Cod at Drift in the Nordic Seas

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Preface

Ever since man started fishing every able fisher had a hypothesis regarding the fluctuations in the fishery. My first encounter with this ancient lore of hypothesis making was with my grandfather out fishing in the outer Oslofjord. Every summer we got nothing and the only hypothesis I can remember him murmuring was that we went out too late in the morning, or that I was fishing too shallow–little did he know that I was terrified to let his best rig sink to the bottom and get stuck. As a true representative of the post-war era mentality, the very anti-thesis of my later graduate studies, I wonder if he ever entertained the thought that resources on this planet are finite, or that it dawned on him that weekend captains like himself could have an impact on the fish. As of late I started to hone my own hypotheses on the matter. A funny coincidence that my first experiences with this hypothesis making were in the same system that my graduate studies were later based upon, but already at that time everybody knew that I would to become a marine biologist.

Thank you Jon, who with a sturdy hand guided our ship through the chaos of the Skagerrak currents. Only with your intimate knowledge of the ocean physics has this thesis become possible. Not to mention your always-constructive attitude to whatever I confronted you with.

Thank you also Even for having the patience with me throughout my graduate studies, and ultimately helped me realise the project that this thesis was built upon. I must say I enjoyed every occasion that we had time for a decent conversation, that being while having a beer when we were out trying to fish mackerel, during workshop dinners, or when just spending the evening with your family.

And finally, thank you Maria who have stood with me through both the good and troubling parts of this journey. I hope we now can finally start to act on our dreams without considering the worries of yesterday or tomorrow.

Mats B.O. Huserbråten, Oslo, February 2017

Contents

Abstract

Gyres shed *Calanus finmarchicus,* and an existential relationship exists between the abundance of *C. finmarchicus* and the recruitment of Atlantic cod (*Gadus morhua*)–but what drives the Gyres? In this synthesis I investigate the entwined fate of cod and *C. finmarchicus*, and how their relationship is modulated by the constantly changing ocean-climate of the North Atlantic and Nordic Seas. In the early 1990s there was a general reversal from a negative to a positive state of the NAO, which led to a northwards retreat of the sub-arctic zooplankton assemblage present in the North Sea. The bottom up forcing represented by this fundamental ecosystem shift severely reduced the replenishment of cod recruits in the southern North Sea, while the northern North Sea was affected to a lesser degree. Since the ecosystem shift in the 1990s, the north-eastern North Sea and Skagerrak appears to have been the southern-most stronghold of cod on the eastern side of the Atlantic–yet even here the cod face challenges of increased temperatures associated with the contemporary ocean-climate. Because of the high spring temperatures that generally comes with positive NAO anomalies, the spring bloom of *C. finmarchicus* is usually already over before cod larvae have time to eat them. Thus in the contemporary ocean-climate, a delay in the phenology of *C. finmarchicus* may be the most important prerequisite to yield strong recruitment, accompanied with a high advection of *C. finmarchicus* onto the European Continental Shelf. To increase the resilience and integrity of our southern cod stocks during this warmer time period when the probability of strong recruitment is low, the general warming should thus be accompanied by a significant reduction in fishing mortality, which to a large degree already have been implemented in the North Sea proper. However, no such reduction in fishing pressure has been given to the stationary and unique coastal populations of Skagerrak, which in practice is a highly over-harvested, open-source fishery. Herein we thus lay down the blueprint of a large-scale zoning scheme of the Norwegian Skagerrak fjords, where no-fishing zones could prove essential to prevent depletion or even extinction of unique fjord populations.

List of papers

Paper I   Huserbråten MBO, Moland E, and Albretsen J. Cod at drift in the North Sea. (*Manuscript*)

Paper II   Huserbråten MBO, Moland E, Knutsen H, Falkenhaug T, and Albretsen J. Refining Hjort's critical period hypothesis in the southern range of cod. (*Manuscript*)

Paper III   Huserbråten MBO, Moland E, and Albretsen J. Dynamics of coastal dispersal. (*Manuscript*)

Introduction

A short recollection of the past ocean-climate of the North Sea, and how it relates to cod

On the eastern side of the Atlantic, spawning aggregations of cod (*Gadus morhua*) are found from the British Isles and the North Sea in the south to the fjords of Finnmark in northern Norway to the north. Along this south to north axis there has historically been two large cod stocks, inhabiting the North Sea and the Barents Sea. The biomass and recruitment levels of these two cod stocks has fluctuated throughout history, and currently the northeast Arctic stock is at a historical high, with a spawning stock biomass (SSB) of 1.600.000 tonnes (ICES 2015a). Whereas the North Sea cod had a maximum SSB of 300.000 tonnes in the early 1970s, but is currently down to around 100.000 tonnes, slightly above the all time low of 50.000 tonnes in the 2000s (ICES 2015b). According to the most recent North Sea-wide surveys a high spawning activity of cod was found along the western slopes of the Norwegian Trench (Fox et al. 2008), and the highest densities of one year old recruits were found in Skagerrak, a small branch of the North Sea (Hjermann et al. 2013, Nicolas et al. 2014, ICES 2015b). This in sharp contrast to the period from the late 1940s to the 1980s when the majority of the biomass was centred around the southern and central North Sea (Engelhard et al. 2014). Moreover, along the coastal margin between the North Sea and the Barents Sea there is a continuous presence, and even an increasing abundance of cod the further north you go. Here along the Norwegian coast, semi-mobile, stationary, and unique populations spawn along the banks, the coastal margin, and inside fjords, where back-migrations to natal spawning grounds are believed be the dominating population structuring mechanism (Robichaud & Rose 2004, Svedäng et al. 2007). Also the coastal cod found along the Norwegian coast undergone a similar reduction in biomass as the North Sea cod, at least as indicated by commercial catches the past three decades (ICES 2015a, Aglen et al. 2016). An even worse trend has been observed along the Swedish west coast, where only a remnant is left of the once so abundant cod in the Kattegat as well as the coastal populations in general (Svedäng & Bardon 2003, Cardinale & Svedäng 2004).

The ocean climate of the North Sea has constantly been changing throughout history, causing major fluctuations in the fisheries stationed there (Alheit & Hagen 1997). In recent times however, there was a notable cold period from the 1960s to the early 1980s. This colder period has later been termed "the gadoid outburst" and was a period associated with a high abundance of the sub-arctic copepod *Calanus finmarchicus* in the North Sea, leading to a

recruitment boom to most of the spring spawning gadoids typically found there (Cushing 1984). Whereas since the late 1980s, the sub-arctic copepod assemblage that is considered beneficial to cod recruitment retreated northwards while more temperate species has taken a hold. These changes appears to have been both gradual, as response to the generally increasing trend in Northern Hemisphere Temperature (NHT), but at the same time accentuated by sudden warm events caused by changes in circulation patterns of the north-eastern Atlantic and sudden phase shifts of the North Atlantic Oscillation (NAO, which in essence is a proxy for the prevalence of westerly winds, associated with higher than normal winter temperatures), causing anomalous flow into to the North Sea as well as increasing water temperatures (Reid et al. 2003, Beaugrand et al. 2008, 2009). This synchronous change in ocean-climate and ecosystem state of the North Sea coincided with a northwards shift of both exploited and un-exploited fish species (Perry et al. 2005). A response in fish communities to the changing ocean-climate of the North Sea can be traced from the English channel to coastal Skagerrak (Genner et al. 2004, Barcelo et al. 2016). Moreover, typical indicator species for the retreating sub-arctic and advancing temperate zooplankton assemblages are the congeners *C. finmarchicus* and *C. helgolandicus*. These two species are morphologically almost identical but have a distinct difference in growth and development rates in response to temperature (Wilson et al. 2015). A high abundance of *Calanus* during the late larval phase and early juvenile stage may be the strongest single factor affecting cod recruitment in the North Sea (Rothschild 1998, Beaugrand & Kirby 2010). However, the sister species' difference in adaption to temperature generally causes *C. finmarchicus* to peak in abundance early in spring while *C. helgolandicus* peaks later in summer or autumn (Wilson et al. 2015). Since the 1960s a decline in *C. finmarchicus* has been noticed throughout the North Sea (Beare & McKenzie 1999), and the most conspicuous decline have been in the Fair Isle current, one of four sources of Atlantic water to the North Sea and the only liable source of *C. finmarchicus* to the southern North Sea (Fransz et al. 1991, Beare et al. 1998). This decline in *C. finmarchicus* led to a significantly lowered recruitment to the cod stock, a decline especially notable in the south, and in combination with the peak fishing pressure exerted to the stock in the 1990s, it collapsed before the 2000s (Engelhard et al. 2014). Although the SSB of cod in the North Sea as a whole has almost doubled since the collapse, most of this biomass is concentrated in the northern North Sea (Engelhard et al. 2014, Holmes 2014), where nursing conditions are believed to be better than in the south (Beaugrand & Kirby 2010). Given the large-scale response in cod biomass to the oscillating ecosystem state of the North Sea, from a notable sub-arctic influence to a more temperate state, it is clear that

a mechanistic understanding of the shifting bio-geographical boundaries has to be gained to be able to foresee a future for cod in the North Sea. Thus below I will review the basin-scale dynamics of *C. finmarchicus* across the North Atlantic and Nordic Seas, which is the scale that the oceanographic and climatic phenomena driving these shifts come into play and can be observed.

Gyres shed C. finmarchicus

As stated above, there is a well established fact that an existential relationship exist between the abundance of *Calanus* and the recruitment of cod (Rothschild 1998, Heath & Lough 2007, Beaugrand & Kirby 2010)–you can even go so far as stating that the presence and persistence of cod populations is governed by the fluctuating bio-geographical boundaries of *C. finmarchicus* (Sundby 2000). There are two distribution centres of *C. finmarchicus*: one in the northern North Atlantic, and one in the Norwegian Sea. The western distribution centre is found within the anti-clockwise North Atlantic Sub Polar Gyre (SPG), which is delimited by the North Atlantic Current (NAC) in the south and by the topography of Iceland, Greenland, and Canada in the north and west. In the SPG most of the production of *C. finmarchicus* happens at the fringes of the gyre in spring and summer, while in late summer and autumn the copepodites descend down into the deep basins in a state of low metabolic activity known as diapause. Underneath the SPG at least three overwintering centra are found: in the Labrador Sea, the Irminger Basin, and the Iceland Basin. When spring arrives the copepodites ascend to the surface from their overwintering grounds to reproduce and feed. The eastern distribution centre of *C. finmarchicus* is found in the Norwegian Sea within several more or less defined gyres that circulates over the deep basins found there, all containing large numbers of overwintering copepodites at depth. However the highest overwintering densities throughout the northern hemisphere are found in the southern Norwegian Sea basin and the Faroe-Shetland Channel (Heath & Jonasdottir 1999, Heath et al. 2004, Melle et al. 2014). What maintains the integrity of the two populations is the basin scale circulation of water masses (Sundby 2000), where the western population is contained by the SPG while in the southern Norwegian Sea the seasonal migration route is slightly more complicated. The copepodites that overwinter in the Faroe-Shetland Channel ascend from diapause in spring and are entrained in the northwards flowing Continental Slope Jet (CSJ) and Norwegian Atlantic Current (NwAC), following the European and Norwegian continental shelves all the way from north of the British Isles to Lofoten. In the mouth of the Norwegian Trench the CSJ

briefly gets topographically steered into the Trench, but leaves on the eastern side aligning with the Norwegian Coastal Current in a northwards direction. When the new generation of copepodites enter diapause in summer they descend to deeper water, eventually sinking into the compensatory flow of Norwegian Sea Deep Water (NwSDW) that follows the continental shelf at great depth although in the opposite direction. This southbound current eventually carries the overwintering copepodites back to the overwintering grounds of the Faroe-Shetland Channel, effectively closing the seasonal migration loop.

Although certain aspects of the basin scale flow dynamics, and thus the transport of *C. finmarchicus* are inertial in nature, they are also highly susceptible to variation in atmospheric forcing and density fluctuations of the water masses. For example, the strength of flow and extent of the SPG is highly influenced by the atmospheric forcing represented by the NAO. Here the strength of the SPG increases initially during episodes of positive NAO due to increased wind forcing, however due to the delayed response in the Atlantic Meridional Overturning Circulation (AMOC) to the increased formation of sinking cold water in the SPG, a compensating flow of warm water from the Sub Tropical Gyre (STG) is advected northward into to north-east Atlantic. However, during NAO negative phases, there is no such compensation in the AMOC, thus less water originating from the STG enters the north-east Atlantic (Häkkinen & Rhines 2004, Hátún et al. 2005, Lohmann et al. 2009). This poleward flow of warm, sub-tropical water during extended positive NAO phases causes a large scale shift in the bio-geographical boundaries of the calanoid copepod assemblages present in the north-eastern Atlantic (Beaugrand et al. 2009, Hátún et al. 2009, 2016). In addition, variation in the meridional overturning circulation (MOC) in the Nordic Seas have large consequences to the southward flow of NwSDW, which has been reduced by more than 20% relative to 1950 (Hansen et al. 2001). This reduction in southward flow of NwSDW has been hypothesised to have a direct connection to the abundance of *C. finmarchicus* copepodites in the Faroe-Shetland Channel (Heath et al. 1999).

It was early on clarified that the North Sea did not contain a self-sustained, overwintering population of *C. finmarchicus* (Fransz et al. 1991). Thus the source of the spring invasion of *C. finmarchicus* to the North Sea can be hypothesised to be supplied by the western and eastern abundance centra as follows, slightly modified from the hypotheses initially put forward by Backhaus *et al.* (1994), later refined by Heath et al. (1999) and Greene et al. (2003): (1) fringe populations of the SPG can be advected from the north-eastern Atlantic through the Faroe-Shetland passage and subsequently into the North Sea through the Fair Isle current, the East Shetland current, and the Norwegian Trench inflow; and (2)

copepodites emerging from diapause in the Faroe-Shetland Channel can by Ekman transport get advected onto the European continental shelf, which is only possible across the open northern boundary between Shetland and the Norwegian Trench. However, the first invasion route have generally only been "open" during extended periods of negative NAO, when the sub-polar water masses have taken precedence in the north-eastern Atlantic (Hátún et al. 2005). This invasion route was probably frequently travelled during the cold period between 1960s to the early 1980s, reflected in the high abundance of *C. finmarchicus* in the Fair Isle current in that cold period (Beare et al. 1998). Whereas spring invasion from the depths of the Faroe-Shetland Channel is generally only possible during positive phases of the NAO, as consequence of an increased frequency of westerly winds that enhances cross-shelf water transport into the northern North Sea east of Shetland. The latter route has been the most common invasion route since the 1990s, albeit with a reduced magnitude due to the decline in the abundance of *C. finmarchicus* copepodites in the Faroe-Shetland Channel as consequence of the reduced MOC (Gallego et al. 1999, Heath et al. 1999). A second variation of the first entry route may also include copepodites spilling out from the Faroe-Shetland Channel during diapause, while being entrained with the NwSDW into the Iceland basin; and this will also probably be strongly dependant on the strength of the MOC (Greene et al. 2003). However, do note that due to the general circulation pattern in the northern North Sea, only the first invasion route will supply the southern North Sea with *C. finmarchicus*. This alternating dominance in invasion routes, which by its forcing mechanism is mutually exclusive in the long run, may explain the shift in relationship between NAO and *C. finmarchicus* in the 1980s (Beaugrand 2012), namely from a negative correlation in the period from the 1960s to the early 1980s, to a positive correlation since the 1980s. Thus in essence, due to the inherent flow dynamics of the North Sea and North Atlantic, a positive (or negative) NAO will disfavour (favour) the southern North Sea as a nursing habitat for cod (Figure 1).
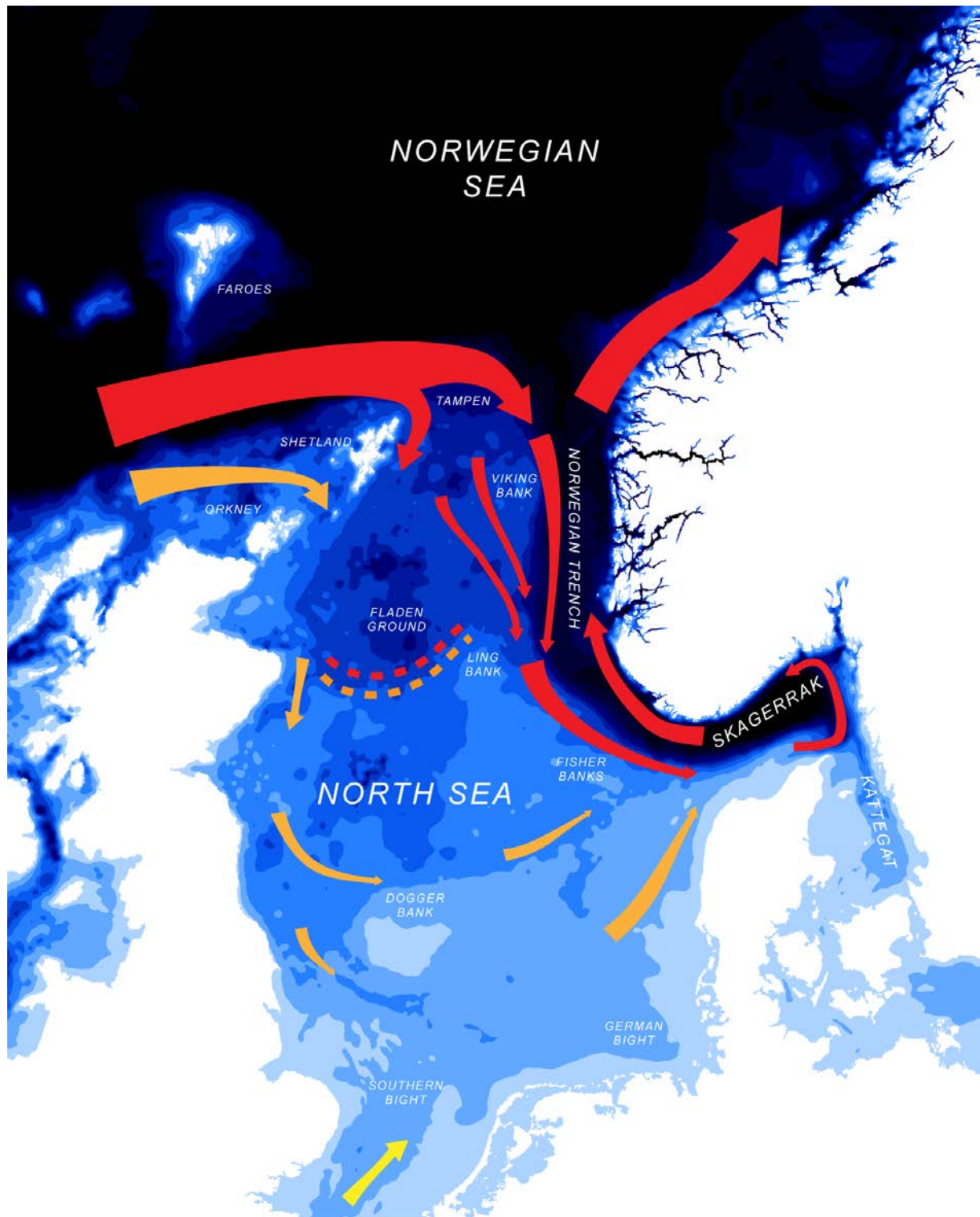
Figure 1. Spring invasion routes of *C. finmarchicus* to the North Sea. Red arrows represent the contemporary entry route, while orange arrows represent the hypothesised entry route only "open" during colder periods. The boundary below the Fladen Ground represents the Dooley current and roughly demarks the division between the northern and central North Sea; where below this border few *C. finmarchicus* copepodites are advected in spring in the present ocean-climate. Arrows are roughly scaled to relative water transport. For further details on the flow patterns of the north-eastern North Sea and Skagerrak, see paper I.

Objectives

Under the over-arching hypothesis that the ecology of *Calanus* dictates the recruitment strength of cod in the North Sea, the main objective of this thesis was to investigate the phenomenon of cod recruitment to the northern North Sea and Skagerrak, which during the warmer period since the 1990s appears to have been the southern-most stronghold of cod on the eastern side of the Atlantic. However, because the pelagic larvae that are produced in the northern North Sea potentially may settle over a large area in the highly advective circulation system, and that processes affecting the survival and settlement thus are expected to vary in space, it was natural to divide this thesis into three main parts. On the largest scale, in paper I, we addressed the dispersal of early pelagic stages of cod in the highly advective northern North Sea. As little was known about the prevalent drift pathways followed by eggs and larvae spawned there, as well as the potential nursery grounds that the juveniles produced here might settle in, we aimed to: (1) model the dispersal of pelagic offspring of cod spawned in the north-eastern North Sea; (2) quantify the potential for settlement to the nursing grounds available to pelagic juveniles in drift; and (3) describe the atmospheric and oceanographic features that forces this circulation system, and thus govern the advection patterns of the north-eastern North Sea cod. The objective of paper II was to evaluate the leading hypothesis on what drives the variation in recruitment of cod in its contemporary southern range. First and foremost, we aimed to (1) apply the widely acclaimed "critical period" hypothesis of Hjort (1914) to the contemporary nursery hotspot of Skagerrak, where challenges to early survival may be fundamentally different from where the concept first was coined in the far northern range of cod. We also wanted to (2) investigate the possible drift routes taken by North Sea cod larvae that have frequently been reported settling into Skagerrak nursery grounds (Knutsen et al. 2004, Stenseth et al. 2006), as well as to (3) evaluate the impact climatic variables may have on recruitment in Skagerrak littoral nursing areas. And finally, under the hypothesis that natal homing and thus spawning location is the prime stock separating mechanism of cod resident to Skagerrak fjords (Svedäng et al. 2007), the focus in paper III was to delimit the hydrographic containment units of pelagic eggs and larvae that match the sub-stock structure suggested by genetic studies (Knutsen et al. 2003). Due to the fragmented structure of the coastal stock they are in high risk of local depletion under the current management regime, as overfishing has already caused the depletion of local populations along the Swedish west coast (Svedäng & Bardon 2003). The secondary goal of

paper III was thus to lay down a blueprint of a coastal-wide network of marine protected areas in Norwegian Skagerrak fjords.

Results and discussion

Inter-ocean drift pathways and their relation to the NAO

Earlier studies that have modelled the drift of cod eggs and larvae in the North Sea have suggested a substantial downstream transport of cod spawning products from the spawning grounds along the western and north-western margin of the North Sea to the southern nursing areas (e.g. Dogger bank). At the same time the retention of eggs spawned over historically important spawning grounds in the southern North Sea, for example around Dogger bank, the Southern Bight, and the German bight appears almost total, although with a leakage up to 35% from the north-eastern extreme of Dogger bank into Skagerrak in some years. By contrast, less than 5% of pelagic juveniles spawned within the north-eastern North Sea are advected into nursing areas in the western and southern parts of the North Sea (Heath et al. 2008, Jonsson et al. 2016). However, little effort has previously been put into describing the dispersal pathways taken by eggs spawned within the northern North Sea-Skagerrak circulation cell in detail–and given the contemporary north-eastern modal distribution of the North Sea cod SSB, where much of the mature fish and newly spawned eggs are found along the western slopes of the Norwegian Trench (Fox et al. 2008, Engelhard et al. 2014), we predicted that the larvae spawned in the highly advective northern North Sea have a high dispersal potential. Our findings indeed suggest that up to a quarter of the total production of North Sea cod larvae is advected out of the North Sea. Here the majority of the year classes we modelled most likely recruited to nursery areas in the Skagerrak, along the western Norwegian coast, or further along the Norwegian Sea continental shelf. In general, most egg release positions in the northern North Sea and Skagerrak yielded a similar drift pathway along the crest of the Norwegian trench in an anti-clockwise direction, albeit with a huge potential settlement area along the crest of the Trench. The degree of leakage of eggs and larvae from the northern North Sea varied considerably between years, where a high NAO within the time frame of pelagic eggs and larvae resulted in higher recruitment potential to the Norwegian west coast and the Norwegian Sea shelf. The mechanistic explanation for the increased export being that a direct result of a high sustained NAO in winter/spring is higher prevalence and intensity of westerly winds, priming the counter-clockwise flow-through of the northern North Sea circulation cell (Winther & Johannessen 2006, Hjøllo et al. 2009,

Mathis et al. 2015).

In contrast to the common advective pathway taken by most eggs spawned in the northern North Sea and Skagerrak, even small differences in spawning location either north or east of the Viking bank would lead to a very different path of advection. As exemplified by Furnes et al. (1986), the qualitative difference in flow dynamics around this small area is probably why large scale drift of saithe (*Pollachius virens*) to the Skagerrak coast is a rare event. The reason being that the North Sea saithe spawns north and east of the Viking bank (in an area known as tampen, see figure 1), which means that their eggs are advected directly across the Trench with the CSJ and avoid the Skagerrak loop altogether. This is also the main pathway taken by the *C. finmarchicus* population that overwinters in the Faroe-Shetland channel, which after rising from diapause in early spring subsequently flows with the CSJ directly across the Trench and further along the Norwegian continental shelf (Gallego et al. 1999, Harms et al. 2000). Becoming entrained in this *C. finmarchicus* highway of the Nordic Seas we hypothesise to be highly beneficial to the cod eggs that are either intentionally or accidentally spawned within it, or advected into it (Figure 2).
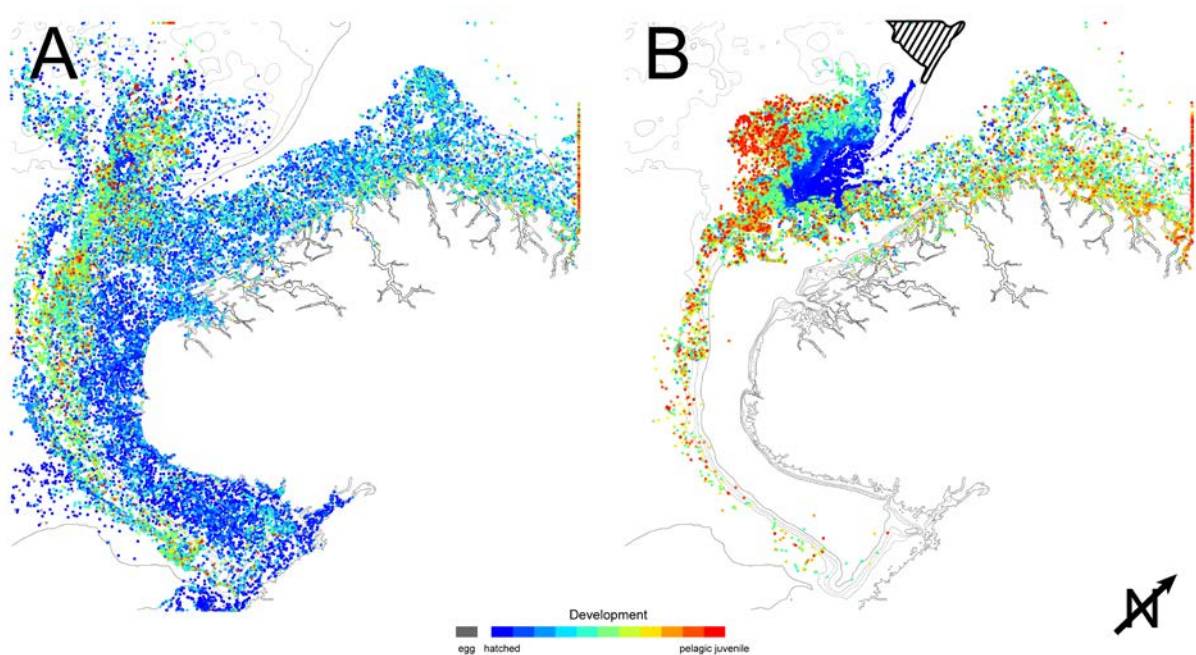
Figure 2. Comparison of flow dynamics of eggs spawned south and north of the Viking bank. Here panel A represents the drift of cod eggs and larvae spawned along the Norwegian Trench as suggested by recent surveys (ICES 2015b). Panel B represents drift of saithe eggs spawned over Tampen (cross-hatched area, see also figure 1), a well-known spawning area for the North Sea saithe (Olsen et al. 2010). Both simulations have been run for 80 days, with eggs spawned every day until day 68, initiated on February 1st 2011 and run until April 22nd 2011. For more details, see paper I.

Recruitment mechanisms of cod in the Skagerrak

In his treatise on "Fluctuations In The Great Fisheries Of Northern Europe" (1914), Hjort put forward the availability of food to pelagic cod larvae as the primary driver of recruitment success in the waters north of Lofoten. His rationale was that the presence or absence of food at the time when the larvae had absorbed their yolk sac would largely decide the year class strength. However, the challenges related to the timing between larval development and zooplankton phenology is expected to be widely different across the latitudinal range of cod. For example, in the Skagerrak, the abundance of *C. finmarchicus* usually peak in April, upon almost disappearing from the upper water column already early in summer. This in contrast to the main spawning ground of the northeast Arctic cod in the Lofoten archipelago, which has a comparably high abundance of *C. finmarchicus* almost year round, except the first few months of the year (Melle et al. 2014). Since the mean hatching date of cod throughout its east Atlantic range is quite conservative, with a peak hatching rate around 1st of April in the Skagerrak and 10th of May north of Lofoten (Suthers & Sundby 1993, Øresland & Andre 2008), the challenge for larval cod in their southern range is rather that the bloom of *C. finmarchicus* is already over before the larvae have time to capitalize on them, in contrast to dying of starvation before the bloom. For example, the previous good year of recruitment of cod to Skagerrak was in 2011, and our investigation in paper II was designed to discern the environmental and biological factors that contributed to that good year class. The only significant deviation from a normal year we found in the physical environment was that the Norwegian coastal water was colder than usual in February, in addition to higher than normal chlorophyll concentrations throughout early spring. We hypothesise that the colder winter temperatures in 2011 may have slowed down the seasonal development of the zooplankton, leading to an unusually late peak as well as stably high availability of *Calanus* copepodites to cod larvae throughout the settlement period in early summer. Hence, in contrast to the traditional interpretation of Hjort's hypothesis, that exemplifies the end of the yolk sac stage as the crux point, we argue that the period from settlement to the transition to benthic feeding is the decisive period for cod in southern latitudes. Our rationale being that during this time period when metabolic requirement is at it's highest, as this coincides with peak summer temperatures, any variability in the zooplankton that the larvae still are dependent on could prove fatal to the year class. This delay in *Calanus* phenology was also what Cushing (1984) identified as central to the general recruitment boom of cod and haddock observed in the North Sea in the 1960s and 1970s. Furthermore, we found no support to the notion that large scale import from the North Sea is the reason for the occasional strong recruitment (e.g.

Knutsen et al. 2004, Stenseth et al. 2006). We rather consider large scale import a prerequisite for strong recruitment in Skagerrak, a precondition that as suggested by both our ocean circulation simulations as well as previous modeling studies (e.g. Mathis et al. 2015) to be met almost every year because of the largely invariant northern North Sea-Skagerrak circulation. This means that as long as there is spawning along the slopes of the Norwegian Trench, large-scale drift of cod larvae into Skagerrak is expected to be a common feature.

Population structuring of Norwegian coastal cod complex and its consequence to management

Although the coastal cod fisheries of Skagerrak all have restrictions to them, in practice they are severely over-harvested, open-access resources. For example, the mortality contributed by recreational fishers on cod along Norwegian Skagerrak coast constitutes more than 40% of total mortality, where commercial fishing only make up 15%, and where the total survival is estimated to 0.3 (Kleiven et al. 2016). Besides the generally intense fishing pressure, a complicating factor to the management of the cod stock in Skagerrak is its fragmented population structure, where most of the major fjords contains genetically distinct populations with limited gene flow among them (Knutsen et al. 2003, 2011). The implication of fishing under the assumptions of no spatial structure where indeed a structure exists is the depletion/extinction of 'cryptic' local populations, a phenomenon that has been observed in historical genetic samples of cod in the North Sea (Hutchinson et al. 2003). The immediate consequences of local depletion can also be seen along the Swedish Skagerrak coast, where most local coastal cod populations have disappeared, yet with scattered recruitment in areas where they somehow have escaped the overfishing (Svedäng & Svenson 2006). From a meta-population perspective, given the low post-settlement connectivity among the fjord and coastal cod populations (e.g. Espeland et al. 2008, Rogers et al. 2014), and now backed up by our dispersal simulations in paper III that predicts a low probability of rescue effects, the resilience of the population as a whole is expected to be low (Hanski 1991). To prevent the further depletion, or even extinction of unique cod populations in Skagerrak, it is clear that the complex stock structure has to be taken into account in its management. And given the documented effect of partially protected areas to reduce mortality of cod (Fernandez-Chacon et al. 2016), a coastal-wide zoning network seems like the most parsimonious solution (Figure 3). In light of the scarcity of good years for recruitment to coastal populations, where only three really good years have been observed the past 20 years, in 1996, 1998, and 2011: to

reduce fishing mortality is tantamount if we want to safeguard our coastal cod populations for the future.
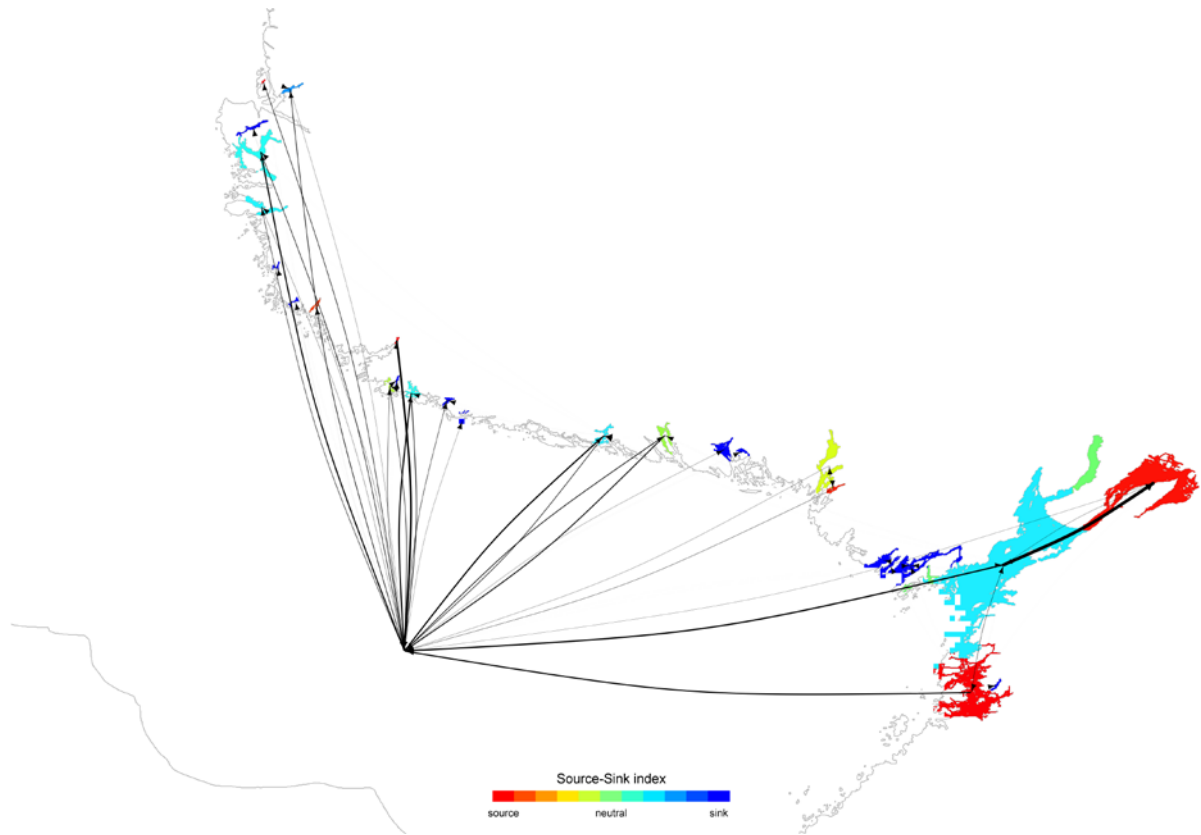
Figure 3. Blueprint for a network of partially protected areas for cod in Skagerrak fjords, to increase the resilience of local populations in a warming ecosystem. Here the identified source populations (i.e. areas of warm colours) should be priority targets for conservation, whereas pure sinks (i.e. areas without local production, dark blue areas) could be fished without compromising local populations. For further details, see paper III.

Future prospects of the cod in the North Sea and Skagerrak

The ocean-climate of the North Atlantic and the Nordic Seas have followed a quasi-periodic cycle of around 65 years since start of the modern record (Knight et al. 2005). However, because of the offset caused by human impact on the general climate, predictions for the future ocean-climate and ecosystem state across the North Atlantic and Nordic Seas looks grim for cod in its present southern distribution (Beaugrand et al. 2008). However, there are aspects of the northern North Sea-Skagerrak circulation that gives the system a certain resilience. For example, as long as there will be a compensatory return flow of the NwSDW

into the Faroe-Shetland Channel, that is, as long as the MOC continues in its present mode, the integrity of the Faroe-Shetland Channel as overwintering habitat to *C. finmarchicus* will probably be maintained (Wilson et al. 2016). However, as discussed in paper II, due to the rapid warming of the surface temperature in Skagerrak in spring, we are already on the limit of the overlap of the cod larvae's development and the phenology of the sub-arctic zooplankton, and where it appears that something extraordinary must occur to yield strong recruitment in the contemporary warm period. Furthermore, if we follow the leading hypothesis on the dynamical properties of the MOC, which ultimately explains a fair share of the ocean-climate of the northern North Atlantic and Nordic Seas; there has been three fundamental states the past 120.000 years, where stadial, interstadial, and Heinrich modes refers to latitudinal shifts in deep convection (as reviewed by Rahmstorf 2002 and Kuhlbrodt et al. 2007). In the interstadial mode, which are associated with the warm periods, the deep convection happens in the Nordic Seas and is naturally associated with a high Atlantic inflow to the Nordic Seas. While in the stadial mode, which is the colder periods, cold water is mostly formed in the SPG, and less Atlantic water enters the Nordic Seas. During Heinrich events the deep convection ceases completely in the North Atlantic, and the deep Atlantic basin is instead filled by cold water originating from the Antarctic. The cause of the Heinrich events is large scale freshwater input indicative of rapid ice-melting, where the freshening of the surface waters prevents the sinking of colder water and the AMOC stops altogether. Moreover, every ~1400 years or multiples thereof are sudden burst of warming, termed Dansgaard–Oeschger events, where average surface temperatures of the North Atlantic increase by more than 10°C in less than a decade. Heinrich events are relatively rare, only occurring about seven times the past 60.000 years, whereas Dansgaard–Oeschger events have happened almost 20 times. It is still unknown though how the heat forcing represented by increased concentrations of green house gases in the atmosphere may affect the dynamical properties of the MOC. On the bright side, considering that the cod populations of Northern Europe maintained their genealogical continuity (i.e. did not go extinct) during the last glacial maximum ca. 21.000 years ago, at least the large oceanic cod stocks seems resilient to these large scale climatic fluctuations (Bigg et al. 2008), probably due to their flexibility in latitudinal range. However, due to the stationary nature of fjord populations, their resilience to climatic fluctuations is expected to be significantly lower, at least under the current management regime in Skagerrak where fishing mortality is sky-high, as discussed in paper III.

Conclusion

In this synthesis we have thoroughly enlightened the role of atmospheric forcing to the North Sea and Skagerrak cod populations. By simulations of drifting cod eggs and larvae spawned in the northern North Sea and Skagerrak, we showed that the majority of pelagic juveniles might settle in Skagerrak, along the western Norwegian coast, or gets advected further along the Norwegian Sea shelf. We also showed and discussed how large-scale wind forcing may enhance the export of eggs and larvae spawned over the northern North Sea in winters of high NAO, by increasing the flow-through of the northern North Sea circulation cell. The consequential north-eastern shift of North Sea cod nursery habitat we consider beneficial to survival of the settling juveniles, considering the marginalisation of the southern North Sea as nursery habitat for juvenile cod compared to historical conditions. Moreover, our findings suggest that there indeed is a critical period that could determine year class strength of cod in the southern range. However, in contrast to the traditional interpretation of Hjort's hypothesis, that exemplifies the end of the yolk sac stage as the crux point, we argue that the period from settlement to the transition to benthic feeding is the decisive period in southern latitudes. Our rationale being that during this time period when metabolic requirement is at it's highest, as this coincides with peak summer temperatures, any variability in the zooplankton that the larvae still are dependent on could prove fatal to the year class. As was concluded from our simulations of the dispersal of cod eggs within Skagerrak fjords, there was a low connectivity among the overfished fjord populations of Skagerrak, putting the relatively isolated fjord sub-populations in high risk of depletion or extinction under the current management regime. To account for the biocomplexity of the stock we recommended the implementation of no-fishing zones within many of the Skagerrak fjords as the next logical step for management. This advice should be accentuated if the general warming of the ocean-climate should continue into the near future, due to the temperature-sensitive recruitment mechanisms of cod discussed herein.

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