists (Barton et al. 2013). As the orthogram analysis revealed that the significant spatial factors included in the study represented processes evident predominantly at coarse to intermediate spatial scales. The observed scale at which these assembly processes are detected depend on the scale of each study, as determined by the smallest distance between sampling locations. In the present study, we aggregated species occurrences within 1.5° grid cells. The distance between centroids of the grid cells thus forms the analytical minimum scale at which we can detect assembly processes, either deterministic or neutral. The ratio of niche-processes to neutral-processes may have been changed if finer environmental and spatial structures had been taken into account.

As was evident from our variation partitioning analysis, compositional changes in marine demersal fish communities are mostly driven by environmental gradients. This signal of niche-based processes were further investigated in detail by investigating the unique or joint contribution of individual or groups of environmental drivers. Temperature has been established as a major determinant of community composition and biogeographic patterns of diversity across taxa in both terrestrial and marine realms (Roy et al. 1998, Gaston 2000, Willig et al. 2003, Fuhrman et al. 2008, Tittensor et al. 2010, Stuart-Smith et al. 2017). Whilst many of these studies have included alpha-diversity, recent studies on the effects of environmental drivers of marine beta-diversity have also found temperature-related variables to be of high importance (Leaper et al. 2011, Smit et al. 2017). In this study, we show that temperature-related variables are the most important determinants for both taxonomic and trait community changes along latitudinal gradients in marine demersal fish. Our study provide
5.4 Discussion

further evidence that contemporary sea temperatures affect the distributions of demersal fish, which is also present on temporal scales, where shifting ranges of species are observed as a result of warming seas (Pörtner 2002, Perry et al. 2005, Pinsky et al. 2013, Sunday et al. 2015, Stuart-Smith et al. 2017). Although evidence suggests that the distribution of fish species are tightly coupled to thermal shifts (Pinsky et al. 2013), the mechanisms by which such a link exists are not fully understood (Rijnsdorp et al. 2009), as temperature affects different levels of organization, from individuals to ecosystems differently. In addition to temperature, depth was identified as an important environmental factor explaining patterns of taxonomic and trait beta-diversity across all coastlines. Compositional variation in marine demersal fish communities across depth gradients have been identified in previous studies (Anderson et al. 2013, Mindel et al. 2016, Zintzen et al. 2017). Although depth has been shown to predict community structure (Reiss et al. 2010, Dencker et al. 2017), it is unlikely that depth differences inherently drive the observed patterns. Rather depth may rather be a proxy for factors of more first order influence, such as water column mixing, light penetration, temperature, and available energy (Carney 2005, Kaiser et al. 2011). Especially available energy has been shown to play an important role in structuring communities in benthic and demersal habitats (Evans et al. 2005), particularly the vertical flux of organic matter supporting the benthic food chain and demersal fish predators globally (van Denderen et al. 2017). Indeed, we find that depth in conjunction with NPP showed a strong effect on taxonomic beta-diversity along all three coastlines and for trait beta-diversity in the Northeast Pacific. This result supports the conclusion that depth is also an important predictor of spatial community structures in marine ecosystems through proxy for important first order determinants, potentially related to the available energy sinking to the seabed conditioned on depth and total NPP (Lutz et al. 2007; Dunn et al. 2005).

Evaluating multiple components of biodiversity and multi-scale processes is crucial for understanding the factors maintaining global patterns of biodiversity, but also for informing management and conservation (Myers & LaManna 2016, Socolar et al. 2016). In this study, we have demonstrated pronounced latitudinal changes in species and trait composition of demersal fish and have distinguished the ecological processes acting on community assembly across latitudes and coastlines by partitioning the total beta-diversity into its two antithetic components, turnover and nestedness. Finally, we have identified a number of key drivers, largely related to differences in temperature, depth and the availability of energy, that separately or in combination with spatial processes, jointly explain a considerable part of the observed variability in beta-diversity across coastlines. This
indicates that latitudinal differences in fish community composition are mainly governed by niche-based assembly processes, channeled through traits and environmental filtering. Our results emphasize the role of investigating beta-diversity in explaining broad-scale patterns of biodiversity. However, further research into local-scale processes governing community assembly, such as food-web dynamics and interactions (Burkle et al. 2016) is warranted as beta-diversity increasingly is used to inform ecological theory and integrated into conservation (Oldén & Halme 2016).

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### Supplementary material

#### Appendix S1

Table S1-1: Trawl survey data overview. Information on bottom-trawl surveys included in the study describing the area, temporal extent, spatial extent, sampling season, gear type, literature reference for each survey.

<table>
<thead>
<tr>
<th>Survey</th>
<th>Year</th>
<th>Latitudinal extent</th>
<th>Sampling season</th>
<th>Gear type</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aleutian Islands</td>
<td>1983-2014</td>
<td>51°-54°</td>
<td>Jun.-Aug.</td>
<td></td>
<td>(Batt et al. 2015)</td>
</tr>
<tr>
<td>Bay of Biscay &amp; Celtic Sea</td>
<td>1997-2016</td>
<td>43°-52°</td>
<td>Oct.-Dec</td>
<td>GOV 36/47</td>
<td>(ICES)</td>
</tr>
<tr>
<td>English Channel</td>
<td>1988-2016</td>
<td>49°-51°</td>
<td>Sep.-Nov.</td>
<td></td>
<td>(ICES)</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>1982-2014</td>
<td>24°-30°</td>
<td>Jan.-Dec.</td>
<td></td>
<td>(Batt et al. 2015)</td>
</tr>
<tr>
<td>Greenland</td>
<td>2002-2012</td>
<td>60°-67°</td>
<td>Oct.-Nov.</td>
<td>140’ bottom trawl with steel bobbins</td>
<td>(Fock 2008)</td>
</tr>
<tr>
<td>Ireland Shelf Sea</td>
<td>2003-2016</td>
<td>50°-57°</td>
<td>Sep.-Dec.</td>
<td></td>
<td>(ICES)</td>
</tr>
<tr>
<td>Portugal Shelf Sea</td>
<td>2002-2014</td>
<td>37°-42°</td>
<td>Sep.-Nov.</td>
<td>NCT</td>
<td>(ICES)</td>
</tr>
<tr>
<td>Southeast US</td>
<td>1989-2014</td>
<td>29°-35°</td>
<td>Apr.-Nov</td>
<td></td>
<td>(Batt et al. 2015)</td>
</tr>
</tbody>
</table>
Appendix S2

Table S2-1: Trait coverage for fish species for each survey

<table>
<thead>
<tr>
<th>Survey</th>
<th>Species-trait completeness (species in surveys/species with full trait information) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aleutian Islands</td>
<td>171/163 (95%)</td>
</tr>
<tr>
<td>East Bering Sea</td>
<td>150/141 (95%)</td>
</tr>
<tr>
<td>Bay of Biscay &amp; Celtic Sea</td>
<td>153/148 (96%)</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>441/343 (77%)</td>
</tr>
<tr>
<td>Gulf of Alaska</td>
<td>206/197 (96%)</td>
</tr>
<tr>
<td>Greenland</td>
<td>53/51 (96%)</td>
</tr>
<tr>
<td>Ireland Shelf Sea</td>
<td>138/133 (96%)</td>
</tr>
<tr>
<td>Northeast US</td>
<td>318/269 (84%)</td>
</tr>
<tr>
<td>Newfoundland</td>
<td>222/185 (83%)</td>
</tr>
<tr>
<td>Irish Sea</td>
<td>75/73 (97%)</td>
</tr>
<tr>
<td>Norway</td>
<td>154/152 (98%)</td>
</tr>
<tr>
<td>North Sea</td>
<td>165/161 (97%)</td>
</tr>
<tr>
<td>Portugal</td>
<td>128/118 (92%)</td>
</tr>
<tr>
<td>Southeast US</td>
<td>191/156 (81%)</td>
</tr>
<tr>
<td>Scotian Shelf</td>
<td>122/109 (89%)</td>
</tr>
<tr>
<td>Scotland Shelf Sea</td>
<td>119/105 (88%)</td>
</tr>
<tr>
<td>West coast US Annual</td>
<td>208/194 (93%)</td>
</tr>
<tr>
<td>West coast US Triennial</td>
<td>185/177 (95%)</td>
</tr>
</tbody>
</table>

Appendix S3

Figure S3-1: Species accumulation curves for each grid cell visualizing sampling differences.

Differences in sampling intensity between grid cells were observed. The number of hauls conducted in grid cells varied from 3 to 1841 (Figure S3-1). We constructed a Species Accumulation Curve (SAC) based on species richness as a function of number of hauls for each grid cell (Figure S3-2). The SACs only reached an asymptote in a small percentage of the grid cells. To standardize for this skewed sampling intensity, we fitted a non-linear curve to each SAC following a Michaelis-Menten model following equation 1:

\[ y(x) = \frac{sx}{a+x} \]

eq. (1)
where $y$ is the number of species, $x$ is the number of hauls, $S$ is the asymptotic species richness (the estimated total species richness of the grid cell), and $a$ is a constant corresponding to the number of samples where we reach half of the asymptote. We used three thresholds (50%, 65% and 80%) of the asymptotic species richness and evaluated the tradeoff between information (number of discarded grid cells versus percentage of estimated total species richness in each grid cell) at each threshold (Table S3-3). A minimum of three hauls is needed to build the SAC, and as such, each grid cell with less than three hauls was discarded. The loss of information in terms of number of grid cells at a threshold of 80% was deemed negligible compared to thresholds of 50% and 65% and as such we chose the highest threshold. We visually checked the location of each discarded grid cell to ensure no spatial bias was present.

![Graph showing species accumulation curves](image)

Figure S3-2: Methodology applied to correct for sampling heterogeneity. 100 species accumulation curves were constructed for each grid cell reaching the maximum observed number of species ($S_{\text{max (observed)}}$). The mean mean (solid black line) was used to estimate the curve asymptote with a Michaelis-Menten function (teal dotted line). The maximum species richness was estimated from the asymptote ($S_{\text{max (estimated)}}$). Here $S_{\text{max (estimated)}}$ is 40 species. Following a threshold value of 80% (80% $S_{\text{max (estimated)}}$), we calculate the number of samples (hauls) needed to reach the threshold. In this case, 6 samples.

Table S3-3: Number of grid cells discarded dependent on strictness of threshold-criterion (percentage of estimated species richness for each grid cell)

<table>
<thead>
<tr>
<th>Threshold-value</th>
<th>Number of grid cells discarded (total left)</th>
</tr>
</thead>
<tbody>
<tr>
<td>50%</td>
<td>3 (719)</td>
</tr>
<tr>
<td>65%</td>
<td>11 (711)</td>
</tr>
<tr>
<td>80%</td>
<td>47 (675)</td>
</tr>
</tbody>
</table>
**Appendix S4 Mathematical formulas for beta-diversity**

All measures of taxonomic and trait beta-diversity and its turnover and nestedness components used in the study were derived from the Jaccard index of dissimilarity (Jaccard 1912). The shared conceptual origin of the used beta-diversity metrics allowed for a comparison between taxonomic and trait measures. Jaccard index of dissimilarity follows equation 2

\[
\text{Jaccard index of dissimilarity } \beta_{jac} = \frac{b+c}{a+b+c} \quad \text{eq. (2)}
\]

In equation 2 \(a\) denotes the number of shared species between two sites of comparison, while \(b\) is the number of species unique to site 1, and \(c\) is the number of species unique to site 2 of the comparison (Jaccard 1912, Koleff et al. 2003, Baselga 2012). \(\beta_{jca}\) formulates the degree of compositional dissimilarity between two sites. This dissimilarity may however be driven by both a difference in species identities (i.e., turnover) and richness differences (i.e., nestedness) as suggested by Baselga (Baselga 2010), and as such, the Jaccard index of dissimilarity can be separated into these two components by following equation 3, 4 and 5. The conceptual outline follows equation 3

\[
\beta_{jac} = \beta_{jtu} + \beta_{jne} \quad \text{eq. (3)}
\]

where \(\beta_{jtu}\) and \(\beta_{jne}\) represent turnover and nestedness components, respectively, of the total beta-diversity (\(\beta_{jca}\)). The turnover component \(\beta_{jtu}\) measures the degree of replacement of species that would occur between communities if both communities had the same number of species (Baselga 2010). This allows for a quantification of replacement without the influence of richness difference (Baselga 2010). \(\beta_{jtu}\) is expressed as equation 4:

\[
\beta_{jtu} = \frac{2\min(b,c)}{a+2\min(b,c)} \quad \text{eq. (4)}
\]

As the highest number of species that can be replaced between two sites is the number of species in the most species poor sample (and not \(a + b + c\)), the numerator is therefore equal to two times the number of species in the most species poor sample. This means that the denominator is expressed as \(a + 2\min(b,c)\) (Baselga 2012). As the total beta-diversity (\(\beta_{jca}\)) is composed of the addition of turnover (\(\beta_{jtu}\)) and nestedness (\(\beta_{jne}\)), the nestedness component can be derived by
\[ \beta_{jne} = \beta_{jac} - \beta_{ftu} \quad \text{eq. (5)} \]

and thus

\[
\beta_{jne} = \frac{b+c}{a+b+c} - \frac{2 \min(b,c)}{a+2 \min(b,c)} = \frac{\max(b,c) - \min(b,c)}{a+2 \min(b,c)} x \frac{a}{a+2 \min(b,c)} \quad \text{eq. (6)}
\]

Total beta-diversity, turnover and nestedness vary between 0 and 1. Turnover increases as species are replaced between sites, and decreases when an increasing number of species are nested across the compared sites. The nestedness-component equals zero when the two sites have the same number of species or when the sites have unique combination of species and share none \((a = 0)\). Nestedness increases when one site is increasingly nested within the other site and a difference in species richness is observed (Baselga 2010).

A similar additive partition of total beta-diversity into its components can be conducted for multiple-site dissimilarity measures (Baselga et al. 2007, Baselga 2010, 2012) if multiple site equivalents to \(a\), \(b\) and \(c\) are used:

\[
\text{Multiple – site } \beta_{jac} = \frac{[\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_{i<j} \max(b_{ij}, b_{ji})]}{[\sum_{i} S_i - S_T] + [\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_{i<j} \max(b_{ij}, b_{ji})]} \quad \text{eq. (7)}
\]

In equation 7, \(S_i\) is the total species richness at site \(I\), \(S_T\) is the total species richness at all sites considered together, and \(b_{ij}, b_{ji}\) are the number of species exclusive to sites \(i\) and \(j\), respectively, when sites are compared as pairs. Thus, \([\sum_{i<j} \min(b_{ij}, b_{ji})]\) and \([\sum_{i<j} \max(b_{ij}, b_{ji})]\) become the multiple-site analogues of the \(b\) and \(c\) parameters of pairwise measures from equation 2, respectively, and \([\sum_{i} S_i - S_T]\) is the analogue of the \(a\)-parameter from equation 2 (Baselga 2010).

Thereafter, the turnover (equation 8) and nestedness (equation 7) components can be calculated in a similar fashion analogous to their pairwise equivalents following equations (4) and (6):

\[
\text{Multiple – site } \beta_{ftu} = \frac{2[\sum_{i<j} \min(b_{ij}, b_{ji})]}{[\sum_{i} S_i - S_T] + 2[\sum_{i<j} \min(b_{ij}, b_{ji})]} \quad \text{eq. (8)}
\]
Multiple site \( \beta_{jne} \) measure

\[
\beta_{jne} = \frac{\sum_{i<j} \max (b_{ij}^j b_{i,j}) - \sum_{i<j} \min (b_{ij}^j b_{i,j})}{\sum_{i} s_i - s_T + \sum_{i<j} \min (b_{ij}^j b_{i,j})} \times \frac{\sum_{i} s_i - s_T + 2 \sum_{i<j} \min (b_{ij}^j b_{i,j})}{\sum_{i} s_i - s_T + 2 \sum_{i<j} \max (b_{ij}^j b_{i,j})} \tag{eq. 9}
\]

Trait-based measures of beta-diversity can be constructed around the same concept of overlap between communities. Instead of species communities, the overlap is between \( n \)-dimensional hyper volumes based on the axes of the \( n \)-number of traits considered in the study (Villéger et al. 2008). In this study, we used the first three principle components from a pCoA on our six life history traits as synthetic trait axes and species loadings along those three PCs as trait values, thus we ended up with three-dimensional trait volumes for each site. The amount of trait space filled within the volume is defined as the trait richness of a community (Villéger et al. 2008) and the overlap between volumes of different sites constitute the trait beta-diversity. The total overlap, replacement of traits and the degree of nestedness can thus be characterized in a similar way to taxonomic beta-diversity through the Jaccard Index of dissimilarity. The conceptual framework is outlined in Figure S4-1 below. Based on the equivalence of the parameters \( a, b \) and \( c \) in the taxonomy-based beta-diversity framework (equation 2), we can outline the mathematical formulas for total trait beta-diversity and its turnover and nestedness components. The volume of each community is measured as the volume inside the convex hull that contains all of its species at a site or in a sample (Cornwell et al. 2006). By analogy with taxonomic beta-diversity, trait beta-diversity can be defined as

\[
\beta_{jac\text{-trait}} = \frac{\text{trait volume not shared}}{\text{total trait volume filled}} \quad \text{eq. (10)}
\]

As the volume of each site is \( \text{volume}_{site1} \) and \( \text{volume}_{site2} \), respectively, and their intersection is \( \text{volume}_{shared} \), we thus have:

\[
\beta_{jac\text{-trait}} = \frac{\text{volume}_{site1} + \text{volume}_{site2} - 2 \times \text{volume}_{shared}}{\text{volume}_{site1} + \text{volume}_{site2} - \text{volume}_{shared}} \quad \text{(equation 11)}
\]
Figure S4-1: Conceptual outline of trait beta-diversity and its turnover and nestedness components. A: Conceptualization of beta-diversity between two sites (site 1 and site 2) and the \( a \), \( b \) and \( c \) parameters expressed as volumes of the convex hull created from points representing the trait values of species in the separate communities (site 1 and site 2). \( a \) is the number of species shared by the two communities and \( b \) and \( c \) are the number of species present only in site 1 and site 2, respectively. B-G: Six examples of changing correspondences between \( a \), \( b \) and \( c \) and volumes of convex hulls for two sites (white for site 1 and grey for site 2). Differences in volume and placement in the trait space defines trait beta-diversity (\( \beta_{\text{jac-trait}} \)) and its turnover (\( \beta_{\text{tu-trait}} \)) and nestedness (\( \beta_{\text{ne-trait}} \)) components. Figure and text adapted and redrawn from (Villéger et al. 2013)

From equation 11 we can formulate the equations for the turnover (\( \beta_{\text{tu-trait}} \)) and the nestedness (\( \beta_{\text{ne-trait}} \)) components of \( \beta_{\text{jac-trait}} \) as following:

\[
\beta_{\text{tu-trait}} = \frac{2 \times \min(volume_{\text{site1}} \times volume_{\text{site2}}) - 2 \times volume_{\text{shared}}}{2 \times \min(volume_{\text{site1}} \times volume_{\text{site2}}) - volume_{\text{shared}}} \quad \text{eq. (12)}
\]

and

\[
\beta_{\text{ne-trait}} = \frac{volume_{\text{site1}} \times volume_{\text{site2}}}{volume_{\text{site1}} + volume_{\text{site2}} - volume_{\text{shared}}} \times \frac{volume_{\text{shared}}}{2 \min(volume_{\text{site1}} \times volume_{\text{site2}}) - volume_{\text{shared}}} \quad \text{eq. (13)}
\]
Multiple-site trait beta-diversity and its turnover and nestedness components are presented in (Villéger et al. 2011).
### Appendix S5

Table S5-1: Pearson’s correlations and Variable Inflation Factor (VIF)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Depth</th>
<th>NPP</th>
<th>NPP</th>
<th>Rugosity</th>
<th>Rugosity</th>
<th>SST</th>
<th>SST</th>
<th>SST_min</th>
<th>SST_var</th>
<th>SST_var</th>
<th>VIF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td>0.002</td>
<td>-0.492</td>
<td>-0.025</td>
<td>0.310</td>
<td>-0.220</td>
<td>-0.492</td>
<td>0.129</td>
<td>0.077</td>
<td>-0.411</td>
<td>0.249</td>
<td>2.221</td>
</tr>
<tr>
<td>Depth²</td>
<td>0.259</td>
<td>0.257</td>
<td>-0.248</td>
<td>0.159</td>
<td>0.061</td>
<td>0.095</td>
<td>0.064</td>
<td>0.067</td>
<td>0.031</td>
<td>1.402</td>
<td></td>
</tr>
<tr>
<td>NPP</td>
<td>0.001</td>
<td>-0.232</td>
<td>0.097</td>
<td>0.384</td>
<td>-0.432</td>
<td>-0.413</td>
<td>0.233</td>
<td>-0.092</td>
<td>2.233</td>
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<td></td>
</tr>
<tr>
<td>NPP²</td>
<td>-0.012</td>
<td>0.068</td>
<td>-0.128</td>
<td>0.283</td>
<td>0.322</td>
<td>0.101</td>
<td>0.106</td>
<td>1.354</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rugosity</td>
<td>0.001</td>
<td>0.071</td>
<td>-0.054</td>
<td>-0.079</td>
<td>-0.121</td>
<td>0.079</td>
<td>1.379</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Rugosity²</td>
<td>0.003</td>
<td>-0.024</td>
<td>-0.005</td>
<td>0.041</td>
<td>-0.125</td>
<td>1.151</td>
<td></td>
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</tr>
<tr>
<td>SST</td>
<td>0.031</td>
<td>-0.017</td>
<td>0.351</td>
<td>-0.225</td>
<td>2.164</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST²</td>
<td>0.623</td>
<td>-0.242</td>
<td>0.149</td>
<td>3.351</td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>SST_min²</td>
<td>-0.050</td>
<td>0.105</td>
<td>4.688</td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>SST_var²</td>
<td>0.011</td>
<td>2.043</td>
<td></td>
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<td>SST_var²</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Variable abbreviations: NPP = net primary production; SST = mean annual sea surface temperature; SST_min = minimum annual sea surface temperature; SST_var = annual variation in sea surface temperature. The $^2$ denotes the quadratic term for each variable.
Appendix S6

Table S6-1: Welch Two Sample t-test results for mean total taxonomic and trait beta-diversity and nestedness component for the Northeast Pacific, Northwest Atlantic and Northeast Atlantic coastlines.

<table>
<thead>
<tr>
<th></th>
<th>t-statistic</th>
<th>p.value</th>
<th>conf.low</th>
<th>conf.high</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total beta-diversity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northeast Pacific</td>
<td>22.30</td>
<td>P&lt;0.01</td>
<td>0.26</td>
<td>0.31</td>
</tr>
<tr>
<td>Northwest Atlantic</td>
<td>13.49</td>
<td>P&lt;0.01</td>
<td>0.14</td>
<td>0.18</td>
</tr>
<tr>
<td>Northeast Atlantic</td>
<td>12.22</td>
<td>P&lt;0.01</td>
<td>0.11</td>
<td>0.15</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nestedness (percentage of total beta-diversity)</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Northeast Pacific</td>
<td>42.29</td>
<td>P&lt;0.01</td>
<td>53.26</td>
<td>58.46</td>
</tr>
<tr>
<td>Northwest Atlantic</td>
<td>27.70</td>
<td>P&lt;0.01</td>
<td>38.77</td>
<td>44.70</td>
</tr>
<tr>
<td>Northeast Atlantic</td>
<td>54.51</td>
<td>P&lt;0.01</td>
<td>48.32</td>
<td>51.93</td>
</tr>
</tbody>
</table>

Appendix S7

Table S7-1: Results of variation partitioning between set of environmental drivers and set of spatial drivers (spatial structures) on total taxonomic and trait beta-diversity along coastlines (contribution to variation explained in percentage)

<table>
<thead>
<tr>
<th></th>
<th>Northeast Pacific</th>
<th>Northwest Atlantic</th>
<th>Northeast Atlantic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Taxonomy</td>
<td>Trait</td>
<td>Taxonomy</td>
</tr>
<tr>
<td>Unique env(^a)</td>
<td>42</td>
<td>13.1</td>
<td>46.1</td>
</tr>
<tr>
<td>Unique spatial(^b)</td>
<td>4.2</td>
<td>8</td>
<td>1.3</td>
</tr>
<tr>
<td>Shared</td>
<td>22</td>
<td>34</td>
<td>14.6</td>
</tr>
<tr>
<td>Unexplained</td>
<td>31.8</td>
<td>44.9</td>
<td>38</td>
</tr>
<tr>
<td>Total env</td>
<td>64</td>
<td>44.9</td>
<td>38</td>
</tr>
<tr>
<td>Total spatial</td>
<td>26.2</td>
<td>42</td>
<td>15.9</td>
</tr>
<tr>
<td>Total variation</td>
<td>68.2</td>
<td>55.1</td>
<td>62</td>
</tr>
</tbody>
</table>

\(^a\) Environmental: all environmental predictors from forward selection as listed in Table 1
\(^b\) Spatial: all significant dbMEMs
Appendix S8

Figure S8-1: Scale assessment of spatial structures explaining total taxonomic and trait beta-diversity. Cumulative adjusted-$R^2$ is plotted against the spatial structures retained for each coastline for dbRDA.D analysis. For each coastline, the coarsest spatial structure is added first and then every consecutive structure is added going towards finer spatial scales.
### Appendix S9

Table S9-1: Cumulative $R^2$-adjusted (Cum. $R^2$) for the parsimonious set of environmental predictor variables explaining total taxonomic and trait beta-diversity. $R^2$-adjusted values are expressed as percentage.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Northeast Pacific</th>
<th></th>
<th></th>
<th>Variable</th>
<th>Northeast Atlantic</th>
<th></th>
<th></th>
<th>Variable</th>
<th>North Atlantic</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxonomy</td>
<td>Traits</td>
<td></td>
<td></td>
<td>Taxonomy</td>
<td>Traits</td>
<td></td>
<td></td>
<td>Taxonomy</td>
<td>Traits</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST</td>
<td>26.22</td>
<td>SST$^2$</td>
<td>52.45</td>
<td>SST</td>
<td>20.86</td>
<td>SST</td>
<td>36.44</td>
<td>SST</td>
<td>32.81</td>
<td>SST$^2$</td>
<td>16.56</td>
</tr>
<tr>
<td>SST$^2$</td>
<td>43.56</td>
<td>SST</td>
<td>60.72</td>
<td>SST$^2$</td>
<td>38.95</td>
<td>SST$^2$</td>
<td>43.07</td>
<td>SST$^2$</td>
<td>40.16</td>
<td>Depth</td>
<td>18.73</td>
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<tr>
<td>SST$^2$min</td>
<td>47.01</td>
<td>Depth</td>
<td>67.21</td>
<td>SST$^2$min</td>
<td>44.34</td>
<td>SST$^2$</td>
<td>46.85</td>
<td>Depth</td>
<td>46.71</td>
<td>NPP</td>
<td>20.43</td>
</tr>
<tr>
<td>Depth</td>
<td>52.87</td>
<td>SST$^2$</td>
<td>73.22</td>
<td>SST$^2$var</td>
<td>48.84</td>
<td>Rug</td>
<td>49.48</td>
<td>Depth</td>
<td>50.63</td>
<td>SST</td>
<td>21.89</td>
</tr>
<tr>
<td>Depth$^2$</td>
<td>54.54</td>
<td>SST$^2$min</td>
<td>74.67</td>
<td>SST$^2$var</td>
<td>52.33</td>
<td>SST$^2$var</td>
<td>50.58</td>
<td>SST$^2$var</td>
<td>52.12</td>
<td>NPP</td>
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<tr>
<td>SST$^2$var</td>
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<td>Rug</td>
<td>75.31</td>
<td>SST$^2$var</td>
<td>54.12</td>
<td>SST$^2$var</td>
<td>52.38</td>
<td>SST$^2$var</td>
<td>53.23</td>
<td>SST$^2$</td>
<td>23.61</td>
</tr>
<tr>
<td>Rug</td>
<td>57.23</td>
<td>SST$^2$var</td>
<td>75.78</td>
<td>SST$^2$var</td>
<td>55.71</td>
<td>Depth</td>
<td>53.16</td>
<td>SST$^2$var</td>
<td>54.20</td>
<td>SST$^2$var</td>
<td>24.35</td>
</tr>
<tr>
<td>SST$^2$var</td>
<td>58.74</td>
<td>Rug$^2$</td>
<td>76.03</td>
<td>NPP</td>
<td>56.52</td>
<td>NPP</td>
<td>53.78</td>
<td>SST$^2$min</td>
<td>54.80</td>
<td>SST$^2$</td>
<td>24.62</td>
</tr>
<tr>
<td>NPP$^2$</td>
<td>58.98</td>
<td>NPP$^2$</td>
<td>76.27</td>
<td>Depth$^2$</td>
<td>54.11</td>
<td>Rug$^2$</td>
<td>54.46</td>
<td>Rug</td>
<td>24.89</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

SST: annual mean sea surface temperature; SST$^2$min: annual minimum temperature; Depth: mean depth of seabed within sampling grid cell; SST$^2$var: Annual variation in sea surface temperature; NPP: net primary production; Rug: rugosity of sampling grid cell. "$^2$" denotes quadratic term.
**Bibliography**


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ICES Database of Trawl Surveys (DATRAS).


Chapter 6

Beyond species richness - turnover, traits and abundances reveal important temporal community changes

Tim Spaanheden Dencker¹, Helmut Hillebrand²,³, Dorothee Hodapp², Martin Lindegren¹

¹ Centre for Ocean Life, National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, Kgs. Lyngby, Denmark
² Helmholtz Institute for Functional Marine Biodiversity (HIFMB), Oldenburg, Germany
³ Plankton Ecology Lab, Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University Oldenburg, Wilhelmshaven, Germany
Abstract
Human activities in marine ecosystems have affected a range of ecosystem processes and caused widespread loss of biodiversity worldwide. Changes in biodiversity have often been investigated by assessing temporal trends in the number of species present in an ecosystem. However, recent studies have found that species richness may be increasing at regional or local scale, while also detecting underlying structural changes in community composition. In this study we investigated temporal trends in biodiversity in marine demersal fish communities across the Northern Hemisphere in both the Pacific and Atlantic Ocean. We utilized a unique standardized multi-decadal survey dataset for ~600 species, incorporating abundance information and life-history traits to assess change across multiple components of biodiversity. Despite no systematic trends in species richness at regional or local scale, we found pronounced short-term and long-term changes in species and abundance structures across multiple survey regions. While trait composition of communities varied on short time scales, we observed relatively high long-term stability. This indicates that while species identities may shift within communities, life-history trait composition remains stable. The temporal changes reflected spatial dynamics, where biotic homogenization was evident in species, suggesting local biotic impoverishment in certain survey regions. Our findings lend further support to the argument that species richness is an inadequate metric to capture important biodiversity changes, and that assessments across multiple components of biodiversity may reveal important community changes more closely linked to ecosystem functioning.
6.1 Introduction

Human activities have left a considerable footprint on marine ecosystems worldwide (Halpern et al. 2008, Jones et al. 2018). This footprint is a result of alterations of biogeochemical cycles (Doney 2010), appropriation of more than 10% of annual marine net primary production through harvesting (Swartz et al. 2010, Haberl et al. 2014), fragmentation of habitats (Valiela et al. 2001, Carpenter et al. 2008, Waycott et al. 2009), unsustainable fishing (FAO 2018), pollution (Bergmann et al. 2017, Chiba et al. 2018), and forcing of the climate system (Pachauri et al. 2014). These long-term and continuous anthropogenic pressures have led to large-scale changes in both shelf and deep-sea ecosystems (McAllister et al. 1999, Lotze et al. 2006, Lindegren et al. 2012, McLean et al. 2018); often evidenced by a marked decline in biodiversity (Lotze et al. 2006). Loss of biodiversity is accelerating worldwide (Butchart et al. 2010), with global losses currently estimated to be 10 or even 1000 times higher than the background extinction rate (Pimm et al. 2014, Ceballos et al. 2015). Consequently, the ensuing loss of biodiversity have led to what is sometimes referred to as the “global biodiversity crisis” (Driscoll et al. 2018). In order to halt further losses of biodiversity efforts to protect vulnerable species and habitats are incorporated into international, regional and national conservation and environmental policies, such as the UN Aichi biodiversity targets (CBD 2010) and the European Marine Strategy Framework directive (Borja et al. 2010). To be effective, these conservation and environmental legislations require quality assessments of biodiversity changes and consensus on how to measure such change. Therefore, reliable and scientifically sound assessments of biodiversity across spatial and temporal scales are imperative for conservation efforts (Ripple et al. 2017, Driscoll et al. 2018).

The most commonly applied metric to assess biodiversity is species richness (Magurran 2004, Morris et al. 2014). However, recent assessments of regional or local species richness change have shown ambiguous trends with a majority of time series indicating no net change or even increases in the number of species (Dornelas et al. 2014, Batt et al. 2017, Vellend, Baeten, et al. 2017, Hillebrand et al. 2018). While such examples have sparked a discussion about biodiversity changes across scales (Cardinale et al. 2018), they have also led to further investigations of biodiversity changes beyond species richness and its underlying mechanisms (Dornelas et al. 2014, McGill et al. 2015, Shimadzu et al. 2015, Hillebrand et al. 2018). One of the clear conclusions stemming from these studies is that no single index can adequately describe and summarize biodiversity changes (Purvis & Hector 2000). This applies especially to species richness, which has been criticized for being ecologically
uninformative, since it ignores differences in relative abundance of species and their ecological roles within food webs and ecosystems (Magurran 2004). To overcome these shortcomings several papers have incorporated alternative measures of biodiversity reflecting changes in species identities, abundance distributions (Hillebrand et al. 2018, Dornelas et al. 2014), and potential homogenization of communities (Keith et al. 2009, Dornelas et al. 2014, Magurran et al. 2015). In particular, McGill et al. (2015) suggested fifteen forms of biodiversity change at various temporal and spatial scales covering both $\alpha$-diversity (i.e., point diversity) and $\beta$-diversity (i.e., differentiation between areas/time steps (Whittaker 1960)) components. The importance of integrating both time and space into assessments of biodiversity is further emphasized by the close link between temporal changes in community compositions and spatial dynamics between sites. Local changes, such as immigrations and local extinctions may be driven by the spreading of cosmopolitan species or loss of more rare, endemic species, respectively (Castro & Jaksic 2008). Both of these dynamics will alter the biotic differentiation between communities (spatial $\beta$-diversity) on a regional scale, leading to decreased heterogeneity between areas within a region (McKinney & Lockwood 1999, Olden 2006). This phenomenon of biotic homogenization has been observed for terrestrial (Castro & Jaksic 2008, Keith et al. 2009), freshwater (Marchetti et al. 2001, Rahel 2002) and marine assemblages (Magurran et al. 2015, Richardson et al. 2018), and represents an additional biodiversity dimension uncoupled from species richness trends (Keith et al. 2009, Magurran et al. 2015), where local “uniqueness” is lost.

Another important, but often overlooked component of biodiversity is the variation in morphological, physiological or phenological traits of species (Violle et al. 2007). Investigations of trait diversity have increased in the last two decades (Pécuchet et al. 2016, Dencker et al. 2017, Villéger et al. 2017, Törnroos et al. 2018), furthering our understanding of the responses of communities to perturbations such as climate variability and fishing (Pecuchet et al. 2017, McLean et al. 2018, Beukhof et al. 2019), and the effects of biodiversity on ecosystem functioning (Gamfeldt et al. 2008, 2015, Maureaud et al. in prep (Appendix C)). Additionally, changes in trait diversity may be uncoupled from taxonomic diversity and may be spatially segregated from it, challenging conservation efforts on which components to protect (Devictor et al. 2010, Mouillot et al. 2014, Dencker et al. 2017). Consequently, a more holistic assessment accounting for multiple aspects of biodiversity, including species abundances and traits is needed to better monitor and understand biodiversity patterns and its changes in time and space.
In this study, we examine changes in marine fish biodiversity using a multifaceted approach that incorporates taxonomic and trait \( \alpha \) and \( \beta \)-diversity. Using a unique, long-term survey data set of fish species abundances and traits sampled across shelf seas in the North Atlantic and Northeast Pacific, we specifically address the following research questions: i) are long-term changes in species richness similar or different across survey areas?; ii) how does net change in species richness compare with underlying gross community changes?; iii) do short-term changes in community structure accumulate over time?; and iv) are changes in biodiversity leading to increased biotic homogenization?

### 6.2 Material & methods

**Bottom trawl survey data**

Abundance data on marine fish species were obtained from seven fisheries-independent scientific bottom trawl surveys covering the continental shelves of the Northeast Pacific, Northwest Atlantic, and Northeast Atlantic. The combined trawl survey data covered a latitudinal gradient from 29\(^\circ\)-81\(^\circ\) N across a total of 50 years from 1968 to 2017 with sampling across multiple seasons between years within each survey (Appendix S1). Occurrence and standardized abundance for 1163 species were reported for 92858 unique georeferenced trawl haul included in this study. As we were primarily interested in temporal community change within surveys, standardization of data was focused on correcting intra-survey discrepancies. To remove seasonal bias in community structures, sampling within surveys was standardized to the same annual quarters. Since depth has been found to influence fish community composition (Anderson et al. 2013, Zintzen et al. 2017), we also removed potential biases from coastal and deep water species not sufficiently sampled by the surveys by restricting our analysis to hauls between 20 meter and the 90\(^{th}\) percentile depth for each survey. Reported species names were checked against the World Register of Marine Species (Horton et al. 2018), and updated to the accepted scientific name when appropriate. All invertebrate and mammalian species were removed, leaving only species in a paraphyletic group consisting of Elasmobranchii, Actinopterygii, Holocephali, Myxini, and Petromyzonti, henceforth referred to as “fish”. Finally, pelagic species not accurately sampled by bottom-trawling gears were excluded, hence restricting the analysis to demersal fish species (based on classification of pelagic fish in Beukhof et al. *in prep* (chapter 7).
Life history traits
We characterized the ecological niche of fish species with respect to their feeding, growth and reproduction life-history characteristics using biological traits. We collected information on six traits: maximum length, life span, trophic level, fecundity, offspring size and parental care. Selection of traits were done on basis of a framework of life-history strategies (Winemiller & Rose 1992) from (Pecuchet et al. 2017). This framework captures three primary life history strategies: equilibrium, periodic and opportunistic species with tradeoffs between different reproductive strategies. The prevalence of these strategies varies with environmental gradients, and the framework is therefore suitable for testing changes in biodiversity in shelf-sea communities (Pecuchet et al. 2017). Detailed trait information can be found in Beukhof et al. in prep (chapter 7). Only fish species with complete trait cover across the six selected traits were retained. A minimum of 82% of species within surveys had complete trait cover (Appendix S2).

Sampling heterogeneity and standardization of sampling effort
To delineate sampling areas with sufficient sampling effort to estimate and compare various measures of biodiversity, a 2.5°x2.5° resolution grid was superimposed on all haul location. The grid size was a compromise between too large cells leading to overlap between adjacent seas across land, and too small grid cells leading to insufficient sampling effort in each year. The grid cells were superimposed on haul locations for each year leading to a total of 2388 grid cells. Sampling effort heterogeneity was prevalent across grid cells and between years. Sampling heterogeneity can bias results and lead to faulty comparisons (Chao & Jost 2012). In order to standardize sampling effort we constructed species accumulation curves (SACs) for each grid cell to assess the level of completeness of sampling. SACs show species richness as a function of the sampled area or of the number of samples. If sufficient sampling is undertaken, the SAC will saturate, reaching an asymptote, signifying that no further sampling is needed to have a representative sample of the underlying true species pool. For multiple grid cells, the constructed SACs did however not reach this asymptote (Appendix S3). In order to compare grid cells, we focused on aligning sampling effort, so a given threshold value of completion was reached. This is in contrast to standardization based on a fixed number of hauls across sites. Using a fixed number of hauls can potentially give biased results depending on the underlying true community structure and may violate the replication principle (Hill 1973, Chao & Jost 2012). For this, we fitted Michaelis-Menten functions to the SAC of each grid cell and estimated the asymptotic species richness based on all available samples for each grid cell using the “vegan”
package in R (Oksanen et al. 2017). Hence, for each grid cell, the number of samples needed to achieve 75% completeness of the estimated asymptotic species richness was calculated. Grid cells with insufficient sampling to reach the required number of hauls for the desired level of completeness were removed from the analysis (Appendix S3). After standardization of taxonomy and trait information, and sampling coverage, 598 species from 73356 unique hauls within 1948 grid cells were included in the analysis.

**Calculation of biodiversity indices**

Each grid cell was randomly resampled through 99 permutations for the required number of hauls to reach 75% of the asymptotic species richness as derived from the SACs. For each permutation, we calculated all taxonomic and trait biodiversity metrics. Rank abundance curves were calculated for each survey to investigate the abundance distribution of species and the degree of rarity (Appendix S4).

Species richness (SRic) was calculated for each year for each grid cell for each survey (Appendix S5). We then calculated the average species richness for each year for each survey (Figure 1) and fitted a linear regression model across years to check for temporal autocorrelation in the residuals. If autocorrelation was detected, we accounted for it with a generalized least squares model with an added correlation structure. Coefficients and significance were checked after autocorrelation correction. If a significant trend was still observed, the linear regression model was compared to the generalized least squares model by AIC (Appendix S6) and the lowest-scoring model was selected.

Secondly, we investigated the net and gross changes of species occurrences on a year-to-year basis. We calculated the inter-annual change in species richness (ΔSRic), as well as the number of species gained and species lost for each grid cell on a one-year time scale (Figure 2). The gross change values of gained and lost species were then used to calculate an occurrence-based species-exchange ratio (SERr) for each grid cell based on Hillebrand et al. (2018) (equation 1)

\[ SER_r = \frac{S_{gained} + S_{lost}}{S_{total}} \]  

where \( S_{gained} \) is the number of new species gained in the later sample, while \( S_{lost} \) is the number of species lost between the two samples, and \( S_{total} \) is the total number of unique species for both samples. While ΔSRic expresses the net change between \( S_{gained} \) and \( S_{lost} \), SERr captures the gross change in
species composition \((S_{gained} + S_{lost})\). \(SER_r\) is expressed as a value between 0 and 1, with 0 being no change and 1 being complete turnover in the community. In order to investigate changes in species abundance distributions, we calculated an abundance-weighted measure of \(SER_r\), termed \(SER_a\) (Hillebrand et al. 2018). \(SER_a\) tracks changes in species proportional abundances, \(p_i\) and \(p'_i\), between two time steps. \(SER_a\) is related to Simpson’s diversity index (Chase & Knight 2013) and is less sensitive to changes in rare species, and more sensitive to changes in the abundance of dominant species.

\[
SER_a = \frac{\sum_i (p_i - p'_i)^2}{\sum_i p_i^2 + \sum_i p'_i^2 - \sum_i p_i p'_i}
\]  
(equation 2)

Like \(SER_r\), \(SER_a\) is bound between 0 and 1. \(SER_a\) approaches 0 if the species identity and dominance structure does not change and 1 if all species are replaced. When the species abundance distribution is equal across samples, \(SER_a\) is similar to \(SER_r\) (Hillebrand et al. 2018).

\(SER_r\) and \(SER_a\) are based on shifts in the taxonomic or abundance structure of communities. To account for possible temporal changes in the trait composition we calculated trait-based beta-diversity (\(\beta_{trait}\)) similar to the Jaccard dissimilarity index (Jaccard 1912). To reflect the taxonomic turnover-metrics, we derived the trait-based turnover-component from the total beta-diversity (Baselga 2010, 2012, Villéger et al. 2013). We refer to this turnover-component as \(\beta_{trait}\). Standardization of trait values between species was performed by using Gower’s distances between species pairs (Gower 1971) as it allows for the use of both continuous and categorical variables. We then performed a principle coordinate analysis (PCoA) on the resulting distance matrix (Villéger et al. 2008, Laliberte & Legendre 2010). The first three axes of the PCoA were retained as they cumulatively explained 87% of the variation in traits. \(\beta_{trait}\) can then be expressed as the trait space not shared between two communities divided by the total trait space of both communities. \(\beta_{trait}\) is bounded between 0 and 1, and similar to \(SER_r\) and \(SER_a\). \(\beta_{trait}\) approaches 0 if the trait composition is identical between time steps and 1 if no overlap between trait composition is detected.

First, we calculated \(SER_r\), \(SER_a\) and \(\beta_{trait}\) on a short-term temporal scale in one-year increments. This was compared to the change in species richness expressed as the change in number of species relative to the total species pool shared between the two years compared (Figure 3). Next, we calculated
ΔSRic, SER\textsubscript{r}, SER\textsubscript{a} and β\textsubscript{trait} from each year to all following years against the temporal distance between the compared years. This allowed us to assess how species richness changes and turnover metrics might accumulate with increasing temporal distance (Figure 4).

Lastly, we assessed the degree of biotic homogenization across years for each survey. We calculated multiple-site β-diversity based on species occurrences (spatial β\textsubscript{occurrence}), species abundances (spatial β\textsubscript{abundance}), and traits (spatial β\textsubscript{trait}). Multiple-site β-diversity expresses the overall dissimilarity across grid cells within each survey and hence shows the degree of spatial biotic homogenization. Spatial β\textsubscript{occurrence} was based on the Jaccard dissimilarity index (Jaccard 1912), while spatial β\textsubscript{trait} was based on a trait-equivalent of the Jaccard Index. In order to reflect the emphasis of turnover in community changes, only the turnover-component of total β\textsubscript{occurrence} and total spatial β\textsubscript{trait} were used (Baselga 2010, Baselga & Orme 2012, Villéger et al. 2013). Spatial β\textsubscript{abundance} was calculated based on abundance-weighted Bray-Curtis dissimilarity. Abundance-weighted Bray-Curtis can be separated into two antithetic components, similar to turnover and nestedness (Baselga 2010, 2017). The turnover-component of abundance-weighted Bray-Curtis, is defined as a shift in the relative abundance of species between sites (Baselga 2017), as opposed to a decrease in overall abundance of the community, but similar relative abundance distribution across species. Similar to species richness trends, we assessed temporal trends of multiple-site β-diversity metrics linear regressions and checked for temporal autocorrelation.

### 6.3 Results

#### Temporal species richness

A majority of surveys across all three coastlines demonstrated increasing trends in species richness (0.09 to 0.35 new species per year) (Figure 1). After correcting for temporal autocorrelation, five surveys showed a significant positive trend (Appendix S5), while only the Barents Sea survey showed a decrease in species richness. The regional trends in species richness were largely consistent at a smaller spatial scale (2.5° x 2.5° grid) (Appendix S7). An increase in SRic was found in 45 out of 59 grid cells (out of which 35 were significant). Decreasing trends in SRic were found in 14 grid cells, with 7 decreasing significantly (Appendix S8). The majority of decreasing grid cells were identified within the Barents Sea survey following the overall declining trend in species richness at regional scale.
6.3 Results

Figure 1: Long-term time-series of species richness in seven surveys shown as mean standardized species richness averaged across grid cell per year. Straight lines represent linear regressions fitted to each time-series.

**Net and gross community changes**

Despite the marked long-term changes in regional species richness across the regions, the magnitude of net change in species richness between years (ΔSRic) was rather moderate (species per year mean across surveys: 1.87±5.12) (Figure 2) and consistent across time and surveys. However, the absolute magnitude of gains and losses was considerably higher (Appendix S9 and Appendix S10), and on average 14.9±6.5% of the standing species richness was replaced by local extinctions/losses and 18.8±10.9% by immigrations/gains. The magnitude of gains and losses showed little variation between years (Figure 2) or between surveys. The highest replacement of species compared to standing species richness was observed in the Northeast US survey with species losses replacing ~50% of the standing species richness, while both the Northeast US and North Sea surveys showed gains up to six-fold larger than ΔSRic.
6.3 Results

Figure 2: Net and gross changes in biodiversity for each survey between years, calculated from each starting year and in one year-increments. Shading represents the 5% and 95% quartiles and colored lines represents median values for net and gross changes. Net species richness ($\text{ΔSRic}$) (blue shading and line) is the result of gross changes in species gains (green shading and line) and losses (red shading and line). Black dashed line represent the zero-line.

**Community turnover**

Considerable short-term turnover based on occurrence ($\text{SER}_o$), abundance ($\text{SER}_a$) and trait information ($\text{B}_{\text{trait}}$) of species was observed for all metrics at low or even no change in species richness, indicating that significant changes in community composition can occur without being detectable by changes in species richness (Figure 3). A high degree of variation in turnover was observed for all turnover metrics. The largest observed values of $\text{SER}_o$ were associated with high $\text{ΔSRic}$, indicating that large increases or decreases in species richness are always associated with high community turnover. $\text{SER}_o$ varied consistently between 0.03 and 0.51 for all surveys, with a mean
turnover of 0.25±0.06. At zero change in species richness $\text{SER}_r$ amounted to 0.23±0.06 across surveys. Variation in $\text{SER}_a$ was consistent throughout the range of species richness change for all surveys, except for the Southeast US survey, where high values of species richness change predominantly led to high values of $\text{SER}_a$.

![Figure 3: Bivariate plots between the relative species richness change and (A) $\text{SER}_r$, (B) $\text{SER}_a$ and (C) $\beta_{\text{trait}}$ for each survey. Y-axes are bound between 0 and 1 and represent turnover. Relative species richness change is calculated as $\Delta \text{SRic}$ divided by $S_{\text{total}}$ between two sample years.]

While mean values were lower for $\text{SER}_a$ than for $\text{SER}_r$ (mean $\text{SER}_a$: 0.17±0.08 across surveys; mean at zero change in species richness: 0.17±0.04), maximum observed values were higher for $\text{SER}_a$ with 80% change in abundance-distribution observed in the East Bering Sea at an observed ~10% change in net species richness. Mean $\beta_{\text{trait}}$ across surveys was similar to mean $\text{SER}_r$ and $\text{SER}_a$ (0.15±0.12).
As with SER_r and SER_a, β\textsubscript{trait} showed considerable variation in the degree of turnover at zero change in net species richness (0.16±0.14) with values ranging from 0.05 to 0.84. Contrary to SER_r and SER_a, maximum values of β\textsubscript{trait} were not observed at the largest changes in species richness, meaning that considerable changes in species richness may not necessarily result in large changes in the trait composition of communities. Correlations between occurrence-, abundance and trait-weighted turnover metrics showed that community changes in either component of biodiversity can happen independently from change in the other metrics, and that no universally consistent relationship between metrics were found across surveys (Appendix S11).

**Cumulative change**

The increases in species richness for a majority of areas were reflected in the pair-wise comparison of ΔSR\textsubscript{ric} between years, where increasing temporal distance led to a significant accumulation of species, except in Barents Sea and Southeast US (Figure 4A, Appendix S12). Likewise, SER_r and SER_a increased significantly with increasing temporal distance, indicating that shifts in both species identities and abundance distribution of the most abundant species accumulated throughout the time period (Figure 4B and 4C, Appendix S12). Furthermore, loss of low turnover values with increasing temporal distance was observed in several surveys for both SER_r and SER_a, indicating directional change with no return to initial species compositions or abundance structures. In contrast to the overall increasing trends in SER_r and SER_a, consistent temporal trends of β\textsubscript{trait} was not observed across surveys (Figure 4D). Significant increasing trends in β\textsubscript{trait} were only observed in the North Sea and Scotian Shelf surveys, while insignificant increases and decreases were observed in the remaining surveys (Appendix S12). At large temporal distances, both low and high values of β\textsubscript{trait} was found for several surveys. This indicates a lack of directional accumulation of change in the trait composition of communities with increasing temporal distance, as seen for both SER_r and SER_a. In the East Bering Sea, the Barents Sea and along the Southeast US coastline, trait turnover over long temporal distances were markedly lower than the rest of the surveys, indicating relatively high stability. All metrics of turnover displayed different rates of change with a faster temporal change in dissimilarity abundance structure with increasing temporal difference (SER_a changing faster than SER_r and β\textsubscript{trait}).
Figure 4: Pair-wise comparisons of species richness and turnover metrics between year one and all following years for each grid cell within surveys. Change in species richness (A), richness-based turnover (SER\(_r\)) (B), abundance-weighted turnover (SER\(_a\)) (C) and trait-based turnover (\(\beta_{\text{trait}}\)) (D) against increasing temporal distance between years. Values are represented by colored shading of 5%–95% quantiles, while black lines represent medians.

**Biotic homogenization**

The strongest signal of biotic homogenization was seen in the species compositions across grid cells within surveys (Figure 5, Appendix S13). Spatial \(\beta_{\text{occurrence}}\) decreased significantly in four out of seven surveys with the fastest rate of homogenization happening in the Barents Sea (Figure S8). No consistent pattern of biotic homogenization was found for abundance-weighted spatial \(\beta\)-diversity (\(\beta_{\text{abundance}}\)), where both significant decreases and increases in \(\beta\)-diversity were observed. The signal of biotic homogenization was weak for trait-based spatial \(\beta\)-diversity (spatial \(\beta_{\text{trait}}\)), where only
Iceland was found to decrease significantly in spatial heterogeneity. Spatial $\beta_{\text{trait}}$ was overall characterized by lower values than spatial $\beta_{\text{occurrence}}$ and spatial $\beta_{\text{abundance}}$, except for the Scotian Shelf survey, where all three spatial $\beta$-diversity metrics varied between 0.1 and 0.6. Spatial $\beta_{\text{occurrence}}$ and spatial $\beta_{\text{abundance}}$ showed little inter-annual variation, except for Scotian Shelf and Northeast US surveys, where short-term variation in values were similar to those observed in Spatial $\beta_{\text{trait}}$.

Figure 5: Temporal trends in spatial $\beta$-diversity expressing degree of biotic homogenization in species (A), species abundance structure (B), and trait composition (C) across grid cells within surveys. Colored shaded areas represent 5%–95% quantiles, while black lines represent medians.
6.4 Discussion

Despite the rapid loss of global diversity reported for a range of organisms (Jackson 2001, Lotze et al. 2006, Pounds et al. 2006, Doherty et al. 2016), we found no systematic trend of either increases or decreases in marine demersal fish species richness at regional or local scales across the North Atlantic and Northeast Pacific. The observed range of temporal trends in species richness lends support to a growing body of evidence indicating inconsistency in temporal trends in species richness at sub-global scales with little or no systematic loss observed (Dornelas et al. 2014, Vellend, Baeten, et al. 2017, Blowes et al. 2018, Hillebrand et al. 2018). However, we observed considerable changes in species composition of communities between years, where on average ~13-15% of the species pool was replaced by local extinctions and immigrations. These changes were not only reflected in high turnover of rare species (SER_r) but also reflected in marked turnover in species abundance distributions of dominant species (SER_a) across both short-term and long-term scales (Figure 2 and 3) in a majority of investigated marine ecosystems. The low values of SER_a at intermediate or high values of net species richness change indicate shifts in rare species, which ultimately doesn’t affect the abundance structure noticeably. The accumulation of turnover and loss of low turnover values found for both SER_r and SER_a indicate directionality in the change, where later years do not revert back to original community structures, but rather deviate increasingly. Conversely, we saw no accumulation of $\beta_{\text{trait}}$ nor loss of low mean $\beta_{\text{trait}}$ values with temporal distance, indicating relative stability in the trait composition of the investigated demersal communities. The chosen multi-trait setup based on life-history traits has been shown to be closely linked to environmental gradients and change (Pecuchet et al. 2017). The temporal long-term stability of the trait composition within certain surveys may indicate that the long-term environmental conditions may have not have changed in such a way to affect the overall trait-composition of the communities, but rather the species composition and abundance structures. The large variation of short-term changes observed in $\beta_{\text{trait}}$ may be a methodological artefact. As $\beta_{\text{trait}}$ is based on traits of occurring species, it is also sensitive to detection of rare species, just as SER_r. Rare species may exhibit rare trait values (Mouillot et al. 2013, Leitao et al. 2016), changing the degree of overlap between trait spaces of communities either separated in time or space, and disproportionally affect short-term fluctuations of $\beta_{\text{trait}}$. Together, these results indicate that biodiversity changes at the community level can occur without being detectable by the most common metric of biodiversity, namely species richness. Additionally, these changes were not consistently correlated to each other, and this suggests that changes in one component of biodiversity
can happen independently of changes in the others. Our result hence further support that multiple metrics need to be considered to for adequately assessing changes in biodiversity.

Observed trends in species richness are the result of underlying changes in community composition caused by local extinctions and immigrations of species, and as such, it is important to understand the mechanisms of such processes. Short-term changes in community composition may be influenced by the prevalence of rarity of species and the low probabilities of detecting these in monitoring (Gotelli & Colwell 2001). All the seven included surveys were characterized by high degrees of rarity (i.e., high dominance in the species abundance distribution; Figure S3) and as such, year-to-year fluctuations of losses and gains of species may reflect a low probability of detecting rare species. However, inter-annual changes in species occurrences may also be caused by factors not inherent in sampling procedures, but rather fluctuations in environmental conditions, such as short-term temperature oscillations, where, for example the range of southerly, more warm-adapted species may expand into more northern regions, but contract again upon cooling (Fisher et al. 2008, Selleslagh & Amara 2008), or sporadically changing food availability (Ruzicka et al. 2012). Such shifts have been found to be prominent at local scales (Selleslagh & Amara 2008, Thiaw et al. 2017).

In contrast to inter-annual changes, long-term biodiversity changes are less sensitive to detection probabilities of rare species and may instead be linked to consistent range shifts of transient and resident species (Batt et al. 2017). Such range shifts are due to more persistent environmental changes, such as long-term temperature increases (Perry et al. 2005, Pinsky et al. 2013) or changes in prey availability (Benson & Trites 2002, Beaugrand 2004, Feary et al. 2014). Range shifts have been reported in several of the investigated areas with a typical pattern of more southern species expanding into boreal systems (Perry et al. 2005, Engelhard et al. 2011, Batt et al. 2017), while boreal species have expanded into arctic regions, such as the Barents Sea (Fossheim et al. 2015, Frainer et al. 2017). Thus, increases in local species richness and the observed accumulated turnover are likely linked to leading/trailing edge dynamics of different ecological types of species (Engelhard et al. 2011). The decline in species richness in the Barents Sea may indicate that resident arctic species have retracted faster in their trailing edges than Boreal species have expanded by their leading edges. While SER captures the turnover underlying the species richness numbers (Dornelas et al. 2014, Hillebrand et al. 2018), it is still sensitive to shifts in rare species and suffers from some of the same issues as species richness, such as sampling sensitivity and detection capabilities (Chase et al. 2011, Magurran &
McGill 2011). SER_a on the other hand is less sensitive to rare species since it takes into account shifts in abundances. It is therefore indicative of shifts in dominance structures among abundant species (Hillebrand et al. 2018). We observed significant short-term abundance-weighted turnover at low or no change in species richness, and accumulated long-term turnover in abundance structures in all investigated areas. Shifts in abundance structure can be attributed to multiple interacting processes affecting marine communities, including fishing (Bell et al. 2017), climate-driven changes in productivity (Behrenfeld et al. 2006) and recruitment success (Lindegren & Eero 2013), as well as species interaction (Lynam et al. 2017). While it is outside the scope of this study to assess the individual or joint contribution of these processes, shifts in species abundance structures in marine ecosystems can drastically change energy flows within food webs (Lindegren et al. 2012), ultimately influencing ecosystem functioning and services (Blenckner et al. 2015). Hence, these shifts and their underlying drivers and mechanisms merit further attention.

Since McKinney and Lockwood’s seminal work (McKinney & Lockwood 1999), the impoverishment of unique local biotas has been a major focus in biodiversity research and conservation (Olden 2006, Socolar et al. 2016). Biotic homogenization has been shown to be closely linked to the temporal dynamics of losses and gains of species and has mainly been focused on taxonomic structures (Olden & Rooney 2006). This focus has now been expanded and biotic homogenization now also encompasses other components of biodiversity (Henriques et al. 2014, Villéger et al. 2014). We integrated spatial β-diversity with community abundance and trait structures, investigating biotic homogenization across multiple components of biodiversity. The significant decreases in spatial β-diversity in species compositions indicate a loss of uniqueness of local biotas, resonating with the increasing body of evidence showing biotic homogenization in multiple taxonomic groups in both terrestrial and aquatic realms (Keith et al. 2009, Baiser et al. 2012, Magurran et al. 2015, Richardson et al. 2018). However, the decreases in heterogeneity observed for taxonomic structures were not reflected in abundance nor trait-structures, except for Iceland, where consistent and significant biotic homogenization was observed across all three investigated components of biodiversity. The lack of consistency between biodiversity components for other surveys suggests that biotic homogenization may be decoupled between different facets of biodiversity. While we quantified the degree of homogenization across multiple components of biodiversity, we do not elaborate on the drivers behind the observed change. Biotic homogenization has been linked to multiple mechanisms (Clavel et al. 2011, Baeten et al. 2012, Baiser et al. 2012,
Villéger et al. 2014, Rosenblad & Sax 2017), and driving mechanisms may differ between different facets of biotic homogenization and across scales (Van Turnhout et al. 2007, Leveau et al. 2017). Our results show that while biotic homogenization could be detected in multiple components of biodiversity, it was not spatially consistent across surveys.

Our study provides a marine perspective to a recent and ongoing debate on long-term changes in biodiversity across scales (Vellend, Dornelas, et al. 2017, Cardinale et al. 2018). While this debate has largely focused on discrepancies between global, regional and local trends in species richness (Vellend, Baeten, et al. 2017), the debate also highlights the dire need and utility of assessing changes across multiple components of biodiversity (McGill et al. 2015). Furthermore, it has sparked a much needed discussion on data availability and quality (Gonzalez et al. 2016, Cardinale et al. 2018). Extensive long-term monitoring programs for marine ecosystems are still relatively rare and costly, at least compared to terrestrial campaigns. However, recent efforts to compile and synthesize available monitoring data from across areas have proven successful (Batt et al. 2015, Dornelas et al. 2018), but further standardization of abundance data and coalescence of extensive trait information remain challenging. Additionally, a pronounced global bias in data availability is obvious with a majority of monitoring data from the Northern Hemisphere and a clear shortage of comparable data from tropical biomes, particularly in developing countries. Therefore, we stress the need for an internationally coordinated effort to better monitor and assess changes across multiple aspects of biodiversity, including species, abundances and traits, in order to best prioritize limited conservation efforts and seek win-win strategies reducing conflict between political, economic and ecological objectives (Tittensor et al. 2014, Klein et al. 2015, Veach et al. 2017, Jones et al. 2018, Lindegren et al. 2018). Such conservation efforts are, however, further challenged by spatial discrepancies between hot spots of different components of biodiversity or rarity of species (Devictor et al. 2010, Stuart-Smith et al. 2013, Mouillot et al. 2014, Parravicini et al. 2014, Wiedmann et al. 2014, Dencker et al. 2017), and temporal mismatches in changes of biodiversity components (see Villéger et al. 2010 and Lefcheck et al. 2014, and results within this study) and in changes in marine and terrestrial realms (Blowes et al. 2018).

Conclusions
Our findings align with recent studies showing considerable changes in community structures beyond those captured by species richness (Dornelas et al. 2014, Magurran et al. 2015, Vellend, Baeten, et
al. 2017, Blowes et al. 2018, Hillebrand et al. 2018). Significant changes in species richness, species identities and abundance structures were observed across seven marine ecosystems from the Northern Hemisphere across both the Pacific and Atlantic Oceans. A trait-based approach to community changes revealed short-term fluctuations in the trait composition, but long-term stability. This was in contrast to directional turnover of species and abundance structures across decades. Additionally, we found signs of spatial biotic homogenization for species, signifying an impoverishment of unique local biotas in marine demersal fish. Collectively, our results indicate that adopting a holistic assessment accounting for multiple biodiversity metrics can serve to “remove the blindfold” of species richness and reveal important community changes of considerable relevance to science and conservation.

Acknowledgements
We wish to thank Esther Beukhof, Aurore Maureaud, and Neil Maginnis for their constructive feedback during the development of the study, Katja Enberg for helping acquiring data for Norway, Jón Sólmundsson for helping acquiring data for Iceland, and Daniel van Denderen for feedback on the manuscript. T.S.D. and M.L. conducted the work within the Centre for Ocean Life, a Villum Kann Rasmussen Center of Excellence supported by the Villum Foundation. M.L. also acknowledges support from a VILLUM research grant (No. 13159).


Bibliography


Supplementary material

Appendix S1

Table S1-1: Trawl survey data overview. Information on bottom trawl surveys included in the study describing the area, temporal extent, spatial extent, sampling season, gear type, and literature reference for each survey.

<table>
<thead>
<tr>
<th>Survey-area</th>
<th>Year</th>
<th>Latitudinal extent</th>
<th>Sampling season</th>
<th>Gear type</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southeast US</td>
<td>1989-2014</td>
<td>29°-35°</td>
<td>Apr.-Nov</td>
<td></td>
<td>(Batt et al. 2015)</td>
</tr>
<tr>
<td>Iceland</td>
<td>1986-2017</td>
<td>63°-67°</td>
<td>Feb.-May</td>
<td>Granton trawl</td>
<td>(Sölmundsson &amp; et al. 2010)</td>
</tr>
</tbody>
</table>
**Appendix S2**

Table S2-1: Trait coverage for fish species for each survey

<table>
<thead>
<tr>
<th>Survey</th>
<th>Species/Species with complete trait information (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Bering Sea</td>
<td>149/141 (94%)</td>
</tr>
<tr>
<td>Iceland</td>
<td>91/88 (96%)</td>
</tr>
<tr>
<td>North Sea</td>
<td>159/155 (97%)</td>
</tr>
<tr>
<td>Northeast US</td>
<td>300/247 (82%)</td>
</tr>
<tr>
<td>Barents Sea</td>
<td>144/142 (98%)</td>
</tr>
<tr>
<td>Scotian shelf</td>
<td>108/97 (89%)</td>
</tr>
<tr>
<td>Southeast US</td>
<td>156/128 (82%)</td>
</tr>
</tbody>
</table>

**Appendix S3**

Figure S3-1: Sampling effort heterogeneity between grid cells (i.e., number of hauls in each grid cell) as shown by species accumulation curves, where species richness is a function of number of hauls within each grid cell.

**Sampling effort standardization**

Differences in sampling intensity between grid cells were observed with number of hauls conducted in grid cells varying between 3 to 138 (Figure S3-1). To avoid sampling effort biases that could affect comparisons of biodiversity measurements, we constructed a species accumulation curve (SAC) based on species richness as a function of number of hauls for each grid cell (Figure S3-1). The SACs only reached an asymptote in a small percentage of the grid cells. In order to get comparable biodiversity measurements, we standardized for this skewed sampling intensity by fitting a non-linear curve to each SAC following a Michaelis-Menten model following

\[
y(x) = \frac{S \times x}{a + x}
\]
where \( y \) is the number of species, \( x \) is the number of hauls, \( S \) is the asymptotic species richness (the estimated total species richness of the grid cell), and \( a \) is a constant corresponding to the number of samples where we reach half of the asymptote. Construction and analysis of SACs were done using the ‘vegan’ R package (Oksanen et al. 2017). We used three thresholds (65%, 75% and 80%) of the asymptotic species richness and evaluated the tradeoff between information (number of species sampled in each grid cell versus the number of grid cells meeting the threshold value) at each threshold (Table S3-3). For each grid cell, we randomly sampled 99 times the required number of hauls needed to reach the selected threshold. A minimum of three hauls is needed to build the SAC, and as such, each grid cell with less than three hauls was discarded. The methodological approach is outlined in Figure S3-2 below.

Figure S3-2: Methodology applied to correct for sampling heterogeneity. 100 species accumulation curves were constructed for each grid cell reaching the maximum observed number of species (\( S_{\text{max (observed)}} \)). The mean mean (solid black line) was used to estimate the curve asymptote with a Michaelis-Menten function (teal dotted line). The maximum species richness was estimated from the asymptote (\( S_{\text{max (estimated)}} \)). Here \( S_{\text{max (estimated)}} \) is 40 species. Following a threshold value of 75% (75% \( S_{\text{max (estimated)}} \)), we calculate the number of samples (hauls) needed to reach the threshold. In this case, 5 samples.

Table S3-3: Number of discarded grid cells per threshold value for species accumulation curves

<table>
<thead>
<tr>
<th>Threshold</th>
<th>Number of discarded grid cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>80%</td>
<td>735</td>
</tr>
<tr>
<td>75%</td>
<td>440</td>
</tr>
<tr>
<td>65%</td>
<td>155</td>
</tr>
</tbody>
</table>
Appendix S4

Figure S4-1: Rank abundance curves for each survey. Relative abundance of species on y-axis with the abundance rank on the x-axis.
Figure S5-1: Temporal trends of species richness per grid cell per survey. Coloration within individual plots represents individual grid cells within surveys.
## Appendix S6

Table S6-1: Regression Figure for temporal trends of species richness for each survey

<table>
<thead>
<tr>
<th>Survey</th>
<th>Coefficient</th>
<th>P-value</th>
<th>Autocorrelation</th>
<th>Corrected-P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Bering Sea</td>
<td>0.16561</td>
<td>&lt;0.01</td>
<td>YES</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Iceland</td>
<td>0.18809</td>
<td>&lt;0.01</td>
<td>NO</td>
<td></td>
</tr>
<tr>
<td>North Sea</td>
<td>0.35427</td>
<td>&lt;0.01</td>
<td>NO</td>
<td></td>
</tr>
<tr>
<td>Northeast US</td>
<td>0.09160</td>
<td>&lt;0.01</td>
<td>YES</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Barents Sea</td>
<td>-0.24408</td>
<td>&lt;0.01</td>
<td>NO</td>
<td></td>
</tr>
<tr>
<td>Scotian Shelf</td>
<td>0.18394</td>
<td>&lt;0.01</td>
<td>NO</td>
<td></td>
</tr>
<tr>
<td>Southeast US</td>
<td>0.09093</td>
<td>0.525</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Bold values are significant at P <0.05.
Appendix S7

Figure S7-1: Boxplot of coefficients from linear regression on temporal species richness (SRic) trends for each grid cell. Solid black line represents the median value, bounded by the upper (75\textsuperscript{th} percentile) and lower (25\textsuperscript{th} percentile) interquartile ranges. Extent of whiskers represent minimum (low) and maximum (high) values of coefficients. Black dots represent outliers. Red dashed line represent the zero line. Each boxplot is colored according to survey.
Appendix S8

Figure S8-1: Bar-plot of the number of either significant or insignificant positive or negative temporal trends of species richness (SRic) per survey. Significance is estimated at P<0.05. Teal represents significance, while red represents insignificance.

Appendix S9

Table S9-1: Magnitude of species loss compared to standing species richness (percentages)

<table>
<thead>
<tr>
<th>Survey</th>
<th>Mean</th>
<th>SD</th>
<th>1st quartile</th>
<th>3rd quartile</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Bering Sea</td>
<td>14.6</td>
<td>6.7</td>
<td>10.0</td>
<td>18.8</td>
<td>2.3</td>
<td>45.2</td>
</tr>
<tr>
<td>Iceland</td>
<td>13.2</td>
<td>5.5</td>
<td>9.3</td>
<td>16.7</td>
<td>2.2</td>
<td>35.1</td>
</tr>
<tr>
<td>North Sea</td>
<td>16.0</td>
<td>5.9</td>
<td>11.8</td>
<td>19.6</td>
<td>2.2</td>
<td>37.5</td>
</tr>
<tr>
<td>Northeast US</td>
<td>15.8</td>
<td>6.3</td>
<td>11.4</td>
<td>19.6</td>
<td>2.3</td>
<td>49.1</td>
</tr>
<tr>
<td>Barents Sea</td>
<td>15.0</td>
<td>6.0</td>
<td>10.7</td>
<td>18.8</td>
<td>2.4</td>
<td>36.4</td>
</tr>
<tr>
<td>Scotian Shelf</td>
<td>14.5</td>
<td>5.4</td>
<td>10.5</td>
<td>17.9</td>
<td>2.5</td>
<td>34.1</td>
</tr>
<tr>
<td>Southeast US</td>
<td>18.6</td>
<td>5.9</td>
<td>14.8</td>
<td>22.0</td>
<td>3.6</td>
<td>41.8</td>
</tr>
</tbody>
</table>
### Appendix S10

**Table S10-1: Magnitude of species gains compared to standing species richness (percentages)**

<table>
<thead>
<tr>
<th>Survey</th>
<th>Mean</th>
<th>SD</th>
<th>1st quartile</th>
<th>3rd quartile</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Bering Sea</td>
<td>12.6</td>
<td>8.4</td>
<td>6.3</td>
<td>17.2</td>
<td>0.0</td>
<td>48.1</td>
</tr>
<tr>
<td>Iceland</td>
<td>11.2</td>
<td>6.8</td>
<td>6.1</td>
<td>15.0</td>
<td>0.0</td>
<td>50.0</td>
</tr>
<tr>
<td>North Sea</td>
<td>15.7</td>
<td>8.3</td>
<td>9.8</td>
<td>20.3</td>
<td>0.0</td>
<td>61.1</td>
</tr>
<tr>
<td>Northeast US</td>
<td>14.5</td>
<td>8.4</td>
<td>8.5</td>
<td>18.8</td>
<td>0.0</td>
<td>61.3</td>
</tr>
<tr>
<td>Barents Sea</td>
<td>12.7</td>
<td>7.3</td>
<td>7.3</td>
<td>17.1</td>
<td>0.0</td>
<td>51.6</td>
</tr>
<tr>
<td>Scotian Shelf</td>
<td>12.7</td>
<td>6.9</td>
<td>7.9</td>
<td>16.9</td>
<td>0.0</td>
<td>41.7</td>
</tr>
<tr>
<td>Southeast US</td>
<td>17.0</td>
<td>7.2</td>
<td>11.9</td>
<td>21.4</td>
<td>1.6</td>
<td>43.5</td>
</tr>
</tbody>
</table>
Figure S11-1: Correlation plots between turnover-metrics of SER\textsubscript{r} and SER\textsubscript{a}, \(\beta\text{-trait}\) across all surveys (“global”) scale and for each survey individually. Histogram plots on the diagonal show frequency distributions of turnover values with a fitted smoother. The left bottom triangle shows scatter plots between turnover metrics with a fitted line. The right upper triangle show values of correlations with significance levels indicated by red stars: *** = P<0.001, ** = P<0.01. Red square indicate P = 0.1.
Appendix S12

Table S12-1: Linear regression coefficient and P-value for temporal distance decay of turnover metrics for each survey.

<table>
<thead>
<tr>
<th>Survey</th>
<th>ΔSRic Coefficient</th>
<th>P-value</th>
<th>SERᵣ Coefficient</th>
<th>P-value</th>
<th>SERₛ Coefficient</th>
<th>P-value</th>
<th>( \beta _{\text{trait}} ) Coefficient</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Bering Sea</td>
<td>0.1711</td>
<td>&lt;0.001</td>
<td>0.0035</td>
<td>&lt;0.001</td>
<td>0.0079</td>
<td>&lt;0.001</td>
<td>0.0004</td>
<td>0.9</td>
</tr>
<tr>
<td>Iceland</td>
<td>0.1969</td>
<td>&lt;0.001</td>
<td>0.0028</td>
<td>&lt;0.001</td>
<td>0.0038</td>
<td>&lt;0.001</td>
<td>0.0006</td>
<td>0.2</td>
</tr>
<tr>
<td>North Sea</td>
<td>0.3674</td>
<td>&lt;0.001</td>
<td>0.0029</td>
<td>&lt;0.001</td>
<td>0.0066</td>
<td>&lt;0.001</td>
<td>0.0020</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Northeast US</td>
<td>0.0888</td>
<td>&lt;0.001</td>
<td>0.0015</td>
<td>&lt;0.001</td>
<td>0.0050</td>
<td>&lt;0.001</td>
<td>0.0001</td>
<td>0.7</td>
</tr>
<tr>
<td>Barents Sea</td>
<td>-0.1997</td>
<td>&lt;0.001</td>
<td>0.0032</td>
<td>&lt;0.001</td>
<td>0.0081</td>
<td>&lt;0.001</td>
<td>-0.0019</td>
<td>0.5</td>
</tr>
<tr>
<td>Scotian Shelf</td>
<td>0.2038</td>
<td>&lt;0.001</td>
<td>0.0033</td>
<td>&lt;0.001</td>
<td>0.0073</td>
<td>&lt;0.001</td>
<td>0.0022</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Southeast US</td>
<td>0.0330</td>
<td>0.14</td>
<td>0.0010</td>
<td>&lt;0.001</td>
<td>0.0050</td>
<td>&lt;0.001</td>
<td>-0.0009</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Significant values are highlighted with bold.
## Appendix S13

Table S13-1: Linear regression results for biotic homogenization for each spatial β-diversity metric. Corrected P-values for significant linear trends where temporal autocorrelation was detected.

<table>
<thead>
<tr>
<th></th>
<th>Spatial β_{occurrence}</th>
<th>Spatial β_{abundance}</th>
<th>Spatial β_{trait}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient</td>
<td>P-value</td>
<td>Corrected P-value</td>
</tr>
<tr>
<td>East Bering Sea</td>
<td>-0.0014</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Iceland</td>
<td>-0.0008</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>North Sea</td>
<td>0.0003</td>
<td>0.51</td>
<td></td>
</tr>
<tr>
<td>Northeast US</td>
<td>-0.0014</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Barents Sea</td>
<td>-0.0083</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Scotian Shelf</td>
<td>0.0021</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Southeast US</td>
<td>0.0006</td>
<td>0.56</td>
<td></td>
</tr>
</tbody>
</table>

Significant values are highlighted with bold.
Bibliography

Batt RD, Morley JW, Selden RL, Pinsky ML (2015) trawlData: Read and Clean Data from Bottom Trawl Surveys.


ICES Database of Trawl Surveys (DATRAS).


Chapter 7

A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas

Esther Beukhof¹, Tim Spaanheden Dencker¹, Maria L. D. Palomares² & Aurore Maureaud¹

¹Centre for Ocean Life, National Institute of Aquatic Resources (DTU-Aqua), Technical University of Denmark, Kgs. Lyngby, Denmark
²Sea Around Us, Institute for the Oceans and Fisheries, The University of British Columbia, British Columbia, Canada
7.1 Background and summary
This dataset containing traits of marine fish is based on fish taxa observed during international scientific bottom-trawl surveys regularly conducted in the Northeast Atlantic, Northwest Atlantic and the Northeast Pacific. These scientific surveys target primarily demersal (bottom-dwelling) fish species, but pelagic species are also regularly recorded. The overarching aim of this dataset was to collect information on ecological traits for as many fish taxa as possible and to find area-specific trait values in order to account for intraspecific variation in traits, especially for widely distributed species. We collected traits for species, genera and families. The majority of trait values were sourced from FishBase (Froese and Pauly, 2019), and have been supplemented with values from primary literature.

7.2 Spatial coverage
The bottom-trawl surveys are performed on and along the continental shelves of the U.S. and Europe, including southern Greenland (Figure 1, Table 1). To collect area-specific trait information, we made use of the division of the world oceans into Large Marine Ecosystems (LMEs; http://lme.edc.uri.edu/) and FAO fishing areas (http://www.fao.org/fishery/area/search/en). The dataset covers 22 LMEs (Table 2) and 7 FAO areas (Table 3).

7.3 Taxonomic coverage
This data includes 1702 unique species, 801 genera, and 236 families occurring across LMEs and FAO areas, resulting in 6216 different taxa with their assigned geographic information. The collection of traits provided here is not complete. The missing information per trait and taxa is further detailed in the sections below.

7.4 Traits
We collected information on 14 traits of marine fish, among which 9 are continuous and 5 are categorical traits (Table 4). Trait information was collected by extracting trait values from an offline version of FishBase from 2015, followed by supplementing missing information with values from primary literature and the most recent version of FishBase (Froese and Pauly, 2019); or by inferring values from closely related species (within genus or family) when no trait information could be found.

Trait data is available for download at https://github.com/timspaanhedendencker/trait-collection
in the literature. Each trait and the trait extraction procedure are described in more detail below. Figure 2 and Table 5 provide information on the number of trait categories per taxonomic group for the categorical traits, whereas Tables 6 and 7 demonstrate some summary statistics for the continuous traits and the availability of trait values per taxonomic group.

Maximum length

Maximum length is the maximum recorded body size in cm. The majority of measurements measure total body length (TL), i.e. from snout to tail. Other types of measurements are standard length (SL; from snout to posterior end of the last vertebra), width of disc (WD; for skates and rays) or fork length (FL; from snout to end of middle caudal fin rays). In other cases, the type of measurement of not given (NG) or is of another type (OT).

Maximum length was extracted from the FishBase table ‘Age/Size’ and from the species page shown on the web version of FishBase (under the heading ‘Length at first maturity / Size / Weight / Age’). Values from the ‘Age/Size’ table were preferred over the ones from the species page, since they are provided with a location specifying where the measurement was taken. Missing values were then supplemented by the ‘Species’ table, values from primary literature, or inferred from genus or family.

Table 1: Bottom-trawl surveys used to collect fish species for which traits were collected. Source of the data and information on the survey are given, if available, in the last two columns.

<table>
<thead>
<tr>
<th>Survey</th>
<th>Area</th>
<th>Source</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>AI</td>
<td>Aleutian Islands</td>
<td>Batt, 2015</td>
<td>Alaska Fisheries Science Center, 2019</td>
</tr>
<tr>
<td>EBS</td>
<td>Eastern Bering Sea Shelf</td>
<td>Batt, 2015</td>
<td>Alaska Fisheries Science Center, 2019</td>
</tr>
<tr>
<td>EVHOE</td>
<td>Bay of Biscay &amp; Celtic Sea</td>
<td>ICES, 2018</td>
<td>ICES, 1997</td>
</tr>
<tr>
<td>FR-CGFS</td>
<td>English channel</td>
<td>ICES, 2018</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>GMEX</td>
<td>Gulf of Mexico</td>
<td>Batt, 2015</td>
<td>Gulf States Marine Fisheries Commission, 2015</td>
</tr>
<tr>
<td>GOA</td>
<td>Gulf of Alaska</td>
<td>Batt, 2015</td>
<td>Alaska Fisheries Science Center, 2019</td>
</tr>
<tr>
<td>Gre-GFS</td>
<td>Greenland</td>
<td>H. Fock</td>
<td>Fock, 2008</td>
</tr>
<tr>
<td>Ice-GFS</td>
<td>Iceland</td>
<td>J. Sólmundsson</td>
<td>Sólmundsson et al., 2010</td>
</tr>
<tr>
<td>IE-IGFS</td>
<td>Ireland shelf Sea</td>
<td>ICES, 2018</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>NEUS</td>
<td>North East US</td>
<td>Batt, 2015</td>
<td>Northeast Fisheries Science Center, 2018</td>
</tr>
<tr>
<td>NI-GFS</td>
<td>Irish Sea - Ireland</td>
<td>ICES, 2018</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>NorBTS</td>
<td>Norwegian Sea, Barents Sea and northern North Sea</td>
<td>Djupervåg, 2018</td>
<td>Mjanger et al., 2006, 2017</td>
</tr>
<tr>
<td>NS-IBTS</td>
<td>North Sea</td>
<td>ICES, 2018</td>
<td>ICES, 2015</td>
</tr>
<tr>
<td>PT-IBTS</td>
<td>Portugal shelf Sea</td>
<td>ICES, 2018</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>ROCKALL</td>
<td>Rockall plateau</td>
<td>ICES, 2018</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>SA</td>
<td>South East US</td>
<td>Batt, 2015</td>
<td>Northeast Fisheries Science Center, 2018</td>
</tr>
<tr>
<td>SCS</td>
<td>Scotian shelf</td>
<td>Batt, 2015</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>SP-NORTH</td>
<td>North of Spain</td>
<td>ICES, 2018</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>SWC-IBTS</td>
<td>Scotland shelf Sea</td>
<td>ICES, 2018</td>
<td>ICES, 2017</td>
</tr>
<tr>
<td>WCANN</td>
<td>West Coast US</td>
<td>Batt, 2015</td>
<td>Keller et al., 2017</td>
</tr>
</tbody>
</table>
7.4 Traits

Table 2: Overview of Large Marine Ecosystem (LME) numbers covered by the dataset and corresponding names.

<table>
<thead>
<tr>
<th>LME number</th>
<th>LME name</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>East Bering Sea</td>
</tr>
<tr>
<td>2</td>
<td>Gulf of Alaska</td>
</tr>
<tr>
<td>3</td>
<td>California Current</td>
</tr>
<tr>
<td>5</td>
<td>Gulf of Mexico</td>
</tr>
<tr>
<td>6</td>
<td>Southeast U.S. Continental Shelf</td>
</tr>
<tr>
<td>7</td>
<td>Northeast U.S. Continental Shelf</td>
</tr>
<tr>
<td>8</td>
<td>Scotian Shelf</td>
</tr>
<tr>
<td>9</td>
<td>Newfoundland-Labrador Shelf</td>
</tr>
<tr>
<td>18</td>
<td>Canadian Eastern Arctic – West Greenland</td>
</tr>
<tr>
<td>19</td>
<td>Greenland Sea</td>
</tr>
<tr>
<td>20</td>
<td>Barents Sea</td>
</tr>
<tr>
<td>21</td>
<td>Norwegian Sea</td>
</tr>
<tr>
<td>22</td>
<td>North Sea</td>
</tr>
<tr>
<td>23</td>
<td>Baltic Sea</td>
</tr>
<tr>
<td>24</td>
<td>Celtic-Biscay Shelf</td>
</tr>
<tr>
<td>25</td>
<td>Iberian Coastal</td>
</tr>
<tr>
<td>26</td>
<td>Mediterranean</td>
</tr>
<tr>
<td>53</td>
<td>West Bering Sea</td>
</tr>
<tr>
<td>54</td>
<td>Northern Bering-Chukchi Seas</td>
</tr>
<tr>
<td>59</td>
<td>Iceland Shelf and Sea</td>
</tr>
<tr>
<td>60</td>
<td>Faroe Plateau</td>
</tr>
<tr>
<td>65</td>
<td>Aleutian Islands</td>
</tr>
</tbody>
</table>

Table 3: Overview of the FAO fishing areas covered by the dataset and their corresponding name

<table>
<thead>
<tr>
<th>FAO number</th>
<th>FAO name</th>
</tr>
</thead>
<tbody>
<tr>
<td>21</td>
<td>Northwest Atlantic</td>
</tr>
<tr>
<td>27</td>
<td>Northeast Atlantic</td>
</tr>
<tr>
<td>31</td>
<td>Western Central Atlantic</td>
</tr>
<tr>
<td>37</td>
<td>Mediterranean and Black Sea</td>
</tr>
<tr>
<td>61</td>
<td>Northwest Pacific</td>
</tr>
<tr>
<td>67</td>
<td>Northeast Pacific</td>
</tr>
<tr>
<td>77</td>
<td>Eastern Central Pacific</td>
</tr>
</tbody>
</table>

Trophic level

Trophic level represents a species’ position in the food web. Two types of trophic level values were extracted from the ‘Feeding’ table, found under the ‘Ecology’ table on FishBase. The trophic level calculated based on the ‘Diet’ table was preferred over the ‘Food items’ table, because the ‘Diet’ table includes information on the proportion of prey items. Data from the ‘Food items’ table was chosen when information from the ‘Diet’ was not available.
7.4 Traits

Age at maturity
Age at maturity is the age at which 50% of the population is mature. In cases where this value was not available, other types of maturity estimates were used, e.g. the lowest reported age at which a mature individual has been found. Values were extracted from the ‘Maturity’ table, which provides a single value and/or a range of ages, for which an average was then calculated. Missing values for age at maturity have been supplemented with values from literature.

Maximum age
Maximum age is the maximum reported age in years. Values were extracted from the FishBase table ‘Age/Size’ and from the species page of the web version of FishBase (under the heading ‘Length at first maturity / Size / Weight / Age’). Values from the ‘Age/Size’ table were preferred over the ones from the species page, since they are provided with a location of where the measurement was taken. Missing values were supplemented by values from primary literature or inferred from genus or family.

Figure 1: Global map with the number of taxa included in the trait database in each Large Marine Ecosystem (LME) (coastal polygons). The major fishing FAO areas are also indicated.
### 7.4 Traits

Table 4: The traits included in the dataset classified as either continuous or categorical traits.

<table>
<thead>
<tr>
<th>Continuous traits</th>
<th>Categorical traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic level</td>
<td>Habitat</td>
</tr>
<tr>
<td>Caudal fin aspect ratio</td>
<td>Feeding Mode</td>
</tr>
<tr>
<td>Offspring size (mm)</td>
<td>Body Shape</td>
</tr>
<tr>
<td>Age at maturity (year)</td>
<td>Caudal Fin Shape</td>
</tr>
<tr>
<td>Fecundity (number of eggs or offspring produced per year by female)</td>
<td>Spawning Type</td>
</tr>
<tr>
<td>Length infinity (cm)</td>
<td></td>
</tr>
<tr>
<td>Von Bertalanffy growth coefficient K (1/year)</td>
<td></td>
</tr>
<tr>
<td>Maximum length (cm)</td>
<td></td>
</tr>
<tr>
<td>Maximum age (year)</td>
<td></td>
</tr>
</tbody>
</table>

Figure 2: Distribution of the number of taxa for each categorical trait. A) Species habitat, B) Feeding mode, C) Body shape, D) Caudal fin shape, E) Spawning Type. Colors indicate the taxonomic level at which the trait value was assigned.
**Von Bertalanffy growth coefficient K**

The growth coefficient K (1/year) is a parameter in the Von Bertalanffy growth equation, describing how fast an individual reaches its asymptotic size (i.e., length infinity). Values were extracted from the FishBase table ‘Growth’.

**Length infinity**

Length infinity (cm) is a parameter in the Von Bertalanffy growth equation and represents the maximum asymptotic size an individual can reach. Values were extracted from the FishBase table ‘Growth’.

**Fecundity**

Fecundity is the number of eggs or offspring a female produces per year (if spawning only once) or per batch (if spawning multiple times per year). Due to limited knowledge for many species on whether they are batch spawners or not, fecundity values per batch have not been corrected to reflect the total fecundity per year. The ‘Fecundity’ table of FishBase provides both the absolute and relative fecundity, the latter being fecundity relative to body size. Since relative fecundity is only rarely available, absolute fecundity was chosen. When both a minimum and maximum fecundity was reported, the mean value was calculated.

Missing values were searched for in primary literature, as well as on the FishBase website under the headings ‘Biology’ and ‘Life cycle and mating behaviour’. If unavailable, values were inferred from the genus or family.

**Offspring size**

Offspring size (mm) represents the egg diameter for fish, length of egg case for skates and rays or body length of a new-born pup for sharks. Values were extracted from the ‘Eggs’ table of FishBase. Missing values were searched for in primary literature, as well as on the FishBase website under the headings ‘Biology’ and ‘Life cycle and mating behaviour’. If unavailable, values were inferred from the genus or family.
7.4 Traits

Table 5: Number of trait values available and not available (separated by a dash) for each categorical trait and taxonomic level ($n_{\text{Family}} = 347$, $n_{\text{Genus}} = 402$, $n_{\text{Species}} = 5467$)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>347/0</td>
<td>402/0</td>
<td>5467/0</td>
</tr>
<tr>
<td>Feeding mode</td>
<td>286/61</td>
<td>400/2</td>
<td>5454/13</td>
</tr>
<tr>
<td>Body shape</td>
<td>347/0</td>
<td>402/0</td>
<td>5467/0</td>
</tr>
<tr>
<td>Caudal fin shape</td>
<td>347/0</td>
<td>402/0</td>
<td>5467/0</td>
</tr>
<tr>
<td>Spawning type</td>
<td>323/24</td>
<td>387/15</td>
<td>5337/130</td>
</tr>
</tbody>
</table>

Table 6: Summary statistics of continuous traits

<table>
<thead>
<tr>
<th>Continuous trait</th>
<th>Minimum value</th>
<th>Mean value</th>
<th>Maximum value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic level</td>
<td>2.00</td>
<td>3.67</td>
<td>4.65</td>
</tr>
<tr>
<td>Aspect ratio</td>
<td>0.08</td>
<td>1.39</td>
<td>7.05</td>
</tr>
<tr>
<td>Offspring size</td>
<td>0.05</td>
<td>24.30</td>
<td>1750</td>
</tr>
<tr>
<td>Age at maturity</td>
<td>0.20</td>
<td>4.54</td>
<td>156</td>
</tr>
<tr>
<td>Fecundity</td>
<td>1</td>
<td>132,000</td>
<td>300,000,000</td>
</tr>
<tr>
<td>Length infinity</td>
<td>2.50</td>
<td>57.13</td>
<td>1000</td>
</tr>
<tr>
<td>Growth coefficient</td>
<td>0.01</td>
<td>0.33</td>
<td>5.90</td>
</tr>
<tr>
<td>Maximum length</td>
<td>1.40</td>
<td>57.39</td>
<td>1000</td>
</tr>
<tr>
<td>Maximum age</td>
<td>0.30</td>
<td>18.00</td>
<td>392</td>
</tr>
</tbody>
</table>

Table 7: Number of trait values available and not available (separated by a dash) for each continuous trait and taxonomic level ($n_{\text{Family}} = 347$, $n_{\text{Genus}} = 402$, $n_{\text{Species}} = 5467$)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic level</td>
<td>337/10</td>
<td>401/1</td>
<td>5462/5</td>
</tr>
<tr>
<td>Aspect ratio</td>
<td>299/48</td>
<td>352/50</td>
<td>4712/755</td>
</tr>
<tr>
<td>Offspring size</td>
<td>324/23</td>
<td>384/18</td>
<td>5223/244</td>
</tr>
<tr>
<td>Age at Maturity</td>
<td>284/63</td>
<td>339/84</td>
<td>4890/577</td>
</tr>
<tr>
<td>Fecundity</td>
<td>317/30</td>
<td>375/27</td>
<td>5122/345</td>
</tr>
<tr>
<td>Length infinity</td>
<td>331/16</td>
<td>387/15</td>
<td>5204/263</td>
</tr>
<tr>
<td>Growth coefficient</td>
<td>331/16</td>
<td>387/15</td>
<td>5213/254</td>
</tr>
<tr>
<td>Maximum length</td>
<td>347/0</td>
<td>402/0</td>
<td>5467/0</td>
</tr>
<tr>
<td>Maximum age</td>
<td>299/48</td>
<td>360/42</td>
<td>5014/453</td>
</tr>
</tbody>
</table>
Caudal fin aspect ratio
The caudal fin aspect ratio is the squared height of the caudal fin divided by the surface area of the caudal fin. It is known to correlate with fish swimming speed, activity, metabolism and food consumption (Sambilay, 1990).

Values were extracted from the ‘Morphology’ table. Missing values were not supplemented with values from primary literature.

Feeding mode
Feeding mode is the type of food consumed and reflects species diet, categorized as: herbivorous (feeding on algae), benthivorous (feeding on benthos), planktivorous (feeding on plankton), piscivorous (feeding on fish) or generalist (feeding on two or more types of food, assigned when the major food type comprised no more than approximately two-thirds of the diet).

Feeding modes were assigned consulting the feeding type and feeding habit from the ‘Ecology’ table, the ‘Biology’ section, and the ‘Diet’ table of FishBase.

Body shape
Information on the lateral body shape and cross section of fish was extracted from the ‘Morphology’ table of FishBase. Based on these two descriptors, the following six body shape categories reflecting the most striking feature (either lateral or cross-sectional): fusiform (or: normal), elongated, eel-like, flat, short and/or deep and compressiform (Figure 3).

Caudal fin shape
Similar to the aspect ratio, the caudal fin shape reflects differences in the mode and behaviour of swimming and locomotion. Information on the caudal fin shape was extracted from the ‘Morphology’ table of FishBase. The categories from FishBase were slightly adapted to the following six categories: forked, rounded, (more or less) truncated, lunate, pointed and heterocercal (Figure 4).

Spawning type
Spawning type reflects the reproductive guild of fish and the amount of parental care. Information was extracted from the ‘Reproduction’ table of FishBase. We aggregated all the categories from FishBase into three categories following (Balon, 1990): ‘non-guarder’ that includes spawning in open
water, on substratum and brood-hiders, ‘guarder’ that includes clutch tenders and nesters, and ‘bearer’ that includes external brooders and internal live bearers.

![Figure 3: Body shape of fish according to six categories with species examples of each category. Pictures from www.phylopic.org under a Creative Commons Public Domain Dedication 1.0 License](image)

**Habitat**

The habitat trait informs the position of a fish in the water column. Information was extracted from the ‘Ecology’ table of FishBase and from the depth distribution of species on the website of the Ocean Biogeographic Information System (OBIS; [http://www.iobis.org/](http://www.iobis.org/)). Categories were classified as follows: pelagic, bathypelagic, demersal, bathydemersal, benthopelagic, reef-associated and non-pelagic. Bathypelagic and bathydemersal fish are either pelagic or demersal fish that occur in waters deeper than the continental shelf. Benthopelagic fish are those that are commonly found in both the pelagic zone and close to the bottom. Fish were classified as non-pelagic when they were clearly not pelagic but it was not possible to distinguish between demersal, bathydemersal, benthopelagic or reef-associated.
7.5 Trait extraction procedure

A Microsoft Access database version of FishBase was provided by M.L. Deng Palomares. The Access database stores, whenever available, information on the location of where the trait value measured or estimated. We assigned all taxa from the bottom-trawl survey data to the LME and FAO fishing area where they were sampled. Taxa were either recorded at the species, genus or family level.

Species trait values for continuous traits were extracted from the Access database as follows:

1.1 Extract the trait value from the LME that corresponds to the area where the species was recorded, and calculate an average value in the cases where multiple trait values are available.

1.2 If unavailable, extract the trait value from the FAO area where the species was recorded, and calculate an average value in the cases where multiple trait values are available.

1.3 If unavailable, extract the trait value from any ocean basin, and calculate an average value in the cases where multiple trait values are available.

1.4 If unavailable, extract the trait value without geographic information.

1.5 If unavailable, calculate the average trait value based on all other species in FishBase from the genus that the species belongs to, and that are also present in the LME where the species has been recorded.

1.6 If unavailable, calculate the average trait value based on all other species in FishBase from the genus that the species belongs to, and that are also present in the FAO area where the species has been recorded.
7.6 Missing trait values

1.7 If unavailable, calculate the average trait value based on all other species in FishBase from the genus that the species belongs to, and that are also present in any ocean basin where the species has been recorded.
1.8 If unavailable, extract the trait value without geographic information.
1.9 If unavailable, repeat steps 1.5-1.8 above by calculating average trait values based on other species that are members of the same family as the species recorded.

When the taxon of interest was specified at the genus or family level, steps 1.4-1.9 were followed. For categorical traits where no information on the location of origin of the trait category was available the following procedure was followed:
2.1 Extract the trait value for the species.
2.2 If unavailable, extract the trait value from members of the same genus.
2.3 If unavailable, extract the trait value from members of the same family.

7.6 Missing trait values

When all previous steps 1.1-1.9 for continuous traits or 2.1-2.3 for categorical traits led to no trait data, we searched for missing trait values in primary literature, preferably for the species of interest, but if unavailable, a trait value was taken from a species that belongs to the same genus or family. If a value was found for a species and, at the same time, another member of the same genus was assigned a family-level value from FishBase, we replaced this value by the species-specific value of the other species of the same genus. In other words, genus-level values were preferred for species or genera over family-level values.

While searching for trait values in primary literature, we did not attempt to find LME or FAO-specific values. One exception is the high-quality trait dataset by Wiedmann et al. (2014), that contains trait values specifically for Barents Sea.

Acknowledgements

We would like to thank Martin Lindegren for his supervision and reviewing the manuscript. A.M., T.S.D, and E.B. conducted the work within the Centre for Ocean Life, a Villum Kann Rasmussen Center of Excellence supported by the Villum Foundation. A.M. received funding from VILUUM research grant to Martin Lindegren (No. 13159). E.B. has received funding from the European Union’s Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No. 675997 (ITN MARmaED).
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Appendix

8.1 Appendix A Beukhof et al. 2018 (accepted)

(Published in MEPS https://doi.org/10.3354/meps12826)

Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change

Esther Beukhof, Tim Spaanheden Dencker, Laurene Pecuchet and Martin Lindegren

Abstract

Marine ecosystems are exposed to a range of environmental and anthropogenic stressors, including climate change and overexploitation. A promising way towards understanding the impacts of such stressors on community composition is by considering species traits rather than species identity. Here, we describe the spatio-temporal dynamics in fish community traits using >30 years of species abundance data from the North Sea combined with trait information on body size, life history, growth rate, reproduction and trophic level for demersal fish species in the area. We assessed whether the derived patterns and trends in community weighted mean traits could be explained by a range of environmental stressors and fishing. Our results revealed strong spatial structuring and long-term changes in the trait composition of North Sea fish, with temporal changes not being uniformly distributed in space. Among the environmental drivers investigated, depth was one of the best predictors, primarily explaining the spatial variation in lifespan, growth rate, trophic level and fecundity. This can be explained by variables that co-vary with depth, e.g. temperature, seasonality, salinity and productivity. Finally, we found only weak relationships between fishing and the spatial variation of traits, suggesting that the spatial trait composition of the community is mostly determined by the environment. Yet, long-term changes in trait composition, primarily in body size, have previously been shown to be affected by size-selective fishing. Our study exemplifies how traits can be used to summarize complex community dynamics and responses to environmental and anthropogenic stressors as well as its usefulness for ecosystem-based management.
8.2 Appendix B Beukhof et al. (in prep)

Traits and environment predict global fish community structure

Esther Beukhof, Romain Frelat, Laurène Pécuchet, Aurore Maureaud, Tim Spaanbenden Dencker, Jón Sólmundsson, Heino Fock, Antonio Punzon, Raul Primicerio, Manuel Hidalgo, Christian Möllmann and Martin Lindegren

Abstract

A fundamental challenge in ecology is to understand why species occur where they are and predict where they are likely to be found in the future. This requires a mechanistic understanding of the underlying factors determining species distributions, particularly the processes whereby species respond to the environment. In contrast to taxonomic studies, trait-based approaches may provide such a mechanistic understanding, since it is the traits and adaptations of species, not their identity, that determine which environments they are capable to inhabit and with which species they interact. Moreover, trait-based approaches may shed light on fundamental principles by facilitating comparisons across ecosystems with different species composition. A critical step following this approach is to identify the key response traits and trait-environment relationships and verify if these relationships hold across ecosystems. Based on a unique survey dataset of species abundances and traits from across the Northern hemisphere and a suit of “big data” analysis tools, we here investigate trait-environment relationships for marine fish and use these to project the global trait composition of marine fish communities. We show that traits related to growth, maturation and lifespan respond most strongly to the environment. This is reflected by a pronounced fast-slow continuum of fish life-histories along coastal-offshore gradients worldwide, revealing that traits vary with latitude and temperature at large spatial scales, but also with depth and seasonality at local scales. Our findings provide key insight into the functional structure of marine fish communities and suggest that global warming will favour an expansion of fast-living species. Knowledge on the global and local-scale drivers of marine fish traits can be used to predict future responses to environmental change and inform ecosystem-based marine management on anticipated changes in the structure and functioning of marine ecosystems.
Testing the biodiversity-ecosystem functioning concept in the ocean: fish biomass is driven by evenness, not by species richness

Aurore Maureaud, Dorothee Hodapp, Pieter Daniël van Denderen, Helmut Hillebrand, Henrik Gislason, Tim Spaanheden Dencker, Esther Beukhof, Martin Lindegren

Abstract

The relationship between biodiversity and ecosystem functioning (BEF) is a topic of considerable interest to scientist and managers because a better understanding of its underlying mechanisms may help us to predict and mitigate the consequences of biodiversity loss on ecosystem functions and services. Our current knowledge of BEF relies heavily on theoretical and experimental studies, typically conducted on a narrow range of spatio-temporal scales, environmental conditions and trophic levels. Hence, whether a relationship holds in nature containing large, complex and highly variable ecosystems is poorly understood, especially in the oceans. Using large-scale observations of marine fish communities and traits, we applied a structural equation modelling framework to investigate the existence and significance of BEF relationships across European Seas. We found that ecosystem functioning, here represented by spatial patterns in total fish biomass was unrelated to species richness, the most commonly used diversity metric in BEF studies. Instead, community evenness, differences in species composition and abiotic variables were found significant drivers. In particular, we found that fish biomass is higher when communities are dominated by a few generalist species with high trophic level able to exploit both the benthic and pelagic energy pathways. Our study provides a better understanding of the mechanisms behind marine ecosystem functioning and allows for the integration of biodiversity into management considerations.
Community ecology in 3D: Tensor decomposition reveals spatio-temporal dynamics of large ecological communities

Romain Frelat, Martin Lindegren, Tim Spaanheden Dencker, Jens Floeter, Heino O. Fock, Camilla Sguotti, Moritz Stäbler, Saskia A. Otto, Christian Möllmann

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 data sets usually derived from large-scale monitoring programs.
Seasonal strategies in the marine environment


Abstract

Throughout much of the world’s oceans a significant part of marine life is dependent and organized around seasonal periods of feast and famine. Here we seek to find and understand the fundamental patterns and processes by which marine organisms contend with seasonal variations in resource availability through various life history strategies primarily related to investment in reserves for overwintering, dormancy and migration. Our perspective is broad, spanning across all trophic levels, from unicellular plankton to whales, and covering all latitudes, from the equator to the poles. First, we develop a series of mechanistic life history models. These simple trait-based models provide a number of general hypotheses primarily conditioned by an organism’s size, namely: (i) small organisms should cope with the scarcity of food and resources during winter by making resting stages or by entering hibernation; (ii) medium-sized organisms should invest in building reserves and perform seasonal vertical migration to reduce predation and survive the winter season; (iii) large organisms should primarily employ latitudinal migrations to follow seasonal peaks in production. Subsequently, these hypotheses are tested against a large assemblage of observations and data reported in the literature. Body size, trophic level, and the intensity and duration of seasonal highs and lows appear to be closely related to seasonal strategies. Some, but not all of these predictions are borne out by our analysis of data. In particular, we find that organisms with a life-span on the order of the seasonal length employ a multitude of strategies.
Unraveling the underlying processes of community thermal shifts
Matthew McLean, David Mouillot, Eric Goberville, Martin Lindegren, Georg Engelhard, Tim Spaanheden Dencker, Tarek Hattab, Arnaud Auber

Abstract
As global warming continues plant and animal communities are becoming increasingly dominated by warm-affinity species, a process usually termed ‘tropicalization.’ Studies have documented such tropicalization by demonstrating increasing community temperature indices (CTI) across large spatial scales in both marine and terrestrial ecosystems. However, the underlying processes of tropicalization are poorly known, especially whether large-scale changes in CTI are being driven primarily by increasing warm-affinity species or decreasing cold-affinity species. Here, we developed a novel index for identifying the underlying processes of community thermal shifts that is applicable across ecosystems and taxa, and can be related to environmental variation. We characterized long-term changes in CTI in marine fish communities using ten scientific bottom-trawl surveys across the Northern Hemisphere, identifying spatial variation in the underlying processes of CTI. We found that CTI increased in only 56% of sampling locations between 1990 and 2015, and of these only 39% were driven by increases in warm-affinity species. Conversely, decreases in CTI were driven primarily by increases in cold-affinity species (64%). Interestingly, increases in CTI were more common in the North Atlantic, while decreases were more common in the Northeast Pacific. These contrasting patterns appeared linked to changes in ocean temperatures, as we found significant association between the rates of change of CTI and sea surface temperatures. Our approach provides a greater understanding of community responses to global warming, enabling large-scale investigations of the underlying processes and drivers of community thermal shifts.