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A trait-based assessment of the Barents Sea fish community: implications for vulnerability under environmental change

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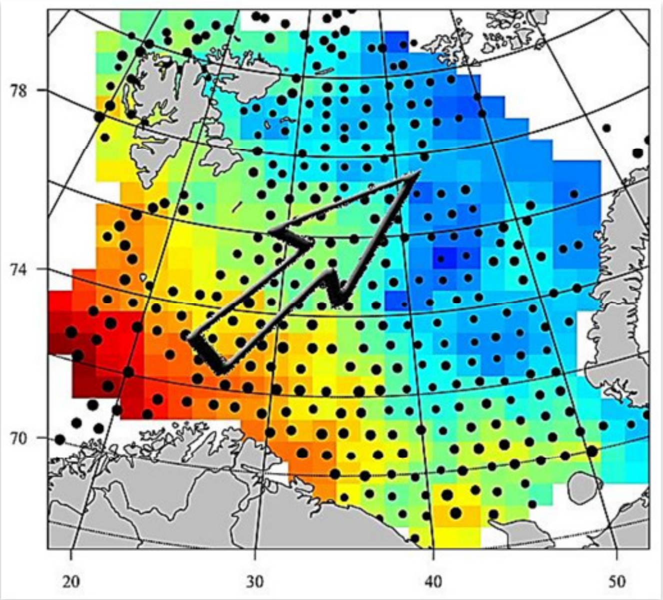
Magnus Aune Wiedmann
A dissertation for the degree of Philosophiae Doctor – March 2014



UNIVERSITY OF TROMSØ

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ACKNOWLEDGEMENTS

I never thought I would write a PhD thesis. I really didn't. But here it is!

Although this has been a lot of work for me, I would never have been able to finalize without all the support, advice and patience from my three supervisors: Michaela Aschan, Raul Primicerio and Benjamin Planque. So thanks a lot to all of you!

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This is a contribution to the BarEcoRe (Barents Sea ecosystem resilience under global environmental change) project. BarEcoRe was funded by the Norwegian Research Council under the NORKLIMA call. BarEcoRe made the access to the Barents Sea ecosystem survey data possible. I want to thank the Institute of Marine Research (IMR) in Norway and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) for sampling these data and making them available to the BarEcoRe; the data were critical to the analyses behind this thesis. Thanks to all BarEcoRe participants, stakeholders, and the scientific advisory panel, for scientific feedback and nice meetings in Tromsø, Bergen and Paris.

Thanks to all the co-authors of the three papers, for feedback, advice and discussions: Michaela, Raul, Benjamin, Andrey, Camilla, Edda, Grégoire and Michael. I will also use this opportunity to thank the head of office Tone Osnes for supporting our institute with coffee beans, which has made my present coffee consumption financially possible.

Finally, I would like to thank my family for all the support throughout my life.

This thesis is dedicated to my wife Ingrid, whose love and patience is so impressing and so appreciated.

SUMMARY

This is a study of the fish community in the Barents Sea and its vulnerability to disturbance such as fishing and climate change. The vulnerability of the fish community depends on its sensitivity to, and adaptability under, stress. To assess these two components of vulnerability, I have combined survey data from the Barents Sea with information about the species properties (i.e., traits), following three approaches. 1) To study the adaptability under disturbance, I have focused on functional diversity, which is a measure of the interspecies functional dissimilarities. 2) To study the sensitivity of the fish community functioning to the loss of species, I have assessed functional redundancy. 3) I have assessed the sensitivity of single species to fishing. For all these three measures, I have mapped the spatial variation throughout the Barents Sea. I have chosen to focus on the time period 2004-2009, a period that was characterized by heating water masses and declining sea ice coverage in the Barents Sea.

The analyses indicate that the fish community has a relatively low vulnerability in the central and south-western parts of the Barents Sea. However, many of the species found there are also fishery-sensitive. Further to the north and east, the community vulnerability appears to be higher due to lower functional diversity and redundancy. The analyses also show that fish that traditionally are found further south moved northwards. This is interpreted as a sign of borealization, which likely occurred due to a heating of the water masses. This pattern is particularly eminent in the northern and north-eastern parts of the Barents Sea, where commercially attractive species establish that are also sensitive to fishing. Since the ecosystem in these northern areas can be vulnerable, and since it is very little studied, cautiousness is required. Future studies that focus on the species' life histories and functional roles will enhance our understanding of the ecosystem vulnerability.

SAMMENDRAG

Dette er et studium av fiskesamfunnet i Barentshavet og dets sårbarhet til stressfaktorer som fiskeri og klimaendringer. Fiskesamfunnets sårbarhet bestemmes av dets sensitivitet til og tilpasningsdyktighet under stress. For å belyse disse to komponentene av sårbarhet har jeg integrert toktdata fra Barentshavet med informasjon om fiskenes egenskaper. Jeg har fokusert på tre innfallsvinkler. 1) For å studere tilpasningsdyktighet under stress har jeg valgt å fokusere på et konsept som heter funksjonell diversitet, som er et mål på hvor ulike fiskene i et fiskesamfunn er funksjonelt. 2) For å studere hvor sensitivt fiskesamfunnets funksjon er til tap av arter har jeg studert et konsept som heter funksjonell redundans. 3) Jeg har også vurdert hvor sensitive enkeltartene er til fiskeri-indusert stress. For alle tre innfallsvinklene har jeg kartlagt romlig variasjon i Barentshavet. Jeg har valgt å fokusere på tidsperioden 2004-2009, en periode som karakteriseres av økende vannmassetemperatur såvel som minkende isutbredelse i Barentshavet.

Undersøkelsene tyder på at fiskesamfunnet som helhet har relativt lav sårbarhet i den sentrale og sørvestre delen av Barentshavet, men at mange av artene her også er sensitive til fiskeri. Lenger nord og øst i Barentshavet ser sårbarheten til fiskesamfunnet ut til å være høyere, på grunn av lavere funksjonell diversitet og redundans. Undersøkelsene viser også at arter som tradisjonelt hører til lenger sør, flytter nordover. Dette tolkes som en borealisering av fiskesamfunnet, og skjer trolig som følge av den pågående oppvarmingen av vannmassene. Dette mønsteret er spesielt tydelig for de nordlige og nordøstre delene av Barentshavet, der arter som er kommersielt attraktive, men også sensitive til fiskeri, nå begynner å etablere seg. Siden økosystemet i disse nordlige områdene kan være sårbart, og siden vi har lite kunnskap om det, bør det utvises forsiktighet her. Fremtidige studier som fokuserer på artenes livshistorier og funksjonelle roller vil kunne styrke kunnskapen om økosystemets sårbarhet.

LIST OF PAPERS AND CONTRIBUTIONS

The following papers are included in this thesis:

I: Wiedmann MA, Aschan M, Certain G, Dolgov A, Greenacre M, Johannesen E, Planque B, Primicerio R (2014) Functional diversity of the Barents Sea fish community. *Marine Ecology Progress Series* 495:205-218

II: Wiedmann MA, Aschan M, Greenacre M, Dolgov A, Primicerio R (unsubmitted manuscript) Functional redundancy in Barents Sea fish: ecological implications of environmental change. Formatted according to the standard of *Marine Ecology Progress Series*.

III: Wiedmann MA, Primicerio R, Dolgov A, Ottesen CAM, Aschan M (manuscript under revision) Life history variation in Barents Sea fish: implications for sensitivity to fishing in a changing environment. *Ecology and Evolution*.

Contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	RP	**MAW**,MA,RP	**MAW**, MA, RP
Study design and methods	**MAW**,MG,BP,RP	**MAW**,MG	**MAW**,RP
Data gathering and interpretation	**MAW**,MA,AD, BP,EJ,GC,RP,MG	**MAW**,MA,AD, MG,RP	**MAW**,AD,CO, MA,RP
Manuscript preparation	**MAW**,MA,AD, EJ,GC,MG,RP	**MAW**,MA,AD,RP	**MAW**,MA,AD, CO, RP

MAW = Magnus Aune Wiedmann; MA = Michaela Aschan; AD = Andrey Dolgov; BP = Benjamin Planque; CO = Camilla A. Meyer Ottesen; EJ = Edda Johannesen; GC = Grégoire Certain; MG = Michael Greenacre; RP = Raul Primicerio

INTRODUCTION

Marine ecosystems currently confront considerable environmental and anthropogenic pressure (Rosenzweig et al. 2008, Worm et al. 2009, Hoegh-Guldberg & Bruno 2010). As the ocean temperatures rise, the species experience new living conditions, which induce migrations towards the poles and thereby altered species distributions and community compositions (Cheung et al. 2009). In addition, a diversity of anthropogenic stressors (e.g. fishing, shipping and oil exploration and exploitation) affects the marine ecosystems. In 2011, the estimated world population passed 7 billion people[1], as compared to 6 billion people only 12 years earlier (i.e., in 1999). Naturally, the anthropogenic pressure upon natural systems increases significantly. As a consequence, we may expect altered ecosystem services in the years to come (Levin & Lubchenco et al. 2008), with associated implications for the capacity of the ecosystems to sustain human communities. This calls for a strengthening of our capacity to manage the ecosystems.

In order to spare the environment and to achieve a more sustainable ecosystem management, the ecosystem-based management approach is argued to be a necessary upgrade from the present-day more common single species management approach (Hilborn 2011). Relative to single-species management, ecosystem-based management should account for a range of additional factors including trophic interactions, climate change and impacts of commercial fishing (e.g., habitat destruction and impact on non-target species) (Levin & Lubchenco 2008, Hilborn 2011). In this regard, synthetic indicators of ecosystem state could work as proxies for important ecosystem properties and processes (Levin et al. 2009).

Concepts such as ecosystem vulnerability are becoming increasingly common in the scientific community as well as among the general public (Figure 1), and most people seem

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[1] http://www.worldometers.info/world-population

to agree that we should take special care of vulnerable ecosystems. Nevertheless, we have still relatively little empirical knowledge of how various types of disturbance influence ecosystem vulnerability, and even less knowledge of how the concept of ecosystem vulnerability can be operationalized and applied to real ecosystem data. This thesis intends to contribute to such understanding by implementing recently developed indicators of ecosystem state and functioning to the Barents Sea fish community.

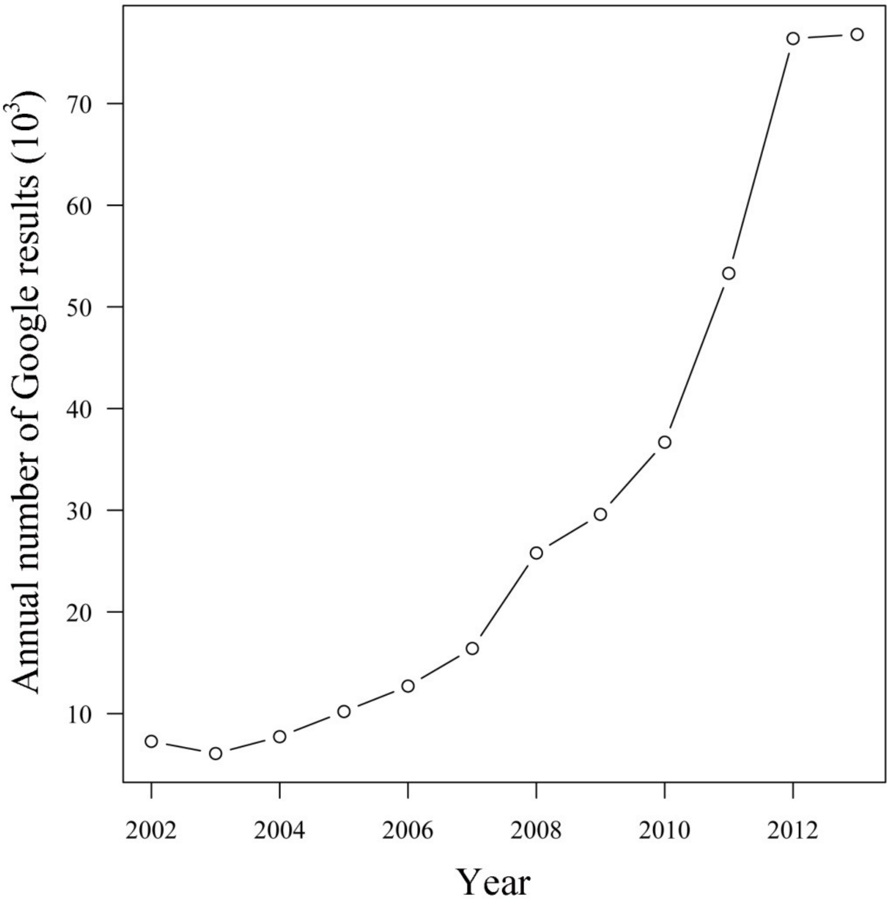

Figure 1. Annual number of Google[2] results when searching for "Ecosystem vulnerability" during the years 2002-2013.

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[2] https://www.google.com

Getting clear on the conceptual basics

This thesis aims to shed light on various facets of the vulnerability of the Barents Sea fish community. But how can we scientifically define the term vulnerability? IPCC (1996, 2007) defined vulnerability as the *extent to which climate change may damage or harm a system. It depends on a system's sensitivity and ability to adapt to new climatic conditions*. Although this definition is in line with the general focus of the IPCC, and therefore has a rather climate explicit imprint, it stresses the different components of vulnerability. However, it does not account for multiple stressors. I therefore decided to expand and rewrite the definition as (Figure 2):

Vulnerability is the extent to which disturbance may damage or harm an ecosystem. It depends on the ecosystem's sensitivity to such disturbance and its adaptability under altered environmental conditions.

As such, the definition resembles common definitions of robustness ("*the capacity of systems to keep functioning even when disturbed*"; Levin & Lubchenco 2008) and ecological resilience ("*the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior*"; Holling 1996). Hence, the latter two terms could constitute conceptual counterparts to the term vulnerability; a vulnerable system would have low robustness and low resilience, and *vice versa*. The resilience concept, which is central to the BarEcoRe project[3], appears to be inextricably connected to the presence of several basins of attraction (Holling 1996, Scheffer et al. 2001), which is something that I do not considered in this thesis. On the other hand, the robustness

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[3] This thesis is a contribution to the BarEcoRe (Barents Sea ecosystem resilience under global environmental change) project

term is mostly applied in connection with studies of food webs (e.g., Allesina et al. 2009). Therefore, I have decided to put emphasis on the vulnerability concept.

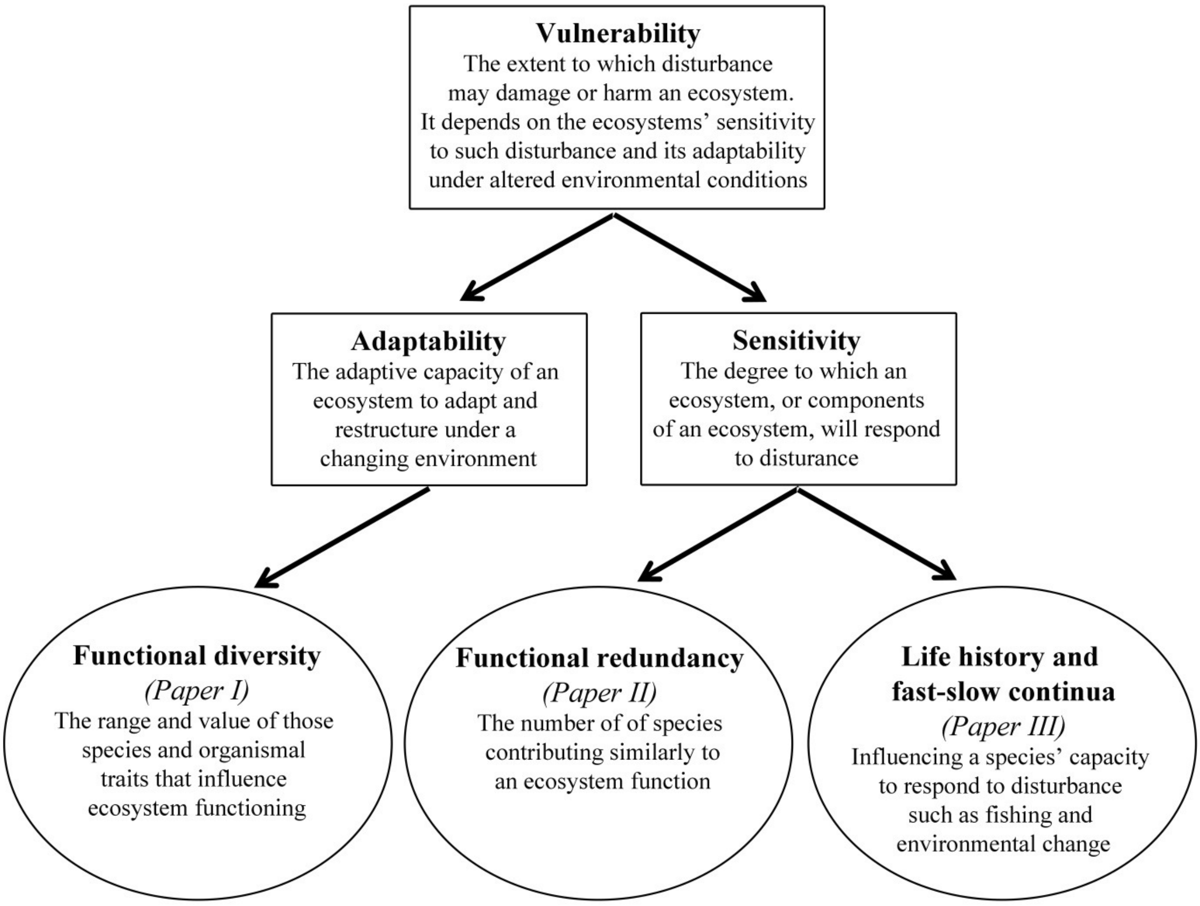

Figure 2: Conceptual framework used in the thesis. Definition of vulnerability is adopted from IPCC (1996, 2007), definition of adaptability is taken from Levin & Lubchenco (2008), the definition of sensitivity is derived from IPCC (1996, 2007) and Zacharias & Gregr (2005), the definition of functional diversity is taken from Tilman (2001), definition of functional redundancy is taken from Laliberté et al. (2010), and descriptions of life histories and fast-slow continua are derived from Perry et al. (2005) and Reynolds et al. 2005.

From my definition of vulnerability, and indeed also from the IPCC (1996, 2007) definition, it is thus clear that the vulnerability of the ecosystem depends on two components: the *sensitivity* to disturbance, and the *adaptability* to the new environmental conditions that are caused by the disturbance. Based on IPCC (1996, 2007) and Zacharias & Gregr (2005), I have defined sensitivity in the following way:

Sensitivity is the degree to which an ecosystem, or components of an ecosystem, will respond to disturbance.

Finally, I have defined adaptability on the basis of Levin & Lubchenco (2008), although IPCC (1996, 2007) defines the concept in a similar way:

Adaptability is the capacity of an ecosystem to adapt and restructure under a changing environment.

Central to the latter three definitions is the term *disturbance*. Although there are many types of disturbance that act on ecosystems (Halpern et al. 2008), I have only focused on disturbance related to fishing and climate change. Recognizing that all biotic ecosystem components have evolved within a given range of environmental conditions, Zacharias & Gregr (2005) defined disturbance (or *stress*) as *a deviation of these environmental conditions beyond the expected range*. Furthermore, according to Zacharias & Gregr (2005), an ecosystem is only vulnerable if it is exposed to a type of disturbance to which it is sensitive. I have presently focused on an implicit approach to disturbance.

Still, we are dealing with normative concepts that are very demanding to approach quantitatively *per se*. This thesis is an attempt to operationalize the concept of ecosystem vulnerability. My solution to this problem has been to combine the species' traits (i.e., properties) with ecosystem survey data. So what are these species' traits, and how can we apply them to assess ecosystem vulnerability?

Traits and trait-based approaches

Probably unaware of the striking relevance to trait-based ecology, George Orwell allowed some of the main characters (the pigs) of his political satire *Animal Farm* (1945) to establish that "*All animals are equal, but some animals are more equal than others*". Although biodiversity is commonly referred to as the number of species present in an ecosystem (Gotelli & Colwell 2001), it is the species' traits that modulate the ecosystems' capacity to respond to and adapt to disturbance (e.g., Jennings et al. 1998, Bellwood et al. 2003). In other words, the fact that species are not equal facilitates ecosystems' response and adaptation under disturbance.

In this thesis, I have focused on two classes of traits: *effect* traits and *response* traits (Lavorel & Garnier 2002). Effect traits (or *functional* traits) are phenotypic properties that determine the species' effect on ecosystem functioning, via their effect on biogeochemical cycling (Lavorel & Garnier 2002). The history of functional traits is tightly associated with the history of niche and competition theory (Elton 1946, Hutchinson 1959; for a review, see Weiher 2011). On the other hand, response traits (such as the *life history* traits), via their demographic implications, determine how species respond to disturbance (Stearns 1992, Lavorel & Garnier 2002).

In the 1990's, the concept of functional diversity started to emerge, mostly with a strong focus on the relation between functional diversity and ecosystem functioning (Steele 1991, Tilman et al. 1997, Walker et al. 1999, Días & Cabido 2001).

> *Functional diversity is the range and value of those species and organismal traits that influence ecosystem functioning* (Tilman 2001).

Most of the work on functional diversity has been carried out in plant communities, where various ecosystem functions (such as photosynthetic activity) can be measured directly (Tilman et al. 1997), but some work has also been done on the functional diversity in marine ecosystems (Micheli & Halpern 2005, Martins et al. 2012). The dendrogram-based approach to functional diversity (Petchey & Gaston 2002, 2006) is the most widely used functional diversity methodology so far, but ordination methods that may account for the species' relative abundances are being developed and are becoming increasingly popular (Villéger et al. 2008, Laliberté & Legendre 2010, Bates et al. 2013, Sabatini et al. 2013). Functional diversity is now recognized as an important driver of ecosystem functioning (Hooper et al. 2005).

Functional diversity can conceptually be regarded as a measure of the number of functional "tools" possessed by a community, which in turn determines what types of functions that the community is able to provide to the ecosystem. In practice, functional diversity can be estimated by using multivariate analyses and species' traits to calculate interspecies dissimilarities. Naturally, functional diversity is positively correlated with the number of species (i.e., the species richness) in an assemblage, since a high number of species often may carry out a high number of ecosystem functions. Intuitively, the expectation that high functional diversity promotes a high adaptability (Levin & Lubchenco 2008) can be illustrated by the craftsman metaphor. A craftsman that has many different tools at his disposal will be able to manage many different types of jobs, i.e., he will be adaptable in a demanding job market. Still, even species-rich systems may undergo major structural changes as a consequence of the loss of one or a few species (Bellwood et al. 2003), a consideration that brings us closer to the concept of functional redundancy.

Functional redundancy is the number of species contributing similarly to an ecosystem function (Laliberté et al. 2010).

A simple measure of the functional redundancy in a community can be obtained by calculating functional diversity and then correcting for the species richness, for instance by regressing functional diversity on species richness and then extracting the residuals from the regression model. For a given species pool, positive residuals (i.e., *functional overdispersion*) will then indicate a higher-than-expected number of functions played by a certain number of species (as compared to the model, i.e., the assemblage mean), and the loss of a species would in theory imply a correspondingly large drop in functional diversity. Likewise, functionally underdispersed communities are expected to be less sensitive to species loss (and thereby be less sensitive to certain types of disturbance), since several species likely play similar functional roles. A community that displays high functional diversity and functional underdispersion could hence be expected to have low vulnerability to disturbance, since it can be expected to be adaptable and insensitive under disturbance.

However, not all species in a community contribute equally to the functional diversity, and thereby to ecosystem functioning (Ehrlich & Walker 1998). It is therefore not uninteresting *which* species is lost, although such a possibility would have opened up for interesting and practical opportunities. Such a practical scenario was presented in the famous poem *The Blacksmith and the Baker*, written by the Danish poet Johan Herman Wessel[4]. The story takes place in a small town. In this town, there is only one blacksmith and only two bakers. One day, the blacksmith kills a man and has to stand before the court, and the expected judgement is execution. However, the members of the town community argue that

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[4] According to http://no.wikipedia.org, the poem was printed for the first time in *Votre Serviteur Otiosis* in the year 1784

they need the presence of a blacksmith in the town. Since there are two bakers in the town, and one of them is even old and weak, the judge decides to acquit the blacksmith. The old baker, on the other hand, is sentenced to death. In other words, the old baker suffers because the town has no redundancy in blacksmiths.

In an ecosystem, it is not enough to know that the species possess a general functional redundancy. We should also strive to understand *which* species play *which* redundant functional roles. This can be approached by dividing the pool of species into *functional groups*, and then assuming that the species within a certain functional group play similar functional roles in the ecosystem. The allocation of species to functional groups can, among other methods, be carried out by cutting a functional dendrogram, so that a species in a given functional group is functionally more similar to the other species in its group than to species in other groups. For a given assemblage in an ecosystem, the functional redundancy can be regarded as the number of species that represent each functional group. This approach allows to identify functional groups that have low redundancy, which may help to assess the sensitivity of the ecosystem to species loss. Furthermore, functional redundancy is commonly approached under the assumption that different species within a given functional group respond differently to disturbance. The functional redundancy concept does not imply that every species should be regarded as critical to ecosystem functioning, nor that we should easily tolerate species loss from redundant functional groups (Ehrlich & Ehrlich 1981, Walker 1995). Rather, a species loss from a redundant functional group may in some instances not lead to immediate, observable effects on ecosystem functioning. Still, a species that go extinct today may very well be the only representative of its functional group that could have been able to withstand a future perturbation (Ehrlich & Walker 1998). A high redundancy may thus be regarded as an ecological insurance, and management plans should therefore aim to maintain high functional redundancy in ecosystems.

Still, one can imagine present species compositions (and associated implications for ecosystem functioning) as results of individual species' capacity to cope with disturbance in earlier time periods. Species that could not handle some sort of disturbance got extinct and are therefore not represented in present-day ecosystems. When managing ecosystems, a general knowledge about individual species' capacity to cope with various stress factors (i.e., their sensitivity to disturbance), such as climate change or fishing, is therefore useful. With regard to the species' sensitivity to fishing, there is evidence that the body size and age at maturity of the fish is particularly important; large-bodied and late-maturing fish are generally more sensitive to fishing than small-bodied and early-maturing ones (Reynolds et al. 2005). While the former can be regarded as having "slow" life histories, the latter have "fast" life histories. Thus, information about the speed of the species' life histories may inform about species' sensitivity to fishing. Such information can be extracted by applying ordination methods on the basis of life history traits. Species with fast life histories (for instance many pelagic species) were shown to display a high capacity to respond to environmental change (Perry et al. 2005), as also observed in the Bering Sea (Overland & Stabeno 2004).

In addition to size- and age related traits, traits that relate to the species' reproduction strategies, such as fecundity and egg size, probably bear important information about the species' capacity to cope with disturbance. A species' egg size and fecundity is often relatively easy to determine from field studies. Due to an allocation trade-off, egg size and fecundity traits are negatively correlated (Stearns 1992). On the basis of ordination, species can be ranked, from species having many, small eggs to species having few, large eggs (i.e., the egg size/fecundity continuum). However, since fish eggs and larvae generally suffers very high as well as very variable mortality rates (Dahlberg 1979), such information is at present difficult to use as indicators of species' sensitivity to disturbance (Denney et al. 2002).

Nevertheless, when assessed in combination, fast-slow information and egg size/fecundity information can inform about spatial variation in dominant patterns of life history strategies.

Setting the environmental and ecological scene: Barents Sea, 2004-2009

The Barents Sea is an arctic-boreal shelf sea in the North Atlantic Ocean, found at 66.7 - 82.5° N and 8 - 68.5° E, which covers 1.6 million km^2 and has an average depth of approximately 220 meters (Ozhigin et al. 2011). The area is spatially delimited by the coasts of Norway and Russia in the south, the shelf break to the Arctic Ocean in the north, the shelf break to the Norwegian Sea in the west and the Novaya Zemlya in the east (Figure 3).

The physical oceanographic conditions vary greatly within the Barents Sea, and are governed by two major flows of water masses (Figure 3). From the south-west, warm Atlantic water masses flow into the Barents Sea, and the bottom temperatures here vary between 3.5 - 7.5°C, depending on the season (Ozhigin et al. 2011). This inflow of Atlantic water masses determines to a large degree the climate of the region (Loeng 1991). From the north, a southward flow of cold Arctic water masses provide an Arctic environment in the north and north-east, with temperatures generally below 0°C (Ozhigin et al. 2011). The ice coverage is at a maximum in early spring, generally covering the areas north of the Polar Front. From April onwards, the ice edge retreats northwards and eastwards until September (Ozhigin et al. 2011).

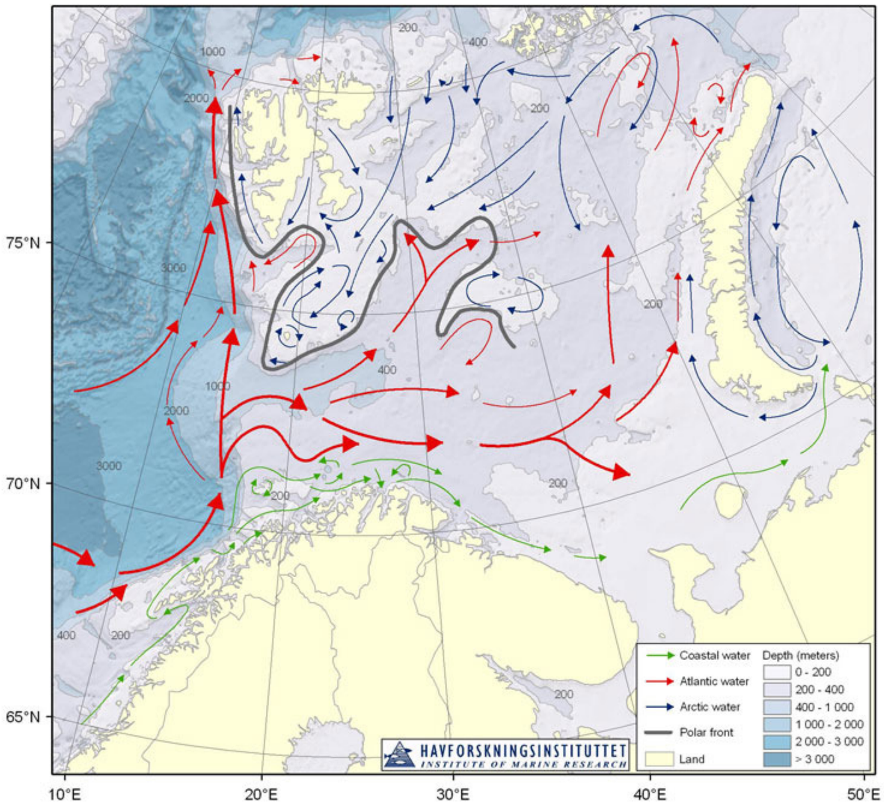

Figure 3. Map of the Barents Sea, with information about bottom depths and main current systems. The thick grey line illustrates the approximate position of the Polar Front, whereas red and blue arrows represent flows of warm Atlantic and cold Arctic water masses, respectively. The figure is obtained from the Institute of Marine Research webpage[5].

In later years, a heating of the Barents Sea water masses has been registered which is mostly due to an increased inflow of Atlantic water masses (Smedsrud et al. 2013). This has resulted in an increasing proportion of warm Atlantic water masses and a declining proportion of cold Arctic water masses in the Barents Sea (Johannesen et al. 2012a, Smedsrud et al. 2013). As such, there seems to be an ongoing atlantification of the Barents Sea water masses. This heating has the main responsibility for the declining sea ice coverage

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[5] http://www.imr.no

in the northern parts of the Barents Sea (Smedsrud et al. 2013), a pattern that is common for the Arctic ocean in general (Overland & Wang 2013). Furthermore, a range of ocean climate models predict almost sea ice free Arctic summers within decades (Overland & Wang 2013).

The mean annual primary production is highest in the south-western part of the Barents Sea, and declines towards the north and north-east (Reigstad et al. 2011). However, the highest short-term primary production rate occurs during the spring bloom along the retreating ice edge (mostly in Arctic water masses), but these high production rates only occur during a short period each year (Titov 1995, cited in Titov & Orlova 2011). A higher proportion (~53%) of the primary production is exported towards the bottom in Arctic areas as compared to the more southern, Atlantic areas (~28%) (Reigstad et al. 2011). This is plausible because the higher trophic levels are not able to make use of such a high production within such a short time frame. The export of organic matter from the surface towards the bottom is the most important source of energy for benthic communities in the Barents Sea (Reigstad et al. 2011).

The Barents Sea is commercially important. Major commercial fish stocks in the area include stocks of the Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), Atlantic halibut (*Hippoglossus hippoglossus*) and redfish (*Sebases norvegicus* and *S. mentella*). The total annual catches in the Barents Sea vary between 0.5-4.5 million tons (Nakken 1998), dominated by the Norwegian and Russian fishing fleets (ICES 2013).

BarEcoRe

This thesis is an output of the BarEcoRe (*Barents Sea ecosystem resilience under global environmental change*) project (project number A37052), and the topics of papers that constitute the thesis are in line with the project deliverables. The overall goal of the BarEcoRe project was to evaluate the effects of global environmental change on the future structure and resilience of the Barents Sea ecosystem. BarEcoRe was divided into four work packages (WP's), and this thesis represents contributions of the WP4. WP4 aimed to "focus on the organismal, population and community properties that influence the Barents Sea ecosystem robustness and resilience, and will assess and forecast changes in resilience that are associated with climate change and fishery"[6].

Objectives

I had two overall objectives for this thesis.

- ***Objective 1.*** There are principally two water masses within the boundaries of the Barents Sea: warm Atlantic water masses and cold Arctic water masses. These two water masses are delimited by the Polar Front. Previous studies have shown that the Barents Sea fish community structure can be characterized by distinct species compositions (i.e., assemblages) depending on spatial allocation (Fossheim et al. 2006, Johannesen et al. 2012b, Aschan et al. 2013). Objective 1 was to assess whether the spatial variation in species composition would be reflected by a spatial variation in the species' functionality and life history. What are the implications of the spatial patterns in trait-based metrics for ecosystem ecology and vulnerability to disturbance?

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[6] BarEcoRe project proposal, submitted to the Norwegian Research council in October 2009

- ***Objective 2.*** The study period (2004-2009) was characterized by a strong heating of the water masses in the Barents Sea, leading to an increasing proportion of Atlantic water masses and a declining proportion of Arctic water masses, as well as declining sea ice coverage. In later years, a rising number of boreal and arcto-boreal fish species and a declining number of Arctic fish species were documented in the northern Barents Sea (Dolgov et al. 2004, cited in Drinkwater et al. 2011). Also, preliminary analyses showed that the species richness increased in the northern parts of the Barents Sea in the later, warmer years of the study period. Objective 2 was to assess whether these events impacted on the spatial variation in ecosystem functioning and life history properties, and to evaluate associated implications for the ecosystems' vulnerability to disturbance.

MATERIAL AND METHODS

Ecosystem survey data

One of the great benefits of being associated with the BarEcoRe project was the access to the high-quality ecosystem survey data that are being collected annually, throughout the Barents Sea, as a co-operation between the Norwegian Institute of Marine Research (IMR) and the Russian Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO)(Wienerroither et al. 2011, Michalsen et al. 2013). The surveys are carried out in August-September, when the sea ice coverage is at a minimum (Figure 4).

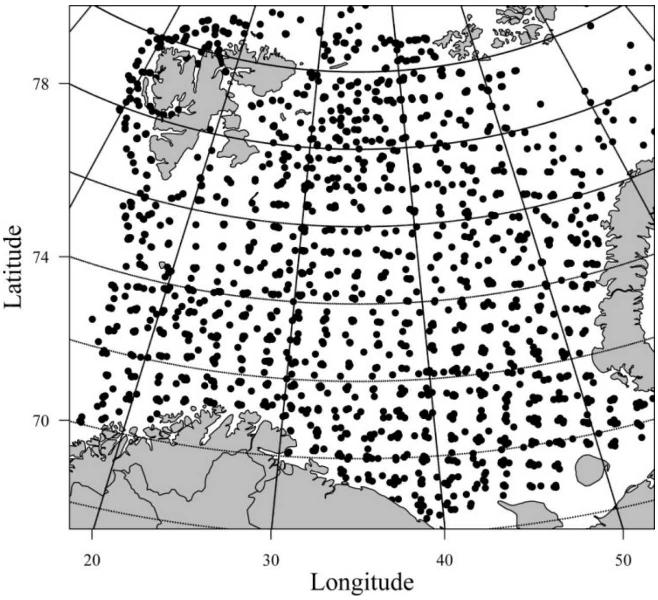

Figure 4. Positions of all (n=1901) survey stations that were used in the present analyses.

Apart from covering the distribution and abundances of fish, which has been the focal taxonomic group throughout my work, these data also comprise ecosystem components such as plankton, benthos, birds and sea mammals, and even abiotic factors such as temperature, salinity, bottom depth and ice conditions. About 200 fish species have been registered in the Barents Sea, but in this thesis I have focused on the ~75 most common ones, based on data obtained from demersal trawl hauls. Throughout this thesis, I have chosen to focus on distributional (i.e. presence/absence) data, based on the assumption that they would be more robust than abundance data. Presence/absence data were assumed not to be strongly affected by some species' strong interannual abundance fluctuations or the interspecies variation in catchability.

Compilation of trait matrices

In addition to the ecosystem survey data, the foundation of this thesis is a collection of species' traits (Table 1). In my work, I have used all available sources of trait information: published papers, reports, personal comments from colleagues, and finally, in a few instances, inferred values based on information about closely (taxonomically) related species.

Table 1. Overview of the traits used in the thesis. The "Trait class" column refers to whether a trait is treated as an effect trait (e), a response trait (r), or both (e/r).

Trait	Trait class
Diet	e
Habitat	e
Longevity	r
Fecundity	e/r
Body shape	e
Offspring size	e/r
Age at maturity	r
Size at maturity	r
Offspring behaviour	e
Maximum body size	e/r
Environmental tolerance range	e

SUMMARY OF RESULTS

Functional diversity

Wiedmann MA, Aschan M, Certain G, Dolgov A, Greenacre M, Johannesen E, Planque B, Primicerio R (2014) Functional diversity of the Barents Sea fish community. *Marine Ecology Progress Series* 495:205-218 **(Paper I)**

Theoretical rationale: Ecosystem functioning and adaptability depends on the biodiversity in general and on the functional diversity in particular. A high number of functions possessed by a community is thought to promote a high capacity to adapt and restructure in the face of disturbance.

Material and methods: We compiled a functional (effect) trait matrix for the 77 most common fish taxa in the Barents Sea (Table 1). On the basis of the traits, we used multivariate analyses to construct a functional dendrogram, which described the interspecies variation in functional trait space. The integration of the survey data and the information from the functional dendrogram allowed us to map spatio-temporal variation in functional diversity for the entire Barents Sea during the period 2004-2009.

Main findings: The functional diversity was persistently high in the central-west due to the high species richness there. The functional diversity rose in the north in later, warmer years. Also, when correcting for species richness, we found a persistent pattern of functional overdispersion in the east and functional underdispersion in the west.

Functional redundancy

Wiedmann MA, Aschan M, Greenacre M, Dolgov A, Primicerio R (unsubmitted manuscript) Functional redundancy in Barents Sea fish: ecological implications of environmental change. Formatted according to the standard of *Marine Ecology Progress Series*. **(Paper II)**

Theoretical rationale: Functional redundancy is regarded to be important because it has implications for the buffering capacity of the ecosystem under disturbance. If several species play similar functional roles in an ecosystem, then a species loss might not lead to immediate effects on ecosystem functioning since other species with similar functional traits may replace the lost one.

Material and methods: We used the ecosystem survey data and an updated version of the fish functional trait matrix that we used in Paper I (Table 1). After constructing a functional dendrogram, we used a permutation approach to decide on a cutting level of the dendrogram so as to define functional groups. Functional redundancy was defined as the number of species representing each functional group in an assemblage of species.

Main findings: Most functional groups displayed a clear spatial preference. This was reflected by the fact that most species within a given functional group had the same biogeographic affiliation, even though information about biogeography was not explicitly accounted for in the trait matrix. While most groups displayed the highest redundancy in the south-west, one group (i.e., the “long demersals”) was redundant in the central Barents Sea, whereas the “small demersals” displayed high redundancy in the north-east. In the later, warmer years, we observed a borealization of the Barents Sea fish community, which occurred in the north-east in particular.

Life history and fast-slow continua

Wiedmann MA, Primicerio R, Dolgov A, Ottesen CAM, Aschan M (manuscript under revision) Life history variation in Barents Sea fish: implications for sensitivity to fishing in a changing environment. *Ecology and Evolution.* **(Paper III)**

Theoretical rationale: Life history traits determine species' capacity to cope with disturbance. For instance, traits such as maximum body size and age at maturity influence the species' response to fishing. Large-bodied species with late maturation were regarded as "slow", and were hence expected to be sensitive to fishing. Species having the opposite properties were regarded as "fast", and were thereby expected to be less sensitive to fishing.

Material and methods: We compiled a life history (response) trait matrix (Table 1). Based on ordination, we extracted species' positions along life history gradients, both with regard to traits such as maximum body size and age at maturity (the "fast-slow continuum"), and with regard to reproduction related traits (the "egg size/fecundity continuum"). Based on the resulting species' ranks, we calculated the average rank for fish assemblages throughout the Barents Sea.

Main findings: There was a clear south-west to north-east gradient in the species' average fast-slow ranks. Also, we observed a similar spatial gradient with regard to the the egg size/fecundity continuum. Compared to the species in the north-east, these findings suggest that the species in the south-west on average are larger, later-maturing, with smaller eggs and higher fecundity. In the later, warmer years, we observed a borealization of the northern areas, implying the average species there had slower life histories, smaller eggs and a higher fecundity as compared to earlier, colder years.

Synthesis: characterising the Barents Sea by using trait-based approaches, 2004-2009

There was a general south-west to north-east gradient in the trait-based metrics that were assessed in this thesis (Figure 5). The fish assemblages in the south-western region of the Barents Sea could be characterized by high numbers of species, high functional diversity, and high redundancy in most functional groups. Furthermore, on the basis of information about the species' fast-slow ranks (Table 2), we showed that the species in the south-west generally possessed slow life histories. Also, the species here generally produced many, small eggs. Finally, the species in the south-west were largely of boreal origin, and they were relatively heterogeneous with regard to phylogeny.

Table 2. The ten most fishery-sensitive fish species[7] in the Barents Sea, as predicted by the fast-slow 1 (FS1) approach (Paper III).

Sensitivity rank	Latin species name	English species name
1	*Somniosus microcephalus*	Greenland shark
2	*Bathyraja spinicauda*	Spinetail ray
3	*Hippoglossus hippoglossus*	Atlantic halibut
4	*Chimaera monstrosa*	Rabbit fish
5	*Amblyraja hyperborea*	Arctic skate
6	*Anarhichas minor*	Spotted wolffish
7	*Sebastes mentella*	Beaked redfish
8	*Gadus morhua*	Atlantic cod
9	*Sebastes norvegicus*	Golden redfish
10	*Anarhichas denticulatus*	Northern wolffish

The central Barents Sea (i.e., in the Polar Front areas), displayed the highest functional diversity. Compared to the south-west, the species in the central Barents Sea displayed faster life histories, larger eggs and lower fecundities. Two groups displayed their highest redundancies in in the central Barents Sea: the "long demersals" and the "demersal planktonfeeders".

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[7] Species names are in accordance with the World Register of Marine Species (WoRMS); http://www.marinespecies.org

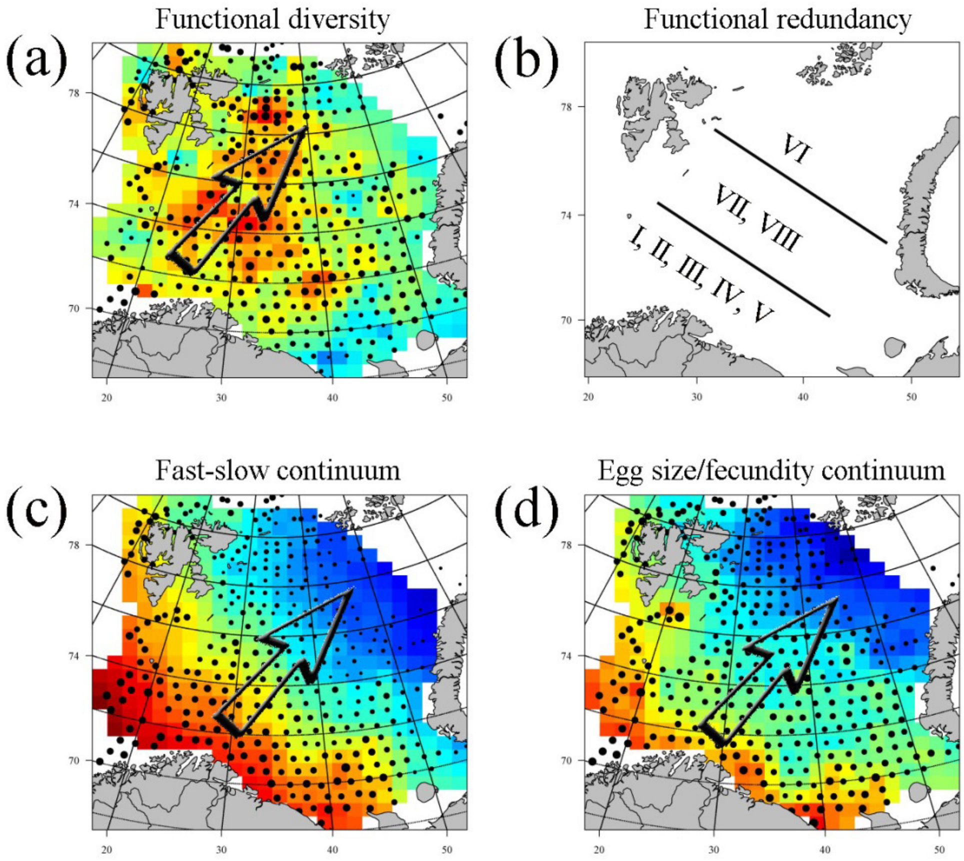

Figure 5. Overview of the most important findings due to trait-based methods applied to the Barents Sea fish community. (a) Functional diversity in 2004 (Paper I). Red colours represent high functional diversity, whereas blue colours represent low functional diversity. The arrow indicates that the field of high functional diversity moved northwards in later, warmer years. (b) Functional redundancy (Paper II). Roman numerals indicate where the functional groups displayed the highest redundancy (i.e., either in the south-west, in the central or in the north-eastern Barents Sea). I: “large demersals”; II: “redfish”; III: “fecund demersals”; IV: “pelagics”; V: “elasmobranchs”; VI: “small demersals”; VII: “long demersals”; VIII: “demersal planktonfeeders”. (c) Fast-slow continuum according to the FS 1 approach, in 2004 (Paper III). Red colours represent high community-level average fast-slow ranks, which entail that the average species is large-sized and late-maturing. Blue colours represent low community-level average fast-slow ranks, which entail that the average species is small-sized and early-maturing. The arrow indicates the expansion of high (red) average fast-slow ranks towards the north-east in later, warmer years. (d) The egg size/fecundity continuum in 2004 (Paper III). Red colours indicate that the average species spawns many, small eggs. Blue colours indicate that the average species spawns few, large eggs. The arrow indicates the northwards expansion during later, warmer years, of species that spawn many, small eggs.

The strongest temporal changes in trait-based metrics occurred in the north-eastern region of the Barents Sea. Here, we observed rising functional diversity and rising average fast-slow ranks in later, warmer years. Also, we observed a northward movement of functional groups dominated by boreal species, such as the "redfish". As such species moved northwards, the average fecundity in these northern areas rose whereas the average egg size declined.

DISCUSSION

Persistent spatial patterns

This thesis suggests that the large-scale patterns in trait-based metrics are governed by water mass characteristics, and plausibly also by the spatial variation in production at lower trophic levels. The water masses of the Barents Sea are not homogeneous, but largely consist of Atlantic and Arctic components, which strongly influence what type of fish that can be found in the different parts of the area. The present results show that there is a clear spatial variation in both effect and response trait based metrics. Such variation can be interpreted as spatial variation in fish community vulnerability to disturbance.

In the south-west, where the influence of inflowing Atlantic water masses is generally strong and the level of primary production is high, also a high number of species could be found. In turn, this probably contributes to a high level of ecosystem functioning and adaptability (Levin & Lubchenco 2008), as predicted due to the high functional diversity in these areas (Paper I). When dividing the species pool into eight functional groups, we found that five of these groups were most redundant in the south-west; these five functional groups predominantly consisted of boreal species (Paper II). This explains the functional underdispersion as shown in Paper I, since each new species from a given functional group that is added to a given assemblage likely contributes relatively little to the functional diversity, provided that the functional group is already represented in the assemblage. I suggest that the high functional redundancy in these south-western areas promotes a relative insensitivity to disturbance (Palumbi et al. 2008). However, the (largely boreal) species found in the south-west are generally large and long-lived (Paper III), which implies high species-level sensitivity to fishing (Jennings et al. 1998, García et al. 2008). Provided that the vulnerability to disturbance is a function of the sensitivity to disturbance and the exposure to such disturbance (Zacharias & Gregr 2005), major directed fisheries may therefore have particularly negative implications for the vulnerability of the fish community in these areas. Large body sizes in the south-west implies high energy demands, which are likely supported by the high levels of primary production in these areas (Reigstad et al. 2011). Still, much of the production is also kept in the upper water layers by the relatively high number of pelagic fish species, which in turn are important prey species for the larger predators (e.g., Hamre 1994). The typical fish species in the south-west had small eggs and therefore high fecundity (Paper III). It has been assumed that high fecundity in fish promotes low sensitivity to fishing, but this is supported by little empirical evidence (Sadovy 2001, Denney et al. 2002). In addition, the interannual variation in fish larvae survival is often highly variable and unpredictable (Dahlberg 1979, Wiedmann et al. 2012), which calls for cautiousness if relations between e.g. fecundity and vulnerability to disturbance are attempted to be established. Furthermore, when it comes to climate-induced disturbance, the opposite situation (i.e., that small eggs promotes high sensitivity) may be plausible. Climate change may induce too long temporal mismatches between the onset of the phytoplankton spring bloom, the onset of zooplankton production, and finally the hatching time of predators such as fish larvae (Koeller et al. 2009). Such a mismatch will negatively influence the survival of the larvae (Cushing 1990). In this regard, larger eggs will commonly produce larger larvae, which in turn may show a higher robustness to such climate change induced time lags (Marshall 1953).

Such larger eggs, and associated lower fecundities, were more common further north in the Barents Sea (Paper III). We suggested that this feature was an adaptation to the strongly seasonal environment in the Arctic, where the capacity of larvae to wait for food for an extended period probably is valuable (Marshall 1953). Likewise, a small body size and association with the benthic environment, which was common in the Arctic (Papers II and

III), can probably also be explained by a scarce access to food during long periods of the year. Even though Arctic fish are generally small-sized, which indicates a relatively low sensitivity to fishing, we argue that a very cautious approach to fisheries in the Arctic is wise; these areas are generally understudied, and little is known about the consequences if they are perturbed by e.g. fishing (Christiansen et al. 2013, Christiansen et al. 2014).

In the central Barents Sea, where the Polar Front is a dominant physical oceanographic feature, the highest functional diversity was observed. The high functional diversity here was partly driven by a very high redundancy in the most species-rich functional group (i.e., the "long demersals"). The Polar Front constitutes a transition between warm Atlantic and cold Arctic water masses, and can therefore also be regarded a natural transition zone between Arctic and boreal species' preferred environmental conditions. In Paper II, we showed that species within a given functional group also shared biogeographic affiliation, even though such information was not explicitly accounted for in the trait matrix. Likewise, we showed that species that shared biogeographic affiliation also often displayed similar life histories (Paper III). For instance, the "small demersals" were largely Arctic, whereas the "large demersals" were mostly of boreal origin. This entails that areas that support both Arctic and boreal species (such as the central Barents Sea in general and the Polar Front in particular) will often display high functional diversity. That being mentioned, individual specimens found in such transition zones between distinct biogeographic regions can be expected to be situated at the outer limits of their distribution ranges. They may thereby be sensitive to climate changes, which suggest that the high community-level adaptability inferred from a high functional diversity potentially is rather artificial.

Climate-induced borealization of the Barents Sea

This thesis suggests that there is an ongoing borealization of the Barents Sea fish community, especially in the northernmost part of the area. This occurs along with the atlantification of the Barents Sea water masses, which in turn is induced by an intensification of the Atlantic water inflow to the area (Smedsrud et al. 2013). The fish community borealization has not only implications for the fish community structure, but also on the ecosystem functionality as well as on the spatial representation of various life history strategies.

This thesis sheds light on major changes in the Barents Sea fish community structure and functionality, particularly in the northern parts of the area. These changes include increasing functional diversity (Paper I), a northward movement of boreal species (Paper II), rising average fast-slow ranks, higher average fecundities and smaller average egg sizes, and a general shift towards northern species assemblages that are phylogenetically more heterogeneous (Paper III). In short, properties that are common in boreal assemblages now appear to get common in the northern parts of the Barents Sea as well, a pattern that is confirmed by recent work by Fossheim et al. (in prep). Furthermore, indications of a corresponding atlantification of the Barents Sea zooplankton community have recently been observed (e.g., Orlova et al. 2011).

The Bering Sea currently undergoes a similar biogeographic transition (Overland and Stabeno 2004), suggesting that the spatio-temporal changes in community structure that we observe in Barents Sea fish represent an ongoing worldwide trend. Cheung et al. (2009) predicted a general poleward movement of biota in response to climate warming. Also, they forecasted the strongest species movements to occur in high-latitude areas, associated with species turnovers of 60% or more (Cheung et al. 2009). Strong empirical evidence for such alterations exists (Doney et al. 2012, Bates et al. 2013, Poloczanska et al. 2013). In the Barents Sea area, an unusually strong inflow of Atlantic water masses led to the re-establishment of the blue mussel (*Mytilus edulis*) in Svalbard after 1000 years of absence (Berge et al. 2005). Also, Kortsch et al. (2012) documented an abrupt shift in Svalbard benthos in recent years, from a community structure dominated by calcareous algae, sea urchins and sea anemones, to a macroalgae dominated community.

Implications for fishing and fisheries

In line with present findings and recent literature (e.g., Johannesen et al. 2012b, Johansen et al. 2013), many commercially attractive species may benefit from the climate change. The reduced proportion of Arctic water masses in the Arctic will probably continue, with associated negative implications for the survival and production of Arctic species (Ellingsen et al. 2008). Still, the primary production is predicted to increase by about 8% over the next ~45 years (Ellingsen et al. 2008), and the primary production in the Barents Sea will possibly support todays' total fish biomass or more, at least during the relatively close future. Interestingly, Everett et al. (1996) suggested that the overall catches will remain largely at todays' level under climate change, but that the location of the catches may change.

Here, we have seen that assemblages in northern regions, north of the Polar Front, will become more heterogeneous as they to an increasing extent will have to share their habitat with boreal species. Many of these boreal species are commercially attractive, which potentially will increase the commercial fishing fleets' interest for the northernmost areas, where there is not much fishing going on today (ICES 2013). However, many of these commercially interesting species are also fishery-sensitive (i.e., they are "slow"; Paper III), and we also know little about the Arctic species that are endemic to the northernmost areas, so I reiterate my recommendation that the fisheries should be cautious here until we have a much better knowledge of the vulnerability of these parts of the Barents Sea ecosystem.

Utility of this work, and future recommendations

This thesis constitutes a first attempt to integrate Barents Sea ecosystem survey fish data with species' traits. I argue that such traits can be applied as translators of ecological knowledge to traditional biodiversity mapping. Today, we have a basic knowledge of how the ecology of typical species varies between different habitats and biogeographic regions, but I contend that trait-based methods make such work much more explicit and structured. Still, it is important to bear in mind that, at the present stage, such methods relies on clear, but very simple theoretical suppositions. For instance, although the life history fast-slow continuum plausibly carries much important information about species ability to cope with fisheries-induced disturbance, other factors are certainly also important for such sensitivity. Furthermore, the desire to study larger ecosystem components (e.g., many species simultaneously) calls for simplifications on the species level, which in turn surely translates into some degree of uncertainty when integrated to higher levels of organisation. Finally, as the effect trait-based methods are largely developed during studies of terrestrial plant communities, we are not guaranteed that the same methods are successful in marine ecosystems (Steele 1991). The present findings should therefore not be treated as a final solution to the vulnerability to disturbance such as fishing or climate change, or used in ecosystem-based management plans as such. Here, I will suggest a number of factors that that may enhance the field of applied trait-based methods in marine ecology.

We should gain a much better knowledge about what the particular species that constitute the ecosystems do, and how they contribute to ecosystem functioning (Jennings & Brander 2010). For instance, a focus on food web interactions may inform about important aspects of ecosystem functioning such as the species' trophic levels and degree of omnivory, as well as food web modularity as a predictor of ecosystems' response to disturbance (Levin & Lubchenco 2008, Stouffer & Bascompte 2011). In the BarEcoRe project, we compiled a food web matrix that includes a majority of the common species found in the Barents Sea, from plankton to birds and sea mammals (Planque et al. in press), which will provide the basis for future work on these aspects of ecosystem functioning. In addition, further information about species' shape, mobility, migratory capacity and habitat use may help to assess ecosystem functioning (e.g., through the species' capacity to utilize local resources or migrate to bring in energy from neighbouring areas), and the species' capacity to cope with disturbance (e.g., through the capacity to avoid fishing gear or migrate in response to climate changes). In this regard, it is important to recognize that building a trait matrix is a never-ending process, because new ecological knowledge always may enhance earlier matrix versions.

In the present work I have solely based the analyses on compositional (presence/absence) data. Still, abundance data indeed contain much information that eventually should be accounted for. Two specimens of the same species would likely have a higher impact on the ecosystem functioning than one specimen would have alone, as a consequence of their increased capacity to contribute to the flow of energy and material. For instance, the Northeast Arctic cod stock (which is the worlds' largest cod stock) dominates the Barents Sea ecosystem, and the relative abundance of the stock has a major impact on the ecosystem (Yaragina et al. 2011).

Finally, future studies should seek to explicitly integrate response traits, effect traits, abundance information and spatially-explicit information about disturbance (e.g., the impact of fisheries activities, or climate scenarios). In this regard, frameworks exist that may prove useful in future assessment of Barents Sea ecosystem functioning and vulnerability (Suding et al. 2008, Laliberté et al. 2010). Relatively speaking, the Barents Sea is considered species poor, which makes it a convenient study area. In springtime 2014, 10 years of Barents Sea ecosystem surveys have been completed, which allows for a higher confidence in the assessment of structural properties and spatio-temporal variation in trait-based metrics.

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Paper 1

Paper 2

Paper 3