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An exploration of patterns, drivers and assembly processes shaping marine fish communities

Beukhof, Esther Deborah

Publication date:
2019

Document Version
Publisher's PDF, also known as Version of record

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Trait-environment relationships in marine fish
An exploration of patterns, drivers and assembly processes shaping marine fish communities

Esther Beukhof
PhD Thesis
June 2019

Supervisor:
Martin Lindegren
Co-supervisor:
Ken Haste Andersen
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 was carried out at the Centre for Ocean Life, a VKR center for excellence funded by the Villum Foundation, at the National Institute of Aquatic Resources (DTU Aqua) in Kongens Lyngby between March 2016 and June 2019. The thesis was supervised by Dr. Martin Lindegren and co-supervised by Prof. Ken Haste Andersen. In addition, three external research stays were carried out at the University of Hamburg, Germany, in collaboration with Dr. Romain Frelat and Prof. Christian Möllmann, at Åbo Akademi University, Finland, in collaboration with Prof. Erik Bonsdorff and Dr. Marie Nordström and their research group, and at the Danish Pelagic Producers Organisation in collaboration with Dr. Claus Reedtz Sparrevohn. This PhD project was part of and funded by MARine MAnagement and Ecosystem Dynamics under Climate Change (MARmaED) – a Marie Sklodowska-Curie Innovative Training Network, grant agreement No. 675997 under the European Union’s Horizon 2020 research and innovation programme. The results of this thesis reflect only the author's view and the Commission is not responsible for any use that may be made of the information it contains. Additional funding was received from the Otto Mønsteds Fond for conference participations.
ACKNOWLEDGEMENTS

During my PhD I have been very fortunate to be supervised by such a kind, enthusiastic, smart and inspiring person. Martin, thank you for all the time and effort that you spent during the last three years. You taught me many things, not only regarding trait-based ecology, but also in terms of developing ideas and projects, writing articles, and not being too self-critical all the time and instead be proud of my achievements. Thank you for all the support and motivation – it has been such a pleasure to be your PhD student. A thanks goes also out to Ken for his help and thoughtful comments – I will now think twice before using the growth coefficient K as a trait.

This thesis would not have been here without the help of the other students and postdocs in Martin’s group. Many thanks to Tim, Laurene, Aurore, Neil, Anna and Jeremy for our group discussions, collaborations and the great amount of help I received from you. Not unimportantly, it has been a lot of fun to share office with you, making it a pleasure to go to work every day. My thanks go also out to the other students and colleagues at DTU Aqua and the Centre for making it a great and inspiring atmosphere. I can only hope my future workplaces will have such nice cookie breaks and lunch breaks, not to mention Friday bars and Christmas parties.

My PhD has been part of the MARmaED network, which has been a great experience from our first meeting in Banyuls. Many thanks to all MARmaED students for the inspiring meetings and riding this PhD rollercoaster together, and thanks to the PIs for bringing us together in the first place. Special thanks to Romain and Camilla for the nice stay in Hamburg, and Christina and Pierre for the good experience in Turku. Romain, it has been such a pleasure and a lot of fun to collaborate with you, and I hope this was not the last time. Thanks to MARmaED I also got the opportunity to do some additional projects for the Danish Pelagic Producers Organisation (together with Rob, which was fun!) and the Pelagic Freezer-trawler Association. Thanks to Claus Reedtz Sparrevoht and Martin Pastoors for those opportunities – they were very interesting and a good introduction to the fishing industry.

Many thanks to my family and friends back in the Netherlands for their support and visits. A special thanks to my parents who have been there for me since the day I became dedicated to ‘save the planet’ with science and knowledge, and for supporting me in my adventures abroad. A final big thank you to Jonas – you are simply amazing and I am lucky to have had you by my side all the way.
Marine ecosystems are exposed to a multitude of environmental and anthropogenic pressures, such as overfishing, habitat loss, invasive species and global warming. Such pressures alter the structure and biodiversity of natural communities, thereby potentially affecting the functions and services that marine ecosystems provide, such as food and coastal protection. The goal of ecosystem-based management is to sustainably make use of marine ecosystems whilst protecting its health and functioning. This requires knowledge on how natural communities respond to the range of environmental and anthropogenic pressures. The trait-based approach may provide such knowledge and understanding. It is based on the traits that species carry, which determine which environments a species can inhabit and how it may respond to disturbances. A trait can be any characteristic that one can measure on an organism, and can be related to its behaviour, morphology, life history or physiology. Moreover, characterizing natural communities in terms of their traits allows for comparing ecosystems with entirely different species compositions, thereby enhancing the possibility of finding general patterns across communities and ecosystems. In this thesis I applied a trait-based approach to marine fish communities with the aim to understand how they are structured in terms of traits, and to use traits to assess how fish communities respond to changes in environment and fishing pressure.

The response of a community to a change in environment or an anthropogenic disturbance can be detected by investigating shifts in the mean trait values expressed by the community. The North Sea fish community has a history of intense fishing pressure, as well as climate-driven changes during the last few decades. Furthermore, there are strong spatial gradients in environmental conditions, from the shallow, southern parts to the deeper, northern parts where the North Sea meets the North Atlantic. We therefore explored if the North Sea fish community shifted in its mean trait values over time, as well as in space, and if this could be explained by the environment and fishing effort. The community showed a strong temporal shift in its trait composition from large, slow-growing, late-maturing and long-living mean trait values to smaller, faster-growing, earlier-maturing and shorter-living ones. Although the high historical fishing pressure on large species, such as Atlantic cod, and the consequent decrease of such species likely contributed to these shifts, we found that they could also be explained by the increases in temperature, salinity and phytoplankton biomass. However, the temporal changes over time were not the same throughout the area, with some areas showing no shift in community trait means. Moreover, the trait composition of the community varied strongly in space, following the gradients in temperature, seasonality and depth. Our results demonstrated that traits can be used to assess how marine fish communities are structured in space and respond to environmental changes over time, and emphasize the importance of taking both spatial and temporal dimensions of marine fish communities into account.

In order for the trait-based approach to be useful in predictive models, it is important to test the generality of the empirical relationships between traits and environment, and to identify which traits respond most strongly to which environmental variables. We therefore combined data on fish communities from the North Atlantic and Northeast Pacific, including >1,200 species, that cover large latitudinal and environmental
gradients. We found that particularly traits related to the fast-slow continuum, i.e. age at maturity, lifespan and the growth coefficient K, varied most strongly with environment. Hence, warm, shallow and seasonal waters were associated with fast-growing, early-maturing and short-living species, whereas cold, deep and stable waters were mostly inhabited by slow-growing, late-maturing and long-living species. When using the observed trait-environment relationships to project the trait composition of marine fish communities worldwide, we found that traits were following both large-scale latitudinal gradients in temperature, as well as local coastal-offshore gradients in depth and seasonality. Given the consistent patterns observed across areas with entirely different species composition our results indicate that these general trait-environment relationships of marine fish may prove useful to predict changes in marine fish communities over time.

Besides knowing how communities are structured in terms of traits, it may provide additional insight to identify the underlying community assembly processes that lead to the observed structure and composition of marine fish communities. Potential community assembly processes could be related to both biotic and abiotic factors. In this thesis, we studied community assembly of marine fish for the first time at a large spatial scale by assessing if the variation in traits within communities was different from random. Some communities were found to be strongly shaped by the environment that acted as a filter by only selecting species with a particular set of traits. For instance, high temperatures filtered out species with a large size and a long lifespan. Several communities were also found to be shaped by biotic interactions, as observed from the high variation in fecundity and offspring size, suggesting that multiple reproductive strategies can coexist within the same community. However, the majority of communities seemed to be randomly assembled, suggesting that both processes may act simultaneously, thereby cancelling each other out, or that stochastic processes like dispersal and immigration/emigration are more important. The strength at which the observed assembly processes were operating varied moderately with environment, particularly with temperature and depth, but not with fishing pressure and primary production. Further knowledge on potential other community assembly processes acting on marine fish and the inclusion of intraspecific trait variation are needed to fully understand the underlying mechanisms of marine fish communities are assembled.

This thesis demonstrated that the structure of marine fish communities is strongly linked to the environment by acting on the trait composition of communities – both in space and time, as well as at small and large spatial scales. We identified key response traits and trait-environment relationships for marine fish that should be further explored and tested in other types of ecosystems. This thesis will hopefully inspire future research to create predictive models that can explore how marine fish communities may change under global warming, in combination with fishing, and to inform ecosystem-based management on the expected changes to come. This will allow users of marine ecosystems to adapt and to continue to benefit from the services provided by marine ecosystems in the future.
**RESUMÉ**


Et samfunds respons til ændringer i miljøet kan betyde at den gennemsnitlige værdi af visse karaktertræk ændres i samfundet. Nordsøens fiskesamfund har igennem historien været udsat for et tydeligt fiskeritryk, samt forandringer relatinger til klimadrevne ændringer i de seneste årtier. Endvidere er der signifikante naturlige variationer i Nordsøen fra den sydlige lavvandede del til de nordlige dybere vande, hvor Nordsøen møder Nordatlanten. Vi undersøgte Nordsøens fiskesamfunds udvikling i tid og rum, med henblik på at kortlægge skift i den gennemsnitlige karaktertræk-sammensætning, og relaterede disse potentielle skift til ændringer i miljøet eller fiskeritrykket. Fiskesamfundet i Nordsøen er generelt skiftet fra store, langsomt voksende, sent modnende og langt levende individer til mindre, hurtigere voksende, tidligt modnende og kortlevede individer. Selvom det høje fiskeritryk har påvirket visse store arter, såsom atlantisk torsk, og har været medvirkende til et skift i samfundssammensætningen, fandt vi også at stigende temperaturer, saltholdighed og phytoplankton biomassen har været afgørende for det observerede skift i samfundssammensætningen. De overordnede skift gennem tid var dog ikke uniformt spredt i rum i Nordsøen, og visse områder viste ingen skift overhovedet. Endvidere betød naturlige graderier i temperatur, sæsonprægning og dybde at sammensætningen også varierede i rum. Resultaterne viser at karaktertræk kan bruges til at beskrive og bedømme hvordan fiskesamfund er struktureret i rum og hvorledes de responderer i tid til miljøforandringer. Dermed konkluderes det yderligere, at det er vigtigt at tage både tid og rum med i analyser af fiskesamfund.

For at gøre den karaktertræk-baserede metode brugbar i prædiktive modeller er det vigtigt at teste hvor generel de empiriske forhold mellem karaktertræk og miljøet er, og identificere hvilke karaktertræk, der responderer kraftigst til ændringer i miljøet. Vi kombinerede derfor data på fiskesamfund fra Nordatlanten og det nordøstlige Stillehav for mere end 1.200 arter på tværs af store graderier i breddegrader og miljøforhold.
Vi identificerede at især karaktertræk relateret til et hurtigt-langsomt spektrum af livsstilstrategier, såsom modningsalder, levealder, og vækst (K) varierede kraftigst langs miljøgrader. Mere specifikt fandt vi, at varme, lavvandede områder præget af sæsonmæssige svingninger favoriserede hurtigt voksende, tidligt modnende og kort levede arter, mens dybere kolde vande med større miljømæssig stabilitet var karakteriseret af langsamt voksende, sent modnende, længe levende arter. Ved brug af disse sammenhænge kunne vi forudsige den globale udbrudds og disse to modsatte livsstil. Vi fandt at livstilene varierede med storkska gradienter i temperatur på tværs af breddegrader, samt gradienter fra kyster til dybere vand og sæsonmæssige prægninger. De generelle mønstre identificeret i studiet betyder, at disse karaktertræk-miljø forhold i marine fisk kan bruges til at forudsige ændringer i fiskesamfund over tid.

Udover kendskab til hvordan fiskesamfund er struktureret i forhold til deres karaktertræk, er det også relevant at øge kendskabet til hvilke mekanismer, der potentielt strukturerer samfundene. Disse strukturerende mekanismer kan både være relateret til biotiske og abiotiske faktorer. I denne afhandling har vi for første gang undersøgt disse mekanismer på stor skala, for at vurdere om samfund er deterministisk struktureret. Visse samfund viste sig at være struktureret udfra miljøet, hvor miljøforhold har virket som et filter, hvor kun bestemte sammensætninger af fiskearter med specifikke karaktertræk kunne overleve. For eksempel fandt vi at høje temperaturer filtrerede store og længstlevede arter fra. Mange fiskesamfund var også struktureret i forhold til biotiske interaktioner, hvor vi fandt stor variation i mengden af afkom og størrelsen på afkom, hvilket tyder på, at flere forskellige reproduktive strategier kan eksistere på samme tid i samme samfund. Dog fandt vi at størstedelen af samfund var mere tilfeldigt sammensat, hvilket enten tyder på at både biotiske og abiotiske mekanismer virker på samme tid, eller at samfund er struktureret i forhold til stokastiske processer såsom spredning og immigration/emigration. Graden hvorved disse mekanismer blev observeret, varierede moderat med miljøgrader, og vi fandt at temperatur og dybde var af stor betydning, modsat fiskeritryk og primærproduktion. Mere viden om andre strukturerende faktorer og brugen af intraspecific variation i karaktertræk er nødvendig for at forstå hvilke mekanismer, der styrer sammensætning af fiskesamfund.

Denne afhandling viser, at strukturen af marine fiskesamfund er stærkt forbundet til miljøforhold gennem filtrering af visse karaktertræk både i tid og rum, samt på lille og stor skala. Vi identificerede generelle mønstre i forholdet mellem karaktertræk og miljøforhold for marine fisk, og foreslår at disse mønstre studeres yderligere i andre typer økosystemer. Forhåbentlig vil denne afhandling inspirere prædiktive modeller og undersøgelser af hvordan marine fiskesamfund reagerer på fremtidige klimaforandringer og fiskeritryk, for at bidrage til en økosystem-baseret forvaltning, og tillade brugere af disse marine ressourcer at tilpasse sig og fortsat gøre brug af de servicen og goder, der kommer fra økosystemerne i fremtiden.
LIST OF PUBLICATIONS

This PhD thesis is based on the following manuscripts:


**Beukhof E**, Frelat R, Pecuchet L, Lindegren M. Community assembly in marine fish: patterns of trait convergence and divergence along large environmental gradients. *In preparation*


The following publications represent minor contributions and were not included in the main thesis:


Maureaud A, Hodapp D, Denderen PD van, Hillebrand H, Gislason H, Dencker TS, **Beukhof E**, Lindegren M. Biodiversity-ecosystem functioning relationships in demersal fish communities: biomass is related to evenness and environmental conditions, not to species richness. *Under review*
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CHAPTER 1

General introduction

1.1. Marine ecosystems under pressure

The Earth is a blue planet: 71% of its surface is covered by oceans. Although humans are a terrestrial species, we have explored and used the oceans for tens of thousands of years (Pinet, 2011). Many people depend in one way or another on the ocean and its resources. For example, fish is an important source of food and livelihood – on average 17% of our animal protein intake comes from fish – and fisheries employ 40 million people worldwide (FAO, 2018). The ocean is also used for shipping, extraction of oil, gas and minerals, and we build kilometres of pipelines and increasing amounts of offshore windfarms to supply our societies with green energy. Moreover, 40% of all people on Earth currently live within 100 km of the sea (Millenium Ecosystem Assessment, 2005). It is therefore not surprising we leave our mark on the ocean and the life it contains.

1.1.1. Pressures on marine ecosystems

The oceans are exposed to a range of human pressures that directly or indirectly impact marine ecosystems and their biodiversity, namely fishing, pollution, habitat destruction, introduction of species and global warming. Since 1974, the percentage of fish populations that are overfished has been increasing from 10 to 33% in 2015 (FAO, 2018). Fishermen may also accidentally catch species that are not targeted by the fishery, thereby influencing the abundance of non-commercial species, including not only fish, but also marine birds and mammals (Jennings et al., 2001). Whaling during the last few centuries has led to strong declines in the abundance, or even extinction, of large marine species (e.g. Stellar’s seacow) (Dulvy et al., 2003; Solan et al., 2012). The centuries-long fishing pressure in the highly disturbed North Sea has likely contributed to the loss of natural oyster reefs and a reduction in the abundance of sharks and rays (Jennings & Kaiser, 1998; Wolff, 2000; Dulvy et al., 2003; Bennema & Rijnsdorp, 2015; Kerckhof et al., 2018). Although fishing may target only a few species within an ecosystem, the strong connection between species through predator-prey interactions and competition may therefore impact the trophic structure of marine ecosystems (Jennings & Kaiser, 1998; Scheffer et al., 2005; Daskalov et al., 2007; Lynam et al., 2017).

Waste and toxic chemicals end up in the oceans via multiple pathways, such as river discharge, water discharge from factories, oil spills and shipping accidents. Pollutants can be ingested by micro-organisms and accumulated throughout the food chain to top predators, where they may reach toxic concentrations and can have severe consequences for health and reproduction of organisms (Pinet, 2011; Lehtonen et al., 2017). Pollution likely decreases biodiversity, but which species are most affected depends on the type of pollution. Top predators may be most vulnerable if the pollutant accumulates in organisms via the food chain. However, large mobile species may be able to move away from polluted areas (e.g. a harmful algal bloom), while smaller and sessile species do not have such opportunities to flee (Solan et al., 2012).
Human activities in coastal areas and at sea may disrupt or even destroy natural habitats (Lotze et al., 2006; Rochette et al., 2010). Bottom-trawl fishing disrupts the seabed, natural coastal systems are replaced by urban areas and harbours, and intense agriculture and aquaculture in the tropics have led to the destruction of a quarter of the world’s mangroves (Barbier, 2016). Habitat destruction can lead to the disappearance of species from particular areas, thereby impacting local biodiversity, whereas man-made structures (e.g. harbours, oil and gas platforms) may also promote biodiversity by creating new habitat (Solan et al., 2012).

The introduction of new species, whether deliberately or accidentally, can have consequences on marine ecosystems (Anton et al., 2019). Invasions of species into new areas, whether through human activities or climate change, may impact local biodiversity and potentially change the trophic structure of marine ecosystems (Solan et al., 2012). For instance, the comb jelly Mnemiopsis leidyi was introduced in the Black Sea via the discharge of ballast water of cargo ships originating from the Northeast Atlantic. It not only competed for zooplankton with anchovy, a pelagic and commercially important fish species, but also predated on its eggs and larvae, thereby contributing to the collapse of the anchovy population with large economic consequences for the fishing industry (Kideys, 2002).

Increasing water temperatures can lead to species shifting in their distribution or phenology in search for more favourable conditions (Parmesan & Yohe, 2003; Perry et al., 2005; Pinsky et al., 2013). Particularly, if a prey species moves faster to another location or peaks in abundance earlier in the year, a predator species may not always be able to keep up with these changes, leading to a spatial or temporal mismatch between predator and prey (Doney et al., 2012; Poloczanska et al., 2016). Higher temperatures may also affect the physiology and metabolism of organisms, which can have either positive or negative consequences for the fitness of individuals and productivity of populations (Doney et al., 2012; Poloczanska et al., 2016; Free et al., 2019). The increasing amount of marine heatwaves is another concern; marine heatwaves may cause instant mortality of organisms, while a series of heatwaves has been shown to reduce overall population densities (Smale et al., 2019). Ocean acidification – a consequence of the increased uptake of CO₂ by the oceans – is also expected to negatively affect organisms, such as corals and shellfish that depend on calcium carbonate for their skeletons or structures (Doney et al., 2012; Poloczanska et al., 2016). Additionally, bleaching is another major threat to corals caused by high temperatures that can lead to the loss of live corals (Hoegh-Guldberg, 1999).

1.1.2. Managing ecosystems

The consequences of these pressures do not only affect life in the ocean, but also the lives of people who depend on the ocean in one way or another. It is therefore of paramount importance to understand the impacts of both natural and anthropogenic pressures on marine ecosystems, in order to stop the degradation of marine ecosystems and make sure we can sustainably use the ocean’s natural resources in the future. The value of ecosystems to society is often described by the functions and services they deliver. Ecosystem functions can be described as fundamental ecological processes that ecosystems support, such as nutrient cycling, biological productivity and carbon storage (Solan et al., 2012; Gamfeldt et al., 2015; Strong et al., 2015). Ecosystems services provide direct value for humanity, for example food, medicine, tourism, clean air and water, climate regulation and coastal protection against storms (Christensen et al., 1996; Solan et al.,
1.1 Marine ecosystems under pressure

Due to the variety of functions and services that marine ecosystems provide and the high demand for marine natural resources, it is challenging to continue exploiting natural resources while maintaining ecosystem functioning and ensuring a sustainable use of resources in the future. This requires an understanding of the interplay between human and ecological systems, which both are highly complex and adaptive systems (Levin & Lubchenco, 2008). Furthermore, there are trade-offs between the two systems and between users (Leslie & McLeod, 2007; Solan et al., 2012). For example, coral reefs provide income and employment for the fishing and tourism industry, but this may come at the cost of the health of reefs and the additional functions or services they provide (Arkema et al., 2006). Therefore, the aim of the ecosystem approach or ecosystem-based management is to take both the human and ecological components of ecosystems into account, thus acknowledging that humans are part of the ecosystems, that our actions affect ecological systems and that both human and ecological factors need to be managed (Leslie & McLeod, 2007). An applied example is for instance the international Convention on Biological Diversity that has the aim to: (i) conserve biodiversity, (ii) ensure sustainable use of natural resources, and (iii) ensure that the benefits of natural resources are fairly distributed (CDB, 1992). For marine ecosystems, the focus has been on developing ecosystem-based fisheries management and to go beyond single-species management. Fisheries scientists have developed multi-species and community models, several single species assessments already include to some extent ecosystem considerations (Link et al., 2002; Pikitch et al., 2004), and the first ecosystem-based management plans have been implemented in marine systems (Thrush et al., 2016). The European Commission aims with its Marine Strategy Framework Directive for “sustainable use of the seas and conserving marine ecosystems”, and adds that “This approach […] should address all human activities that have an impact on the marine environment” (European Commission, 2008; L164/19).

1.1.3. The complexity of ecosystems and communities

An ecosystem-based approach to the management of marine ecosystems requires information on and understanding of the biological, physical and socio-economic aspects of ecosystems and their interlinkages. This thesis aims to provide a piece of the puzzle by studying the structure and drivers of marine fish communities. Communities themselves consist of populations of species, which are composed again of individuals. Individuals and populations interact with each other through processes like competition, predation and facilitation. Moreover, the environment and anthropogenic pressures may act at any level of organization – individuals, populations or communities, and a change at one level may cascade on to another. Community ecology is by some considered as ‘a mess’ (Lawton, 1999) due to the enormous complexity and difficulty of finding general patterns, rules and processes that govern communities (Lawton, 1999; Simberloff, 2004; Vellend, 2010). In response to that claim, McGill et al. (2006) suggested a trait-based approach to “clean up the mess, bringing general patterns to community ecology” (p. 178). The complexity of communities may be captured by the simplicity of the trait-based approach, because all individuals and/or species within the community are captured by only a few traits that are based on evolutionary principles (Kisørboe et al., 2018). This is also the approach that inspired this thesis and that I apply to explore the patterns and drivers of marine fish communities. The following section describes the trait-based approach to community ecology and its usefulness for ecosystem-based management, whereas the section thereafter gives an introduction to the data used in this study and the current knowledge we have on the effects of fishing and climate change on fish. I end this Chapter with the objectives of my thesis.
1.2. The trait-based approach

1.2.1. Definition and aim of trait-based ecology

Trait-based ecology is centred around the idea that individuals and species can be characterized by the traits that they carry. A trait is a characteristic of an individual that can be measured and is related to its physiology, behaviour, phenology, life history or morphology (McGill et al., 2006; Violle et al., 2007). Traits determine an individual’s performance and ultimately its fitness through the three Darwinian missions in life: to survive, to feed and to reproduce (Violle et al., 2007; Litchman et al., 2013). Traits that are known to affect an organism’s fitness are often called key traits or functional traits (McGill et al., 2006; Violle et al., 2007; Litchman & Klausmeier, 2008; Litchman et al., 2013). Since not all missions can simultaneously be maximized, individuals have to allocate the limited amount of energy available between the three processes, thereby leading to trade-offs. Traits can be used to quantify these trade-offs and to understand how individuals should allocate their energy to maximize their overall fitness (Westoby & Wright, 2006; Litchman et al., 2013; Kiørboe et al., 2018). Besides identifying such trade-offs and the traits that drive them, trait-based ecologists study how trait values vary with environment or change in response to a disturbance, and how this affects organismal performance (McGill et al., 2006). Traits may also shed light on species’ niches and with which other individuals or species they can coexist and interact with (McGill et al., 2006). Ultimately, trait-based ecology aims to understand and to predict how traits of individuals and species determine community structure and the provision of ecosystem functions and services (Díaz & Cabido, 2001; Lavorel & Garnier, 2002). A useful framework is the classification of traits as response and/or effect traits (Lavorel & Garnier, 2002; Suding et al., 2008), where response traits vary with a change in environment or an anthropogenic disturbance, while effect traits determine ecosystem functioning (Figure 1.1). This thesis will focus on the identification of response traits for marine fish by studying how traits of marine fish vary with environment and fishing pressure, the latter as an example of an anthropogenic disturbance. The following two sub-sections describe in more detail trait-based approaches in community ecology. However, many examples and references will come from terrestrial plant ecology, as it is this field for which the trait-based approach is most developed.

1.2.2. Trait-based approaches in community ecology

Community assembly

Community ecologists have embraced the trait-based approach; it enables them to find general rules that describe the composition and structure of communities, and that can be used to make predictions, as well as comparisons between communities with entirely different species compositions (Keddy, 1992; Weiher & Keddy, 1995; McGill et al., 2006). The critique in the 1970s and 1980s on community ecology was that it was only a ‘soft science’ (i.e. descriptive rather than predictive). A common approach was to use null models that create randomly assembled communities based on observational data, and that can test if the observed community is different from what one would expect by chance alone (Morin, 2011). Keddy (1992) argued that finding that a community is non-randomly assembled is not an assembly rule in itself. He therefore introduced the concept of filtering as a framework to make community assembly predictive. According to
1.2 The trait-based approach

In this framework, the environment can be seen as a filter through which species from a regional species pool have to pass in order to be part of a local community (Figure 1.2). Species with unsuitable traits will then be excluded. The research field has since then progressed by studying traits in relation to the environment in order to identify which traits and which environmental filters determine community composition. Especially for terrestrial plants, this line of research has been extremely popular and has led to the compilation of a global database on plant traits and studies (TRY; www.try-db.org), and to the identification of key plant traits for several ecosystem functions and trait-environment relationships that have been tested at local, regional and global scales (Reich et al., 1997; Wright et al., 2005; Brueelheide et al., 2018).

**Figure 1.1** Representation of the response/effect trait framework. The aim is to identify response and effect traits by which individuals or species can be characterized. A trait can be a response or effect trait at the same time. Knowing the response and effect traits of all species within a community allows for studying the effect of environmental or anthropogenic change or disturbance on the structure and diversity of the community, as well as the consequences for ecosystem functioning. Figure adapted from Lavorel & Garnier (2002).

Environmental filtering on traits can limit the variation in trait values in a community and can lead to a more narrow or ‘converged’ trait distribution (Keddy, 1992) (Figure 1.2). In harsh environments, such as dry areas with low moisture and little rainfall, plant and tree height is reduced due to hydraulic constraints in water transport that could limit photosynthesis in tall plants. Dry environments thus filter out tall plant species (Koch et al., 2004; Le Bagousse-Pinguet et al., 2017). Areas where competition is strong, e.g. tropical rainforests, may support high trait variation. This is due to a biotic process called limiting similarity caused by separation of niches among closely related species, thereby indirectly avoiding competitive exclusion (MacArthur & Levins, 1967; Grime, 2006). The trait distribution of the community is then likely more ‘diverged’, allowing for multiple strategies to coexist (Figure 1.2). Although somewhat counterintuitive, several studies recently pointed out that biotic interactions may also lead to filtering (Mayfield & Levine, 2010; HilleRisLambers et al., 2012; Kraft et al., 2015; Cadotte & Tucker, 2017). For instance, species may be excluded from a community due to local competition, grazing or predation (Cadotte & Tucker, 2017). Moreover, the environment itself may determine the strength of biotic interactions and of their importance as a filter.
1.2 The trait-based approach

Figure 1.2 During community assembly species can be selected from a regional species pool. Community A has been assembled mainly via the process of filtering, leading to low trait variation and a converged trait distribution. Community B has been assembled mainly via the process of limiting similarity, leading to high trait variation and a diverged trait distribution. It is also possible that neither processes are dominating, or that neutral processes are most important. Redrawn from Mouillot et al. (2007). Fish images from phylopic.org.

Dispersal is now also recognized as a filter in that it can hinder species to enter a community when they have limited dispersal abilities (Cadotte & Tucker, 2017). Finally, as a result of both assembly processes acting simultaneously, a community may seem to be randomly assembled (Weiher & Keddy, 1995). However, community assembly can also happen through stochastic processes (Hubbell, 2001). Neutral theory assumes that all species are ecologically similar, and that instead demographic processes (e.g. immigration, emigration, survival), dispersal, ecological drift, or extreme events or disturbances are important. This contrasts the niche-based theory (as described above) that relies on deterministic processes (e.g. filtering, biotic interactions) and interspecific variation as the mechanisms behind community assembly and coexistence (Chase & Myers, 2011). More recently, it is recognized that communities can have both deterministic and stochastic components (D’Amen et al., 2017; Viana & Chase, 2019).
Within the field of niche-based theory, there is still ongoing debate about which filter is acting on which trait and in which direction. Plant ecologists have reported both limiting similarity and filtering acting at the same time on the same trait (Cornwell & Ackerly, 2009), whereas others detected environmental filtering of plant traits at both ends of a soil depth and resource availability gradient, suggesting that trait convergence may happen in both productive and unproductive areas (Bernard-Verdier et al., 2012). The use of different null models, traits, environmental gradients, ecosystem types, presence/absence versus abundance data, and different spatial scales likely adds to the discrepancy in results (Bernard-Verdier et al., 2012). Weiher & Keddy (1995) already predicted the chance of finding trait divergence due to limiting similarity reduces when the spatial scale increases due to increased environmental heterogeneity. This stresses the importance of collaboration among trait-based ecologists working in different ecosystems, particularly marine ecosystems that are comparably poorly studied, to combine and integrate all these aspects (Viana & Chase, 2019).

**Trait distributions and community-level metrics**

The frequency of trait values within a community provides information about community structure in terms of traits. The abundance or biomass of each species adds additional insight and can be incorporated as a weight to each trait value. The most commonly used community-level trait metric, which is also the first central moment of a frequency distribution, is the mean. When trait values are weighted by abundance or biomass, this is referred to as the community-weighted mean (CWM). The CWM trait originally stems from the ‘mass-ratio hypothesis’ (Grime, 1998), which states that species with the highest biomass and the traits that they carry will have the strongest impact on ecosystem functioning. The CWM reflects the most common trait value and can thus considered to be the value most important for ecosystem functioning in an uneven community (Garnier et al., 2004; Violle et al., 2007). Gardarin et al. (2014), for instance, used CWMs of a set of plant traits in grasslands to identify the most important effect traits for digestibility – an ecosystem service related to the nutritious value that grasslands provide for herbivorous animals.

CWMs are also commonly used to identify response traits that indicate community shifts in response to changes in environment or to an anthropogenic disturbance (Ricotta & Moretti, 2011; Mouillot et al., 2013). A shift in CWM trait values along an environmental gradient is interpreted as a shift in the optimal trait value, reflecting the optimal strategy (Figure 1.3A). Van Der Sande et al. (2016) observed differences in the CWM traits of trees in five tropical rain forests that varied in soil fertility and rainfall. In forests with relatively little rain fall, the most common strategy observed was to have small leaves to reduce water loss during the dry season, whereas trees in the wettest forests invested in a high ratio of leaf area to leaf mass (called specific leaf area) in order to capture as much light as possible despite the high density of trees in such forests. Trends in CWM traits may thus help in identifying the optimal strategy under a given set of environmental conditions. CWMs have also been used to study changes in the structure of communities to detect the effects of a disturbance. For instance, declines in the mean size, age and length at maturity of a fish community in the North Sea were attributed to the intense size-selective fishing pressure on the community (Jennings et al., 1999).
1.2 The trait-based approach

Figure 1.3 Schematic representation of how the trait distribution of a community may shift in response to a change in environment or an anthropogenic disturbance. The CWM trait of the community may shift in response by either increasing or decreasing – the latter shown in panel A. The community may also respond by increasing or decreasing its CWV, as for the latter case shown in panel B. The shifts in CWM and/or CWV are caused by changes in the underlying species abundances. Note that in A the CWV and in B the CWM remain the same after the shift, but multiple combinations of shifts in CWM and CWV are possible.

The second moment of a frequency distribution is the variance. The community-weighted variance (CWV) has often been used in the context of community assembly and trait-environment relationships. A decrease in CWV along an environmental gradient indicates a decreased variation in trait values, thereby supporting filtering (through the environment and/or biotic interactions) as the main community assembly process (Cornwell & Ackerly, 2009; Enquist et al., 2015). Vice versa, an increase in CWV along the gradient may be a result of increasing importance of limiting similarity. Changes in CWV over time may also show community responses to changes in environment or management measures (Figure 1.3B). For instance, Chollet et al. (2013) found that the CWV of plant height was reduced in response to increased grazing pressure and fertilization over time, leading to a homogenization of the community.

The CWM and CWV complement each other. A decreasing CWV along a gradient does not reveal if either lower or higher trait values are selected for while moving along the gradient. The direction of change in the CWM along the gradient can provide this insight (Bernard-Verdier et al., 2012; Le Bagousse-Pinguet et al., 2017). A similar metric to the CWV is Rao’s Q that represents the dissimilarity in trait values between species of a community (based on species’ relative abundance) and is therefore also used as a single-trait metric of functional diversity, although it can incorporate multiple traits (Botta-Dukat, 2005; Lepš et al., 2006; Ricotta & Moretti, 2011). Similar to the CWV, a low Rao’s Q reflects low variation in trait values and supports the filtering hypothesis, whereas a high Rao’s Q indicates high trait variation and supports the process of limiting similarity. For simplicity, this thesis will only focus on the CWV as a metric of trait variation.
Trait-environment relationships and trait biogeography

Biogeography tries to understand the spatial and temporal distributions of species and ecosystems and the underlying mechanisms that explain them (Violle et al., 2014). Species-environment relationships are useful to model and predict species distributions (Guisan & Zimmermann, 2000). Joint species distribution models are now also available that consider multiple species simultaneously and can incorporate correlations between the abundance or occurrence of species (Clark et al., 2014; Pollock et al., 2014; Harris, 2015). Although such approaches are useful for predictive purposes and for identifying the drivers of species distributions, they cannot always provide a mechanistic understanding of why species occur where they do. Moreover, in a community or ecosystem context, a species-based approach does not easily allow for inferring consequences of environmental change on ecosystem functions and services. Instead, trait biogeography, including trait-environment relationships and modelling trait distributions in time and space, has the promise to improve our mechanistic understanding of species distributions and to incorporate knowledge on response and effect traits into models that can predict community structure and ecosystem functioning under different environmental conditions (Violle et al., 2014; Kiørboe et al., 2018). For example, the previously mentioned study by Gardarin et al. (2014) on plant traits important for digestibility of plants in grasslands was followed up by a study where they related the CWM traits to the environment, and used these relationships to predict the spatial patterns of digestibility across France (Violle et al., 2015).

Although trait-based ecology for organisms other than terrestrial plants is not yet as advanced (explaining the high number of examples and references from plant ecology in this chapter), recent progress have been made on identifying key traits and the exploration of trait-environment relationships also for marine organisms. Aquatic scientists have studied trait biogeography of corals (Sommer et al., 2014; McWilliam et al., 2018) and plankton (Litchman & Klausmeier, 2008; Barton et al., 2013; Litchman et al., 2013; Brun et al., 2016; Thomas et al., 2016), with a recent study using key traits of zooplankton to calculate their effect on carbon cycling in the ocean – an important ecosystem function in marine systems (Brun et al., 2019). For marine benthos and fish a strong focus has been on response traits to fishing and climate change (Jennings et al., 1998; Tillin et al., 2006; Fisher et al., 2010; Greenstreet et al., 2012; Baudron et al., 2014; van der Linden et al., 2016), while for benthos also effect traits have been identified, e.g. the effect of burrowing species on oxygen and nutrient fluxes in the sediment (Mermillod-Blondin et al., 2004; Thrush et al., 2006; Norling et al., 2007; Bremner, 2008). A recent study investigated trait-environment relationships of fish in estuaries at a global scale (Henriques et al., 2017), whereas others showed fish community changes in multiple traits over time as a response to environmental change (Frainer et al., 2017; McLean et al., 2018a).

1.3. Studying marine fish communities

This thesis investigates marine fish communities living in the continental shelf seas of the North Atlantic and Northeast Pacific. Chapter 4 studies local changes in the trait composition of the North Sea fish community in both space and time, whereas Chapter 5 and 6 explore the regional and continental scale variation in traits of fish communities and community assembly in the North Atlantic and Northeast Pacific. To provide some general background to these Chapters, I will discuss the bottom trawl surveys that sample marine fish
1.3 Studying marine fish communities

communities, some common traits studied for marine fish and a brief overview of two of the main pressures on marine fish communities, fishing and climate change, and how traits have been used in studying the effects of these pressures so far.

1.3.1. Bottom trawl surveys
The geo-referenced abundance and biomass data of fish used in this thesis stem from national and international scientific bottom trawl surveys conducted in the continental shelf seas of the North Atlantic and Northeast Pacific (Figure 1.4). The goal of these surveys is typically to sample demersal (bottom-dwelling) fish and invertebrate communities in order to collect abundance and biomass data for each species, but also length and age information needed for stock assessment of commercial species. Surveys typically follow a strict protocol that describes a variety of gear deployment procedures, vessel speed, net opening, duration and distance of the hauls, and procedures of subsampling, length and age measurements and species identification. They often follow a stratified survey design, where stratification may occur a priori, for instance, by depth or the spatial distribution of certain commercial fish stocks. Surveys either randomize samples within the predefined strata or have fixed sampling stations (ICES, 2017). The frequency of surveys varies: they are commonly conducted annually, biannually or twice a year, often within a fixed season.

Figure 1.4 Overview of the 22 bottom trawl surveys used in this thesis. Points represents hauls from 2005-2015 and are coloured by survey.

Bottom trawl surveys are now an important source of information to study marine fish communities, as they include a wide range of demersal species. Pelagic species are also regularly caught, but their catchability is, not surprisingly, lower than for demersal species. Moreover, between demersal species or between age groups within species catchability may differ. It is therefore important to keep in mind that surveys may provide a biased view of the fish community, at least in terms of abundances (Fraser et al., 2008; Walker et al., 2017). Nevertheless, bottom trawl surveys have been successfully used to study population and
community dynamics answering both fundamental and applied scientific research questions. An increasing amount of studies made an effort to combine data from multiple surveys, allowing for the comparison of large-scale patterns within and across populations and communities at a high spatial resolution (e.g. Pinsky et al., 2013; Jansen et al., 2015; Batt et al., 2017; Pecuchet et al., 2017; Thorson et al., 2018; Dencker, 2019; Frelat, 2019). However, when combining multiple surveys, it is important to be aware of the differences in survey protocols, and to standardize the reported abundances or biomasses as best as possible in order to make valid comparisons across surveys.

1.3.2. Trait information of marine fish

Traits, as previously mentioned, are measurable characteristics of an organism that describe its physiology, behaviour, phenology, morphology or life history. In case they strongly affect fitness and (one or more of) the three missions of life, we speak of functional traits or key traits (McGill et al., 2006; Violle et al., 2007; Litchman & Klausmeier, 2008; Litchman et al., 2013). This section describes the traits of marine fish used in this thesis, and explains why they can be considered as key traits for marine fish due to their link with life-history strategies and the fast-slow continuum. I also briefly touch upon traits used in other studies.

Traits used in trait-based studies of marine fish

Fish demonstrate a wide range of diets and feeding strategies, which can broadly be divided into planktivores, benthivores, herbivores, detritivores, piscivores or a combination of these categories. Trophic level reflects the position and role of species in the food web and is calculated based on prey items. Feeding can also be characterized by morphological traits, such as size and position of the mouth and the eyes (the latter related to visual searching for prey) (Villéger et al., 2010; Lefcheck et al., 2014; Gravel et al., 2016).

Body size is a key trait for many organisms, since it scales with metabolic rates and survival (Hendriks, 1999; Brown et al., 2004). Especially in aquatic systems food webs are strongly size-based (big eats small, small eats even smaller) (Shurin et al., 2006), and body size is seen as a key trait to study complex ecological networks (Woodward et al., 2005). For fish, body size is often measured as the length of an individual, or at the species level as the maximum length reported.

Growth is strongly related to the three missions in life because of the limited amount of energy available to an organism. Energy spend on growth cannot be used anymore for reproduction or survival (e.g. maintenance, storage or repair) (Litchman et al., 2013). Individual growth rate varies with temperature and food availability (Brown et al., 2004), and hence, also strongly with the environment. For this reason and time-consuming efforts needed to measure growth rate, trait-based studies requiring information on many species often choose proxy traits for growth. In this thesis I use the growth coefficient $K$ from the Von Bertalanffy growth equation as a proxy for individual growth rate of fish. The Von Bertalanffy growth equation describes the relationship between age and size, where the parameter $K$ (in 1/year) describes how fast an individual reaches its asymptotic size (often named length infinity $(L_\infty)$ in cm).

There is a large variation in the size and age at which fish mature. Maturing early at a small size ensures reproduction before mortality, but leaves little energy left for growing to a large size. Large and late
maturing fish have also often a long lifespan, thereby still ensuring high reproductive output, but this requires a high investment in growth earlier in life (Winemiller & Rose, 1992). Because of the high correlation between age and size at maturity as well as between body length and length at maturity, this thesis focuses on age at maturity only. Age at maturity is often reported as the age at which 50% of the population is mature or as the lowest age at which a mature individual has been found.

Some teleost fish and elasmobranchs may become surprisingly old, such as species from the genus *Sebastes* (rockfish) (205 years for *Sebastes aleutianus*) and the Greenland shark (almost 400 years), making the latter the longest-lived vertebrate on earth (Nielsen *et al.*, 2016). A long lifespan allows for many opportunities to reproduce and thus to overcome years of bad environmental conditions for reproduction, but this may also require high maintenance costs. Here I use the maximum reported age to represent lifespan.

The number of eggs or offspring produced by a female, i.e. fecundity, can differ by several orders of magnitude between fish species. Fecundity is also closely correlated with the size of eggs and offspring: the sunfish (*Mola mola*) produces up to 300 million small eggs of 1 mm, whereas some shark species only produce one or two pups each time but of one meter long or more. There is thus a clear trade-off between the number of eggs or offspring produced versus their size (Smith & Fretwell, 1974). Closely related to this trade-off is the amount of parental care or investment by the parents (Winemiller & Rose, 1992). Large eggs require extra maternal energy to create a large yolk sac, but this increases survival of the larvae after hatching. Several fish species are known to guard or hide their eggs in a nest, to perform mouth brooding or to keep eggs or larvae in a pouch on their belly, as done by male seahorses. Little to no parental care often correlates with the production of many small eggs, where the high mortality of eggs causes many to be eaten or larvae to starve, but the large amount of eggs produced ensures few survivors that are enough to contribute to the recruitment to the population (Winemiller & Rose, 1993).

Other traits typically used in trait-based and functional diversity studies of fish are related to morphology and behaviour. For instance, body shape and caudal fin shape are proxies for behavioural aspects such as mobility, swimming speed and position in the water column (Wiedmann *et al.*, 2014a; Sunday *et al.*, 2015; Pecuchet *et al.*, 2016), whereas other studies use morphometrics, e.g. caudal fin aspect ratio or elliptical Fourier transformation, to quantify morphology (Villéger *et al.*, 2010; Lefcheck *et al.*, 2014; Caillon *et al.*, 2018). In reef fish studies, gregariousness (degree of schooling) and diel activity patterns are important behavioural traits that have implications for species’ functions on reefs (Stuart-Smith *et al.*, 2013; Mouillot *et al.*, 2014; Duffy *et al.*, 2016).

**Life-history strategies and fast-slow continuum**

Several of the traits described above have been combined to form and test conceptual models of life-history strategies. The most common model for fish was developed by Winemiller & Rose (1992). This framework classifies fish into three life-history strategies, equilibrium, periodic and opportunistic species, based on traits related to generation time, fecundity and offspring survival. Equilibrium species have a low fecundity but high investment in offspring survival and long generation time (long lifespan, late maturation). This allows them to live in stable and predictable environments. Periodic species share the long generation time, but have
a high fecundity and intermediate offspring survival, enabling them to thrive in unstable but predictable environments. Finally, opportunistic species are successful in both unstable and unpredictable environments due to their short generation time, despite their low fecundity and low offspring survival (Winemiller & Rose, 1992). The framework has been found to be appropriate in describing life-history variation in both marine and freshwater fish (Mims et al., 2010; Fisher et al., 2011; Pecuchet et al., 2017). Note that these axes form continua and that many species fall somewhere in between the endpoints.

A second common framework used to describe life-history variation in animals is the fast-slow continuum, which has been observed for mammals, birds (Stearns, 1983; Gaillard et al., 1989; Read & Harvey, 1989; Promislow & Harvey, 1990), lizards (Clobert et al., 1998) and fish (Rochet et al., 2000; Juan-Jordá et al., 2013; Wiedmann et al., 2014b). After correcting for body size, it ranks species from fast-growing, early-maturing and short-living to slow-growing, late-maturing and long-living. Mortality and temperature that the organisms experience have been suggested to explain the continuum (Promislow & Harvey, 1990; Brown et al., 2004; Gislason et al., 2010; Juan-Jordá et al., 2013).

The traits used in this thesis are linked to the life-history framework and/or the fast-slow continuum. Thus, the link between the frameworks, traits, the three missions in life and the environment make them suitable to study trait-environment relationships.

1.3.3. Pressures on marine fish
Two main pressures on marine fish are fishing and climate change. Although this thesis focusses on communities, these pressures have profound consequences for lower levels of organization, namely individual fish and fish populations. This section will therefore briefly summarize some of the main effects of fishing and global warming on the individual and population level with the aim to better understand potential effects visible at the community level.

Fishing
As previously mentioned, one-third of the world’s fish stocks are currently overfished (FAO, 2018), and it is therefore not surprising that harvesting has had profound consequences on fish population and communities. Several cases are known of collapsing fish stocks, such as herring in the North Sea in the 1970s and several Atlantic cod (Gadus morhua) stocks in the 1980s, leading to fishing moratoria and enormous economic consequences for the fishing sector and countries highly depending on those sectors (Myers et al., 1996; Dickey-Collas et al., 2010). High fishing pressure on Atlantic cod in Newfoundland even led to cascading effects altering the food web (Frank et al., 2005; Scheffer et al., 2005). However, before any such collapses occur, high fishing pressure in combination with a strong size selection may cause phenotypic or even genetic changes, termed fishing-induced evolution. Several fish stocks have shown a reduction in age and length at maturity, since the selection on large sizes imposes a selection to reproduce earlier and at a smaller size to ensure reproduction before being caught by the fishery (Law, 2000; Jørgensen et al., 2007). Another observation has been a reduction in annual growth and an increased growth coefficient K (Jørgensen et al., 2007; van Walraven et al., 2010). A strong spatial selection of the fishery may also lead to changes in the
spatial distribution of fish stocks, although such changes in growth, size or spatial distribution can sometimes partially be attributed to increased temperatures (Engelhard et al., 2011a, 2014).

The life history strategy framework and the fast-slow continuum, together with the theory of $r,K$-selection, have led to some application of traits to fisheries management and marine conservation, for instance by identifying species that are most vulnerable to fishing (Adams, 1980; Jennings et al., 1998; Rochet et al., 2000; Winemiller, 2005; Juan-Jordá et al., 2015; Pinsky & Byler, 2015; Kindsvater et al., 2016; Quetglas et al., 2016). Exploited fish species with a large maximum size and late maturation decreased more in abundance during a 20-year period of fishing than close relatives with a smaller size and earlier maturation (Jennings et al., 1998). By comparing tuna species, Juan-Jordá et al. (2015) observed that species with slow life histories and occurring at higher latitudes had declined most strongly in response to fishing and had the highest chance of collapse due to overfishing compared to species with a fast life history. They attributed this to the fact that smaller tuna species and species living in warmer environments experience higher natural mortality and are thereby already adapted to experience high mortality. Additional fishing mortality may therefore be more problematic for larger tuna species living in colder environments that are not adapted to such conditions. Although large species may be more vulnerable to overfishing, small, fast-growing species may more quickly get overexploited, since they are also quick to respond to environmental variability. Fisheries management may therefore not always have acted quickly enough in reducing fishing pressures when environmental conditions turned for the worse (Pinsky & Byler, 2015). These studies highlight the need to incorporate both environmental and anthropogenic drivers in fisheries management and vulnerability assessments based on life-history traits.

**Climate change**

Human-induced climate change has multiple consequences for marine ecosystems and the life they contain, such as increasing temperatures, ocean acidification, loss of sea ice, marine heatwaves, increased stratification and an expansion of oxygen minimum zones (Keeling et al., 2010; Poloczanska et al., 2016; Frölicher et al., 2018; Smale et al., 2019). Since covering all of these effects is beyond the scope of this thesis, I will mainly focus on discussing the consequences of warming.

One important prediction is that global warming will lead to smaller body sizes in ectotherms. There are multiple, and probably synergetic, explanations for this. Since metabolic rate scales with temperature, metabolic rates are expected to increase when ectothermic organisms experience higher temperatures (Gillooly et al., 2001; Brown et al., 2004). This results in a smaller body size when individuals are not able to compensate for the increased metabolic rate by increasing their food intake, or by allocating their resources differently. Since individuals may likely not compensate their maintenance or reproduction to a large extent, they may instead limit their growth, leading to a smaller body size (Sheridan & Bickford, 2011). Moreover, higher temperatures also accelerate processes such as maturation and development, resulting in an earlier maturation at a smaller adult size despite an increased growth rate (Atkinson, 1994; Sheridan & Bickford, 2011). When taking biotic interactions into account, the lower mass-specific metabolic rate of small individuals and their lower relative energy requirements compared to large individuals at high temperatures potentially make them better competitors, leading to a selection for smaller body sizes at high temperatures.
temperatures in combination with strong competition (Edeline et al., 2013). Several studies have now indeed observed a decrease in body size within fish populations in response to warming (Daufresne et al., 2009; Genner et al., 2010; Edeline et al., 2013; Baudron et al., 2014).

Besides physiological changes, fish may also respond to higher temperatures by moving to cooler, deeper waters or towards the poles, seeking for more a favourable habitat (Parmesan & Yohe, 2003; Perry et al., 2005; Dulvy et al., 2008; Nye et al., 2009; Fossheim et al., 2015). Yet, there is considerable variation in the direction and the rate at which species and populations shift, and neither do they always comply with the expectation (deeper, colder, poleward) (Genner et al., 2004; Pinsky et al., 2013; Poloczanska et al., 2013). Furthermore, the extent to which traits (e.g. body size, mobility, range size) explain species distributional shifts is still under debate (Perry et al., 2005; Pinsky et al., 2013; Sunday et al., 2015; Schuetz et al., 2019).

Another indirect climate change effect on fish is changes in food availability and predator-prey interactions. Zooplankton species have responded rapidly to increasing temperatures, with subtropical species now being found in temperate waters and a decline in sub-Arctic and Arctic species at high latitudes (Poloczanska et al., 2016). Since warm-water zooplankton species are often smaller and are less rich in lipids, this may have negative consequences for fish larvae and planktivorous fish species (Beaugrand et al., 2003; Poloczanska et al., 2016). Early life stages of fish may also be particularly vulnerable to global warming due to their narrow temperature range and their limited swimming capacity (particularly for temperate species) to move towards areas with more favourable temperatures (Rijnsdorp et al., 2009). It may therefore be that global warming affects fish populations most strongly through negative effects on recruitment (Rijnsdorp et al., 2009).

Several studies have reported community-wide shifts for temperate marine fish with increases in warm-water species and decreases in cold-water species (Engelhard et al., 2011b; Auber et al., 2017). Such changes coincided with decreases in the mean body size of communities and an increase in small pelagic species (Engelhard et al., 2011b; ter Hofstede & Rijnsdorp, 2011; McLean et al., 2018b). Recently, Free et al. (2019) showed that across fish stocks worldwide, some stocks already benefitted from the historic warming during the last few decades (as the authors estimated an increase in maximum sustainable yield throughout the study period), while other stocks showed signs of a decrease in productivity due to warming. Climate change will most likely produce winners and losers, and shifts in species abundances and composition may have consequences for entire ecosystems and their functioning. For instance, the increasing abundance of Atlantic cod in the Barents Sea, which is a generalist species feeding on both benthos and pelagic prey, will likely alter energy flows within this system that used to be dominated by small Arctic benthivorous species (Frainer et al., 2017). Moreover, the loss of sea ice will provide a window of opportunity for pelagic visual predatory fish, while it will likely have severe negative consequences for typical Arctic fish species that depend on the sea ice for food, shelter or spawning (Christiansen, 2017; Langbehn & Varpe, 2017). Besides ‘borealization’ in the Arctic, ‘tropicalization’ may occur in temperate marine ecosystems. Several cases have already been reported where poleward shifts of tropical herbivorous fish species led to overgrazing in sub-tropical and temperate macrophyte-dominated systems (Vergés et al., 2014).
1.4. Objectives

The general aim of this thesis was to contribute to the trait-based ecology of marine fish communities with a focus on exploring the relationships between traits of marine fish, the environment and fishing pressure. We compiled bottom trawl survey datasets from continental shelf seas of the North Atlantic and Northeast Pacific to study these relationships, and combined the survey data with an extensive trait collection. I first focus on the North Sea fish community to study both the temporal and spatial dynamics of community-weighted mean traits. The long time series (> 30 years), strong environmental gradients, and history of intense fishing pressure in this ecosystem allowed us to address the following questions in Chapter 4:

- How do community-weighted mean traits of North Sea fish vary in time and space?
- Are temporal trends in community-weighted mean traits homogeneous in space?
- To what extent can the environment and fishing effort explain the trends and patterns of community-weighted mean traits?

In Chapters 5 and 6 I increase the geographical area by including more than 20 bottom trawl surveys from the North Atlantic and Northeast Pacific. This allowed us to investigate if one would find similar trait-environment relationships within and across multiple ecosystems. In Chapter 5, I set out to find key response traits for marine fish by answering the following questions:

- Which traits of marine fish vary most strongly with environment and fishing pressure?
- What is the direction and shape of the relationships between traits and environment and fishing pressure?
- Using the observed trait-environment relationships: how does the projected trait composition of marine fish communities across continental shelf seas worldwide look like?

Knowing how community-weighted mean traits of marine fish vary with environment and fishing pressure across large spatial scales, I wanted to further explore the variance in trait values around the observed community-weighted means. The community-weighted variance can provide insights into community assembly, and may reveal which processes of community assembly, filtering or limiting similarity, may shape marine fish communities. I therefore wanted to answer the following questions in Chapter 6:

- Do marine fish communities show patterns of trait convergence or divergence, indicating filtering or limiting similarity, respectively, or does neither assembly process dominate, resulting in random (neutral) assembly?
- Does the strength of filtering and limiting similarity vary with environment and fishing pressure?

Lastly, Chapter 7 describes the trait dataset used in Chapter 5 and 6, including its collection procedure.
CHAPTER 2

Synopsis

2.1. Patterns, trends and drivers of fish community traits in the North Sea

Traits are useful to explore variation in community structure in space and time, especially in response to changes in environment or an anthropogenic disturbance (Greenstreet et al., 2012; Mouillot et al., 2013). During the last few decades, the North Sea demersal fish community has been exposed to a range of environmental changes, e.g. an increase in temperature, as well as a decrease in fishing effort (Beaugrand, 2004; ter Hofstede et al., 2010; Engelhard et al., 2015). I applied a trait-based approach to this community in order to assess its response to several environmental and anthropogenic drivers by studying temporal, spatio-temporal and spatial patterns of community-level traits (Chapter 4).

Fish abundance data from the North Sea were extracted from the online database of the International Council for the Exploration of the Sea (http://datras.ices.dk) for the years 1983 to 2014, which were collected as part of the annual North Sea International Bottom Trawl Survey. For each demersal species, information was collected on eight traits (trophic level, body length, age and length at maturity, lifespan, growth coefficient K, fecundity and offspring size) that together represent important aspects of fish ecology, such as diet, life history, growth and reproduction. For 78 species complete trait information was found and their abundance was converted to biomass. To represent the spatial patterns and temporal dynamics I then calculated community-weighted mean (CWM) traits (i.e. the average trait value of the community, weighted by the relative biomass of each species) (Garnier et al., 2004) in three different ways. Firstly, I calculated the CWM traits for each year based on spatially averaged fish biomasses, resulting in time series of CWMs. Secondly, for each survey grid cell I calculated CWMs based on annual averages, which I used to produce maps of the CWM traits. Lastly, CWMs were calculated for each year in each grid cell, resulting in time series in CWMs per grid cell. Linear regressions were performed on these time series to assess the strength and direction of temporal change in the grid cells to reflect the spatio-temporal patterns of the CWMs. To identify the key drivers of trait changes in space and time the temporal and spatial CWM traits were modelled using a set of environmental variables as predictors (including temperature, salinity, Phytoplankton Colour Index (PCI) representing phytoplankton biomass, seabed substrate richness and seasonality in temperature), as well as fishing effort. The models used were generalized additive models (GAMs) and included corrections for temporal or spatial autocorrelation where necessary, in which case these constituted generalized additive mixed models (GAMMs).

Our results demonstrated pronounced temporal changes in the North Sea fish community, with a shift in dominant traits from large, long-living, late-maturing and slow-growing species to smaller, shorter-living, earlier-maturing and faster-growing species during the 1980s and 1990s. The GAMs revealed that increases in PCI, temperature and salinity, themselves caused by changes in large-scale ocean-
2.2 Identifying key response traits and trait-environment relationships

Atmospheric forcing in the North Atlantic (Reid *et al.*, 1998, 2001; Letterme *et al.*, 2005; Beaugrand, 2009), underpinned these structural changes. Furthermore, literature indicates that the high historical fishing pressure on the North Sea fish community played a large role by removing biomass of large-bodied species (Engelhard *et al.*, 2015). Interestingly, the temporal trends were not homogeneously spread throughout the North Sea, but instead seem to have taken place mostly in the central part. The spatial patterns of CWM traits revealed strong spatial structuring of traits in the community. For instance, the high biomass of elasmobranchs in the southwestern North Sea was reflected by high CWMs of offspring size and low CWMs of fecundity. In the southeast, high biomass of benthivorous species resulted in low CWMs of trophic level. Along the Norwegian trench and the continental shelf edge with the North Atlantic a distinct community of large, late-maturing and long-living species was found. The south-north gradients in depth, temperature, seasonality and phytoplankton biomass all contributed to explaining the spatial variation in CWM traits according to the models.

Although the North Sea is one of the most studied systems worldwide, we derived new insights by showing temporal trajectories and spatial dynamics of a range of CWM traits of fish that reflect the underlying species dynamics and are the result of changes and variation in lower trophic levels, environmental conditions and fishing pressure. We also showed that the spatial patterns of the temporal trends are not homogeneous, thereby confirming the importance of taking the spatial-temporal dynamics of fish communities into account when managing marine ecosystems. Moreover, we demonstrated that multiple drivers play a role in determining the trait composition of the North Sea fish community and that some traits are better candidates for use as ecological indicators than others. Several traits revealed strong community-level responses to changes in environment over time (e.g. body length, age at maturity) but showed weak correlations with environmental gradients in space. In Chapter 5 I therefore expanded the spatial scale of our analysis to seek more general trait-environment relationships across large environmental gradients, whereas in Chapter 6 I go beyond the CWM trait by looking at the variation around this mean.

### 2.2. Identifying key response traits and trait-environment relationships

Trait-environment relationships can increase our understanding of why species are found where they are, and how community structure varies across systems with entirely different species compositions. Moreover, they can be used to predict how communities may change under different scenarios of, for instance, climate change and fishing intensity. In Chapter 5 I therefore set out to find general trait-environment relationships for marine fish in continental shelf seas and identify which traits are most responsive to which environmental gradients.

We expanded the spatial scale of our study by combining fish abundance data from 21 scientific bottom trawl surveys that run regularly in the shelf seas of the North Atlantic and Northeast Pacific. The data span large latitudinal gradients that range from subtropical waters in the Gulf of Mexico to sub-Arctic to Arctic conditions around southern Greenland, the Eastern Bering Sea and the Barents Sea. Fish abundances were standardized either by the duration of the haul or the area swept by the fishing gear over the seafloor. Abun-
dances were then converted to relative abundances per haul or per grid cell. From each survey we selected the years 2005-2015 and retained all taxa that were described at the species, genus or family level. Our final dataset consisted of 1,464 unique taxa (1,256 species, 142 taxa at the genus level and 66 taxa at the family level). We assigned each taxon to the Large Marine Ecosystem (LME) it was sampled in, which allowed us to match taxa with LME-specific trait values whenever possible (26% of taxa had LME-specific trait values for at least one trait). We included the same traits here as in Chapter 4, but excluded length at maturity due to its high correlation with maximum body length and age at maturity. In terms of environment, we extracted data on sea bottom temperature and seasonality in temperature (taken as the range), sea bottom salinity, chlorophyll $a$ concentration and seasonality in chlorophyll (taken as the range), depth and a cumulative metric for demersal fishing pressure (see Chapter 5 for all sources of data).

![Figure 2.1](image-url) **Figure 2.1** Overview of the data and methodological approach taken in Chapter 5. In **Step 1**, all three datasets (species abundances per site (L), species traits (Q), and environmental variables per site (R)) are simultaneously used in the RLQ and fourth-corner analysis that explore the associations between traits and environment (i.e. the missing fourth corner). In **Step 2**, CWM trait values are calculated per site based on the species abundances, and their variation across environmental gradients is modelled using multiple random forests. In **Step 3**, the random forests are used to project the CWM traits across shelf seas worldwide. (World map from Wikimedia Commons.)

To assess the relationships between traits and environment, we performed three different but complementary analyses: RLQ analysis, fourth-corner analysis and random forests (Figure 2.1). The RLQ analysis is a multivariate statistics approach that summarizes the structure across the three datasets – fish abundances per sampling site, traits and environmental variables per sampling site – by maximizing the cross-covariance between traits and environmental variables and making use of the abundance data (Dray et al., 2014). The resulting structure among the three datasets is summarized through so-called RLQ axes on which species, traits, environmental variables, sampling sites all get scored. These scores then reveal the associations between and among them. The fourth-corner analysis assesses the significance of the associations between each trait and each environmental variable separately, again through species abundances and by comparing correlations between traits and environment with correlations based on 5,000 permutations of the fish abundance dataset (Dray et al., 2014). Finally, we investigated trait-environment relationships by calculating CWM traits per grid cell based on fish abundances and their trait values, and modelled the CWMs of each trait with the set of environmental variables and fishing pressure as predictors by constructing random forests. These allowed us to explore potential non-linear relationships between traits and environment, and to
generate projections of the distribution of CWM traits on continental shelf seas worldwide based on environmental conditions and fishing pressure.

All three analyses revealed the same traits and environmental variables to be strongly related. Age at maturity and lifespan were positively associated with depth and negatively with sea bottom temperature and temperature seasonality. In contrast, the growth coefficient K was positively related to temperature and temperature seasonality and negatively with depth. The spatial patterns of traits, environmental variables and their associations confirmed the presence of a ‘fast-slow continuum’ of fish life histories, with short-living, early-maturing and fast-growing species dominating in warm, highly seasonal and shallow waters, and long-living, late-maturing and slow-growing species dominating communities in colder, more stable and deeper waters. When projecting the CWM traits based on the random forests onto continental shelf seas worldwide, the fast-slow continuum appeared to be present at all latitudes, following coastal to offshore gradients of depth, temperature and seasonality. The remaining traits (maximum length, trophic level, fecundity, offspring size) and predictor variables (salinity, fishing pressure, chlorophyll a concentration and seasonality therein) showed consistently less strong relationships across the three methods. Yet, all traits responded at least to some extent to depth and temperature, confirming the importance of these drivers for structuring marine fish communities.

Our results identified three key response traits (age at maturity, lifespan and growth) that varied strongly across large environmental gradients (e.g. latitudinal gradient in temperature) as well as along more regional gradients (e.g. coastal-offshore gradients in depth, temperature and seasonality). The expansion of the spatial scale in Chapter 5 allowed us to identify drivers of trait variation that were not clearly detected at local scales, as for the North Sea in Chapter 4. This emphasizes the importance of studying trait-environment relationships at different spatial scales to identify the relevant drivers and response traits at each scale. Furthermore, when substituting space for time, our work in Chapter 5 suggests that under future global warming communities in colder environments are likely to become more dominated by fast-living species as temperatures increase. This can have pronounced consequences for not only community structure itself, but also for ecosystem functioning and the services that are provided, such as the type of fish that can be harvested. Policy makers, marine ecosystem managers and the fishing industry can thus benefit from future research on trait-based models that predict the response of fish communities to environmental changes and the consequences for ecosystems under different management scenarios.

2.3. Trait-mediated community assembly

While in Chapters 4 and 5 I explored how communities are structured, a key question in ecology is how communities are assembled. Understanding the processes underlying community assembly can inform predictive models to see how communities will change under environmental change. From a niche- and trait-based perspective, there are two major community assembly processes: filtering and limiting similarity. Harsh environmental conditions or a strong competitive environment may act as a filter by excluding species with unsuitable traits (Keddy, 1992). In such cases communities likely show reduced trait variation and a
2.3 Trait-mediated community assembly

relatively ‘narrow’ trait distribution, a phenomenon named trait convergence. Limiting similarity, on the other hand, is a result of biotic interactions whereby species that share a common resource differentiate themselves (MacArthur & Levins, 1967). Communities may then show a relatively high variation in trait values and a ‘wide’ trait distribution, named trait divergence (Weiher & Keddy, 1995; Bernard-Verdier et al., 2012). Based on the strong trait-environment relationships and spatial variation in CWM traits observed in Chapter 4 and 5, marine fish communities are potentially shaped by these two trait-mediated assembly processes. Therefore, in Chapter 6, I aimed to (i) uncover signals of filtering and limiting similarity in marine fish communities, and (ii) to investigate if the strength of these processes may depend on the environment or the intensity of fishing. I did so by making use of the community-weighted variance (CWV), with the idea that a higher CWV than expected by chance is a sign of trait divergence due to limiting similarity, while a lower CWV than expected is an indication of trait convergence caused by filtering (Cornwell & Ackerly, 2009; Bernard-Verdier et al., 2012).

As in Chapter 5, I combined 21 bottom trawl surveys from across the North Atlantic and Northeast Pacific, and selected data from the years 2005-2014. To define local communities, I performed a randomization procedure to standardize the biomasses per species across a spatial grid of 1° by 1° cells. Each grid cell was then considered to be a community. I selected the same seven traits as used in Chapter 5 (maximum length, trophic level, age at maturity, lifespan, growth coefficient K, fecundity and offspring size) and found complete trait information for 1,138 unique species. For each community and trait, I calculated the CWV and created null models to test if the observed CWV was significantly higher or lower than expected by chance, indicating limiting similarity or filtering, respectively. The difference between the observed CWV and those of the null models was quantified with the standardized effect size (SES). Finally, I aimed to assess if the strength of the assembly processes varied with environment and fishing pressure. I did so by modelling the variation in SESs using a set of environmental variables and fishing pressure using random forests.

Several traits demonstrated significant signs of trait convergence, namely lifespan, maximum length, age at maturity and the growth coefficient K. This indicates that there is selection on specific values for these traits, and that other values are excluded from the community. Fecundity and offspring size showed signs of trait divergence, suggesting that several reproductive strategies can coexist within the same local community and that no strategy is strongly selected for. However, a majority of communities neither showed significant signs of trait convergence nor of divergence, particularly for trophic level. This indicates that neither filtering nor limiting similarity dominated, or that other assembly processes not studied here are more important (e.g. dispersal, demographic processes related to neutral theory) (Weiher & Keddy, 1995; Hubbell, 2001). The random forests revealed some variation in the strength of community assembly processes that could be explained by the environment. For instance, filtering was strongest in deep waters, at medium to high temperatures and in areas with low seasonality in temperature. None of the traits showed strong relationships with chlorophyll a concentration or fishing pressure.

Our results confirm and expand on previous small-scale studies by showing that both limiting similarity and filtering shape marine fish communities (Mouillot et al., 2007; Ingram & Shurin, 2009; Pecuchet et al., 2016; Dencker et al., 2017). We found filtering to be particularly strong for body length and traits related to the...
fast-slow continuum at medium to high temperatures and at greater depths. This indicates that, together with the results from Chapter 5, at high temperatures there is a strong selection for small and fast-living species, and that large and slow-growing species do not pass the ‘high temperature filter’. At greater depths, large, slow-growing species are selected for. At the same time, communities allow for a diversification in reproductive strategies, as observed from the trait divergence in fecundity and offspring size. No strong relationship was found between the SESs and fishing, but such a relationship can potentially be detected when studying the effect of fishing on the trait composition of fish communities over time. For instance, the phenomenon of fishing down the food web (Pauly et al., 1998) implies that fishing acts as a strong selective pressure by filtering out large, high trophic level species. The absence of statistically significant results indicating specific assembly processes for the majority of communities in our study suggests future research is needed to explore the importance of other assembly processes, such as those invoked by neutral theory. However, effort should also be made to collect intraspecific trait variation to capture as much of the true variation in traits present in communities as possible. This will likely increase the detection of trait-mediated assembly processes.

2.4. Collection of marine fish traits

The trait-based approach requires trait information on the individuals or species present in the community. The marine fish communities studied here are sampled by scientific bottom trawl surveys from across the North Atlantic and Northeast Pacific and included approximately 1,700 fish species, 800 genera and 230 different families. To permit trait-based analyses based on these surveys, we systematically sourced 14 traits from a Microsoft Access version of FishBase (Froese & Pauly, 2015a). The traits included, in addition to the ones used in Chapter 4-6, caudal fin aspect ratio, asymptotic size, habitat, feeding mode, body shape, caudal fin shape and spawning type. The occurrence of each taxon was georeferenced with the Large Marine Ecosystem (LME) and FAO major fishing area it was sampled in. This allowed us to extract LME or FAO-specific trait values whenever such area-specific trait information was available. When information was missing, values were searched for in the primary literature or taken from a member from the same genus or family. The dataset has been made publicly available and will hopefully make more large-scale trait-based studies of marine fish possible.
CHAPTER 3

Synthesis

This thesis studied trait-environment relationships of marine fish communities by exploring how the trait composition of communities is structured in time and space and how well the observed trends and patterns can be explained by the environment and fishing pressure. Here I synthesize the results of Chapters 4-7 and describe the overall contribution to the field in light of previous studies. I highlight the benefits of the trait-based approach I took, but also discuss some caveats and improvements the field needs to address in order to move forward. Finally, I discuss the current application of trait-based indicators in marine ecosystem-based management, and provide an outlook on moving from response traits to effect traits in relationship to biodiversity and ecosystem functioning.

3.1 Trait-environment relationships in marine fish

3.1.1 The value of the trait-based approach
It has been more than two decades since Keddy (1992) proposed his community assembly framework of filtering via traits, and Keddy & Weiher (1995) encouraged community ecologists to look for patterns of traits in space and time across ecosystems and study their importance for community assembly. Their ideas were further expanded in McGill and colleagues’ influential paper in 2006 – with the overall aim to turn community ecology into a predictive science by studying species niches in relation to and interaction with traits, environment and organismal fitness. Much progress has been made in our understanding of key functional traits (e.g. Wright et al., 2004; Litchman et al., 2013; Violle et al., 2014; Andersen et al., 2016; Funk et al., 2017; Villéger et al., 2017), patterns and drivers of trait variations and community assembly (e.g. Reich et al., 1997; Cornwell & Ackerly, 2009; Brun et al., 2016; Pecuchet et al., 2016), and the first predictive models have been created (e.g. Shipley et al., 2006; van Bodegom et al., 2014; Kiørboe et al., 2018). The large body of work that has been done has shown two benefits of taking a trait-based approach to study communities: (i) it provides a mechanistic understanding of the underlying drivers of species distributions and community assembly, and (ii) it goes beyond taxonomy by being able to compare communities from ecosystems with entirely different species compositions. For marine fish, in particular, the life-history strategy framework based on traits has greatly increased our understanding of the different ecological strategies that fish exhibit under a given set of conditions, and thereby also which groups of fish are most vulnerable to (over)fishing – an immense pressure on marine fish communities (Winemiller & Rose, 1992; Jennings et al., 1998; Reynolds et al., 2005; Charnov et al., 2013; Juan-Jordá et al., 2015; Pinsky & Byler, 2015; Kindsvater et al., 2016; Pecuchet et al., 2017) and to climate change (Perry et al., 2005; Sunday et al., 2015).
In this thesis I scaled up from marine fish species and populations to entire communities to explore how the trait composition of communities varies with environment and fishing pressure, and how communities have responded to environmental changes in the past. We collected information on traits for 1,700 species (Chapter 7) that are related to the life history and ecology of marine fish, and that describe and quantify their size, feeding, growth and reproduction. We then used community-level trait metrics – community-weighted mean (CWM) and community-weighted variance (CWV) – and multivariate approaches (e.g. RLQ analysis) to study the response of communities while taking the underlying species dynamics in abundances or biomasses into account. Chapter 5 and 6, together with the large trait collection described in Chapter 7, clearly demonstrate the benefit of the trait-based approach, as it allowed us to compare the community structure of hundreds of fish communities across ocean basins and large environmental gradients. The trait-environment relationships were found to be consistent across different ecosystems, thereby enabling us, for the first time to our knowledge, to predict the trait structure of communities in continental shelf seas worldwide (Chapter 5). We employed a range of methods to study these trait-environment relationships at multiple scales. The consistent response of traits related to the fast-slow continuum (age at maturity, lifespan, growth) to local and larger-scale gradients in temperature, depth and seasonality across these analyses demonstrates the robustness of our findings. As expected based on the strong patterns in CWM traits across environments, Chapter 6 demonstrated that trait values of marine fish, such as maximum length and lifespan, are being selected for, although in some areas more than others. Interestingly, I also found evidence that limiting similarity is in some cases the main process determining variation in fecundity and offspring size. Overall, Chapter 5 and 6 indicate that marine fish communities show strong shifts in CWM traits, but that there is still considerable variation in trait values around the means, with filtering sometimes being the dominant assembly process, whilst on other occasions neither filtering nor limiting similarity dominate. These are new insights into the variation in traits within and across marine fish communities, as well as the drivers that shape communities under given environmental conditions.

Chapter 4 was the only study where I explored the variation in community traits in both space and time. I took the North Sea fish community as a case study and assessed the response of CWM traits to a range of environmental variables as well as fishing effort. I found that some areas within the North Sea had undergone many more changes over time in the CWM traits than others. Moreover, some environmental drivers in time were not necessarily driving patterns in space. Similarly, other studies revealed a variety of spatio-temporal dynamics in marine fish communities in terms of trait variation, and taxonomic and trait diversity (Greenstreet & Hall, 1996; Wiedmann et al., 2014a; Engelhard et al., 2015; Granger et al., 2015; Lamy et al., 2015; Dencker et al., 2017; Frelat et al., 2018; McLean et al., 2018b; Rincón-Díaz et al., 2018). Overall, such spatio-temporal analyses, including Chapter 4, emphasize the importance of taking both spatial and spatio-temporal dimensions into account when studying trends in trait-based community metrics over time.

3.1.2 Response traits
Among the traits and trait-environment relationships identified in this thesis, some traits were more responsive to the environment than others. In all Chapters (4-6) community-level metrics of age at maturity, growth coefficient K and lifespan responded strongly to the environment, both in time and in space. The
3.1 Trait-environment relationships in marine fish

clear statistical relationships suggest that these are key response traits for marine fish. All of these traits are related to the fast-slow continuum of life histories (Rochet et al., 2000; Juan-Jordá et al., 2013; Wiedmann et al., 2014b). Body length also responded to a range of environmental variables, and is a key trait due to its importance for determining the structure of communities and food webs, its spanning across trophic levels, and its relation to life history traits, vital rates, metabolism and ecological processes (Brown et al., 2004; Andersen & Beyer, 2006; Andersen et al., 2009, 2016). The strong relationships between the CWMs of these four traits and temperature confirm that individual and population-level physiological responses to temperature scale up to higher levels of organization, i.e. communities, as also predicted by metabolic theory of ecology (Brown et al., 2004).

In contrast to these traits, the relationships between the CWMs of fecundity and offspring size were more variable across studies. For example, no trait-environment relationships were found for offspring size within the North Sea area (Chapter 4), whereas fecundity revealed only weak and non-linear relationships with environment across large environmental gradients studied in Chapter 5. This suggests that the strength of the relationships between these traits and environment at the community-level are scale-dependent, or that other environmental variables not studied here are better candidates. Indeed, egg size of marine fish is not solely explained by temperature, but also by environmental predictability and the strength of density-dependence that eggs and larvae experience (Olsson et al., 2016; Barneche et al., 2018). The survivorship of juveniles is also included in the life-history strategy framework of Winemiller & Rose (1992) as an explanation for the diversity in strategies. Future trait-based studies should include such variables.

The most consistent trait-environment relationship found for trophic level was the increase in trophic level with depth up till approximately 100 m, after which the relationship either levelled off or slightly decreased again (Chapter 4, 5). This is consistent with the fact that shallow waters are often used as nursery areas for young fish and inhabited by small benthivorous and planktivorous species, whereas adults and larger species feeding at higher trophic levels tend to occur in deeper waters. However, in this thesis no individual-level trophic information was included, resulting in juveniles being assigned the same trophic level as adults. If such information would have been included, the derived trait-environment relationship would likely have strengthened, since juveniles often feed at lower trophic levels and/or occur in shallower waters than adults. The results of thesis also indicate that trophic level does not vary as strongly with temperature as body size and the traits related to the fast-slow continuum, potentially due to trophic level being less controlled by physiological mechanisms that are temperature-driven. Trophic level neither showed strong signs of trait convergence or divergence (Chapter 6), confirming the results from Chapter 4 and 5 that the environment does not strongly select for certain trophic levels within fish communities or that there are no specific environments that support a greater (or lower) variety in trophic levels than one would expect by chance alone. Since fish can vary in their feeding strategy and traits within the same trophic level (van Denderen et al., 2017; Mihalitsis & Bellwood, 2019), it is rather recommended to select other traits than trophic level to represent diet and feeding strategy (Gravel et al., 2016; Villéger et al., 2017). This will likely lead to more insightful relationships with environment and better represent the diversity in feeding strategies and resource use, which can help to detect community assembly processes.
3.1.3 The effect of environment and fishing

In all of Chapters 4-6 depth, temperature and seasonality in temperature were identified as the main drivers of trait variation, both within the North Sea (Chapter 4), as well as across coastal-offshore gradients across the North Atlantic and Northeast Pacific (Chapter 5). These variables were also the best explanatory variables for the variation in trait convergence and divergence across communities (Chapter 6). This supports other trait-based studies on marine fish that have found strong responses of community-level traits and trait diversity to these predictors (Fisher et al., 2010; ter Hofstede & Rijnsdorp, 2011; Dencker et al., 2017; Frainer et al., 2017; Pecuchet et al., 2017; McLean et al., 2018a, 2018b). Overall, many of the trait-environment relationship observed in this thesis were non-linear, and both the models (generalized additive models, random forests) and RLQ-analysis revealed that multiple environmental variables were driving the variation in traits. Future work should direct attention to potential interacting effects of environmental variables, e.g. the effect of temperature on CWM traits may change with increasing chlorophyll $a$ concentration. Such knowledge may disentangle the underlying mechanisms and community assembly processes behind the trait-environment relationships even further.

In this thesis two proxies for food availability were used: the phytoplankton colour index (PCI), used in Chapter 4, and chlorophyll $a$ concentration (Chl), used in Chapter 5 and 6. The PCI is based on data from the Continuous Plankton Recorder (SAHFOS, 2016), which has a long time series and represents phytoplankton biomass, whereas Chl is based on satellite observations and is a proxy for primary production (Maritorena et al., 2010). The North Sea fish community showed strong temporal responses to changes in the PCI. These results were explained by top-down cascading effects via high fishing pressure on predatory fish and a regime shift that took place in the 1980s. During this regime shift, temperatures and salinity changed, as well as the size and community composition of the phytoplankton and zooplankton community, which in turn negatively affected the recruitment of large-sized commercial species, such as cod (Chapter 4; Lynam et al., 2017). However, only the growth coefficient $K$ had a strong spatial relationship with the PCI, and the large-scale analyses in Chapter 5 and 6 revealed only weak spatial relationships between traits and Chl. These differences across and between temporal and spatial scales and studies might be attributed to the interpolated observational data of the PCI, the differences in meaning of the two metrics (proxy for biomass vs. production), or the opposing trends found for the PCI and Chl in the North Sea (Capuzzo et al., 2017). Chl has been shown to correlate with fish production, landings and recruitment (Jennings & Brander, 2010; Capuzzo et al., 2017) and has the benefit of global observations at a high spatio-temporal resolution.

However, here I showed that community-level traits of fish do not strongly respond to Chl variation in space, perhaps due to the stronger effects of depth, temperature and seasonality. Huston & Wolverton (2011) suggested using evolutionary and ecologically net primary production (eNPP), which is the NPP observed during the growing season. They found that the average maximum length of fish species in Large Marine Ecosystems was strongly related to eNPP, with the explanation that high primary production during the short growing season in temperate areas on the Northern hemisphere leads to the largest animal body sizes in these areas. However, other proxies for food should also be looked at in relation to fish community traits, e.g. benthos and zooplankton biomass and production, which are closer proxies to the actual food items that fish consume.
The effects of fishing on marine fish communities are relatively well-studied: it may change the community size spectrum and reduce the mean trophic level (Rice & Gislason, 1996; Jennings & Kaiser, 1998; Pauly et al., 1998; Blanchard et al., 2005; Essington et al., 2006; Branch et al., 2010). Although I could not test for the effect of fishing on the CWM traits of the North Sea fish community over time, literature suggested that the intense historical fishing pressure on this community has likely affected the temporal trends, also those of other traits than size and trophic level (Chapter 4). However, other drivers, such as increased temperature due to climate change, may have similar effects. Indeed, it may be difficult to disentangle the effects of warming and fishing (Daan et al., 2005; Piet & Jennings, 2005). Often both drivers are found to have an effect on the dynamics of populations, and although fishing pressure has been reduced in areas such as the North Atlantic, a stock may not necessarily recover (Fisher et al., 2010; Engelhard et al., 2014; Rouyer et al., 2014; Sguotti et al., 2019). In the Northeast Atlantic, large-bodied stocks seem on their way to recovery (van Gemert & Andersen, 2018), and so does the proportion of large individuals within the North Sea fish community, potentially due to improved fisheries management (Engelhard et al., 2015). However, here I showed strong responses of community trait-based metrics to temperature, emphasizing that it remains important to take into account the possibility that increasing water temperatures may hamper further recovery and alter community dynamics (ter Hofstede & Rijnsdorp, 2011; Engelhard et al., 2015; Queirós et al., 2018; Free et al., 2019).

In none of Chapters 4-6 did I found strong evidence that fishing has spatially affected the community trait composition. Theory and previous observations predict that high fishing pressure and removal of large fish would lead directly, or indirectly, to a decrease in the mean size of the community (Nicholson & Jennings, 2004). Although this has been observed across temporal scales, it has been difficult to detect such changes across space, when looking at a similarly high resolution as in this thesis (Blanchard et al., 2005; Piet & Jennings, 2005). Studying fishing effects at such small scales cannot take into account the fact that fish easily swim in or out of grid cells. Therefore, intense fishing in one grid cell may easily affect neighbouring grid cells and distort relationships (Piet & Jennings, 2005). The effect of fishing pressure on the trait composition of marine fish communities can thus better be assessed at temporal scales, or at spatial and spatio-temporal scales with larger grid cells or areas than used here.

Furthermore, several ecosystems, such as the North Sea, have been trawled for more than 100 years, which has likely contributed to the strong declines of elasmobranchs (which were also targeted by the fishery) and a shift towards more smaller and warm-water elasmobranch species (Jennings & Kaiser, 1998; Wolff, 2000; Bennema & Rijnsdorp, 2015; Sguotti et al., 2016). Such historic fishing effects may have blurred some of the trait-environment relationships found in this thesis, given that we know that species typical of the slow end of the fast-slow continuum (Chapter 5) have lived in the relatively shallow and seasonal waters of the North Sea. It remains therefore important to keep the history of ecosystems in mind, particularly in terms of its past exploitation.
3.2 Limitations of the data and methodology

3.2.1 Intraspecific trait variation
The inclusion of intraspecific trait variation in this thesis was only done in Chapters 5 and 6 for a few, abundant species. Although interspecific variation in body size of fish is larger than the intraspecific variation (Alofs, 2016), the lack of intraspecific trait information for the majority of species has implications for the results of this thesis and their meaning. Firstly, fish undergo large ontogenetic changes in both size and diet. Assigning all individuals the same size and trophic level leads to underestimations of the actual trait variation present in the community, resulting potentially in less variation in CWM traits and lower CWV. Secondly, there is a mismatch in the level at which fish abundances and environmental data are collected compared to the level at which traits are collected. The former are collected at either the haul-level or at a high spatial resolution (maximum 1° by 1° grid cells), while the resolution at which traits are collected is often much larger. Species may even get assigned a trait value that has been measured in a different ecosystem under different environmental conditions. This mismatch may have influenced our observed trait-environment relationships. Including intraspecific trait information can thus enhance the finding of more representative trait-environment relationships and niche-based community assembly processes (Violle et al., 2012). Since most bottom-trawl surveys provide length information, intraspecific variation in size can be included in future studies. It might also be possible to separate juvenile and adult individuals based on length and age-length relationships and estimate trophic levels for juveniles and adults separately – such trophic information is available on FishBase (Froese & Pauly, 2015b) and can be found in literature. Fecundity values can be improved by using relative fecundity (fecundity per gram of ovary) and fecundity-size relationships.

3.2.2 Biotic interactions
Although the environment explained a considerable part of the variation in traits (Chapter 4-6), biotic interactions may also play an important role in trait-based community assembly and trait variation through processes like competition, predation and facilitation (Adler et al., 2013; Kraft et al., 2015; Cadotte & Tucker, 2017). Our results in Chapter 6 showed that several communities display more variation in reproductive traits than expected by chance, reflecting that multiple reproductive strategies can coexist – typically many, small eggs for teleost fish and a few large offspring for elasmobranchs. Several evolutionary explanations exist for the coexistence of these strategies in the same environment. For instance, teleost fish and elasmobranchs show different mechanisms of dispersal: teleost fish often produce drifting pelagic eggs, whereas female elasmobranchs carry internal offspring across large distances (Goodwin et al., 2005). The strength of density-dependence experienced by offspring can also explain the emergence of two strategies: strong density-dependence favours many, small offspring, while weak density-dependence favours few, large offspring (Olsson et al., 2016). Both explanations reveal a diversification of reproductive strategies that cannot be solely explained by abiotic factors acting on the abundance and distribution of the adults.

The traditional community assembly process ‘environmental filtering’ has in more recent years been questioned, since biotic interactions may also lead to filtering (Mayfield & Levine, 2010; Adler et al., 2013;
3.2 Limitations of the data and methodology

Kraft et al., 2015; Cadotte & Tucker, 2017). For example, Edeline et al. (2013) showed that the effect of temperature on body size of fish (whereby temperature can be considered as an environmental filter) in rivers across France depended on the strength of biotic interactions. The strongest effect of temperature on body size was observed under medium and high levels of competition and predation. This can be explained by the increased competitive advantage for small-sized individuals at high temperatures, as their net energy gain (difference between food intake and maintenance costs) increases faster with increasing temperature than for large individuals (Edeline et al., 2013; Ohlberger, 2013). Selection for small sizes will likely go hand in hand with early maturation and short lifespan, and therefore, the fast-slow continuum observed in Chapter 5 and the filtering for these traits in Chapter 6 may be the result of the interaction of both biotic and abiotic factors. It is therefore of great importance to further disentangle the effect of biotic and abiotic assembly processes in order to make trait-based models mechanistic and predictive (Adler et al., 2013).

3.2.3 Methodology

This thesis has used a variety of methods to explore trait-environment relationships in marine fish. The CWM trait is a simple and intuitive metric that reflects the most dominant trait value in the community (Garnier et al., 2004; Funk et al., 2017). A correlation between CWMs and environment suggests that individuals and/or species adapt to this environment through different expressions of the trait along the environmental gradient (Ackerly, 2003; Ricotta & Moretti, 2011; Laughlin et al., 2018). CWMs have the benefit that they summarize all underlying species dynamics and interactions and reduce complexity (Funk et al., 2017; Laughlin et al., 2018), thereby being very suitable for large-scale and big data analyses, as in Chapter 5 and 6.

The use of CWMs also comes with some disadvantages. Firstly, the aggregation of individual or species dynamics into one metric leads to loss of information. Multivariate methods, e.g. RLQ, fourth-corner analysis, use all available information (traits, species abundances, environmental variables) directly without any aggregation, thereby making use of the full variation within the data (Kleyer et al., 2012). Multi-level or community-level models also maintain the entire structure of the data. These models are often extensions of species distribution models, and jointly model all species abundances simultaneously in relation to environment, while incorporating species traits to control the effect of environment on species abundances (Pollock et al., 2012; Jamil et al., 2013; Brown et al., 2014; Warton et al., 2015; Ovaskainen et al., 2017; Nieto-Lugilde et al., 2018; Wüest et al., 2018). Although often based on known model structures (e.g. generalized linear (mixed) models), large datasets can make running such models computationally demanding. Secondly, some recent studies have reported serious errors with the use of simple correlations between CWM traits and environmental variables (Peres-Neto et al., 2017; Miller et al., 2018; ter Braak et al., 2018). Simulation analyses showed that correlations between CWMs and an environmental variable could lead to inflated Type I error and low statistical power, possibly because the CWMs are not truly independent from each other. Species may occur in multiple sites and very abundant species may have a relatively large influence that cannot be accounted for in simple correlations. The aforementioned community-level models, fourth-corner analysis and multivariate approaches are therefore deemed more suitable (Kleyer et al., 2012; Peres-Neto et al., 2017; Miller et al., 2018; ter Braak et al., 2018). The
consistent trait-environment relationships observed with the RLQ, fourth-corner analysis and random forests in Chapter 5, suggest that the latter is another appropriate tool to study such relationships.

3.3 Application and perspectives

3.3.1 Community indicators and predictions

Trait-based community metrics such as the CWM can be used to detect community trends in space and time. These metrics are already in use, particularly in studying the effect of fishing on marine fish communities. For example, the Oslo/Paris (OSPAR) commission (https://www.ospar.org/), which aims to assess and protect the health of marine ecosystems in the Northeast Atlantic, has stimulated the development of ecosystem indicators, such as mean trophic level, mean maximum length and the large fish indicator (LFI), which is the proportion of large fish (> 40 cm) in the community (Greenstreet & Rogers, 2006; Greenstreet et al., 2011; Engelhard et al., 2015; OSPAR, 2017). The LFI was developed to show and monitor the response of large fish to fishing pressure and has been applied to bottom trawl survey data of the North Sea and Celtic Sea. For both areas a recovery has been observed, albeit with a time-lag of more than a decade (Greenstreet et al., 2011; Engelhard et al., 2015; OSPAR, 2017). The mean maximum length is essentially equal to the CWM of maximum length and was used to detect declines in large and particularly vulnerable species, e.g. elasmobranchs. Some inconsistent trends were observed for this indicator, with an overall decline in the North Sea, increases in the English Channel, Bay of Biscay and Iberian coast and no consistent trends in the Celtic Sea (OSPAR, 2017). On a larger scale is the work done by the Indicators for the Seas (IndiSeas) working group (http://www.indiseas.org/) including members from 36 countries worldwide. They combined bottom trawl survey data and fisheries landings from multiple ecosystems and used indicators such as mean lifespan, mean length and mean trophic level to compare fishing effects and the status of marine fish communities over time (Bundy et al., 2010; Shannon et al., 2014; Fu et al., 2015; Coll et al., 2016; Shin et al., 2018). Both OSPAR and IndiSeas recognize, however, that their indicators may be sensitive to stressors or drivers other than fishing, e.g. climate change. A decrease in mean size or LFI may not reflect a decline in large species but an increasing abundance of small-sized species and individuals (Baudron et al., 2014; Engelhard et al., 2015; Fu et al., 2015; OSPAR, 2017; Queirós et al., 2018; Shin et al., 2018). As shown in this thesis in Chapter 4, the temporal trends of the CWM traits were sometimes explained more than 70% by environmental variables. More detailed assessments and simulation studies are therefore needed to understand the cumulative impacts and relative importance of fishing, temperature and other environmental drivers on trait-based indicators for marine fish communities (ter Hofstede & Rijnsdorp, 2011; Queirós et al., 2018; Shin et al., 2018).

As CWM traits can be used to detect historical changes in marine fish communities, our knowledge of trait-environment relationships may also be used to predict the trait composition of marine fish communities in the future (Violle et al., 2014). For instance, how will the trait composition change under various scenarios of warming, fishing pressure, or both? Our results from Chapter 4 and 5 suggest that under increasing temperatures, small, fast-growing, early-maturing and short-living species will become more abundant. The bottom trawl survey datasets used in Chapter 5 and 6 would allow investigating if historical data already
support such a prediction and can be used to create and test predictive models. Such models may inform marine ecosystem-based management and the fishing industry on expected changes in the ecosystem, particularly with regards to which type of (commercial) species may disappear and which may enter. Such knowledge is important for stakeholders taking part in marine ecosystem-based management to discuss and adapt to the changes to come.

3.3.2 From response to effect traits

The rationale of this thesis was based on the response-effect traits framework (Lavorel & Garnier, 2002; Suding et al., 2008), as explained in Chapter 1, with the aim to identify response traits for marine fish. A natural next step is to identify effect traits – traits that determine ecosystem functions of communities. For example, benthic invertebrates that burrow in the sediment have a significant effect on benthic fluxes of oxygen and nutrients through bioturbation (Mermillod-Blondin et al., 2004; Norling et al., 2007; Bremner, 2008), whereas plant height is an important determinant for primary production in aquatic plants communities (Gustafsson & Norkko, 2018). The majority of studies using the response/effect trait framework are still from vegetative systems (Lavorel, 2013; Hevia et al., 2017), but some recent outlook papers have been published for zooplankton (Hébert et al., 2016) and fish (Villéger et al., 2017) that can guide future work on identifying effect traits and quantifying their effects on functions of marine ecosystems. Moreover, traits can be both response and effect traits. Studying them simultaneously in relation to the environment, anthropogenic pressures and ecosystem functioning may provide insightful information to ecosystem-based managers (Suding et al., 2008).

For a great variety of organisms, including marine fish, there is an ongoing debate on the relationship between biodiversity and ecosystem functioning (Duncan et al., 2015; Gamfeldt et al., 2015; Strong et al., 2015; Daam et al., 2019). For instance, Duffy et al. (2016) found that species richness and functional diversity both enhanced biomass of reef fish, whereas Maureaud et al. (Appendix B) found that not species richness, but species evenness was important for demersal fish biomass in European waters, with the highest biomass of fish reached when only few high trophic level and generalist species were dominating. The specific inclusion of traits in such models may increase our understanding of the biodiversity-ecosystem functioning relationship. Furthermore, it is important to identify and explore ecosystem functions of fish other than biomass, such as production, productivity and nutrient cycling (Holmlund & Hammer, 1999; McIntyre et al., 2008; Greenstreet et al., 2012; Villéger et al., 2017).

Recently, past climate change effects on carbon cycling in the North Atlantic, an important ecosystem function of pelagic ecosystems, could be partially attributed to copepod diel vertical migration thanks to a mechanistic model that incorporated key traits of copepods (Brun et al., 2019). Studies like these and the growing number of studies in other aquatic and terrestrial systems (e.g. Thrush et al., 2006; Frainer & McKie, 2015; Violle et al., 2015; Cadotte, 2017) will hopefully further inspire marine ecologists to better understand and predict the effect of climate change and variability on community traits and its implications for the overall structure, functioning and services of marine ecosystems.
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Appendix

Appendix A: Dencker et al.


Tim Spaanheden Dencker, Laurene Pecuchet, Esther Beukhof, Katherine Richardson, Mark R. Payne and Martin Lindegren

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 biomass 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 these differences 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.
Appendix B: Maureaud et al.

Biodiversity-ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness. *Under review*

Aurore Maureaud, Dorothee Hodapp, P. Daniël van Denderen, Helmut Hillebrand, Henrik Gislason, Tim Spaanheden Dencker, *Esther Beukhof* and Martin Lindegren

The relationship between biodiversity and ecosystem functioning (BEF) is a topic of considerable interest to scientists and managers because a better understanding of its underlying mechanisms may help us mitigate the consequences of biodiversity loss on ecosystems. 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 the natural environment is poorly understood, especially in exploited marine ecosystems. Using large-scale observations of marine fish communities, we applied a structural equation modelling framework to investigate the existence and significance of BEF relationships across North western European seas. We find that ecosystem functioning, here represented by spatial patterns in total fish biomass, is unrelated to species richness – the most commonly used diversity metric in BEF studies. Instead, community evenness, differences in species composition, and abiotic variables are significant drivers. In particular, we find that high fish biomass is associated with fish assemblages dominated by a few generalist species with high trophic level, who are able to exploit both the benthic and pelagic energy pathway. Our study provides a better understanding of the mechanisms behind marine ecosystem functioning and allows for the integration of biodiversity into management considerations.
Appendix C: Chapter 4

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.

This chapter has been published as Beukhof E, Dencker TS, Pecuchet L, Lindegren M (2019) Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Marine Ecology Progress Series 610:205–222.
Appendix D: Chapter 5

**Marine fish traits follow fast-slow continuum across oceans**

Esther Beukhof¹, Romain Frelat¹, Laurene Pecuchet, Aurore Maureaud, Tim Spaanheden Dencker, Jón Sólmundsson, Antonio Punzon, Raul Primicerio, Manuel Hidalgo, Christian Möllmann and Martin Lindegren

**Abstract**

A fundamental challenge in ecology is to understand why species are found where they are and predict where they are likely to occur in the future. Trait-based approaches may provide such understanding, because it is the traits and adaptations of species that determine which environments they can inhabit. It is therefore important to identify key traits that determine species distributions and investigate how these traits relate to the environment. Based on scientific bottom-trawl surveys of marine fish abundances and traits of >1,200 species from across the Northern hemisphere, we investigate trait-environment relationships and project the trait composition of marine fish communities across continental shelf seas worldwide. 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, revealing that traits vary with temperature at large spatial scales, but also with depth and seasonality at more local scales. Our findings provide insight into the structure of marine fish communities and suggest that global warming will favour an expansion of fast-living species. Knowledge of the global and local drivers of trait distributions can thus be used to predict future responses of fish communities to environmental change.

¹ These authors contributed equally to this work.
Appendix E: Chapter 6

**Community assembly in marine fish: patterns of trait convergence and divergence along large environmental gradients**

Esther Beukhof, Romain Frelat, Laurene Pecuchet and Martin Lindegren

**Abstract**

Understanding how communities are shaped by environment, biotic interactions and anthropogenic pressures is a major challenge in ecology. Community assembly processes, such as filtering and limiting similarity, provide insight into the mechanisms that shape communities, including its drivers. The relative importance of these processes across environmental gradients and in different geographic areas has hardly been investigated for marine fish. Here we study community assembly processes of marine fish across the North Atlantic and Northeast Pacific by assessing whether the variance in a range of ecological and life-history traits in marine fish communities is lower (indicating trait convergence due to filtering) or higher (indicating trait divergence due to limiting similarity) than expected by chance. Furthermore, we investigated if the strength and spatial variation in community assembly processes could be explained by a combination of environmental variables and fishing pressure. Lifespan and body length were the traits that showed the strongest signs of community assembly by generally converging within communities, as observed from the lower variance in trait values than expected by chance. Age at maturity and growth were also converging, whereas fecundity and offspring size were generally diverging, as indicated by the higher variance in trait values than expected by chance. This indicates that both filtering and limiting similarity shape marine fish communities by acting on different traits. However, in the majority of communities neither process was dominating, indicating non-deterministic assembly processes or that both deterministic processes are simultaneously at play. The strength and relative importance of filtering and limiting similarity varied moderately with temperature, seasonality and depth, but not with fishing pressure. Our large-scale analysis revealed the processes and traits involved in the assembly of marine fish communities, and the extent to which the environment moderates the strength of these processes. Such knowledge may be used in trait-based models to predict the future composition and structure of marine fish communities under environmental change.
Appendix F: Chapter 7

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

Esther Beukhof, Tim Spaanheden Dencker, Maria L.D. Palomares and Aurore Maureaud

Abstract
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 and have been supplemented with values from primary literature.