Population dynamics and trophic interactions of Atlantic cod along the Greenland shelf

Dissertation

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Preface

The results of this cumulative PhD dissertation summarize the findings of the research I have conducted as part of my PhD project from Mai 2016 to December 2019. This work was funded by the CLIMA project, reference RER 15/0008, Ministry of Foreign Affairs Norway. Biological samples were collected on nine research cruises with FRV Walther Herwig 3 between 2006 and 2017. I participated in the survey in 2016 as staff scientist and in 2017 as cruise leader.

The work was focussed on investigating the impacts of natural variability and anthropogenic pressures on stock productivity and body condition of Atlantic cod (*Gadus morhua*) in Greenland waters. Because climate change and fishing have already affected all cod stocks in the North Atlantic and changes in abundance of cod affect ecosystems and socio-economic stability of coastal communities, it is important to disentangle the role of natural variability and fishing on population replenishment.

This thesis consists of an introduction (Chapter 1), six publications presented below (Chapter 2-7) and a synoptic discussion (Chapter 8). The concept of this PhD dissertation was designed by myself with support of my advisors Heino O. Fock and Christian Möllmann.

Chapter 2

Karl Michael Werner, Hans-Joachim Rätz, Søren Anker Pedersen, Christian Möllmann

Population and abundance dynamics in the offshore stock of Atlantic cod in Greenland waters

The concept was mainly developed by myself with support from Hans-Joachim Rätz and Christian Möllmann. Data were taken from the Thünen Institute data base. The literature review was conducted by mself. Hans-Joachim Rätz and myself extracted and prepared the data from our database. Hans-Joachim Rätz ran the virtual population analysis. The first draft of the paper was written by myself and all co-authors contributed with comments and advice. The manuscript is currently in preparation for submission.

Chapter 3

Camilla Sguotti, Saskia A. Otto, Xochitl Cormon, Karl Michael Werner, Ethan Deyle, George Sugihara, Christian Möllmann

Non-linearity in stock-recruitment relationships of Atlantic cod: insights from a multi-model approach

The concept was mainly developed by Camilla Sguotti and Christian Möllmann. I contributed data from the stock assessment in chapter 2. The first draft was written by Camilla Sguotti and all authors contributed with comments and advice afterwards. The manuscript was published in the ICES Journal of Marine Science (2019), doi:10.1093/icesjms/fsz113.

Chapter 4

Fabian Zimmermann and Karl Michael Werner**

**both authors contributed equally to this study*

Improved management is the main driver behind recovery of Northeast Atlantic fish stocks

Both authors developed the concept. Data analysis was mainly conducted by Fabian Zimmermann, writing of the first draft mainly by myself. The paper is published in Frontiers in Ecology and the Environment (2019), 17(2): 93-99

Chapter 5

Karl Michael Werner, Marc. H. Taylor, Rabea Diekmann, Josep Lloret, Christian Möllmann, Raul Primicerio, Heino O. Fock

Evidence for limited adaptive responsiveness to large-scale spatial variation of habitat quality

The concept was developed by myself and Heino O. Fock. And data were collected by myself and Heino O. Fock. Samples were taken and stomachs dissected by myself, Heino O. Fock and five master students. Samples were collected on Thünen surveys in Greenland between 2006 and 2016. Data were analysed by myself, Marc H. Taylor and Rabea Diekmann. I wrote the first draft of the manuscript and all co-authors contributed with comments and advice. The paper is published in Marine Ecology Progress Series (2019), 629: 179-191.

Chapter 6

Ina Stoltenberg, Karl-Michael Werner, Stefanie M.H. Ismar-Rebitz, Heino Fock

Trophic niche variability influences body condition on organosomatic and biochemical level of mature female Atlantic cod (*Gadus morhua*) in offshore Greenland waters

The concept was developed by Ina Stoltenberg and myself as part of supervising Ina Stoltenberg's Master thesis. Heino O. Fock, Stefanie Ismar-Rebitz and myself supervised Ina. Data were collected on the Thünen Greenland survey 2017, where I was cruise leader, by Ina Stoltenberg and myself. Ina Stoltenberg and myself wrote the first draft of the manuscript and Heino O. Fock and Stefanie M. H. Ismar-Rebitz contributed with comments and advice. The paper is in preparation for publication.

Chapter 7

Robert Boenish, Jacob P. Kritzer, Kristin Kleisner, Robert Steneck, Karl Michael Werner, Wenbin Zhu, Frederick Schram, Douglas Rader, William Cheung, Jose Ingles, Yongjun Tian, John Mimikakis

The global rise of crustacean fisheries

Robert Boenish compiled the data and conducted the analysis. Robert Boenish and myself developed the current draft of the manuscript and all co-authors contributed with comments and advice. The paper is currently under revision in Frontiers in Ecology in the Environment (major revisions, 22.01.2020, FEE19-0294).

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Thesis Summary

Atlantic cod (*Gadus morhua*) is the most abundant high-trophic-level fish predator in continental shelf habitats in the North Atlantic and has been a vital economic and nutritious resource for many nations. Climate change and overexploitation have already affected all stocks of Atlantic cod and changes in their abundance influence entire ecosystems and the socioeconomic stability of fishing communities. The short, medium and long-term future of marine ecosystem compositions and global fishery patterns will depend on global warming and how marine resources are managed. Investigating how wild fish stocks respond to environmental change and anthropogenic pressures and how they can be sustainably managed in a changing environment is one of the most important questions to be investigated in marine ecology and fishery science.

Although Atlantic cod is one of the most important fishery resources in Greenland, scientific knowledge on the stock is patchy ever since the fishery collapsed. Here, the cod stock belonged to the once largest cod stocks worldwide with a total stock biomass of ~ 4 million tons. The stock supported a fishery with annual landings up to 460.000 tons until it collapsed in the 1970s. It is the objective of this thesis to investigate natural and anthropogenic drivers impacting the life history and abundance of cod in Greenland waters. In particular, I focus on fishing as anthropogenic driver and on the influence of habitat heterogeneity as reflected through diet composition as natural driver.

The thesis consists of six scientific publications, which deal with **1)** fishing and environmental change as drivers of abundance of the cod stock in Greenland waters since 1955; **2)** non-linear stock-recruitment dynamics of North Atlantic cod stocks and their implications for recovery potential; **3)** the impacts of natural variation and fishing as drivers of Northeast Atlantic fish stocks; **4)** the influence of diet composition on energy reserves and the ability of Greenland cod to adapt to spatial and temporal variability of habitat quality and how this influences their body condition; **5)** if different trophic niches impact the reproductive capacities and body condition of the cod population in East Greenland and **6)** how anthropogenically altered

marine ecosystems including an example from West Greenland influence the composition of fishery harvests and if these changes come with ecological and socioeconomic trade-offs.

Results of our review in **publication 1** show that while the collapse of the Greenland cod stock in the 1970s was mainly driven by recruitment failure associated with dropping temperatures, overfishing in the late 1980s and early 1990s induced hysteresis effects, which have ever since the collapse in the 1970s prevented a recovery. The stock can benefit from irregular influx events of eggs and larvae from Iceland, which periodically support recruitment in Greenland waters. Over the past 60 years, the year classes of 1973, 1984 and 1985 drifted in high amounts to Greenland, where they triggered an unsustainable boom and bust fishery on a largely immature stock. These irregular influx events are reflected in a chaotic stock-recruitment relationship. Analyses from **publication 2** show similarities among the cold-water Northwest-Atlantic cod stocks, where abrupt changes and discontinuous dynamics are more common than in Northeast-Atlantic stocks. This has implications for reference points and that without harvest control rules in place, a precautionary management approach should be in place for these stocks. In order to compare management success of the Greenland cod stock with a suite of well-managed fish stocks, **publication 3** aimed to investigate historic drivers of fish populations from the North-East Atlantic. The results show that when management action and stricter regulations are in place, fish populations can collectively recover. Between 1960 and 2000, decreasing productivity and increasing fishing pressure caused fish stocks in the Northeast Atlantic to decline. After 2000, enforced management actions facilitated fish abundance to increase on a large scale.

After investigating the historic role of management and the influence of climate variability on recruitment success, **publications 4 and 5** focus on trophic interactions and their influence on energy reserves and body condition with implications for organism health. In **publication 4** we show that Greenland cod exhibits limited abilities to adapt its distribution to spatial and temporal variation to food availability and habitat quality. In particular areas, cod individuals show persistently higher energy reserves than in other areas, which was mainly explained by differences in the diet composition. It appears that individuals rather remain in sub-optimal habitats to avoid costly searching behaviour to screen the environment for better areas. Based on the results from **publication 4**, three distinct habitats where chosen for the study in **publication 5** and it was investigated how different habitats can influence body condition and reproductive potential of mature female cod as indicated by fatty acid composition and fat content in the liver and the gonads. Stable isotope signatures revealed different trophic niches, aligning with the spatial distribution of pelagic and benthic diets revealed in **publication 4**. Fatty acid profiles and fat contents differed between these trophic niches. In areas with high somatic condition, cod showed high fat contents in the organs and large amounts of poly-unsaturated fatty acids, which are crucial for fish health because they are important components of cell membranes and involved in energy storage and hormone production. Because individuals with healthy fatty acid compositions have a higher reproductive potential, these results suggest that the abilities to adapt to spatial habitat heterogeneity influences fish health and likely the reproductive output.

In order to synthesize the impacts of overfishing and anthropogenic ecosystem alterations, **publication 6** investigates the ecologic and socio-economic trade-offs between formerly finfish and afterly crustacean dominated ecosystems. In West Greenland, where cod was once the most important fishery, the populations of deep sea shrimp (*Pandalus borealis*) rose after the cod collapse. Today, deep sea shrimp is one of the most important fishery resources in Greenland waters. Results from **publication 6** illustrate that crustacean dominated fisheries often come with high carbon emissions, provide low nutritional yield but have the potential for more wealth. This synthesizes a complicated picture and highlights the need for managers to carefully weigh up these trade-offs.

1. Introduction

Because fish populations are a major source for food, nutrition and income for a rising human population, increased fishing pressure on all trophic levels has caused a global decline of many marine fish populations (Christensen *et al.*, 2003; Worm *et al.*, 2009; Branch *et al.*, 2010; Pauly *et al.*, 2012; Fernandes *et al.*, 2017; FAO, 2018; Rousseau *et al.*, 2019). Since 1800, energy use and economic productivity grew many times faster than global human population grew and as consequence, natural resources, such as fish stocks, diminished while fuelling industrial growth and feeding the world (Crutzen, 2002; Christensen *et al.*, 2003; Steffen *et al.*, 2011; Zalasiewicz *et al.*, 2011; Pauly *et al.*, 2012; Lewis and Maslin, 2015).

Fish populations are subject to natural variation and anthropogenic pressure (Hjort, 1914; Finney *et al.*, 2002; Worm *et al.*, 2009; Pauly *et al.*, 2012). Anthropogenic impacts can act as direct or indirect drivers (Halpern *et al.*, 2006; Anderson *et al.*, 2008; Lynam *et al.*, 2017). Humans indirectly influence fish in various ways such as through eutrophication, greenhouse gas emissions, marine installations or size-selective fishing (Heino *et al.*, 2013; Perry *et al.*, 2014; Casini, Käll, *et al.*, 2016; Zimmermann and Jørgensen, 2017; Todd *et al.*, 2019). The most important direct anthropogenic driver of fish population abundance and size composition is fishing, which increases mortality through removal of individuals and truncates population size spectra by catching individuals at a species-specific high age (Heino *et al.*, 2013; Zimmermann and Jørgensen, 2017).

Because fish populations are a major source for food, nutrition and income for a rising human population, increased fishing pressure on all trophic levels has caused a global decline of many marine fish populations (Christensen *et al.*, 2003; Worm *et al.*, 2009; Branch *et al.*, 2010; Pauly *et al.*, 2012; Fernandes *et al.*, 2017; FAO, 2018; Rousseau *et al.*, 2019). In addition to directly affecting fish abundance, overexploitation and extensive fishing effort have caused ecosystems to alter and ecosystem functions to change (Frank *et al.*, 2005; Möllmann *et al.*, 2008; Pauly *et al.*, 2012; Szuwalski *et al.*, 2016). Through the removal of high trophic-level predators, regional trophic cascades can emerge and sometimes change ecosystems to such extent that they do not recover, but remain in the alternative, changed state (Frank *et al.*, 2005; Steneck and Wahle, 2013; Conversi *et al.*, 2015; Sguotti, S. Otto, *et al.*, 2019).

However, when harvested on safe single stock levels and with low impacts on the seabed and non-target species, wild finfish products often come with low CO2 emissions, high nutrient loadings and compared to agriculture, no negative impacts caused by factors such as eutrophication-causing fertilizers or pesticides (Hilborn et al., 2018; Parker et al., 2018; Hallström et al., 2019; Hicks et al., 2019). Then wild capture fish products can belong to the most sustainable choices of animal protein worldwide and can be a vital part of global food security (Hilborn et al., 2018; Parker et al., 2018; Hallström et al., 2019; Hicks et al., 2019). In light of current climate change and a rising and more wealthy human population, which sets high value on seafood meals (Smith et al., 2010; Clark et al., 2018), a maximized and sustainable exploitation of marine resources has become increasingly important. However, as wild fish populations are as well affected by natural environmental variability, it is important to understand and disentangle the role natural and anthropogenic drivers play for exploited fish populations.

For many centuries, people believed that fish as marine resource is infinite and that fluctuations in abundance were only driven by natural variation (Kurlansky, 2011). Because striking amounts of evidence for widespread overfishing have accumulated, the question if natural variability or fishing is the main driver of exploited fish populations has arose and fuelled many scientific and political discussions (Skud, 1975; Worm *et al.*, 2006; Branch, 2008). Natural (biotic and abiotic) drivers can also directly or indirectly influence individual fish or entire populations (Hjort, 1914; Casini, Käll, *et al.*, 2016; Lynam *et al.*, 2017). For example, natural drivers can indirectly influence abundance through altering species behaviour, interactions and trophic links, or directly through changes in the abiotic environment such as temperature, salinity and nutrients (Casini, Käll, *et al.*, 2016; Akimova, Hufnagl and Peck, 2019; Zimmermann, Claireaux and Enberg, 2019).

Changes in the natural environment usually begin with changing physical parameters, such as temperature, salinity or acidity. Throughout a fish’s life cycle, direct dependence of survival on beneficial environmental conditions is highest during its early life stages as eggs, larvae and juveniles, when mortality caused by predation or starvation shapes the abundance of a cohort as adult population (Hjort, 1914; Jennings, Kaiser and Reynolds, 2001; Stachura *et al.*, 2014;

Zimmermann, Claireaux and Enberg, 2019). During adult stages, when individuals become more mobile to avoid potentially lethal environments and are less susceptible to predation, the suitability of the environment to sustain well-conditioned organisms is reflected in somatic growth and the amount of energy individuals can acquire (Lloret, Shulman and Love, 2013; Casini, Eero, *et al.*, 2016; Casini, Käll, *et al.*, 2016). Surplus energy storages, which are not needed for basic metabolism, can be invested in reproduction and fish in superior condition have a higher reproductive potential (Marshall *et al.*, 1999; Lloret *et al.*, 2012; Mcbride *et al.*, 2015). First at the level of an individual, somatic condition and energy storages directly influence health and productivity of whole populations (Sutherland, 1996; Rätz and Lloret, 2003; Casini, Eero, *et al.*, 2016).

The present thesis aims at investigating natural variation and anthropogenic pressure as drivers of abundance and body condition Atlantic cod (*Gadus morhua*), a commercially and ecologically important marine predator (Kurlansky, 2011; Rose, 2019). Because the influence of temperature on stock productivity on Greenland cod as direct effect has been investigated in the past (Buch, Horsted and Hovgård, 1994; Pedersen and Rice, 2002; Hovgård and Wieland, 2008), I chose to assess the influence of diet composition and behavioural responsiveness on body condition as indirect effects linked to natural variability and fishing as direct anthropogenic factor on population dynamics of Atlantic cod in offshore Greenland waters. Here, cod inhabits one of its most northern areas of distribution, where recruitment and body condition is strongly correlated to environmental change (Pedersen and Smidt, 2000; Rätz and Lloret, 2003; Fock, 2007; Bonanomi *et al.*, 2015).

1.1 Atlantic cod

Atlantic cod (*Gadus morhua*) (Figure 1) is the most abundant high-trophic-level fish predator in the North Atlantic and has been a vital economic and nutritious resource for many nations (Kurlansky, 2011; Rose, 2019). It is distributed throughout the whole North Atlantic and for fishery management purposes, the populations are divided into different stocks, covering its whole area of distribution (Figure 2).

Climate change and overexploitation have already affected all stocks of Atlantic cod and changes in their abundance influence entire ecosystems and the socioeconomic stability of fishing communities (Drinkwater, 2005; Lilly *et al.*, 2008; Kurlansky, 2011; Rose, 2019). All cod stocks have collapsed at a certain point during the second part of the 20th or the early 21st century and for most of them, these collapses were associated with increasing fishing mortalities (e.g. catch rates) during periods of population decline, which is a clear sign of overfishing (Myers, Hutchings and Barrowman, 1996; Lilly *et al.*, 2008; Rose, 2019). Collapsed cod stocks can lead to ecological cascades through reduced predation on prey species lower in the food chain (Worm and Myers, 2003; Steneck and Wahle, 2013; Christie *et al.*, 2019). Throughout the whole North Atlantic, such cascades have led to proliferation of commercially important crustacean species, such as American lobster (*Homarus Americanus*), snow crab (*Chionocetes opilio*), edible crab (*Cancer pagurus*) and northern shrimp (*Pandalus borealis*), which has also changed local fishery catch compositions (Worm and Myers, 2003; Steneck and Wahle, 2013; Hamilton *et al.*, 2014; Christie *et al.*, 2019).

Figure 1 Picture of Atlantic cod (*Gadus morhua*) taken in East Greenland (© Thünen-Institut).

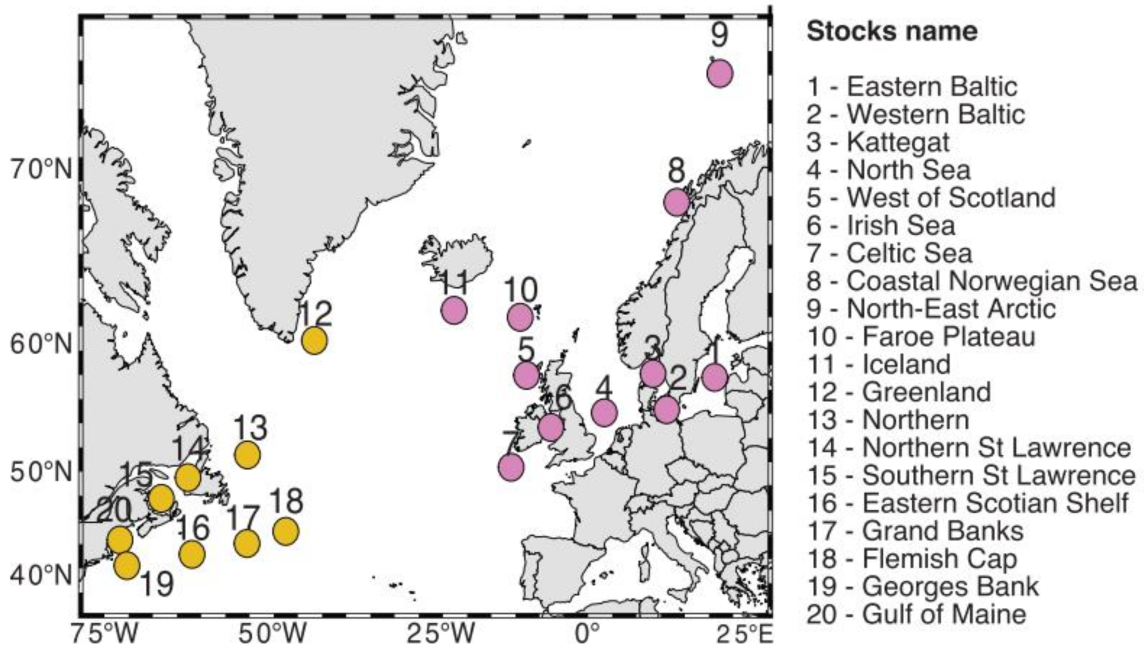

Figure 2 Distribution of North Atlantic cod stocks. Taken from (Sguotti, S. A. Otto, *et al.*, 2019) (see chapter 3). Orange dots denote western, pink dots denote eastern cod stocks.

Nevertheless, cod stocks are also affected by natural variation in the environment, which influences recruitment success, growth, body condition and natural mortality (Marshall *et al.*, 1999; Dutil *et al.*, 2006; Lilly *et al.*, 2008; Beaugrand and Kirby, 2010; Casini, Eero, *et al.*, 2016). Diet composition and availability of different prey resources are important for condition of individual fish and entire populations (Kjesbu *et al.*, 1991, 1998; Yaragina and Marshall, 2000; Pardoe, Thórdarson and Marteinsdóttir, 2008; Casini, Käll, *et al.*, 2016). For most arcto-boreal cod stocks, such as the stocks from the Barents Sea, Iceland and off Labrador and Newfoundland, body condition and stock productivity of cod are positively correlated with capelin recruitment and capelin abundance, which is the most important forage-fish species in these regions (Yaragina and Marshall, 2000; Rose and O'Driscoll, 2002; Rideout and Rose, 2006; Sherwood *et al.*, 2007; Pardoe, Thórdarson and Marteinsdóttir, 2008; Frater *et al.*, 2019; Holt *et al.*, 2019). High abundance of capelin, which is a lipid-rich species, has been linked to high energy reserves and higher recruitment through greater spawning potential and lower chances of skip-spawning (Kjesbu *et al.*, 1998; Rideout and Rose, 2006; Sherwood *et al.*, 2007; Lilly *et al.*, 2008; Mcbride *et al.*, 2015). In other areas of distribution, body condition of cod has already been linked with diet composition and population replenishment. For instance, in the Baltic Sea, recent collapses of the cod populations have been linked to increased natural mortality and reduced fecundity caused by low body condition (Casini, Eero, *et al.*, 2016; Casini, Käll, *et al.*, 2016; Mion *et al.*, 2018).

1.2 Atlantic cod in Greenland waters

The Greenland cod stock belongs to the cold-water stocks of the Northwest Atlantic (Stock 12, Figure 2), which are characterized by lower average condition and growth, lower recruitment potential especially at low levels of spawning biomass and higher vulnerability to exploitation in comparison to warn-water cod stocks (Rätz and Lloret, 2003). Global warming is changing sub-arctic and arctic regions faster than any other area in the world and thus acts as additional challenge to other natural fluctuations (Hoegh-Guldberg and Bruno, 2010; Fossheim *et al.*, 2015; Griffith *et al.*, 2019; Peck and Pinnegar, 2019). In the 1920s and 1930s, the cod stock in Greenland waters benefitted from a regime shift in the North Atlantic; increased sea temperatures and reduced sea ice conditions supported higher stock productivity (Buch, Horsted and Hovgård, 1994; Drinkwater, 2006). Annual fishery catches went up to 460.000 tons, when abundance peaked in the 1950s and 1960s (Figure 3) (Horsted, 2000). During this time, cod supported Greenland's once most valuable fishery and represented one of the largest stocks of Atlantic cod in the world (Horsted, 2000; Hovgård and Wieland, 2008).

In the late 1960s and 1970s, a cooling of the northern North Atlantic caused a reduction in primary production and zooplankton abundance in Greenland waters (Pedersen and Smidt, 2000; Drinkwater and Kristiansen, 2018). These changes induced a bottom-up decline of the Greenland cod stock, likely triggered by recruitment failure through low larval food availability and decreased growth (Pedersen and Smidt, 2000; Pedersen and Rice, 2002; Drinkwater and Kristiansen, 2018). During this period, fishing pressure was not reduced and as consequence the cod stock collapsed and fisheries landings declined by the late 1970s (Horsted, 2000; Hovgård and Wieland, 2008; Bonanomi *et al.*, 2015).

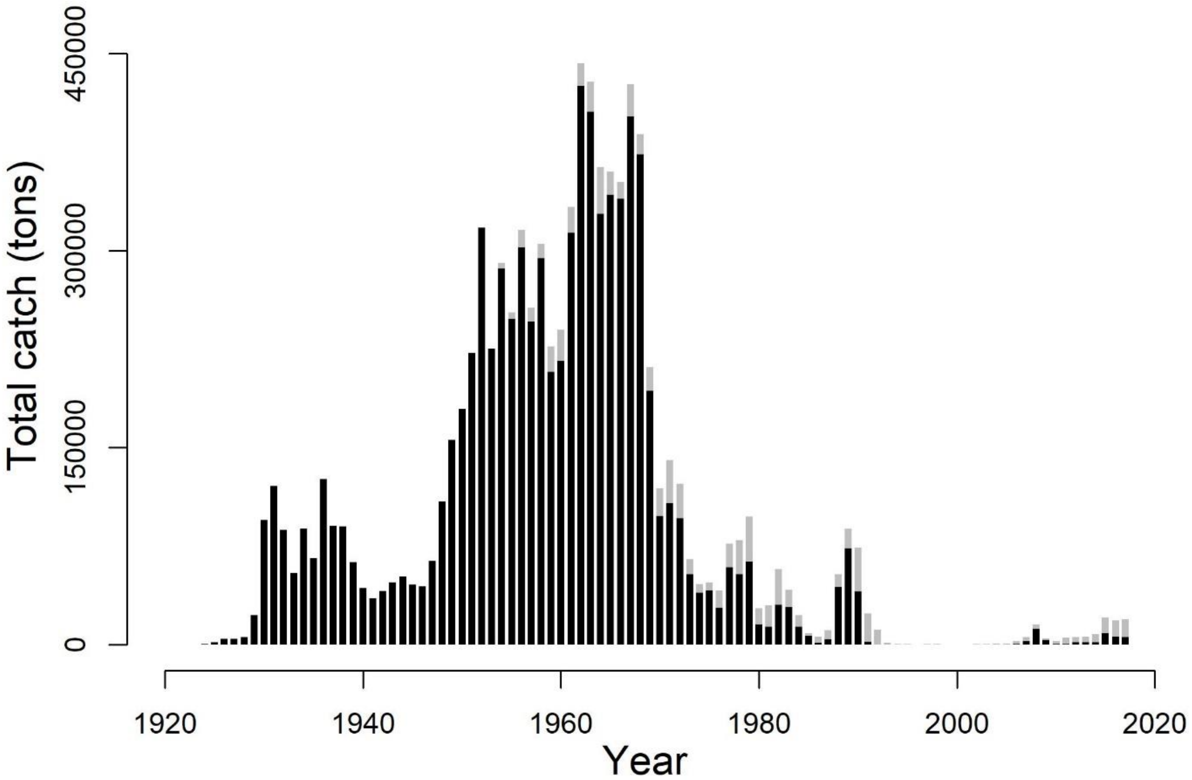

Figure 3 Total landings of Atlantic cod in Greenland waters from 1924-2017. Black bars represent catches of the West Greenland offshore stock component (NAFO 1A-1F), grey bars represent catches of the East Greenland offshore stock component (ICES 14b).

Habitat heterogeneity and trophic interactions

In Greenland waters, cod inhabits shelf and slope areas to depths of ~ 400 m, where the stock was annually monitored by the Thünen Institute of Sea Fisheries since 1982 (Rätz, 1996, 1999). In this heterogeneous environment, cod inhabits shelf-like, shallow areas and deeper banks on underwater mountains (Rätz, 1996; Fock, 2007; Sutherland and Pickart, 2008). These areas differ in their fish assemblages and are stronger dominated by boreal species in East and South Greenland and more sub-arctic and arctic species in West Greenland (Rätz, 1999; Fock, 2007). Environmental heterogeneity within the ecosystems surrounding Greenland is reflected in the diet composition of cod, which differs spatially (Jensen and Hansen, 1931; Hansen, 1949; Rasmussen, 1953; Sidorenko, 1963; Tiedtke, 1988; Grunwald and Köster, 1994; Nielsen and Andersen, 2001; Hedeholm *et al.*, 2016) (Table 1). Because the West Greenland component of the Greenland cod stock used to be several times as large and of larger importance for the fishery than the component in East Greenland (Horsted, 2000), most scientific studies and diet investigations took place in West Greenland (Table 1). Capelin and krill are important diet items in nearly all areas of distribution (Jensen and Hansen, 1931; Hansen, 1949; Grunwald and Köster, 1994; Nielsen and Andersen, 2001; Hedeholm *et al.*, 2016). In West Greenland cod exhibits high predation rates on northern shrimp (*Pandalus borealis)*, sandeel (*Ammodytes sp*.) and benthic crabs (Brachyura), whereas in East Greenland prey species are mainly amphipods and redfish (Sebastes sp.). Because West Greenland covers different climatic zones with more arcto-boreal conditions in the South and more high-arctic conditions in the North, diet composition varies spatially, but spatially discrete information is rare (Grunwald and Köster, 1994; Hedeholm *et al.*, 2016). In more northern regions, cod exhibits higher predation rates on northern shrimp, whereas in more southern regions cod preys more on capelin, cod and redfish as well as krill (Euphausiacea) (Grunwald and Köster, 1994; Hedeholm *et al.*, 2016). In the early 20th century, when fishery catches and biomass of the offshore cod in West Greenland increased steeply, both capelin and sandeel complemented by northern shrimp, benthic crabs and krill were important parts of cod diet in West Greenland (Table 1). Although Rasmussen (1953) did not describe the occurrence of capelin in cod stomachs during their investigations in July 1952, they observed that cod was feeding on “great swarms of sandeel and capelin” in July 1951 (Rasmussen, 1952, 1953). This implies that capelin was still an abundant food source in the 1950s, with a likely interannual and spatial variation in intensity. In the early 1980s, sandeel more or less disappeared from cod diet in West Greenland (Table 1). Krill and benthic crabs showed declines in consumption in the 1980s and 1990s (Table 1). Northern shrimp was an important food source throughout almost all periods of the 20th century (Table 1).

Most of the investigations about diet of cod in Greenland waters took place before the collapse of the stock but ever since the severe collapse in the 1990s, investigations on how diet composition might affect body condition and stock productivity are rare. The present thesis aims to fill these missing gaps and to investigate the impacts of natural variability and fishing on the offshore cod stock in Greenland waters with an emphasize on the role diet composition and trophic niches may play for population replenishment of cod in these heterogeneous and high-latitude environments.

Table 1 Diet composition of Atlantic cod in West and East Greenland throughout the 20th century based on different sources (numbers 1-8). Because most diet investigations took place in West Greenland, only two studies were available for East Greenland. For these studies, results for West Greenland are denoted with "W" and for East Greenland with "E". Colours were used to indicate feeding intensity (White = no feeding; light grey = low feeding intensity; dark grey = increased feeding intensity; black = main diet item).

Prey	1	2	3	4	5W	6	7	8	9W	5E	9E
Fish (general)	█	█	█	█	█	░	▓	█	░	█	█
Crustaceans (general)	█	█	█	█	█	█	▓	█	█	▓	░
Capelin (*Mallotus villosus*)	█	█		░	▓		▓	█	░	░	░
Sandeel (*Ammodytes spp.*)	▓	▓	▓	█							
Atlantic Cod (*Gadus morhua*)		░		░	░		░		░		
Greenland Cod (*Gadus ogac*)		░									
Redfish (*Sebastes spp.*)					▓	░	░			█	░
Greenland Halibut (*Reinhardtius hippoglossoides*)	░	░									
American plaice (*Hippoglossoides platessoides*)					▓	░					
Northern shrimp (*Pandalus borealis*)	▓	█	█	▓	▓	█	█	░	█	░	
Other shrimps	░	░		░	░	░		░		░	
Gammaridea	░							░			
Crabs (Brachyura)	▓	█	▓	▓				█			
Bivalves	░							░			
Cephalopods	▓		▓							░	
Krill	▓	▓	▓	█	▓	░		░	█	▓	░
Amphipoda		█			░	░				▓	
Hyperiidae		░						░			
Jellyfish		░	▓	░							
Other molluscs				▓						░	
Pteropoda		░	▓								
Polychaetes		░		▓	░			░			
Sea cucumbers			▓	▓							
Starfish				░	░					░	

Sources: 1 = (Jensen and Hansen, 1931), 2 = (Hansen, 1949), 3 = (Rasmussen, 1953), 4 = (Sidorenko, 1963), 5 = (Tiedtke, 1988), 6 = (Köster and Schober, 1990), 7 = (Grunwald and Köster, 1994), 8 = (Nielsen and Andersen, 2001), 9 = (Hedeholm et al., 2016)

1.3 Objectives of the thesis

The aim of this thesis is to provide new insights into how environmental variability on temporal and spatial scales as well as fishing affects abundance, productivity, trophic interactions and energy acquirements of the cod populations in Greenland waters. The knowledge originating from this thesis is expected to support a sustainable management of the Greenland cod stock and to integrate scientific advice in an ecosystem-based fishery management

In order to tackle these questions, **a) stock assessments** were used to investigate historical abundance, **b) meta analyses** were conducted for large-scale and inter-taxonomic comparisons, **c) stomach analyses** were carried out to gain insight into spatial and temporal diet patterns and **d) body condition indices**, such as liver size and fatty acid composition, were chosen to relate diet composition to habitat quality to draw conclusions on aspects of natural resource management.

The main objectives of this dissertation are:

1. Summarize population dynamics and update historic abundance estimates to compare the impact of natural variability and fishing on Greenland cod with other North Atlantic fish stocks (Chapters 2, 3 & 4)
2. Investigate the influence of diet composition on energy acquirements and the responsive abilities of the cod populations to adapt to spatial and temporal variability of habitat quality (Chapter 5)
3. Assess the spatial distribution of trophic niches and how they might influence body condition and fish health of large mature females on biochemical level (Chapter 6)
4. Investigate the implications of a global transition from finfish to crustacean dominated fisheries with a case study from West Greenland (Chapter 7)

1.4 Bibliography

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2 Publication 1

Population and abundance dynamics in the offshore stock of Atlantic cod in Greenland waters

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Abstract

Atlantic cod (*Gadus morhua*) has historically been the most important fishery resource in Greenland waters with annual landings of up to 450.000 tons in the 1960s. We firstly summarize egg and larval drift patterns and migrations between the Greenland and Iceland cod stocks and secondly use updated survey data to calculate stock assessment time series for the period 1993-2015. The cod stock around Greenland can benefit from irregular influx events of eggs and larvae from Iceland, although some of these individuals migrate back to Iceland, when maturity is reached. These drift and migration patterns show strong interannual variability, which seem to be highly dependent on cohort sizes of the different stock components and drift properties of ocean currents around Greenland and Iceland. There is little indication for systematic and interannually repeating connectivity between spawning grounds in Greenland and Iceland waters. The stock collapsed in the early 1970s, which was driven by a combination of high fishing effort and low temperatures, which likely caused recruitment failure. After 1970, increasing fishing mortality in combination with growth and recruitment overfishing diminished the stock's reproductive potential, which has ever since not recovered.

2.1 Introduction

Atlantic cod (*Gadus morhua*) constituted historically the most important fishery resource in Greenland waters (Horsted, 2000). Cod total stock biomass (TSB) in Greenland waters has fluctuated between one million tons during a low-abundance period in the early 20th century and four million tons during a high-abundance period in the 1950s, before the stock collapsed in the 1960s (Bonanomi et al., 2015; Buch et al., 1994; Horsted, 2000; Hovgård and Wieland, 2008; Jensen and Hansen, 1931). These fluctuations supported the emergence and collapse of a large international fishery with annual landings up to 450.000 tons (Figure 1) (Horsted, 2000; ICES, 2017). Historic and current commercial fishing on the offshore stock takes places on the banks of the Greenland shelf and along the slope in West and East Greenland (Figure 1). When the stock was thriving in the early and mid-part of the 20th century, more than 90 % of the total landings were taken in offshore areas in West and Southwest Greenland and only small proportions in the East (Figure 1) (Horsted, 2000). The European long-distance fishing fleets of Germany, Portugal, France, Norway and the Faroe Islands took historically largest parts of these offshore landings (Horsted, 2000). Domestic, Greenland fishing was restricted to fjords and coastal areas until four larger and more mobile long-liners, which could reach the offshore areas, were built in 1966 (Horsted, 2000). In 1974, catch quotas were introduced but not enforced until 1977, when the 200 nautical mile EEZ was introduced. Before, the offshore area was considered an unregulated open-access fishery (Horsted, 2000). The fact that most of the offshore landings were taken by non-Greenlandic vessels does not affect the biological perspective of the stock but it adds a socio-economic issue, because native Greenlandic residents barely benefitted from this productive and profitable fishery.

Until 2012, the cod populations in Greenland waters were treated as one stock, when separate stock assessments were for the first time conducted for the western inshore component and a combined western and eastern offshore component including the management subareas NAFO 1A-1E and ICES 14b (Figure 2) (ICES, 2012). In 2015, the offshore component was further divided into a western offshore (NAFO 1A-1E) and an eastern offshore stock (NAFO 1F & ICES 14b) (Figure 2) (ICES, 2015), meaning that ICES considers now three different stocks in Greenland waters. While eastern offshore and the Iceland offshore stocks are separated for management purposes, they belong genetically to the same population (Bonanomi et al., 2015; ICES, 2015; Therkildsen et al., 2013).

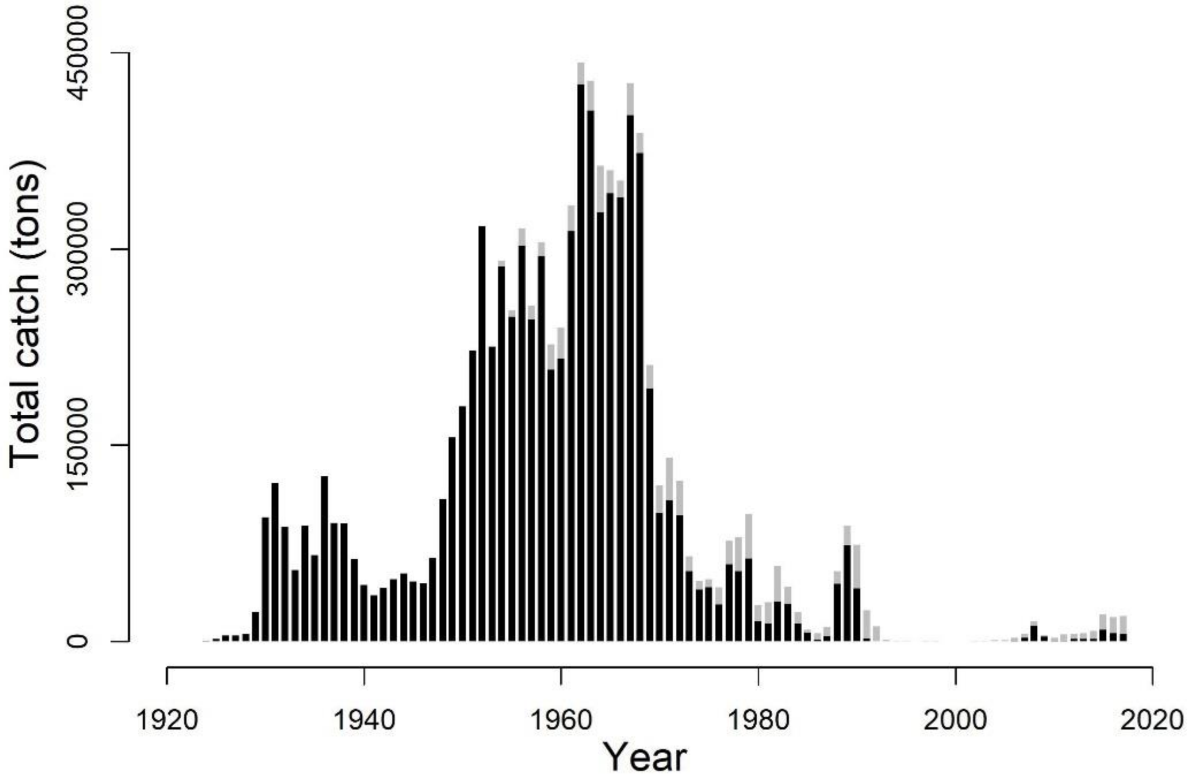

Figure 1 Total landings of Atlantic cod in Greenland waters from 1924-2017. Black bars represent catches of the West Greenland stock component (NAFO 1A-1F), grey bars represent catches of the East Greenland stock component (ICES 14b).

Despite the historic size of the stocks and their large importance for fishing fleets from many different nations, the existing literature clearly lacks a comprehensive review of population dynamics and historic drivers of abundance. Additionally, no analytical stock assessment for the combined East and West Greenland offshore stock has been conducted since 1992 and because historic input data are only available for the combined offshore stock, important data dating back to 1955 would be excluded from the stock and the fisheries analyses using separated East and West stocks. In order to carry out a stock synthesis of cod in Greenland waters, we conducted a review, which is split into two parts. The first part focuses on a summary of the existing literature on population dynamics including egg and larval drift and migrations. The second part contains stock assessment from 1955-2015 of the combined West and East Greenland offshore stock using updated data for the period 1993-2015, which we will use to illustrate historic trends of abundance. At the end, the results from the review and our new stock assessment time series will be used to investigate historic drivers of population structure and abundance with special emphasize on the impact from the fisheries on abundance of cod.

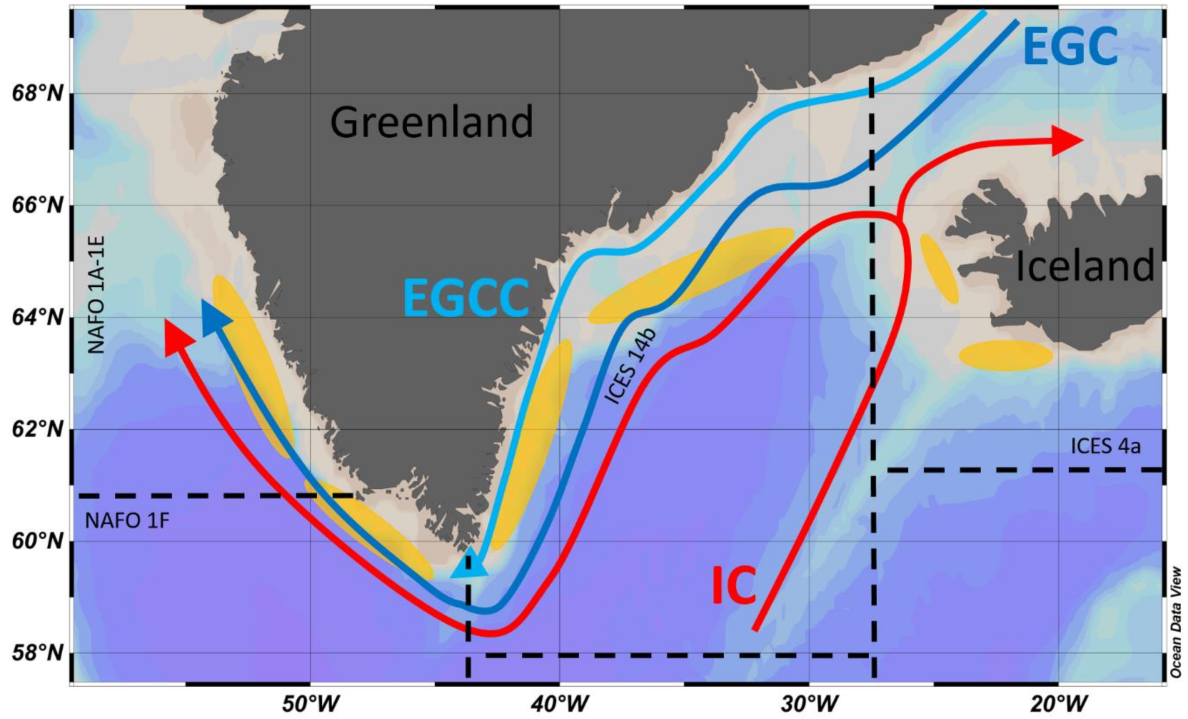

Figure 2 Schematic of major ocean currents, spawning grounds and relevant stock management units for Atlantic cod around Greenland and Iceland. Lines and arrows show directions of the Irminger current (IC), East Greenland current (EGC) and East Greenland coastal current (EGCC). Orange areas show locations of spawning grounds, dotted lines show borders of different stock management units. The map was done using ocean data view (Schlitzer, 2018).

2.2 Material and methods

Population dynamics

In order to review and summarize available information on egg and larval drift, migrations and historical abundance, we used google scholar to conduct a keyword search using different combinations containing the following character strings: “Gadus morhua”, “Greenland”, “Recruitment”, “Eggs”, “Larvae”, “Migration”, “Drift”, “Abundance”, “Fishery”, “Dynamics” and “Iceland”. The titles were screened for publications focusing on abundance and population dynamics of cod around Greenland and Iceland. Suitable references were chosen for review and afterwards screened for topic-related references not available through the google scholar search. These references were found to be mainly research and survey reports covering the ecosystems around Greenland and Iceland, which were only available through the ICES online library (http://ices.dk/publications/library/Pages/default.aspx) or per demand through the ICES librarians.

Stock assessment

In order to illustrate historic developments of abundance, recruitment and fishing mortality, we reconstructed the Greenland cod stock applying the age-based model extended survivor analysis (XSA) (Darby and Flatman, 1994). In order to make use of the historic data and to avoid significant assessment uncertainty caused by variable migration, we combined both stocks off West and East Greenland as it was formulated in the past and maintains the important historical perspectives in our assessment. The XSA was set to default settings, in order to make it consistent with the historical assessment (ICES, 1996). It is believed that discards in Greenland cod fisheries are negligible.

Age-based input data for XSA were derived from two data sources: i) annual commercial catch-at-age data in numbers for the period 1955 – 1992 (ICES, 1996), and ii) abundance indices and biological data from the annual German offshore bottom trawl survey in Greenland for the period 1982 – 2015 (Fock, 2007). Commercial landings have been low during the past three decades and biological monitoring of commercial catches has been scarce, hence, no representative catch-at-age information is available for recent periods. In order to replace the missing catch-at-age data for the period 1993-2015, catch and biological data from the survey were used. The German bottom trawl survey, which is in detail described in (Fock, 2007; Rätz, 1999), covers shelf areas and areas along the slope in East and West Greenland and is primarily designed for the monitoring of cod (Rätz, 1999).

During the whole procedure, we thus assumed that survey catches were representative in terms of length frequencies, length-at-age and weight-at-age for the whole stock, respectively commercial catches. In order to scale total reported landings to an age-based catch matrix, we calculated stratified length frequency distributions from the survey catches for every year, summarized for each 3 cm length class. This length-based survey index was extrapolated to the total survey area, by which we calculated the total number of fish per 3 cm length class being residential in the survey area and potentially subject to commercial fishing. Small fish, which would not have been caught by a commercial net, were removed from the survey abundance index, by taking selectivity parameters l_{50} and sr estimated for a 135 mm mesh size codend of a cod bottom trawl (Kvamme and Isaksen, 2004) and Eq. (1), where p_r is the retention probability, l_{50} the length at a retention probability of 50 %, l the fish length and sr the selection range to calculate retention probability of an individual fish in a 135 mm codend (Bethke, 2004).

$$p_r = (1+{}^{9(l_{50}-l)/sr})^{-1} \qquad (1)$$

Retention probabilities per 3 cm length class were multiplied with frequencies of the corresponding length classes of the abundance index, by which we obtained the number of fish in every length class retained in a commercial catch for each year. An age-length key for every 3 cm length class was calculated by taking all available individuals with age and length information and calculating a probability of every single cm class to be composed of the corresponding ages. As last step, we multiplied total number per age class per year with the corresponding individual mean weight at age to get a potential total catch weight per year and age class and by adding all ages together for the whole stock. This total surveys catch weight was divided by the officially reported offshore landings (ICES, 2017) to determine each year's real catch rate. Finally, this rate was multiplied with total catch weights of every age class to create a catch-at-age matrix.

XSA was tuned with an age-based abundance index derived from survey catch data. This abundance index is based on survey catches in numbers at age for each for year per trawled area (nm²) and raised to the total area surveyed. Natural mortality (M) was set to 0.2 for ages classes 3 and 4, and 0.3 for age classes 5-11+. The higher M for older age-classes accounts for the emigration of a part of the stock to Iceland (ICES, 1996; Schopka, 1994, 1993). Maturity ogives for the period 1955 – 1992 were taken from (ICES, 1996) and annual means of this period were considered representative for years 1993-2015 as well.

2.3 Results

Drift patterns of eggs and larvae

Spawning in Greenland waters takes place between March and early June on the shelf, along the slope and in coastal and fjord areas in East and West Greenland (Figure 2) (Hansen, 1949; ICES, 2017; Jensen, 1926; Wieland and Hovgård, 2002). The warm and high saline Atlantic Irminger current and the cold, low saline Arctic East Greenland and East Greenland coastal currents are the major determinants of oceanographic patterns around Greenland (Figure 2) (Sutherland and Pickart, 2008). Ocean currents carry eggs and larvae westwards from Greenland and Iceland spawning grounds to Southwest and West Greenland (Begg and Marteinsdottir, 2000; Bonanomi et al., 2015; Jensen, 1926; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984; Wieland and Hovgård, 2002). These spawning and drift patterns lead to a spatial overlap of four genetically different stocks in Greenland waters: 1.

Iceland inshore, 2. Iceland and East Greenland offshore, 3. West Greenland offshore and 4. West Greenland inshore (Bonanomi et al., 2015; Therkildsen et al., 2013).

Because the Greenland and Iceland stocks are separated for management purposes but cod individuals from different spawning stocks mix in Greenland waters, intensive discussion arose whether year classes appearing in Greenland waters were of Iceland or Greenland origin (Hovgård and Wieland, 2008; ICES, 2018; Wieland and Hovgård, 2002). Stock origin and drift patterns of eggs and larvae of cod around Greenland and Iceland can be derived using the distribution of eggs and larvae from ichthyoplankton surveys, the distribution of juveniles from commercial catches and trawl surveys and by genetic assignment of individuals to the different populations (Begg and Marteinsdottir, 2000; Bonanomi et al., 2016, 2015; Therkildsen et al., 2013; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984; Wieland and Hovgård, 2002). Ichthyoplankton surveys were carried out from the 1950s-1980s and targeted the distribution of eggs and larvae in Greenland waters (Begg and Marteinsdottir, 2000; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984; Wieland and Hovgård, 2002). The distribution of juveniles from trawl surveys and fisheries catches can be used to identify stock origin, because individuals from eastern areas are generally more southerly distributed than year classes from West Greenland (Bonanomi et al., 2015; ICES, 1976; Therkildsen et al., 2013). When strong cohorts are mainly distributed in Southwest Greenland (NAFO 1F & 1E), they likely drifted as eggs and larvae from the Iceland inshore or the Iceland & East Greenland offshore stocks and settled in Southwest Greenland (Bonanomi et al., 2015; ICES, 1976; Therkildsen et al., 2013). Over the past 60 years, the year classes of 1961, 1973, 1984 and 1985 drifted in high amounts as eggs and larvae from Iceland spawning grounds to East and West Greenland (Begg and Marteinsdottir, 2000; Hovgård and Wieland, 2008; ICES, 1976; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984; Wieland and Hovgård, 2002). In most recent years, influx from Iceland was considerably high in 2003, although ever since the large influx events in 1984 and 1985, no cohort has drifted again in such high numbers from Iceland to Greenland waters (Begg and Marteinsdottir, 2000; ICES, 2018; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984; Wieland and Hovgård, 2002). As investigated with drift and modelling experiments, the probability for eggs and larvae to drift from Iceland spawning grounds to Greenland is generally low (Brickman et al., 2007; Schmidt, 1931a) and restricted to discrete influx events. Difficulties to determine the stock origin of particular year classes intensify, because the East Greenland offshore and Iceland offshore stocks belong to one genetic unit and while spawning regularly takes place in Iceland waters, the contribution of the East Greenland spawning assemblages to a self-sustaining East Greenland stock remains difficult to estimate. Influx events from Iceland appear to be of much larger importance for the East Greenland component than production of juveniles from the East Greenland stock itself (ICES, 2018).

Larvae from the inshore spawning grounds in Iceland rarely drift to Greenland waters and account for the quantitatively smallest contribution of all four populations to the Greenland stocks (Bonanomi et al., 2015; Therkildsen et al., 2013). As the close proximity to cod stocks in North America suggests a similarly strong connectivity between stocks in West Greenland and Canada, both morphometric and genetic studies have shown that exchange between these areas is negligible and much weaker pronounced than the connection to Iceland (Schmidt, 1930; Therkildsen et al., 2013).

To conclude, major drift events of eggs and larvae from Iceland to Greenland waters are infrequent, temporally highly variable events but which have the potential to periodically support recruitment in Greenland cod stocks (Begg and Marteinsdottir, 2000; Hansen, 1949; Tåning, 1937; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984). The spatial overlap in Greenland waters between all four stocks, West Greenland inshore, West Greenland offshore, East Greenland/Iceland offshore and Iceland inshore is large, but relative contributions of the different stocks are highly variable over time and space, which seems to depend on interannual variation of year class strengths of the different stocks and current properties, which carry eggs and larvae to West Greenland (Begg and Marteinsdottir, 2000; Bonanomi et al., 2015; Hovgård and Wieland, 2008; ICES, 1976; Schopka, 1993; Shepherd and Pope, 1993; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984).

Recruitment and migration of adults

Because ocean currents carry eggs and larvae from all spawning grounds in Iceland and East Greenland to Southwest and West Greenland (Figure 2) (Bonanomi et al., 2016, 2015; Hansen, 1949; Hovgård and Wieland, 2008), the large majority of all juvenile cod in Greenland waters, independent of stock origin, can be found west of Cape Farewell, the southern tip of Greenland. Migration routes have historically been investigated using tags and their reported recaptures from commercial fishing vessels. Over the past 100 years, the vast majority of cod tagged in Greenland waters was tagged in Southwest and West Greenland and only few specimens were tagged in East Greenland, of which almost all were recovered either in East Greenland or Iceland, emphasizing the pronounced stock connectivity between these areas (Hansen, 1949; ICES, 2018, 1976). For cod tagged West of Cape Farewell (Hansen, 1949; Hovgård and Christensen, 1990; Hovgård and Wieland, 2008; ICES, 2018; Schmidt, 1931b; Storr-Paulsen et al., 2004; Tåning, 1937) four main patterns can be identified: i) a high proportion of stationary fish without signs of migratory behaviour, ii) a higher proportion of migration to Iceland from Southwest Greenland, than from more northern parts of West Greenland, iii) higher migration from the offshore banks than from inshore fjord areas and iiii) migration to East Greenland and Iceland increases with age.

Despite of the general pattern that a high proportion of individuals was stationary, migration to Iceland was considerably large for certain years and areas. For example, more than 70 % of all individuals tagged in Southwest Greenland were in some years recaptured in Iceland, whereas in other years, migration to Iceland was negligible (Hansen, 1949; Schopka, 1993; Shepherd and Pope, 1993). This migration to East Greenland and Iceland mainly concerns individuals from the mixed East Greenland offshore & Iceland offshore and Iceland inshore stocks, which grow in Southwest and West Greenland, where they recruit to the fishery and migrate back to East Greenland and Iceland when maturity is reached (Bonanomi et al., 2016; Hansen, 1949; Hovgård and Christensen, 1990; ICES, 2018, 1976; Jensen and Hansen, 1931; Schopka, 1994, 1993; Storr-Paulsen et al., 2004; Tåning, 1937; Therkildsen et al., 2013; Wieland and Hovgård, 2002). This slow migration takes years and because it is not an annually repeating spawning migration with returns to Greenland, the eastbound movement should rather be considered as stepwise displacement of ageing fish (Hovgård and Wieland, 2008; ICES, 2017). This pattern is manifested in an age stratification around Greenland, with generally older and larger fish further eastwards (Hovgård and Wieland, 2008; ICES, 2017). As spawning also occurs in East and Southeast Greenland (Wieland and Hovgård, 2002), there is potential for juveniles to settle and recruit in eastern areas but it appears that the majority of juveniles drift to Southwest and West Greenland and do not recruit in East Greenland (Bonanomi et al., 2015; Hovgård and Wieland, 2008).

In rare cases, fish from spawning grounds in inshore and fjord areas in West Greenland move offshore and support the West Greenland offshore stock (Bonanomi et al., 2015; Hansen, 1949). However, in general, the contribution of inshore-born cod to offshore areas is low, because they are mainly sedentary (Storr-Paulsen et al., 2004).

Migration to East Greenland and Iceland shows a similarly high interannual variability as drift of eggs and larvae from East Greenland and Iceland to West Greenland (Hansen, 1949; Hovgård and Christensen, 1990; ICES, 2018; Schmidt, 1931b; Storr-Paulsen et al., 2004; Tåning, 1937). Especially in the early and mid-part of the 20th century, when the cod stock in West Greenland emerged and abundance was high, high percentages of fish migrated from West Greenland to Iceland (Hansen, 1949; ICES, 1976; Tåning, 1937), what has in the mid-part of the 20th century also been described as "*the great spawning migration of the cod to Iceland, a phenomenon of the greatest importance for the Greenland fishery…*" (Hansen, 1949). During the second half of the 20th century, migration was strongly reduced with a low and constant movement as well as infrequent and less pronounced migratory events, like the migrations of the 1973 and 1984 year classes (Schopka, 1993; Shepherd and Pope, 1993; Storr-Paulsen et al., 2004). Quantifying an accurate difference between stationary and migratory fish from mark-recapture experiments is notoriously difficult, because tagged individuals are recaptured by commercial fishing vessels and fishing effort is often variable between areas and years, what impacts recapture probabilities (Tåning, 1937). An increased proportion of migration to Iceland in relation to stationary fish in West Greenland from 2003-2016 (ICES, 2018) has likely been caused by little to absent fishing effort in West Greenland and the fact that tagging in West Greenland began further South (NAFO 1F), from where fish have a higher probability of being recaptured in Iceland, than from more Northern areas (NAFO 1A-1E).

Considering the different migration patterns and interannual variabilities, the question arises, what triggers the migration to East Greenland and Iceland. One hypothesis is that migrations are to a large degree triggered by natal homing. This hypothesis has recently found strong evidence through genetic investigations (Bonanomi et al., 2016), which showed that more than 95 % of fish which were tagged in West Greenland and recaptured in Iceland originated from the Iceland offshore spawning stock. Historic drift and migration patterns support this hypothesis further, because migration to Iceland was often documented for cohorts, which drifted in unusually large numbers as larvae to Greenland, such as the year classes of 1961, 1973 and 1984 (ICES, 1976; Schopka, 1993; Shepherd and Pope, 1993; Vilhjálmsson and Fridgeirsson, 1976; Vilhjálmsson and Magnússon, 1984; Wieland and Hovgård, 2002). Observations that cohorts originating from Iceland and East Greenland are mainly distributed in Southwest Greenland waters, from where the highest proportions of migrations to Iceland were observed, further indicate natal homing (Bonanomi et al., 2015; Hansen, 1949; ICES, 1976; Storr-Paulsen et al., 2004). However, old and new data contain signals that not all cod which migrated to Iceland were of Iceland origin (Hansen, 1949; Jensen and Hansen, 1931; Schopka, 1993; Shepherd and Pope, 1993). For example, in the 1950s, when the Greenland cod stock was a highest levels, the year classes of 1950 and 1953, which likely originated from West Greenland, were observed immigrating to Iceland waters (ICES, 1976; Schopka, 1993). This suggests that density dependent factors may have contributed to increased migratory behaviour, when the offshore stock in Greenland throve. Despite the fact that homing behaviour is a strong driver for these migrations, the less pronounced annual constant movement of adult fish to Iceland appears to be a part of regular movements of the mixed offshore East Greenland and offshore Iceland cod stocks, which belong genetically to the same population (ICES, 2018; Schopka, 1993; Shepherd and Pope, 1993; Therkildsen et al., 2013).

Stock assessment

Fishing mortality was with values around 0.3 on comparably low levels between 1955 and 1960 and increased slowly towards a first temporal peak around 1975 (Figure 3, Table 1). After another increase in the early 1980s, followed by low levels in the late 1980s, fishing mortality reached its maximum with rates above 2 in 1992. Ever since that peak, fishing mortality fluctuated around an average of 0.3. Spawning stock biomass (SSB) peaked with levels close to two million tons in 1955, the first year of the assessment. A steady decline of SSB between 1955 and the early 1970s was followed by a collapse around 1975. SSB has ever since not shown considerable trends of increase. Although the year classes of 1973 and 1984 facilitated short increases in stock size, the stock vanished in the early 1990s, when SSB corresponded to less than 0.1 % of its historic maximum size. Recruitment showed highest average values from 1955-1970, when SSB was at highest levels. After 1970, recruitment has been negligible with a few sporadically occurring stronger year classes, as the ones from 1973 and 1984. Over the past 10 years, the stock has started to recover but is in size not comparable to historic levels.

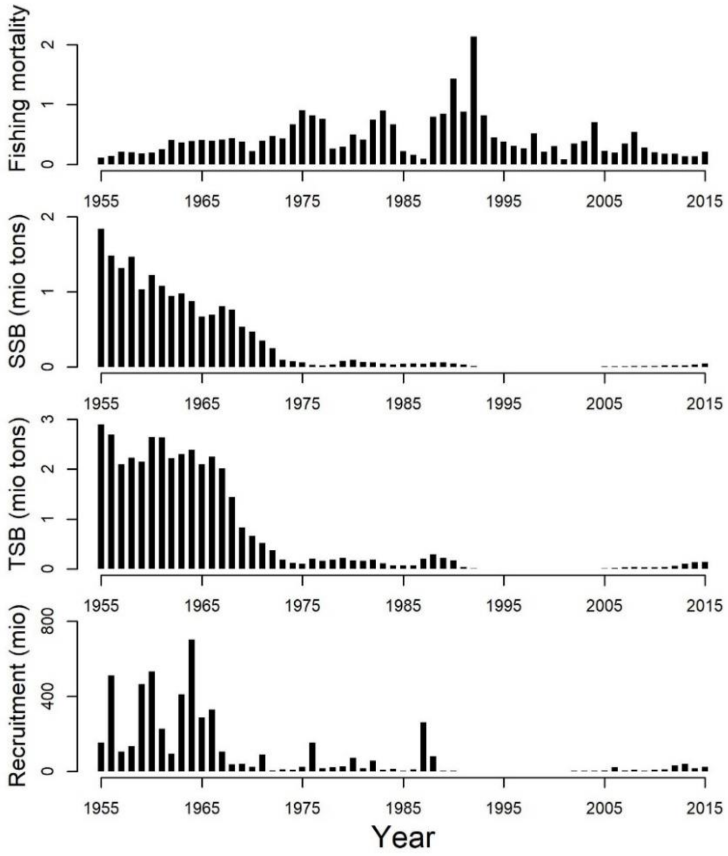

Figure 3 Fishing mortality, spawning stock biomass (SSB), total stock biomass (TSB) and recruitment at age 3 for the offshore stock of Atlantic cod in Greenland waters for the period 1955-2015 as estimated by extended survivor analysis (XSA). Fishing mortality as mean fishing mortality for ages 5-8.

Table 1 Stock assessment time series as calculated with extended survivor analysis (XSA) for the offshore stock of Atlantic cod in Greenland waters. Fbar = Mean fishing mortality of age classes 5-8. Recruitment is presented in thousand individuals, total stock biomass and spawning stock biomass in tons.

Year	Recruitment (age 3)	Total stock biomass	Spawning stock biomass	Fbar 5-8
1955	153802	2891904	1835483	0.109
1956	511983	2693441	1478576	0.149
1957	104904	2097026	1316870	0.210
1958	134529	2223973	1467708	0.202
1959	463649	2140837	1035650	0.189
1960	531662	2640090	1224436	0.194
1961	226870	2632533	1077353	0.257
1962	93567	2213164	944307	0.404
1963	409559	2299338	975549	0.369
1964	703359	2391432	875179	0.387
1965	286690	2096278	669360	0.412
1966	329963	2240044	695173	0.403
1967	105573	2009033	807464	0.414
1968	37493	1438284	764388	0.440
1969	39073	832841	532539	0.379
1970	22749	661186	472018	0.219
1971	87981	516070	350699	0.398

1972	4193	373266	245998	0.473
1973	9182	186617	90031	0.431
1974	6197	119335	74053	0.670
1975	24612	108300	56561	0.906
1976	154648	203580	27579	0.821
1977	16628	167155	16904	0.764
1978	20221	185002	34938	0.267
1979	26789	224506	78451	0.293
1980	73533	176285	92705	0.501
1981	14247	163094	66448	0.413
1982	56733	180250	60225	0.744
1983	7696	116546	44222	0.895
1984	13741	74945	31513	0.672
1985	1978	75749	41150	0.222
1986	10835	69795	44192	0.159
1987	262860	209706	38050	0.099
1988	79937	295667	62079	0.797
1989	1216	222744	62162	0.845
1990	1443	176441	47070	1.432
1991	530	46561	29349	0.884
1992	237	15881	12666	2.135
1993	384	1658	915	0.821
1994	248	1782	785	0.450
1995	272	1329	590	0.378
1996	235	1285	430	0.315
1997	123	1589	546	0.274
1998	195	1295	556	0.519
1999	352	1059	491	0.212
2000	464	978	398	0.306
2001	667	2077	506	0.088
2002	1104	2924	685	0.350
2003	1542	4291	960	0.390
2004	1960	5495	1206	0.700
2005	3890	12709	2545	0.227
2006	20230	24615	4137	0.196
2007	5416	32842	6305	0.352
2008	7189	43030	11792	0.542
2009	3211	29603	10807	0.280
2010	6414	29449	13058	0.207
2011	10773	40537	16947	0.176
2012	33036	62958	18502	0.180
2013	40056	101635	21230	0.136
2014	16895	135198	31930	0.141
2015	24060	143220	45357	0.209

2.4 Discussion

Top down vs. bottom up control of the stock

The discussion of top-down vs bottom-up control on fish stocks has been an ongoing debate for many decades, especially since the famous “Thompson-Burkenroad” debate crystallized this question (Skud, 1975). We dedicate our discussion to the issue, if environmental drivers or fishing caused historic abundance fluctuations and how this has changed over time. While detailed information and interpretation is available on the environmental aspects of the collapse of the Greenland cod stock during the late 1960s and early 1970s (Bonanomi et al., 2015; Buch et al., 2003; Rätz and Lloret, 2005), the importance of fishing for the demise of the stock especially during recent decades is poorly explored and will be discussed in light of our new assessment time series.

Both emergence and collapse of the offshore cod stock in Greenland waters coincided with temperature changes. While the steep increase of abundance from the 1920s – 1950s was driven by a regime shift caused by rising temperatures in the North Atlantic, the stock collapse in the late 1960s and 1970s was supported by steep declines in sea surface temperatures (Buch et al., 2003; Drinkwater, 2006; Hovgård and Wieland, 2008; Stein, 2007). The increase of SSB by more than 2 million tons from 1935-1950 (Buch et al., 1994) shows that the cod stock in Greenland waters has the capability for fast recovery under favourable environmental conditions. During the stock collapse in the late 1960s, dropping temperatures caused low abundance of copepod species *Calanus finmarchicus* and *Calanus hyperboreus* in West Greenland (Pedersen and Smidt, 2000), what likely had a detrimental impact on recruitment (Buch et al., 2003; Hansen and Buch, 1986; Pedersen and Smidt, 2000; Rätz and Lloret, 2005). These sudden environmental changes in Greenland waters in the late 1960s were linked to the "Great Salinity Anomaly", a high inflow of Artic water with the East Greenland current (Dickson et al., 1988). Drawing direct connections between these oceanographic phenomena and ecological consequences has, however, been difficult (Dickson et al., 1988; Pedersen and Rice, 2002). In the 1970s, detrimental impacts of dropping temperatures on stock productivity were magnified by increasing fishing mortalities in an international open access fishery and a combination of both factors caused the collapse of the spawning stock (Bonanomi et al., 2015; Hovgård and Wieland, 2008; Lilly et al., 2008; Pedersen and Rice, 2002). During this period, not only the direct removal of mature fish but also indirect effects through age truncation with a reduced number of old fish (Hovgård and Wieland, 2008; Rätz, 1996) can have had a negative impact and might have harmed the reproductive potential of the spawning stock (Hixon et al., 2014; Longhurst, 2002; Ottersen et al., 2006; Wright and Gibb, 2005).

After the decline of the stock and commercial fishing in the early 1970s, the strong year classes of 1984 and 1985 facilitated a boom-and-bust fishery on largely immature individuals between 1988 and 1991, which harmed the stock's long-term reproductive potential (Horsted, 2000;

ICES, 1996; Rätz and Lloret, 2005). Exploitation of these year classes as pre-mature and just-maturing individuals is well documented in form of low mean ages in commercial landings in the late 1980s (ICES, 1996; Rätz, 1996). Additionally, these immature year classes were caught as unwanted bycatch in the Greenland shrimp fishery and discarded at unknown volumes. Such mortality of juveniles likely magnified the impacts of the commercial target fishery (Pedersen and Kanneworff, 1995). Removing fish before recruiting to the spawning stock, known as growth overfishing, has led to a minimum stock size in the mid-1990s of ~ 500-1000 tons, corresponding to < 0.1 % of the stock's historic maximum size. These low SSB values have not been capable of producing above average year-classes ever since, what is a phenomenon generally known as depensation or Allee effect (Hilborn and Walters, 2013; Hutchings, 2014). The vulnerability of the stock to high fishing mortalities becomes even more pronounced, considering that the year classes of 1973, 1984 and 2003, which represented the strongest year classes after the collapse of the stock in the 1970s, originated from Iceland. Our analysis confirms this perspective and demonstrates that when the stock shrinks below a particular level, potentially due to high fishing pressure, it might take many decades for it to recover (Rowe and Rose, 2017). Although the stock has ever since its historic collapse not recovered or shown signs of the potential for a self-sustaining fishery, Greenlandic management has continued to ignore scientific advice and frequently set TAC quotas above scientifically recommended levels in the past decade (ICES, 2017).

While our analysis shows a long-term negative effect of fishing, migration of large amounts of fish to Iceland likely magnified negative trends of cod abundance in Greenland waters (Schopka, 1993; Shepherd and Pope, 1993). The year classes 1984 and 1985, which were strongly supported by influx from Iceland, drove the boom and bust fishery around 1990. It remains speculative, if individuals of these year classes would have migrated to Iceland as mature individuals anyways, even if they had not been fished beforehand. The evidence for a periodic large degree of homing and historic spawning migration to Iceland is certainly prevalent (Bonanomi et al., 2016; Hansen, 1949; Schopka, 1994; Shepherd and Pope, 1993), but existing information does not allow a quantification of this migration and the contribution of spawning grounds in East Greenland as source for recruits remains unsolved (Bonanomi et al., 2016, 2015; Hansen, 1949; Schopka, 1994; Shepherd and Pope, 1993; Storr-Paulsen et al., 2004; Wieland and Hovgård, 2002). Genetic analyses show that a small proportion of recruits in the late 1980s originated from offshore and inshore areas in West Greenland (Bonanomi et al., 2015) and would likely have not been a part of the homing migration to Iceland. Hence, these individuals could have supported a stock rebuilding process in Greenland waters if they had not been caught. Because the largest year classes in recent decades were strongly supported by influx from Iceland, it seems that the Greenlandic component of the stock was already harmed by the early 1970s and because of high fishing mortalities never received the opportunity to recover.

The collapses of cod stocks in their northern ranges of distribution highlight the need to consider its biology when evaluating long-term sustainable commercial fishing yields. Cod in particular has a large reproductive potential with high fecundity, enabling it to produce large cohorts in years with beneficial growth conditions, survival and drift properties for eggs and larvae. The cod’s high fecundity is likely the species’ adaptation to survival in areas with harsh and often disruptive environments, such as at West Greenland and East Canada (Longhurst, 1998). Longhurst, 1998, suggests that cannibalism may be for cod a necessary adaptation for the maintenance of large individuals and a large reproduction potential in the population in fluctuating environmental conditions. Additionally, removal of old, experienced and very fecund fish might have supported recruitment failure and more effort should be invested to test this hypothesis empirically (Barneche et al., 2018; Longhurst, 2002; Ottersen et al., 2006). While temperature driven ecosystem changes currently happen, a rise of the cod stock in Greenland waters has not occurred. This indicates that the historic impacts of commercial fishing and the current quotas, which exceed scientific advice especially in West Greenland (ICES, 2017), harm the stock and prevent rebuilding. That underlines an apparent difference between the Greenlandic offshore cod stock and other cod stocks from the North Atlantic, such as the ones from the Barents Sea or Iceland, which had also declined in abundance but later recovered (ICES, 2017, 2016). Especially the Barents Sea cod stock, which also inhabits a subarctic environment, shows how increasing temperatures can benefit the productivity of high-latitude cod stocks (Kjesbu et al., 2014), from which the Greenland cod stock apparently could have benefitted under historically lower fishing pressure.

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3 Publication 2

Non-linearity in stock-recruitment relationships of Atlantic cod: insights from a multi-model approach

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Abstract

The stock-recruitment relationship is the basis of any stock prediction and thus fundamental for fisheries management. Traditional parametric stock-recruitment models often poorly fit empirical data, nevertheless they are still the rule in fish stock assessment procedures. We here apply a multi-model approach to predict recruitment of 20 Atlantic cod (*Gadus morhua*) stocks as a function of adult biomass and environmental variables. We compare the traditional Ricker model with two non-parametric approaches; (i) the Stochastic cusp model from catastrophe theory and (ii) Multivariate Simplex Projections, based on attractor state-space reconstruction. We show that the performance of each model is contingent on the historical dynamics of individual stocks, and that stocks which experienced abrupt and state-dependent dynamics are best modelled using non-parametric approaches. These dynamics are pervasive in western stocks highlighting a geographical distinction between cod stocks which has implications for their recovery potential. Furthermore, the addition of environmental variables always improved the models´ predictive power indicating that they should be considered in stock assessment and management routines. Using our multi-model approach, we demonstrate that we should be more flexible when modelling recruitment and tailor our approaches to the dynamical properties of each individual stock.

3.1 Introduction

Forecasting complex trajectories of marine resources is essential for fishery management and one of the major challenges of our time (Schindler and Hilborn, 2015; Ye *et al.*, 2015). An important factor to be considered in fisheries management is the stock-recruitment relationship (SRR), which serves as a basis for any stock assessment procedure to ultimately calculate reference points (Hilborn, 2002; ICES, 2017, 2018). SRRs are based on the assumption that recruitment (the number of fishes that enter the adult population) is directly related to adult stock size (Kraus *et al.*, 2000; Jennings *et al.*, 2001). Parametric approaches, such as the Ricker model, were developed around the 1950s (Ricker, 1954) and in some cases still represent the method of choice in stock assessments (ICES, 2017). These models are very specific in the type of functional response curve to describe the SRR, and are linear, in the sense that, the relationship between recruitment and biomass can be linearized through log-transformation (Ye *et al.*, 2015). However, they often fail to capture the high variability in recruitment data and this has led to questioning the existence of the relationship itself (Szuwalski *et al.*, 2015; Britten *et al.*, 2016; Perlala *et al.*, 2017). The fit of the SRR is sometimes so poor, that short-term predictions of spawning stock biomass are conducted using an average of recruitment over a particular number of years, instead of a SRR model (Deyle *et al.*, 2018). Both approaches, using average recruitment or a parametric model, assume that natural systems behave in a linear way, which may lead to biased fisheries management decisions when stocks show complex dynamics such as aperiodic chaos, non-linearity or non-stationarity (Ye and Sugihara, 2016; Perlala *et al.*, 2017; Deyle *et al.*, 2018).

Chaos and non-stationary dynamics are pervasive in natural systems and characterize many marine ecosystems and populations (May and Oster, 1976; Scheffer *et al.*, 2001; Möllmann *et al.*, 2015). These dynamics emerge from the inherent complexity of nature, governed by a multitude of factors (Ye *et al.*, 2015; Deyle *et al.*, 2016; Tu *et al.*, 2018). Assuming linearity and stability in recruitment models can, thus, result in wrong stock predictions (Glaser *et al.*, 2014; Ye *et al.*, 2015). As a consequence, new non-parametric modelling frameworks were developed to predict stock trajectories accounting for state-dependent and chaotic behaviour, such as the Empirical Dynamic Modelling (EDM) framework (Sugihara *et al.*, 2012; Ye *et al.*, 2015; Deyle *et al.*, 2018). EDM is a minimal assumptive approach based on time series observations, which reconstructs the temporal dynamics of a system by constructing a so-called attractor manifold (Sugihara *et al.*, 2012; Ye *et al.*, 2015). EDM is able to predict the future system trajectory based on its past dynamics (Ye *et al.*, 2015; Deyle *et al.*, 2018), thus accounting for state-dependent dynamics (Sugihara, 1994). This approach, and in particular Multivariate Simplex Projection (MSP) has been applied to predict non-linear fish recruitment dynamics in a range of studies, and has also been applied directly to management, e.g. for the menhaden stocks along the East Coast of the USA (Perretti *et al.*, 2015; Ye *et al.*, 2015; Deyle *et al.*, 2018).

Another non-parametric approach suitable for modelling state-dependent and discontinuous recruitment dynamics is the Stochastic cusp model (SCM), which is based on catastrophe theory (Zeeman, 1976; Thom, 1977; Grasman *et al.*, 2009; Petraitis and Dudgeon, 2016; Sguotti *et al.*, 2019). Here, a state variable *z* (for instance recruitment), depends on two control variables *alpha* and *beta*. The model allows *z* to move from a state A (e.g. high recruitment) to a state B (e.g. low recruitment) following either a continuous or discontinuous path (Diks and Wang, 2016). SCM has been widely applied to economic and behavioural studies (van der Maas *et al.*, 2003; Diks and Wang, 2016), but to a lesser degree to marine ecological studies (Jones and Walters, 1976; Jones, 1977; Petraitis and Dudgeon, 2015; Sguotti *et al.*, 2019).

Another point often neglected in recruitment prediction is the effect of multiple external drivers and potential interactions such as predation, competition and environmental variables (Myers *et al.*, 1995; Brander, 2005; Ottersen *et al.*, 2006; Stiasny *et al.*, 2016). However, in multiple cases the relationship between recruitment and environment can be spurious, non-linear or non-stationary, and therefore is often not considered in stock assessments (Myers, 1998; Perlala *et al.*, 2017). Traditional stock-recruitment models, which often are parametric models, assuming fixed parameters, usually fail to correctly incorporate the environmental information, since they often just consider additive effects of SSB and climate variables. Instead, non-parametric models such as MSP and SCM, can model interactions between the different drivers (i.e. biomass and climate variables) and thus may be able to integrate the climate information correctly (Ye *et al.*, 2015; Deyle *et al.*, 2018; Sguotti *et al.*, 2019). This is important since for effectively predicting the status of living marine resources the integration of environmental variables is becoming crucial given the widespread impacts of climate change on ecosystems and marine resources such as commercially important fish (Britten *et al.*, 2016; Gaines *et al.*, 2018).

Atlantic cod (*Gadus morhua*) is an iconic species from ecological, cultural and economic points of view (Myers *et al.*, 1996). In recent decades, most North Atlantic cod stocks have collapsed, followed by prolonged periods of no recovery even after the application of strict management measures (e.g. fishing moratoria) (Myers *et al.*, 1996; Hutchings, 2000; Hutchings and Rangeley, 2011; Frank *et al.*, 2016; Sguotti *et al.*, 2019). This failed recovery of Atlantic cod stocks suggests the presence of discontinuous dynamics and hysteresis (Frank *et al.*, 2011; Steneck *et al.*, 2011; Sguotti *et al.*, 2019). Eastern and western Atlantic stocks differ in life history traits, exploitation trajectories and recovery potential (Pörtner *et al.*, 2008; Wang *et al.*, 2014; Frank *et al.*, 2016). Indeed, stocks in the West collapsed more abruptly compared to stocks in the East which on average show more gradual declines (Frank *et al.*, 2016). Cod recruitment is highly state-dependent, depending on the dimension of the stock and environment conditions. Recruitment is fundamental to Atlantic cod recovery (Myers and Barrowman, 1996; Brander, 2005) and influenced by climate change (Myers and Drinkwater, 1989; Planque *et al.*, 1999; Stige *et al.*, 2006; Pörtner *et al.*, 2008; Pershing *et al.*, 2015). We here used stock assessment data from 20 Atlantic cod stocks to i) investigate whether cod recruitment can be best described by the parametric Ricker model, by the non-parametric, “discontinuous” SCM, or by the non-parametric, state-dependent MSP approach, and ii) test whether the model's predictive power can be improved when including environmental variables. We show that the adoption of a multi-model approach should be considered when modelling stocks presenting different dynamics.

3.2 Materials and Methods

Data

We used recruitment (i.e. number of fish for a particular age and stock that recruit to the adult biomass in thousands, R) and spawning stock biomass (i.e. biomass of mature fish in tonnes, SSB) data derived from stock assessments of 20 Atlantic cod stocks (Fig. 1, Supplementary material Fig. S1). Data were provided by the International Council for the Exploration of the Sea (ICES), the National Oceanic and Atmospheric Administration of the USA (NOAA), the Northwest Atlantic Fisheries Organization (NAFO), the Department of Fisheries and Ocean in Canada (DFO) and by personal communication (Supplementary material, Tab. S1). Recent assessments for cod stocks in the Kattegat, the Western Baltic as well as the Norwegian coast have been conducted only for reduced periods. Therefore, we combined recent and older stock assessments after consistency checks of SSB and R time-series, by simply replacing the newer part of the time series of the older assessments with the newer time series assessment (see Supplementary material, Fig. S2).

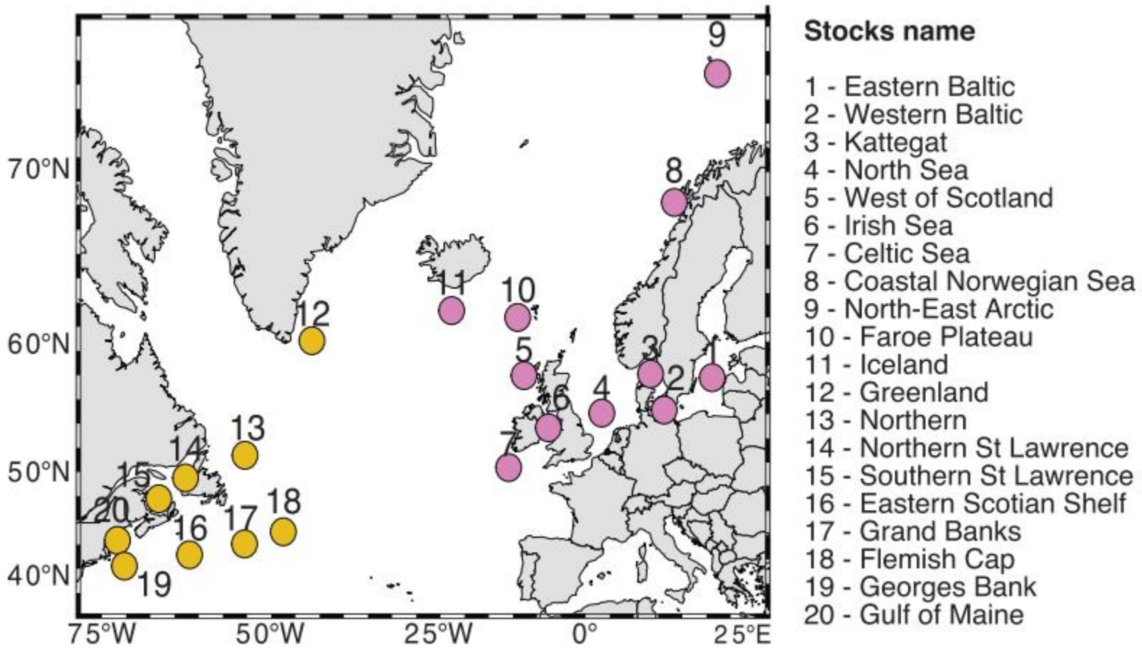


Figure 1 Map of cod stocks in the North Atlantic. Each circle corresponds to the centre of distribution of an Atlantic cod stock. The colour code corresponds to the division between western (orange) and eastern stocks (pink).

We selected sea surface temperature (SST) and the indices of the North-Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) as climate predictors in our models. SST data were collected from the NOAA Extended Reconstructed Sea Surface Temperature dataset (ERSST, www.ncdc.noaa.gov) version 4. The dataset represents a reconstruction of SST from 1854 to the present and comprises monthly anomalies computed with respect to the period 1971-2000, resolved in a 2°x 2° grid of spatial resolution. The data were averaged per year and per management unit. SST was chosen because of its importance for recruitment of Atlantic cod and is also a proxy for climate change at a local scale (Planque *et al.*, 1999). NAO and AMO were used as indices of climate variability at the supraregional scale. In particular NAO has been shown to highly correlate with Atlantic cod recruitment (Stige *et al.*, 2006), while AMO is a good proxy for climate change at longer time scales in this area. The NAO is a large scale, high frequency (7-25 years) climatic index depending on the different atmospheric pressure at sea level between Iceland and Azores. The AMO is instead a large-scale, low frequency (60 years) multi-decadal index representing climate-related SST changes in the Atlantic Ocean. The data for both indices were collected from the Earth System Research Laboratory of NOAA (www.esrl.noaa.gov), and the AMO was averaged to annual values, while the NAO was averaged annually but just between December and March.

Modelling strategy

We compared multiple stock-recruitment models, the traditional *Ricker* model, the *Stochastic Cusp Model* (SCM) and *Multivariate Simplex Projections* (MSP, from the Empirical Dynamic Modelling (EDM) framework). Recruitment models include either SSB alone or SSB in combination with one of the climate variables (i.e. SST, NAO and AMO) as predictors. Since recruitment can be influenced by climatic factors at different life-stages (i.e. eggs, larvae and juveniles), we applied multiple lags on the climate variables depending on recruitment age (Supplementary material, Tab. S1). We assessed the predictive power of the different models (three modelling approaches and explanatory variables and corresponding lags selection) on the test data using 5-fold cross validation, which randomly splits the time series in 5 parts, fitting the model on 4 (training data) and using the results to predict the last one (test data). In each of the five iterations, we compared the predicted with the observed test values using Pearson correlation coefficients (ρ) (Ye *et al.*, 2015; Deyle *et al.*, 2018). We repeated this procedure 100 times to increase the robustness and eventually used the median of the 500 values of ρ for model comparison (Fig.2).

The recruitment models

The *Ricker* Model fits a curve between recruitment and SSB depending on parameters *a* and *b* (Ricker, 1954). These parameters allow the curve to bend in the middle, so that at very high spawning stock biomass values recruitment will be low due to density dependent effects. However, this model is log-linear, i.e. the relationship between recruitment and biomass can be linearized through log-transformation, thus, we will refer to it as a linear model throughout the text. Climate effects can be added through a new parameter (*c*) (Fig.2c):

$$R_t = SSB_t \exp(a - b * SSB_{t-ageR}) \tag{1a}$$

$$R_t = SSB_t \exp(a - b * SSB_{t-ageR} + c * climate_{t-lags}) \tag{1b}$$

where *ageR* is the age at recruitment, and *lags* the offset between the effect of a *climate* variable and *R* depending on the age of recruitment (i.e. for each stocks the climate variables were lagged from R_t to R_{t-ageR} depending on the age at recruitment (Supplementary material, Tab. S1)).

The starting values for the parameters were estimated from the linearized version of the function using the *FSA* (Ogle, 2016) package (Eq.2):

$$\log(\frac{R_t}{SSB_t}) = SSB_t \exp(a - b * SSB_{t-ageR} + c * climate_{t-lags}) \tag{2}$$

Subsequently the Stock-Recruitment function was fitted to the data using a non-linear model with as response variable the log-transformed recruitment.

Stochastic Cusp Modelling (SCM) is based on the cusp**,** one of the seven canonical forms of catastrophe theory that describe sudden changes in a system due to small changes of external drivers (Thom, 1977; van der Maas *et al.*, 2003; Petraitis and Dudgeon, 2016; Sguotti *et al.*, 2019). The cusp model is based on a cubic differential equation (3) and describes discontinuous transitions in a state variable z_t, controlled by two control variables α and β, and thus can be used to describe discontinuous dynamics in recruitment (Fig.2a).

$$-V(z_t;\alpha,\beta) = -\frac{1}{4}z_t^4 + \frac{1}{2}\beta z_t^2 + \alpha z_t \tag{3}$$

where $V(z_t;\alpha,\beta)$ is a potential function representing the rate of change of the system (z_t), depending on the two control variables (α, β).

Since natural processes and empirical data often include stochasticity, Eq.3 was reformulated as a stochastic differential equation, adding the Wiener process ($\sigma_z \mathrm{d}W_t$) with variance σ^2:

$$-\frac{\partial \mathrm{V}(\mathrm{z};\alpha,\beta)}{\partial \mathrm{z}} = (-\mathrm{z}_t{}^3 + \beta z_t + \alpha)\mathrm{dt} + \sigma_z \mathrm{d}W_t = 0 \tag{4}$$

where the first part of the equation is the drift term, $\sigma_z$is the diffusion parameter and W_t represents the Wiener process.

The state variable, z_t, and the parameters, α and β (Eqs. 3,4) are estimated as a linear function of one or more exogenous variables using a likelihood approach (Eq.5a,b,c).

$$z = w_0 + w_1 y_1 + w_2 y_2 + \cdots w_y y_y \tag{5a}$$

$$\alpha = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 + \cdots \alpha_y x_y \tag{5b}$$

$$\beta = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots \beta_y x_y \tag{5c}$$

where α_0, β_0 and z_0 are the intercepts and α_1, β_1 and z_1 the slopes of the models.

In our study z_t, the state variable, is a linear function of recruitment. α is the so called asymmetry parameter and controls the size of z_t, thus in our study is a function of SSB. β is called the bifurcation parameter since it controls whether the state variable follows a continuous or discontinuous path (Petraitis and Dudgeon, 2015; Diks and Wang, 2016; Sguotti *et al.*, 2019), and in our study is a function of the environmental variables (climate, see below Eqs. 7a,b,c).

The system presents multiple equilibria if it follows a discontinuous path (i.e. two stable and one unstable) and just one if it follows a continuous path. The number of equilibria of the system depends on the solution of equation (4), from which the Cardan´s discriminant (δ) is derived:

$$\delta = 27\alpha^2 - 4\beta^3 \tag{6}$$

If $\delta > 0$, the system has one equilibrium, indicating a continuous path. Whereas if $\delta \leq 0$ the system has three equilibria, indicating a discontinuous path (Diks and Wang, 2016). Therefore, SCM allows the detection of interactive effects of the two control variables on the state variable. Any changes in the bifurcation parameter β, will lead to changes in the relationship between α and z_t and consequently dramatic changes of the state variable (Fig.2a, Supplementary material, Fig. S3).

The model is represented by:

$$zt = w_0 + w_1 R_t \tag{7a}$$

$$\alpha = \alpha_0 + \alpha_1 SSB_{t-ageR} \tag{7b}$$

$$\beta = \beta_0 + \beta_1 SSB_{t-ageR} \text{ or } \beta = \beta_0 + \beta_1 climate_{t-lags} \tag{7c}$$

In order to test the predictive power of the model, we first produced the linear predictors of the parameters and the state variable. These were then fit into the equation 8 to predict the new points on the surface.

$$V'(\hat{z}) = \alpha + \beta\hat{z} - \hat{z}^3 \ = 0 \tag{8}$$

Multivariate Simplex Projection is based on the EDM framework. The cornerstone of this framework is the Simplex projection method. The principle of EDM is to reconstruct the dynamics of one or multiple time series in a multidimensional space, i.e. an attractor manifold, and predict the future trajectory of the system based on these past dynamics (Fig.2a) (Sugihara *et al.*, 2012; Ye *et al.*, 2015; Chang *et al.*, 2017). Reconstructing the past dynamics of a system (in our case recruitment) is possible either using multiple variables (i.e. SSB or climate indices) or just time lags of the system itself (i.e. recruitment) (Sugihara *et al.*, 2012). We here used differentiated recruitment time series to build the attractor for each cod stock, and Simplex Projection (Eq.9-10) to approximate the attractor dynamics of the system (Sugihara *et al.*, 2012; Ye *et al.*, 2015; Deyle *et al.*, 2018). The time series is transformed in a set of time-delayed coordinate vectors:

$$x = \{x_t, x_{t-\tau}, x_{t-2\tau}, x_{t-3\tau}, \dots x_{t-(E-1)\tau}\}, \tag{9}$$

where *x* is the system, in our study recruitment, *t* is time, τ is the time lag and *E* the Embedding dimension. E represents the dimensionality of the attractor (Ye *et al.*, 2015). E is selected by predicting the attractor manifold one step ahead into the future (using leave-one-out cross validation) then comparing the predictive power of models with a varying E. In order to predict the system into the future, $\hat{x}_{t+1}$, Euclidean Distance is used and the system is predicted using nearest neighbourhood estimations

$$\hat{x}_{t+1} = \left(\sum_{i=1}^{E+1} w_{i,t}\, x_{i,t+1}\right) \Big/ \sum_{i=1}^{E+1} w_{i,t} \tag{10}$$

where w_i represents the weights (Eq. 11), which are the Euclidean distance to the neighbour vector *i* relative to the nearest neighbour $\bar{d}$.

$$w_i = \exp\left(-\frac{d(x_t, x_i)}{\bar{d}}\right). \tag{11}$$

Multivariate Simplex Projection (MSP) uses Eq. 9 but with multiple variables. In our study, the attractor reconstruction of recruitment was based on SSB alone or together with climate variables (climate) (Eq.12a,b):

$$R_t = \{SSB_{t-ageR}\} \tag{12a}$$

$$R_t = \{SSB_{t-ageR}, climate_{t-lags}\} \tag{12b}$$

Performing MSP requires two preliminary tests, the S-Map and the Convergent Cross Mapping (CCM), to unravel recruitment dynamics and the relationship between recruitment and explanatory variables, respectively.

EDM-specific preliminary tests S-Map & CCM

The S-Map, was performed after the attractor reconstruction with Simplex Projection. This test includes a tuning parameter θ that controls the weights $w_i$from Eq. 10, and, if bigger than 0 indicates non-linearity (Sugihara, 1994; Klein *et al.*, 2016; Dakos *et al.*, 2017). Significance of non-linearity was assessed using a null distribution generated from 500 surrogate time series for each S-Map model. The surrogate time series were created following Deyle *et al.* (2018) and were phase-randomized which preserves the basic statistical properties of the original time series (Ebisuzaki, 1997). We averaged the S-Map results for all Atlantic cod recruitment time series to understand the overall dynamics.

We performed Convergent Cross Mapping (CCM) between R and SSB and the climate variables (SST, NAO and AMO), a technique to understand causality between time series without assuming any distribution (Sugihara *et al.*, 2012; Deyle *et al.*, 2016; Pierre *et al.*, 2018). CCM is based on the principle that, if SSB or climate variables have an influence, then the R time series will contain information about the past state of these variables. CCM is performed using Eq. 10 (see Deyle *et al.*, 2018)~~.~~

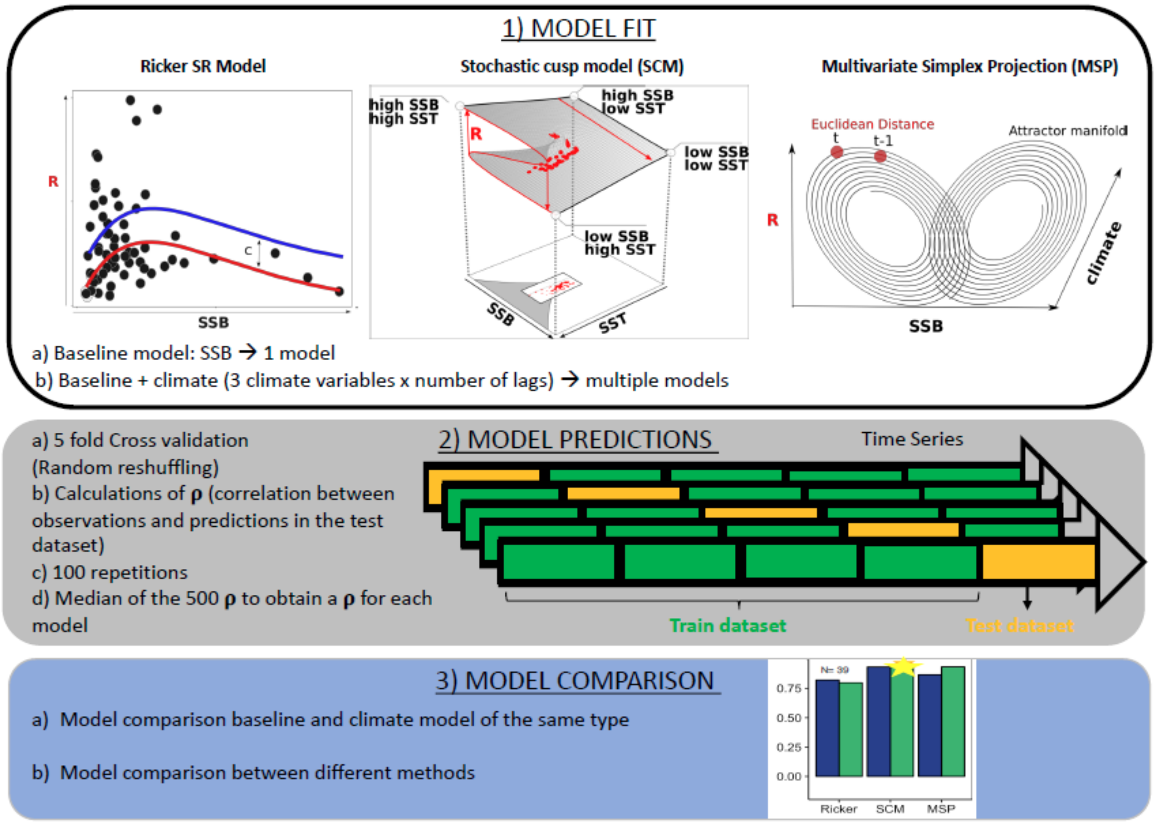
Software

All analyses were performed in the programming environment R (R Core Team, 2017, version 3.3.1) using the packages *FSA* (Ogle, 2016), *cusp* (Grasman *et al.*, 2009), *rEDM* (Ye *et al.*, 2016).

3.3 Results

In our multi-model approach, we compared the parametric, linear Ricker model with two non-parametric, state-dependent approaches, i.e. the Stochastic cusp model (SCM) and the state-dependent Multivariate Simplex Projection (MSP), with or without environmental variables as predictors (Fig. 2). The two preliminary tests of the Empirical Dynamic Modelling (EDM), necessary to perform the MSP, revealed on average significantly non-linear dynamics in recruitment of Atlantic cod stocks, and an appropriate choice of explanatory variables (Supplementary material, Fig. S4-S5), thus allowing us to proceed with the analyses. For most of the Atlantic cod stocks, the best performing models produced high correlations between observed and predicted values ($0.7 < \rho < 0.8$). An exception were North-East Arctic, Iceland and Gulf of Maine cod stocks where the predictive power was lower compared to the other stocks (about $\rho = 0.4$). Differences between the three model types were in general low (Fig. 2). The Ricker model performed best for seven stocks, the SCM for eight stocks and the MSP for five stocks (Fig. 3, Supplementary material, Tab. S2). For stocks where SCM was the best, the MSP generally showed also a high predictive power, indicating that both models can well describe abrupt dynamics (e.g. Fig. 3-$_{12,13,14,17}$). The addition of climate variables as explanatory variables to the baseline SSB models generally increased the predictive power, independently of the model type, even though SSB was often the most correlated explanatory variable (Fig. 3, Supplementary material Tab. S2 and as shown in CCM, Fig. S5). SST and AMO were selected, based on the predictive power of the model, in respectively eight stocks and NAO in the remaining four stocks, generally agreeing with CCM results (Fig. 4, Supplementary material, Fig. S5). However, adding a climate variable had only a weak or even no additional effect when the baseline SSB model performed already poorly (e.g. Fig. 3-$_{8}$, Ricker model).

The Ricker model best represented more gradual declines in recruitment, typical for cod stocks around the British Isles (i.e. North Sea, West of Scotland and Irish Sea), those closer to the Arctic (i.e. Faroe Plateau, North-East Arctic and Iceland cod) and Georges Bank cod (Fig. 4a-g, Supplementary material, Tab. S3), as illustrated by their individual time series (Supplementary material, Fig. S1). All of these stocks, except Georges Bank, displayed strong density-dependence in recruitment (Supplementary material, Tab. S3), which is characteristic for the Ricker model. Furthermore, Ricker models clearly revealed that recruitment in warmer years is usually lower for the same level of SSB when compared to colder conditions (as indicated by low SST, NAO or AMO in Fig. 3a,d,g). The only exception with the reverse pattern of higher recruitment values at warmer conditions was North-East Arctic, hence the only cod stock that really profited from climate warming (Fig. 4-$_{9}$).



1) MODEL FIT

a) Baseline model: SSB → 1 model

b) Baseline + climate (3 climate variables x number of lags) → multiple models

2) MODEL PREDICTIONS

a) 5 fold Cross validation (Random reshuffling)

b) Calculations of ρ (correlation between observations and predictions in the test dataset)

c) 100 repetitions

d) Median of the 500 ρ to obtain a ρ for each model

3) MODEL COMPARISON

a) Model comparison baseline and climate model of the same type

b) Model comparison between different methods

Figure 2 Schematic summary of the modeling approach. Box 1 shows the three model types applied. In the Ricker model (left) a curve depending on parameter a and b is fitted to show the relationship between recruitment (R) and SSB. A third parameter c, allows the introduction of a climate variable and thus allows the curve to change between different climate states (i.e. above the mean in red, below the mean in blue). The stochastic cusp model (SCM; center) is shown both in from of a 3D landscape and its projection in 2D. In SCM the state variable R depends on 2 control variables (i.e. SSB and temperature). While SSB controls the dimension of R, i.e. if R is found at the upper or lower shield, temperature controls the type of path that R will follow, either linear or discontinuous (s-haped, i.e. the 2 red paths). The 3D landscape can be projected on the 2D plane in which the folded area, i.e. the area of discontinuous dynamics, is shown in grey. In the attractor reconstruction of R depending on SSB and climate made with multivariate simplex projection (MSP; right) every point in the attractor correspond to a time step of the system. MSP allows for the prediction of the future step of the system based on Euclidean Distance Calculations and thus is a state-dependent approach. All methods were fit as baseline models using just SSB as control variable and then adding the environmental variable. Box 2 shows the model evaluation procedure using 5-fold cross validation. From this procedure, the predictive power of all the models was calculated and finally compared (Box 3) to assess performance among models of the same type and between the three different methods.

Figure 3 Stock-recruitment model comparison. The comparison between the predictive power of the best models resulting from the model selection between the Ricker, Stochastic cusp (SCM) and Multivariate Simplex Projection (MSP) models. The median of the predictive power, derived from the cross-validation is shown for the three models without (blue) and with (green) the inclusion of climate variables. The best model among the three, i.e. the model presenting the highest Pearson ρ between observed and predicted values of the test dataset, is indicated by a yellow star for each stock. Black

stars indicate the best models which however had a poor fit to recruitment and thus were substituted by the second-best model. The environmental variable that resulted in the best predictions can be found in Fig. 4 and Supplementary material, Tab. S2. The number of years in the time series are indicated for each stock. The colours underlying the names of the stocks correspond to the geographical location of the stock, pink in the East Atlantic, and orange in the West. The numbers correspond with the stocks number in Fig.1.

SCM instead is an approach from catastrophe theory which models best discontinuous dynamics characterized by abrupt sudden shifts and hysteresis (i.e. in this case delayed recovery). The recruitment and SSB time series of Canadian stocks on the Western Atlantic side, but also Greenland and Eastern Baltic cod (Supplementary material, Fig. S1) show this type of dynamics, and hence SCM was the best approach for these stocks. SCM identified discontinuous stock-recruitment dynamics caused by the interaction of SSB and the climate variable. Moreover, SCM can identify catastrophic collapse which occurs when SSB is found in the "folded" area, or area of instability (see blue shaded areas in Fig. 4h-o, Supplementary material, Fig. S3). Recruitment collapsed in these stocks, when in the instability area, in response to only small reductions in stock size (Fig. 4-$_{12-18,1}$). Consequently, SSB was a significant predictor in all SCMs, controlling the stocks dimension, while the climate variables modified the relationship between recruitment and SSB rendering it discontinuous, and thus inducing hysteresis (Supplementary material, Tab. S4). These two factors lead to the presence of stable low recruitment levels towards the end of the time-series. Low SSB coupled with warming (as indicated by climate variables SST, NAO and AMO, Supplementary material, Tab. S4) had the potential to stabilize low recruitment. This is indicated by values outside the bifurcation area as best demonstrated by Northern and Grand Banks cod (Fig. 4-$_{13,17}$). Other cod stocks such as those from the Gulf of St. Lawrence, on the Eastern Scotian Shelf and off Greenland were at the boarder of stable low recruitment levels (Fig. 4-$_{12,14-16}$).

Eventually, we found MSP to be the best model for recruitment of stocks that did not show collapses, but mostly fluctuating dynamics such as cod in the Western Baltic, the Kattegat (since, even if the SCM was the best the model, the fit was invalid), the Celtic Sea, the Norwegian coast and in the Gulf of Maine (Fig. 4$_{3,2,7,8,20}$, Supplementary material, Fig. S1). The MSP however, seemed also appropriate to model catastrophic dynamics, but less effectively than the SCM. In contrast to the stocks best modelled with SCM and Ricker, stocks best modelled with MSP showed a mixed response to recent warming with a clear negative effect on recruitment in the Western Baltic only (Fig. 3-$_{2}$).

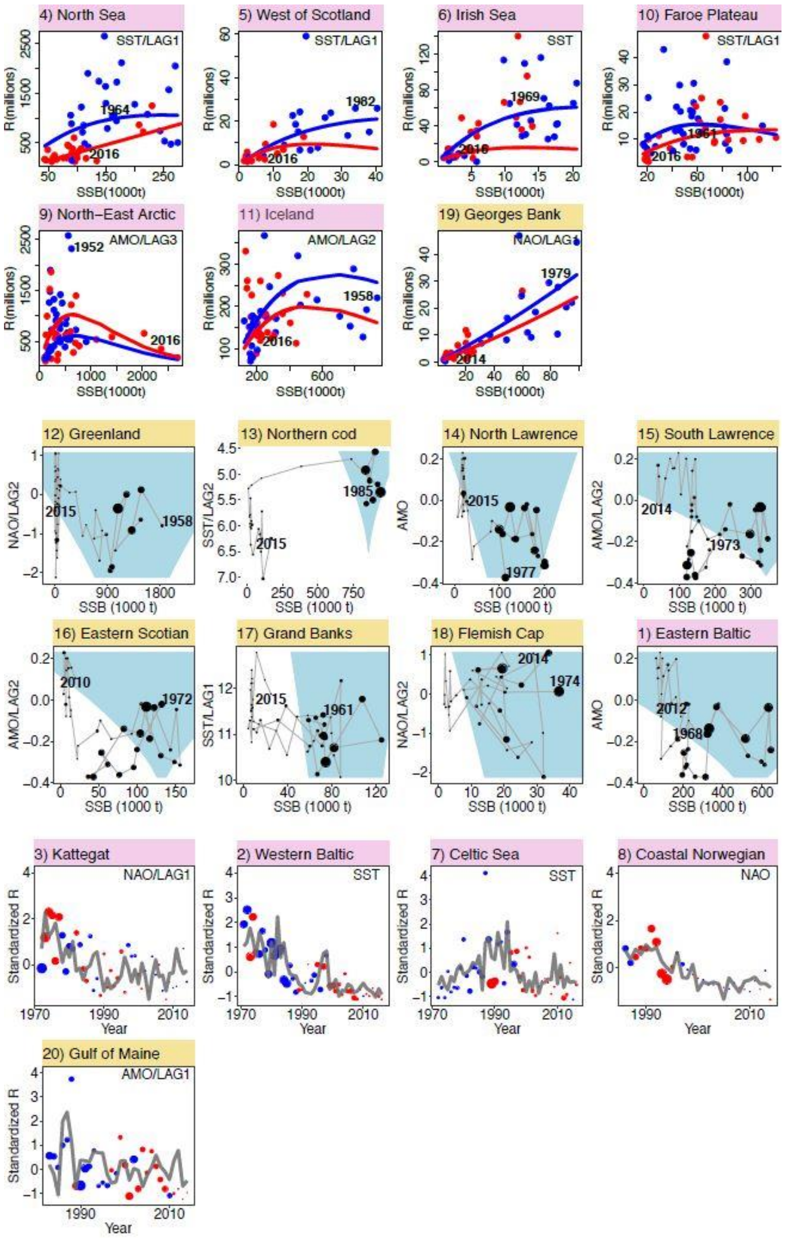


Figure 4 Visualization of stock-recruitment relationships (SRR) for Atlantic cod stocks. Every panel contains a representation of the best model for each of the stocks. 4,5,6,10,9,11,19) Results for cod stocks best represented by the Ricker model; SSB – spawning stock biomass, R – recruitment. The colour of the dots corresponds to the state of the climate variable, red above the mean, blue below the mean. The two lines indicate separate SRRs for the two climate states (above and below the mean).12-18,1) Results for cod stocks best represented by the Stochastic cusp model (SCM); SST – Sea Surface Temperature, NAO – North Atlantic Oscillation, AMO – Atlantic Multidecadal Oscillation. Dots are scaled to the size of R. The blue area corresponds to the instability area, thus the fold in the 3D visualization (Fig.2, Supplementary material Fig.S3) where 3 equilibria are possible. 3,2,7,8,20) Results for cod stocks best represented by Multivariate Simplex Projection (MSP); Dots are scaled to the size of SSB. Colours correspond to the state of the climate variable indicated, red above the mean, blue below the mean. The lines show the predicted trends of R over time. The colours in the small boxes closed to the names of the stocks correspond to the geographical location of the stock, pink in the East Atlantic, and orange in the West. The numbers correspond to stock numbers in Fig.1. The comparison between observed and predicted values for each model can be seen in Supplementary Material Fig.S6.

3.4 Discussion

Short-term predictions of the size of an incoming year-class is essential to modern assessments of commercial fish species, but often suffers from the accuracy of available models predicting recruitment based on continuous, linear relationship with spawning stock biomass (SSB). In our study, we investigated (i) whether recruitment dynamics in Atlantic cod stocks are better predicted by non-parametric, state-dependent or catastrophic statistical methodology compared to traditional parametric, linear approaches such as the Ricker stock-recruitment model, and (ii) whether using climate variables as predictors in addition to SSB improves the predictive performance of such models.

The main result of our study is that predicting fish stock recruitment can be improved by tailoring the modelling approach to the dynamical properties of each individual stock. We found cod stocks with more gradual and mostly linear dynamics to be best predicted by the traditional linear Ricker model, while stocks that experienced sudden abrupt changes in recruitment and stock size are best described by the Stochastic cusp model (SCM). SCM, based on catastrophe theory, is well suited to represent such discontinuous regime shift dynamics (Thom, 1972; Grasman *et al.*, 2009; Diks and Wang, 2016;s Sguotti *et al.*, 2019). SCM allows for the identification of drivers and how their interactions result in unstable recruitment dynamics and hence provides a form of vulnerability assessment that can be instrumental in management (Petraitis and Dudgeon, 2015; Diks and Wang, 2016; Sguotti *et al.*, 2019). Eventually, Multivariate Simplex Projection (MSP) was most appropriate for stocks that displayed more chaotic and fluctuating behaviours (Sugihara *et al.*, 2012; Ye *et al.*, 2015). Indeed, being a minimally assumptive model the most complex dynamics are better captured by it. MSP as part of the EDM (Empirical Dynamic Modelling) suite of methods is based on attractor reconstruction and accounts for state-dependent dynamics (Ye *et al.*, 2015). which makes it a suitable approach to model also discontinuous dynamics (Ye *et al.*, 2015; Deyle *et al.*, 2018). Mostly, both SCM and MSP models performed similarly in our analysis and their relatively high predictive power indicated the importance of using state-dependent and/or discontinuous approaches to model recruitment (Ye *et al.*, 2015; Deyle *et al.*, 2018; Munch *et al.*, 2018).

Our study highlights that important differences exist between cod stocks in the Eastern and Western areas of the North Atlantic (Frank *et al.*, 2016). Stocks from the Western Atlantic and in particular off Canada and Greenland often experienced pronounced catastrophic dynamics, i.e. abrupt and sudden changes in stock size and recruitment. Eastern Atlantic stocks instead showed more continuous dynamics and thus a higher degree of stability. In general Western Atlantic cod stocks seemed to be less resilient to abrupt collapses due to more fragile life history traits, an overall more extreme and difficult environment, and different exploitation histories (Rätz and Lloret, 2003; Pörtner *et al.*, 2008; Wang *et al.*, 2014; Frank *et al.*, 2016). Moreover, sea surface temperature (SST) was selected in Eastern Atlantic cod stocks models, while for Western stocks the climate indices explained better the recruitment variability. This difference might indicate that the Eastern cod stocks are more influenced by local processes, while in the Western Atlantic large scale climatic fluctuations are more important. Nevertheless, the addition of the climate factors in the best stock-recruitment models almost always increased its predictive power and thus highlights the importance of using environmental information also in stock assessment and management considerations to consider broader ecosystem dynamics (Punt *et al.*, 2013; Skern-Mauritzen *et al.*, 2015).

These results highlight the presence of multiple dynamics in cod stocks which are also supported by the results of the preliminary S-Maps tests revealing a significant level of non-linearity in recruitment time-series of Atlantic cod stock. However, the non-linearity signal is lower than expected, which we assume is due to the nature of the stock assessment data we used, and thus could be an underestimation (Brooks and Deroba, 2015). Such model output tends to be smoother and more linear than survey data (Storch *et al.*, 2017), which are unfortunately not available for all cod stocks and longer time-periods needed for our study.

Finally, the different models allow us to draw conclusions about the recovery potential of collapsed Atlantic cod stocks. Most of the stocks are negatively influenced by warming and climate variability, since the lowest recruitment and SSB coincide with the highest temperature (Brander, 2005; Drinkwater, 2005; Pörtner *et al.*, 2008). The only exception is North-East Arctic cod where a warming environment positively influences recruitment, since this stocks resides at the northern distribution limit of the species (Pörtner *et al.*, 2008). Apart from North-East Arctic and Iceland cod where SSB has recently reached high levels, the stocks for which the traditional Ricker model performed best, such as the ones from the North Sea and around the British Isles, show continuously low recruitment and SSB in recent years and a continuous relationship between these parameters. These imply that, with low exploitation pressure these stocks have a higher recovery potential, but with climate change the productivity will likely remain low (Drinkwater, 2005). The situation is even worse for stocks that are best described by the SCM such as the Western Atlantic stocks where the relationship between recruitment and SSB is discontinuous and thus the stocks display a strong hysteresis effect. Most of them are at present in a stable low state, suggesting that recovery might be even further delayed and productivity will remain low.

3.5 Conclusions

We demonstrated that discontinuous, state-dependent dynamics are pervasive in at least half of Atlantic cod stocks and need to be considered when predicting year-class strength. Indeed, even if our study does not necessarily reflect the goodness of the models to predict future recruitment, since the cross validation included years after those predicted, we highlight the presence of different dynamics between stocks. Furthermore, we show the importance of accounting for environmental factors in recruitment predictions. Our findings indicate the need for more flexibility in the stock assessment process and highlight the importance for an adaptive multi-model approach that accounts for the inherent dynamics of living marine resource populations (Punt *et al.*, 2016). Flexible models and adaptive management are fundamental to move towards an ecosystem-based management approach, especially in the face of climate change. To achieve this, we need to move away from fixed and established model procedures and explore other options, to be ready to adapt to the new challenges that climate change will pose (King *et al.*, 2015).

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Conflict of interest

The authors declare no conflict of interests

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Supplementary material

Table S1 The stocks assessment models of the Atlantic cod stocks. Stock number and corresponding name have been listed together with management area code, stock assessment models used, age at recruitment (in years), and the institution (or working group within the institution) conducting the stock assessment. Last column provides the person or organisation responsible for the data

Stock name	Stock N°	Management area	Stock assessment models*	Age at R	Institution/ group	Contact person or other data source
Eastern Baltic[1]	1	25-32	SAM	2	ICES/ WGBAFS	Margit Eero
Western Baltic[2]	2	22-24	SAM	1	ICES/ WGBAFS	Margit Eero
Kattegat[1,2]	3	IIIa/21	SAM	1	ICES/ WGBAFS	Johan Lövgren
North Sea	4	IV – VIId – IIIa	SAM	1	ICES/ WGNSSK	Alexander Kempf
West of Scotland	5	VIa	TSA	1	ICES/ WGCSE	Rui Catarino
Irish Sea	6	VIIa	SAM	1	ICES/ WGCSE	Colm Lordan
Celtic Sea	7	VIIe – VIIk	XSA	1	ICES/ WGCSE	Colm Lordan
Coastal Norwegian Sea[2]	8	I – I	Survey SSB and F from VPA	2	ICES/ AFWG	Gjert Endre Dingsor
Northeast Arctic	9	I – II	XSA	3	ICES/ AFWG	Gjert Endre Dingsor
Faroe Plateau	10	Vb1	XSA	2	ICES/ NWWG	Petur Steingrund
Iceland	11	Va	Forward based statistical catch at age model	3	ICES/ NWWG	Einar Hjorleifsson
Greenland	12	1	XSA	2	Thünen Institute of Sea Fishery	Karl Micheal Werner
Northern cod	13	2J3Kl	State space model	2	DFO	DFO(2016)[3]
Northern Gulf of st. Lawrence	14	3Pn4Rs	SPA	3	DFO	Claude Brassard
Southern Gulf of st. Lawrence	15	4T4Vn	SCA	2	DFO	Doug Swain
Eastern Scotian Shelf	16	4VsW	VPA	2	DFO	Swain & Mohn (2012)[4]
Grand Banks	17	3NO	SPA	2	NAFO	NAFO (2015)[5]
Flemish Cap	18	3M	Bayesian model	2	NAFO	Diana Gonzalez
Georges Bank	19	5z	Age structured model	1	NOAA	Loretta O´Brien
Gulf of Maine	20	5y	Age structured model	1	NOAA	Mike Palmer

* SAM – State-space assessment model, TSA – Analytical age-based assessment (time series analysis), XSA – Extended survivor analysis, SPA – Sequential population analysis, SCA – Statistical catch at age, VPA – Virtual population analysis

[1] Stocks that in the last year failed the assessment

[2] Stocks where, in order to have longer time series, we mixed old assessments and new ones, after checking for same trends and stock dimensions.

[3] DFO (2016) Stock Assessment of Northern Cod (NAFO Divs. 2J3KL) in 2016. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/026

[4] Swain DP, Mohn RK (2012) Forage fish and the factors governing recovery of Atlantic cod (Gadus morhua) on the eastern Scotian Shelf. Can. J. Fish. Aquat. Sci. 69: 997–1001.

[5] NAFO (2015) Assessment of the Cod Stock in NAFO Divisions 3NO. NAFO SCR Doc. No. 15/034.

Table S2 Results of the model selection for each stock

Stock name	Model	Selected variables	Predictive power (ρ)	MAE	Stock name	Model	Selected variables	Predictive power(ρ)	MAE
Eastern Baltic	Ricker	SSB	0.65	0.35	**Western Baltic**	Ricker	SSB	0.62	0.68
		+ NAO_lag2	0.73	0.36			+ AMO_lag1	0.73	0.59
	Cusp	SSB	0.69	9.4E4		Cusp	SSB	0.69	3.8E4
		+ AMO	0.83	7.6E4			+ AMO_lag1	0.73	3.3E4
	EDM	SSB	0.37	0.76		EDM	SSB	0.76	0.55
		+ SST	0.7	0.55			+ SST	0.81	0.52
Kattegat	Ricker	SSB	0.31	0.53	**North Sea**	Ricker	SSB	0.67	0.55
		+AMO	0.36	0.52			+ SST_lag1	0.81	0.43
	Cusp	SSB	0.64	4.2E3		Cusp	SSB	0.7	3.46E5
		+ NAO_lag1	0.67	4.1E3			+ SST_lag1	0.74	3.43E5
	EDM	SSB	0.52	0.82		EDM	SSB	0.39	0.75
		+ NAO_lag1	0.5	0.82			+ AMO_lag1	0.72	0.58
West of Scotland	Ricker	SSB	0.85	0.46	**Irish Sea**	Ricker	SSB	0.8	0.6
		+ SST_lag1	0.87	0.44			+ SST	0.85	0.54
	Cusp	SSB	0.8	4.3E3		Cusp	SSB	0.82	1.4E4
		+ SST_lag1	0.79	4.5E3			+ SST	0.84	1.6E4
	EDM	SSB	0.52	0.65		EDM	SSB	0.64	0.61
		+ SST_lag1	0.69	0.48			+ AMO_lag1	0.83	0.59
Celtic Sea	Ricker	SSB	0.26	0.7	**Coastal Norwegian**	Ricker	SSB	0.81	0.24
		+ SST_lag1	0.28	0.7			+ SST	0.8	0.24
	Cusp	SSB	0.37	3.2E3		Cusp	SSB	0.76	9.2E3
		+ SST_lag1	0.34	3.2E3			+ SST_lag1	0.82	7.9E3
	EDM	SSB	-0.14	0.98		EDM	SSB	0.81	0.53
		+ SST_lag1	0.51	0.77			+ NAO	0.88	0.49
North-East Arctic	Ricker	SSB	0.49	0.53	**Faroe Plateau**	Ricker	SSB	0.49	0.53
		+ AMO_lag3	0.54	0.52			+ SST_lag1	0.64	0.47
	Cusp	SSB	-0.09	3.8E5		Cusp	SSB	0.29	7E3
		+ NAO_lag3	0.42	3E5			+ SST_lag1	0.53	6.5E3
	EDM	SSB	0.26	0.77		EDM	SSB	0.15	0.92
		+ AMO_lag2	0.27	0.78			+SST_lag1	0.36	0.5
Iceland	Ricker	SSB	0.2	0.28	**Greenland**	Ricker	SSB	0.64	1.6
		+ AMO_lag2	0.47	0.25			+ SST_lag2	0.81	1.1
	Cusp	SSB	0.25	4.8E4		Cusp	SSB	0.85	4.5E4
		+ AMO_lag2	0.44	4.4E4			+ NAO_lag2	0.85	4.5E4
	EDM	SSB	0.19	0.96		EDM	SSB	0.76	0.41
		+ NAO_lag3	0.36	0.8			+ NAO_lag2	0.84	0.37
Northern	Ricker	SSB	0.82	0.58	**Northern Lawrence**	Ricker	SSB	0.84	0.5
		+ AMO	0.8	0.56			+SST	0.86	0.53

	Cusp	SSB	0.93	1.2E5		Cusp	SSB	0.92	1.9E4
		+ SST_lag2	0.95	1.1E5			+AMO	0.94	1.9E4
	EDM	SSB	0.87	0.79		EDM	SSB	0.82	0.46
		+ SST	0.93	0.31			+ SST_lag3	0.91	0.31
Southern Lawrence	Ricker	SSB	0.69	0.36	**Easter Scotian Shelf**	Ricker	SSB	0.76	0.54
		+ AMO_lag2	0.76	0.34			+ NAO_lag2	0.75	0.48
	Cusp	SSB	0.78	5.2E4		Cusp	SSB	0.65	2.4E4
		+ AMO_lag2	0.8	5.2E4			+ AMO_lag2	0.76	2.1E4
	EDM	SSB	0.36	0.76		EDM	SSB	0.56	0.7
		+ AMO	0.78	0.53			+ NAO_lag2	0.67	0.64
Grand Banks	Ricker	SSB	0.73	1.02	**Flemish Cap**	Ricker	SSB	0.64	1.43
		+ NAO	0.82	0.87			+ SST	0.64	1.42
	Cusp	SSB	0.87	2.1E4		Cusp	SSB	0.63	1.3E4
		+ SST_lag1	0.83	2.3E4			+ NAO_lag2	0.68	1.2E4
	EDM	SSB	0.65	0.55		EDM	SSB	0.24	0.65
		+ AMO_lag2	0.82	0.36			+ SST_lag1	0.6	0.53
Georges Bank	Ricker	SSB	0.89	0.47	**Gulf of Maine**	Ricker	SSB	0.31	0.49
		+ NAO_lag1	0.9	0.48			+ NAO	0.43	0.5
	Cusp	SSB	0.87	4.8E3		Cusp	SSB	0.41	3.7E3
		+ AMO_lag1	0.85	5.1E3			+ NAO_lag1	0.36	3.9E3
	EDM	SSB	0.81	0.46		EDM	SSB	0.06	0.86
		+ SST	0.79	0.51			+ AMO_lag1	0.52	0.74

For every stock the results of the best Ricker model, SCM, and EDM with and without environmental variable is shown. The Predictive power corresponds to the median of the 500 Pearson rho, obtained from the cross-validation. The Mean Absolute Error shown is calculated with the same process of the predictive power.

Table S3 Results of the best Ricker stock-recruitment model

	North Sea	West of Scotland	Irish Sea	Faroe Plateau
a	6.052*	1.437*	5.243*	5.829e-01*
b	2.316e-06	3.988e-05*	5.243e-05	1.644e-05*
c	-4.727e-01*	-3.202e-01*	-5.93e-01*	-3.581e-01*
Variance Explained	55	54.4	75	32
Better than BH	***	*	**	***

	North-East Arctic	Iceland	Georges Bank
a	3.297e+00*	1.017e+00*	2.403e-01*
b	1.474e-06*	1.716e-06*	-1.220e-06
c	1.229e+00*	-9.752e-01*	-2.692e-01*
Variance Explained	13.8	8.1	56
Better then BH	*	***	*

The table shows the results of the Ricker model for the stocks where this model resulted the best (see Table S2 and Fig.3). a,b,c are the parameter fitted in the model for the climate effect (scaled) (c) and the density dependent effects (a and b). The asterisk indicates models where the confidence interval did not include 0, thus significant parameters. The percentage of variance explained by the model is indicated. The last line of the table shows whether the Ricker model constitutes a significant improvement from a Beverton and Holt model and the associated asterisks show the different levels of significance (*0.05, **0.005, ***0.0005).

Table S4 Results of the best Stochastic Cusp Model

	Greenland	**Northern cod**	**Northern St Lawrence**	**Southern St Lawrence**
$\alpha 0$	-2.409**	-7.6**	-1.75**	-2.234**
$\alpha 1$	1.824e-06**	8.872e-06**	1.347e-05**	6.511e-06*
$\beta 0$	3.614***	9.375**	2.403***	3.082***
$\beta 1$	0.7237**	-1.432*	2.21E+00	8.301***
Z0	-2.268e+00***	-2.451***	-2.21***	-3.013***
z1	7.06e-06***	3.08E-06	2.246e-05***	8.978e-06***
ΔAIC	1416	834	884	1009
R squared	0.78	0.81	0.79	0.64

	Eastern Scotian Shelf	**Grand Banks**	**Flemish Cap**	**Eastern Baltic**
$\alpha 0$	-1.546**	-3.306***	-2.333**	-1.554**
$\alpha 1$	1.175e-05*	3.575e-05**	7.044e-05*	2.873e-06**
$\beta 0$	1.999**	-0.2526	2.784***	2.701***
$\beta 1$	4.51**	0.2357	0.2302	5.27***
Z0	-2.27***	-2.142***	-2.187***	-2.826***
z1	2.873e-05***	1.734e-05***	3.697e-05***	6.834e-06***
ΔAIC	836	1260	877	1107
R squared	0.5	0.66	0.69	0.73

The table shows the results of the stochastic Cusp model (SCM) for the stocks where this model resulted the best (see Table S2, and Fig.3).The SCM estimated the parameter as a linear function of exogenous variables using a likelihood approach (see Methods). Thus the significance of the parameters α, β and z, respectively the asymmetry variable (linear function of SSB), the bifurcation variable (linear function of climate) and the State variable (linear function of R), is assessed through a linear model where $\alpha 0$, $\beta 0$ and z0 are the intercepts of the models, while $\alpha 1$, $\beta 1$ and z1, are the coefficients. The stars indicate the significance (*=0.05, **=0.005, ***<0.0005). Delta AIC (ΔAIC) shows the improvement of the Stochastic Cusp Model (SCM) compared to the simpler linear model fitted as R=SSB+SST+ϵ. This is routinely done in the package Cusp in order to test the improvement from the linear to the Cusp model. Finally, the R squared show how well the SCM fits to the data.

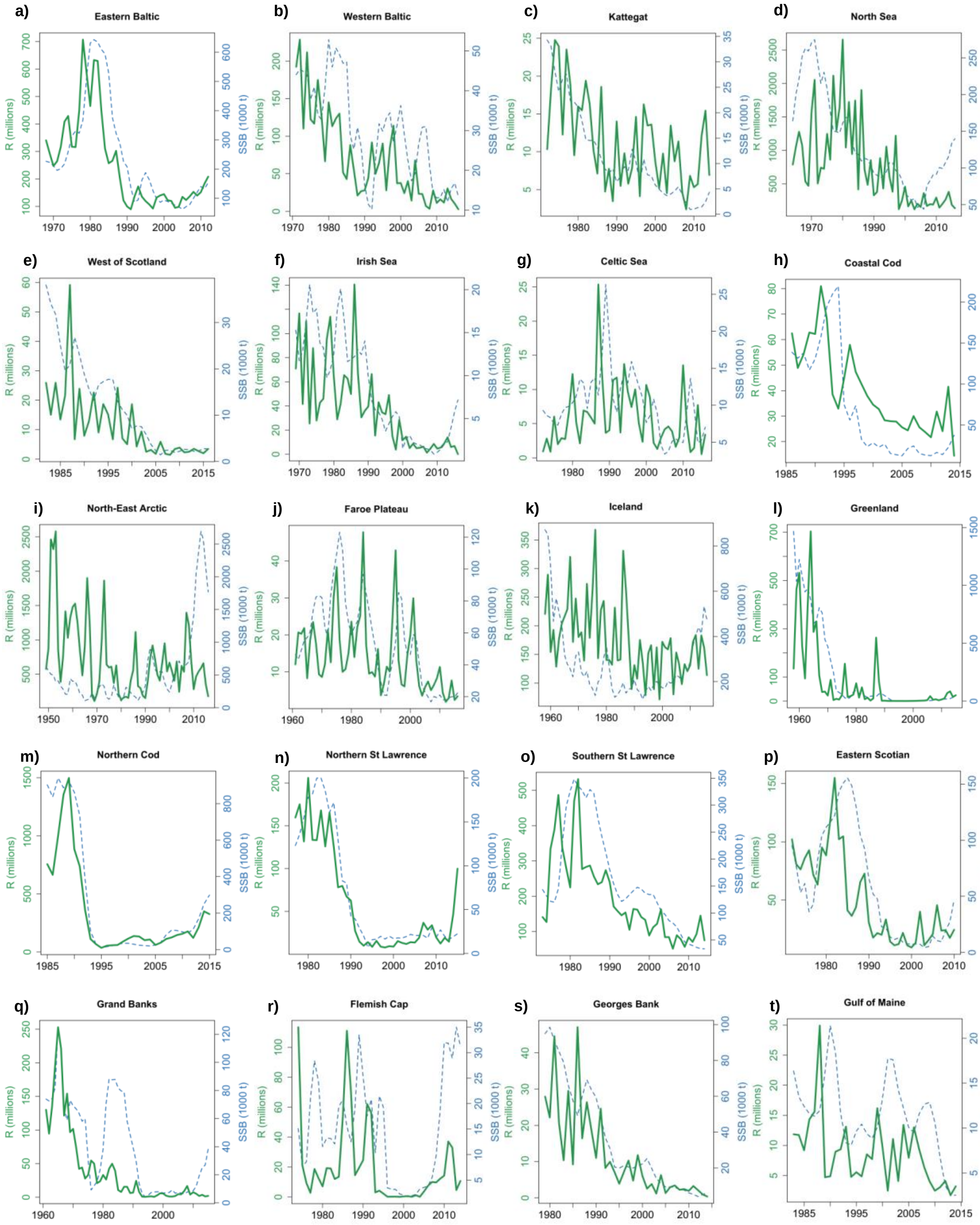

Figure S1 Recruitment and Spawning Stock Biomass (SSB) trend over time for Atlantic cod stocks. On the x axis year, on the y axis recruitment in millions and SSB in thousands tons. Recruitment is shown in green, while SSB in blue dotted line. The data come from the stock assessment indicated in Supplementary material, Tab.1.

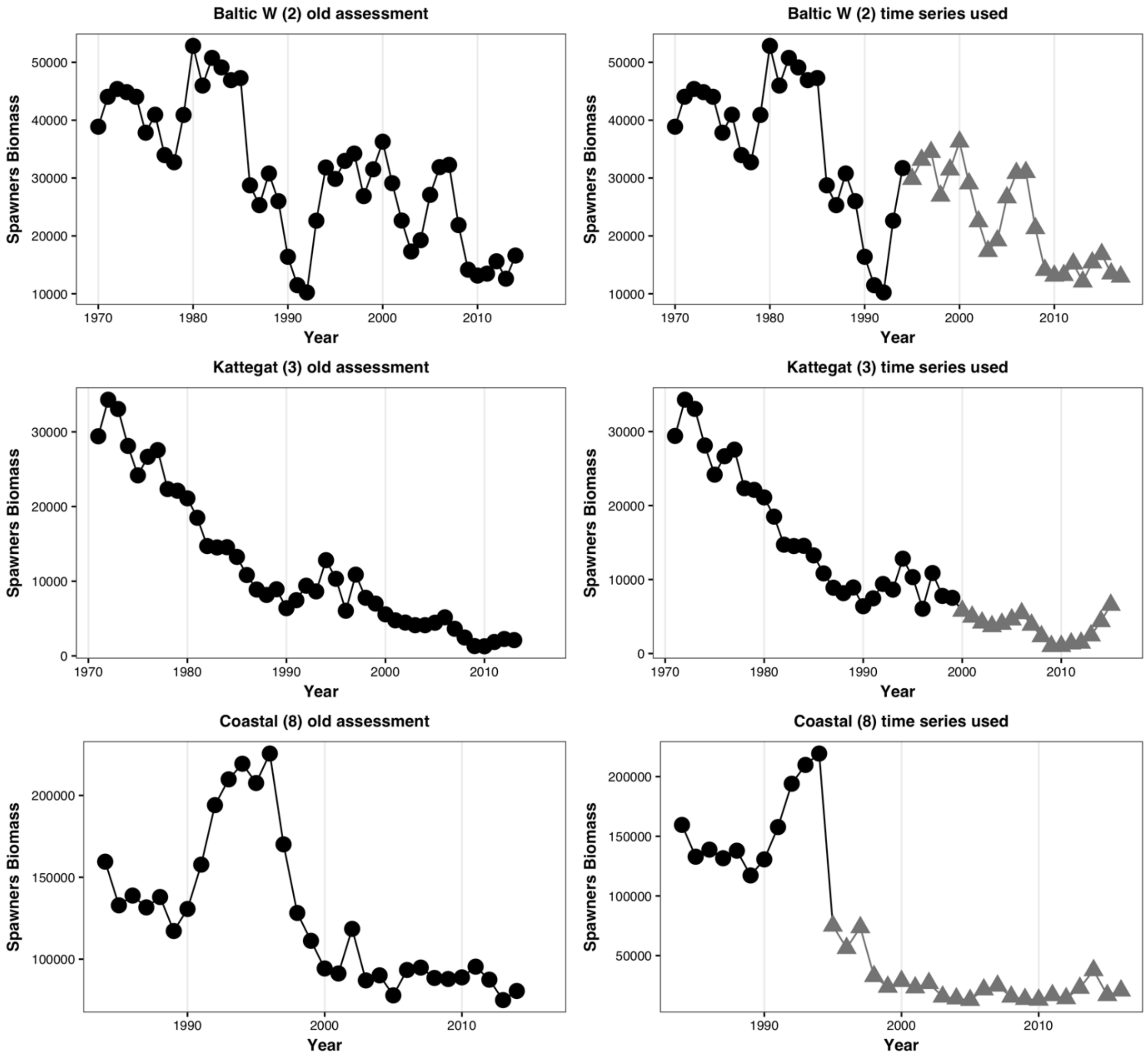

Figure S2 Stock assessment used for short time series stocks. The plots represent SSB in tonnes over time. On the left panel, the older stock assessments. On the right panel the new stock assessment, represented by the lighter grey line and triangles, merged with the old stock assessment represented by the darker black line and dots. We merged them together because we needed a long time series, but also we wanted to have the more recent stock assessments, from 2017.

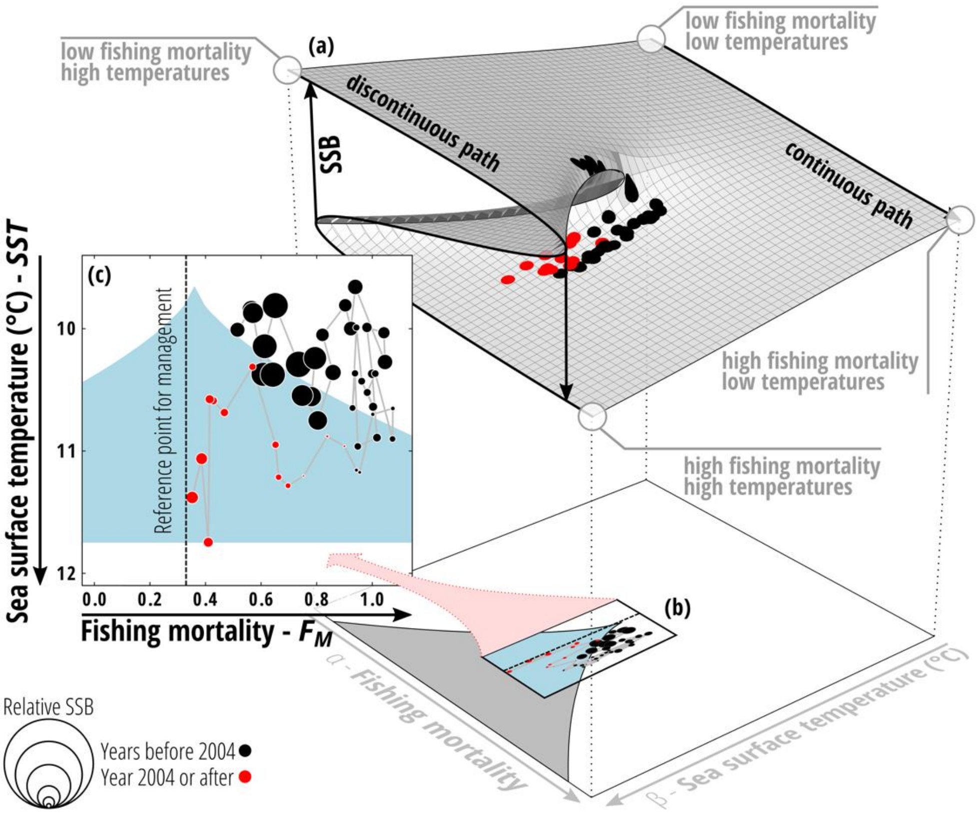

Figure S3 Example of the Stochastic Cusp model, **from Sguotti *et al.*, 2019.** In this example, the state variable is spawning stock biomass (SSB) and the predictors are seat surface temperature (SST) and fishing Mortality (F). The Cusp model can be visualized as a 3D landscape (a) in which SSB is controlled by two control variables, here Fishing Mortality (F, α) and SST (β). F is the so called "asymmetry variable" and controls the dimension of SSB; indeed, SSB will be in the higher fold (i.e. high SSB) when F would be low and in the lower fold (i.e. low SSB) when F would be high. Instead, SST, the "bifurcation variable" controls whether the moving on SSB happens in a continuous or discontinuous way. In this example, at low SST the SSB will have a continuous dynamic and will respond in a continuous way to increase in F, while at high SST, the SSB will cross the fold, indicating a discontinuous path. The fold is the so called "instability areas", where 3 equilibria (2 stable, 1 unstable) are possible. The same representation can be seen in 2D (b-c). The instability area is the blue area in the plot. The SSB follows a discontinuous path, since it is always closed or crossing the instability area. (c) At the beginning of the time series F was low and SSB high. At the increasing of F, SSB started to oscillate close to the instability area to finally collapse in the lower fold and into the unstable state (small dots). Even with reduction of F, SSB is now in a low state and it is pushed from the higher SST even more into the instability area, thus the stock resilience is low. Therefore, higher SST modifies the relationship between F and SSB, causing hysteresis and discontinuous, non-linear dynamics.

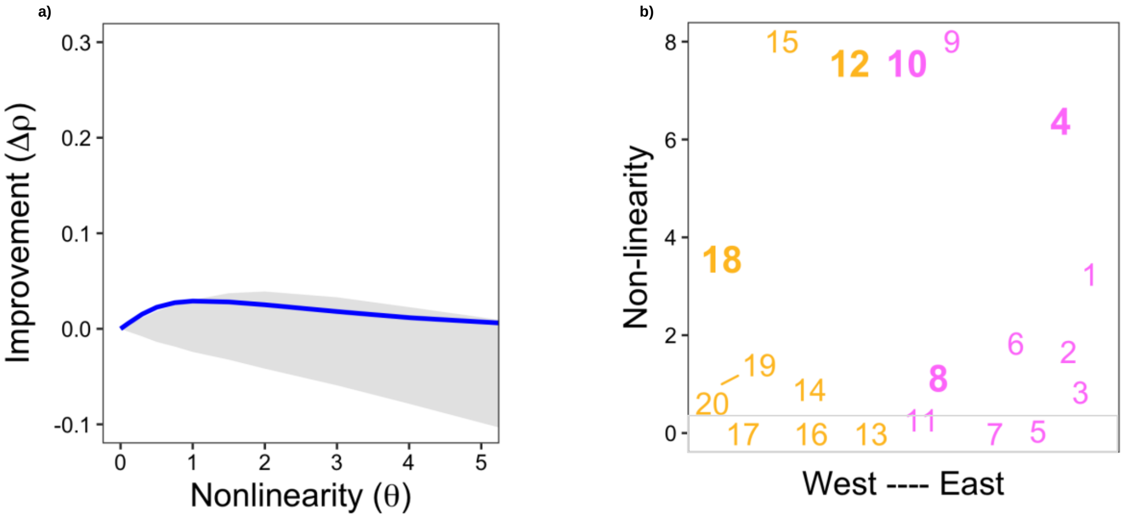

Figure S4 Non-linearity test on Recruitment data. a) Average of the S-map results among Atlantic cod stocks. The y axis shows the improvement in the predictability (ρ), while the x axis show the parameter θ, which represent the non-linearity. The grey area represents the null distribution of the non-linearity test. The best prediction was obtained at a θ of 1 and outside of the null distribution, indicating a significant non-linear trend in recruitment time series. b) The results of the non-linear test for each stock (represented by the numbers showed in Fig.1 and Table S1). Y axis represent the value of θ which corresponded to the best prediction. The stocks above the grey area show non-linear trend, and the stocks in bold are significantly non-linear. The colour of the numbers refers to the East (pink) West (orange) division.

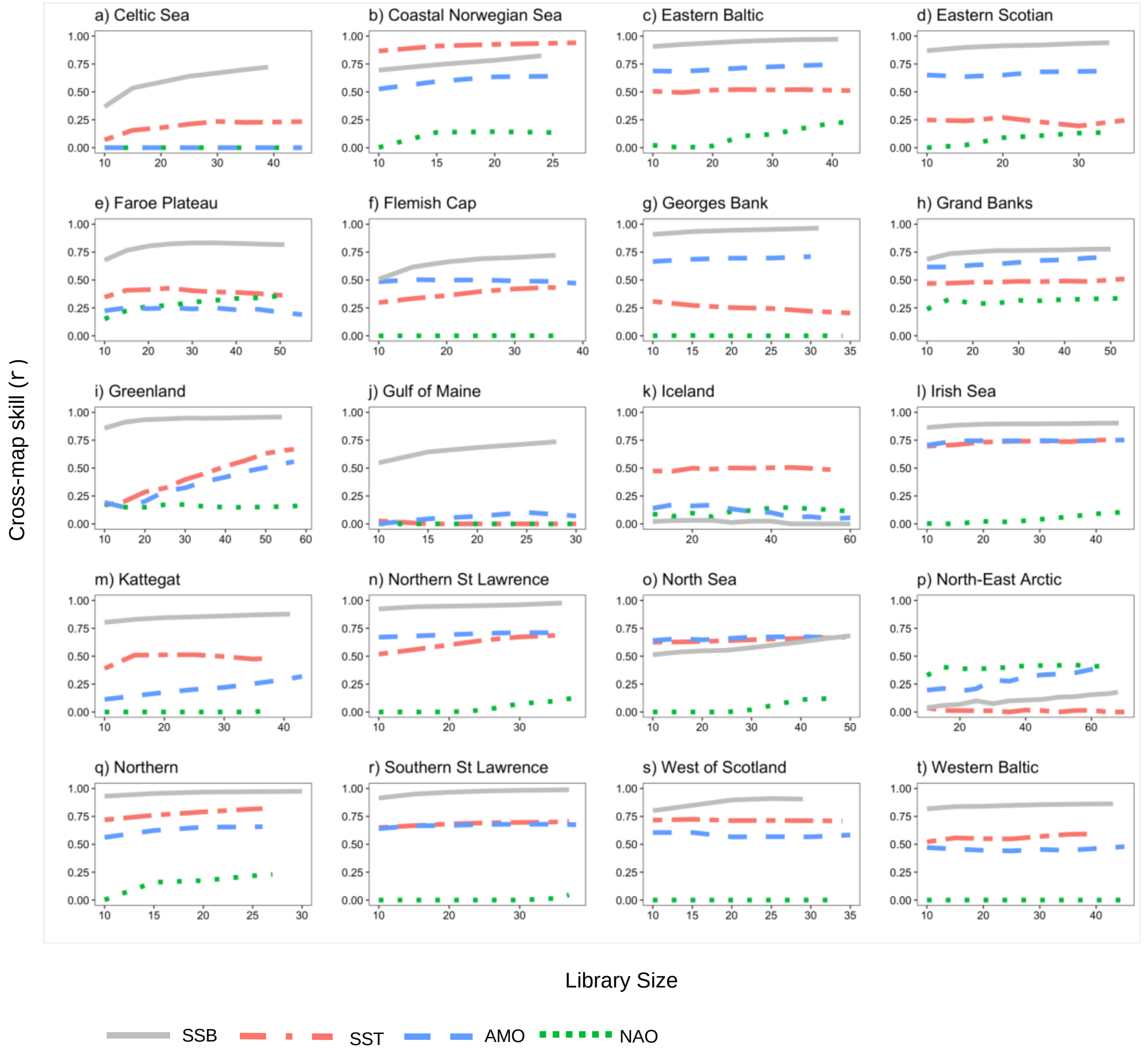

Figure S5:Convergent Cross Mapping (CCM) – correlation of recruitment (R) with spawning stock biomass (SSB) and environmental drivers. Cross-mapping skills are calculated as Pearson ρ between observed and predicted values using equation (2). Library size represents the time series length. The different explanatory variables (SSB, SST, AMO, NAO) are showed with different colours and different line types as indicated in the legend. CCM aims to detect correlation between variables, in our case R, SSB and environment. In a full deterministic system with zero noise, we expect the cross-map skill to increase with increasing time series length, i.e. with the reconstruction becoming denser.

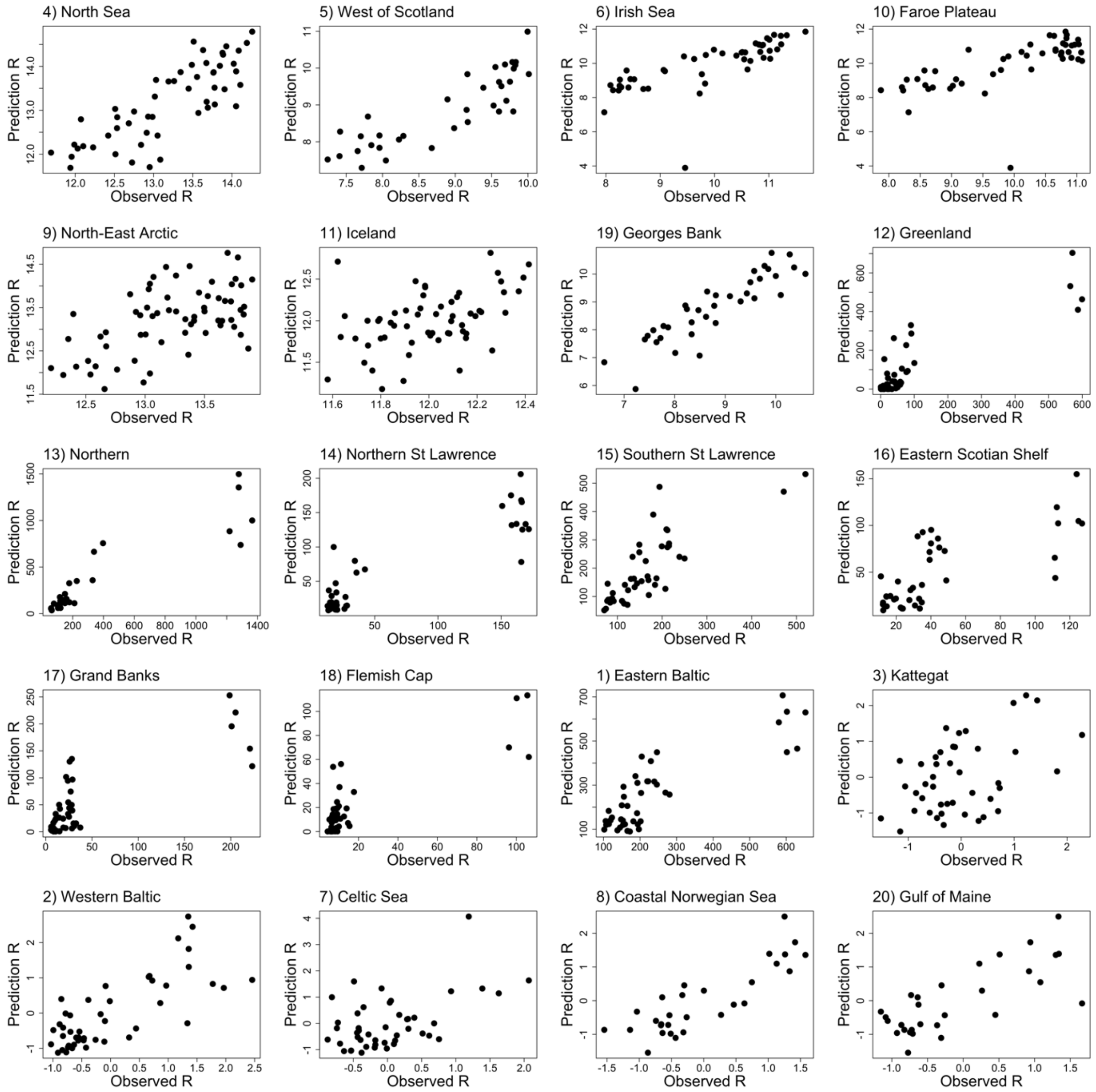

Figure S6 Predicted vs Observed values for each model. The predicted values of recruitment against the observed values for each cod stocks. The prediction was done using the best model for each stock (Fig.4, Tab. S2). The values are shown for the Ricker model (from North Sea to Georges Bank) in log values, for the stochastic cusp model (from Greenland to Eastern Baltic) in hundred thousand individuals and for the multivariate simplex projection (from Kattegat to Gulf of Maine) in scaled values.

4 Publication 3

Improved management is the main driver behind recovery of Northeast Atlantic fish stocks

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Abstract

Decades of intense fishing have not only caused widespread declines in marine fish populations but in recent years have also spurred progress in the development of resource policies, coinciding with reports of positive trends for selected fish stocks in several ecosystems. Anthropogenic pressures and environmental changes affect fish populations, but it is unclear whether improved fisheries management or natural conditions are responsible for the observed recoveries. We show that, for a large set of Northeast Atlantic fish stocks, long-term declines in biomass from 1960 to 2000 were due largely to fishing, suggesting that external drivers caused stock fluctuations at a time when catch regulations were weak or largely absent. After the year 2007, a general pattern of increasing biomass and decreasing catches was observed across most taxa and geographic regions. Implementation of adequate policies to reduce fishing mortality is crucial for overexploited stocks to recover, underlining the positive impacts of science-based management. Because attempts to rebuild Northeast Atlantic fisheries have been only partially successful, and management targets were not fully achieved, policy-making efforts must continue.

4.1 Introduction

It has been widely documented that overfishing poses a major threat to the world's oceans because it can cause stock collapses, reduce biodiversity, and negatively alter ecosystem functions (eg Christensen et al. 2003). Global trends of increased fishing pressure on all trophic levels (Branch et al. 2010) and declining or collapsed fish stocks (Pauly et al. 2005) contrast with indications of improving stock states and fisheries sustainability in several regions worldwide in recent years (Worm et al. 2009), including the Northeast Atlantic (Fernandes and Cook 2013). Fundamental to this development were the implementation of policies (EU 2002) designed to reduce overfishing and facilitate the recovery of depleted or collapsed stocks. Within the European Union (EU), the underlying targets of these policies have been to attain maximum sustainable yield (MSY) in all stocks by 2015 and end overfishing in European waters by 2020.

In addition to anthropogenic exploitation, environmental drivers can also cause changes in stock sizes. In particular, the occurrence of strong or weak cohorts (Stachura et al. 2014) can shape population dynamics for many subsequent years and result in large fluctuations in population biomass (Figure 1; Hjort 1914). These dynamics can be traced back to before the onset of industrial fishing, and are especially well documented for the smaller pelagic species that constitute a major proportion of global catches (Finney et al. 2002). The strength of cohorts is determined during the early life stages, when eggs, larvae, and juveniles are highly vulnerable to predation or environmental conditions. Interannual differences in mortality during the early life stages strongly influence the number of fish recruiting to the mature stock. It is this mature stock – the so-called "spawning stock" – that largely determines the reproductive potential of a population. The combined biomass of the sexually mature individuals in a population and the number of juvenile individuals in each cohort that survive to join the population (which we define here as "spawning stock biomass" [SSB] and "recruitment", respectively) represent important measures of the state of a fish population and its overall productivity (Figure 2a).

An unusually strong decline in population size can often be attributed to a combination of unsustainable fishing pressure and detrimental natural conditions, which can suppress somatic growth and diminish physical condition, increase mortality, and cause periods of weak recruitment when affecting the early life stages. This interplay of excessive fishing pressure and environmental fluctuations has been well illustrated by the collapse of major fisheries, such as those of the Norwegian spring-spawning herring (*Clupea harengus*; Dragesund et al. 1997) and the northwestern stocks of Atlantic cod (*Gadus morhua*; Myers et al. 1997). Although a fishing moratorium was implemented in both cases, only the herring stock has fully recovered, due to an exceptionally strong year class.

Figure 1 Capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus*) caught in the Barents Sea. Populations of both species, which are important forage fish in the Barents Sea and Norwegian Sea ecosystems, are known to fluctuate strongly over time because of large variability in recruitment and mortality; moreover, because capelin is a major prey item for juvenile herring, the cohort strength of herring depends on the stock biomass of capelin, and vice versa. Photo credit: ©L Nøttestad/Havforskningsinstituttet

The interplay between regulation and natural fluctuation demonstrates that implementation of sustainable fisheries policies and rebuilding plans form a crucial foundation for stable recovery of fish stocks, but year-class variability and unpredictably large cohorts may also be important contributors to increases in stock size. To test this hypothesis and evaluate the current state of commercially exploited fish stocks in the Northeast Atlantic Ocean, we analyzed time-series data over the period 1960–2015 relating to SSB, recruitment, fishing mortality (F), and catches for all Northeast Atlantic fish stocks, using data reported by the International Council for the Exploration of the Sea (ICES) (see WebTable 1 for details). We also assessed trends over time, examined the potential influence of fisheries catches and recruitment on SSB, assessed the performance of stock size and fishing rates against official management reference points, and included fishing effort data from all EU fleets as an indicator of changes in fishing activity.

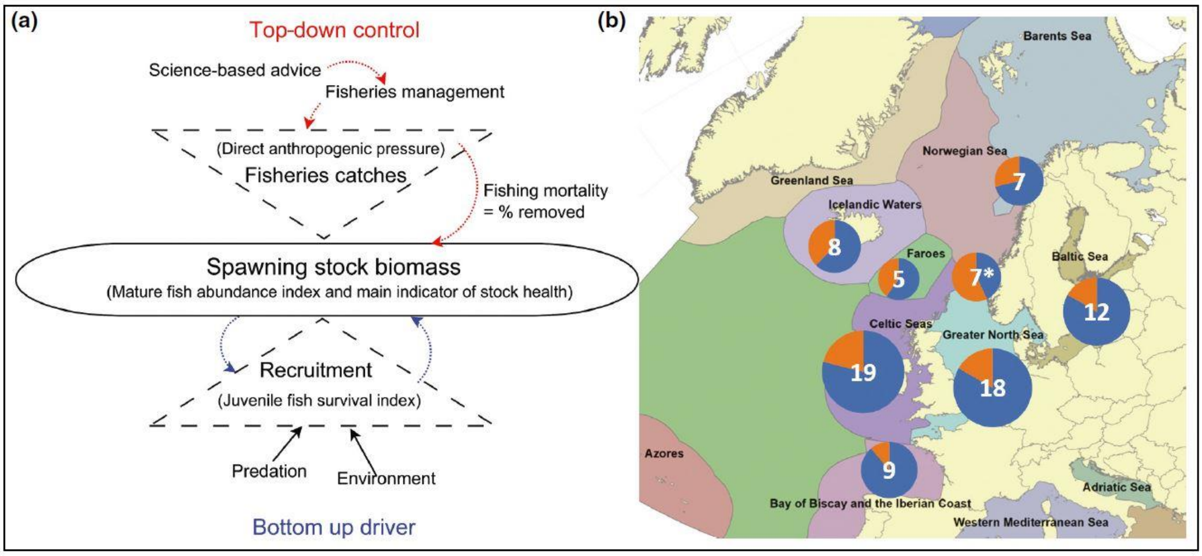

Figure 2 (a) Conceptual diagram of population and fisheries dynamics and (b) map of the study area showing for each region on the map a pie chart that details the number of associated populations and indicates changes in stock size. Changes are shown as the proportion of fish stocks with positive (blue) and negative (red) changes in spawning stock biomass between 2007 and 2015. Fish stocks associated with the Barents Sea and Norwegian Sea were pooled together in one pie chart (placed at the border of the two regions), and stocks with substantial distributions over more than one region are shown separately in the pie chart indicated with an asterisk. The map was provided by the International Council for the Exploration of the Sea (personal communication).

4.2 Methods

Data

In our analysis, we used data from stock assessment reports published by ICES for all European fish stocks with available time-series of annual SSB, recruitment numbers, F, and catches. In total, the study considered 85 different fish stocks from the entire ICES area, encompassing most of the Northeast Atlantic Ocean (WebTable 1). Subareas consisted of the Baltic Sea, Barents Sea, North Sea, Norwegian Sea, Icelandic and East Greenlandic waters, the Iberian coast, Bay of Biscay, and the waters around the British Isles (Figure 2b). Fishing effort data were derived for all available years from the database of the EU Joint Research Centre’s Scientific, Technical and Economic Committee for Fisheries (https://stecf.jrc.ec.europa.eu/dd/effort), and summed annually over all gear types and regions.

To achieve a coherent standardization of SSB, recruitment, and catch among all stocks, we normalized all data to the mean and standard deviation of each time-series. We then calculated general trends using the mean over all stocks and 95% confidence intervals based on the variation around the mean (ie variation among the point estimates in all stocks). We relied on all available data points in each year, and consequently stocks were added gradually after 1960 as data availability permitted. Trends for recent decades aligned well among different subsets of stocks, independent of time-series length (WebFigure 1).

Stock-specific reference points for F and SSB are available from ICES for all fish stocks in the Northeast Atlantic. These reference points are designed to be target levels of stock size and fishing pressure against which the current state of the stock and its fishery can be evaluated in order to determine their sustainability, and to provide guidance for future harvesting (see Table 1 for definitions of five stock-specific reference points: F_{MSY}, F_{MP}, $B_{trigger}$, and B_{PA}). The underlying principles applied to calculate these reference points are based primarily on the individual stock's reproductive potential at different stock sizes, which can differ widely among stocks. We calculated the relationship between SSB and its stock-specific management reference point $B_{trigger}$ or, if $B_{trigger}$ was unavailable, B_{PA}. A given stock is considered to be safe within precautionary limits with a very low risk of collapse when this ratio is equal to or above 1. Similarly, we calculated the ratio between F and F_{MSY} or, if F_{MSY} was unavailable, F_{MP}. Harvesting of a stock is considered to be sustainable if this ratio is at or below 1. Harvesting a stock at F_{MSY} over a longer period is ideal because it should ensure MSY. Because the two reference points for SSB and F (that is, $B_{trigger}$ and B_{PA} for SSB; F_{MSY} and F_{MP} for F) are very similar or identical in most ICES stocks where two or more reference points are available, we combined the different reference points to increase the number of stocks analyzed. Furthermore, because $B_{trigger}$ and F_{MSY} were available for the majority of stocks with reference points, we included only six stocks with BPA and two stocks with F_{MP} in the analysis. Geometric means were used to calculate the means of the ratios between SSB or F and the corresponding reference points. Reference points are subject to current knowledge and the specific assessment methodology applied by the assessing institution (in this case, ICES), and so they may vary over time and among approaches; as such, in our analysis, we also considered standardized trends of SSB and F in addition to reference point ratios. These complementary approaches resulted in a more complete picture that does not rely solely on potentially biased reference points.

For further analysis, two subsets of stocks were generated based on taxonomic or geographic criteria: (1) Atlantic cod, other gadiformes, clupeids, and flatfish; and (2) stocks with eastern, western, northern, or wide distributions. The areas and stock comprising the second subset consisted of: for the western region, the Bay of Biscay, Celtic Sea, Irish Sea, and Southern Shelf (ICES areas VI–XI); for the eastern region, the Baltic Sea and North Sea (ICES areas III–IV); for the northern region, the Barents Sea, Norwegian Sea, Faroese Plateau, and Icelandic Sea (ICES areas I–II, V, and XIV); and finally, for widely distributed stocks, those stocks with substantial geographic distributions or migration patterns encompassing more than one region. Widely distributed stocks are blue whiting (*Micromesistius poutassou*), boarfish (*Capros aper*), the northern stock of European hake (*Merluccius merluccius*), Atlantic mackerel (*Scomber scombrus*), spiny dogfish or spurdog (*Squalus acanthias*), and western horse mackerel (*Trachurus trachurus*).

Table 1 Definition of management reference points

Reference point	Description
F_{MSY}	The exploitation rate expected to produce maximum sustainable yield (MSY) over the long term, given a <5% probability that SSB is below B_{PA}; fishing mortality is reduced below F_{MSY} if SSB is < MSY B_{trigger}
F_{MP}	Fishing mortality reference point adapted to a stock-specific management plan; an alternative for stocks for which F_{MSY} or F_{PA} are not yet available; rarely used in recent years
B_{trigger}	Biomass reference point, usually denoted as “MSY B_{trigger}”, at or above which F_{MSY} is applied in harvest control rules; when SSB < B_{trigger}, fishing mortality is proportionally reduced ($F = F_{\mathrm{MSY}} \times \mathrm{SSB}/B_{\mathrm{trigger}}$)
B_{PA}	Precautionary limit of biomass; biomass limit based on uncertainty estimates that ensure a 95% probability of true SSB being above a critical lower threshold (limiting biomass, B_{lim}) and having full reproductive capacity

Statistical analysis

We used piecewise regression models to search for the main breakpoint (ie the point in a time series when a linear trend switches direction from negative to positive or vice-versa) within the observed trends of SSB. To explore recent trends of individual stocks following major SSB low points and initial policy implementations, we assessed linear regressions of SSB, recruitment, F (and alternatively catch) against time for the period 2000–2015. We also applied multiple regression analyses to the time-series of each fish stock to determine whether F or recruitment (and alternatively whether catch or recruitment) was more strongly correlated with changes in SSB. First-order differences in SSB, depicted as $\Delta SSB(t) = SSB(t) - SSB(t-1)$ were used to represent annual changes in stock size:

$\Delta SSB(t) = a + bF(t-1) + cR(t-1)$

(Eq 1)

and

$\Delta SSB(t) = a + bC(t-1) + cR(t-1)$

(Eq 2),

where t are the years from 1961 to 2015; ΔSSB are first-order differences in SSB from year t–1 to year t; and F, C, and R are fishing mortality, catch, and recruitment in year t–1, respectively, a the intercept, and b and c the regression parameters. All time-series were normalized prior to analysis to facilitate direct comparisons between the parameters.

4.3 Results

Historical fluctuations and breakpoints

Mean standardized SSB indicated that Northeast Atlantic fish stocks declined to a minimum at the beginning of the 21st century and then sharply increased to levels comparable to those of the 1970s (Figure 3). Notably, catches and SSB fluctuated in synchrony from 1960 to the early 2000s, with both variables exhibiting long-term declines until they began to diverge in subsequent years, when SSB increased but catches remained stable and low. Recruitment fluctuated strongly around the mean over the entire time-series, with a decreasing long-term trend and a historical low in the late 1970s. In recent years, recruitment was relatively weak, with a particularly low productivity among stocks spawning around Iceland, along the Norwegian coast, and in the North Sea in the years 2010 and 2011. The last strong recruitment period occurred around 2000, with the highest proportions of productivity occurring among stocks west of the British Isles and in northern areas.

The combined trends of catches and SSB reflected the three major historical phases in Northeast Atlantic fisheries: (quasi-)unregulated fishing activities before 1980, overcapitalized fleets and increasingly severe overfishing between 1980 and 2000, and widespread establishment of stock rebuilding and management plans after 2000 (Cardinale et al. 2013). Implementation of these plans was mirrored by the total effort of the EU fishing fleet, which fell by 25% from 2003 to 2014 (Figure 3). Because this fleet's total fishing effort was highly positively correlated ($P < 0.01$) with the total catches of all analyzed stocks, it can therefore serve as an effective proxy for the overall fishing effort within the Northeast Atlantic Ocean.

When looking at the development of mean normalized SSB values, a breakpoint was found in 2007 ($P < 0.05$). Around this time, the previous downward trend reversed and SSB subsequently increased by 54% until 2015. A significant breakpoint with a positive trend change, as found on aggregated levels, also occurred in 76% of all individual stocks (WebFigure 2): that is, SSB increased after the breakpoint more strongly than before the breakpoint (ie the trend switched from negative to positive or, when positive before the breakpoint, became more steeply positive). Sixty-two percent of SSB breakpoints for these stocks occurred between 2000 and 2010, corresponding to one-third of all stocks.

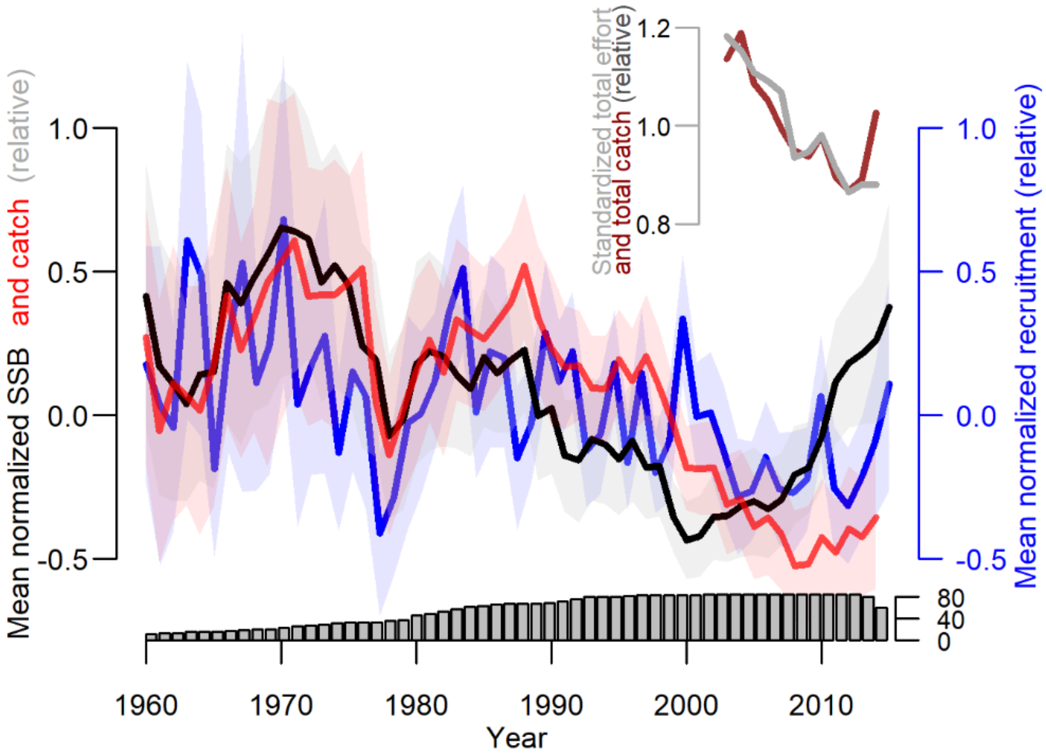

Figure 3 Mean normalized spawning stock biomass (SSB, black line), catches (red line), and recruitment (blue line) of 85 Northeast Atlantic fish stocks from 1960 to 2015, along with standardized total effort (inset graph, gray line) of the EU fleet and total catches (inset graph, dark red line) for the years 2003–2014. For each stock, time-series of SSB, recruitment, and catch data taken from official stock assessment reports were normalized to the mean and standard deviation of each time-series, and subsequently used to calculate the mean over all stocks from all available data in each year. Total annual fishing effort (kilowatts × days at sea) and summed annual catch (kilograms) were standardized to the mean of their entire time-series. Bars along x axis denote number of stocks with available data in each year. Shaded areas around point estimates indicate the 95% confidence intervals.

Indications of the recent recovery

After the 2007 breakpoint, biomass trended upward for most stocks across all ecoregions and taxonomic groups (WebFigure 3). Exceptions to this pattern were the northern and sub-Arctic stocks, which began to increase around 2000 and therefore started to level out toward the end of the decade. Among taxonomic groups, the clupeids also exhibited early-onset increases in biomass, reaching a peak in 2009. The median increase of total SSB over all stocks was 36% between 2007 and 2015, albeit with considerable variability (WebTable 2). The largest increases in SSB during this period occurred in stocks of European hake (551%), plaice (*Pleuronectes platessa*; 455%), and whiting (*Merlangius merlangus*; 451%), whereas the SSB values of specific stocks of European pilchard (*Sardina pilchardus*) and haddock (*Melanogrammus aeglefinus*) fell by more than 50% in 2007. Similar variability was found among the most important commercial stocks, including large (>50%) increases in total SSB for northeast Arctic stocks of Atlantic cod and haddock in the Barents Sea, for North Sea plaice, and for Atlantic mackerel, whereas the SSB values of Icelandic and Norwegian spring-spawning herring were substantially reduced (>37%) after 2007. However, the general pattern of increasing SSB and decreasing catch resulting in lower F was qualitatively consistent among different taxonomic groups and geographic areas (Figure 4).

Overall, exploitation rates declined substantially, with 43% of all stocks below F_{MSY} in 2015 as compared to 25% of stocks in 2007; only Atlantic cod stocks remained substantially above F_{MSY} on average in 2015 (Figure 4). Over the same time period, the SSB values of the majority of stocks (>70%) were higher than the corresponding reference point $B_{trigger}$, but those of Atlantic cod stocks were not (WebFigure 3). SSB shifted, on average, outside of the zone of sustainable stock sizes ($SSB/B_{trigger} > 1$) in the early 2000s, when SSB was at historically low levels, but has shown clear improvements since then (WebFigure 4). At the same time, fishing rates have been moving toward sustainable levels, and have come close to MSY levels ($F/F_{MSY} = 1$). This positive trend has been stable over recent years, is reflected in aggregated indicators (WebFigure 4) and individual stocks (WebFigure 5), and differs markedly from the period around 2000, when the mean of stocks was within the zone of critical stock sizes.

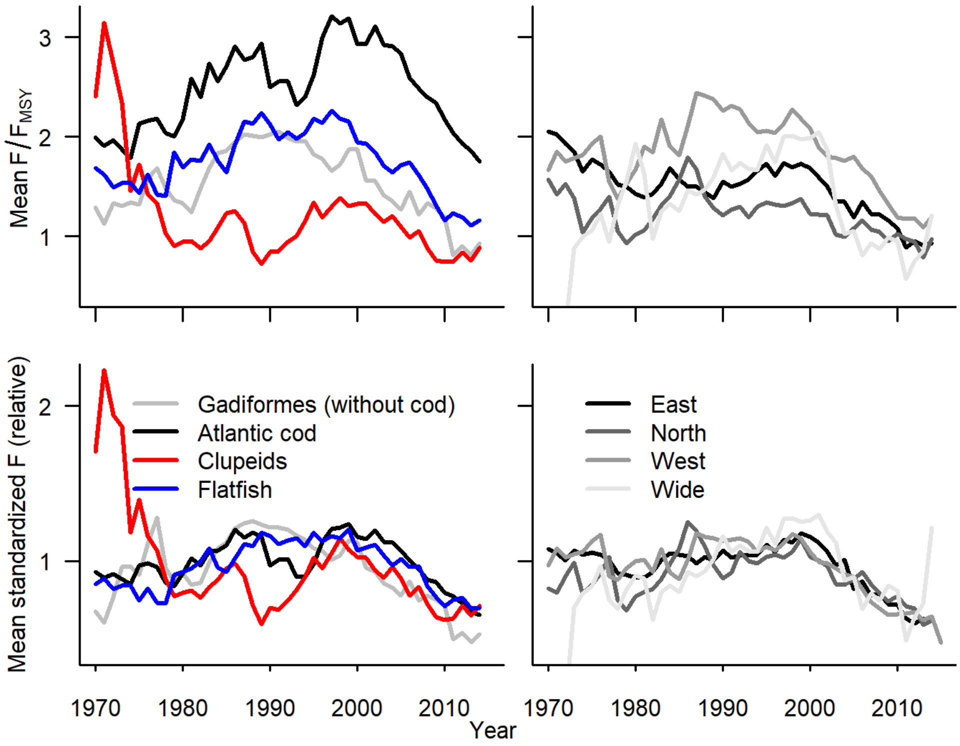

Figure 4 Geometric mean of F/F$_{MSY}$ ratio (top) and standardized fishing mortality F (bottom) for (a) taxonomic groups and (b) geographic regions for the years 1960–2014. F/F$_{MSY}$ was calculated for 59 stocks with available reference points as the ratio between stock-specific annual fishing mortality F and, according to availability and with decreasing priority, F$_{MSY}$ (57 stocks) or F$_{MP}$ (two stocks). F was standardized by dividing the F of each of the 85 stocks by the mean F over the entire time-series.

Statistical analyses revealed strong indications for interdependent effects of F and recruitment on changes in SSB (Figure 5). Statistically significant ($P < 0.05$) positive trends in SSB since 2000 were detected in 34 stocks, whereas negative trends were found for 15 stocks and no clear trends were discernible for 29 stocks. Although these positive trends in SSB were strongly associated with declining F (83% of stocks with statistically significant positive trends in SSB displayed negative F trends), negative trends in F were also found in 50% of stocks with negative trends in SSB (WebTable 3). In contrast, negative trends for recruitment were detected in only 6% of stocks that exhibited increasing SSB. Furthermore, in 24 stocks where SSB did not increase after 2000 despite significant declines in F, recruitment showed negative trends in 11 stocks, no clear trends in 12 stocks, and a positive trend in only one stock. Stocks for which there were no increases in SSB despite a statistically significant negative trend in F included six of 11 cod stocks and five of 11 herring stocks.

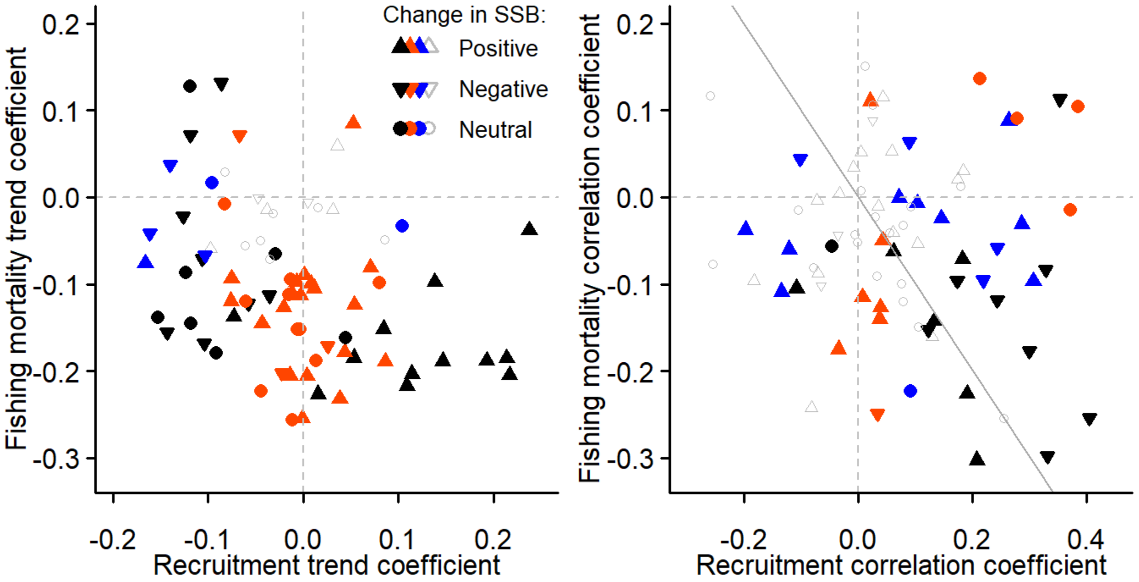

Figure 5 (a) Linear trends and (b) correlation coefficients of multiple regression analysis for F and recruitment. F and recruitment of 82 stocks were (a) linearly regressed against time for the period 2000–2015 or (b) used in multiple regression against SSB for the period 1960–2015. Linear trends for SSB over the period 2000–2015 were used to determine statistically significant (49 stocks for which P < 0.05 and three stocks for which P < 0.1) positive or negative or no change (P > 0.1) in SSB. Statistical significance in both F and recruitment (black), only F (red), only recruitment (blue), or none (no fill) of the coefficients are shown. All time-series were normalized and coefficients are dimensionless. The solid gray line (right) represents the identity line.

Multiple regression analysis over the entire time-series revealed – in the majority of stocks – negative correlations between F and changes in SSB as well as positive correlations between recruitment and changes in SSB (Figure 5), independent of the stock's trend over the past two decades. For stocks in which both covariates were statistically significant, recruitment had a stronger effect than F in stocks with decreasing SSB (78%) and F tended to be stronger in stocks with increasing SSB (67%) (WebTable 4). The results were similar when catch was substituted for F (WebFigure 6), except that increasing SSB was strongly associated with increasing catches, and vice versa.

4.4 Conclusions

Most Northeast Atlantic fisheries experienced unsustainable rates of exploitation for several decades, resulting in a persistent downward trend in stock biomasses. Subsequently, changes in catches followed natural fluctuations in SSB while fishing exceeded sustainable levels, a strong indication that insufficient catch regulations were widespread throughout the region. Representing the largest fraction of total fishing effort within the Northeast Atlantic area, fishing effort by the EU fleet – which was active in almost all fisheries analyzed in this study – decreased substantially and in synchrony with total catches over the past 15 years. These results suggest that the recent recovery of Northeast Atlantic fish stocks was primarily facilitated by improvements in and implementation of more stringent management regulations that reduced effort and exploitation rates, resulting in catches that no longer tracked increases in SSB and that have remained comparatively low ever since. Although statistical analyses of individual stocks indicated the presence of a very strong link between decreasing F and greater stock sizes, our results also suggested that stocks failed to increase in the absence of positive trends in recruitment. Aggregated trends corroborated this pattern, indicating that a period of strong recruitment around 2000 likely contributed to the subsequent reversal of the downward trends in SSB.

For the few Northeast Atlantic stocks that have undergone markedly strong recoveries, such as Atlantic mackerel and European hake, record strong year classes likely initiated and supported increases in stock sizes, as fishing pressures remained above sustainable levels, highlighting that beneficial environmental conditions can facilitate recoveries of individual stocks and can shift regimes toward greater productivity. On the other hand, our analyses suggested that decreasing productivity might prevent stock recoveries in cases where fishing pressure was reduced. Nevertheless, reductions in fishing effort were crucial for reducing exploitation rates and initiating recovery of spawning stocks, and the negative correlations between F and interannual changes in SSB observed for most stocks serve to illustrate the top-down effect of fishing. Our results emphasize that large-scale fisheries can be managed sustainably but only if policies include more cautious regulations that specifically account for periods of lower productivity.

Environmentally driven variability in recruitment is a key factor determining population dynamics in marine fish (Cushing 1982), which was underscored by the statistically significant positive correlations between recruitment and SSB revealed in our analysis. Recruitment data are, however, confounded by population density, and typically affect population dynamics over longer periods and with lags of several years, making it difficult to detect clear signals in aggregated data from the assessment models used in this study. Historically, collapses of single fish stocks typically occurred when severe overfishing coincided with weak recruitment and general downward trends, whereas the combination of stringent regulations and beneficial environmental conditions resulted in large stock biomasses. Consequently, variations in year-class strength are a strong determinant of changes in SSB, and fishing can magnify these fluctuations in stock productivity (Anderson et al. 2008), demonstrating the need for management strategies that can be adapted to periods of low productivity.

In addition to the direct impacts of fishing on spawning stock size, selective fishing can also potentially reduce a stock's reproductive output via removal of the oldest and most fecund individuals (Wright and Gibb 2005). These demographic shifts in populations may also extend to an evolutionary level (Heino et al. 2013), particularly in the absence of adequately regulated fishing selectivity (Zimmermann and Jørgensen 2017). Lower productivity as a long-term consequence of past overfishing could account for why recovery of some stocks was slow or non-existent despite reductions in fishing pressure. Ongoing progress in policy development (EU 2013) notwithstanding, the legacy of overfishing, periods of weak recruitment, and long-term impacts of changes in environmental conditions may therefore undermine the observed increases in SSB, and require adequate responses in continued management and policy-making efforts.

Species distributions, as well as ocean physical conditions and marine ecosystem compositions, will continue to shift in response to climate change, with impacts on commercially relevant stocks (Parmesan and Yohe 2003). In particular, the ranges of several major stocks, including northeast Arctic cod (Kjesbu et al. 2014), Atlantic mackerel (Hughes et al. 2015), and northern European hake (Cormon et al. 2016), may subsequently have expanded; such expansions can be the cause of or serve to intensify conflicts over marine fish resources and ecosystem disturbances. To achieve the stated goal of ending overfishing by 2020 among EU members and reap the benefits of rebuilt fisheries, resource managers and decision makers will require continued improvements to fisheries policies and management strategies, greater cooperation among member states, and reductions in fishing capacity to further decrease exploitation rates, resolve future challenges, and remain effective during phases of lower productivity due to less favorable environmental conditions. Additional challenges remain, especially for species with little or no commercial value or for which data are deficient, and for specific regions, such as the Mediterranean Basin (although not considered in the present study, areas like the Mediterranean are highly relevant for marine biodiversity and regional subsistence; Fernandes et al. 2017). Our findings highlight the need for marine resources to be managed in a manner consistent with the science, and that also considers interactions between ecosystems and non-commercial species, which contrasts sharply with current practices (Skern-Mauritzen et al. 2016). Over the long term, recovered stocks and well-managed marine ecosystems can be expected to provide higher and more stable fisheries yields with less effort, resulting in substantial societal benefits (Costello et al. 2016).

4.5 Acknowledgements

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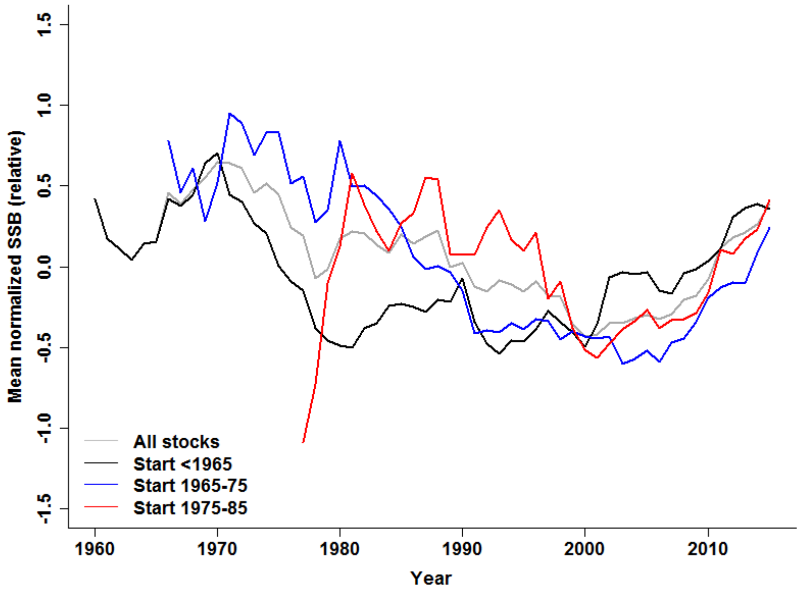
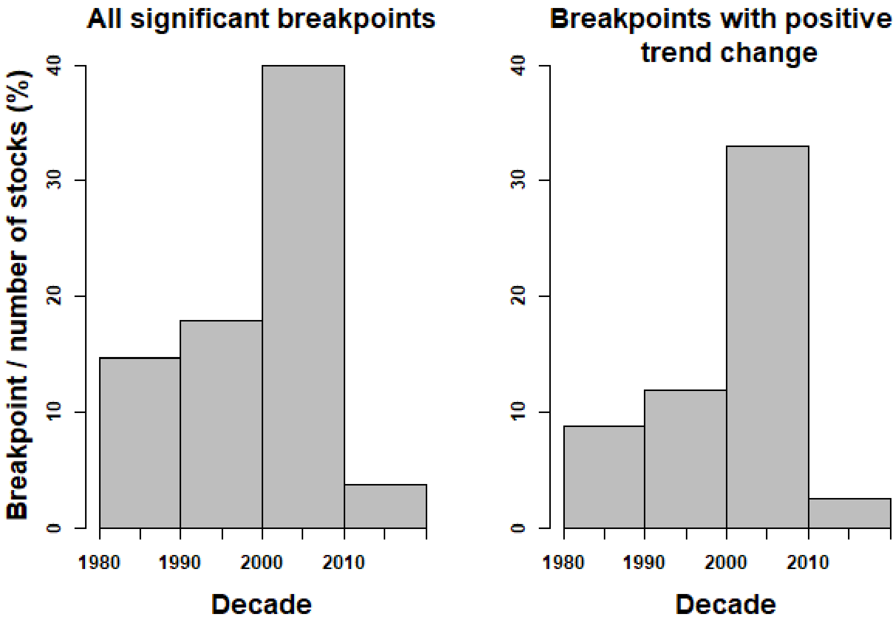
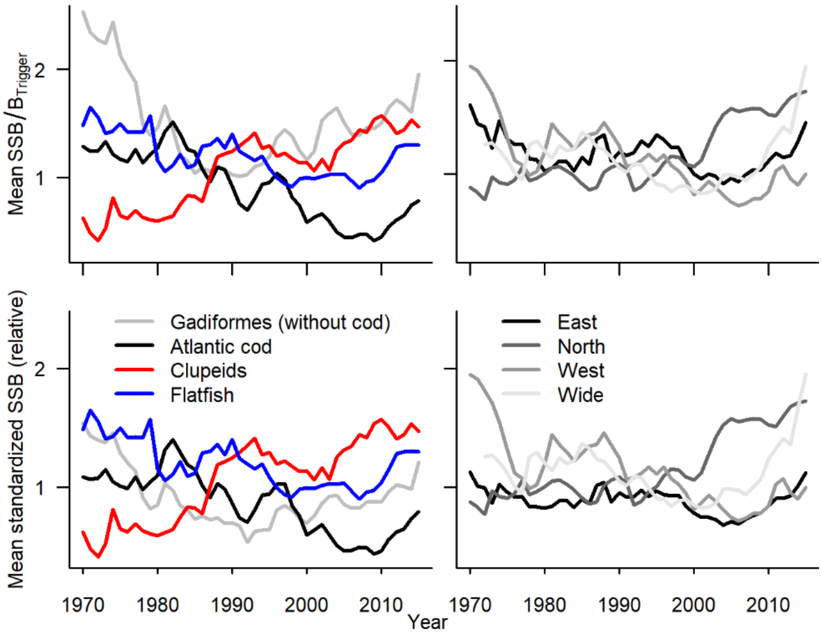
F ZIMMERMANN and KM WERNER – Supporting Information



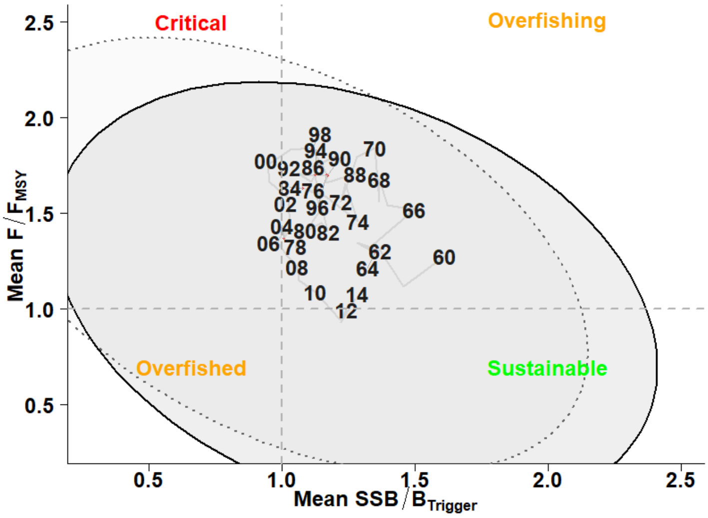
WebFigure 1 Mean standardised spawning stock biomass (SSB) for different subsets of all stocks included in the study: All 85 stocks (grey line), stocks with time series starting before 1965 (16 stocks, black line), stocks with time series starting between 1965 and 1975 (29 stocks, blue line), and stocks with time series starting between 1975 and 1985 (16 stocks, red line).



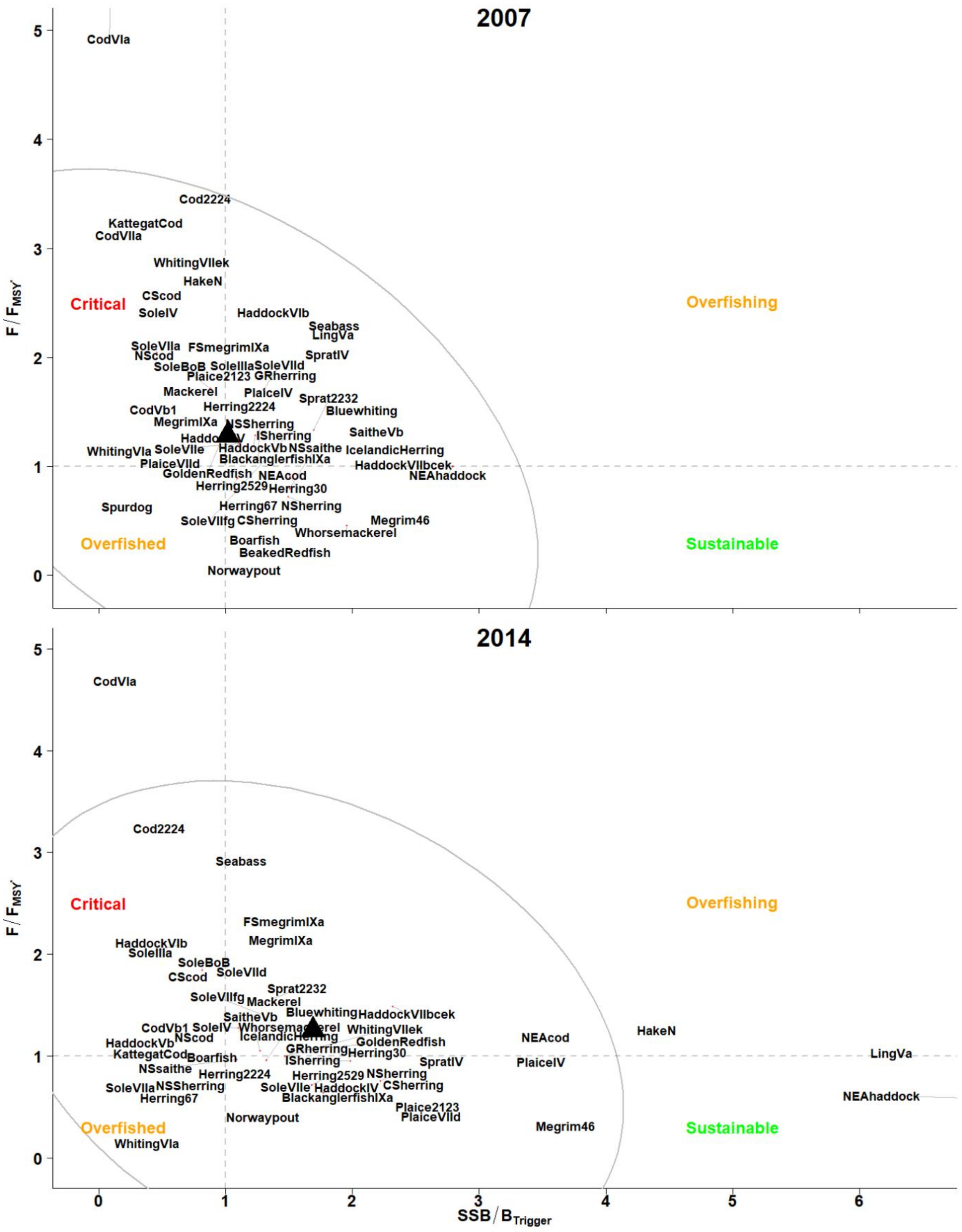
WebFigure 2 Proportion of breakpoints in SSB trends of individual stocks for all significant ($p < 0.05$) breakpoints (left) and breakpoints with positive trend change only (right) in relation to the number of stocks assessed in each decade. Breakpoints were estimated with piecewise regression models in the entire available SSB time series of all 85 stocks. Positive trend change was defined as an increase in the slope value from before to after the breakpoint (slope 1 < slope 2).



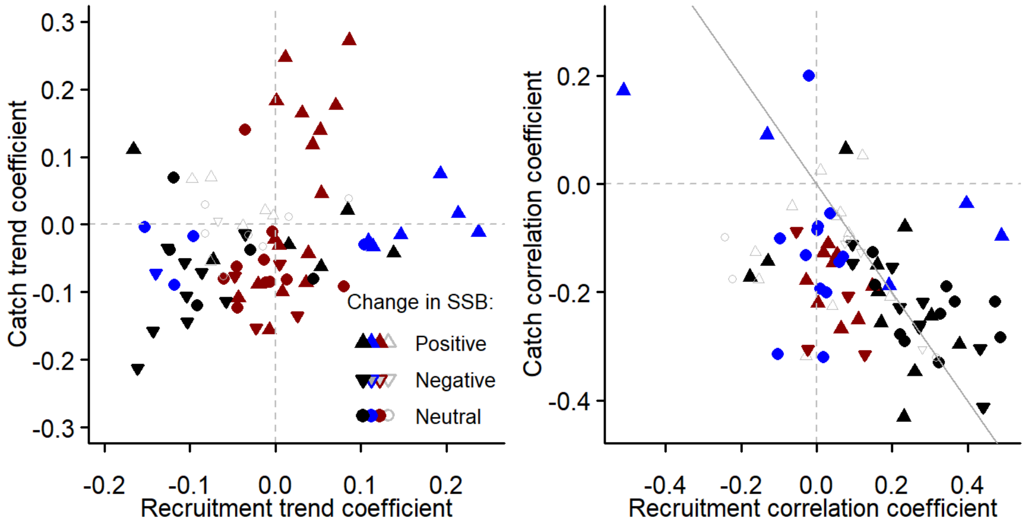
WebFigure 3 Mean SSB/B$_{Trigger}$ ratio (top) and mean standardised SSB (bottom) for taxonomic groups (left) and geographic regions (right) for the years 1970 to 2014. SSB/B$_{Trigger}$ was calculated for 62 stocks as the ratio between stock-specific annual SSB and, according to availability and with decreasing priority: B$_{Trigger}$ (the biomass above which F_{MSY} is applied, 56 stocks) and B$_{PA}$ (F as defined by the precautionary approach; 6 stocks). SSB was standardised by dividing with mean SSB over the entire time series for each of all 85 stocks. Geographic regions include for West: Bay of Biscay, Celtic and Irish Sea, Southern Shelf (ICES areas: VI-XI); East: Baltic and North Sea (ICES areas: III-IV); North: Barents and Norwegian Sea, Faroese Plateau, Icelandic Sea (ICES areas: I-II, V, XIV); Wide: Five stocks with substantial distribution over areas within more than one region.



WebFigure 4 Kobe plot of geometric mean SSB/B$_{Trigger}$ and geometric mean F/F_{MSY} in the years 1960-2014 for all 55 stocks with both biological reference points B$_{Trigger}$ and F_{MSY}. Numbers denote the years and the four different quadrants separated by dashed lines describe the four possible states: no overfishing but overfished ("Overfished": SSB/ B$_{Trigger}$ < 1, F/F_{MSY} < 1) overfishing but not overfished ("Overfishing": SSB/B$_{Trigger}$ > 1, F/F_{MSY} > 1), overfishing and overfished ("Critical": SSB/B$_{Trigger}$ < 1, F/F_{MSY} > 1) and no overfishing and not overfished ("Sustainable": SSB/B$_{Trigger}$ > 1, F/F_{MSY} < 1). Only even numbered years are displayed. Circles indicate the 50% probabilities for the years 2000 (dashed line) and 2014 (solid line).



WebFigure 5 Kobe plot of SSB/$B_{Trigger}$ and F/F_{MSY}* for all 55 stocks with both biological reference points $B_{Trigger}$ and F_{MSY}* in the years 2007 (top) and 2014 (bottom). The mean (black triangle) and 95% probability (solid circle) for each year are shown. The four different quadrants separated by dashed lines describe the four possible states: no overfishing but overfished SSB (“Overfished”: SSB/$B_{Trigger}$ < 1, F/F_{MSY}* < 1), overfishing but not overfished SSB (“Overfishing”: SSB/$B_{Trigger}$ > 1, F/F_{MSY}* > 1), overfishing and overfished SSB (“Critical”: SSB/ $B_{Trigger}$ < 1, F/F_{MSY}* > 1) and no overfishing and not overfished SSB (“Sustainable”: SSB/$B_{Trigger}$ > 1, F/F_{MSY}* < 1).



WebFigure 6 Linear trend coefficients (left) and correlation coefficients of multiple regression analysis (right) for catch and recruitment. Catch and recruitment of 82 stocks were linearly regressed against time for the period 2000-2015 or in multiple regression against SSB for the period 1960-2015. Linear trends for SSB in 2000-2015 were used to determine statistically significant (49 stocks with $p < 0.05$ and 3 with $p < 0.1$) positive or negative as well as no changes ($p > 0.1$) in SSB. Statistical significance in both catch and recruitment (black), only catch (dark red), only recruitment (blue), or none (no fill) of the coefficients is shown. All time series were normalized and coefficients dimensionless. The grey solid line (right) represents the identity line.

Stock ID	Species	Definition	Time series	Source
SandeelSA1	*Ammodytes*	Sandeel in the Dogger Bank area (SA 1)	1983-2015	(1)
SandeelSA2	*Ammodytes*	Sandeel in the South Eastern North Sea (SA 2)	1983-2015	(1)
SandeelSA3	*Ammodytes*	Sandeel in the Central Eastern North Sea (SA 3)	1983-2015	(1)
TuskVa	*Brosme brosme*	Tusk in Division Va and Subarea XIV	1980-2015	(2)
Boarfish	*Capros aper*	Boarfish in ICES Subareas VI, VII, VIII	1991-2014	(3)
Herring2224	*Clupea harengus*	Herring in Division IIIa and Subdivisions 22 - 24 (Western Baltic spring spawners)	1991-2015	(4)
Herring2529	*Clupea harengus*	Herring in Subdivisions 25 - 29 (excluding Gulf of Riga) and 32	1974-2015	(4)
Herring30	*Clupea harengus*	Herring in Subdivision 30 (Bothnian Sea)	1973-2015	(4)
Herring31	*Clupea harengus*	Herring in Subdivision 31 (Bothnian Bay)	1980-2014	(4)
Herring67	*Clupea harengus*	Herring in Divisions VIa and VIIb,c (West of Scotland, West of Ireland)	1957-2015	(5)
CSherring	*Clupea harengus*	Herring in Division VIIa South of 52° 30' N and VIIg,h,j,k (Celtic Sea and South of Ireland)	1958-2015	(5)
GRherring	*Clupea harengus*	Herring in Subdivision 28.1 (Gulf of Riga)	1977-2015	(4)
IcelandicHerring	*Clupea harengus*	Herring in Division Va (Icelandic summer-spawners)	1987-2015	(2)
ISherring	*Clupea harengus*	Herring in Division VIIa North of 52° 30' N (Irish Sea)	1961-2015	(5)
NSherring	*Clupea harengus*	Herring in Subarea IV and Divisions IIIa and VIId (North Sea autumn spawners)	1947-2015	(1)
NSSherring	*Clupea harengus*	Herring in Subareas I, II, V and Divisions IVa and XIVa (Norwegian spring-spawning herring)	1950-2015	(6)
Seabass	*Dicentrarchus labrax*	Seabass in Divisions IVb and c, VIIa, and VIId,e,f,g,h (Central and South North Sea, Irish Sea, English Channel, Bristol Channel, Celtic Sea)	1985-2015	(5)
AnchovyBoB	*Engraulis encrasicolus*	Anchovy in Subarea VIII (Bay of Biscay)	1987-2016	(7)
Cod2224	*Gadus morhua*	Cod in Subdivisions 22-24 (Western Baltic Sea)	1970-2015	(4)
CodVb1	*Gadus morhua*	Cod in Subdivision Vb1 (Faroe Plateau)	1959-2015	(2)
CodVIa	*Gadus morhua*	Cod in Division Via (West of Scotland)	1981-2015	(5)
CodVIIa	*Gadus morhua*	Cod in Division VIIa (Irish Sea)	1968-2013	(8)
CoastalCod	*Gadus morhua*	Norwegian coastal cod	1984-2014	(3)
CScod	*Gadus morhua*	Cod in Division VIIe-k (Celtic Sea)	1971-2015	(5)
IcelandicCod	*Gadus morhua*	Cod in Division Va (Iceland grounds)	1955-2015	(2)
KattegatCod	*Gadus morhua*	Cod in Division IIIa East (Kattegat)	1997-2014	(4)
NEAcod	*Gadus morhua*	Cod in Subareas I and II (Northeast Arctic)	1946-2015	(3)
NScod	*Gadus morhua*	Cod in Subarea IV and Divisions VIId and IIIa West (North Sea, Eastern English Channel, Skagerrak)	1963-2015	(9)

Cod2532	*Ghadus morhua*	Cod in Subdivisions 25-32 (Eastern Baltic)	1966-2014	(4)
FSmegrimIXa	*Lepidorhombus boscii*	Four-spot megrim in Divisions VIIIc and Ixa	1986-2015	(7)
Megrim46	*Lepidorhombus spp*	Megrim in Divisions IVa and Via	1985-2014	(5)
Megrim78	*Lepidorhombus whiffiagonis*	Megrim in Divisions VIIb-k and VIIIa,b,d	1984-2014	(5)
MegrimIXa	*Lepidorhombus whiffiagonis*	Megrim in Divisions VIIIc and IXa	1986-2015	(7)
BlackanglerfishIXa	*Lophius budegassa*	Black-bellied anglerfish in Divisions VIIIc and IXa (Cantabrian Sea, Atlanic Iberian Waters)	1980-2015	(7)
AnglerfishIXa	*Lophius piscatorius*	White anglerfish in Divisions VIIIc and IXa (Cantabrian Sea, Atlanic Iberian Waters)	1980-2015	(7)
IcelandCapelin	*Mallotus villosus*	Capelin in Subareas V and XIV and Division IIa west of 5°W (Iceland and Faroes Grounds, East Greenland, Jan Mayen area)	1979-2014	(2)
NEACapelin	*Mallotus villosus*	Capelin in Subareas I and II (Barents Sea)	1973-2014	(3)
HaddockIV	*Melanogrammus aeglefinus*	Haddock in Subarea IV and Divisions IIIa West and VIa (North Sea, Skagerrak and West of Scotland)	1963-2015	(9)
HaddockVb	*Melanogrammus aeglefinus*	Haddock in Division Vb	1957-2015	(2)
HaddockVIb	*Melanogrammus aeglefinus*	Haddock in Vib (Rockall)	1991-2015	(5)
HaddockVIIa	*Melanogrammus aeglefinus*	Haddock in Division VIIa (Irish Sea)	1992-2015	(5)
HaddockVIIbcek	*Melanogrammus aeglefinus*	Haddock in Divisions VIIb,c,e-k	1993-2015	(5)
IcelandicHaddock	*Melanogrammus aeglefinus*	Haddock in Division Va (Icelandic haddock)	1979-2015	(2)
NEAhaddock	*Melanogrammus aeglefinus*	Haddock in Subareas I and II (Northeast Arctic)	1950-2015	(3)
WhitingIV	*Merlangius merlangus*	Whiting in Subarea IV and Divisions VIId	1990-2015	(9)
WhitingVIa	*Merlangius merlangus*	Whiting in Division Via	1981-2015	(5)
WhitingVIIek	*Merlangius merlangus*	Whiting in Division VIIbc,e-k	1982-2015	(5)
HakeN	*Merluccius merluccius*	Hake in Subareas IV, VI, and VII and Divisions IIIa, VIIIa,b,d (Northern stock)	1978-2015	(7)
HakeS	*Merluccius merluccius*	Hake in Divisions VIIIc and IXa (Southern stock)	1982-2015	(7)
Bluewhiting	*Micromesistius poutassou*	Blue whiting in Subareas I-IX, XII and XIV (Combined stock)	1981-2014	(6)
BluelingVb	*Molva dypterygia*	Blue ling in Vb (Faroes)	1966-2014	(10)
LingVa	*Molva molva*	Ling in Division Va	1982-2015	(2)
LingVb	*Molva molva*	Ling in Vb	1996-2014	(10)
Plaice2123	*Pleuronectes platessa*	Plaice in Subdivisions 21-23 (Kattegat, Belts, and Sound)	1999-2014	(4)
Plaice2432	*Pleuronectes platessa*	Plaice in Subdivisions 24 - 32 (Baltic Sea)	2002-2014	(4)
PlaiceIV	*Pleuronectes platessa*	Plaice in IV (North Sea)	1957-2015	(9)

PlaiceVIIa	*Pleuronectes platessa*	Plaice in Division VIIa (Irish Sea)	1993-2014	(5)
PlaiceVIId	*Pleuronectes platessa*	Plaice in Division VIId (Eastern Channel)	1980-2015	(9)
PlaiceVIIe	*Pleuronectes platessa*	Plaice in Division VIIe (Western Channel)	1980-2014	(5)
PlaiceVIIfg	*Pleuronectes platessa*	Plaice in Divisions VIIf,g (Celtic Sea)	1993-2013	(5)
PlaiceVIIhk	*Pleuronectes platessa*	Plaice in Divisions VIIh-k (Southwest of Ireland)	1993-2014	(5)
SaitheVa	*Pollachius virens*	Saithe in Division Va (Icelandic saithe)	1980-2015	(2)
SaitheVb	*Pollachius virens*	Saithe in Division Vb (Faroe Saithe)	1961-2015	(2)
NEAsaithe	*Pollachius virens*	Saithe in Subareas I and II (Northeast Arctic)	1960-2015	(3)
NSsaithe	*Pollachius virens*	Saithe in Subarea IV (North Sea) Division IIIa West (Skagerrak) and Subarea VI (West of Scotland and Rockall)	1967-2015	(9)
Greenlandhalibut	*Reinhardtius hippoglossoides*	Greenland halibut in subareas I and II	1992-2014	(3)
SardineIXa	*Sardina pilchardus*	Sardine in Divisions VIIIc and IXa	1978-2015	(7)
Mackerel	*Scomber scombrus*	Mackerel in the Northeast Atlantic (combined Southern, Western and North Sea spawning components)	1972-2015	(6)
TurbotIV	*Scophthalmus maximus*	Turbot in Subarea IV	1975-2014	(9)
BeakedRedfish	*Sebastes mentella*	Beaked redfish in Subareas I and II	1992-2013	(3)
GoldenRedfish	*Sebastes norvegicus*	Golden Redfish in Subareas V, VI, XII and XIV	1971-2015	(2)
SoleIIIa	*Solea solea*	Sole in Division IIIa and Subdivisions 22-24 (Skagerrak, Kattegat, the Belts and western Baltic)	1984-2014	(4)
SoleIV	*Solea solea*	Sole in Subarea IV (North Sea)	1957-2015	(9)
SoleVIIa	*Solea solea*	Sole in Division VIIa (Irish Sea)	1970-2015	(5)
SoleVIId	*Solea solea*	Sole in Subarea VIId (Eastern Channel)	1982-2015	(9)
SoleVIIe	*Solea solea*	Sole in Division VIIe (Western Channel)	1969-2015	(5)
SoleVIIfg	*Solea solea*	Sole in Divisions VIIf,g (Celtic Sea)	1971-2015	(5)
SoleVIIhk	*Solea solea*	Sole in Divisions VIIh-k (Southwest of Ireland)	1993-2014	(5)
SoleBoB	*Solea solea*	Sole in Divisions VIIIa, b (Bay of Biscay North and Central)	1984-2015	(7)
SpratIV	*Sprattus sprattus*	Sprat in Subarea IV (North Sea)	1974-2015	(1)
Sprat2232	*Sprattus sprattus*	Sprat in Subdivision 22-32 (Baltic Sea)	1974-2015	(4)
Spurdog	*Squalus acanthias*	Spurdog in the Northeast Atlantic	1980-2013	(11)
HorsemackerelIXa	*Trachurus trachurus*	Horse mackerel in Division IXa (Southern stock)	1992-2015	(7)
Whorsemackerel	*Trachurus trachurus*	Western horse mackerel in Divisions IIa, IVa, Vb, VIa, VIIa-c, e-k, VIII (Western stock)	1982-2015	(6)

Norwaypout	*Trisopterus esmarkii*	Norway Pout in Subarea IV (North Sea) and IIIa (Skagerrak - Kattegat) - Autumn assessment	1983-2015	(9)

WebTable 1 Details of the stock assessments used in the analyses. The table shows the stock ID as defined for this study, the species name, the stock definition, the available years of each time series and the specific source of the data.

References

1. ICES. Report of the Herring Assessment Working Group for the Area South of 62ºN (HAWG). International Council for the Exploration of the Sea (ICES), 2015.
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3. ICES. Report of the Arctic Fisheries Working Group (AFWG). International Council for the Exploration of the Sea (ICES), 2015.
4. ICES. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). International Council for the Exploration of the Sea (ICES), 2015.
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6. ICES. Report of the Working Group on Widely Distributed Stocks (WGWIDE). International Council for the Exploration of the Sea (ICES), 2015 ICES CM 2010/ACOM:15.
7. ICES. Report of the Working Group for the Bay of Biscay and the Iberian waters Ecoregion (WGBIE). International Council for the Exploration of the Sea (ICES), 2015 ICES CM 2010/ACOM:15.
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11. ICES. Report of the Working Group on Elasmobranch Fishes (WGEF). International Council for the Exploration of the Sea (ICES), 2015 ICES CM 2015/ACOM:19.

Stock	$B_{trigger}$	B_{PA}	B_{MP}	SSB 2007	Final SSB*	Change (%)	F_{MSY}	F_{PA}	F_{MP}	F 2007	Final F	Change (%)
SandeelSA1	215000	215000	-	222246	178712	-19.59	-	-	-	0.28	0.37	34.42
SandeelSA2	100000	100000	-	86901	91545	5.34	-	-	-	0.04	0.07	75.61
SandeelSA3	195000	195000	-	70118	202124	188.26	-	-	-	0.62	0.52	-16.53
TuskVa	-	-	-	5.05	6.03	19.44	0.20	-	-	0.35	0.26	-25.71
Boarfish	347889	-	-	429320	312898	-27.12	0.18	-	-	0.06	0.13	119.30
Herring2224	110000	-	-	122516	129845	5.98	0.32	-	-	0.49	0.26	-47.21
Herring2529	600000	600000	-	655926	1000071	52.47	0.22	0.41	-	0.20	0.16	-19.43
Herring30	316000	-	-	477347	669461	40.25	0.15	-	-	0.14	0.15	13.24
Herring31	-	-	-	0.54	1.24	129.13	-	-	-	0.97	0.78	-20.10
Herring67	410000	410000	-	486991	194194	-60.12	0.16	-	-	0.10	0.09	-8.45
CSherring	54000	54000	-	72019	89937	24.88	0.26	-	-	0.13	0.19	43.46
GRherring	60000	-	-	88226	90347	2.40	0.32	0.40	-	0.58	0.34	-41.57
IcelandicHerring	-	300000	-	702111	341973	-51.29	0.22	-	-	0.25	0.26	1.46
ISherring	9500	9500	-	13377	17633	31.81	0.26	-	-	0.30	0.25	-16.37
NSherring	-	1000000	-	1497039	2215525	47.99	0.27	-	-	0.19	0.20	4.85
NSSherring	5000000	5000000	5000000	6276000	3946000	-37.13	0.15	0.15	0.13	0.16	0.11	-30.45
Seabass	8000	8000	-	14854	6925	-53.38	0.13	-	-	0.30	0.38	27.45
AnchovyBoB	-	-	-	31381	152711	386.64	-	-	-	0.00	0.17	4150.00
Cod2224	38400	38400	-	32370	23742	-26.65	0.26	-	-	0.90	0.84	-6.44
CodVb1	40000	40000	-	17387	18781	8.02	0.32	0.35	-	0.49	0.41	-15.52
CodVIa	22000	22000	-	2428	3363	38.54	0.19	0.60	-	1.10	0.89	-19.40
CodVIIa	10000	10000	-	1584	3109	96.28	0.40	0.72	-	1.25	1.16	-7.20
CoastalCod	-	-	-	63540	64356	1.28	-	-	-	0.28	0.22	-22.39
CScod	10300	10300	-	5157	7676	48.85	0.32	0.56	-	0.82	0.57	-30.50
IcelandicCod	220000	-	-	207394	546376	163.45	-	-	-	0.51	0.28	-45.31
KattegatCod	-	10500	-	3868	4347	12.38	-	-	0.40	1.28	0.54	-57.80
NEAcod	460000	460000	-	666542	1139000	70.88	0.40	0.40	-	0.37	0.48	29.46
NScod	165000	165000	-	72911	148896	104.22	0.33	-	-	0.67	0.39	-41.17
Cod2532	-	88200	-	72620	122516	68.71	-	-	-	0.86	0.45	-47.51

FSmegrimIXa	4600	4600	-	4732	6573	38.91	0.17	-	-	0.35	0.39	10.95
Megrim46	0.50	-	-	1.18	1.84	55.42	1.00	-	-	0.46	0.32	-30.74
Megrim78	-	-	-	0.74	1.40	89.34	-	-	-	1.43	0.87	-39.29
MegrimIXa	910	910	-	780	1089	39.62	0.17	-	-	0.25	0.36	47.12
BlackanglerfishIXa	0.50	-	-	0.70	0.98	41.29	1.00	-	-	1.06	0.59	-44.62
AnglerfishIXa	-	-	-	6071	7546	24.30	0.19	-	-	0.31	0.25	-19.35
IcelandCapelin	-	-	-	410000	424000	3.41	-	-	-	-	-	-
NEACapelin	-	-	-	844000	873000	3.44	-	-	-	-	-	-
HaddockVIIa	-	-	-	1.52	2.93	93.60	-	-	-	-	-	-
HaddockIV	88000	88000	-	79630	145650	82.91	0.38	-	-	0.47	0.24	-49.16
HaddockVb	35000	35000	-	43113	18133	-57.94	0.25	0.25	-	0.32	0.29	-11.01
HaddockVIb	9000	9000	-	12411	13052	5.16	0.20	0.40	-	0.48	0.42	-12.37
HaddockVIIbcek	10000	10000	-	24065	33387	38.74	0.40	0.89	-	0.41	0.60	46.19
IcelandicHaddock	45000	-	-	162863	78357	-51.89	-	-	-	0.56	0.31	-44.80
NEAhaddock	80000	80000	-	223463	770000	244.58	0.35	0.47	-	0.35	0.15	-56.45
WhitingIV	-	-	-	185089	263195	42.20	-	-	0.15	0.26	0.23	-10.85
WhitingVIa	-	39900	-	4186	23058	450.84	0.22	-	-	0.25	0.03	-88.31
WhitingVIIek	40000	40000	-	29473	83052	181.79	0.32	-	-	0.92	0.32	-65.17
HakeN	46200	46200	-	38250	249017	551.02	0.27	-	-	0.73	0.34	-53.42
HakeS	-	-	-	12786	18856	47.47	0.24	-	-	0.94	0.68	-27.24
Bluewhiting	2250000	2250000	-	4672000	3965000	-15.13	0.30	0.32	-	0.45	0.20	-56.42
BluelingVb	-	-	-	0.24	0.35	45.83	-	-	-	0.10	0.03	-70.00
LingVa	9500	-	-	17596	66421	277.48	0.24	-	-	0.53	0.25	-53.58
LingVb	-	-	-	12729	34402	170.26	-	-	-	0.36	0.16	-56.42
Plaice2123	5553	5553	-	5277	14402	172.92	0.37	0.67	-	0.68	0.20	-70.80
Plaice2432	-	-	-	1677	3748	123.49	-	-	-	0.63	0.62	-0.96
PlaiceIV	230000	230000	-	309077	901694	191.74	0.19	0.6	-	0.32	0.18	-43.75
PlaiceVIIa	-	-	-	11704	16817	43.69	-	-	-	0.15	0.10	-32.41
PlaiceVIId	25826	25826	-	14626	81191	455.11	0.25	-	-	0.26	0.11	-56.44
PlaiceVIIe	-	-	-	0.55	1.96	256.83	-	-	-	1.35	0.50	-62.97

PlaiceVIIfg	-	-	-	1888	2577	36.49	-	-	-	0.76	0.96	26.08
PlaiceVIIhk	-	-	-	0.35	0.62	78.00	-	-	-	1.39	0.73	-47.16
SaitheVa	65000	-	-	151684	138502	-8.69	-	-	-	0.28	0.19	-32.16
SaitheVb	55000	55000	-	120818	82089	-32.06	0.30	0.30	-	0.40	0.32	-20.45
NEAsaithe	-	220000	-	530725	337357	-36.43	-	0.35	-	0.26	0.29	10.00
NSsaithe	200000	200000	-	301555	199270	-33.92	0.32	0.40	-	0.26	0.31	20.78
Greenlandhalibut	-	500000	-	582071	733870	26.08	-	-	-	0.03	0.03	11.11
SardineIXa	-	-	-	476945	139409	-70.77	-	-	-	0.25	0.27	8.73
Mackerel	3000000	3000000	-	2191288	3620056	65.20	0.22	0.25	-	0.37	0.34	-9.12
TurbotIV	-	-	-	0.39	0.44	12.95	-	-	-	0.99	1.14	15.08
BeakedRedfish	600000	-	-	884928	832597	-5.91	0.065	-	-	0.01	0.01	-42.86
GoldenRedfish	220000	-	-	216300	346700	60.29	0.097	-	-	0.13	0.10	-18.40
SoleIIIa	2000	2000	-	2027	1252	-38.23	0.22	0.3	-	0.40	0.41	4.55
SoleIV	37000	37000	-	17465	41137	135.54	0.2	-	-	0.48	0.26	-47.11
SoleVIIa	3100	3100	-	1426	992	-30.43	0.16	0.30	-	0.33	0.11	-67.71
SoleVIId	8000	8000	-	10388	8143	-21.61	0.30	0.40	-	0.51	0.55	7.84
SoleVIIe	2800	1800	-	3095	4452	43.82	0.27	-	-	0.33	0.19	-41.70
SoleVIIfg	2200	2200	-	2883	2620	-9.12	0.31	0.37	-	0.33	0.44	32.93
SoleVIIhk	-	-	-	0.77	0.97	25.29	-	-	-	0.93	0.70	-25.00
SoleBoB	13000	13000	-	11423	12012	5.16	0.26	0.42	-	0.45	0.48	7.87
SpratIV	142000	142000	-	255703	576000	125.26	0.70	-	-	1.41	0.65	-54.25
Sprat2232	570000	570000	-	967000	753000	-22.13	0.26	0.32	-	0.35	0.41	17.27
Spurdog	963700	-	-	215591	243135	12.78	0.03	-	-	0.02	0.01	-22.22
HorsemackerelIXa	-	-	-	417138	529830	27.02	0.11	-	-	0.06	0.04	-29.78
Whorsemackerel	634577	-	-	1241670	723560	-41.73	0.13	-	-	0.06	0.12	109.33
Norwaypout	150000	150000	-	172482	227638	31.98	0.60	-	-	0.02	0.23	913.04

WebTable 2 Reference points, spawning stock biomass (SSB) and fishing mortality (F) for all stocks used in the analysis. Information provided contains the identifier of the stock, reference points $B_{trigger}$, B_{PA}, B_{MP}, F_{MSY}, F_{PA}, F_{MP}, SSB and F in 2007 and at the end of available time series (see Table 1 for details) as well as corresponding change within this period. All values were rounded to two digits after the decimal point.

Stock	**SSB**	**p-value**	**F**	**p-value**	**Catch**	**p-value**	**Rec**	**p-value**
AnchovyBoB	0.10	0.10	**-0.10**	**0.02**	**-0.09**	**0.08**	0.08	0.22
Anglerfish9a	**0.10**	**p<0.01**	-0.01	0.22	0.00	0.94	-0.04	0.13
Bluewhiting	**-0.13**	**0.02**	**-0.16**	**0.01**	**-0.16**	**0.01**	**-0.14**	**0.02**
Cod3.2224	**-0.08**	**0.01**	**-0.20**	**p<0.01**	**-0.15**	**p<0.01**	-0.02	0.12
Cod3.2532	**0.02**	**0.01**	**-0.23**	**p<0.01**	**-0.03**	**p<0.01**	**0.02**	**0.06**
Cod5b1	**-0.08**	**p<0.01**	-0.07	0.22	**-0.14**	**p<0.01**	**-0.10**	**0.01**
Cod6a	**-0.03**	**p<0.01**	**-0.11**	**0.01**	**-0.01**	**0.05**	**-0.04**	**0.07**
Cod7a	-0.01	0.33	**-0.07**	**p<0.01**	**-0.04**	**p<0.01**	**-0.03**	**0.02**
CoastalCod	0.00	0.73	**-0.10**	**p<0.01**	**-0.05**	**0.01**	-0.01	0.21
CScod	0.03	0.49	**-0.11**	**0.01**	-0.03	0.33	-0.02	0.74
IcelandCod	**0.11**	**p<0.01**	**-0.21**	**p<0.01**	**-0.03**	**0.04**	0.00	0.88
KattegatCod	**-0.08**	**0.01**	**-0.17**	**p<0.01**	**-0.13**	**p<0.01**	0.03	0.67
NEAcod	**0.24**	**p<0.01**	**-0.18**	**p<0.01**	**0.12**	**p<0.01**	0.04	0.11
NScod	**0.09**	**p<0.01**	**-0.25**	**p<0.01**	**-0.02**	**p<0.01**	0.00	0.91
Haddock4	-0.02	0.54	**-0.15**	**p<0.01**	**-0.01**	**p<0.01**	0.00	0.42
Haddock5b	**-0.23**	**p<0.01**	-0.04	0.12	**-0.21**	**p<0.01**	**-0.16**	**0.01**
Haddock7b	-0.03	0.53	**-0.18**	**p<0.01**	**-0.12**	**p<0.01**	**-0.09**	**0.06**
Haddock7bcek	0.08	0.14	-0.07	0.16	**0.14**	**p<0.01**	-0.04	0.59
IcelandHaddock	-0.05	0.45	**-0.14**	**p<0.01**	0.00	0.96	**-0.15**	**0.02**
NEAhaddock	**0.30**	**p<0.01**	**-0.09**	**p<0.01**	**0.18**	**p<0.01**	0.00	0.99
Greenlandhalibut	**0.15**	**p<0.01**	-0.06	0.28	0.07	0.12	-0.10	0.23
HakeN	**0.26**	**p<0.01**	**-0.19**	**p<0.01**	**0.27**	**p<0.01**	0.09	0.17
HakeS	**0.05**	**p<0.01**	-0.01	0.55	**0.16**	**p<0.01**	0.03	0.62
Herring3.2224	**-0.04**	**0.03**	**-0.17**	**p<0.01**	**-0.11**	**p<0.01**	**-0.10**	**p<0.01**
Herring3.2529	**0.12**	**p<0.01**	**-0.22**	**p<0.01**	-0.02	0.11	**0.11**	**0.05**
Herring3.30	**0.10**	**p<0.01**	**0.08**	**0.03**	**0.14**	**p<0.01**	0.05	0.26
Herring3.31	**0.09**	**p<0.01**	**-0.11**	**0.02**	0.01	0.63	0.00	0.96
Herring67	**-0.11**	**p<0.01**	**-0.02**	**0.02**	**-0.03**	**p<0.01**	**-0.13**	**p<0.01**
CSherring	**0.17**	**p<0.01**	**-0.20**	**p<0.01**	-0.03	0.35	*0.11*	*0.05*
GRherring	0.03	0.20	**-0.12**	**p<0.01**	**-0.08**	**p<0.01**	-0.06	0.37
IcelandHerring	0.01	0.85	**-0.15**	**p<0.01**	-0.09	0.18	**-0.12**	**0.04**
ISherring	**0.12**	**p<0.01**	**-0.15**	**p<0.01**	**0.02**	**0.01**	**0.08**	**0.01**
NSherring	0.01	0.66	-0.02	0.13	-0.02	0.66	-0.03	0.42
NSSherring	0.01	0.55	**-0.01**	**0.01**	-0.01	0.70	-0.08	0.11
Ling5a	**0.24**	**p<0.01**	**-0.10**	**0.01**	**0.25**	**p<0.01**	0.01	0.86
Ling5b	**0.21**	**p<0.01**	**-0.19**	**p<0.01**	0.07	0.21	**0.19**	**p<0.01**
Horsemackerel9a	0.02	0.77	-0.05	0.13	0.04	0.24	0.09	0.13
Whorsemackerel	0.01	0.71	**-0.09**	**0.05**	**-0.04**	**0.03**	*-0.12*	*0.07*
Mackerel	**0.23**	**p<0.01**	**-0.08**	**0.02**	**0.18**	**0.01**	0.07	0.27
Megrim78	*0.11*	*0.05*	**-0.12**	**0.03**	-0.05	0.32	-0.08	0.25
Megrim9a	0.02	0.50	-0.01	0.80	0.01	0.61	0.02	0.50
FSmegrim9a	**0.22**	**p<0.01**	**-0.12**	**p<0.01**	**0.05**	**0.04**	0.05	0.32
Norwaypout	0.04	0.48	-0.03	0.28	-0.03	0.23	*0.10*	*0.06*
Plaice3.2123	**0.15**	**0.01**	**-0.21**	**p<0.01**	-	-	-0.01	0.82
Plaice3.2432	**0.24**	**p<0.01**	**-0.20**	**p<0.01**	-	-	**0.22**	**p<0.01**
Plaice4	**0.31**	**p<0.01**	**-0.23**	**p<0.01**	**-0.04**	**0.05**	0.04	0.24

Plaice7a	**0.11**	**p<0.01**	**-0.10**	**p<0.01**	**-0.16**	**p<0.01**	-0.01	0.91
Plaice7d	**0.23**	**p<0.01**	**-0.19**	**p<0.01**	0.02	0.78	**0.21**	**p<0.01**
Plaice7e	**0.16**	**0.02**	**-0.19**	**p<0.01**	-0.02	0.43	**0.15**	**p<0.01**
Plaice7fg	**0.21**	**p<0.01**	0.06	0.31	**-0.09**	**p<0.01**	0.04	0.63
Plaice7hk	**-0.08**	**0.01**	p<0.01	0.99	**-0.08**	**p<0.01**	-0.05	0.21
BeakedRedfish	**0.10**	**p<0.01**	*-0.04*	*0.08*	-0.01	0.88	**0.24**	**p<0.01**
GoldenRedfish	**0.14**	**p<0.01**	**-0.11**	**p<0.01**	0.02	0.11	-0.01	0.76
Saithe5a	**0.09**	**0.05**	**-0.09**	**p<0.01**	0.07	0.10	-0.08	0.12
Saithe5b	*-0.11*	*0.06*	0.04	0.32	-0.07	0.19	**-0.14**	**0.05**
NEAsaithe	**-0.06**	**0.04**	**0.07**	**p<0.01**	0.01	0.87	-0.07	0.32
NSsaithe	-0.04	0.12	0.02	0.42	-0.02	0.13	**-0.10**	**0.01**
Sandeel4SA1	0.03	0.15	**-0.22**	**p<0.01**	**-0.12**	**0.03**	-0.04	0.33
Sandeel4SA2	0.04	0.10	**-0.15**	**0.01**	**-0.09**	**p<0.01**	-0.01	0.86
Sandeel4SA3	*0.07*	*0.05*	**-0.18**	**p<0.01**	**-0.06**	**0.01**	*0.05*	*0.06*
Sardine9a	**-0.13**	**p<0.01**	**0.13**	**0.03**	**-0.07**	**p<0.01**	**-0.09**	**0.01**
Seabass	-0.04	0.40	**0.13**	**p<0.01**	**0.07**	**0.03**	**-0.12**	**p<0.01**
Sole3a	**-0.14**	**p<0.01**	**0.07**	**0.03**	-	-	**-0.12**	**p<0.01**
Sole4	0.02	0.31	**-0.19**	**p<0.01**	**-0.08**	**p<0.01**	0.01	0.62
Sole7a	**-0.11**	**p<0.01**	**-0.12**	**p<0.01**	**-0.11**	**p<0.01**	**-0.06**	**p<0.01**
Sole7d	0.06	0.29	0.03	0.48	0.03	0.56	-0.08	0.16
Sole7e	**0.15**	**p<0.01**	**-0.14**	**p<0.01**	**-0.05**	**0.01**	**-0.07**	**0.08**
Sole7fg	-0.01	0.56	-0.06	0.19	-0.08	0.13	-0.06	0.25
Sole7hk	**0.08**	**0.02**	**-0.15**	**p<0.01**	**-0.11**	**p<0.01**	-0.04	0.53
SoleBoB	**0.09**	**0.03**	**-0.13**	**0.02**	**-0.09**	**p<0.01**	-0.02	0.70
Sprat4	**0.11**	**0.04**	**-0.10**	**0.03**	**-0.04**	**0.04**	*0.14*	*0.06*
Sprat3.2232	**-0.06**	**0.01**	-0.01	0.86	**-0.06**	**0.01**	0.01	0.92
Spurdog	0.00	0.66	**-0.16**	**p<0.01**	**-0.08**	**p<0.01**	**0.04**	**p<0.01**
Turbot4	-0.02	0.34	-0.05	0.29	**-0.06**	**p<0.01**	-0.04	0.42
Tusk5a	**0.11**	**p<0.01**	-0.08	0.13	**0.11**	**0.08**	**-0.17**	**0.01**
Whiting4	**-0.09**	**0.05**	**-0.07**	**0.01**	**-0.06**	**p<0.01**	*-0.11*	*0.05*
Whiting6a	0.01	0.68	**-0.26**	**p<0.01**	**-0.09**	**p<0.01**	-0.01	0.74
Whiting7ek	**0.11**	**0.02**	**-0.10**	**p<0.01**	**-0.10**	**0.02**	0.01	0.87

WebTable 3 Correlation coefficients and p-values for linear regressions of SSB, fishing mortality, catch and recruitment against time (years) for the period 2000-2015. Bold values indicate statistically significant (p<0.05) and values in italic marginally significant (p<0.1) correlation coefficients.

Stock	F	p-value	Rec	p-value
AnchovyBoB	-0.08	0.61	-0.26	0.15
Anglerfish9a	-0.04	0.43	**-0.20**	**p<0.01**
Bluewhiting	*-0.12*	*0.07*	**0.24**	**p<0.01**
Cod3.2224	0.09	0.30	0.03	0.76
Cod3.2532	-0.01	0.87	**0.10**	**0.01**
Cod5b1	**-0.15**	**0.01**	**0.12**	**0.04**
Cod6a	0.06	0.15	*0.09*	*0.05*
Cod7a	0.14	0.11	**0.21**	**0.02**
CoastalCod	-0.10	0.26	0.08	0.35
CScod	-0.01	0.89	**0.37**	**p<0.01**
IcelandCod	0.03	0.45	-0.01	0.83
KattegatCod	*-0.25*	*0.09*	0.03	0.73
NEAcod	-0.06	0.26	*-0.12*	*0.06*
NScod	**-0.11**	**p<0.01**	0.01	0.84
Haddock4	-0.02	0.91	-0.11	0.41
Haddock5b	*-0.08*	*0.07*	**0.33**	**p<0.01**
Haddock7b	-0.25	0.16	0.25	0.16
Haddock7bcek	0.15	0.47	0.01	0.96
IcelandHaddock	0.11	0.29	0.02	0.80
NEAhaddock	*-0.06*	*0.07*	*0.06*	*0.07*
Greenlandhalibut	0.00	0.91	-0.03	0.41
HakeN	*-0.10*	*0.05*	**-0.11**	**0.04**
HakeS	**0.11**	**0.01**	0.02	0.59
Herring3.2224	-0.10	0.36	-0.07	0.51
Herring3.2529	0.00	0.98	*0.07*	*0.05*
Herring3.30	-0.01	0.83	0.03	0.46
Herring3.31	-0.02	0.66	**0.14**	**0.02**
Herring67	-0.06	0.36	**0.24**	**p<0.01**
CSherring	0.05	0.23	0.06	0.22
GRherring	0.10	0.25	**0.38**	**p<0.01**
IcelandHerring	0.09	0.34	**0.28**	**0.01**
ISherring	**-0.14**	**0.01**	0.04	0.49
NSherring	-0.04	0.31	-0.01	0.91
NSSherring	0.01	0.78	0.00	0.89
Ling5a	**-0.13**	**p<0.01**	0.04	0.21
Ling5b	-0.10	0.33	**0.31**	**0.01**
Horsemackerel9a	*-0.22*	*0.09*	0.09	0.44
Whorsemackerel	-0.05	0.42	0.00	0.97
Mackerel	0.05	0.51	0.00	0.95
Megrim78	0.12	0.31	0.04	0.70
Megrim9a	-0.15	0.16	0.10	0.32
FSmegrim9a	-0.09	0.36	-0.07	0.48
Norwaypout	0.01	0.94	0.18	0.32
Plaice3.2123	**-0.30**	**p<0.01**	**0.21**	**p<0.01**
Plaice3.2432	0.09	0.32	**0.26**	**0.02**
Plaice4	**-0.14**	**p<0.01**	**0.13**	**p<0.01**

Plaice7a	-0.04	0.73	0.06	0.62
Plaice7d	*-0.07*	*0.09*	**0.18**	**p<0.01**
Plaice7e	**-0.23**	**0.01**	**0.19**	**p<0.01**
Plaice7fg	0.02	0.93	0.17	0.42
Plaice7hk	0.04	0.40	*-0.10*	*0.08*
BeakedRedfish	0.00	0.96	-0.07	0.29
GoldenRedfish	*-0.05*	*0.09*	0.04	0.11
Saithe5a	-0.05	0.49	0.10	0.17
Saithe5b	-0.10	0.11	**0.22**	**p<0.01**
NEAsaithe	-0.04	0.26	-0.04	0.36
NSsaithe	-0.09	0.10	0.03	0.56
Sandeel4SA1	0.12	0.59	-0.26	0.24
Sandeel4SA2	0.29	0.17	**-0.50**	**0.02**
Sandeel4SA3	-0.24	0.18	-0.08	0.64
Sardine9a	**0.11**	**0.05**	**0.35**	**p<0.01**
Seabass	-0.12	0.15	0.08	0.32
Sole3a	**-0.18**	**0.02**	**0.30**	**p<0.01**
Sole4	-0.08	0.53	-0.08	0.51
Sole7a	**-0.10**	**0.03**	**0.17**	**p<0.01**
Sole7d	-0.03	0.87	0.08	0.68
Sole7e	**-0.18**	**0.01**	-0.03	0.60
Sole7fg	-0.01	0.86	0.09	0.13
Sole7hk	-0.16	0.26	0.13	0.36
SoleBoB	-0.03	0.76	**0.29**	**0.01**
Sprat4	0.03	0.80	0.18	0.13
Sprat3.2232	**-0.25**	**p<0.01**	**0.40**	**p<0.01**
Spurdog	**-0.06**	**p<0.01**	**-0.05**	**p<0.01**
Turbot4	-0.02	0.48	0.03	0.35
Tusk5a	-0.11	0.14	*-0.13*	*0.07*
Whiting4	**-0.30**	**0.04**	**0.33**	**0.02**
Whiting6a	-0.04	0.50	0.05	0.34
Whiting7ek	-0.10	0.70	-0.18	0.27

WebTable 4 Correlation coefficients and p-values from multiple regressions of first order differences in SSB against fishing mortality and recruitment. Bold values indicate statistically significant (p<0.05) and values in italic marginally significant (p<0.1) correlation coefficients.

5 Publication 4

Evidence for limited adaptive responsiveness to large-scale spatial variation of habitat quality

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Abstract

The ability of organisms to adapt their foraging behaviour to spatial variations in food availability and habitat quality is crucial to maximize energy intake and hence fitness. Under ideal conditions, habitat selection should result in a spatial distribution of individuals such that their fitness (energy reserves or condition) is roughly equal across habitats of varying quality. Using 11 years of field data on Atlantic cod (*Gadus morhua*) distribution along the Greenland shelf, we investigated the foraging behaviour and life history of cod in heterogeneous environments. We combined information on energy reserves of cod with spatially-resolved diet composition data to derive a measure of habitat quality and heterogeneity. Energy reserves in individual fish were best explained by the particular area they inhabited, whereas growth, population density, food quantity and interannual effects were of minor importance. Condition differed on relatively small spatial scales, at which cod would be capable of redistributing in favour of high quality habitats. Our results indicate that particular areas may persistently allow higher fitness by sustaining high-conditioned individuals but suggest that replenishment of well-conditioned individuals in these high-quality habitats may take longer than expected. We conclude that cod exhibited limited scope in its behavioural response to spatial variation of habitat quality, leading to spatio-temporal persistent differences in energy reserves. Current climate change and fishing activities alter ecosystems and affect habitat heterogeneity and the adaptive responsiveness of species to such changes in habitat quality is important in natural resource management.

5.1 Introduction

Habitat selection is an important aspect of foraging behaviour influencing many life-history traits, such as growth and maturation schedules and fecundity (Sutherland 1996, Stamps 2009, Morris 2011, Lloret et al. 2013). Use of poor quality habitats leads to reduced condition and fitness due to low food intake, whereas surplus energy storages obtained in high quality habitats can enhance reproductive potential (Sutherland 1996, Morris 2011, Lloret et al. 2013, Hixon et al. 2014). The amount of energy that individuals can acquire in a habitat mainly depends on resource richness, number of consumers and their competitive abilities (Sutherland 1996, Munday 2001, Morris 2011). Ultimately, energy intake reflects an individual’s ability to respond to environmental heterogeneity in space and time (Sutherland 1996, Munday 2001, Morris 2011, Casini et al. 2016b).

A successful model of habitat choice predicting consumer distribution in relation to resource availability is called “ideal free distribution” (IFD) (Fretwell & Lucas 1969, Sutherland 1996, Stamps 2009, Morris 2011). It is a conceptual model, which predicts that all individuals in particular areas and populations should have approximately the same realized fitness, because they distribute themselves according to the available food resources (Fretwell & Lucas 1969, Kacelnik et al. 1992, Sutherland 1996, Morris 2006, 2011). The theory assumes that all individuals are equal in their competitive abilities, can freely move in the environment, have perfect knowledge of resource distribution, always choose the best habitat and that traveling between habitats has no costs (Fretwell & Lucas 1969, Kacelnik et al. 1992, Kennedy & Gray 1993, Sutherland 1996, Stamps 2009). As a result, individuals should move to areas with the highest resource availability first, until increasing density causes a reduction of fitness, whereby individuals start to utilize less suitable habitats (Fretwell & Lucas 1969, Kacelnik et al. 1992, Sutherland 1996). However, the assumptions on ideal behaviour and equal competitive abilities are simplifications and while studies conducted on smaller scales, such as tank experiments or field studies from freshwater lakes, often show similar fitness across food patches, distribution patterns on large scales often show discrepancies to IFD predictions (Kacelnik et al. 1992, Van Duren & Glass 1992, Tregenza 1995, Sutherland 1996, Haugen et al. 2006, Stamps 2009, Morris 2011, Meager et al. 2017). Reasons for these discrepancies are mainly imperfect knowledge of resource distribution, interference, unequal competitive abilities and varying travel cost, all of which violate the assumptions behind IFD (Abrahams 1986, Van Duren & Glass 1992, Kennedy & Gray 1993, Tregenza 1995). Especially on larger scales, animals are often not capable to correctly perceive the true distribution of resources, because searching behaviour and extensive screening of the environment is too costly and may increase the risk of mortality (Sutherland 1996, Stamps 2009). This often implies that individuals would rather accept lower-quality habitats, and the resulting relative density in each particular habitat or food patch does not correctly reflect its intrinsic resource quality (Stamps 2009). It appears that the optimization processes necessary to obtain equal fitness in a heterogeneous environment require high degrees of behavioural plasticity and responsiveness. Considering the rapidity and magnitude of expected environmental changes under global warming, it is important to investigate whether animals can quickly respond adaptively to spatial variation of habitat quality (Sutherland 1996, Morris 2011, Fossheim et al. 2015).

We investigated large-scale habitat selection, adaptive behaviour and the influence of habitat quality on food intake and energy acquisition of Atlantic cod (*Gadus morhua*), a widely distributed marine predator and an ecologically and economically iconic species (Kurlansky 2011). Cod is an ideal study species for this purpose, because it is considered to be an opportunistic feeder, where stomach contents reflect the species composition in the environment and individuals can be used as environmental samplers (Lilly & Parsons 1991, Fahrig et al. 1993, Link & Garrison 2002). The study was carried out on the populations located on the subarctic Greenland shelf (Figure 1a), which is at one of its northernmost areas of distribution. The environment is considered to be quite heterogeneous resulting in a relatively patchy distribution of mature cod among the banks of the area. Here, the cod populations respond rapidly and extensively to environmental fluctuations and climate change will likely alter ecosystem structure and habitats (Rätz & Lloret 2003, Drinkwater 2005, 2006, McBride et al. 2014, Fossheim et al. 2015). Throughout the study area, energy reserves (i.e. liver condition) and growth of cod vary spatially, indicating that the populations might not be ideally distributed and that fitness might vary between areas (Figure 1, for methodology, see methods section). We used cod diet to draw direct conclusions about the surrounding habitat structure (Lilly & Parsons 1991, Fahrig et al. 1993, Link & Garrison 2002)

In this study we used data collected over 11 years, allowing us to investigate spatio-temporal patterns of energy reserves and their relationship with spatial variability of food quality, fish density and growth. By combining spatially resolved data of food composition and energy reserves, which was used to infer habitat quality and resource distribution, we investigated the research question, if energy reserves and distribution patterns were adapted to different environments.

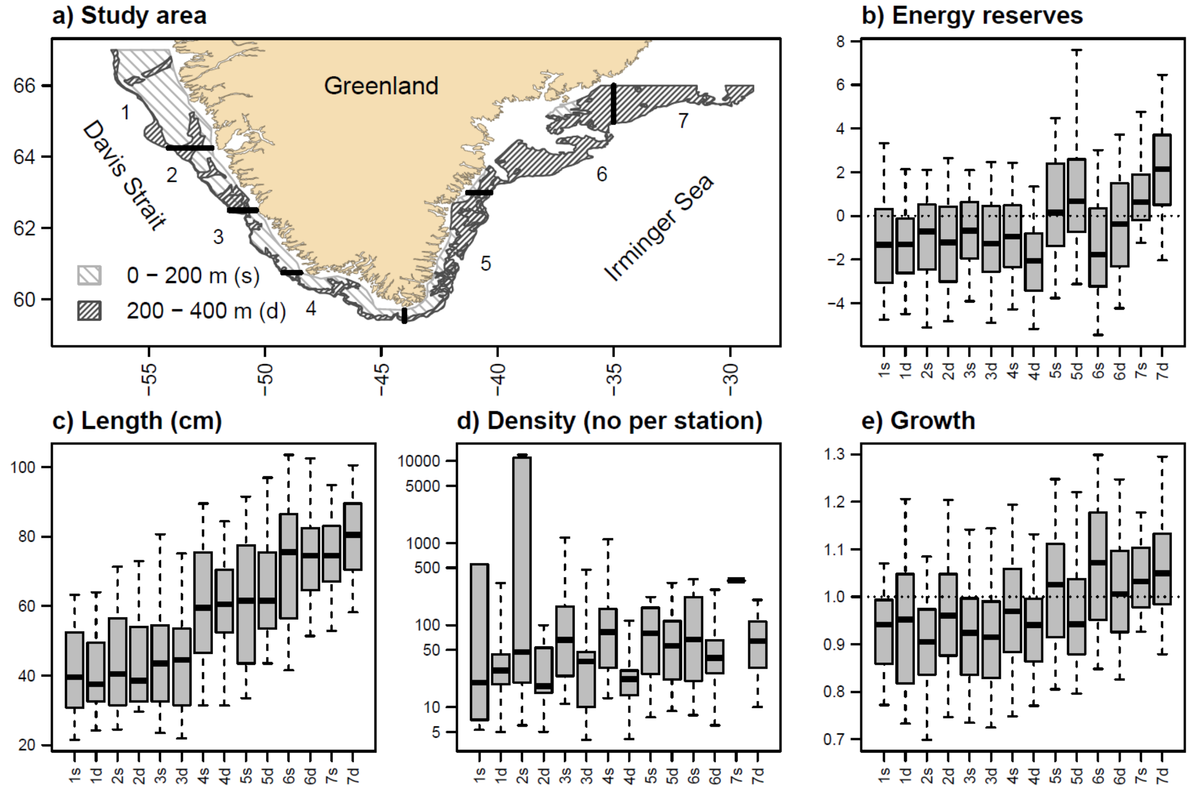

Figure 1 a) Study area as divided into seven subareas (1-7). Each subarea was further subdivided into a shallow (0-200 m, s) and a deep (200-400 m, d) zone b) Spatial variation of energy reserves c) Length distribution over the 14 different subareas d) Spatial variation of cod density e) Spatial variation of growth (residual length at age). For all box-whisker plots, box limits are the 25% and 75% quantiles, with the median denoted by the bold line. Whiskers show the 90% quantiles (5% and 95%).

5.2 Material and methods

Data collection and sampling strategy

We based all analyses on samples collected during eight groundfish surveys with FRV Walther Herwig III in Greenland waters during the periods of 2006-2011 and 2015-2016 (Fig. 1a). Each year, the survey started East off Greenland in mid-October from where sampling was carried out southwards towards the southern tip and northwards to West Greenland during an approximate total sampling duration of four weeks. In order to collect samples, we used a fisheries survey bottom trawl net. The survey area was pre-stratified into seven subareas with a maximum depth of 400 m (Fig. 1a), of which each subarea was subdivided in a shallow (0-200 m) and a deep (200 – 400 m) part. At least five 30 minute hauls in each of the 14 subareas at fixed locations were planned for each survey. Because poor weather conditions often restricted sampling effort in November, sample coverage was generally better in East and South Greenland (Subareas 4-7) than in West Greenland (Subareas 1-3) (Appendix S1). If catches allowed, at least 30 fish were sampled to obtain a representative length distribution of the total catch. Total length was measured to the nearest 1 cm and eviscerated weight and liver weight to the nearest 1 decigram. Only fish whose stomachs were not everted, were used for the study. Stomachs were removed from the abdominal cavity and individually frozen at -30 °C for later analysis. Age was determined by reading annual rings in the ear stones (i.e. otoliths) and used to compute the mean length at age for each age class.

Diet composition and habitat heterogeneity

In order to gain insights into the spatial habitat heterogeneity of the area inhabited by cod along the Greenland shelf, diet composition was determined by analysing stomach contents, which were assumed to roughly represent the prey composition in the environment (Lilly & Parsons 1991, Fahrig et al. 1993, Link & Garrison 2002). Diet composition is one of the strongest predictors of energy storage levels in cod and influences vitality, fertility, egg quality and mortality (Danulat 1986, Jobling 1988, Lie et al. 1988, Kjesbu et al. 1991, DeBlois & Rose 1996, Marteinsdottir & Steinarsson 1998, Lambert & Dutil 2000, Morais et al. 2001, Rosenlund et al. 2004, Rideout & Rose 2006, Rideout et al. 2006, Sherwood et al. 2007, Pardoe et al. 2008, Lloret et al. 2013, Casini et al. 2016a b). Identification of fish species was conducted either visually or by examining the species-specific shape of the ear stone, which was compared with the available literature (Whitfield & Blaber 1978, Whitehead et al. 1984, Härkönen 1986, Scott & Scott 1988, Campana 2004) and a reference collection available at the Thünen Institute of Sea Fisheries. Wet weight of each prey item was measured to the nearest 1 mg. Statistical analyses and the comparison of feeding habits required the grouping of some taxa into taxonomically or functionally distinct categories. Rarely occuring species or groups were grouped based on their position in the water column, i.e. pelagic or benthic. If this could not be distinguished (mainly for decapoda and cephalopoda), taxa were assigned to one of the three groups “crustacea others”, “fish others” or “others”. Due to its relative importance and ease in identification, capelin (*M. villosus*) was given its own taxonomic category. Diet items were identified as “benthic remains”, when they could not be clearly identified but related to benthic feeding (i.e. stones, sponges). Altogether 14 prey categories were used in the statistical analyses (Appendix S2). In some cases digestion was far developed and no identification was possible. Stomachs which consisted of more than 70 % of unidentified prey material, were excluded from the analysis. All other samples were standardised by setting the total weight of prey categories to 1. In total, 3315 samples were in the analysis. In order to indicate, if diet quantity was important to predict energy reserves, we calculated the total fullness index for each individual (TFI) (Daan 1973, Lilly & Parsons 1991), relating stomach content weight to fish length, using the equation:

Total fullness index = $\frac{full\ stomach\ weight - empty\ stomach\ weight}{fish\ length^3 * 1000}$

Energy reserves and growth performance

To indicate individual growth performance and long-term feeding success we calculated a growth index by dividing each individual's length at age of capture by the mean length at age for the corresponding age class.

Growth index = $\frac{individual\ length\ at\ age}{mean\ length\ of\ that\ age\ group}$

In cod, the amount of energy acquired is reflected in the liver size, because cod stores energy in the liver which increases in weight during the feeding season and from where energy is transferred to the gonads prior to reproduction (Bogucki & Trzesinski 1950, Eliassen & Vahl 1982, Kjesbu et al. 1991, Lambert & Dutil 1997, Mello & Rose 2005, Røjbek et al. 2012, Lloret et al. 2013). Large energy storages indicate high-quality food supply and a lipid-rich diet, which is advantageous during reproduction and leads to increased fecundity of cod (Lie et al. 1986, 1988, Kjesbu et al. 1991, 1998, Marteinsdottir & Steinarsson 1998, Marshall et al. 1999, Lambert & Dutil 2000, Morais et al. 2001, Rideout et al. 2006, Pardoe et al. 2008, Lloret et al. 2013). However, while energy reserves as represented in the liver index provide one of the most important parental effects on fitness (Kjesbu et al. 1991, Lambert & Dutil 1997, Marshall et al. 1999, Lloret et al. 2013), using it has limitations because it cannot capture all factors driving the reproductive success of an individual. The liver index reacts to changing diets within 8-12 weeks, what makes it a seasonally and spatially dynamic index but it cannot reflect long-term patterns and might have spatially differed several months before or after our field sampling (Lie et al. 1988, Morais et al. 2001, Pardoe et al. 2008). Fatty acid composition in the gonads can vary with differing diets and influence reproductive success, but remaining undetected through liver size (Røjbek et al. 2012, Stoltenberg 2019).

The liver index was used as proxy for the size of energy reserves and calculated using the equation:

Liver index = $\frac{liver\ weight}{eviscerated\ weight\ *100}$

Because the mean and the variance of liver index increased with fish length and hence varying liver indices could be an artefact of fish lengths, we fitted a generalized additive model with log link ($p<0.001$)

$L_i = exp\ (\beta_{0i} + s(T_i) + \beta_{1i} A_i\ ) + \varepsilon_i,$

where the dependent variable *L* is the liver index and the independent variables *T* is total fish length and *A* the year for each sample *i* and *s* a penalized spline and *ε* the gamma distributed error. Year was used as a factor to consider interannual differences e.g. due to fluctuations in population size or feeding conditions. Model residuals were subsequently used to visualize the spatial variation of energy reserves (Fig. 1b).

Statistical analysis

In order to test the validity of ideal free distribution and relate energy reserves to fish density, individual growth and temporal and spatial patterns of diet, we divided our statistical approach into a univariate and a multivariate part. All statistical analyses were conducted using the R software (R: Development Core Team. 2016) using the packages *vegan* (Oksanen et al. 2018), *MuMIn* (Bartoń 2012) and *mgcv* (Wood 2011). *ggplot2* (Wickham 2016) was used for visualization of the results.

In order to test if individuals have the same condition across different areas, univariate multiple regression models were used to explore variables influencing the liver index. A Generalized Linear Model (GLM) with gamma distribution and log link was used with liver index as response and fish length, subarea, year, density (number of cod per station), total fullness index and growth as explanatory variables. Subarea and year were used as factors and additionally two-way interactions were tested between length and subarea respectively year, as well as between year and subarea. The most parsimonious model was selected by backward selection (Crawley 2005) using Bayesian Information Criterion (BIC) (Schwarz 1978) and the "dredge" function of the MuMln package (Bartoń 2012). BIC was chosen over Akaikes Information Criterion (AIC) (Akaike 1974) because BIC adapts better to the number of samples and punishes complex models based on high sample sizes (3315 in our study) (Aho et al. 2014). The most parsimonious model was

$L_i = exp\ (\beta_{0i} + \beta_{1i} * T_i + \beta_{2i} S_i) + \varepsilon_i,$

where *L* is the dependent variable liver index, *T* the total fish length and *S* the subarea for each sample *i*. The error term *ε* was assumed to be gamma distributed.

Patterns in diet composition were explored using Canonical Correspondence Analysis (CCA), a multivariate approach, which uses gradients in an independent set of explanatory variables to explain variability in a multivariate response data matrix (Greenacre & Primicerio 2013). The response matrix was the individual diet composition according to the 14 main prey categories. Explanatory variables encompassed fish length (numeric), energy reserves (numeric), subarea (factor) and year (factor). In accordance to the above described GLM, the model included all single-effect terms, all two-way interaction terms between fish length, energy reserves and subarea, and an additional two-way interaction between subarea and year in order to account for potential inter-annual spatial differences of environmental conditions. Significance of variables was tested with PERMANOVA (Anderson 2001). The CCA model was used to predict diet composition based on the explanatory variables and to visualize trends in dietary changes as related to fish length and energy reserves. Predicted values by sample were aggregated according to five length classes (20-40 cm, 40-60 cm, 60-80 cm, 80-100 cm and > 100 cm) and four liver index classes (0-4, 4-8, 8-12 and > 12) combinations. These aggregated values were rescaled to be within a positive range of 0-1, followed by conversion into percent contribution for visualization in stacked bar plots. A biplot of the two leading CCA dimensions further demonstrated the relationship between feeding strategies and the four explanatory variables fish length, energy reserves, subarea and year.

5.3 Results

Is cod distributed according to ideal free distribution?

The model revealed a strong spatial gradient of energy reserves, with increasing values from west to east (Fig. 1b). The most parsimonious model explaining energy storages included subarea and fish length as single terms (lowest BIC) (Table 1), providing evidence against an ideal and free distribution. Subarea (F = 151.4) had higher explanatory power than fish length (F = 86.4), although both were highly significant (p-value < 0.001) (Fig. 1a, Fig. 1b, Appendix S3). Deep stations in subarea 7, an area in East Greenland bordering on the northern slope of the Irminger Sea showed highest energy storages for three out of five length classes (Appendix S4). Interestingly, in West Greenland (subareas 1-4) energy reserves of cod below 60 cm did not spatially vary as it was detected for larger fish. Year and stomach fullness were included in the second best model. The growth index, combined for all age classes, showed an increasing trend from west to east, indicating that faster growing fish were more easterly distributed. Although the west-east gradient was prevalent for both, energy reserves and growth, they strongly differed on smaller scales (Fig. 1b, Fig. 1e). For example, subareas 6 and 7 were occupied by individuals with similar individual long-term growth, but energy reserves differed strikingly between these subareas (Fig. 1b, Fig 1e). Energy reserves were generally higher in deeper than shallower subareas, whereas faster growing fish tended to be distributed in shallower areas, especially in subareas 4, 5 and 6 (Fig. 1b, Fig. 3).

Table 1 Generalized linear models testing the effects of year, fish length, density and subarea on energy reserves (liver index) of Greenland cod. Ranked from lowest to highest BIC. Term inclusion in a given model is indicated by a plus symbol (+). The interactions Year:Fish length, Year:Subarea, Fish length:Density and Subarea:Density were not included in the top 10 models

Rank	Year	Fish Length	Density	Sub-area	Stomach Fullness	Growth	Length: Subarea	Df	BIC
1		+		+				16	15456
2	+	+		+	+		+	37	15456
3	+	+		+	+			24	15457
4		+		+			+	29	15458
5	+	+		+			+	36	15458
6		+		+	+			17	15459
7	+	+		+				23	15460
8	+	+	+	+	+		+	38	15461
9		+		+	+		+	30	15462
10		+		+		+		17	15462

Df = degrees of freedom, BIC = Bayesian information criterion.

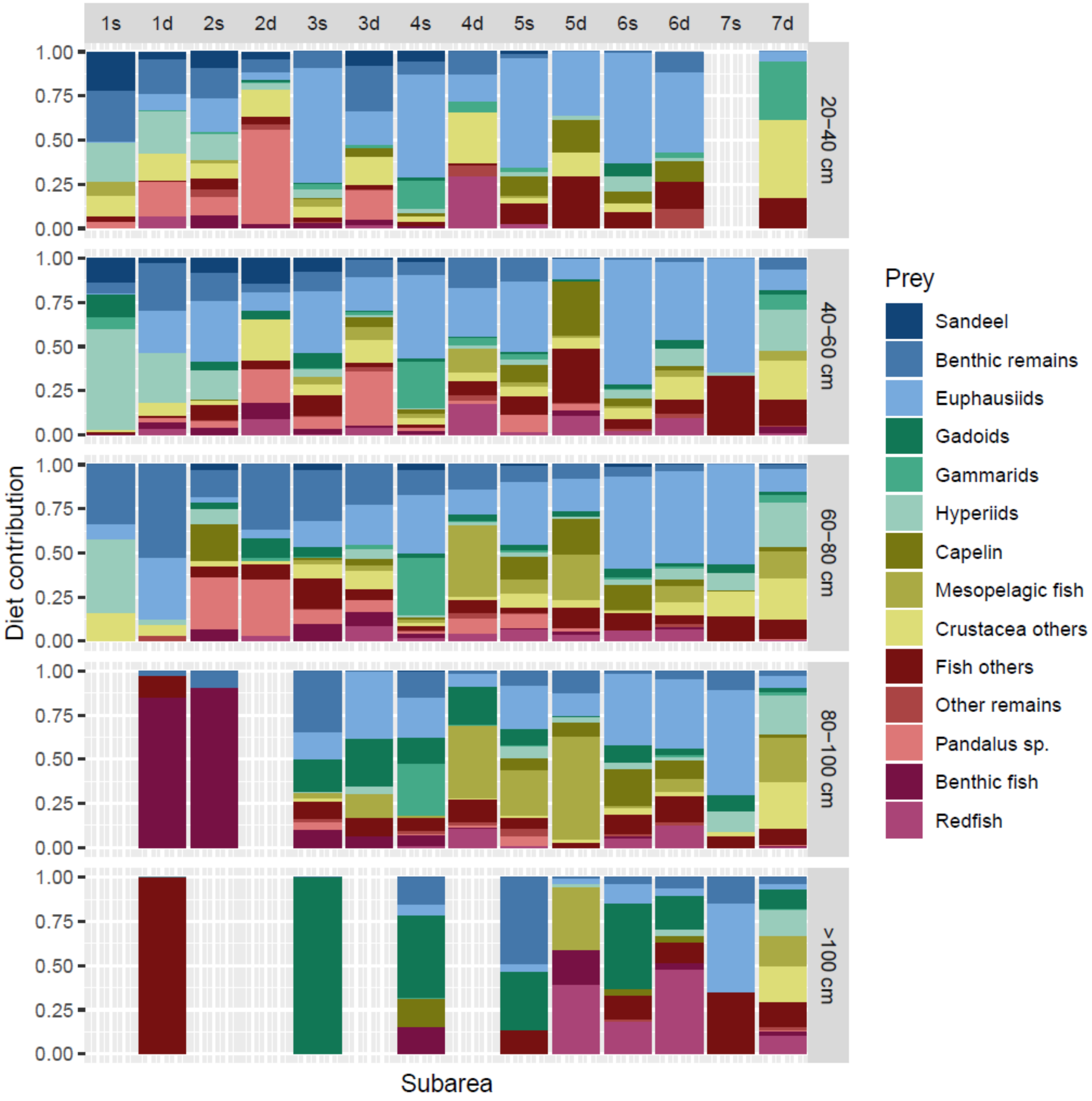

Figure 2 Spatial and size-dependent variation of Atlantic cod diet composition off Greenland.

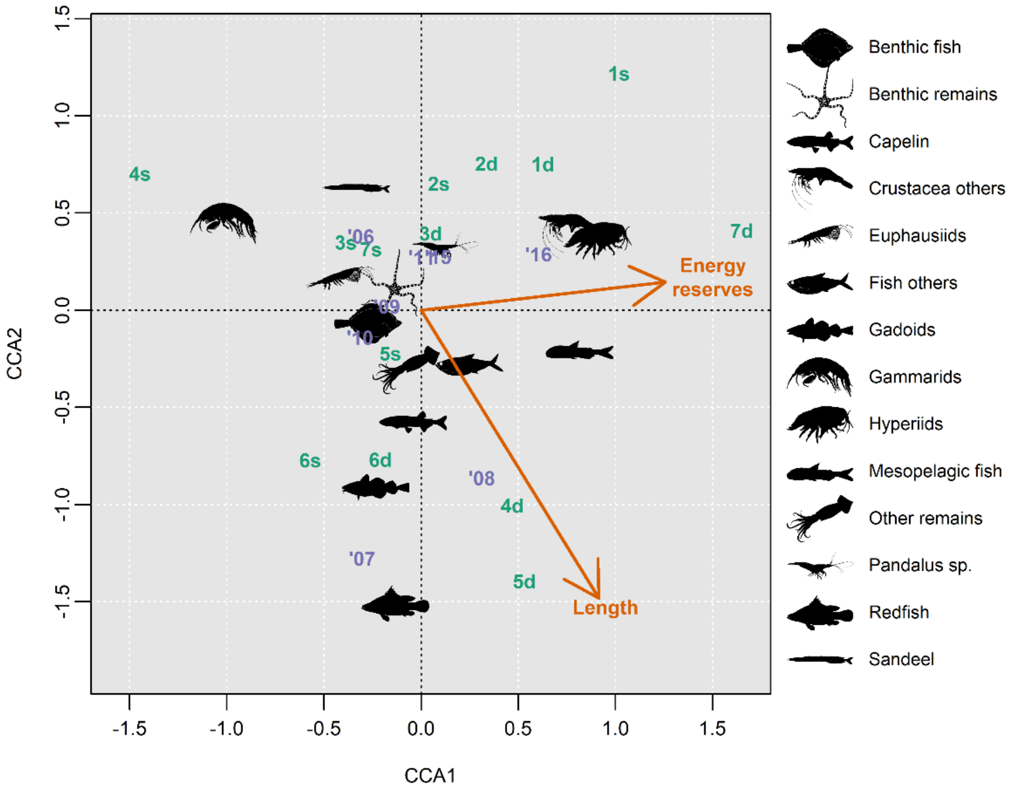

Figure 3 Ordination diagram based on canonical correspondence analysis showing ordination axes 1 (CCA1) and 2 (CCA2), relating cod feeding patterns to energy reserves, length, subarea and year. All explanatory variables were used as single predictors for diet composition. Diet item biplot scores are shown by the silhouette symbols. Arrows indicate biplot scores of continuous explanatory variables, while scores of factor variables year (purple) and subarea (green) are indicated by text.

Habitat heterogeneity, diet quality and their influence on energy reserves

Energy reserves in different subareas showed distinct relationships to particular diet compositions, which we used to infer habitat heterogeneity (Fig. 2, Fig. 3, Fig. 4). Canonical correspondence analysis was used to explore the influence of several biotic and abiotic factors on diet composition. The prediction revealed that at for a given size, fish diet composition is related to energy reserves. All predictors except of the interaction term of length and energy reserves were found to be highly significant (Appendix S5). Single terms were most significant, as revealed by pseudo-F values, with fish length and energy reserves being of highest significance in explaining diet composition (Appendix S5). Fish above 60 cm with high liver weights and large amounts of energy stored, were associated with a diet of mesopelagic fish, hyperiids (pelagic amphipods) and other crustaceans , which were found in the deep areas off north-eastern Greenland (deep subarea 7) (Fig. 3). Low energy reserves (i.e. negative CCA1 coordinates, Fig. 3) values were associated with increasing proportions of benthic remains, gammarids (benthic amphipods), euphausiids, gadoids and related to shallow parts in subareas 3, 4, 5 and 6. Piscivory, independent of the main prey species, was related to larger energy values for the two smallest length groups, 20-40 cm and 40-60 cm, with especially capelin showing a positive correlation (Fig. 4). At all length groups the proportion of euphausiids, gammarids and benthic remains in the diet were especially high when energy reserves were found to be low (Fig. 3, Fig. 4). Above 80 cm, cod showed stronger piscivorous feeding behaviour and the proportion of euphausiids in the diet decreased accordingly (Fig. 4). Consumption of gadoids, which includes cannibalism, was related to lower average energy values in all but the smallest length group (Fig. 4). Overall, euphausiids, especially *Meganyctiphanes norvegica*, were the most abundant food item over all samples, being the dominant prey in one third of all stomachs across all length classes (Fig. 1, Appendix S2).

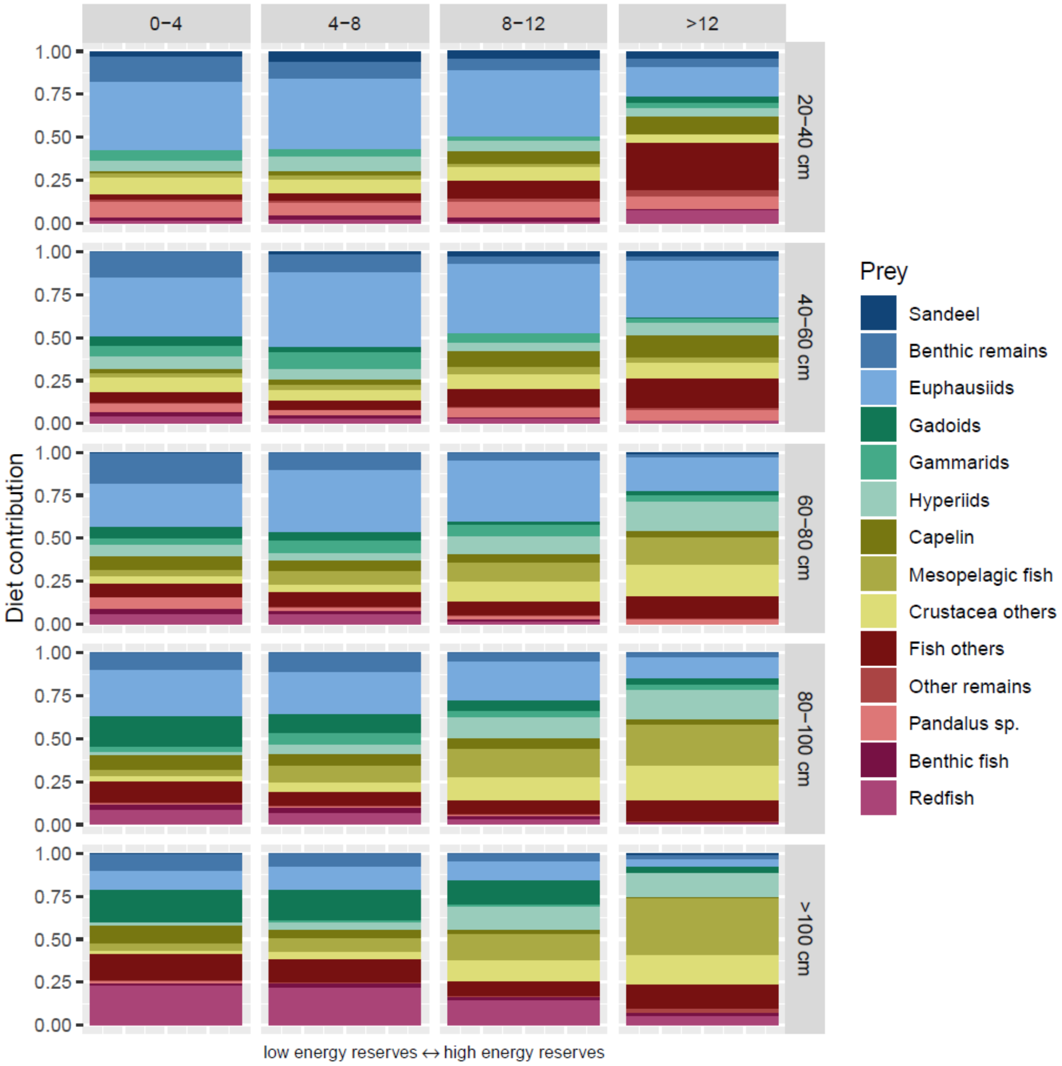

Figure 4 The influence of fish length and energy reserves on diet composition of Atlantic cod off Greenland predicted by canonical correspondence analysis for different length (20-40 cm, 40-60 cm, 60-80 cm, 80-100 cm and > 100 cm) and energy reserves (liver index) (0-4, 4-8, 8-12 and > 12) categories.

5.4 Discussion

We showed that significant spatial differences in energy reserves in cod populations from the Greenland shelf were likely caused by variable food quality as result of pronounced habitat heterogeneity. Growth indices, which we assume to be related to competitive abilities, did not predict the amount of energy stored. Even on smaller scales, where cod appears to be physiologically capable to switch between food patches, energy reserves differed between habitats. We conclude that cod individuals often remained in suboptimal habitats, leading to spatio-temporal persistent patterns of fish with different amounts of energy reserves. These observations are not consistent with an ideal free distribution, not even at the smaller spatial scales for which it is more readily applicable.

Different diet compositions cause fluctuations in energy reserves

Spatial differences in the observed energy reserves were likely influenced by food quality, indicated by diet composition. Mesopelagic fish are often very rich in lipids (Falk-Petersen et al. 1986, Lea et al. 2002, Spitz et al. 2010, Grimaldo et al. 2018), which probably had a positive influence on energy levels in subareas 5 and 7 because these areas are rich in this type of fish. Our results showed that here cod had access to food from the mesopelagic realm from the deep scattering layer in the Irminger Sea. Highest energy reserves might be partially explained with bottom trapping mechanisms, as they are found around seamounts (Genin & Dower 2007), which retain large amounts of high quality food and make it easily accessible for feeding. This advantage might have contributed to the differences in energy reserves between deep subarea 7 and subareas 4 and 5, where also considerable amounts of mesopelagic fish were found in the diet. Benthic feeding on e.g. brittle stars, polychaetes, sea cucumbers or gammarids, typically for cod inhabiting shallower banks, resulted in lower energy gains, what is likely driven by the low levels of organic matters and caloric content in many benthic invertebrates (Tyler 1973, Atkinson & Wacasey 1976, Percy & Fife 1981, Norrbin & Båmstedt 1984, Wacasey & Atkinson 1987). It must be further considered that *M. norvegica*, which is generally a lipid-rich organism, has its annual peak in lipid content in January and its minimum in July (Falk-Petersen et al. 2000), which means that cod caught during the autumn season covered by the surveys were feeding on krill with comparatively low lipid content. General assumptions about lipid contents and energy levels of food organisms could however not be made, because caloric content of different zooplankton and fish species can vary between regions, seasons, habitats, sexes and maturity stages (Henderson et al. 1984, Falk-Petersen et al. 1986, 2000, Anthony et al. 2000, Lee et al. 2006, Färber-Lorda et al. 2009, Spitz et al. 2010, McBride et al. 2014, Grimaldo et al. 2018).

Causes of large-scale deviations from ideal habitat selection theory

IFD as conceptual ecological model and framework to predict consumer distributions related to resource availability has been tested for a variety of areas, scales and taxa (Fretwell & Lucas 1969, Kennedy & Gray 1993, Tregenza 1995, Sutherland 1996, Stamps 2009, Morris 2011). Because it is not unusual that observations in ecology contradict the ideal and free assumptions, our results of large-scale unequal patterns of energy reserves are not surprising, considering the spatial extent and heterogeneous environments of our study area (Stamps 2009). It appears that a lack of knowledge on the spatial distribution of resources combined with limited capacities to risk potentially fitness-costly searching behaviour likely cause large-scale deviations from an ideal and free habitat selection. Because large and mature cod is patchily distributed on underwater banks in East Greenland, we hypothesize that traveling between these banks through “food valleys”, areas of low food availability and quality, would cost too much energy and impose substantial risks of starvation, what probably precludes extensive screening of the environment. Fish from areas with poor habitat quality, such as southern Greenland, might exhibit increasingly restricted explorative behaviour because of low energy reserves, which can amplify poor condition because weak fish have a lower probability of discovering high-quality habitats (Stamps 2009). It seems that active habitat selection in the sense of choosing the ideal environment to maximize fitness based on perfect knowledge of the environment, did not take place, because cod individuals did not extensively screen the environment for food availability. The observed length-stratification of cod around Greenland shows that the main areas of distribution of juvenile and adult fish do not overlap because maturing individuals migrate eastwards with increasing age (Hovgård & Wieland 2008). The timing of the migration from west to east Greenland seems to be related to higher growth rates, because mean length at age was higher in east Greenland. These results indicate that individuals start to migrate eastwards as soon as they reach a certain size, independent of age, because faster-growing fish tend to be more easterly distributed than conspecifics of the same age but with slower growth. It remains speculative, why particular individuals migrate to and occupy high quality habitats, such as deep banks in subarea 7, and others to low-quality habitats, such as shallow areas in subarea 6, which are divided by a distance adult cod would be physiologically capable of overcoming. A possible explanation is that these distribution patterns were caused by “natal habitat preference induction” (Stamps 2009), which is a common behaviour and driver of migration patterns in cod (Stamps 2009, Bonanomi et al. 2016). Once an individual has ended up in a particular area, potentially attracted by natal habitat cues, it might not only be the lack of behavioural plasticity leading to the acceptance of low-quality habitats, but simply the impossibility to behave ideally because of increasing risks of death. It seems that once an individual found a suitable habitat for surviving and reproducing, even if fitness is not maximized, it accepts imperfect conditions rather than risking costly traveling to potentially better habitats.

Implications for ecosystem-based management

Although our observed violations of ideal habitat selection were not unexpected, we identified two important aspects that may have far-reaching implications for eco-evolutionary processes and natural resource management. Firstly, the observed spatial differences in energy reserves were temporally stable over our study period and secondly spatial differences were only influenced to a minor degree by density, food quantity, growth, or interannual effects. Hence, density-dependence and individual competitive abilities seemed to be of minor importance restricting energy gain. Greenland cod did not show increased density in high-quality habitats, which would have been the expected behavioural response to spatial variations in resource quality. These results confirm that important life-history traits, such as growth, reproduction, condition and survival, may depend on habitat type and quality and the ability to adapt to heterogeneous environments. They furthermore add to the eco-evolutionary perspective, that missing capabilities to balance these spatial differences may lead to persistent differences in fitness between individuals, which have occupied and fed in different environments. Hence, our results indicate that the observed patterns are not an evolutionarily stable strategy (ESS), where all competitors would have been found in the environment with the highest resource rewards (Smith & Slatkin 1973, Parker & Sutherland 1986, Cressman & Křivan 2010). Because condition affects reproduction, growth and natural mortality of fish (Kjesbu et al. 1991, Marteinsdottir & Steinarsson 1998, Lambert & Dutil 2000, Lloret et al. 2013), we hypothesize that deep areas off north-eastern Greenland may contribute significantly to the productivity of the Greenland cod stock and may therefore be potential ‘essential fish habitats’ (Benaka

1999). Deep rocky bottoms, as are often found in eastern Greenland, are known to represent a high quality habitat for other species such as rockfish species (*Sebastes* spp) (Yoklavich et al. 2000) and therefore should deserve particular management measures to protect them, including the establishment of marine protected areas (Rosenberg et al. 2000). It must be noticed that the importance of the physical health of exploited stocks, is an essential element of sustainable and profitable fisheries (Lloret et al. 2012, Casini et al. 2016a) and therefore the results of this study can be of importance for an ecosystem-based approach of fisheries management in Greenlandic waters. In the face of climate change and fishing impacts, ecosystems are expected to alter dramatically, which will impact energy content and the distribution of forage species of cod in Greenland and by this change habitat suitability (Hansen 1949, Pedersen & Rice 2002, Drinkwater 2006, McBride et al. 2014). Because of the lack of a correlation between habitat quality and density, it appears that cod populations were not able to adapt to habitat changes and persistently inhabited areas with suboptimal food availability. To conclude, our study results support the idea that particular areas in Greenland should receive increased attention and protection in natural resource management, because these areas might disproportionally contribute to population stability by sustaining high-conditioned fish, which, once they were removed, might not be replenished immediately.

5.5 Acknowledgements

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Supporting Information

Table S1 Number of samples collected in each year and subarea

Stratum & Year	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2
2006	10	10	39	28	96	34	91	26	15	10	37	27	-	42
2007	9	30	6	-	35	-	64	27	29	33	31	54	-	42
2008	3	-	19	9	16	4	26	3	10	39	5	37	-	24
2009	-	-	14	9	37	33	20	21	28	10	29	71	-	32
2010	-	-	-	-	45	19	52	10	12	-	29	65	-	34
2011	-	-	-	-	-	3	95	32	74	25	77	56	-	122
2015	12	38	47	17	70	16	144	17	71	14	92	82	35	162
2016	-	-	-	-	19	-	68	7	38	21	67	47	-	157

Table S2 Classification of all identified species into the 14 taxonomically or functionally distinct diet groups. When a diet item was too far digested or too fragmentary to be identified to species level, the diet item was classified to a higher taxonomic level.

Diet group/Species	No of occurrence
Benthic fish	
Anarhichas lupus	11
Anarhichas minor	1
Anarhichas sp.	19
Artediellus atlanticus	8
Benthic fish	2
Cottidae sp.	9
Enchelyopus cimbrius	3
Eumicrotremus sp.	1
Gymnelus sp.	2
Hippoglossoides platessoides	14
Icelus spatula	1
Leptoclinus maculatus	1
Lycodes vahlii	2
Macrourus berglax	1
Pleuronectiformes	5
Raja radiata	1
Reinhardtius hippoglossoides	7
Rhinonemus cimbrius	2
Scorpaeniformes	3
Stichaeidae sp.	1
Triglops sp.	14
Triglops pingeli	2
Triglops murrayi	27
Benthic remains	
Actiniaria	5
Annelida	10
Anthozoa	3
Aphrodita spp.	1
Asteroidea	6
Benthic remains	364
Bivalvia	59

Brachyura	8
Chaetognatha	1
Echinodermata	9
Gastropoda	19
Holothuria	145
Hyas spp.	4
Isopoda	59
Lithodes maja	63
Lithodes spp.	1
Majidae	16
Octopoda	12
Ophiuridae	163
Opisthobranchia	10
Paguroidea	2
Polychaeta	262
Sclerocrangon sp.	3
Capelin	
Mallotus villosus	286
Crustacea unidentified	
Acanthephyra pelagica	21
Amphipoda	15
Calanoida	12
Caprellidae	75
Caridea	213
Copepoda	17
Crangonidae	4
Crustacea	370
Cumacea	4
Decapoda	237
Dendrobranchiata	3
Ephyrina hoskynii	2
Eucopia grimaldii	1
Gnathophausia sp.	68
Gnathophausia zoea	19
Lebbeus polaris	15
Lophogastrida	2
Mysida	18
Neognathophausia gigas	3
Ostracoda	1
Paraeuchaeta norvegica	5
Pasiphaeidae	8
Pasiphaea multidentata	22
Pasiphaea tarda	3
Phyllocarida	1
Sclerocrangon sp.	3
Sergia robusta	3
Sergestidae	18
Tanaidacea	7

Euphausiids	
Euphausiacea	994
Meganyctiphanes norvegica	1175
Thysanoessa spp.	21
Thysanoessa inermis	1
Thysanoessa rachii	1
Fish unidentified	
Anguilliformes	2
Argentina silus	2
Clupea harengus	1
Hoplostethus atlanticus	1
Osmeriformes	2
Perciformes	1
Teleostei	818
Gadoids	
Arctogadus glacilis	1
Boreogadus saida	2
Brosme brosme	1
Gadiformes	24
Gadus morhua	131
Gadus ogac	3
Gaidropsarus argentatus	4
Lotidae	3
Melanogrammus aeglefinus	14
Microgadus tomcod	3
Micromesistius poutassou	43
Pollachius virens	3
Gammarids	
Gammaridae	689
Gammarus spp.	104
Hyperiids	
Hyperiidae	334
Hyperia medusarum	2
Hyperia galba	10
Themisto spp.	65
Themisto abyssorum	60
Themisto compressa	252
Themisto libellula	714
Mesopelagic fish	
Alepocephalus spp.	4
Alepocephalus agassizii	3
Argyropelecus hemigymnus	1
Bathylagus spp.	1
Bathylagus euryops	16

Benthosema glaciale	147
Borostomias antarcticus	7
Chauliodus sloani	12
Chauliodus sp.	2
Chiasmodon spp.	2
Cyclothone spp.	75
Gonostoma bathyphilum	1
Gonostomatidae	12
Holtbyrnia macrops	1
Lampadena speculigera	1
Lampanyctus spp.	23
Lampanyctus ater	5
Lampanyctus festivus	2
Lampanyctus intricarius	4
Lampanyctus macdonaldi	31
Lobianchia spp.	1
Malacosteus niger	6
Maurolicus mülleri	3
Myctophidae	154
Myctophum punctatum	77
Myctophum selenops	2
Myctophum spp.	1
Nemichthyidae	8
Notoscopelus spp.	28
Notoscopelus caudispinosus	1
Notoscopelus kroyeri	88
Notolepis rissoi	5
Paralepis atlantica	3
Paralepididae	25
Platytroctidae	7
Poromitra megalops	1
Protomyctophum arcticum	1
Scopelogadus beanii	3
Scopelosaurus lepidus	1
Serrivomer beanii	81
Sternoptychidae	1
Stomias boa boa	7
Stomiidae	1
Trigonolampa miriceps	1
Xenodermichthys copei	3
Other remains	
Cephalopoda	29
Coleoidea	29
Hydrozoa	1
Medusozoa	6
Salpidae	5
Teuthida	83
Pandalus sp.	

Pandalidae	98
Pandalus borealis	113
Pandalus montagui	3
Redfish	
Sebastes sp.	144
Sebastes fasciatus	3
Sebastes norvegicus	23
Sebastes mentella	43
Sebastes viviparus	3
Sandeel	
Ammodytes sp.	63
Ammodytes marinus	12
Ammodytes dubius	3

Table S3 Summary table of the best generalized linear model relating energy reserves (liver index) of cod to fish length and subarea. Df, degrees of freedom.

Predictor	Df	Deviance	Residual Df	F-value	p-value
Subarea	13	219.4	424.45	151.4	< 0.001***
Fish length	1	9.6	414.81	86.4	< 0.001***

Figure S1 Variation of the energy reserves (liver index) of cod in relation to the 14 different subareas. Subarea numbers (1-7) correspond to a west-east gradient off Greenland. Data are presented for five different fish length classes. In order to reduce the effect of fish size on energy reserves, model residuals (GAM with energy reserves as response and year and length as predictors) instead of raw values were used. Box limits are the 25% and 75% quantiles, with the median denoted by the bold line. Whiskers show the 90% quantiles (5% and 95%).

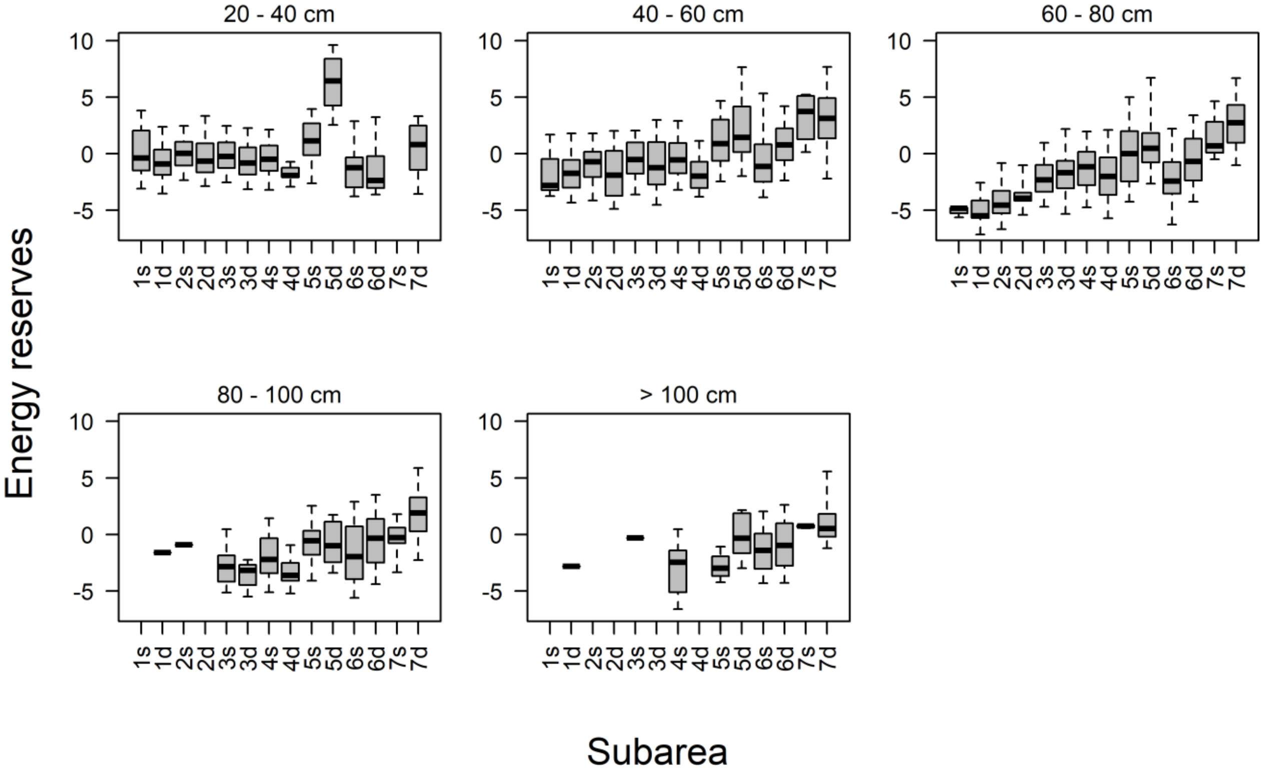

Table S4 Generalized linear models testing the effects of year, fish length, density, subarea and bottom temperature on energy reserves (liver index) of Greenland cod. Ranked from lowest to highest BIC. Term inclusion in a given model is indicated by a plus symbol (+).

Rank	Year	Fish Length	Density	Sub-area	Stomach Fullness	Growth	Year: Fish Length	Year: Subarea	Length: Subarea	Fish Length: Density	Sub-area: Density	Bott. Temp.	BIC
1	+	+		+								+	13124
2	+	+		+	+							+	13125
3	+	+	+	+						+		+	13130
4	+	+	+	+								+	13130
5	+	+	+	+	+							+	13132
6	+	+	+	+	+					+		+	13132
7	+	+		+		+						+	13132
8	+	+		+	+	+						+	13133
9	+	+		+									13135
10	+	+		+	+								13136

Table S5 Results of permutation tests (PERMANOVA) for canonical correspondence analysis relating Atlantic cod diet composition to different constrained variables (adjusted r²: 0.20).

Predictors	Df	Chi²	pseudo-F	p-Value
Fish length	1	0.12	51.2	0.001***
Energy reserves	1	0.07	32.8	0.001***
Subarea	13	0.76	25.7	0.001***
Year	7	0.24	15.2	0.001***
Subarea:Year	64	0.84	5.9	0.001***
Fish length : Energy reserves	1	0.00	1.4	0.096
Fish length : Subarea	13	0.10	3.4	0.001***
Energy reserves : Subarea	13	0.06	2.0	0.001***

6 Publication 5

Trophic niche variability influences body condition on organosomatic and biochemical level of mature female Atlantic cod (*Gadus morhua*) in offshore Greenland waters

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Abstract

In many fish species, body condition and energy reserves are important indicators of organism health and predictors for the reproductive success, which represents the ability to respond to changing environmental conditions in space and time. In Greenland waters, Atlantic cod (*Gadus morhua*) inhabits heterogeneous environments covering shallow and deep habitats on top of the shelf and along slopes. We investigated the influence of habitat heterogeneity and trophic niche on body condition and fish health using organosomatic indicators, e.g. the morphometric index K, hepatosomatic and gonadosomatic indices, and biochemical indicators, e.g. lipid content and fatty acid compositions, of mature female cod caught at three different sites in eastern and southern Greenland. Energy reserves and body condition differed between these sites and indicated best body condition in north-eastern regions below 300 m towards the slope of the northern Irminger Sea. Trophic niches as indicated by stable isotope values and stomach compositions varied between sites, which was likely related to depth and differences between benthic and pelagic feeding regimes. Lipid content and fatty acid profiles important for reproduction were highest in deepest waters and associated to a pelagic diet comprised of different mesopelagic fish and crustacean species. We conclude that habitat heterogeneity and trophic niches affect body condition and organism health of female Atlantic cod. These results emphasize that particular areas might be of increased importance for population stability of the cod stocks in Greenland waters.

6.1. Introduction

In Greenland waters, Atlantic cod (*Gadus morhua* Linnaeus, 1758) inhabits a wide range of habitat structures from inshore areas shallower than 100 m to offshore areas deeper than 400 m along the slope of Greenland shelf (Rätz, 1999). The heterogeneity of these habitats caused by different oceanographic and geologic conditions influences the trophic interactions within these habitats (Fock, 2008, Sutherland and Pickart, 2008, Werner et al., 2019). In north-eastern Greenland, cod inhabits deep areas close to the continental slope and influenced by the cold, arctic East Greenland Current and the warmer Irminger current (Figure 1). Here, cod diet mainly consists of mesopelagic fish such as the myctophid *Benthosema glaciale*, hyperiids, which are pelagic amphipods, as well as other pelagic crustaceans (Hedeholm et al., 2017, Werner et al., 2019). In coastal areas in East Greenland as well as in South Greenland, the species lives on top of the shallower continental shelf, which is influenced by resident eddy systems, circular flowing water currents, between the East Greenland and the East Greenland Coastal Current (Figure 1) (Rätz, 1999, Sutherland and Pickart, 2008). Across these areas, cod feeds on benthic invertebrate, such as benthic crabs (Majidae), brittle stars (Ophiuroidea), northern shrimp (*Pandalus borealis*) and sea cucumbers (Holothuroidea), as well as fish species, including capelin (*Mallotus villosus*), sandeel (*Ammodytes* spp.), redfish (*Sebastes* spp.) and northern krill (*Meganyctiphanes norvegica*) (Jensen and Hansen, 1931, Hansen, 1949, Nielsen and Andersen, 2001, Hedeholm et al., 2017, Werner et al., 2019). These particular diet compositions are stably associated with particular areas and linked to habitat heterogeneity in Greenland waters (Hedeholm et al., 2017, Werner et al., 2019).

These different diet compositions are associated with differences in body condition and energy intake, as for example feeding on mesopelagic fish and crustaceans in deep waters is associated with high energy reserves and benthic feeding on echinoderms and gammarids in shallower waters with low energy reserves (Werner et al., 2019). Diet composition is a strong predictor of body condition, fatty acid composition, fertility and egg quality in cod (Kjesbu et al., 1991, Morais et al., 2001, Dalsgaard et al., 2003, Røjbek et al., 2014). High body condition and large energy reserves positively influence fecundity and egg size, likely increasing offspring survival and recruitment success (Kjesbu et al., 1991, Marshall et al., 1999, Mion et al., 2018). Low condition can lead to mortality and skip-spawning, which can trigger population collapses and are linked to reduced stock productivity (Kjesbu et al., 1998, Rideout et al., 2006, Casini et al., 2016). In Greenland waters, low body condition and energy reserves of cod in particular areas is linked to the populations' missing capabilities to perceive the spatial variation of habitat quality and as result, cod is often found in suboptimal environments (Werner et al., 2019), e.g. South Greenland. Because of lower body condition and less productivity, cod populations in Greenland are generally more susceptible to high fishing pressure than more southern cod stocks and climate change will likely alter ecosystem structure of these high-latitude areas (Rätz and Lloret, 2003, Drinkwater, 2005, Fossheim et al., 2015).

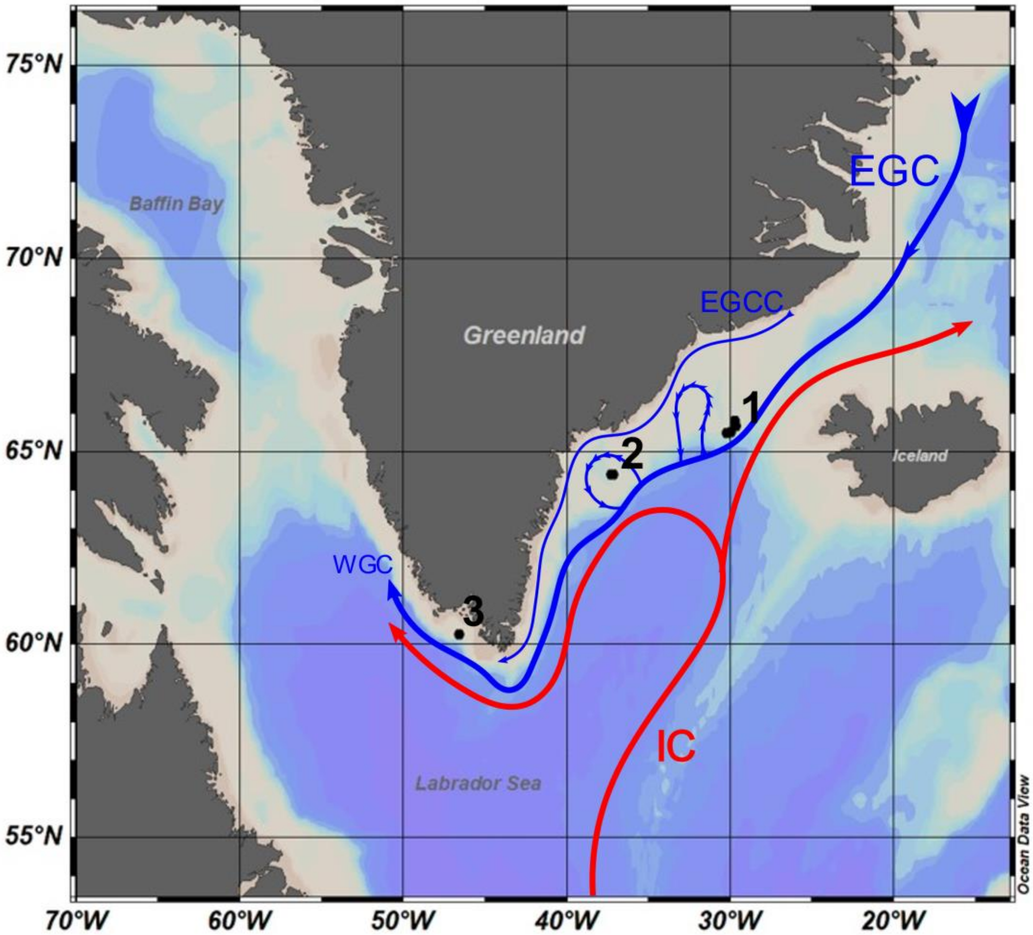

Figure 1 Sampling locations around the Greenland shelf. Currents adapted from Sutherland & Pickart 2008. Arrows are indicating EGC East Greenland current, EGCC East Greenland coastal current, IC Irminger current, WGC West Greenland current. Red arrows depict warm currents, blue arrows depict cold currents. The graph was done using Ocean Data View (Schlitzer, 2018).

Fatty acids are involved in many main functional and structural traits of life, such as energy storage hormone production and cell membranes. (Dalsgaard et al., 2003). In fish they are the preferred source of metabolic energy used for growth, movement and therefore migration and also reproduction (Tocher, 2003). There are three major groups of fatty acids, saturated fatty acids (SFA), mono-unsaturated fatty acids (MUFAs) and poly-unsaturated fatty acids (PUFAs). All groups together are here referred to as total fatty acids (TFAs). Especially long chain PUFAs are beneficial for health. The most common PUFAs, which are often connected to human health, but also to other vertebrates including fish, and recommended for a healthy diet, are eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA) and arachidonic acid (ARA) (Tocher, 2003). They belong to the group of omega-3 and omega- 6 fatty acids, which are essential. In cod, ARA and EPA levels influence the reproductive potential; high ARA levels in a diet and a low EPA/ARA ratio in gonads lead to greater numbers of viable larvae per kilogram of cod (Røjbek et al., 2012, Røjbek et al., 2014, Norberg et al., 2017).

We investigated, if the missing adaptive capabilities and rather stationary behaviour of cod in offshore Greenland waters can lead to lower energy intake and reduced organism health as indicated by morphometric (Condition factor "K"), organosomatic (Hepatosomatic index (HSI); gonadosomatic index (GSI) and biochemical (Total fat content in gonads and livers; fatty acid composition in gonads) body condition indicators. In addition, stomach and stable isotope data were collected to link these body condition indicators to short and long-term feeding patterns and determine trophic niches. Because they are relatively easy to collect, condition indices, such as K, HSI and GSI are the most frequently used condition indices for gadoid fish species, such as cod (Lambert and Dutil, 1997, Lloret et al., 2013). While these indices provide indications about general body condition and energetic fitness, biochemical indicators, such as fatty acid composition and total fat content in organs, are rarely used (Lloret et al., 2013). These biochemical indicators were chosen to provide more in-depth information about functional activity, organism health and reproductive potential and especially fat content in organs is thought to be one of the best biochemical indicators for fish condition (Lambert and Dutil, 1997, Lloret et al., 2013). Field data were collected on so called "BOFFFFs" (big old fat fecund female fish), which have higher potential fecundity and a lower chance of skip spawning than younger females and contribute disproportionally more to the reproductive output of a population (Marteinsdottir and Begg, 2002, Hixon et al., 2013, Barneche et al., 2018). By combining short and long term trophic interactions with body condition parameters, focussing on biochemical indicators, we investigated, if i) condition indices are correlated with diet composition and the trophic niche, ii) the spatial variation of organosomatic body condition indices is reflected in the fatty acid composition and organ fat contents and iii) the missing capabilities to perceive the spatial variation of habitat quality can cause variation in organism health.

6.2. Methods

Data collection and study area

All samples were collected during the annual German groundfish survey in Greenland waters, carried out by Thünen Institute for Sea Fisheries with FRV Walther Herwig III from 06.10.2017 to 17.11.2017. Three sites in East and Southwest Greenland (Figure 1), where cod previously showed persistent diet compositions (Werner et al., 2019), were sampled. In order to collect only mature female cod, a size range of 75-90 cm was chosen (Begg and Marteinsdottir, 2002, Marteinsdottir and Begg, 2002). At least 10 individuals were sampled per site using a bottom trawl net. Samples were randomly taken from the catch. Total length was measured to the nearest 1 cm and gutted weight, gonad weight and liver weight to the nearest decigram. The otoliths were dissected from the head for age determination. Stomachs were removed from the abdominal cavity and frozen at -30°C. The gonads and livers were kept on ice until tissue sampling for total lipid content and fatty acid composition. Gonad tissue was taken from the right lobe, even though ovaries of Atlantic cod are presumed to be homogenous (Witthames et al., 2009). Liver tissue was taken from the smallest lobe, after carefully removing visible liver parasites, to make sure only pure liver tissue was sampled. Tissue samples were stored in liquid nitrogen. Tissue samples for stable isotopes were taken from the left side of the dorsal muscle behind the head and were frozen at -30 °C.

Diet composition and trophic niche

Stomach content analyses were conducted to indicate short-term patterns of feeding and stable isotope analyses were conducted for a better understanding of trophic interactions and long-term feeding preferences (Fry, 2006). Based on home ranges and estimated evacuation rates, we assume the stomach contents represent local feeding. Studies showed that 50% of stomach contents are usually evacuated within 24 hours (Dos Santos and Jobling, 1991). Additionally, home ranges of cod are considered to be relatively small (Neat et al., 2006). Stomachs were defrosted, and full and empty stomachs weights were taken to the nearest 1 mg. Stomach contents were identified to the lowest possible taxonomic level. Fish prey was identified through comparison of the species-specific otolith shapes with the available literature (Campana, 2004) and the reference collection available at the Thünen Institute of Sea Fisheries. Invertebrates were identified by using the following literature: Schneppenheim and Weigmann-Haass 1986; Baker et al., 1990; Hayward and Ryland 1990a, Hayward and Ryland 1990b. In order to analyze and compare feeding patterns, particular species had to be grouped together to taxonomically distinct groups (Table S 1).In order to indicate whether an individual fed more on pelagic or benthic prey, a prey index I_i for prey i was calculated (1) by using the following formula and prey categories c as weighting factor:

$$I_i = c * \frac{W_i}{W_S}$$

I = prey index

i = prey

W_i = prey weight

W_s = total weight of stomach content

c = Prey categories (1 = Benthic, 2 = Unknown, 3 = Pelagic)

In order to determine differences in the prey diversity, the Shannon-Index, which considers both the number of species and its proportion, was calculated for each stomach by using the following equation (2) (Allaby, 2003):

$$H = -\sum_{i=1}^{S} p_i * lnp_i \qquad (2)$$

H = the Shannon diversity index

p_i = proportion of individuals belonging to species i

S = numbers of species encountered

For stable isotope analyses of δC and δN, the muscle tissue was freeze dried for at least 12 hours (Christ Alpha 1-2 LDplus freeze-dryer). Afterwards tissue was grinded to a fine powder using a mortar and pestle. Tissue powder was weighed into tin capsules (3.2x4mm, HEKAtech GmbH,Wegberg/Germany), using a Sartorius micro-balance with a resolution of 10^{-4}mg. The analyses were done following the methods from Hansen et al. 2009 (Hansen et al., 2009). A sample of 0.04-0.06mg was used for analysis. The analysis was done by a high sensitivity elemental analyser (CE INSTRUMENTS EA1110) coupled with an isotope mass spectrometer (DeltaPlus Advantage, Thermo Fisher Scientific). Acetanilide (C_8H_9NO) was used as internal standard and measured in between samples to calibrate the measurements.

Body condition and parasite infection

In order to gain insights into morphometric body condition and organosomatic indices, the HSI, the GSI and the condition factor K were calculated using the equations (Lloret et al., 2013):

$$\text{Condition factor K} = \frac{\text{Eviscerated weight}}{\text{Total length}^3} * 100 \qquad (3)$$

$$\text{Hepatosomatic index (HSI)} = \frac{\text{Liver weight}}{\text{Eviscerated weight}} * 100 \qquad (4)$$

$$\text{Gonadosomatic index (GSI)} = \frac{\text{Gonad weight}}{\text{Eviscerated weight}} * 100 \qquad (5)$$

Because gadoid fish store energy in the liver, the HSI is most sensitive to diet variability and can reflect the spatial impact of diet variability (Pardoe et al., 2008, Jobling and Leknes, 2010, Lloret et al., 2013). As additional indicator for liver health and condition, liver macro parasites were dissected from the liver tissue. Parasites are related to fish condition and fish health, because low energy reserves decrease the immunity and poor-conditioned fish have a higher disease prevalence and mortality (Dutil et al., 2006, Lloret et al., 2013). In order to relate parasite loadings to liver weight, a simple liver parasite index was calculated by using formula (6):

$$\text{Ectoparasite index} = \frac{\text{Total parasite weight}}{\text{Liver weight}} * 100 \qquad (6)$$

Energy content

The extraction of lipids was done using a modified version of the methods described in Bligh and Dyer (1959) and Folch et al. 1957. Subsamples of liver and gonad tissue were freeze dried for at least 24 hours (Christ Alpha 1-2 LDplus freeze-dryer). Afterwards the tissue was extracted three times for 24h at -20 °C, using a 1:1:1 Chloroform/ Dichloromethane/ Methanol extraction mix. The total fat content was afterwards determined gravimetrically by subtracting the weight of the extracted tissue from the tissues dry weight.

Fatty acid profiles

Total quantities of fatty acids measured in nanograms (ng) were chosen, to gain an overview about the actual energy storage and resource stocks of the gonads. Gonad tissue was chosen for analyses in order to incorporate offspring health and survival (Røjbek et al., 2014). Together with the percentage values, depletions or enrichments in certain fatty acids or fatty acid groups can be determined. Subsamples of gonads were freeze dried for at least 12 hours

(Christ Alpha 1-2 LDplus freeze-dryer). Fatty acids were extracted using a modified version of the methods described in Bligh and Dyer (1959) and Folch and colleagues (1956). Lipids were extracted in a 1:1:1 Chloroform/ Dichloromethane/ Methanol ($CHCl_3/CH_2Cl_2/CH3OH$) extraction mix. Two internal standards (C19:0 (Nonadecanoic acid) as fatty acid methyl ester, C21:0 (Heneicosanoic acid) as fatty acid), were added as a reference for concentration and a check for esterification efficiency, respectively. Esterification was done in a 50 °C sand bath for at least 12 h in a 1 % H_2SO_4 in CH_3OH solution. Fatty acid methyl esters were finally solved in n-Hexane and analysed using a fast gas-phase chromatograph (Thermo ELECTRON CORPORATION Trace GC Ultra) coupled with an autoanalyzer (Thermo SCIENTIFIC AS 3000). The injection was splitless on a capillary column and hydrogen was used as carrier gas. An external standard of 37 Component FAME Mix (Supelco®) with a concentration of 40ng C19 per 1µl and a Bacterial Acid Methyl Ester (BAME) Mix (Supelco®, 1ng $µl^{-1}$) were run three times before every set of analysis, to check for peak separation. Peak identification was done by retention times, comparing the external standard to the actual sample.

Statistical Analyses

To compare condition indicators at different sites the non-parametric Kruskal-Wallis rank sum test was used. In addition, the post-hoc pairwise Wilcoxon rank sum was used to test pairwise differences between sites. SIMPER (similarity percentage analysis based on Bray-Curtis dissimilarities) and redundancy analysis (RDA) were done using the package vegan (Oksanen et al., 2018). SIMPER was used to identify the contribution of variables, i.e. prey items or hydrography, to the dissimilarity of fatty acid profiles between sites. The four most influential species based on cumulative contributions to the overall Bray-Curtis dissimilarity were chosen as explanatory variables for the RDA. Fatty acid composition in nanograms was used as response matrix. The response matrix was fourth root transformed prior to the analysis to emphasize the importance of fatty acids with low total weight. The level of significance was set to $p < 0.05$. All analyses were conducted in R (R Core Team, 2019) and figures were produced using the package ggplot2 (Wickham, 2016).

6.3. Results

Stomach content and stable isotope analyses

Diet composition at site 1 was dominated by mesopelagic fish, a mix of pelagic crustaceans and hyperiids, a pelagic amphipod (Figure 2). Mesopelagic fish and hyperiids were mainly consumed at site 1 and occurred only sporadically in other regions. Prey composition at site 2 was dominated by capelin and euphausiids (Figure 2). Main diet items at site 3 were *Hyas sp.*, a genus of benthic crabs, sea cucumbers (Holothuroidea) and brittle stars (Ophiuroidea), indicating a diet dominated by benthic organisms. Four individuals at site 3 had small amounts of pelagic prey (euphausiids, hyperiids and mesopelagic fish) in their stomachs (Fishes # 23, 24, 25, 26; Figure 2). Site 1 showed the highest Shannon diversity in the prey, which differed significantly between sites and was mainly related to a large number of species grouped as mesopelagic fish (Table 1).

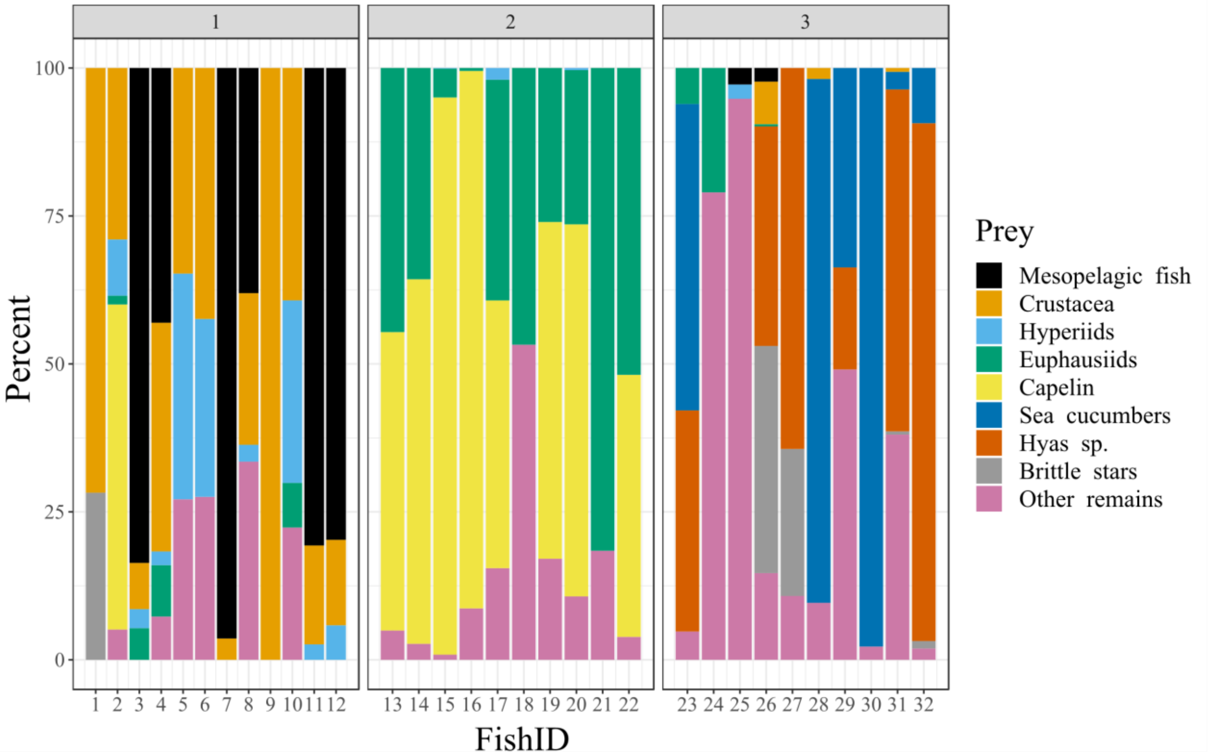

Figure 2 Site dependent diet composition of each individual of Atlantic cod in southern and eastern Greenland.

The stable isotope data showed a clear separation of site 3 from sites 1 and 2, with lower values for δ^{13}C. Sites 1 and 2 had similar values for δ13C and δ15N (Figure 3). This overlaps with the prey composition at sites 1 and 2, which is characterized by a pelagic diet. Three individuals from site 3 (Fishes # 24, 25, 26) are within the pelagic cluster of sites 1 and 2. Interestingly, these three individuals were among the four individuals at site 3 with a small proportion of pelagic food items. Combined results of stomach and stable isotope analyses indicate different trophic niches, reflecting short-term diet patterns from stomach analyses.

Table 1 Biological characteristics of sampled female cod individuals and depth per site displayed as mean and standard deviation.

	Site 1			Site 2			Site 3		
	n = 12			n = 10			n = 10		
Age (years)	6.17	±	0.90	6.11	±	1.20	7.27	±	0.96
Eviscerated Weight (g)	5990.58	±	838.39	4782.50	±	829.48	5709.55	±	602.00
Length (cm SL)	84.75	±	3.98	81.60	±	3.88	84.00	±	3.29
HSI	10.46	±	1.97	5.81	±	2.27	5.36	±	1.28
GSI	2.36	±	0.33	1.36	±	0.37	2.30	±	0.98
K	0.98	±	0.06	0.87	±	0.08	0.96	±	0.07
Parasite index	0.04	±	0.02	0.08	±	0.08	0.62	±	0.49
Gonad lipids (% of dry weight)	12.38	±	1.15	10.99	±	2.39	12.78	±	1.24
Liver lipids (% of dry weight)	91.78	±	1.44	89.42	±	3.44	87.69	±	3.18
H'	1.19	±	0.42	0.72	±	0.37	0.74	±	0.44
Depth	358.25	±	22.34	168	±	14.53	92	±	0

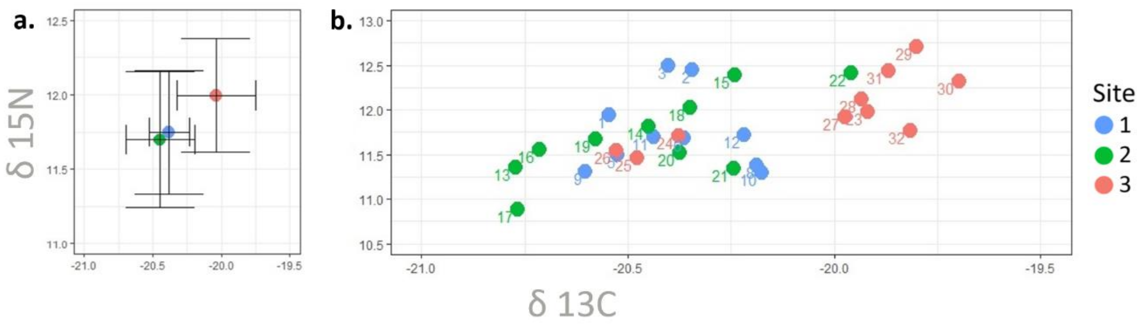

Figure 3 Stable isotope ratios of 30 fish, data for fish 4 and 7 were not available. On the x axis δ C13 and on the y axis δ N15. Sites are indicated by color. a) Mean ratios of the sites, error bars show standard deviation. b) Stable isotope signature for each individual. Numbers depict Fish-ID.

Fish condition and liver ectoparasites

HSI values were significantly higher at site 1 compared to both other sites (Tables 1 and 2). K was high at site 1 and 3 (Table 1) and significantly lower at site 2 (Table 2). Site 2 also showed significantly lower GSI values than sites 1 and 3 (Tables 1 and 2). The parasite index between sites differed significantly (Table 2) with site 3 showing highest proportions of liver ectoparasites (Table 1). Individuals at site 3 were on average approximately one year older than individuals at the same size from sites 1 and 2 (Table 1).

Total lipid content in gonads and livers

Total fat content of gonads was highest at site 3 (Table 1), even though differences were not found to be significant. The lowest mean fat content in gonads was found at site 2. Fat content in livers was highest at site 1 and gradually decreased towards sites 2 and 3. Liver fat contents at site 1 were significantly higher than at site 3 (Tables 1 and 2).

Fatty acid profiles of gonads

Site 1 showed highest total amounts for gonad fatty acids in all four sub-groups (TFA, SFA, MUFA and PUFA) and highest values for ARA and DHA (Figure 4). Site 1 had a significantly larger amount of mono unsaturated fatty acids (MUFAs) than sites 2 and 3 (Table 2, Figure 4). The differences between TFAs was significant in a Kruskal Wallis test (Table 2), but the post hoc Wilcoxon test was insignificant for the combination of all sites. The amount of ARA was similar between sites 1 and 2, but lower at site 3. For EPA, site 3 showed the highest mean value resulting in the highest EPA:ARA ratios at site 3 (Table 2,Figure 4). For DHA, site 1 showed the highest mean values. SFAs showed similar patterns at all sites, with site 1 being slightly higher than sites 2 and 3. Mean total amounts of PUFAs was highest at site 1 but did not differ significantly between sites (Figure 4).

Although site 1 showed highest total values of gonad fatty acids in all four sub-groups (SFAs, MUFAs, PUFAs, TFAs), these differences were not as pronounced when looking at proportional values (Figure 4). Only EPA and MUFAs showed significant differences among sites (Table 2). Proportional contribution of EPAs was higher at site 3 than at both other sites (Table 2) and MUFAs were highest at site 1 (Table 2). PUFAs showed the highest contribution to total fatty acids at site 3. ARA showed highest values at site 2 (Figure 4), whereas site 1 and 3 did not differ in terms of their means.

Regional influences on fatty acids

SIMPER analysis revealed capelin, crustaceans, euphausiids, mesopelagic fish, *Hyas* sp. and sea cucumbers as the most influential species, although only crustaceans were found to be significant (p-value= 0.042). Sea cucumbers (Holothuria) and *Hyas* sp. are positively correlated and can be found in the same quadrant (Figure 5). Euphausiids and capelin lie in close proximity in the ordination diagram and are negatively associated with consumption of mesopelagic fish, crustaceans and depth. Consumption of mesopelagic fish and crustaceans is positively correlated with depth on the first axis. Mesopelagic fish and crustaceans are associated with enrichments in DHA, EPA, C18:1n7, C16:1, C20:1n9c and C14:0 and depth is associated with an enrichment in C16:0, C18:0, and C18:1n9c.

Table 2 Kruskal-Wallis and pairwise Wilcoxon tests testing the between-sites significance of body condition indices. Only significant results are shown.

Index/ Compared sites		Test	chi-square	p-value
HSI		Kruskal-Wallis	19.008	<0.001
	1:2	Pairwise Wilcoxon		<0.001
	1:3	Pairwise Wilcoxon		<0.001
GSI		Kruskal-Wallis	17.899	<0.001
	1:2	Pairwise Wilcoxon		<0.001
	2:3	Pairwise Wilcoxon		0.004
K		Kruskal-Wallis	11.07	0.004
	1:2	Pairwise Wilcoxon		0.005
	2:3	Pairwise Wilcoxon		0.006
TFLiver		Kruskal-Wallis	8.4688	0.014
	1:3	Pairwise Wilcoxon		0.006
Parasites		Kruskal-Wallis	14.299	<0.001
	1:3	Pairwise Wilcoxon		<0.001
	2:3	Pairwise Wilcoxon		0.004
Prey		Kruskal-Wallis	22.766	<0.001
	1:2	Pairwise Wilcoxon		0.007
	1:3	Pairwise Wilcoxon		<0.001
	2:3	Pairwise Wilcoxon		<0.001
Prey diversity		Kruskal-Wallis	8.2384	0.016
	1:2	Pairwise Wilcoxon		0.01
EPA:ARA		Kruskal-Wallis	13.318	0.001
	1:3	Pairwise Wilcoxon		0.004
	2:3	Pairwise Wilcoxon		0.002
EPA [%]		Kruskal-Wallis	13.475	0.001
	1:3	Pairwise Wilcoxon		<0.001
	2:3	Pairwise Wilcoxon		0.01
DHA [ng]		Kruskal-Wallis	6.6818	0.035
MUFA [ng]		Kruskal-Wallis	8.6506	0.013
	1:2	Pairwise Wilcoxon		0.025
	1:3	Pairwise Wilcoxon		0.025
MUFA [%]		Kruskal-Wallis	12.055	0.002
	1:2	Pairwise Wilcoxon		0.045
	1:3	Pairwise Wilcoxon		0.002

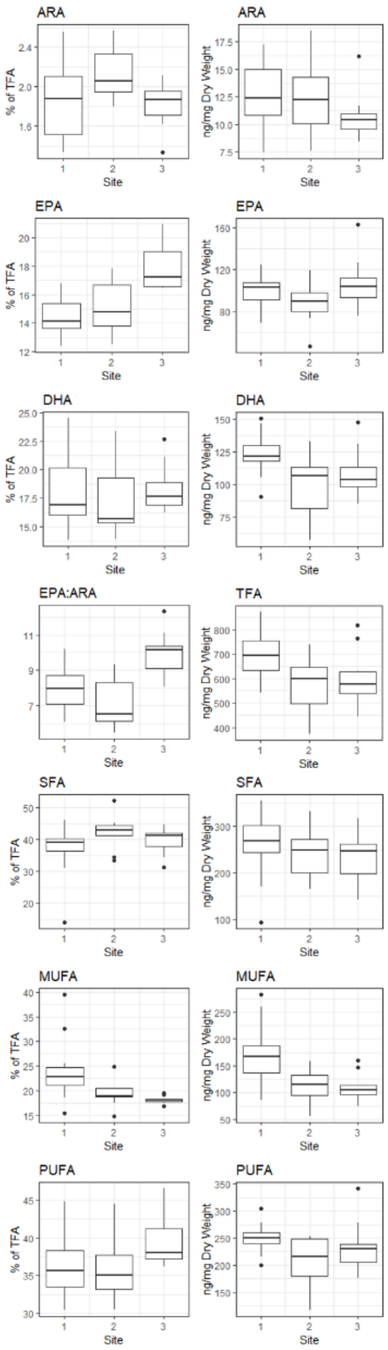

Figure 4 Essential PUFAs and fatty acid groups each in percentage contribution to total fatty acids (TFAs), as well as in total amounts (ng/mg tissue dry weight) and the EPA:ARA ratio. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). The upper/lower whisker extends from the hinge to the largest value/smallest value no further than 1.5 * IQR from the hinge (where IQR is the inter-quartile range, or distance between the first and third quartiles

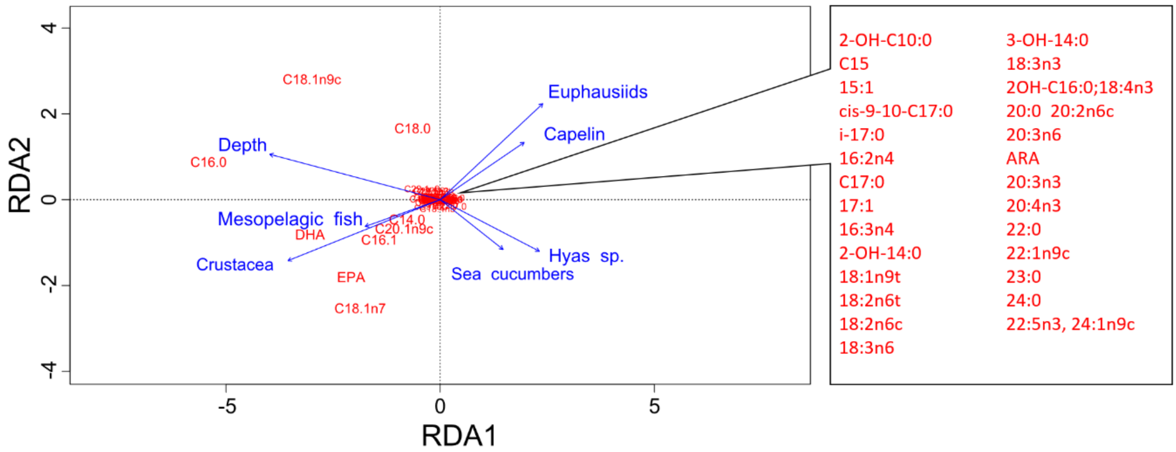

Figure 5 Ordination diagram based on redundancy analysis (RDA) showing ordination axes 1 and 2 and relating fatty acid profiles to feeding patterns. Arrows indicate biplot scores of diet items.

6.4. Discussion

Our results show that body condition and fatty acid composition of female mature cod varies between sites in South and East Greenland waters, which was likely driven by differences in the available resources detected through short- and long-term feeding patterns. These results further indicate that habitat quality differences fish condition and body health at organosomatic and biochemical level. Differences in energy storages, fat content and gonad fatty acids between sampling sites imply that not only health but also reproductive output of female mature cod might be influenced by capabilities to perceive habitat quality differences.

Spatial agreement of body condition indicators

Total lipid content in livers showed similar spatial patterns to the HSI, indicating a positive correlation between liver size and liver fat content, which agrees with earlier studies and confirms that liver size is a suitable proxy for liver fat content (Lambert and Dutil, 1997). Highest HSI and liver fat content as well as lowest amounts of liver parasites were found in individuals coming from deep areas at the most north-eastern sampling site. Similarly, in Icelandic waters, high HSI was associated to deeper areas, which was linked to high abundance of capelin, indicating strong trophic effects on condition and deep water habitats being beneficial for cod condition (Pardoe et al., 2008). Although individuals from site 3 showed low liver fat content, they showed both high GSI and high gonad total lipid values (Table 1). In cod, HSI and liver and gonad fat contents decrease prior and during spawning and GSI increases, because energy is transferred from the livers to the gonads, where it is needed for egg production (Eliassen and Vahl, 1982, Schwalme and Chouinard, 1999, Røjbek et al., 2012). Low HSI, liver fat content and K values indicate that fish at site 3 have already began with transferring energy from the liver to the gonads prior to spawning season (Schwalme and Chouinard, 1999, Røjbek et al., 2012). Consistent with high lipid contents of livers, individuals from site 1 showed highest total amounts of all groups of fatty acids (TFAs, SFAs, MUFAs and PUFAs) in their gonads. Along with low energy reserves and body condition at site 3, EPA:ARA ratios were highest at site 3. In cod, high EPA:ARA ratios and low ARA levels in the diet of females are reflected in the eggs and linked to low egg production and a low number of viable eggs (Røjbek et al., 2014). Hence low body condition and high macroparasite loadings coincided with EPA:ARA ratios known to be associated with reduced egg production indicating low reproductive potential and poor fish health at site 3 (Røjbek et al., 2014).

Comparing the total amounts of fatty acids to the percentage contribution of fatty acids, site 3 has the lowest total amounts of PUFAs, but the highest percentage contribution of PUFAs to total fatty acids and hence low SFA and MUFA contribution. MUFAs and SFAs are the preferred source of energy and essential fatty acids like PUFAs are rather stored than used directly for energy production (Müller-Navarra, 2008). When comparing sites 1 and 2, it stands out that site 1 shows considerably higher HSI, GSI, K and liver fat content values but similar ARA values and EPA:ARA ratios. This indicates that biochemical indicators must not always reflect body condition as measured with organosomatic indices and that a diet mainly consisting of capelin and krill might not lead to large energy storages but valuable enrichments of important fatty acids. This might add further explanation to why capelin appears to be the most important prey resource for stock productivity and recruitment success in most Arcto-boreal cod stocks (Kjesbu et al., 1998, Rose and O'driscoll, 2002).

Potential causes for spatial variation of body condition

Diet composition was dominated by benthic species and associated with low body condition in South Greenland and dominated by pelagic species and associated with higher body condition in East Greenland, which is consistent with previous studies (Nielsen and Andersen, 2001, Hedeholm et al., 2017, Werner et al., 2019). Although a stable isotope baseline for trophic level determination was not available, the stable isotope values and stomach compositions revealed two distinct trophic niches, indicating a strong difference between a benthic diet at site 3 and a pelagic diet at sites 1 and 2 (Figure 3,Figure 5). SIMPER analyses revealed that all three sampling sites can be linked to specific diet characteristics. Individuals with a mesopelagic diet frequently had liver weights accounting for more than 10 %, sometimes even more than 15 % of their total eviscerated weight. These energy levels indicate a lipid-rich diet and were among the highest values described for cod in the wild and comparable to individuals fed to satiation in experiments or aquaculture trials (Lie et al., 1988, Kjesbu et al., 1991, Morais et al., 2001, Pardoe et al., 2008). Interestingly, fish at site 1 showed highest prey diversity in the stomachs (Table 1), indicating that a diverse diet is beneficial for body condition and fish health. HSI of females ranged from 15.8 at site 1 to 2.8 at site 2, covering the whole spectrum from *"very well fed"* to *"about to starve"* (Kjesbu et al., 1991, Pardoe et al., 2008). This might have been associated with liver parasite loadings, having a negative impact on their immunity and making individuals at site 3 more vulnerable for infections (Table 1) (Dutil et al., 2006, Lloret et al., 2013).

Fatty acid composition and lipid content in cod strongly depend on diet quality, in other words "you are what you eat" (Lie et al., 1988, Dalsgaard et al., 2003, Røjbek et al., 2014). Fatty acids are channelled up the food web from the lower trophic levels. In marine systems these lower trophic levels are formed by phytoplankton, like diatoms and dinoflagellates and zooplankton, like copepods. In addition, fatty acid profiles can be altered by abiotic factors, such as temperature, climate and latitude (Dalsgaard et al., 2003, Tocher, 2003, Kattner and Hagen, 2009). RDA revealed a negative correlation between depth and benthic prey and a positive correlation between depth and mesopelagic fish as well as crustaceans. Depth and the proximity to the continental margin are therefore probably the reason for differing prey compositions. Mesopelagic fish can have lipid contents twice as high as capelin and can even have higher lipid contents than euphausiids, what might have caused high HSI values and lipid-richness at site 1 (Henderson et al., 1984, Falk-Petersen et al., 1986, Anthony et al., 2000). Enrichments of three saturated fatty acids, Myristic acid (C14:0), Palmitic acid (C16:0), Stearic acid (C18:0) and four mono unsaturated fatty acids, Palmitoleic acid (C16:1), Vaccenic acid (C18:1n7), Oleic acid (C18:1n9c), Gadoleic acid (C20:1n9c), as well as two essential poly unsaturated fatty acids, DHA and EPA, were associated with larger depth and consumption of mesopelagic fish and crustaceans at site 1. This agrees with earlier findings, where mesopelagic fish showed high amounts of Gadoleic acid, Palmitoleic acid and Myristic acid (Falk-Petersen et al., 1986). Except from PUFAs, none of these fatty acids are linked to particular physiological traits in fish but are rather common fatty acids in lipids in general (C18:1n9c), in animal lipids (C14:0) and in fish oil (C18:1n7, C20:1n9c) and are mainly used as energy storage (Tocher, 2003). On the other hand, DHA and EPA are essential PUFAs and crucial for fish physiology. Consumption of crustaceans was the only significant explanatory variable and associated with enrichments in DHA and EPA. Crustaceans are related to high concentrations of astaxanthins (Czeczuga, 1976), a pigment belonging to the group of carotenoids, which are important antioxidants in cod (Miki et al., 1982, Grung et al., 1993). Due to their double bonds, PUFAs are sensitive against free radicals and peroxidation (Sargent et al., 2002). Astaxanthin can protect PUFAs against free radicals and helps to preserve them (Edge et al., 1997). Species summarized as "crustaceans", mainly consisted of mesopelagic, shrimp like and deep-red crustaceans, which are due to the coloration likely to have high astaxanthin concentrations. Therefore, consumption of crustaceans may have contributed to higher amounts of EPA and DHA.

Larger amounts of capelin and euphausiids at site 2 were linked to a depletion of storage fatty acids (e.g. 14:0 and 16:1) and EPA, DHA and PUFAs. This contradicts previous investigations, because capelin and euphausiids are known to be rich in lipids (Sargent and Falk-Petersen, 1981, Henderson et al., 1984, Falk-Petersen et al., 2000, Tocher, 2003) and especially capelin is known to be an important food source for cod in other areas in the North Atlantic (Yaragina and Marshall, 2000, Sherwood et al., 2007, Pardoe et al., 2008). Sampling site 2 is located within a resident eddy system between the East Greenland Current and the East Greenland Coastal Current (Sutherland and Pickart, 2008). This hydrographical feature decouples the primary production of sampling site 2 from adjacent areas, which results in earlier spring blooms (Waniek et al., 2005) and might cause differences in the phytoplankton community composition. The system is controlled by climatic influences and shows inter annual fluctuations in zooplankton community compositions (Stippkugel, 2018), which may include changes in abundance between lipid rich zooplankton species and species with a lower total fat and fatty acid content. This might have caused a bottom-up effect influencing the fat storages and fatty acid profiles of capelin and euphausiids in the area. A second explanation for poor fish health at site 2 might include a trade-off, because for large cod preying on a fast pelagic species such as capelin might cost more energy than they gain (Lilly and Fleming, 1981, Bogstad and Gjøsæter, 2001, Sherwood et al., 2007). Hence, capelin might be of better nutritional quality for smaller individuals than for fish in the size class 75-90 cm (Sherwood et al., 2007, Werner et al., 2019).

Site 3 was characterized by benthic feeding on sea cucumbers and *Hyas* sp. and associated with high EPA:ARA ratios and a depletion in SFAs and MUFAs (C16:0, C18:0 and C18:1n9c). On the other hand site 3 females showed high percentage contributions of PUFAs. This indicates either a selective incorporation of PUFAs into gonads, or a general lack in energy storages of female cod caught at site 3, due to poor food quality. Poor condition and low energy storages of individuals with a benthic diet, e.g. sea cucumbers or brittle stars, were likely related to low organic and caloric levels of many benthic invertebrate (Atkinson and Wacasey, 1976, Norrbin and Båmstedt, 1984).

Implications for an ecosystem-based fishery management

Building on the results from Werner et al. 2019, the results of this study imply that limited capabilities to perceive the spatial variation of habitat quality does not impact body condition on organosomatic but also biochemical level, likely influencing the health of adult cod in Greenland waters. Because individuals with higher condition and better health have a higher reproductive potential (Kjesbu et al., 1991, Marshall et al., 1999, Mion et al., 2018), areas supporting individuals with a better health might be of increased importance for population stability. Low energy levels trigger females to skip spawning and increase post-spawning mortality (Lambert and Dutil, 2000, Rideout et al., 2006, Tomkiewicz et al., 2010). Higher contents of total fatty acids and especially of health supporting PUFAs in the gonads of cod feeding in the mesopelagic realm might have a positive influence on the reproductive outcome of the individuals in this area. These habitats seem to be of high value for the maintenance of well-conditioned individuals, which produce healthy and vital offspring and should therefore receive special protection in natural resource management. Fisheries of cod in these areas but also bycatch of mesopelagic fish should be carefully managed to keep these valuable habitats intact.

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Supporting Information

Table S 1 Groupings of diet items from cod stomachs into taxonomically distinct prey groups.

Prey group	Diet item
Mesopelagic fish	*Alepocephalus sp., Bathylagos euryops, Benthosema glaciale, Cyclothone sp.,* Myctophidae, *Lampanyctus_sp., Protomyctophum arcticum, Serrivomer beanii, Stomiidae*, other mesopelagic fish remains
Crustacea	Decapoda unidentified, Gammaridae unidentified, *Gnathophausia sp.,* Mysidae, other unidentifiable crustacea remains
Hyperiids	*Themisto libellula,* other unidentified hyperiids
Euphausiids	*Meganyctiphanes norvegica*, other unidentified euphausiids
Capelin	*Mallotus villosus*
Sea cucumbers	No species or genus could be identified
Brittle stars	No species or genus could be identified
Others	*Artediellus_atlanticus,* Bivalves unidentified, Gastropoda unidentified, Theutidae unidentified, other fish remains

Table S 2 mean and standard deviation of each fatty acid and for fatty acid groups per site, in ng mg^{-1}. Fatty acids ARA, EPA, DHA are highlighted in green.

in ng mg^{-1} Fatty Acid	Site 1 n=12	Site 2 n=10	Site 3 n=10
2-OH-C10:0	0.414 ± 1.37	0.00 ± 0.00	0.00 ± 0.00
14:0	29.576 ± 11.97	20.76 ± 5.34	21.99 ± 4.95
C15	5.236 ± 1.69	4.04 ± 1.58	4.77 ± 1.03
15:1	0.000 ± 0.00	0.23 ± 0.70	0.00 ± 0.00
16:0	169.509 ± 59.46	163.37 ± 34.18	157.25 ± 33.86
16:1	38.074 ± 16.18	29.69 ± 9.40	32.27 ± 8.02
cis-9-10-C17:0	0.982 ± 1.60	0.61 ± 1.22	2.61 ± 2.03
i-17:0	5.692 ± 0.81	4.22 ± 1.47	5.20 ± 1.77
16:2n4	0.243 ± 0.37	0.21 ± 0.51	0.28 ± 0.42
C17:0	1.515 ± 1.33	0.90 ± 0.76	1.07 ± 0.97
17:1	2.821 ± 1.28	1.27 ± 1.08	1.38 ± 1.18
16:3n4	1.014 ± 0.93	0.78 ± 0.96	0.42 ± 0.44
2-OH-14:0	0.517 ± 0.48	0.40 ± 0.51	0.72 ± 0.51
18:0	42.652 ± 20.01	46.94 ± 12.81	38.13 ± 9.47
18:1n9t	5.909 ± 3.37	4.76 ± 1.14	3.55 ± 1.12
18:1n9c	68.436 ± 35.60	50.42 ± 17.96	43.12 ± 10.13
18:1n7	31.299 ± 23.31	15.21 ± 3.61	16.53 ± 4.68
18:2n6t	3.097 ± 1.81	1.37 ± 0.63	2.48 ± 0.96
18:2n6c	4.607 ± 1.66	3.41 ± 0.91	3.21 ± 1.01
18:3n6	0.768 ± 0.79	1.19 ± 0.81	0.76 ± 0.66
3-OH-14:0	0.025 ± 0.08	0.00 ± 0.00	0.00 ± 0.00
18:3n3	0.642 ± 0.78	0.40 ± 0.51	0.64 ± 0.58
2OH-C16:0;18:4n3	3.078 ± 1.76	2.12 ± 1.05	4.00 ± 1.67
20:0	0.535 ± 0.63	0.55 ± 0.86	0.15 ± 0.31
20:1n9c	18.002 ± 14.81	9.06 ± 5.21	10.69 ± 4.01
20:2n6c	0.547 ± 0.37	0.28 ± 0.25	0.36 ± 0.39
20:3n6	0.672 ± 0.57	0.50 ± 0.45	0.14 ± 0.29
20:4n6c	12.831 ± 2.71	12.40 ± 3.03	10.72 ± 2.04
20:3n3	0.839 ± 1.12	0.51 ± 0.90	0.59 ± 0.91
20:4n3	1.493 ± 4.95	0.00 ± 0.00	0.00 ± 0.00
22:0	0.910 ± 0.96	1.06 ± 1.01	3.93 ± 3.48
20:5n3c	100.040 ± 14.45	87.29 ± 18.35	106.62 ± 22.84
22:1n9c	5.494 ± 2.40	3.14 ± 2.81	1.78 ± 0.77
23:0	0.000 ± 0.00	0.02 ± 0.07	0.00 ± 0.00
24:0	1.211 ± 0.64	1.17 ± 0.84	1.23 ± 0.33
22:5n3, 24:1n9c	12.332 ± 5.49	10.06 ± 2.32	11.47 ± 4.21
22:6n3c	123.105 ± 15.68	100.46 ± 23.31	108.17 ± 18.17
SFA	258.774 ± 70.96	244.03 ± 51.48	237.06 ± 51.24
MUFA	170.035 ± 57.08	113.78 ± 29.53	109.31 ± 25.33
PUFA	249.896 ± 25.80	208.80 ± 42.09	234.41 ± 44.97
HUFA	239.527 ± 26.26	201.43 ± 41.40	226.61 ± 42.76
TFA	694.114 ± 108.40	601.66 ± 107.72	596.24 ± 115.15
EPA/ARA Ratio	7.624 1.94	7.19 ± 1.35	9.97 ± 1.21

Table S 3 mean and standard deviation of each fatty acid and fatty acid groups per site, in percent of total fatty acids. Fatty acids ARA, EPA, DHA are highlighted in green.

in % of TFA	Site 1	Site 2	Site 3
Fatty Acid	n=12	n=10	n=10
2-OH-C10:0	0.07 ± 0.25	0.00 ± 0.00	0.00 ± 0.00
14:0	4.22 ± 1.31	3.55 ± 0.45	3.68 ± 0.42
C15	0.75 ± 0.25	0.70 ± 0.25	0.80 ± 0.10
15:1	0.00 ± 0.00	0.04 ± 0.11	0.00 ± 0.00
16:0	24.34 ± 7.67	28.27 ± 2.76	26.28 ± 2.06
16:1	5.35 ± 1.88	5.04 ± 1.14	5.38 ± 0.59
cis-9-10-C17:0	0.13 ± 0.21	0.09 ± 0.18	0.40 ± 0.29
i-17:0	0.83 ± 0.14	0.77 ± 0.34	0.88 ± 0.28
16:2n4	0.04 ± 0.05	0.03 ± 0.08	0.04 ± 0.07
C17:0	0.21 ± 0.18	0.17 ± 0.15	0.18 ± 0.15
17:1	0.42 ± 0.19	0.24 ± 0.20	0.24 ± 0.20
16:3n4	0.15 ± 0.15	0.14 ± 0.17	0.07 ± 0.07
2-OH-14:0	0.08 ± 0.08	0.07 ± 0.10	0.12 ± 0.10
18:0	6.07 ± 2.90	8.21 ± 2.17	6.41 ± 1.33
18:1n9t	0.84 ± 0.46	0.84 ± 0.20	0.58 ± 0.12
18:1n9c	9.59 ± 4.69	8.59 ± 2.23	7.19 ± 0.40
18:1n7	4.67 ± 3.86	2.61 ± 0.29	2.75 ± 0.30
18:2n6t	0.47 ± 0.34	0.24 ± 0.10	0.41 ± 0.08
18:2n6c	0.66 ± 0.23	0.58 ± 0.12	0.53 ± 0.07
18:3n6	0.11 ± 0.11	0.20 ± 0.12	0.13 ± 0.11
3-OH-14:0	0.00 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
18:3n3	0.09 ± 0.11	0.07 ± 0.08	0.11 ± 0.10
2OH-C16:0;18:4n3	0.45 ± 0.25	0.37 ± 0.16	0.66 ± 0.16
20:0	0.08 ± 0.10	0.10 ± 0.14	0.03 ± 0.06
20:1n9c	2.41 ± 1.86	1.52 ± 0.77	1.76 ± 0.40
20:2n6c	0.08 ± 0.05	0.05 ± 0.04	0.06 ± 0.06
20:3n6	0.10 ± 0.10	0.09 ± 0.07	0.02 ± 0.05
20:4n6c	1.87 ± 0.40	2.13 ± 0.27	1.82 ± 0.21
20:3n3	0.12 ± 0.17	0.09 ± 0.15	0.08 ± 0.13
20:4n3	0.27 ± 0.89	0.00 ± 0.00	0.00 ± 0.00
22:0	0.13 ± 0.13	0.17 ± 0.16	0.66 ± 0.64
20:5n3c	14.50 ± 1.40	15.08 ± 1.81	17.90 ± 1.53
22:1n9c	0.82 ± 0.40	0.54 ± 0.43	0.32 ± 0.16
23:0	0.00 ± 0.00	0.00 ± 0.01	0.00 ± 0.00
24:0	0.18 ± 0.11	0.19 ± 0.12	0.21 ± 0.07
22:5n3, 24:1n9c	1.81 ± 0.84	1.76 ± 0.40	1.98 ± 0.76
22:6n3c	18.08 ± 3.27	17.44 ± 3.31	18.33 ± 1.97
SFA	37.11 ± 7.97	42.30 ± 5.06	39.65 ± 3.87
MUFA	24.09 ± 6.10	19.41 ± 2.45	18.21 ± 0.71
PUFA	36.53 ± 4.61	36.16 ± 4.62	39.50 ± 3.29
HUFA	35.01 ± 4.62	34.89 ± 4.71	38.21 ± 3.29
EPA/ARA Ratio	7.62 1.94	7.19 ± 1.35	9.97 ± 1.21

7 Publication 6

The global rise of crustacean fisheries

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Abstract

Global decapod crustacean fisheries are growing faster than any other major group, but to date, little attention has been given to the costs and benefits of this shift. We examined over six decades of global fisheries catch data to evaluate the socioeconomic and ecological implications of the compositional change in global fisheries landings. First, we suggest that direct and indirect human enhancements continue to benefit crustaceans, which are more resilient to human alterations than other fished species. Second, crustaceans are among the most valuable seafood, but provide among the lowest nutritional yield and highest carbon emissions. Effectively, increased reliance on crustacean fisheries carries a mix of social, economic, and environmental costs and benefits. There exists strong potential for more wealth, but also largely unevaluated risks, highlighting the need for a nuanced perspective on global fisheries tradeoffs across ecological drivers, anthropogenic enhancement, economics, nutrition, and greenhouse gas emissions. Changes in science, fishing technology, and management are needed to address this unique suite of trade-offs.

7.1 Introduction

Beginning during the latter part of the 20th century, more people in developing, newly industrialized and developed countries have been able to afford highly prized seafood, such as lobsters, prawns or fresh fish (Clark *et al.* 2018). This development emerged as part of globalized trading systems, which make it possible to ship vulnerable fresh goods, alive or chilled, at any time to almost every location on the planet (Kearney 2010). In wealthy societies, which set high values on healthy and fancy seafood meals, seafood has consequentially arisen to a luxury food product and social status symbol. These increases in consumption rates, trade, and trade routes can largely be explained by changes in individual wealth (Watson *et al.* 2016). Notwithstanding innovations in food production, wild fisheries are, and will continue to be, a requisite of global food security, especially for vulnerable populations in coastal zones (Golden *et al.* 2016). Although there continue to be many success stories in fisheries management, target biomass levels of many species have decreased considerably through time (Pauly 1995). Globally, many populations of large predator species have been depleted (*9*, but see *10*), and what remains is often heavily size truncated, prime evidence of overexploitation. Further, the reductions of top predators and keystone species have resulted in regional trophic cascades (Worm and Myers 2003) and meso-predator release (proliferation) to varying degrees. Decapod crustaceans, including crabs, lobsters, and shrimps, are an increasingly important component of this ecological transition (Anderson *et al.* 2011).

Relative increases in crustacean landings have outpaced all other major species groups since 1990, and in that time, have nearly doubled their share from 4.4 to 7.8% of global landings (Table S1, Figure 1). Overall global landings have not appreciably changed over this period, but show a declining trend if crustaceans are omitted. While the largest individual contribution to the increase in crustacean landings is attributed to China, crustacean fisheries have risen globally in lieu of declining vertebrate catches with or without the inclusion of China (Figures 1, S2). As the global composition of fisheries changes, a new set of ecological and socioeconomic trade-offs will become important due to the unique ecological, nutritional, socioeconomic, and environmental attributes of these fisheries. To understand their role, we compiled global fisheries catch data from 1950-2016 and information on price, nutrition, and carbon emissions for four major groups of wild capture fisheries (crustaceans, cephalopods, pelagic fish, and demersal fish). We relate these global patterns to taxonomically and geographically diverse crustacean fisheries.

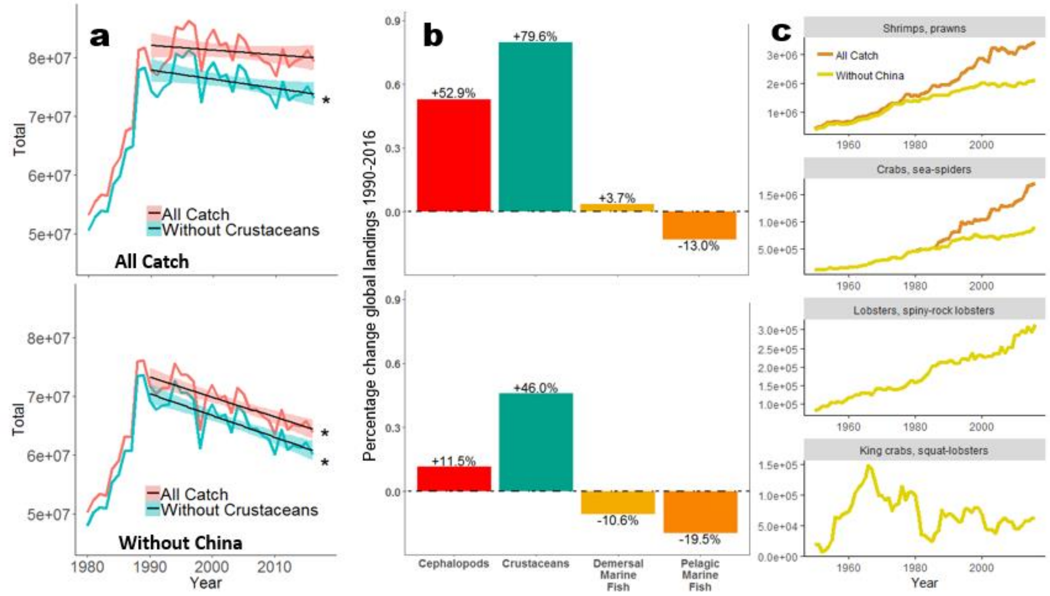


Figure 1 The role of crustaceans in global wild capture fishery landings. a) Total global landings with and without the inclusion of China (1980-2016). Between 1950 and 1980 global landings increased linearly. Landings from all countries suggest no significant positive or negative trend in global landings since 1990 (two-tail t-test, p=0.28), unless crustaceans are removed in which case the trend become negative (p=0.02). Removing China suggests that global landings have been declining since 1990, with or without crustaceans (two-tailed t-test p<0.001). (b) Total percentage change in global landings of four major species groups representing 81.3 % of global marine wild capture landings from 1990-2016 with (top) and without (bottom) China. (c) Catch trajectories of four main crustacean groups with and without the inclusion of China (as categorized by the FAO, 1950-2016).

7.2 Materials and Methods

Experimental design

Catch and value data were obtained from the FAO wild capture fisheries database (FishstatJ, 2018). Taxonomic grouping was done in accordance with defined "FAOSTAT" groups. We considered only marine capture fisheries, thus excluded groups such as freshwater crustaceans. The final four groups were selected based on taxonomic consistency and magnitude. Large amorphous groups such as "Marine Fish NEI" were excluded due to their diversity of life histories. However it should be noted that particularly in Asian countries, this group has increased markedly in recent decades, likely due to some of the same ecological forcing that have facilitated unprecedented increases in crustaceans.

For our study, we use global crustacean catches in order to relate the landed volume to catch value, to predict greenhouse gas emissions, and to draw conclusions on global crustacean abundance. Data besides catch only exist for a small number of global crustacean stocks. Ironically, fisheries-independent data or quantitative information based on stock assessments are often considered restricted to the most valuable species in data-rich regions, while crustaceans which are often the most valuable fisheries, are omitted. The question if catch reflects abundance has been an ongoing debate for several years and there is evidence for both, catch indeed reflecting abundance and catch and abundance becoming decoupled (Zimmermann and Werner 2019). Species with implemented management regimes that limit catch theoretically decouple catch and abundance when management phases in. Hence, we assume that catches are a suitable index to indicate crustacean abundance (NOAA 2015; Gaudian *et al.* 2019), although we cannot exclude that trends can diverge for particular, single stocks.

Nutritional analysis

Data related to percentage yield were obtained from the FAO (Torry Research Station, Aberdeen 1989), and other published sources when available (n=143, 132 based on FAO data, 11 from other sources). When available, percentage yield referenced raw flesh and muscle tissue. For example, with shrimp species, this would refer to the accepted practice of consuming the portion of muscle distal to the carapace, the 'tail'. Certainly, nutritional yield could be based on consuming the entire organism, but this is not particularly common practice with the exception of very small crustaceans. Nutritional data were extracted from the GENuS database (Golden *et al.* 2016). Taxonomic distinctions were accordingly made based on "FAOSTAT" groups. Relative caloric yield represents the effective yield in relation to live mass. For example, results suggest that for a 1 kg crustacean and pelagic fish, the caloric yield for the crustacean is 43% that of the pelagic fish. Due to sample size, cephalopod caloric yield was calculated as product of cephalopod percentage yield and pooled mollusk nutritional information from (Golden *et al.* 2016).

Emission projections

Short-term emission projections were based off current catch trends for included "FAOSTAT" taxonomic groups (crustaceans, cephalopods, pelagic, and demersal fish). We estimated catch trends estimated as average annual change in catch (Table S1, column 2) divided by the number of years (n=27). It is important to note that for these four groups over the selected years, intergroup total landings changed little, while intragroup landings changed considerably (Figure 1). We assumed group-specific emission intensities from (Parker *et al.* 2018). For pelagic species specifically, catch-weighted averages (small and large pelagic) were assumed based on available data. The overall result of changes in pelagic fish catch and carbon footprint were robust to the weighted or simple arithmetic mean. For the 14 year projection (2017-2030), per-capita emissions intensities were assumed stationary (i.e., the respective fisheries did not become more or less efficient). The combined 'pelagic' category is used for discussion purposes and aids in the brevity of results. We should highlight that our approach does not explicitly highlight stocks that have catch trends in opposition to the group trend. For example, global tuna catches have increased in recent years, despite a very modest overall group trend for pelagic fishes.

Socioeconomic factors

In order to calculate the volumes and values as the contributions of each taxonomic group to global total, we used data from the FAO Yearbook on Fishery and Aquaculture Statistics 2017 (FAO 2019), covering the period from 2011-2017. Although yearbooks published before 2017 contain data going back further in time than the year 2011, we did not use earlier yearbooks because prices for several taxonomic groups were revised in the most recent report and changed considerably compared to the prior yearbooks. Hence, using older yearbooks for years prior to 2011 would have caused a bias and change for the value of each taxonomic group after 2010.

7.3 Results

Biological and ecological traits

Crustaceans exhibit several important traits that increase their inherent productivity and resilience (Box 1), promoting continued increases in catch despite widespread overfishing and depletion of other species. These traits have enabled crustaceans to not only adapt but to benefit from a wide array of anthropogenic alterations to their life cycles and ecosystems, some that are direct and intended to enhance crustacean populations, and others that are indirect and the effect of unintended outcomes of other interventions (Figure 2).

Direct enhancement includes stocking (including invasive species) (Lorentzen *et al.* 2018), the use of bait to supplement diets, (Grabowski *et al.* 2010), or catching wild individuals to be raised in net pens (Shelley and Lovatelli 2011).

Box 1. Characteristics facilitating crustacean success

- **Feeding plasticity** – Many crustaceans are feeding generalists (Schram, 1986) facilitated by an extensive battery of mouth parts may process all sorts of food live or dead, plant or animal, large or microscopic.
- **Thermal tolerance** – Relatively low temperature sensitivity (Watson *et al*. 2014) may allow crustaceans to remain in particular habitats as ocean temperatures change and more easily colonize new areas.
- **Natural defenses** – Tough exoskeleton and cryptic tendencies may contribute to disproportionate decreases in natural mortality (Steneck and Wahle, 2013). Some harvested species possess large claws on the first pereiopods, adding to defense capabilities (Schram, 1986), whereas many species further reduce predation through nocturnal feeding.
- **Relatively fast growth** – Many commercially-exploited crustaceans exhibit rapid growth and/or a short life history.
- **Parental care** – Most species (i.e., suborders Dendrobranchiata and Pleocyemata) brood eggs on the mother's pleopods, producing highly-competent larvae with more than one free larval stage, thus minimizing competition among themselves (Schram, 1986).

Indirect enhancement includes instances where a species' top-predator biomass has been reduced or habitats have been altered so that habitat and/or ecosystem components become more favorable for crustaceans. All of these enhancements either supplement food and reproduction or reduce competition, natural mortality, and predation risks (Heithaus *et al.* 2008) (Figure 2). In fact, indirect consequences of anthropogenic actions can have comparable or even greater impact on crustacean populations. For example, as has been documented in the north Atlantic, intense urchin (*Stronglyocentrotus droebachiensis*) harvesting has resulted in the proliferation of microalgae, and hence the unintended expansion of key nursery habitat and enhanced juvenile survival for a variety of invertebrates (Steneck *et al.* 2013). This adds to previous challenges (Klinger *et al.* 2013) of the notion that wild-capture crustacean fisheries are fully 'wild'. It is perhaps more appropriate to consider crustacean fisheries existing on a relative 'enhancement' spectrum (Figure 2), where populations persist in ecosystems ranging from a relatively unperturbed state or thrive under nearly artificial (aquaculture) conditions. Indeed, historically overfished and simplified ocean ecosystems around the world are home to most of the largest and most valuable crustacean fisheries (Jackson 2008). This is especially true in Southeast Asia, where ecosystem overfishing and predator removal have contributed to remarkably fast growth of wild crustacean landings over the past three decades (Szuwalski *et al.* 2017; Ye *et al.* 2017).

Beyond targeted and system-specific alterations, global climate change is bringing about larger scale transitions and tipping points in the oceans, and with it, creating 'winners' and 'losers' (Cheung *et al.* 2013). Emerging from this mix of changes are mid to low-trophic level generalists: species more resilient to exploitation and changes in temperature, less restricted to a particular geography, and with a tendency for rapid growth. The same traits that provide crustaceans with robustness and adaptability in the face of overfishing may also make these species more successful facing climate change. The fossil record provides evidence that the general crustacean bauplan has proven to be remarkably successful through past iterations of global change (Clark 2009; Bracken-Grissom *et al.* 2014; Rozenberg *et al.* 2015). Coinciding with the radiation of modern fishes (early invertivores), the diverse assemblage of extant decapods evolved under high adult mortality.

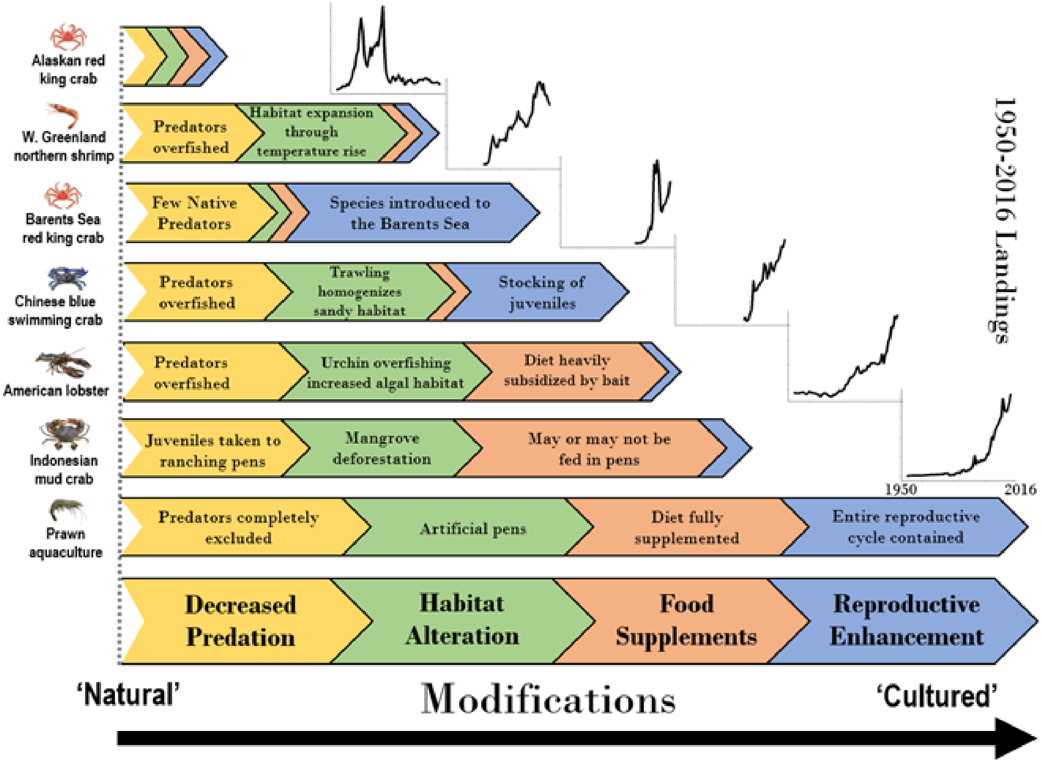


Figure 2 Conceptual spectrum of fishery enhancements through four major types of interventions, with examples from global crustacean fisheries illustrating a range of system alterations. Using prawn aquaculture as an extreme, we qualitatively consider wild crustacean fisheries with various interventions (the arrow size is conceptual). Species exist throughout the spectrum for all attributes, and when considered together, similar results may be seen from different circumstances of enhancement. (Modified from framework developed by (Klinger *et al.* 2013). References for each species: Alaska red king crab, *Paralithodes camtschaticus* (Kruse *et al.* 2010), West Greenland northern shrimp, *Pandalus borealis* (Arboe and Kingsley 2013; Hedeholm *et al.* 2017), American lobster, *Homarus americanus* (Grabowski *et al.* 2010; Steneck *et al.* 2013), Chinese blue swimming crab, *Portunus trituberculatus* (Hamasaki *et al.* 2006), Norwegian red king crab, *P. camtschaticus* (Lorentzen *et al.* 2018; Christie *et al.* 2019), and Indonesian mud crab, *Scylla serrata* (Shelley and Lovatelli 2011).

Ocean acidification and epizootic disease

Among the most discussed, but poorly understood topics related to projecting climate effects on marine ecosystems is the ability of calcifying organisms, including crustaceans, to persist with increasing ocean acidification. Studies examining the effects of acidification on the life histories of both vertebrates and invertebrates are mixed, but crustaceans may experience surprisingly modest effects, albeit with important regional and taxonomic variability (Branch *et al.* 2013; Dodd *et al.* 2015). Additional biological characteristics that could dampen the effects of acidification for some species include high capacity of osmoregulation, a biogenic and cyclically-replaceable covering (Ries *et al.* 2009), mobility, and energy allocation plasticity (Arnold *et al.* 2009).

An underappreciated threat posed by climate change is the possibility of increased epizootic disease. Substantial evolutionary top-down control has caused many crustacean species to endure cryptic lifestyles (Steneck and Wahle 2013). As has been seen in systems such as the western North Atlantic, the removal of predators over time creates an environment sufficient to allow increases in decapod density and carrying capacity far above historically top-down controlled levels. This may facilitate density-dependent emergence and spread of disease, which is further exacerbated by increasing temperatures. Work across invertebrate phyla suggests an increasing propensity of disease outbreaks given rising temperature and population density (Miner *et al.* 2018), however, the study of disease across wild crustacean populations is relatively nascent (Stentiford *et al*. 2012), so it is uncertain whether and by how much future risks will change.

Socioeconomic Factors

Despite a relatively modest contribution to landings volume (7.8%), crustaceans represent a disproportionate 22.6% of global fisheries value, making them the most valuable group by landed mass (Figure 3) (FAO 2016). The four highest-valued taxonomic seafood groups are invertebrates, of which the top three are crustaceans (lobsters, crabs, and shrimps and prawns; (FAO 2018)). In recent years prices have continued to rise. From 2011-2017, global crustacean catches and prices have increased the fastest among all other major groups (catch +13%, price +4.1%). This general trend is seen worldwide (Figure S1). Since 1990, annual crustacean catches have more than doubled in Africa and Asia (+134 and +101%, respectively), and increased substantially in all regions except Oceana (-4%) (Figure S1).

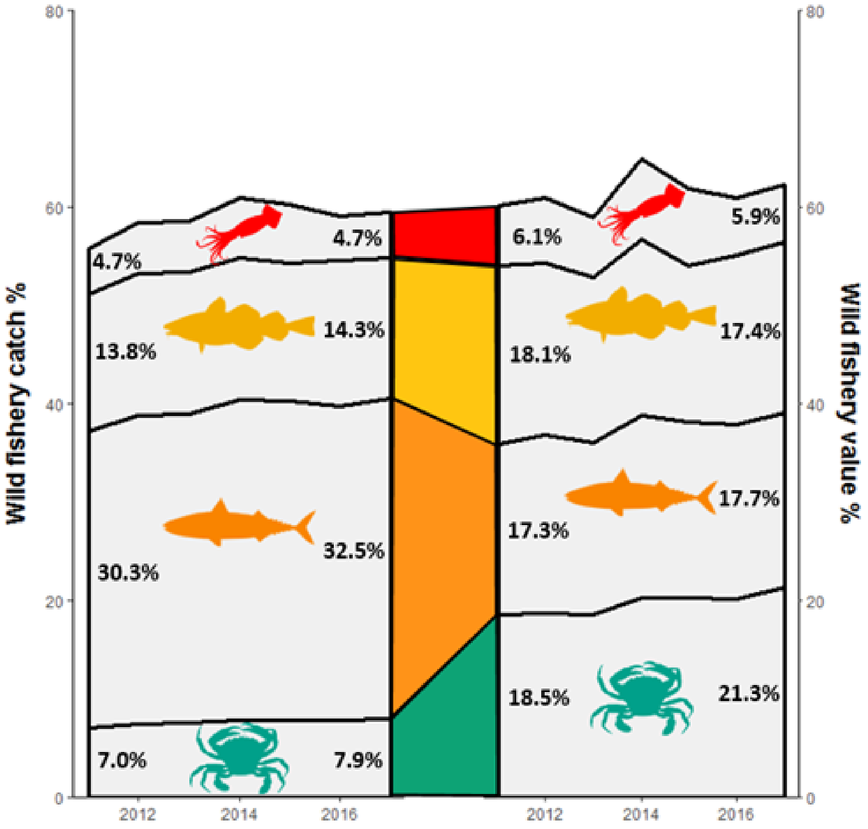


Figure 3 Landings and value for four major wild capture fisheries groups (Crustaceans (green), Pelagic fishes (orange), Demersal fishes (yellow), and Cephalopods (red)) spanning 2011-2017. Percentages denote beginning and ending percentage contribution to global total based on (FAO 2019).

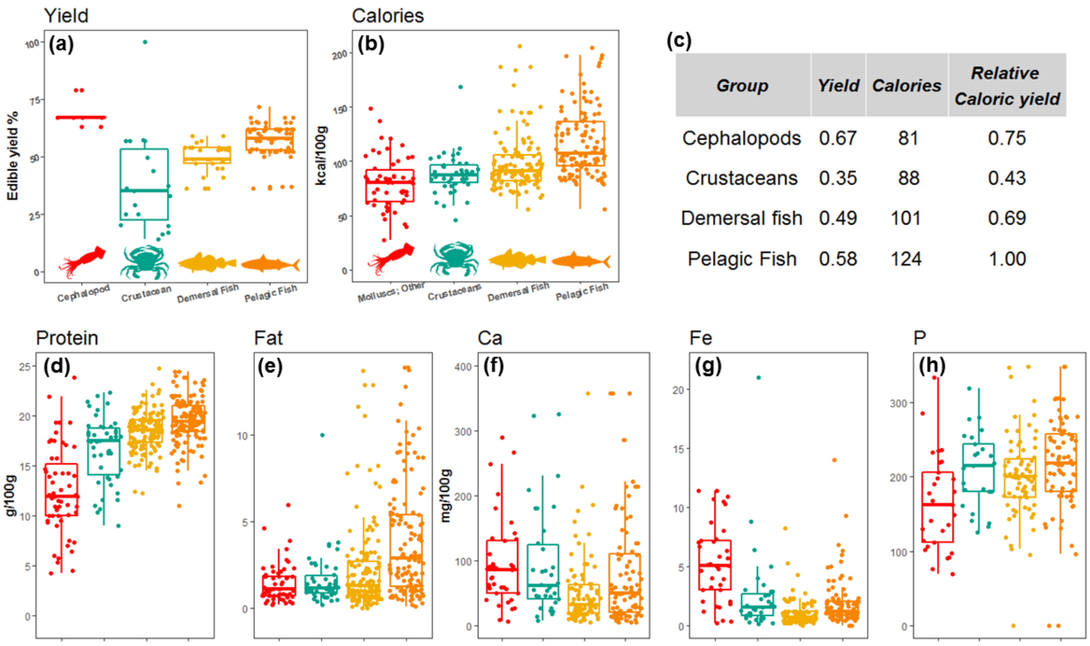
The shift towards crustaceans is signaling a global shift down (or through) the foodweb (Essington *et al.* 2006), but is providing an important monetary counterbalance to the decline in many finfish fisheries. For example, following the historic collapse of Atlantic cod in Canada, from 1990-2016, total fishery catches in Atlantic Canada have declined 51% while overall value (adjusted for inflation) has increased 92%. Lobster catch alone now accounts for 84% of Atlantic Canada's total wild fishery value (landings have increased 89% since 1990) (DFO). Particularly, in less affluent countries, rising crustacean catches can empower communities to leverage emerging economic opportunities, with export-oriented luxury foods serving as a crucial step for poverty alleviation.

These benefits are not without substantial risks. Reliance on high-value species brings added potential for overexploitation (Anderson *et al.* 2011), over-dependence, overcapitalization, and social traps (Steneck *et al.* 2011). In the event of a collapse, or even moderate fluctuation, over-reliance on a small number of resources can decrease social resilience irrespective of the value of a species. Moreover, harmful incentives such as government fuel subsidies will continue to play a role in compounding the risks of overcapitalization and overdependence (Sumaila *et al.* 2010). Undoubtedly, most social and ecological externalities will occur in vulnerable coastal fishing communities (Asian countries account for 69% of crustacean landings). Diversified fishing portfolios provide greater resilience, however, the high value of certain species combined with harmful subsidies can hinder the motivation to rebuild and sustainably manage a broader array of species.

Food and nutrition

Based on our analysis of the yield and nutritional composition, the consumable weight of invertebrates is on average lower than that of most other seafood (Figure 4a). Approximately 60% of the landed biomass of large vertebrates such as salmon and tuna is normally consumed, and the proportion is even higher for most cephalopods (~70%). Conversely, for a large crustacean like American lobster (*Homarus americanus*), the yield is 15-25%, depending on season. After accounting for overall yield and caloric content of consumable mass, the mean ‘caloric yield’ per landed mass for crustaceans is only 62% and 43% that of demersal and pelagic fish, respectively (Figure 4c). Thus, high-value crustaceans are little direct relief for food-insecure people. From the portion that is normally yielded, the micronutrient composition of crustaceans is generally comparable to finfish (Figure 4, S3).

Seafood is a major source of protein and micronutrients for 1.4 billion people (Golden *et al.* 2016). Therefore, reductions in food security due to declining fisheries are a global concern for which the growth of crustacean fisheries has mixed implications (Golden *et al.* 2016). It appears that the high economic value of many crustacean species can provide fishing communities with the income needed to secure sufficiently nutritious food, provided that fishery benefits are distributed broadly and equitably. However, the growth of crustacean fisheries is changing the nature of food harvested from the ocean. If crustaceans are to replace yields from historically finfish-dominated fisheries, landed biomass provides an incomplete measure of the realized amount of food and nutrition from seafood in much the same way that it provides an incomplete measure of economic contribution. The rising importance of crustaceans seems to shift the relative socioeconomic contribution of the fisheries away from nutrition contributions and towards generation of wealth.



Group	Yield	Calories	Relative Caloric yield
Cephalopods	0.67	81	0.75
Crustaceans	0.35	88	0.43
Demersal fish	0.49	101	0.69
Pelagic Fish	0.58	124	1.00

Figure 4 Nutritional summaries of four major species groups in global fisheries. (a) Edible yield (100 x [edible biomass/total biomass]), (b) caloric content [Kcal/100g edible biomass], and (c) mean caloric yield (edible calories per unit of total biomass relative to pelagic fishes) of globally representative species (See supplementary Materials for sources). (d-h) Nutritional breakdown for 387 species (see Figure S3 for data on additional micronutrients). Nutritional information for molluscs are pooled due to data availability. Pelagic fish exhibit a high percentage yield and caloric content, thus have the highest relative caloric yield. Crustaceans have the lowest yield and low caloric content, amounting to a mean caloric yield of 43% relative to pelagic fish.

Carbon footprint

Crustaceans are harvested in many different ways but overall are the most energy-intensive form of seafood production (Parker *et al.* 2018; Hilborn *et al.* 2018). Trap and trawl fisheries for crustaceans accounted for 22% of global fishery carbon emissions in 2011, but only 6% of landings. We calculated the average change in fishery landings from 1990 through 2016 (the period that global fishery landings have remained relatively stable) for four major fishery groups and extrapolated this increase from 2017 through 2030 to compare with emission intensity estimates (Parker *et al.* 2018) (Figure 5). While the modest projected decrease in emissions from pelagic fish catches approximately cancels out the increase of emissions from cephalopods and demersal fish catches, overall emissions from fishing operations are projected to increase by 22 million metric tons (15.0%) (Figure 5). Crustaceans dictate this increase, causing overall emissions to rise, although their increase in catches is relatively low (Figure 5).

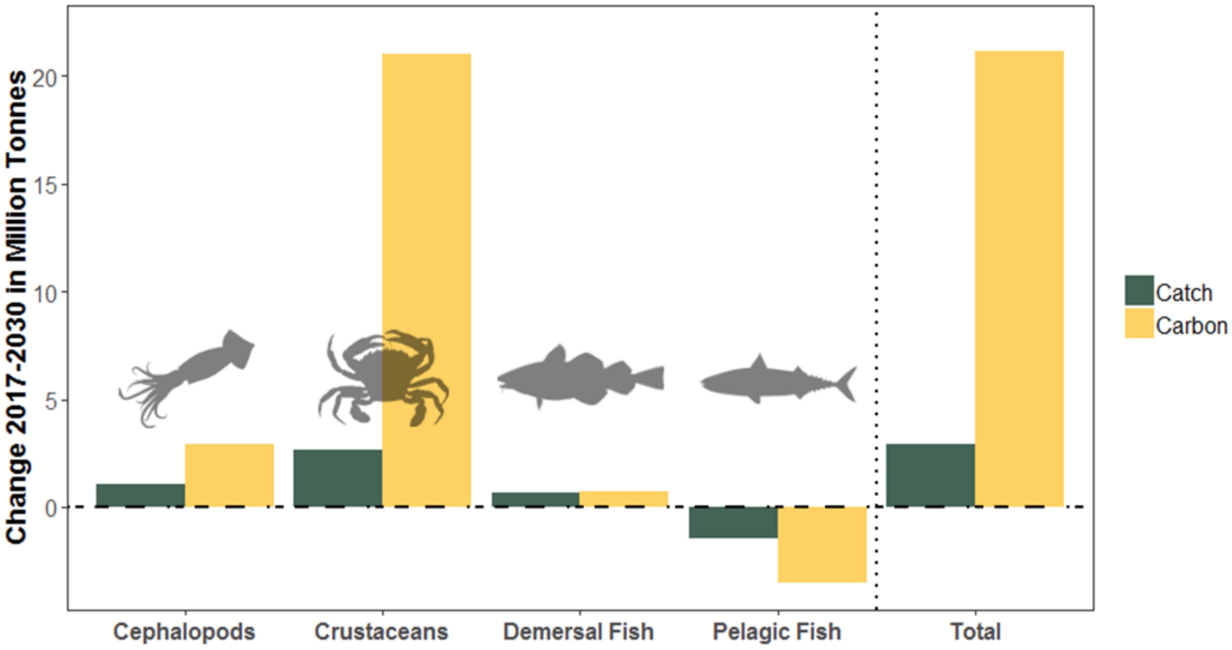


Figure 5 Projected change in global fisheries catch and CO_2 emissions from 2017-2030 for four major fisheries groups comprising 81.3% of landings. Change in overall catch (green bars) is based on mean annual change from 1990-2016 (FAO 2016). CO_2 emissions (yellow bars) based on indices from (Parker *et al.* 2018). Due to the lower per-capita fuel consumption of non-crustacean groups, net carbon emissions are effectively offset increases in crustacean catches dictate the overall increase in system emissions. Despite a projected modest increase of 1.78 million tons in overall catches, CO_2 emissions increase by 22.25 million tons, equivalent to 15.0% of the overall global fishery emissions in 2016.

Comparatively, the emissions intensity (kg CO_2/per kg) of small pelagic fish (< 30 cm) is nearly 40 times lower than for crustaceans, while cephalopods, pelagic fish and demersal fish are in the range of 24-35 % of the greenhouse gas emission intensities of crustacean fisheries (Parker *et al.* 2018). Furthermore, published figures only consider the carbon footprint associated with active procurement of the target species, and not the costs of catching and transporting bait, or the emissions associated with increasingly global supply chains. This implies that overall greenhouse gas emissions associated with crustacean fisheries are considerably higher than those from the fishery process. Illustratively, based on 2016 catch records, the economically important American lobster fishery in New England, USA, has a bait:landings ratio of approximately 1:1, and exports a significant portion of the catch live to Asian markets.

The total contribution of the fisheries sector to global food production emissions is, however, < 5 %, and ~1 % overall (Hilborn *et al.* 2018). Whereas nutritional attributes are essentially fixed, and economic factors are subject to complex dynamics, it appears that carbon footprint is an aspect that could be changed through improvements in gear and vessel technology, fishing behavior, and supportive management strategies.

7.4 Conclusions

In nearly all regions of the global ocean, more crustaceans are being caught for more value than ever before, providing new socioeconomic opportunities. Crustaceans are increasing on a spectrum of altered systems that draw striking similarities to partial domestication. Counterintuitively, the fishery production value of these crustacean dominated systems may be more lucrative than the previous "pristine state".

The risks connected to this transition are largely untested, opening possibilities that the more profitable ecosystem state may be unstable. Although results from this study paint a complicated picture of the trade-offs associated with rising crustacean landings, they demonstrate that more lucrative alternative ecosystem states may decrease fisheries yields and increase carbon emissions. In the cases of West Greenland shrimp and American lobster, overall edible seafood did not only decrease due to generally lower edible yield percentage in crustaceans (Figure 4) but also due to lower total landings from the fishery in comparison to previously cod-dominated ecosystems (Worm and Myers 2003). In less developed countries, a shift towards higher value crustaceans may mean a larger reliance on exporting to other markets, and could be especially important in creating jobs and improving livelihoods, even if crustaceans are not being directly consumed. However, any market externalities (increased risk of cascading ecosystem effects, CO_2 emissions, disease potential, decreased system resilience, market variability, and social traps) will be realized by these same communities.

Reliability concerns are often raised with global fisheries data (Pauly and Zeller 2017). To address our own data quality concerns it was important to examine inter-regional consistency of fishery trends. Furthermore, the long debate over using catch data to represent abundance did not go unheeded (Pauly *et al.* 2013). With sole use of catch records, disentangling the relationship between catch and abundance is difficult. Additionally, the broad scale of our approach could not address individual stocks or shifts in population structure that may maintain overall crustacean productivity despite local depletion. We focused our analysis on decapod crustaceans where long catch records and ecological literature exists for many (albeit, data-rich) regions. This evidence (Figs S1, S2), lends support that the global increase of crustacean fisheries is simultaneously the result of aided ecological and market drivers.

Our analysis demonstrates that the global hunger for luxurious seafood products comes with trade-offs. For future policies, management should carefully weigh these tradeoffs. Overall, we recommend more diversified portfolios as logical approaches to reduce long-term social and ecological risks. Further, governments should avoid the use of subsidies to reduce the propensity of overcapitalization and over-reliance. Fortunately, many environmental effects can be mitigated with improvements of gear efficiency and management. While the global rise of crustaceans brings social opportunities for poverty alleviation, and wealth generation, based on our analysis, attaining the optimal balance between economic and ecological integrity will be a necessary challenge as we traverse the Anthropocene.

7.5 Acknowledgements

The authors would like to sincerely thank Cayla Calderwood, Timothy Fitzgerald, Emilie Litsinger, and Alexis Rife for many helpful comments on previous versions of this paper. This research was supported through a gift to Environmental Defense Fund from the [High Meadows Foundation, Kravis Scientific Research Fund] for post-doctoral fellowships. The authors claim no conflict of interest. K. M. Werner received financial support from CLIMA project (RER 15/0008, Ministry of Foreign Affairs Norway).

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List of Supplementary Materials

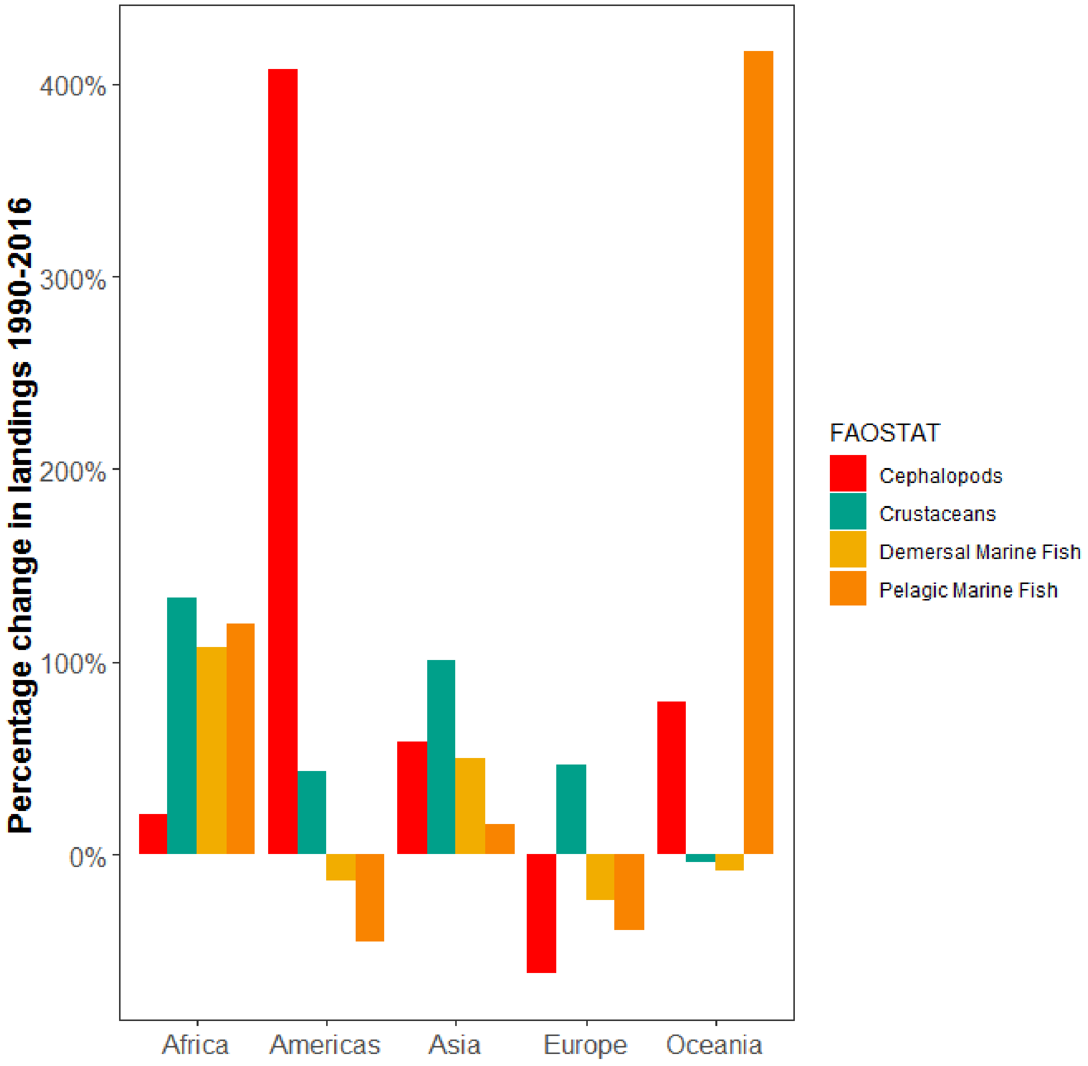

Figure S1 Global catch composition. Total percentage change in 1990-2016 regional landings for 4 dominant marine fishery groups comprising 81.3% of global catch.

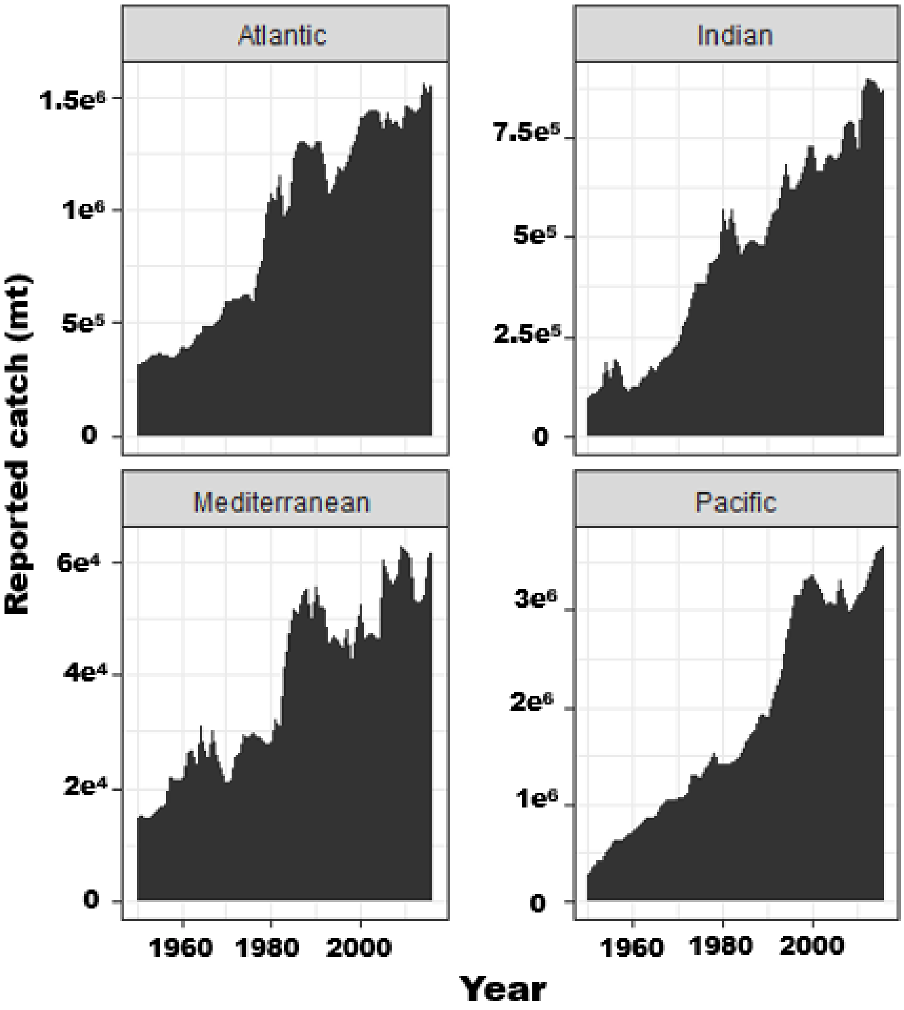

Figure S2 Global marine crustacean catch by ocean from 1950-2016 (Data source: FAO 2018). Note difference in y-axes between subplots.

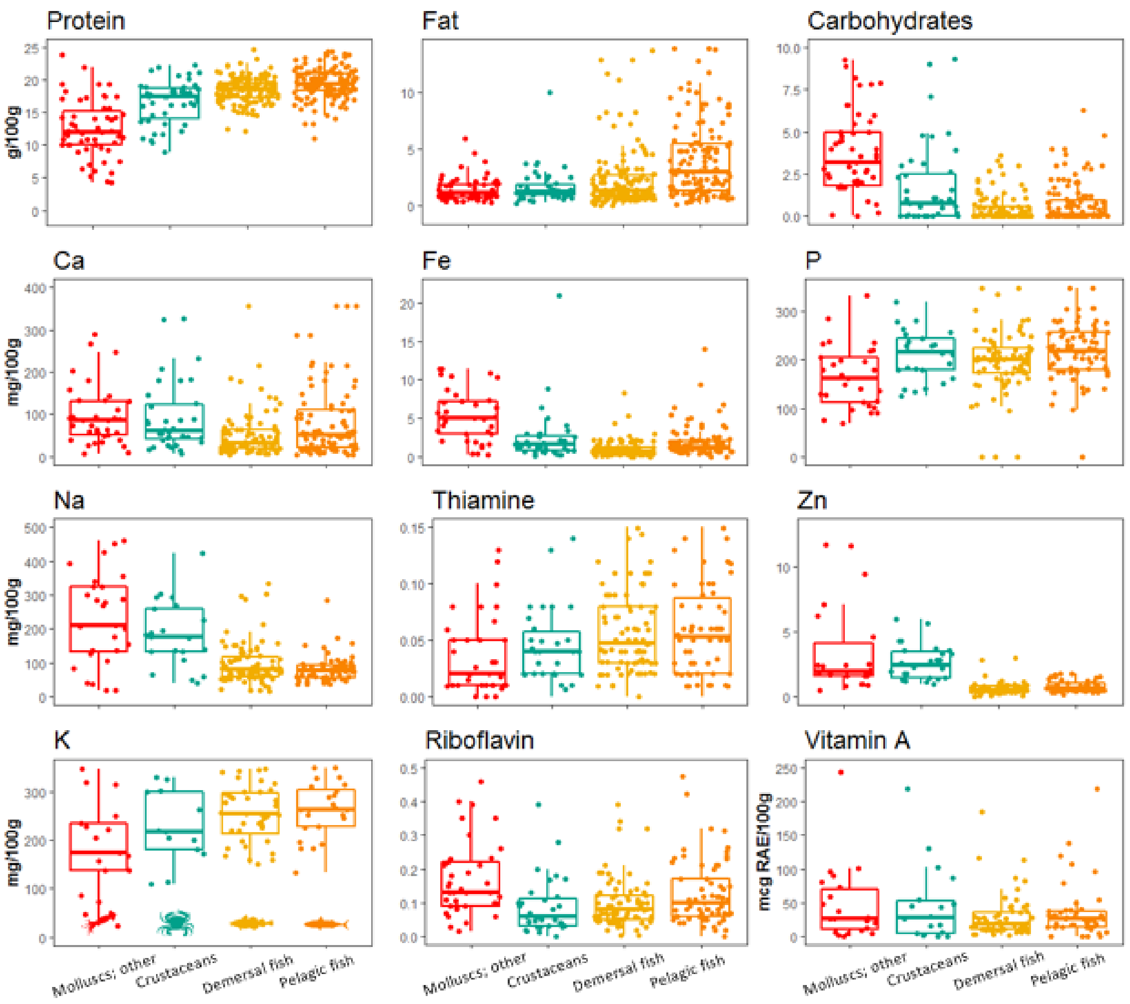

Figure S3 Nutritional summaries of four categories of global fisheries. Twelve subplots denote nutrient breakdown based on data from GENuS database, covering 387 species (raw, unprocessed flesh when available). Micronutrients if not spelled out are labeled with elemental signature. Nutritional information for molluscs are pooled due to data availability. Boxes represent interquartile range, whiskers extend to estimated 95% confidence interval.

Table S1 Overall percentage change, compositional change, and current breakdown of wild capture fishery yield for four major taxonomic groups comprising in excess of 80% of global landings from 1990-2016 (Source FAO, 2018).

Taxonomic Group	1990-2016 Δ Landings (%)	(%) Total 1990 global landings	(%) Total 2016 global landings	(%) 1990 catch from China	(%) 2016 catch from China
Cephalopods	52.9	3.1	4.6	3.2	29.4
Crustaceans	79.6	4.4	7.8	25.9	39.7
Demersal Marine Fish	3.7	26.4	26.8	5.3	18.4
Pelagic Marine Fish	-13.0	49.4	42.1	2.6	9.8
Total		**83.2**	**81.4**		

8 Synoptic discussion and conclusions

The aim of the present thesis was to investigate how natural drivers and anthropogenic pressures affect abundance, body condition and trophic interactions of Atlantic cod in offshore Greenland waters and how this might be associated with potential impacts on population replenishment.

In order to address these questions, we analysed **1)** historical time series of abundance and fishing mortality of Greenland cod, how natural variation and fishing influence population dynamics and how these dynamics compare to other cod and North Atlantic fish stocks, **2)** if spatial and temporal variability of diet composition influences energy acquirements and if the cod populations are able to adapt to habitat quality differences, **3)** if habitat heterogeneity can influence body condition of large mature female cod using organosomatic and biochemical indicators, such as total fat content and fatty acid composition, and **4)** the impact of ecosystem changes and overfishing on the composition of fishery landings and associated socio-economic and ecological trade-offs including an example from the West Greenland cod fishery.

I will begin the subsequent and final chapter with a comprehensive summary of the publications, which I will use to discuss how combined results across the different chapters align to address the objectives of the thesis. Five questions were chosen, designed to discuss these results:

1. Why are recruitment patterns chaotic?
2. How is diet composition linked to stock productivity?
3. Is capelin important for Greenland cod?
4. How should the Greenland cod stock be managed?
5. How can results contribute to an ecosystem approach to fisheries?

Afterwards, I will summarize how climate change is expected to impact temperature, primary productivity and fisheries productivity around Greenland. This information will be combined with the results from the previous chapters to discuss, how climate change might affect the Greenland cod stock and how it might interact with other natural and anthropogenic drivers in the future. The thesis will be closed with an outlook trying to identify research gaps, which could provide further insight into the understanding of fishing and natural variation as drivers of exploited wild fish populations and how the socioeconomic and ecological challenges of the Anthropocene might affect fishery science and natural resource management.

8.1 Comprehensive summary and discussion - The role of fishing, natural variability and diet on cod abundance and stock productivity in Greenland

Disentangling the impacts of fishing pressure and natural variability on exploited fish populations has been a seminal part of fishery science for over a hundred years. In the 20th century, this question crystallized as result of the collapse of the Pacific halibut (*Hippoglossus stenolepis*) stock in the 1920s (Skud, 1975; Hilborn and Walters, 2013). From the 1930s to the 1950s, the scientists W. F. Thompson and M. D. Burkenroad brought forward two hypotheses, why the stock of Pacific halibut had collapsed: Thompson believed that overfishing caused the stock to collapse and Burkenroad believed that natural variation was the reason for low juvenile survival, which triggered a decline in halibut abundance (Skud, 1975; Hilborn and Walters, 2013). Although it still remains unclear, what had caused this in the end, the theme of natural variation and fishing as drivers of abundance of commercially exploited fish stocks is by no means less important or up-to-date than 100 years ago (Hilborn and Walters, 2013) and because this issue has not been addressed for many commercially exploited fish stocks, it is important to be investigated.

This thesis has shown that fishing as anthropogenic driver had strong impacts on abundance of Greenland cod from 1955-2015 (Chapter 2). Commercial fishing likely magnified natural fluctuations in abundance and had through growth and recruitment overfishing long-term negative effects on stock replenishment (Chapter 2). Because interannual patterns of recruitment are chaotic and affected by temperature and an irregular influx of larvae from Iceland, population replenishment is difficult to predict and relies on infrequent spikes of recruitment (Chapter 2 and 3). Recovery patterns of other Northeast Atlantic fish stocks show that effective fishery management works, highlighting the contrast between Greenland cod and more sustainable management regimes (Chapter 2 and 4). This emphasizes that a reduction in exploitation rates or even a catch moratorium might be sufficient to initiate a recovery of the Greenland cod stock.

Habitat quality and responsive behaviour was shown to affect body condition, which likely affects population replenishment (Chapter 5 and 6).This implies that habitat is an important and often overlooked aspect, which has impacts on important life-history traits, such as growth and reproduction (Chapter 5 and 6). Greenland cod was shown to exhibit limited behavioural responsiveness to the spatial variation of habitat quality and tended to stay in sub-optimal habitats, leading to low body condition (Chapter 5 and 6). This was not only observed on organosomatic level, as through the liver index, but also through biochemical indices of body condition, such as fatty acid profiles (Chapter 5 and 6). These results show how natural variability can act indirectly through trophic relationships on population dynamics, life-history traits and likely on population replenishment.

Finally, results of this thesis indicate that changes fishery catch compositions can have socioeconomic implications (Chapter 7). A global transition from a fish to a crustacean dominated fishery, as it happened in West Greenland, when the cod collapsed and northern shrimp began to proliferate, comes with high CO_2 emissions, low food security but potentially more wealth (Chapter 7).

Why are recruitment patterns chaotic?

The work, which is part of this thesis, has shown that the offshore cod stock in Greenland waters has experienced chaotic recruitment patterns in the past (Chapter 2 and 3). Year class strength depends on influx of larvae from Iceland and beneficial environmental conditions for survival of the early life stages (Chapter 2 and 3). Historically, fishing mortalities were almost always at unsustainable levels (Chapter 2). Overfishing contributed to the decline of the Greenland cod stock in the late 1960s and catches of immature individuals likely prevented a recovery since the first population collapse (Chapter 2). Although it appears that the first stock collapse in the 1960s was initiated by recruitment failure caused by a decline of temperature, fishery catch rates were not lowered to adapt to this decrease of natural stock productivity (Chapter 2 and 3). As cod inhabits areas close to its lower thermal boundary in Greenland

(Drinkwater, 2005; Pörtner *et al.*, 2008), declining productivity as response to declining temperature is not unexpected and typical for other arcto-boreal gadoid species, such as haddock (*Melanogrammus aeglefinus*), ling (*Molva molva*), saithe (*Pollachius virens*) and tusk (*Brosme brosme*) (Hansen, 1949; Drinkwater, 2006; Drinkwater and Kristiansen, 2018). The dependency of Greenland cod recruitment on abrupt changes in the environment, such as a cooling, as well as on influx of larvae from the Icelandic cod stocks are likely the main reason for chaotic recruitment patterns and unpredictable recruitment spikes (Chapter 2 and 3). These patterns, which are common in Atlantic cod stocks, make it difficult to accurately predict future recruitment success (Chapter 3).

Looking across cod stocks of the North Atlantic, it stands out that recruitment success, growth and stock productivity depend on body condition (Rätz and Lloret, 2003). Warm-water cod stocks with higher growth and body condition, which are mainly found in the southern part of the Northeast Atlantic, such as the North Sea, are more productive especially at low spawning biomass than the arcto-boreal cold-water stocks of the North and Northwest Atlantic (Rätz and Lloret, 2003). Because recruitment is affected by body condition and growth, which depend on the diet composition, the question of how important diet composition is for population replenishment of the Greenland cod stock, must be raised (Kjesbu *et al.*, 1998; Yaragina and Marshall, 2000; Rose and O'Driscoll, 2002; Mcbride *et al.*, 2015; Frater *et al.*, 2019; Link and Sherwood, 2019).

How is diet composition linked to stock productivity?

Food availability and energy acquisition are predictors of reproductive potential and offspring health in many fish species (Marshall *et al.*, 1999; Lloret, Shulman and Love, 2013; Mcbride *et al.*, 2015). The amount of energy an individual can acquire depends directly on the availability of food resources as well as on its abilities to respond to changing environments (Sutherland, 1996; Lloret, Shulman and Love, 2013; Casini *et al.*, 2016).

Abundance of the offshore cod stock in Greenland waters is at historically lowest levels and especially the West Greenland population, which used to be of considerably larger size than the East Greenland population and supported a big international fishery in the 1950s and 1960s, has suffered from overfishing and low recruitment (Chapter 2) (Therkildsen *et al.*, 2013; Bonanomi *et al.*, 2015; ICES, 2019c). Despite low cod biomass and density in West Greenland, which could lead to density-dependent higher food intake for the remaining individuals, body condition and energy reserves are low (Chapter 2, 5 and 6). This indicates that in addition to overexploitation, ecological effects currently deteriorate body condition and growth of cod in West Greenland. Because body condition of Greenland cod benefits from above average temperatures , this is surprising, because temperatures have been generally high over the past two decades (Lloret and Rätz, 2000; Drinkwater, 2005; ICES, 2018). As results from chapter 5 indicate, cod in Greenland shows limited abilities to adapt its distribution to the spatial variation of habitat quality and is not ideally distributed, going against ecological theory. If cod individuals in West Greenland were currently not able to detect high quality habitats, but continuously stuck in areas with low-quality food resources, this might be one of the reasons for low body condition. However, because scientific advice continues to be ignored and catches remain high (ICES, 2019c), it remains complicated to disentangle the impacts of natural variability and fishing (Chapter 2).

In comparison to diet composition in West Greenland in the early and mid 20th century (Table 1, see introduction), it becomes clear that consumption of forage fish species such as capelin or sandeel (*Ammodytes* spp.) has been low in West Greenland over the past decade (Chapter 5 and 6). Instead, from 2006-2016 cod diet in West Greenland mainly consisted of crustaceans and benthic organisms, such as brittle stars and sea cucumbers, of which especially benthic echinoderms are known to have low organic and caloric content and can be considered to be a rather low-quality food source for cod in Greenland offshore waters (Chapter 5 and 6) (Atkinson and Wacasey, 1976; Percy and Fife, 1981; Norrbin and Båmstedt, 1984; Wacasey and Atkinson, 1987).

In contrast to these observations from Greenland, it was hypothesized that limited access to benthic prey organisms may negatively affect body condition of Eastern Baltic cod (Casini *et al.*, 2016). Eastern Baltic cod showed a strong decline in body condition over the past decades, which was related to limited access to the giant isopod *Saduria entomon* (Casini *et al.*, 2016). *S. entomon* was a major food item of cod but decreased especially in the central Bornholm basin due to more frequently occurring and stronger pronounced hypoxic conditions (Casini *et al.*, 2016). The hypothesis that benthos accessibility can be also positively related to body condition of cod might be further supported by the fact that over the last decades cod from Western parts of the Western Baltic Sea feeding mainly on benthic invertebrates such as the common shore crab (*Carcinus maenas*), showed a higher body condition than Eastern Baltic cod feeding mainly on clupeids (Funk et al., unpublished; S. Funk, pers. comm.). However, whether these differences can be more related to differences in food quality or more to a general difference in food accessibility and related differences in the overall consumption rates between the two cod stocks, could not be clarified so far (S. Funk, pers. comm.).

Capelin constituted a large fraction of cod diet in West Greenland, when the stock rose in the first part of the 20th century (Table 1, see introduction). This forage fish species is known to be a valuable food source for all arcto-boreal cod stocks in the North Atlantic and low capelin recruitment and abundance is often linked to low body condition, growth and recruitment (Yaragina and Marshall, 2000; Rose and O'Driscoll, 2002; Lilly *et al.*, 2008; Pardoe, Thórdarson and Marteinsdóttir, 2008; Frater *et al.*, 2019; Link and Sherwood, 2019).

As discussed in the beginning of this chapter, the Greenland cod stock generally shows low growth and body condition, leading to lower recruitment especially at low spawning stock sizes in comparison to warm-water cod stocks (Rätz and Lloret, 2003). In contrast to only a few or just one abundant forage fish species as food supply in Greenland waters, cod in the North Sea can choose from a wide array of abundant forage fish species, such as Atlantic herring (*Clupea harengus*), sprat (*Sprattus sprattus*), sandeel (*Ammodytes* spp.), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), dab (*Limanda limanda*) or plaice (*Pleuronectes platessa*) (Daan, 1973; Adlerstein and Welleman, 2000). Here it seems that cod could likely cover periods with a shortage of one species by switching to another, comparable species (Lilly *et al.*, 2008; Link and Sherwood, 2019). Because many clupeids, flatfish and gadoid species, which constitute important parts of the diet in the North Sea, are not very abundant in Greenland waters, they only account for a tiny fraction of cod diet in the area (Chapter 5 and 6) (Table 1, see introduction). This generally more stable food-supply could be one factor making the southern cod stocks less susceptible to overexploitation (Rätz and Lloret, 2003). These patterns indicate that the warm-water cod stocks, such as North Sea cod, show higher adaptive capacities to natural environmental variation, which affect abundance of different prey species, than the Greenland cod stock. Availability of just one or few abundant forage-fish species might be a reason for the vulnerability of cold-water cod stocks to overexploitation and chaotic stock-recruitment dynamics (Chapter 2, 3, 5 and 6) (Lilly *et al.*, 2008; Link and Sherwood, 2019).

However, because resilience to overfishing increases in the warm water cod stocks (Rätz and Lloret, 2003), low body condition and growth linked to low temperatures in West Greenland could to some degree be the natural state of the population. Nevertheless, although the results of this thesis show that consumption of mesopelagic fish is superior for energy acquirements and body condition in comparison to consumption of capelin (Chapter 4 and 5), it appears that capelin or sandeel as additional food source to crustaceans and benthic organisms could currently have a positive effect on body condition and stock productivity of cod in West Greenland.

Is capelin important for Greenland cod?

Interestingly, this thesis has shown that capelin is beneficial for body condition and energy acquirements for small and medium-large cod (20-60 cm), but not for cod larger than 60 cm (Chapter 5). In the Barents Sea and in Labrador-Newfoundland, consumption of capelin decreases with body size and is most important for cod below 80 cm (Sherwood *et al.*, 2007; Holt *et al.*, 2019). Similarly to patterns observed in Greenland, body condition of cod feeding on capelin decreases with size in Labrador-Newfoundland, indicating that for large cod the energetic costs of hunting a fast pelagic species, such as capelin, might offset the benefits (Chapter 5 and 6) (Sherwood *et al.*, 2007). It might be beneficial for large cod to consume larger prey, albeit of lower quality (Chapter 5 and 6) (Sherwood *et al.*, 2007). Assuming that capelin is important for recruitment and growth, this indicates that population replenishment is related to body condition of medium-size cod.

In fishery science, it has previously been hypothesized that the oldest and most experienced females in a population constitute the reproductive backbone (Hixon, Johnson and Sogard, 2014). The fact that recruitment of arcto-boreal cod stocks might depend more on condition of medium-size individuals questions the importance of these so called “BOFFFFs” (big old fat fecund female fish) for population replenishment (Andersen, Jacobsen and van Denderen, 2019).

Results from this thesis reveal that high consumption rates of mesopelagic fish, but not capelin, lead to highest energy reserves in Greenland cod (Chapter 5 and 6). Interestingly, fatty acid analyses show that consumption of capelin was linked to a low ratio of the polyunsaturated fatty acids eicosapentaenoic acid (EPA) to arachidonic acid (ARA) in the gonads (Chapter 6). Fatty acids are involved in many functional and structural traits of life, such as maturation, cell membrane integrity and reproduction (Tocher, 2003; Røjbek *et al.*, 2014). Feeding experiments with cod have shown that a low EPA:ARA ratios in the diet lead to highest egg production and the highest number of viable eggs per kg of female cod (Røjbek *et al.*, 2014). Hence, although capelin consumption did not cause large energy reserves as indicated by liver size and liver lipid storages, it was associated with a low EPA:ARA ratio, a fatty acid composition in the gonads linked to increased production of viable eggs (Chapters 5 and 6). This provides evidence for why capelin might be of great importance for stock productivity of the arcto-boreal cod stocks and shows how variability in abundance of a forage fish species might affect the reproductive success in fish populations (Lilly *et al.*, 2008; Link and Sherwood, 2019).

How does this have implications for management?

Productivity of the Greenland cod stock is susceptible to abrupt changes in the environment and to overfishing (Chapter 2, 3 and 4). Historic abundance and exploitation patterns of Greenland cod contrast with large-scale developments in Northeast Atlantic waters, where enforced management measures, such as effort reductions and a stricter compliance with scientific quota recommendations, have facilitated an increase of commercially exploited fish stocks over the past two decades (Chapter 2 and 4). While the past has evidently shown that unregulated fisheries will most likely lead to overfishing, these patterns paint a clear picture and show that only when the political will exists and rules are in place, fish stocks are sustainably managed and can recover from previous overfishing (Chapter 2 and 4). In cases, where overfishing is not haltered, stock recoveries must solely rely on favourable environmental conditions and unpredictable recruitment spikes, what has often not led to sustainable exploitations (Chapter 2 and 4).

According to the latest advice the East Greenland cod stock is currently not overfished and the biomass is above the sustainable reference point MSY $B_{trigger}$, although total allowable catches have exceeded scientific advice since more than a decade (ICES, 2019c, 2019a). In 2019, the total allowable catch was almost four times higher than the scientific advice (ICES, 2019a). The West Greenland offshore stock is currently handled as a data-limited “category 3” stock (ICES, 2019b). While these information suggest that the Greenland cod stocks, as they are currently treated separately, are managed sustainably in East Greenland, our results from chapter one show that cod biomass in West and East Greenland combined is compared to historic dimensions on a very low level (Chapter 2). This discrepancy likely arises because the historic dimension is ignored with the current stock separation, which dates back to 1973 in East Greenland (ICES, 2019c). In addition, drift patterns of eggs and larvae from Iceland distort the perception of historic cod abundance in East Greenland and are the main reason for very low biomass and very high fishing mortality reference points (ICES, 2019a). Because drift from Iceland occurred in years, where cod biomass was on levels among the lowest in the time series, it appears that the stock can tolerate high levels of exploitation (Precautionary fishing mortality > 1) and be fished down to negligible biomass levels and still replenish itself (ICES, 2019a, 2019c). Considering that the by far largest year classes going into the assessment, 1973, 1984, 1985 and 2003 were of Icelandic origin, it becomes clear that the self-sustaining proportion of East Greenland recruitment is considerably lower. Although reference points indicate that the East Greenland cod stock is currently managed sustainably, it seems highly probable that current exploitation rates exceed the potential of the stock to replenish itself. For West Greenland, the results of this thesis are in line with current perception of the stock status as severely depleted (ICES, 2019c).It appears that a combination of the East and West Greenland offshore stocks into one assessment (Chapter 2), could increase the quality of current scientific advice by lifting the West Greenland stock from a data-limited to a "category 1", full quantitative, assessment and getting rid of unrealistic reference points in East Greenland.

Both knowledge and evidence exist, which can lead the way to a sustainable fish stock management (Chapter 4) (Hilborn *et al.*, 2020). It appears that in order to rebuild the Greenland cod stock, only a catch moratorium would help. Rebuilding of the stock could, however, be hindered by unfavourable environmental conditions, as indicated by low body condition in West Greenland (Chapter 5, 6 and 8). Results from the comparative modelling approach in chapter 2, showing that the stochastic cusp model, which is best at identifying catastrophic dynamics, is the most suitable approach for explaining stock-recruitment relationships of the Greenland cod stock, stress the stock's vulnerability to overexploitation and the need for a precautionary management approach (Chapter 2, 3 and 4).

Overfishing of the West Greenland stock led to ecological cascades through a strong reduction of a top-predator biomass, which has been associated with proliferation of the Northern shrimp *Pandalus borealis* (Chapter 2 and 7) (Worm and Myers, 2003; Hamilton *et al.*, 2014; Hedeholm *et al.*, 2016). This case is not the only global example, of where ecosystem alterations have led to such cascades or changes in the fishery composition towards being more crustacean-dominated (Chapter 7) (Worm and Myers, 2003; Möllmann *et al.*, 2008; Anderson *et al.*, 2011; Szuwalski *et al.*, 2016). However, this change from a formerly finfish to a crustacean-dominated fishery comes with trade-offs (Chapter 7). Although crustaceans can bring potential for more income and wealth, they are associated with high CO_2 emissions due to inefficient capture methods and low edible yields compared to most fish species (Chapter 7). Hence, they are little relief for food-insecure communities, but might have the potential to increase fishery revenues and provide socio-economic stability (Chapter 7).

In Greenland, two important fishing communities, Sisimiut and Paamiut experienced the cod-to-shrimp transition differently (Hamilton *et al.*, 2014). While Sisimiut, which is more northern at the West Greenland coast than Paamiut, prospered during and after this transition, Paamiut did not because it was more specialised in cod fishing (Hamilton *et al.*, 2014). Sisimiut had begun to invest in shrimp trawlers and specialised fishing capacities earlier in the transition phase, which was of great advantage (Hamilton *et al.*, 2014). Yet, these early advantageous investments in Sisimiut were a result of human capital, namely skills and education (Hamilton *et al.*, 2014). Sisimiut had a historically more diverse economic landscape supporting a wider range of workforce skills than Paamiut, which was an adaptive advantage (Hamilton *et al.*, 2014). Even when the shrimp stock spread southwards, Sisimiut's new fishing capacities enabled them to continue to pursue this natural resource (Hamilton *et al.*, 2014). These results indicate a socio-ecological tipping point induced by a shift from a cod-dominated to a shrimp-dominated ecosystem (Hamilton *et al.*, 2014).

I can only speculate that the political will to rebuild the Greenland cod stocks might be low, taking into consideration that a cod recovery might lead to a decline of the valuable stock of Northern shrimp again. In order to answer the question of how a recovery of the cod stock might affect abundance of shrimp, detailed spatial and temporal information on the predator-prey relationship between cod and northern shrimp would be necessary, especially considering the importance of habitat for diet composition (Chapter 5 and 6). Latest results indicate that northern shrimp is mainly an important diet item in northern parts of West Greenland (Chapter 5) (Hedeholm *et al.*, 2016). However, it seems generally agreed upon that the collapse of the cod stock in West Greenland led to reduced predation pressure and a proliferation of the shrimp stock (Hamilton *et al.*, 2014; Hedeholm *et al.*, 2016). If economic profitability and not ecological sustainability was the main objective of natural resource management in Greenland, current management practice might be successful. Reliance on one species as resource comes, however, with risks, because abrupt changes in abundance can have far-ranging consequences (Chapter 7).

How can these results contribute to an ecosystem approach to fisheries?

Ecosystem based management or ecosystem based fisheries management has the goal to include multiple stressors on multiple components of marine ecosystems into the management of natural resources (Möllmann *et al.*, 2014). This does not only include anthropogenic impacts but also species interactions, which can affect life-history parameters important for stock assessment and single-species advice, such as natural mortality (Möllmann *et al.*, 2014). Hence, in an ideal management world, management would not only take into consideration single-species abundance and historic population dynamics but include changing ecosystem composition, trophic relationships and their impact on the biological state of a fish population, as for example reflected through body condition (Lloret, Shulman and Love, 2013).

Habitat selection and adaptive responsiveness was chosen as central topic of this thesis (Chapter 5 and 6). In Greenland waters, cod inhabits habitats different in their abiotic and biotic properties (Chapter 5 and 6) (Rätz, 1999; Fock, 2007; Sutherland and Pickart, 2008). In East Greenland, cod lives in deep areas at 300-400 m at the slope of the shelf towards the northern Irminger Sea (Rätz, 1999). In southeastern, southern and western Greenland, the species mainly inhabits areas on top of the shelf from 50-150 m (Rätz, 1999). These areas differ in their resource availability, which is reflected in different diet compositions throughout the species' area of distribution (Chapter 5 and 6) (Rätz, 1999; Fock, 2007; Hedeholm *et al.*, 2016). These different diet compositions were linked to spatial differences in body condition (Chapter 5 and 6). Although some of these regions are separated by a distance, adult cod would be physiologically capable of overcoming, the species was persistently found in suboptimal areas (Chapter 5 and 6).

These results indicate that cod was over more than 10 years not capable of perceiving the spatial variability of habitat quality, which could have led to a redistribution in favour of high-quality habitats (Chapter 5 and 6). Missing capabilities to perceive the spatial distribution of habitat qualities did not only lead to lower energy intake, but also to a lower intake of polyunsaturated fatty acids, lower lipid content in gonads and livers and higher macroparasite loadings (Chapter 5).

Fatty acids are produced by phyto- and zooplankton species on low trophic levels, from where they are channelled up the food web. This is important because fatty acids are important for body condition and reproduction, but can only be taken up over the diet, which is a strong predictor of energy acquirements, body condition and fatty acid composition in cod (Lie, Lied and Lambertsen, 1988; Kjesbu *et al.*, 1991; Marshall *et al.*, 1999; Dalsgaard *et al.*, 2003; Røjbek *et al.*, 2014).

These results suggest sedentary behaviour of cod in southern and eastern Greenland, because differences in condition as measured with energy reserves in the liver as well as fatty acid profiles can only develop when differences in the diet persisted over several months (Chapter 5 and 6) (Morais *et al.*, 2001; Røjbek *et al.*, 2014). If adult cod constantly travelled and explored, they would all have similar spatio-temporal diets and the stable patterns in different body condition would not have emerged (Chapter 5 and 6). It can be concluded, that this limited adaptive responsiveness to habitat quality caused by behavioural constraints can influence body condition, what likely has implications for the stock productivity. Hence, particular areas might be more important for population replenishment than others and should receive increased attention in natural resource management (Chapter 5 and 6). Our results furthermore indicate that habitat is such an important factor for many physiological processes that it should receive increased attention in marine biology and fishery science (Chapter 5 and 6). Due to the apparently strong connection of fish to their surrounding habitat, assumptions of movement, migration and ideal behaviour should be re-considered. This aspect is often overlooked when investigating trophic relationships, behaviour and when spatial data are pooled, leading to potentially wrong conclusions.

8.2 Projections of Greenland ecosystems under climate change

Climate change is already happening and projected to happen fastest in sub-arctic and arctic regions (Hoegh-Guldberg and Bruno, 2010; Fossheim *et al.*, 2015; Griffith *et al.*, 2019; Peck and Pinnegar, 2019). As response to increasing temperatures, fish communities in arctic and sub-arctic waters have already shifted their distribution (Fossheim *et al.*, 2015; Griffith *et al.*, 2019). While temperature is predicted to increase steepest in the Norwegian Sea, Barents Sea and Canadian Atlantic Arctic regions, temperature increase in the Irminger Sea, the subpolar gyre region and the southern Labrador Sea, which surround southern Greenland, is predicted to be moderate (IPCC [van Oldenborgh *et al.*, 2013; Peck and Pinnegar, 2019). Temperature increase in the high-arctic Greenland region is expected to be stronger than in more southern regions (IPCC [van Oldenborgh *et al.*, 2013; Peck and Pinnegar, 2019).

Primary productivity is predicted to decrease by 10 – 30 % in the Labrador Sea, the Davis Strait, the Irminger Sea and increase by 10 – 30 % further North in the Greenland and Iceland Seas and the Arctic Greenland region (Peck and Pinnegar, 2019). This projected increase in primary productivity is mainly linked to ice-free summers, which might benefit phytoplankton production (Peck and Pinnegar, 2019). Along with increasing primary productivity in subarctic and arctic regions, fish biomass is generally predicted to increase, which can have positive effects on the maximum fishery catch potential in these regions (Blanchard *et al.*, 2012; Bindoff *et al.*, 2019).

To summarize, climate change will have mixed impacts on ecosystem dynamics in Greenland waters. Because coastal shelf regions in East Greenland are heavily affected by arctic water masses, which are transported southwards with the East Greenland current, these regions will likely see more productivity-enhancing effects than the adjacent Irminger Sea (Sutherland and Pickart, 2008; Bindoff *et al.*, 2019). However, increases in temperature, primary productivity and fishery catch potential, which appear to support commercial fishing, will have strong implications for the trophic structure and species interactions (McBride *et al.*, 2014; Fossheim *et al.*, 2015; Griffith *et al.*, 2019).

Increasing temperatures and trophic changes might alter habitat structure and suitability as well as growth and body condition of cod in Greenland waters (McBride *et al.*, 2014; Våge *et al.*, 2018; Bindoff *et al.*, 2019). Abundance of boreal pelagic species blue whiting (*Micromesistius poutassou*) and Atlantic mackerel (*Scomber scombrus*) has already increased in East Greenland waters, which does not only have ecological but also socioeconomic implications through changes in the distribution of a fishery resource (Nøttestad *et al.*, 2015; Jansen *et al.*, 2016; Post, Fock and Jansen, 2019). From a regime shift in the North Atlantic towards warmer waters in the early part of the 20th century it is known that abundance of benthic boreal fish species, such as haddock, saithe, tusk or ling, positively correlates with temperature in Greenland waters and in the future it can be expected that these species benefit from increasing temperatures (Hansen, 1949; Drinkwater, 2006). In contrast, more cold-water species, such as capelin, will likely retreat northwards (Drinkwater, 2006).

Importantly, changes might be unexpected. For example, in more northern regions in East Greenland, sea ice loss has enabled stronger air-sea interaction through increased convection, leading to increased heat loss to the atmosphere (Våge *et al.*, 2018). As consequence, water temperatures will likely not increase proportionally with air temperatures and through southerly water transports these changes will have implications for coastal ecosystems along the Greenland coast (Våge *et al.*, 2018). Changes in the upper water column can exceptionally fast reach deeper waters and change trophic interactions throughout the whole water column within months (Soltwedel *et al.*, 2016). Hence, it can be expected that not only direct effects of temperature will occur, but also trophic changes through for example sea ice loss or changes in primary productivity, which might affect resource availability and body condition of the cod populations in Greenland waters (Casini *et al.*, 2016; Soltwedel *et al.*, 2016; Møller and Nielsen, 2019; Peck and Pinnegar, 2019).

8.3 Research gaps, outlook and future challenges

Compared to areas with high research effort, such as the North Sea, the Barents Sea, the Gulf of Maine or the California current system, the shelf and slope areas around Greenland are notoriously under-researched and ecological time series are rare. The annual ground fish monitoring survey, which has been conducted by the Thünen Institute since 1981, is the only long-term time series for benthic fish communities and their abundance in the area. The Thünen institute research survey spans shelf and slope areas from 59 °N to 67 °N and from 29 °W to 57 °W with a depth from 0-400 m, which cover the most important areas of distribution and fishing grounds of Atlantic cod (Rätz, 1996). In addition to the German survey, the

Greenland Institute of natural resources has begun annual demersal fish stock monitoring on shelf and slope areas in 2005 (ICES, 2018).

Along the Greenland coast north of 67 °N, ground fish communities and their temporal changes are largely unknown and research is limited to the more recently started ground fish survey in West Greenland and an acoustic monitoring of the capelin stock in East Greenland (ICES, 2019c). If areas in East Greenland north of 67° N become ice free, the ecosystems along the East Greenland and likely the West Greenland shelf can be expected to change and likely become more suitable as habitat for cod as arcto-boreal predator (Drinkwater, 2005; Christiansen *et al.*, 2016; Strand *et al.*, 2017; Andrews *et al.*, 2019). Under conditions mainly north-easterly dominated winds in the Lofoten area, the main spawning ground of Northeast Arctic cod, cod larvae can drift in considerable numbers with the West Spitsbergen and Return Atlantic currents to the East Greenland shelf, where juveniles have already been observed (Christiansen *et al.*, 2016; Strand *et al.*, 2017; Andrews *et al.*, 2019). Hence, if conditions in these regions becomes increasingly favourable, the likelihood seems high that cod as opportunistic predator spreads to these regions (Strand *et al.*, 2017; Andrews *et al.*, 2019).

Because the area of distribution of capelin already spans to areas north of 67° N, cod might have begun following the capelin stock to these high-latitude regions without being caught on research surveys. Current scientific monitoring does not include these areas and if climate change happens as fast as predicted, governments and scientists are challenged to adapt monitoring practices. Recently, the island of Jan Mayen, which is located north of Iceland, has received increased attention, because spawning activity of cod was discovered around the island, which indicates that climate change has already opened up this region as new habitat for cod populations (Source: https://www.hi.no/en/hi/news/2019/may/the-cod-spawns-at-jan-mayen, accessed 30.01.2020). Here, almost 60 % of all samples were of Barents Sea origin (Source: https://www.hi.no/en/hi/news/2019/may/the-cod-spawns-at-jan-mayen, accessed 30.01.2020), showing that new habitats can be colonized by drifting larvae from the northern route via the West Spitsbergen and Return Atlantic currents (Christiansen *et al.*, 2016; Strand *et al.*, 2017; Andrews *et al.*, 2019).

Even if temperature in southern parts of Greenland is not predicted to increase as fast as in northernmost regions, reductions in sea ice cover and primary productivity might affect food webs and trophic interactions (Soltwedel *et al.*, 2016; Våge *et al.*, 2018; Griffith *et al.*, 2019;

Peck and Pinnegar, 2019). In order to detect rapidly cascading trophic changes induced by changes in the upper water columns, information on abundance and community composition of the planktonic part of the food web is necessary. Annual monitoring of these components is currently not a part of the ground fish surveys but would be a valuable and necessary addition to detect changes and cascades in the food web. Monitoring these lower trophic levels would likely provide valuable information about the implications of changes in primary productivity and the impacts of natural variability on body condition and habitat suitability of cod.

However, it appears that the most important and central challenge to ensure a sustainable exploitation of marine resources under climate change is to increase adaptability of monitoring bodies, intergovernmental science organizations and fishery management to changing fish distributions (Baudron *et al.*, 2020). Through the intrinsic character of the retrospective approach in all stock assessment models and our way of using forecasts for quota advice, fishery advice always lacks behind ecological changes (Jennings, Kaiser and Reynolds, 2001).

Abundance indices from fishery-independent surveys are based on a standardized sampling design, which is one of the most important assumption in order to collect time series data. These standardized sampling locations, once developed to cover the areas of distribution of the most important commercial fish species in the respective areas, have to be re-evaluated, when established species move out and new move in (Pinsky *et al.*, 2013; Perry *et al.*, 2014; Baudron *et al.*, 2020). This requires politicians, scientists and fisherfolk to be adaptive and work together (Stephenson *et al.*, 2016; Baudron *et al.*, 2020). Fisherfolk are usually the first to detect changes in fish distributions and their knowledge is essential in this context (Stephenson *et al.*, 2016).

The probably most prominent example of scientific and political challenges as consequence to changes in natural productivity and fish distribution, is Atlantic mackerel (Nøttestad *et al.*, 2015; Jansen *et al.*, 2016; Spijkers and Boonstra, 2017; ICES, 2019d). From 2007 to 2014, abundance of the mackerel stock in the North Atlantic benefitted from increasing temperatures in the Irminger Sea and spread its distribution westwards to Greenland waters (Nøttestad *et al.*, 2015; Nikolioudakis *et al.*, 2019). As consequence of this stock appearance in national jurisdictions, where the species has not occurred before this expansion, scientific catch recommendations were ignored and countries began to set unilateral quotas (Jansen *et al.*, 2016; Spijkers and Boonstra, 2017). As a so far unsuccessful management of the stock has shown, diplomacy and international collaborations are challenged, when fish populations expand to new fishing jurisdictions (Jansen *et al.*, 2016; Spijkers and Boonstra, 2017; ICES, 2019d; Baudron *et al.*, 2020). This case highlights that current practices are far away from being adaptive enough and suitable not to risk achievements, which were made and to ensure sustainable fisheries in the 21st century.

8.4 Bibliography

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Eidesstattliche Versicherung

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