Cod at Drift in the Nordic Seas

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Doctoral Dissertation at University of Agder
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University of Agder
Faculty of Engineering and Science
2017

ISSN: 1504-9272
ISBN: 978-82-7117-868-0 (trykt utg.)

Trykk: Wittusen & Jensen
Oslo

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 fish stocks. 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 Ph.D. studies were later based upon, but already at that time everybody knew that I would 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 helping 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.

Thanks to researchers Halvor, Geir, Øystein, Leif, and Joel that provided a stimulating work environment and engaging discussions. And thanks to friends, office mates, and fellow candidates Anna, Kristina, Rebekah, Tonje, Kim, Sussanna, Giovanni, Leana, Leonie, and Kaixing for making these three years a more fun experience.

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 Huserbråten

Mats B.O. Huserbråten, Oslo, February 2017

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 varying 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 North Atlantic Oscillation (NAO, a major driver of variability in the ocean-climate across the North Atlantic and Nordic Seas), which contributed to the 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 this ecosystem shift in the 1990s, the northern North Sea and Skagerrak appears to have been the southern-most stronghold of cod on the eastern side of the Atlantic–yet even there the cod face challenges of increased temperatures associated with the contemporary ocean-climate. Because of the high spring temperatures that generally entail the positive NAO anomalies the seasonal peak of *C. finmarchicus* usually pass before cod larvae have time to capitalise on this vast resource. Thus, in the contemporary ocean-climate a delay in the phenology of *C. finmarchicus* may be the most important prerequisite to yield strong recruitment. To increase the resilience and integrity of our southern cod stocks during warmer episodes and the future scenario of general warming, these short and long term trends should be accompanied by a significant reduction in fishing mortality. This reduction in fishing mortality has to a large degree already been implemented in the North Sea proper, however, no

such reduction in fishing pressure has been afforded the stationary and unique coastal populations of Skagerrak, which in practice is a highly over-harvested, open-source fishery. Herein I thus lay down the blueprint of a large-scale zoning scheme of the Norwegian Skagerrak fjords, in which spatially differentiated protection measures could prove essential to prevent depletion or even extinction of unique fjord populations.

Contents

1 Introduction

1.1 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 occurred 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 1.6 million tons (ICES 2015a). Whereas the North Sea cod had a maximum SSB of 300 thousand tons in the early 1970s, but is currently down to around 100 thousand tons, slightly above the all time low of 50 thousand tons in the 2000s (ICES 2015b). According to recent North Sea-wide surveys a high spawning activity of cod is found along the western slopes of the Norwegian Trench (Fox et al. 2008), and the highest densities of one year old recruits are found in Skagerrak, a small branch of the North Sea (Hjermann et al. 2013, Nicolas et al. 2014, ICES 2015b). This stand 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 has 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 located 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 in bio-geographical boundaries appear 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), 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 variation in species composition of fish communities as response 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 zooplankton indicator species for the retreating sub-arctic and advancing temperate 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 ssp.* during the late larval phase and early benthic juvenile stage of cod may be the strongest single factor affecting cod recruitment in the North Sea (Rothschild 1998, Beaugrand & Kirby 2010). However, the two sister species' difference in adaption to temperature generally causes *C. finmarchicus* to peak in abundance early in spring while *C. helgolandicus* peaks in late summer or autumn (Wilson et al. 2015). This difference in adaption to temperature is probably the main reason why *C. helgolandicus* plays a marginal role as a food source for cod larvae, as the pelagic diet is generally phased out for benthic prey in June-July (Bastrikin et al. 2014). Furthermore, since the 1960s a decline in *C. finmarchicus* has been noticeable throughout the North Sea (Beare & McKenzie 1999), but 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 advection pathway 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 (Beaugrand & Kirby 2010). And in combination with the peak fishing pressure exerted on the cod stock in the 1990s the fishery in the south 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). Given the large-scale response in cod biomass (and spring spawning gadoids in general) to the oscillating ecosystem state of the North Sea, between a notable sub-arctic influence to more temperate states, 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 that is the scale at which the oceanographic and climatic phenomena driving these shifts come into play and can be observed.

1.2 Gyres shed C. finmarchicus

As stated above, there is a well established fact that an existential relationship exist between the abundance of *Calanus ssp.* 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 contained 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 habitat 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 circulate 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 currently 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), trailing 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, where a small fraction of its mass follow the Trench edge into Skagerrak, before doing an anti-clockwise loop in Skagerrak and leaving on the eastern side, aligning with the bulk of the mass flowing underneath the Norwegian Coastal Current along the north-western Norwegian coast 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 also follows the continental shelf, although at great depth in the opposite direction. This deep, southbound current eventually carries the overwintering copepodites back to the overwintering grounds of the Faroe-Shetland Channel, effectively closing the seasonal migration loop (Heath et al. 1999, Greene et al. 2003).

Although the basin/ocean-scale flow patterns of the northern North Atlantic and Nordic Seas seem inertial by nature–and thus also the biogeographical boundaries of *C. finmarchicus*–these ocean flow dynamics is highly susceptible to variation in atmospheric forcing and density fluctuations of the water masses. For example, the structure and strength of the SPG is highly influenced by the atmospheric forcing represented by the NAO, where the counter-clockwise flow increases significantly during episodes of positive NAO by the increased westerly wind forcing. Another consequence of the increased wind stress is increased heat loss of upper water masses that results in increased formation and sinking of cold water in the SPG. As response to this increased sinking, a compensatory flow of warm, saline water from the Sub Tropical Gyre (STG) is advected northward into the north-east Atlantic, and with a delay of up to a decade this effectively causes the SPG to shrink. However, during negative NAO phases, there is no such compensatory flow, thus little warm water originating from the STG enters the north-east Atlantic (Häkkinen & Rhines 2004, Hátún et al. 2005, Lohmann et al. 2009). This see-saw like oscillation in poleward flow of warm, sub-tropical water in response to phase shifts in the NAO causes a large scale translocation of the biogeographical boundaries of the calanoid copepod assemblages present in the north-eastern Atlantic (Beaugrand et al. 2009, Hátún et al. 2009, 2016). Moreover, variation in the meridional overturning circulation (MOC, of which the thermo-haline circulation is an important driver) 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 variation 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 shelf 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 onto the North Sea shelf 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 overwintering hotspot can by Ekman transport get advected onto the European Continental Shelf, which due to the position of the channel and dominant flow patterns in the channel 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 the extended periods of negative NAO between the 1960s and 1980s, when the sub-polar water masses have taken precedence in the north-eastern Atlantic (Hátún et al. 2005), reflected in the high abundance of *C. finmarchicus* in the Fair Isle current in that colder 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 prevalence 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 general 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). However, do note that due to the inflow regime and general circulation pattern in the North Sea, only the first invasion route through the Fair Isle current will supply the southern North Sea with *C. finmarchicus* in spring. This alternating dominance in invasion routes, which by its forcing mechanism is mutually exclusive in a long term perspective, may explain the shift in relationship between NAO and *C. finmarchicus* in the 1980s (Beaugrand 2012), namely from a negative correlation in the cold 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).

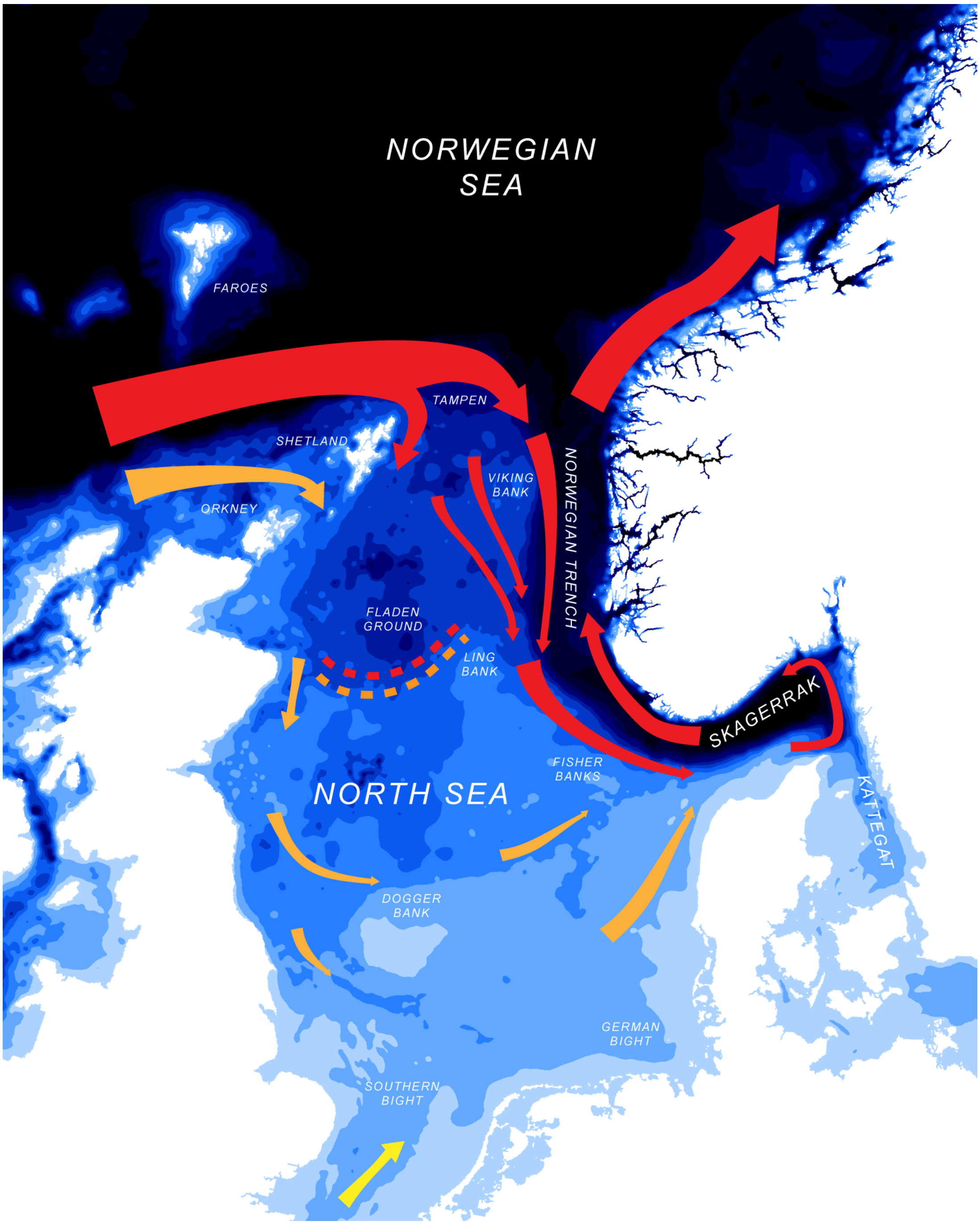

Figure 1. Spring invasion routes of *C. finmarchicus* to the North Sea. Red arrows represent the contemporary entry route, while orange arrows represent the hypothesised entry route “closed” during prolonged periods of positive NAO anomalies (i.e. warmer periods). The boundary south to the Fladen Ground 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 1.

2 Objectives

Under the over-arching hypothesis that the ecology of *Calanus ssp.* 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 the thesis into three main parts. On the largest scale, in paper 1, I 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 there might settle in, I aimed in paper 1 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 2 was to evaluate the leading hypothesis on what drives the variation in recruitment of cod in its southern range. First and foremost, in paper 2 I aimed to (1) apply the widely acclaimed “critical period” hypothesis of Hjort (1914) to the contemporary southern 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. I also wanted to (2) investigate the possible drift routes taken by North Sea cod larvae that have frequently been reported settling in 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 3 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 population structure of the coastal stock they are at 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 3 was thus to lay down a blueprint for a new management strategy, namely by the use of area based protection, a widely implemented management tool to impede overfishing.

3 Results and discussion

3.1 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 propagules 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), I predicted in paper 1 that the larvae spawned in the highly advective northern North Sea have a high dispersal potential. My 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 I 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 period 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 north-eastern 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*) propagules 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 across the Trench with the CSJ and avoid the Skagerrak loop altogether (Bjørke & Sætre 1994). This is also the pathway taken by the vast majority of the *C. finmarchicus* population that overwinters in the Faroe-Shetland channel, which after rising from diapause in early spring flows with the CSJ (Gallego et al. 1999, Harms et al. 2000). Becoming entrained in this *C. finmarchicus* highway of the Nordic Seas I hypothesise to be highly beneficial to the cod eggs that are either intentionally or accidentally spawned within it, or advected into it (Figure 2).

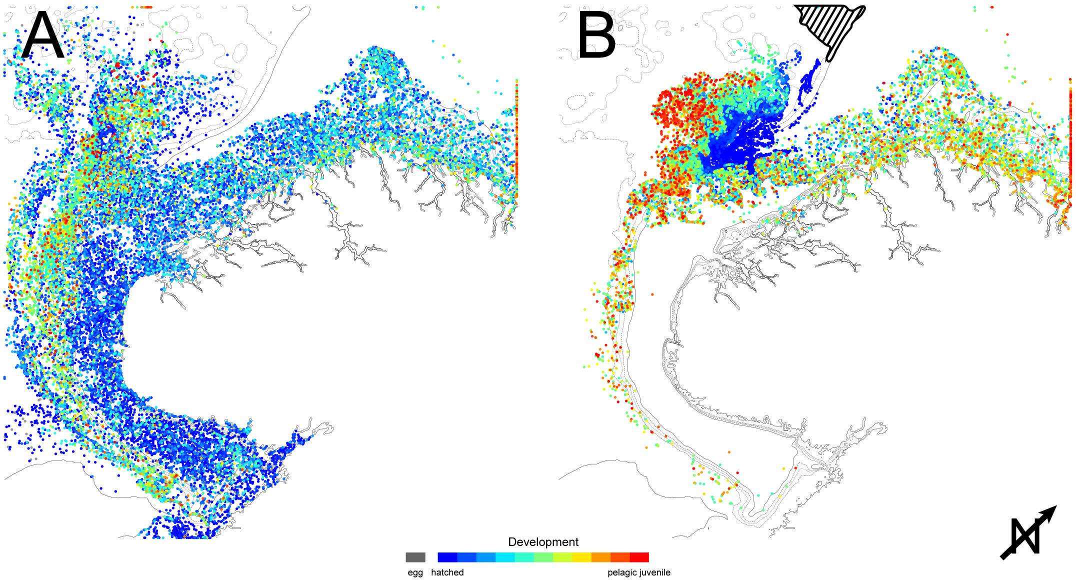

Figure 2. Comparison of flow dynamics of eggs spawned south and north of the Viking bank. Here panel A represents the drift of cod eggs and larvae spawned along the Norwegian Trench as suggested by recent surveys (ICES 2015b). Panel B represents drift of saithe eggs spawned over Tampen (cross-hatched area, see also figure 1), a well-known spawning area for the North Sea saithe. 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 1.

3.2 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 along 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 2 was designed to discern the environmental and biological factors that contributed to that strong year class. The only significant deviation from a normal year found in the physical environment therein was that the Norwegian coastal water was colder than usual in February, in addition to higher than normal chlorophyll concentrations throughout early spring. I hypothesised 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 ssp.* copepodites to cod larvae throughout the settlement period in early summer (Figure 3). Hence, in contrast to the traditional interpretation of Hjort's critical period hypothesis, that exemplifies the end of the yolk sac stage as the crux point, I argue that the period from settlement to the transition to benthic feeding is the decisive period for cod in southern latitudes. My 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 *C. finmarchicus* phenology (and generally high abundance in summer) was also what Cushing (1984) identified as central to the general recruitment boom of cod and haddock observed in the North Sea in the colder 1960s and 1970s. Moreover, I 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). I rather consider large scale import a prerequisite for strong recruitment in Skagerrak, a precondition that is met almost every year because of the largely invariant northern North Sea-Skagerrak circulation (Mathis et al. 2015). In other words, 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.

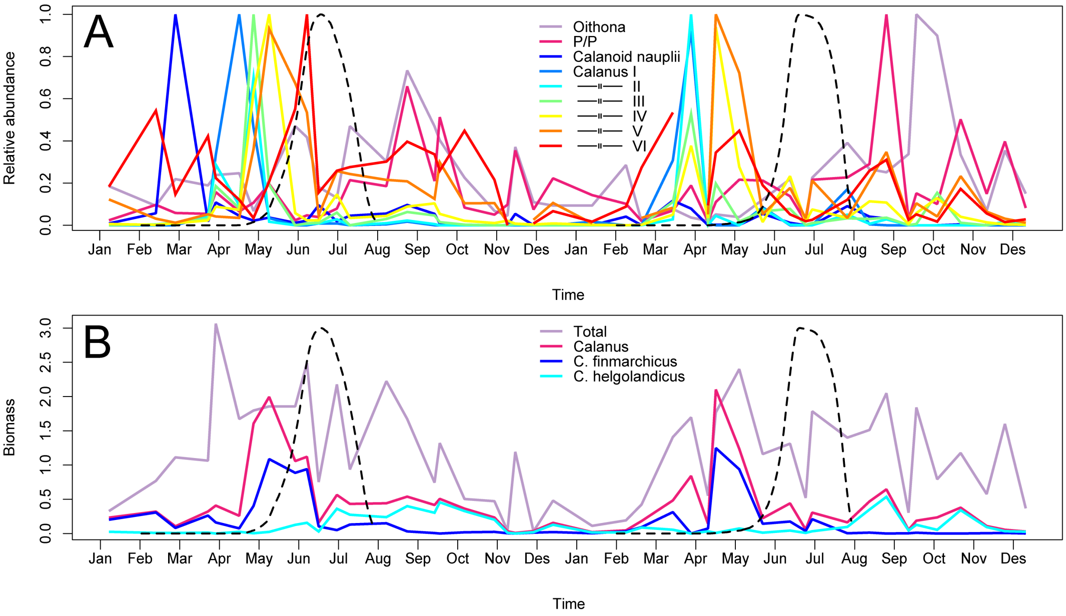

Figure 3. (A) Relative abundance of the three most favoured copepod species/groups throughout pelagic and early settlement stage of cod larvae (according to Heath & Lough, 2007) scaled by the peak abundance of each species/stage, and modeled development of settlement phase (i.e. when larvae where between 25 mm and 49 mm, stapled curve). (B) Total biomass of zooplankton and *Calanus spp.* (for further details see paper 2).

3.3 Population structuring of the Norwegian coastal cod complex and its consequence for management

Although the coastal cod fisheries of Skagerrak all have restrictions to them (minimum landing size of 40 cm), 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 annual survival is estimated to 30% (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 contain 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 3 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 4). In light of the scarcity of good years for recruitment to Skagerrak coastal populations, where only three really good years have been observed the past 20 years, in 1996, 1998, and 2011 (see paper 2): to reduce fishing mortality is paramount if we want to safeguard our coastal cod populations for the future.

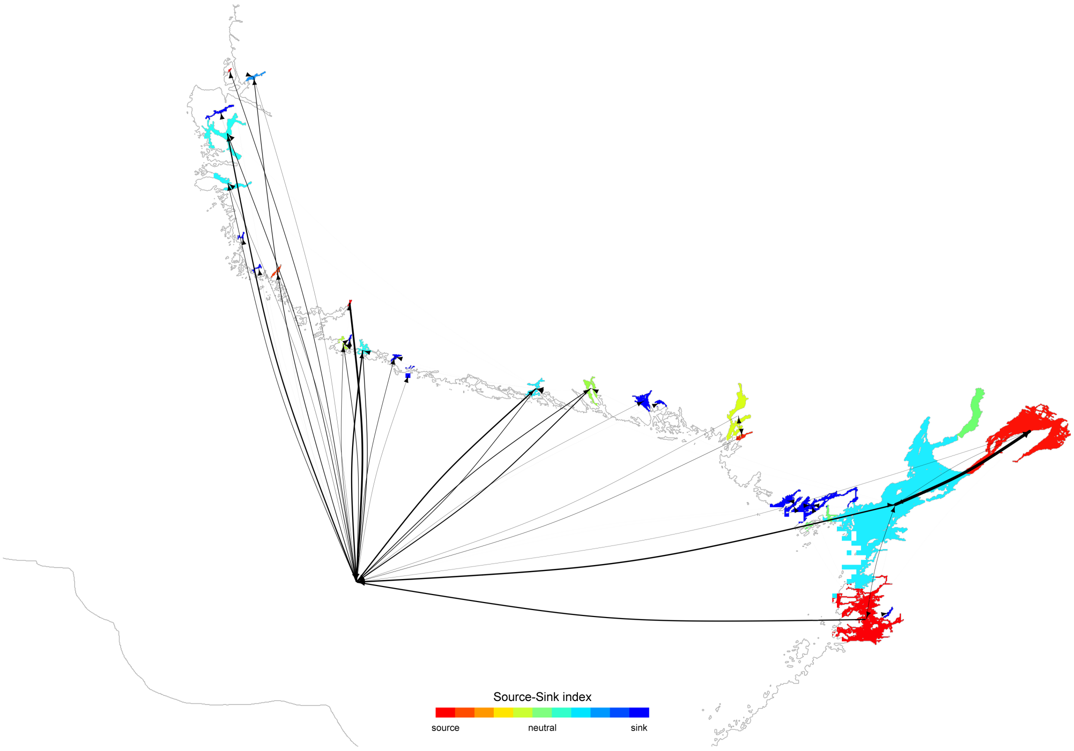

Figure 4. Blueprint for a network of partially protected areas for cod in Skagerrak fjords, to increase the resilience of local populations in a warming ecosystem. Here the identified source populations (i.e. areas of warm colours) should be priority targets for conservation, whereas for example pure sinks (i.e. areas without local production, dark blue areas) could be fished without compromising local populations. For further details, see paper 3.

3.4 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 the 1880s (Knight et al. 2005). However, because of the offset caused by the 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 the south, due to the projected continuing retreat of the sub-arctic zooplankton assemblage (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 (Rahmstorf 2002, Kuhlbrodt et al. 2007), 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 2, 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. On the bright side, considering that the cod populations of Northern Europe have maintained their genealogical continuity (i.e. did not go extinct) during the past 20 thousand years, at least the large oceanic cod stocks seem 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 both fishing and natural mortality is high (Anderson et al. 2008). Thus as discussed in paper 3, to safeguard the coastal cod complex for the future a significant reduction in fishing mortality is recommended, and a spatially explicit moratorium/fishing reduction within selected southern fjords seems like the most parsimonious solution. 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.

In summary; in this synthesis I have thoroughly illuminated/explored 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, I showed that the majority of pelagic juveniles might settle in Skagerrak, along the western Norwegian coast, or become advected further along the Norwegian Sea shelf. I 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/spring of high NAO, by increasing the flow-through of the northern North Sea circulation cell. The consequential north and eastern shift of North Sea cod nursery habitat I 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, my findings suggest that there is indeed 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, I argue that the period from settlement to the transition to benthic feeding is the decisive period in southern latitudes. My 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 are still dependent on could prove fatal to the year class. As was concluded from my 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 I recommended the implementation of spatially differentiated management measures such as no-take zones and partially protected areas within many of the Skagerrak fjords as the next logical step for management.

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5 List of papers

Paper I	Huserbråten MBO, E Moland, and J Albretsen. Cod at drift in the North Sea. (*Manuscript*)
Paper II	Huserbråten MBO, E Moland, T Falkenhaug, H Knutsen, and J Albretsen. Refining Hjort's critical period hypothesis in the southern range of cod. (*Manuscript*)
Paper III	Huserbråten MBO, E Moland, and J Albretsen. Dynamics of coastal dispersal. (*Manuscript*)

Cod at drift in the North Sea

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Target journal: Progress in Oceanography, Fisheries Oceanography (No page limits)

Abstract. There has been a large-scale reduction and geographical re-distribution of the North Sea cod stock over the past century, and recent surveys indicate a north-eastern modal distribution. Here we assess the consequences of the contemporary distribution of North Sea cod (*Gadus morhua*) spawning biomass to inter-ocean recruitment potential. By simulations of drifting cod eggs and larvae spawned in the northern North Sea and Skagerrak, we show that the majority of pelagic juveniles most likely settle in Skagerrak, along the western Norwegian coast, or gets advected further northward along the Norwegian Sea shelf. We also show how large-scale wind forcing may enhance the export of eggs and larvae spawned in the northern North Sea during episodes of high NAO, by increasing the flow-through of the northern North Sea circulation cell. The northern and eastern extension of the North Sea cod nursery habitat may be beneficial to survival of the settling juveniles, considering the marginalisation of the North Sea proper as nursery habitat for juvenile cod compared to historical conditions. Looking back at a century of overfishing, warming, and variable nursery conditions for settling cod juveniles in the North Sea, getting entrained in the Norwegian coastal current seems like a viable strategy to larvae, considering the contemporary prevalence of cod spawning in the north-east.

Introduction

There has been a large scale shift in the distribution of the North Sea fish assemblage the past decades, with a general northward, deepened distribution of both exploited and unexploited species (Perry et al. 2005, Dulvy et al. 2008). This observed shift has been accompanied by dramatic decline in abundance of many commercially important species. The most famous example is perhaps the decline of the North Sea cod (*Gadus morhua*)–boasting a spawning stock biomass (SSB) of 300.000t in the 1970s, plummeting down to an all time low of 50.000t in the mid 2000s (ICES 2015). As fishing mortality almost mirrored the cod SSB in this period, the immediate and natural explanation for the observed decline is that fishing curtailed the abundance of cod (Engelhard et al. 2014). However, throughout the modern record there has been large inter-annual as well as decadal variation in the recruitment of cod, and the single factor that explains the most of this variation is the abundance of copepod *Calanus finmarchicus* (Beaugrand & Kirby 2010), a fundamental prey for early life stages of cod (Heath & Lough 2007). For example, in the 1970s there was a succession of exceptional years for recruitment of cod correlated with high abundance of *C. finmarchicus,* a period later known as the 'gadoid outburst' (Cushing 1984, Rothschild 1998); whereas throughout the 1990s the abundance of *C. finmarchicus* diminished, leading to cod recruitment collapse (Beaugrand & Kirby 2010). Irrespective of whether driven by bottom up, top down, or socio-economic processes, the spatial distribution of the North Sea cod seems to have constantly been changing over the last century, but in the past decades the bulk of the SSB has been found in the north east (Fox et al. 2008, Engelhard et al. 2014). This north-eastern spawning assemblage of cod also constitutes a distinct genetic unit that spawns in vicinity of the Viking bank, in distinction to the south-western genetic unit that generally spawns in the southern and western margin of the North Sea, as well as west of Shetland (Heath et al. 2014). This division into two distinct genetic population units is highly parsimonious with the large-scale circulation pattern of water masses in the North Sea, where several more or less defined currents effectively divide the North Sea in two. The first division is made by the Fair Isle current that enters the North Sea between Orkney and Shetland, and this current transports coastal water originating from west of the British Isles into the North Sea. Its path continues south past the Scottish coast, and before reaching 57°N it turns east in an anti-clockwise fashion, while deflecting parts of its mass south along the English coast (in some sources referred to as the 'Fulton drift', e.g. in Franz et al. 1991) and onto the shallower central/southern North Sea plateau. The second barrier is the East Shetland current, which transports Atlantic water into the North Sea in a southern direction along the eastern side of Shetland. Upon reaching 58°N, the East Shetland current also turns east and aligns with the Fair Isle current in a double-entrainment, and together they form an anti-clockwise gyre over the Fladen ground. A branch of this double Fair Isle/East Shetland current (together referred to as the 'Dooley current') turns around the Ling bank and into Skagerrak, although with diminished strength (Svendsen et al. 1991, Turrell et al. 1996). This double barrier not only splits the North Sea cod stock in two, it also roughly demarcates the southern limit above which *C. finmarchicus* is usually found in large numbers in spring, while being a rare guest south of it (Fransz et al. 1991)–and since the cod fishery in the North Sea collapsed in the time period 1980s-1990s, catches of cod have been steadily high north-east of these currents, while dismally low to the south (Engelhard et al. 2014, Holmes 2014). Even further separating the northern and southern North Sea is a an unnamed current traversing the northern plateau along the diagonal between Shetland and the southern slope of the Norwegian Trench (hereby referred to as the 'traverse' current) transporting relatively cold, saline water into the Norwegian Trench (Ljøen & Sætre 1987, Svendsen et al. 1991). Moreover, sweeping along the open northern boundary to the Norwegian Sea and into the Norwegian Trench (a current referred to as the Continental Slope Jet) we find the main inflow of Atlantic water to the North Sea (Winther & Johannessen 2006, Hjøllo et al. 2009). However, the majority of this inflowing Atlantic water gets retroflected and eject underneath the Norwegian coastal current on the eastern side of the Trench before reaching 59°N (Furnes et al. 1986). Although little is known of how the flow is organised in the conjunction were the traverse current, the double Fair Isle/East Shetland current, and the Atlantic inflow in the Norwegian Trench meet, we do know that the outflowing northern North Sea water gets topographically steered in a south-eastern and eastern direction along the western and southern slopes of the Norwegian Trench and into the Skagerrak (Furnes et al. 1986). And here, south of Norway within the more or less permanent front between the westward propagating, low saline Norwegian coastal current, a continuation of the Baltic current, the eastward flowing northern North Sea and Atlantic water, and the West-Jutlantic coastal current carrying coastal water from the southern North Sea, high abundances of cod larvae are found (Munk 2007, 2014). Now, the origin of these larvae is not known for certain, but peak abundances are found in water-masses typical of the northern North Sea in terms of salinity and temperature and also in respect to the assemblage of copepod species present. However, to date there have been no high-resolution drift studies addressing the dispersal of early pelagic stages of cod in the highly advective northern North Sea, hence little is known about the prevalent drift pathways taken by eggs and larvae spawned there, as well as potential nursery grounds they may settle in. Thus here we aim to: (1) describe the dispersal of pelagic offspring of cod spawned in the north-eastern North Sea; (2) quantify the potential for settlement to the various nursing grounds available to pelagic juveniles in drift; and (3) describe the oceanographic features that gives structure to this complex circulation system. Given the contemporary north-eastern modal distribution of the North Sea cod SSB, where most of the mature fish and newly spawned eggs are found along the western slopes of the Norwegian Trench (Fox et al. 2008), we predict that the eggs spawned in the highly advective northern North Sea have a high dispersal potential. In light of our findings we will round off with a discussion on the potential reasons why the north-eastern North Sea cod is seemingly unaffected by the recruitment collapse observed in the southern North Sea.

Materials and methods

Indices of potential egg production and particle release scheme

To derive an estimate of the spatial distribution of egg production in the North Sea, and the relative contribution of northern North Sea cod spawners, we extrapolated potential egg production from the annual ICES international bottom trawl survey (IBTS, quarter 1). This survey is run between January and March every year, and is mainly designed to assess the spawning stock biomass of cod. We used the coordinates of the survey trawl-hauls as release points in our drift simulations, and the number of eggs released at each coordinate was calculated from the number of fish of different size classes caught at that location. The potential egg production at each location was calculated using a simple equation for fecundity of cod: $F = 5.4xL^3-13000$ (eqv. [3] in Oosthuizen & Daan 1974), where F is number of eggs, and L is length class of cod binned into 10 cm intervals (See figure 1 for the distribution of egg production estimates). The average fraction of estimated North Sea egg production that was within our model's domain was 57% for the past decade (2005-2015). The estimated egg production at a given site was then portioned out over the spawning season typical of the North Sea cod in a normal distribution, from February 2nd to May 9th (Brander 1994). To simulate spawning behaviour observed in the wild (e.g. as described in Rose 1993), the eggs were released uniformly from one meter above the sea bottom, up to 40% of bottom depth (e.g. 20 m above sea bottom when total depth was 50 m) at each release site.

The individual based model for eggs and larvae

At the initiation of each drift simulation, eggs were assigned an individual buoyancy value measured in practical salinity units. As no studies have quantified buoyancy of North Sea cod eggs, we used values typical of Arcto-Norwegian cod, between 33 and 34 psu (Sundby 1997). Density of eggs was then calculated as a function of its pre-set salinity equivalent and the eggs' in-silico sea temperature (Coombs et al. 1981). At each time step of ten minutes, the egg was then pushed either upwards or downwards depending on the hydrostatic pressure acting on it. Egg incubation time was calculated as a function of temperature (Peterson et al. 2004), and larvae experienced temperature dependant growth (Folkvord 2005). In the wild, young cod larvae are generally found within or immediately below the pycnocline (Munk 2014), while older larvae are found deeper (Lough & Potter 1993). Cod larvae are also known to display a vertical movement of up to 10 m over the course of 24 hours (Höffle et al. 2013, Munk 2014), indicating some active movement in the water column. However, during episodes of high wind-induced turbulence, smaller larvae have been shown to be mixed homogenously in the water column (Ellertsen et al. 1984). Thus, from hatching until time of first feeding our modelled larva had little swimming capability (max 10 cm per 10-minutes), vertical position was mainly regulated by their density (Saborido-Rey et al. 2003), and they were programmed to attract towards the pycnocline. After the time of first feeding, we hypothesised that vertical position was regulated by larva's behaviour in response to light. The rationale is that a certain amount of light is needed to feed, while too much light would increase predator exposure. Thus, the feeding larvae were programmed to swim upwards if situated below the isolume of 1 W/m^2, downwards if above the isolume of 10 W/m^2, and remain still at onset of total darkness (see figure 2 for a sample of the vertical movement profile of eggs, larvae, and pelagic juveniles). Maximum swimming speed of feeding larva smaller than 10 mm was set to 0.5 m per 10 min, while bigger larvae could swim up to 1 m per 10-minute time step. The potential integrated vertical swimming distances used in the model was well below critical swimming speeds observed in laboratory experiments (Guan et al. 2008), however, there are no empirical evidence for extensive swimming activity in the wild. When larvae reached a size between 25 mm and 35 mm they were defined as ready to settle (larvae within this size range is hereby referred to as pelagic juvenile), as this is the size range of newly settled larvae observed along the Skagerrak coast (Johannessen 2014). To account for vertical mixing experienced by eggs and larvae, a pre-set vertical perturbation component was added at each time step. If mixed into the transition layer and when situated below the upper mixing layer, one tenth of the mixing coefficient was used. The mixing layer depth was calculated as the depth where the vertical gradient in water density was highest. Particle advection in the horizontal plane was modelled using a fourth-order Runge-Kutta scheme with the velocity field arrays from the hydrodynamic model. We included no horizontal swimming behaviour to larvae in our model.

Circulation model of the northern North Sea

The circulation model used was the Regional Ocean Modelling System (ROMS, http://myroms.org), a free-surface, hydrostatic, primitive equation ocean model (e.g. Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). The circulation model was run with 800m resolution in the horizontal and was forced over a time period of 2 × 180 days (from February 1st to August 1st) for two consecutive years (2011 and 2012), using daily averages of currents and hydrography along the open boundaries from a large-scale model covering the Nordic Seas (Lien et al., 2014), high-resolution wind fields (Weather Research and Forecasting model, WRF, using 3km horizontal resolution, see Skamarock et al. [2008]) and realistic freshwater discharge from all rivers in the model domain (provided by the Norwegian Water Resources and Energy Directorate, see Beldring et al. [2003]). The time-varying arrays from the ROMS model had a temporal resolution of two hours, 35 depth layers, and contained velocity fields and physical variables covering a total area of 880 × 850 grid points, giving a total model area of approximately 704 km × 680 km (Figure 1). More details on the ROMS simulation can be found in Albretsen et al. (2011). To validate the ocean model we compared its physical output variables (salinity and temperature) with hydrographical data routinely sampled within the model domain. Overall, the model compared well with observations, with no significant biases in predicted salinity or temperature, equivalent to former and more comprehensive validation analysis of the same modelling system shown in e.g. Myksvoll et al. (2013).

Furthermore, to evaluate the relationship between the variation in ocean circulation in the study area and the dominant mode of variability in the wind field, namely the North Atlantic Oscillation (NAO); we performed correlation analyses between transport estimates at various transects and the normalised daily NAO (retrieved from the Climate Prediction Centre, National Oceanic and Atmospheric Administration). We also wanted to know the response time between the two variables, and thus ran correlation tests with filtered NAO indices, from the ‘raw’ daily estimated values to 20-day running average filters.

Results

The majority of the eggs released over the plateau east and south of the Viking bank were “funnelled” into and along the crest of the Norwegian Trench, entering just northeast of the Ling bank. The main drift route of eggs spawned south of the Viking bank, for example over the Ling bank and the Fisher banks, was also along the southern slopes of the Trench before entering Skagerrak. Subsequently, the eggs and larvae followed the counter-clockwise Skagerrak loop and drifted with the Norwegian coastal current out of Skagerrak, further along the western Norwegian coast, or into the Norwegian Sea (Figure 3A). In total, ≈50% of all individual particles spent at least one day in Skagerrak in both 2011 and 2012 simulations. There was also a second export route taken by eggs and larvae spawned over the north-eastern plateau and the Viking bank; those that got mixed into the northward propagating eddies of the Norwegian coastal current already in the North Sea, effectively short-circuiting the northern North Sea-Skagerrak circulation cell. A variation of this short-circuit pathway was also followed by the majority of eggs released north-east of the Viking bank and over Tampen, getting entrained with the Continental Slope Jet and directly mixed into the Norwegian coastal current upon floating towards the surface layer, but also through horizontal mixing with the deflected Atlantic water at different depths (Figure 3B). The percentage of eggs and larvae spawned over the north-eastern North Sea that was retained on the plateau declined from an initial 74%, where 19% of the eggs were released from locations in the Skagerrak, down to 24% at the end of August 2011. In 2012 there was an overall higher retention rate in the north-eastern North Sea, starting with 68% of the eggs, declining down to around 36%. The proportion of eggs and larvae that was located within Skagerrak at a given time was fairly constant, but slightly declining over time. The number of particles that was advected into Kattegat was insignificant in both years. The proportion of eggs and larvae that was advected into the Norwegian Sea increased linearly with time in both years, starting at

3% and ending up at 68% in 2011, and from 1% to 53% in 2012 (Figure 4A). The average date of first feeding (i.e. upon reaching ≈ 5 mm) of the larvae in the model was similar in the two years of simulation, in 2011 the mean date was March 29th (95%CI: March 2nd – April 26th), and in 2012 March 28th (95%CI: February 28th – April 22nd). The average modelled pelagic larval duration (i.e. time from hatching until reaching 25 mm) was 83 days (95%CI: 64 – 101 days) in 2011 compared to 78 days in 2012 (95%CI: 64 – 92 days). Total proportion of days spent by pelagic juveniles (with a size between 25 mm and 35 mm) over unsuitable habitat, i.e. over a bottom depth deeper than 200 m, integrated over the two years was 26% (See figure 5 for drift routes of pelagic juveniles for 2011). The percentage of days spent by settling pelagic juveniles over the North Sea plateau and Skagerrak coastal margin in drift simulations was 30% in 2011 and 49% in 2012. The percentage of days that was spent by pelagic juveniles in the Norwegian Sea, while being advected out of the northern model domain boundary, was very different between the two years, with 39% advected out in 2011 and only 21% in 2012. Thus integrated over the two years, about 56% of pelagic juveniles originating from the northern North Sea and Skagerrak spent their potential "settlement window" along the western Norwegian coast, or further along the Norwegian Sea shelf (Figure 4B).

When reaching Skagerrak, the northern North Sea outflow had a peak correlation coefficient of 0.43 with the 5-day filtered NAO, and the current there extended all the way from the bottom of the channel towards the surface (Figure 7). There were also two jet cores flowing out from Skagerrak, both responding significantly to the NAO, being the returning flow of the northern North Sea outflow bundle after having completed the counter-clockwise loop around Skagerrak as well as the fresher continuation of the Baltic current and freshwater input from Norwegian rivers. The average daily transport estimates of water masses leaving the North Sea and entering Skagerrak varied between 0.5 Sv (1 Sv = 10^6 m^3 s^{-1}) to 1.8 Sv, but averaged around 1 Sv. The daily average transport responded significantly to the daily NAO, but had a maximum correlation with the 5-day filtered NAO ($\mathrm{cor}_{\mathrm{Sv-NAO}\,5} = 0.36$, $p<0.001$, Figure 6). In 2012 however, the relationship between the daily NAO and the northern North Sea outflow was not significant ($\mathrm{cor}_{\mathrm{Sv-NAO}} = 0.14$, $p=0.09$). From the temperature vs. salinity profiles systematically sampling the modelled water masses occupying the Norwegian Trench, it was clear that Atlantic water in its undiluted form (with a salinity around 35 and temperature of 8-9°C in spring) does not intrude further than the saddle-point north of transect D, west of Stavanger (Figure 6, and see Figure 1).

Discussion

Based on the contemporary distribution of North Sea cod SSB, our results suggest that more than a quarter of the total production of North Sea cod larvae is advected out of the North Sea. The vast majority of the year classes modelled here most likely recruited to nursery areas in Skagerrak, along the western Norwegian coast, or further along the Norwegian Sea shelf. In general, most spawning locations in the northern North Sea and Skagerrak yielded a similar drifting pathway, albeit with a huge potential settlement area along the Trench crest, Norwegian southern and western coast, and Norwegian Sea continental shelf–whereas even small differences in spawning location around the Viking bank would lead to highly variable dispersal paths. The degree of leakage of eggs and larvae from the northern North Sea varied considerably between years, with high NAO within the time frame of pelagic eggs and larvae most likely resulting 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-Skagerrak circulation cell (Furnes 1980, Winther & Johannessen 2006, Hjøllo et al. 2009). Actually, in the time period between 1960 and 2000, the wind forcing represented by the NAO explained 44% of the total variation in winter circulation of the North Sea (Mathis et al. 2015). Generally positive phases yield positive anomalies in Atlantic inflow between Orkney and Shetland as well as an increased eastward and southward flow over the entire North Sea; whereas in extreme negative phases the circulation in the southern and central North Sea effectively stops, and most of the Orkney and Shetland inflow follows the Dooley current, rather than flowing into the southern North Sea. There is also a second mode of variation in winter circulation, independent of the NAO, explaining 22% of the variation in the past half-century (Mathis et al. 2015). This second mode is characterised by episodes of high and low pressure system build up over the British Isles, which results in increased prevalence of north-western wind anomalies, leading to increased inflow of Atlantic water in the Norwegian Trench and over the open northern boundary between Shetland and the Trench, but also significantly decreasing the English channel inflow as well as reducing flow along continental Europe. Concurrent with the dominant flow patterns of the North Sea water masses; earlier drift studies suggest 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 there seems to be almost total retention of eggs spawned over historically important spawning grounds in the southern North Sea, around Dogger bank, Southern Bight, and German bight, although with a leakage of up to 35% of spawning products from the north-eastern extreme of Dogger bank into Skagerrak in years of high NAO. By contrast, less than 5% of pelagic juveniles spawned within the north-eastern North Sea reaches nursing areas in the western and southern parts of the North Sea (Heath et al. 2008, Jonsson et al. 2016). Thus based on old and new information on the major drifting pathways of cod eggs and larvae in the North Sea, it is increasingly clear that the southern spawning assemblage is oceanographically decoupled from the highly advective northern part, as outlined in the introduction. However, what we consider novel in our study is the large extent of the potential settlement area of the larvae spawned within the northern North Sea, as well as the large-scale shift in spatial recruitment potential within the circulation cell in response to the wind forcing represented by the NAO.

There is to date no unifying theory explaining a direct link between atmospheric forcing and variability in the pelagic ecosystem of the North Sea. But given the highly correlated relationship between recruitment strength of cod and abundance of *C. finmarchicus* (Sundby 2000, Beaugrand & Kirby 2010), we find it necessary to briefly review the ecology of *C. finmarchicus* in the northern North Sea circulation system. The closest upstream overwintering ground of *C. finmarchicus* in the region is situated in the Faroe-Shetland channel (Heath & Jonasdottir 1999), and the overwintering copepodites' least variable entry point to the highly productive Norwegian coastal current is through the mouth of the Norwegian Trench (Gallego et al. 1999, Harms et al. 2000). Here, most of the inflowing, *C. finmarchicus* enriched Atlantic water gets retroflected and eject underneath the Norwegian coastal current on the eastern side of the channel before 59°N (Heath et al. 1999). This agrees well with our ocean model, where Atlantic water in its undiluted form did not intrude beyond the Trench saddle point at ≈58°N, as also pointed out by Furnes et al. (1986). After the brief visit in the Trench mouth the outflowing Atlantic water aligns with the Norwegian coastal current, and at ≈63°N (offshore off Svinøy) the highest abundances of *C. finmarchicus* throughout the northern hemisphere is found (Melle et al. 2014). Spawning at a location that ensures eggs and larvae are being entrained in this *C. finmarchicus* highway of the Nordic Seas seems to be a successful spawning strategy for the North Sea gadoids. For example, the main spawning grounds used by the North Sea saithe (*Pollachius virens*) is to release their eggs over the far northern, deep end of the North Sea/European continental shelf (Bjørke & Sætre 1994). Most of the saithe eggs and larvae spawned there subsequently follow the same short-circuit pathway across the Norwegian Trench that we sketched out for the cod eggs spawned north and east of the Viking bank (see figure 3B). The comparably vast SSB of North Sea saithe since the 1990s of between 100.000 and 300.000 tonnes bears witness to the recruitment potential that lies in this spawning strategy (ICES 2015), even in the seemingly unfavourable climatic period since the start of the 90s. In fact, when looking at catch data of North Sea cod aggregated into their respective north-eastern and south-western genetic units, the Viking unit spawning biomass has remained at its present level for at least 30 years, while the southern and north-western stocks drastically declined (Holmes 2014). It thus appears that despite the declining trends and overall low abundance of *C. finmarchicus* in the North Sea proper (Beare & McKenzie 1999), the Trench inflow regime has facilitated a stable supply of *C. finmarchicus* to the drifting and settling cod larvae spawned there–although not having the same recruitment potential to cod as the now relic state of the southern North Sea nursery grounds in the colder periods of the 20s, 60s, and 70s (Beaugrand & Kirby 2010). Moreover, over a longer time perspective, the ocean-climate of the North Atlantic and the Nordic Seas have followed a natural quasi-periodic cycle of around 65 years–where the two latest cold periods coincided with the strong recruitment years for cod of the 20s and 60s-70s (Knight et al. 2005). But because of continual emission of green house gasses, and hence a general warming of the ocean-climate of the North Atlantic and Nordic Seas, the sub-arctic zooplankton assemblage is projected to continue their northward retreat into the foreseeable future (Beaugrand et al. 2008), painting a grim future for the spring spawning gadoids in the North Sea. 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 Norwegian Sea deep water into the Faroe-Shetland Channel, that is, as long as the meridional overturning circulation continues in its present mode (Rahmstorf 2002, Kuhlbrodt et al. 2007), the integrity of the Faroe-Shetland Channel as overwintering habitat to *C. finmarchicus* will probably be maintained (Wilson et al. 2016). Thus in essence, due to the inherent flow dynamics of the northern North Sea and the upstream position of the Faroe-Shetland Channel containing overwintering *C. finmarchicus*, even in climatically unfavourable periods the Trench inflow regime can facilitate favourable nursing conditions to the spring spawning gadoids choosing to, or accidentally spawning there.

A major weakness of our particle-tracking algorithm is that convectional forces were not resolved. For example, when a heavier water mass gets subducted under a lighter water mass, which constantly happens in for example Skagerrak where water masses of different densities meet creating complex frontal dynamics, a particle flowing with the heavier water mass is not pushed down to follow the flow. The consequence is that the particle gets advected into flows/water masses of qualitatively different dynamics. This is to some extent compensated by buoyant eggs following the water mass identical to their innate density, but the vertical displacement was not instant. Although the particle-tracking algorithm had its weaknesses, our individual based model seemed to represent the development stages of cod well, with a pelagic juvenile settlement window coinciding with timing of settlement observed in the wild (Bastrikin et al. 2014, Johannessen 2014), and the high abundance of larvae and pelagic juveniles in the front north of the Danish Jutland coast compare well with field observations (Munk 2007, 2014). The few data points that are available for the abundance of cod larvae along the western Norwegian coast indicates some agreement with our model (Riley & Parnell 1984, Nedreaas et al. 2008). But since the sampling outside the western Norwegian coast were taken early in the season (April-May) and not during the pelagic juvenile stage (June), the data give an inconclusive answer on the abundance of pelagic juveniles “in drift” along the western Norwegian coast originating from the northern North Sea or Skagerrak. Thus, further field studies have to be performed to confirm our hypothesis on the prevalence of North Sea originated juveniles at nursing grounds along the Norwegian western coast and Norwegian Sea shelf, although it is well known that North Sea pelagic juveniles settle in for example coastal Skagerrak (Knutsen et al. 2004, Stenseth et al. 2006, Øresland & Andre 2008). Added to that, pelagic juveniles of saithe spawned in the northern North Sea is found in large numbers north-east of the mouth of the Norwegian Trench and beyond, which lend strong support for the hypotheses of continuous settlement habitat from the northern North Sea, across the Trench, and along the Norwegian north-western coast in the wake of the Norwegian coastal current (Bjørke & Sætre 1994).

To conclude, 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 along the western Norwegian coast or gets advected further along the Norwegian Sea shelf. We also showed and discussed how large-scale climatic 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 and eastern extension of North Sea cod nursery habitat we consider beneficial to survival of the settling juveniles, considering the marginalisation of the North Sea as nursery habitat for recently settled juvenile cod compared to historical conditions. Although the particle-tracking algorithm had its weaknesses, the main patterns compare well with observations in the wild. However, further field studies have to be performed to confirm our hypothesis of the north-eastern extension of the North Sea cod nursery grounds.

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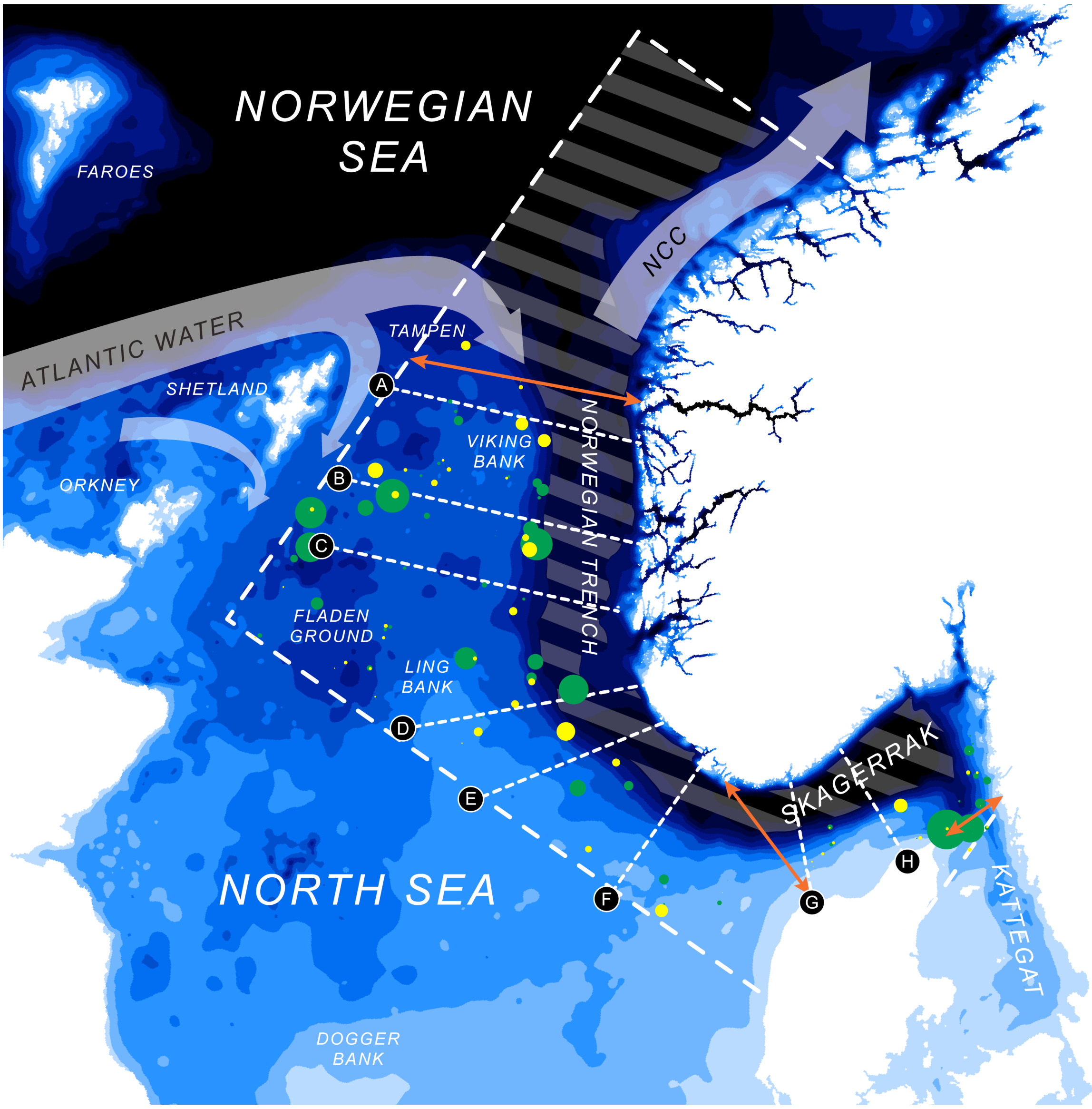

Figure 1. Bathymetry of the study area. White arrows represent the main inflow routes of Atlantic water, and the only outflow of North Sea water masses through the Norwegian coastal current. Yellow and green circles represent the spatial distribution and estimated egg production in 2011 and 2012, extrapolated from the ICES IBTS survey. The double-headed, orange arrows denote the boundaries between the North Sea-Skagerrak, Skagerrak-Kattegat, and North Sea-Norwegian Sea. Lines A-H refers to transects where salinity and temperature was extracted for figure 6. The hatched area in the Norwegian Trench represents hypothesised unsuitable settlement habitat for settling pelagic juveniles. Stapled box represents the boundaries of the circulation model.

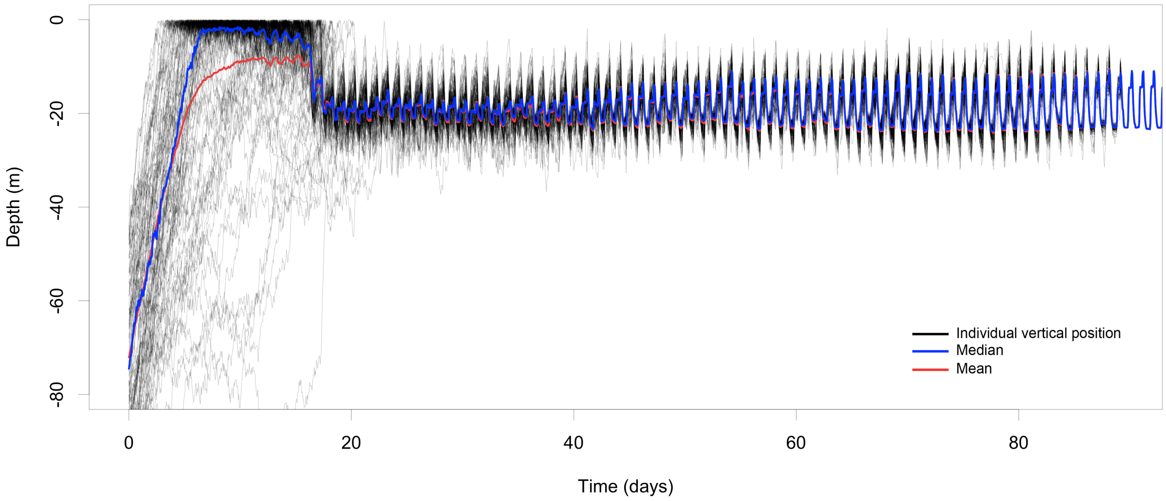

Figure 2. Vertical distribution through development of 100 eggs, larvae, and pelagic juveniles. Blue line represents the median depth, while red represents mean depth.

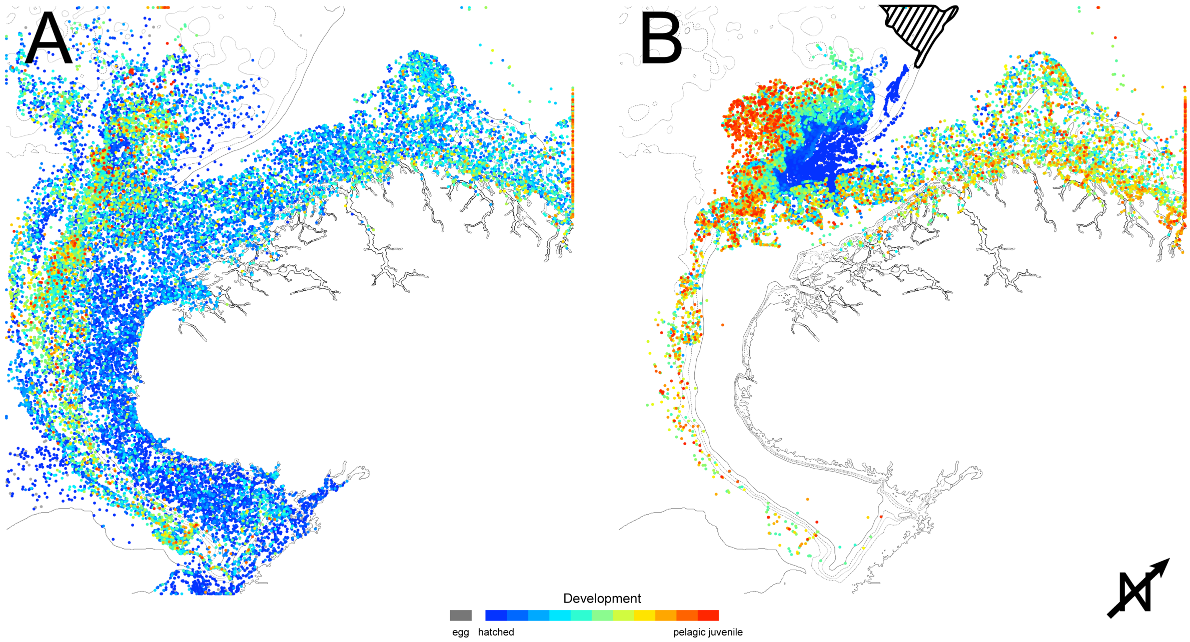

Figure 3. Comparison of flow dynamics of eggs spawned south and north of the Viking bank. Here panel A represents the drift of cod eggs and larvae spawned along the Norwegian Trench as suggested by recent surveys (ICES 2015). For illustrative purposes, panel B represents drift of eggs released over Tampen typical of North Sea Saithe (amount of particles in panel B is arbitrary, and not comparable to panel A). Both simulations have been run for 80 days (when all eggs were hatched), with eggs spawned every day until day 68, initiated on February 1st 2011 and run until April 22nd 2011.

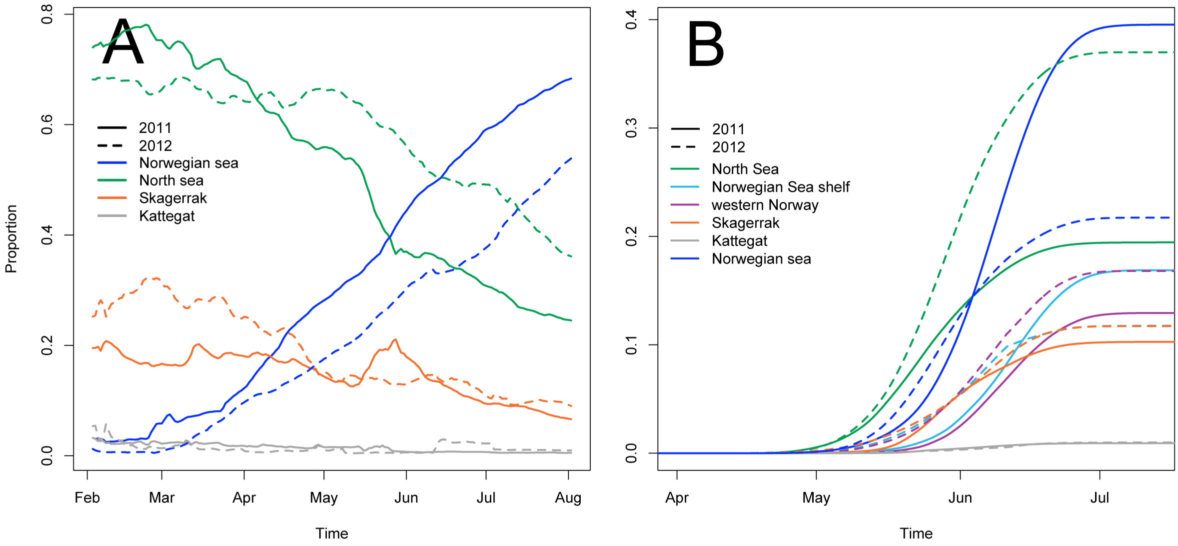

Figure 4 (A) Proportion of eggs and larvae spawned in the northern North Sea and Skagerrak situated in the North Sea, Skagerrak, Kattegat, or Norwegian Sea through the simulation period. (B) Proportion of days spent over the possible nursery habitats within our model domain by larvae ready to settle, between 25 and 49 mm in body size (see spatial distribution of settlement days in figure 5).

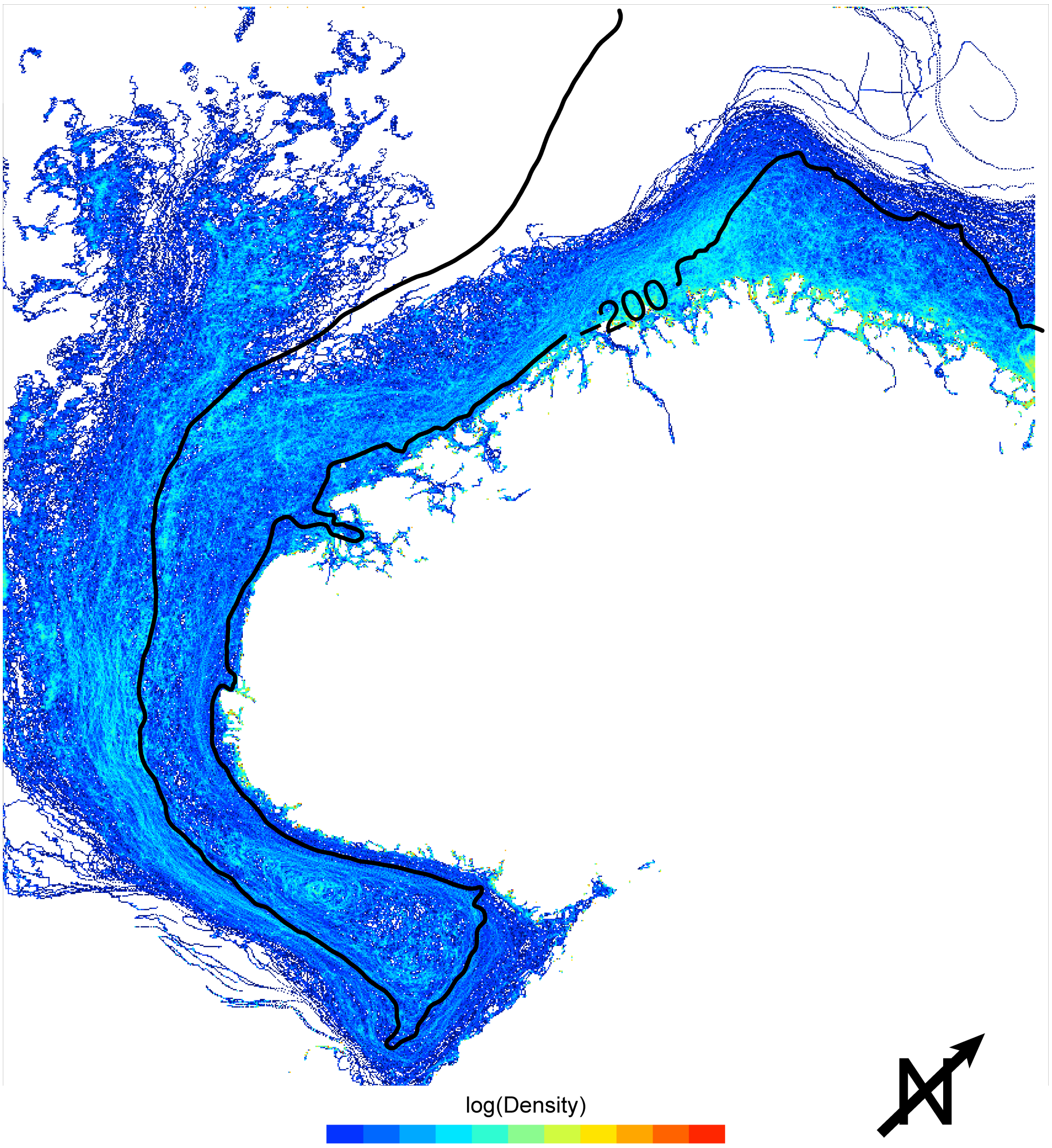

Figure 5. Spatial distribution of accumulated settlement days for pelagic juveniles spawned in the north-eastern North Sea and Skagerrak in 2011 (see figure 4 for summary of the proportion of settlement days spent in the different oceans/areas).

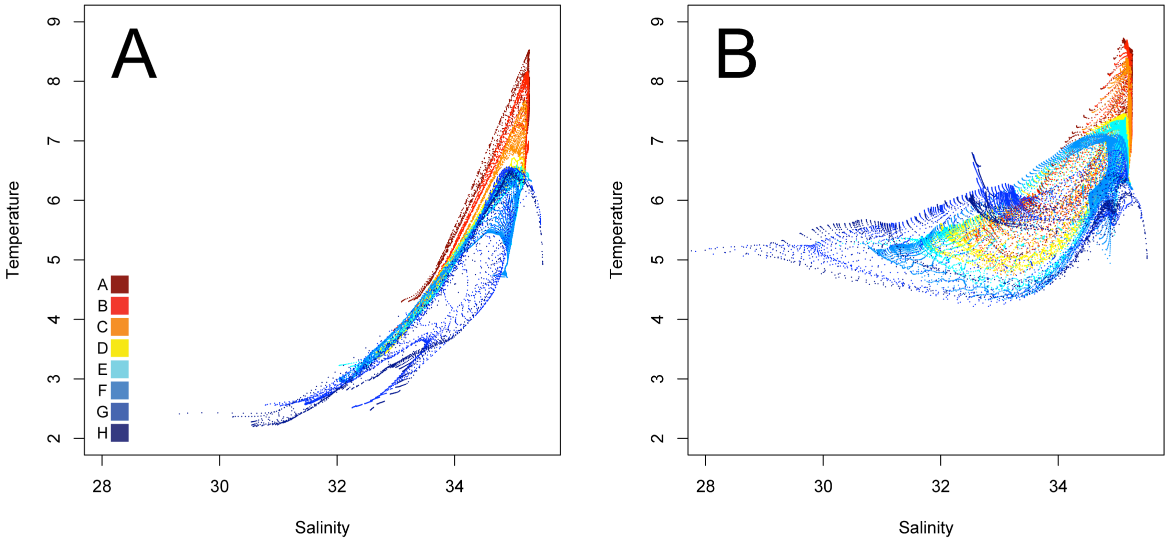

Figure 6. Monthly average salinity and temperature extracted from ocean model in all depth-layers at transects A-H in figure 1. Panel A represents average values for March 2011, and B is for April 2011.

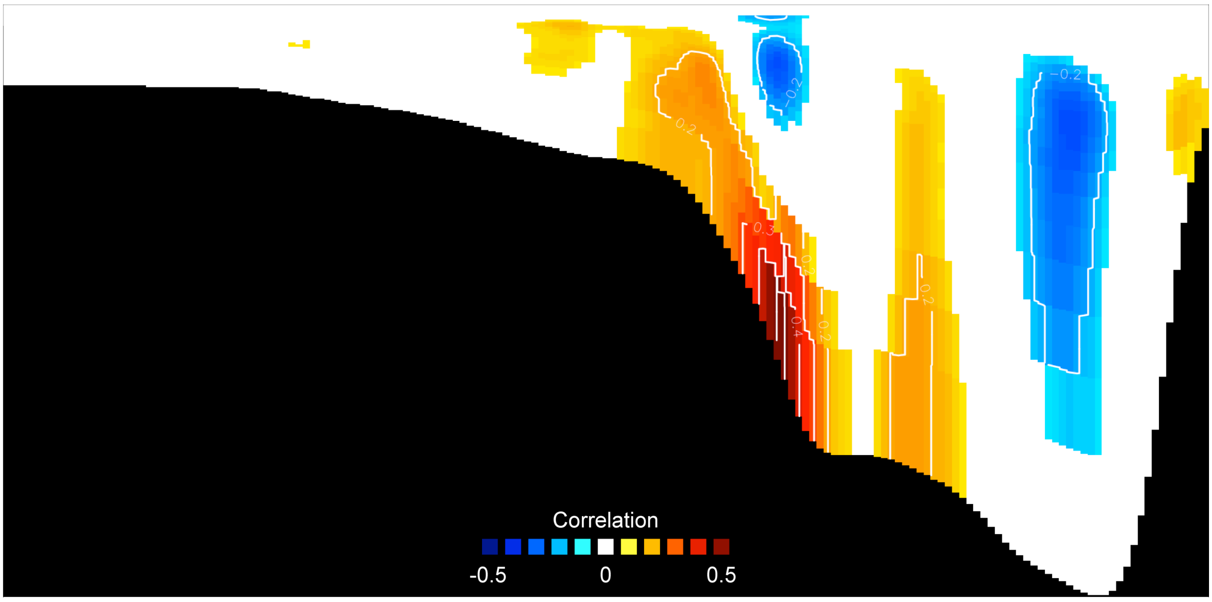

Figure 7. Cross-section of currents across the Norwegian Trench (at transect "F" in figure 1) correlated with the 5-day running average of NAO. Coloured areas of the cross-section identifies areas with a significant correlation between currents and NAO (white numbers and isolines indicates strength of correlation), and warm and cold colours represents currents. entering or leaving Skagerrak.

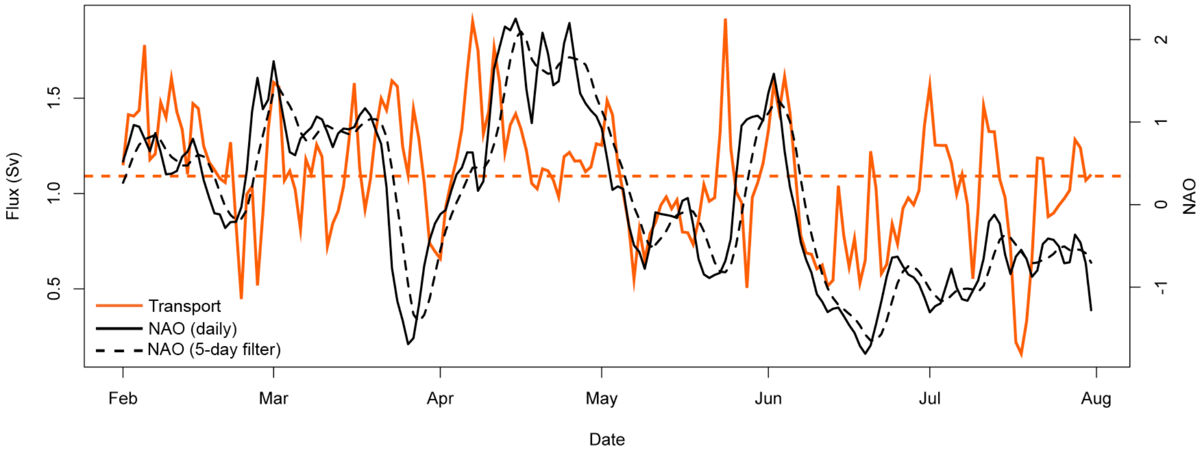

Figure 8. Daily average transport estimates of water masses leaving the northern/central North Sea and entering Skagerrak (orange line, transport estimates based on transect "F" in figure 1) and the daily NAO (solid line, with the 5-day running average of NAO, stapled line).

Refining Hjort's "critical period" hypothesis to the southern range of cod

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Target journal: Progress in Oceanography, Fisheries Oceanography, or ICES Journal of marine science (i.e. no page limits)

Abstract. Hjort put forward the availability of food to first feeding larvae of Arcto-Norwegian cod (*Gadus morhua*) as the primary driver of recruitment variability in the Barents Sea, later known as the "critical period" hypothesis. However, given the large latitudinal range of the Atlantic cod and the boreal affinity of its most important prey during the larval stage, the copepod *Calanus finmarchicus*, the challenges of matching larval development with the seasonal dynamics of *C. finmarchicus* is expected to vary. In this study we set out to apply Hjort's widely acclaimed critical period hypothesis to the recruitment of cod (*Gadus morhua*) in Skagerrak nursing grounds, which according to recent surveys is among the most southern nursery grounds of significance for the species on the east side of the Atlantic. Our investigation was designed to discern the environmental and biological factors that contributed to a good year class for recruitment of cod in the Skagerrak, including potential drift of pelagic juveniles from the North Sea validated by field sampling and genetic assignment of settled juveniles. We put special attention in our analyses to the year of 2011, as this was by far the best year class for cod in the Skagerrak throughout the past decade. The only significant deviation from a normal year found in the physical environment was that the Norwegian coastal water was colder than usual in winter. We hypothesis that the colder winter temperatures may have slowed down the seasonal development of the zooplankton, leading to a later peak as well as stably high availability of *C. finmarchicus* copepodites to cod larvae throughout the settlement period. Thus, in contrast to the popular interpretation of Hjort's hypothesis, that proclaims the end of the yolk sac stage to be the crux point for the year class of cod, we hypothesise that the period from settlement to the transition to benthic feeding is the decisive period in Skagerrak nursing grounds. The rationale being that during this time period when metabolic requirement is at it's highest, as this coincides with peak temperatures, any variability in the zooplankton that the larvae still are dependent on could prove fatal.

Introduction

One of the oldest conundrums in fisheries biology is the determinants of year class strength. In his treatise on “Fluctuations In The Great Fisheries Of Northern Europe” (1914), Hjort put forward the availability of food to pelagic larvae as the primary driver of recruitment success. He observed that at the time of spawning of the Arcto-Norwegian cod (*Gadus morhua*) the water around Lofoten was devoid of zooplankton and remarked that the cod probably spawned at that particular time in anticipation of the spring bloom, to ensure that larvae hatched when the availability of food would be at its peak. 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. Cushing (1990) later generalised this notion that a coinciding (or separate) peak in prey abundance with the extent of the larval phase would prevent (or induce) bottlenecks in population numbers, and termed it the Match-Mismatch hypothesis. However, in for example the North Sea, high recruitment of cod has been found to be dependent on high abundance of zooplankton throughout the early phases of life, and even more so at the end of the larval stage (Cushing 1984, Rothschild 1998). This by no means discredit the “critical period” as a concept, because it was already loosely coined in the first place, as we can read under the header *Origin of the fluctuations in renewal of the stock* (Hjort 1914, p.202), where Hjort summarises his thoughts on the causality of the variability of the great fisheries of herring, cod, and haddock in the Nordic Seas: “It … appear most probable that the renewal of the fish stock … is dependent upon many factors, all necessary, and all more or less variable. Thus in each individual instance, the *missing factor* will appear to be that which *determines the ultimate result*”. Given the large latitudinal range of the Atlantic cod (spawning from 50°N to 70°N on eastern side of Atlantic) and the boreal affinity of its main pelagic prey during the early stages of life, the copepod *Calanus finmarchicus* (Heath & Lough 2007, Melle et al. 2014), the challenges of matching larval development with the seasonality of *C. finmarchicus* is expected to vary along their range (Sundby 2000). For example, in the Skagerrak the abundance of *C. finmarchicus* usually build up from next to nothing in early February towards a peak in April, upon almost disappearing from the upper water column in summer. This in contrast to the main spawning ground of the Arcto-Norwegian cod in the Lofoten archipelago, which has a comparably vast abundance almost year round, except a short period of absence in February to March (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 capitalise on them, unlike dying of starvation before the bloom. If we also take into account that summer temperatures are at least ten degrees warmer in the littoral nursery habitat in the Skagerrak than in the Barents sea, and knowing that metabolic requirement of fish increases exponentially with temperature (e.g. Clarke & Johnston 1999), any variability in *C. finmarchicus* abundance during that critical summer period may prove sharply defining to the year class strength.

Since the restructuring of the survey program of the North Sea cod stock in 1992, the international bottom trawl survey (IBTS) now encompasses the entire North Sea as well as the southern Skagerrak (ICES 2015). Recent surveys suggest that most of the one year old recruits of the North Sea cod stock are found in the southern Skagerrak nursery areas (Hjermann et al. 2013, Nicolas et al. 2014, ICES 2015). Northern Skagerrak nursery habitats have also been surveyed along the Norwegian coast since the dawn of the 19th century, and together these two data sets offer a unique perspective on long-term as well as short-term recruitment patterns in the Skagerrak. The variability in recruitment to Skagerrak nursery areas is large, and typically has a series of mediocre and bad years, interrupted by a good year now and then. The good years of the past three decades are by far the seasons of 1996, 1998, and 2011, and in these years we find good recruitment across the entire Skagerrak. Explanations have been many on what creates the variation in cod recruitment to Skagerrak nursing grounds, from overfishing (Cardinale & Svedäng 2004), inter -and intra cohort competition (e.g. Fromentin et al. 2001), variable import from the North Sea (Stenseth et al. 2006), to variability in the prevalent wind field and large scale climatic phenomena (Lekve et al. 2002). However, more similar to the match-mismatch hypothesis of Cushing and critical period hypothesis of Hjort, Johannessen (2014) put forward an interesting hypothesis regarding recruitment of cod in Skagerrak. His studies suggest that recruitment in general is decoupled between the pelagic to benthic phase, largely because the number of cod larvae surviving the settlement phase is dependant on food conditions in terms of quantity and/or quality during summer. In short, the answer to this question remains many-faceted. The scope of this study was thus quite simply to evaluate the leading hypothesis on what drives recruitment of cod in Skagerrak. Our primary objective was to apply the “critical period” hypothesis of Hjort to nursery habitat in the southern range of cod, where challenges to the development of larvae may be fundamentally different than were the concept first was coined. Our secondary objectives was to investigate the possible drift routes taken by North Sea cod larvae that have frequently been reported settling into coastal Skagerrak nursery grounds (Knutsen et al. 2004, 2011, Stenseth et al. 2006) as well as to evaluate the impact climatic variables may have on recruitment in Skagerrak littoral nursing areas (Lekve et al. 2002, Rogers et al. 2011). Our investigation was designed to discern the environmental and biological factors that contributed to a good year class for recruitment of cod in Skagerrak and contrast it to a mediocre year. We put special attention to the year of 2011, as this was by far the best year class for cod in these waters throughout the past decade. To evaluate the impact of food availability on recruitment, we analyse the phenology of the copepod community sampled bimonthly over the two years. In our analyses we focused on the species of copepods that has been shown to be important food items of cod larvae, in decreasing order of importance: *Calanus spp.*, Paracalanus/Pseudocalanus, and *Oithona sp.* (Heath & Lough 2007). Our queries on the role of import of larvae and pelagic juveniles from the North Sea to Skagerrak nursing grounds were addressed by the deployment of a biophysical dispersal model of the Skagerrak and the northern North Sea, coupled with empirical data on the distribution of potential cod egg production. We validated our modelled drift trajectories and settlement distribution with recruitment data of half-year old cod collected in the Skagerrak as well as genetic assignment of the recruits. And lastly, to evaluate the climatic impact on recruitment, we analysed empirical data on the physical environment experienced by eggs and larvae over the two contrasting years, both the early pelagic habitat and the later benthic nursery areas.

Materials and methods

The biophysical dispersal model of cod early life stages

To derive an estimate of the potential spawning distribution in the northern North Sea, we extrapolated potential egg production from the annual ICES international bottom trawl survey (IBTS, quarter 1). This survey is run between January and March every year, and is designed, among other things, to assess the spawning stock biomass of cod. We used the coordinates of the survey hauls as release points in our drift simulations, and the number of eggs released was calculated from the number of fish of different size classes caught at that location (see Fig. 1 for spatial distribution of calculated egg production within model domain). The potential egg production at each location was calculated using a simple equation for fecundity of cod: F = 5.4xL^3-13000 (eqv. [3] in Oosthuizen & Daan 1974), where F is number of eggs, and L is length class of cod binned into 10 cm intervals. The long-term average fraction (i.e.

over the last decade) of potential North Sea egg production that was within our model's domain was 58%. The modelled egg production at a given site was then portioned out over the spawning season typical of the North Sea cod in a normal distribution, from February 2nd to May 9th (Brander 1994). To simulate spawning behaviour observed in the wild (e.g. Rose 1993), the eggs were released uniformly from one meter above the sea bottom, up to 40% of bottom depth (e.g. up to 20 m when total depth was 50 m) at each release site.

At the initiation of each drift simulation, eggs were assigned an individual buoyancy value measured in practical salinity units. As no studies has quantified buoyancy of North Sea cod eggs, we used values typical of Arcto-Norwegian cod, between 33 and 34 (Sundby 1997). Density of eggs was then calculated as a function of its pre-set salinity equivalent and the eggs' in-situ sea temperature (Coombs et al. 1981). At each time step of ten minutes, the egg was then pushed either upwards or downwards depending on the hydrostatic pressure acting on it. Egg incubation time was calculated as a function of temperature (Peterson et al. 2004), and larvae experienced temperature dependent growth (Folkvord 2005). In the wild, young cod larvae are generally found within or immediately below the pycnocline (Munk 2014), while older larvae are found deeper (Lough & Potter 1993). Cod larvae are also known to display a vertical movement of up to 10 m over the course of 24 hours (Höffle et al. 2013, Munk 2014), indicating some active movement in the water column. However, during episodes of high wind-induced turbulence, smaller larvae have been shown to be mixed homogenously in the water column indicating that their vertical position is not maintained if convectional forces are too high (Ellertsen et al. 1984). Thus, from hatching until time of first feeding our modelled larva had little swimming capability (max 10 cm per 10-minutes), vertical position was mainly regulated by their density (Saborido-Rey et al. 2003), and they were programmed to attract towards the pycnocline. After the time of first feeding, we hypothesised that vertical position was regulated by larva's behaviour in response to light.

The rationale is that a certain amount of light is needed to feed, while too much light would increase predator exposure. Thus, the feeding larvae were programmed to swim upwards if situated below the isolume of 1 W/m^2, downwards if above the isolume of 10 W/m^2, and remain and remain at their vertical level at onset of total darkness. Maximum swimming speed of feeding larva smaller than 10 mm was set to 0.5 m per 10 min, while bigger larvae were allowed to swim up to 1 m per 10-minute time step. The potential integrated vertical swimming distances used in the model was well below critical swimming speeds observed in laboratory experiments (Guan et al. 2008), as there is no empirical evidence that the maximum swimming ability is realised in the wild. To account for vertical mixing experienced by eggs and larvae, a pre-set vertical perturbation component was added at each time step. If mixed downward into the transition layer with higher density and when situated below the upper mixing layer, one tenth of the mixing coefficient was used. The mixed layer depth was calculated from the hydrodynamic model as the depth where the vertical gradient in water density was highest. Particle advection in the horizontal plane was modelled using a fourth-order Runge-Kutta scheme with the velocity field arrays from the hydrodynamic model. We included no horizontal swimming behaviour to larvae in our model. When larvae reached a size between 25 mm and 50 mm they were defined as ready to settle (this size class of larvae is henceforth termed the pelagic juvenile stage), as this is the size range of newly settled cod observed along the Skagerrak coast, down to no deeper than 40 m (Johannessen *et al.* 2014). To quantify the spatial distribution of settlement along the coast, we integrated the number of days spent by pelagic juveniles in proximity of each grid point of our hydro-dynamical model that was shallower than 40 m. The bottom areas of our model constrained by the upper 40 m were thus defined as nursery habitat of the cod along the Norwegian Skagerrak coast.

The circulation model used was the Regional Ocean Modelling System (ROMS, http://myroms.org), a free-surface, hydrostatic, primitive equation ocean model (e.g. Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). The circulation model was run with 800m resolution in the horizontal and using 35 topography-following levels in the vertical over a time period of 2 × 180 days (from February 1st to August 1st in addition to spin-up) for two consecutive years (2011 and 2012), and was forced using daily averages of currents and hydrography along the open boundaries from a large-scale 4km-model covering the Nordic Seas (Lien et al., 2014), high-resolution wind fields (Weather Research and Forecasting model, WRF, using 3km horizontal resolution, see Skamarock et al. [2008]) and realistic freshwater discharge from all rivers in the model domain (provided by the Norwegian Water Resources and Energy Directorate, see Beldring et al. [2003]). The time-varying arrays from the ROMS model had a temporal resolution of two hours and contained horizontal current fields and hydrographic variables covering a total area of 880 × 850 grid points, giving a total model area of approximately 704 km × 680 km. More technical details on the ROMS simulation can be found in Albretsen et al. (2011). To validate the ocean model, we compared its physical output variables (salinity and temperature) with hydrographical data routinely sampled within the model domain. Overall, the model compared well with observations, with no significant biases in predicted salinity or temperature, equivalent to former and more comprehensive validation analysis of the same modelling system shown in e.g. Myksvoll *et al.* (2014).

Field sampling and statistical analyses

Every year since 1919, with a few exceptions during WWII, there has been an annual collection of half-year-old juvenile cod along the Norwegian Skagerrak coast using a standardised beach seine-sampling regime. Average catches vary substantially among years in this survey, and there is considerable spatial variation in abundance both within and between years at the ca. 135 stations sampled today. To be able to directly compare the modelled distribution of settlement from the northern North Sea with the abundance of the half-year-old cod sampled in nursery habitat in September, we projected both of the geo-located spatial abundances onto a new axis running parallel to the southern Norwegian coast, corresponding to the horizontal axis of the ocean model (rotated ≈45° relative to true north), binned into 800 m intervals corresponding to the resolution of the model. Prior to a correlation test, we applied a mild smoother to the spatial abundance projected on the new axis, effectively averaging the 800 m bins that had several observations between each grid point, and giving the grid points along the new axis with no sampling coverage an interpolated value. We thus imposed a spatial autocorrelation on the raw data; however this is already a common feature in the data set, with significant spatial auto-correlation out to more than 30 km (Rogers et al. 2014). Note that cod found along the Skagerrak coast belongs to at least two genetic groups where one is similar to the North Sea cod and dominates the outer parts of the coast, while the Norwegian coastal cod is more prevalent in more sheltered locations (Knutsen et al. 2011). Thus to validate the origin of the half-year-old cod collected by beach seine along the Norwegian coast in 2011 (i.e. North Sea-like or coastal cod), a total of 815 individuals from 11 locations were scored for genetic origin, identified by 26 single nucleotide polymorphisms unique to either the North Sea or Norwegian coastal cod. Because genetic assignment of individuals only had two possible outcomes applying this method and that origin-estimates from larger beach seine hauls (up to 800 individuals per haul) were sub-samples of what was actually caught, we deemed the Wilson interval as appropriate for estimating the confidence interval of the true proportions present in the area (Brown et al. 2001). To compare recruitment level on the Norwegian Skagerrak coast with recruitment in southern Skagerrak, we used the data from the ICES IBTS for the third quarter. This sampling cruise is done in autumn and is designed (among many things) to survey the abundance of half-year-old cod in the North Sea and southern Skagerrak. We thus tested for a correlation between mean yearly abundance per trawling hour in the Skagerrak division of the IBTS with the mean annual abundance in beach seine hauls along the Norwegian Skagerrak coast, which had a temporal overlap of 21 years, from 1992 to 2013.

The environmental variables analysed in this study were collected along a regular transect with ten fixed, nearly equidistant stations running across Skagerrak, between Torungen (Norway) and Hirtshals (Denmark). The variables collected were: salinity, temperature, chlorophyll, nitrogen, phosphorous, and oxygen; all measured at 0, 5, 10, 20, and 50 m. These measurements have been taken approximately once a month from 1988 until 2012. Coarsely we can divide the sampling stations into three groups based on what water mass they are sampling: (1) the stations closest to the Danish coast sample the water coming from the southern North Sea, high in nutrients and with a noticeable freshwater content coming from the major rivers of continental Europe; (2) the stations in mid Skagerrak has a thin layer of fresher water on top with a mixed origin but mostly samples the Skagerrak mid and deep waters, which is similar to the water found in the northern North Sea; and (3) the stations closest to the Norwegian coast usually samples the Norwegian coastal water and the coastal current, with a high influence of freshwater from the Baltic and the major Norwegian rivers running out in Skagerrak (Kristiansen & Aas 2015). To get an overview of the primary modes of variability of the sampled physical environment in the period winter to early summer (i.e. encompassing the period from spawning to settlement), we did a principal component analyses on the physical variables. To give each of the variables equal weight in the analyses, we did a Hellinger transformation of the raw data (i.e. the data was standardised and square-root transformed). Additionally, to get a more detailed overview of how the temperature in 2011 developed compared to the normal the past three decades, we fitted a generalised additive mixed model (GAMM) to the ≈monthly measured temperature at 20 m, at the ten stations across Skagerrak; as this is the closest depth segment sampled that the cod larvae are usually found (e.g. Munk 2014). A random intercept was also included in the temperature model, allowing the yearly intercept at each station to vary according to normal distribution (i.e. a random intercept mixed model). Moreover, to evaluate the impact temperature in the littoral zone may have on recruitment, which is the primary nursery habitat for cod along the Norwegian Skagerrak coast; we also measured temperatures daily at 1 m, from 2009 to 2012. These temperature measurements were done at two different locations, in the Flødevigen bay, just inshore of Torungen, and in Drøbak situated in the mid-Oslofjord (roughly 175 km apart). To quantify the anomalies in summer temperature, we fitted a GAMM to the daily mean temperature, also here allowing the yearly intercept at each location to vary according to the normal distribution.

Approximately one nautical mile offshore from Torungen (at the second sampling station of the hydrography transect 58°23'N 8°49'W, see figure 1) we collected zooplankton samples bimonthly, from January 2011 to December 2012. Zooplankton sampling was done by vertical hauls with a WP2 net (180 µm mesh, 0.25 m^2 mouth opening), from 50 m to the surface. The zooplankton vertical hauls were thus sampling the coastal water and coastal current for the most part, and a small part of the deeper Skagerrak water. Samples were preserved in 4% borax buffered formaldehyde-seawater solution for species identification and enumeration. To determine the contribution of the single-most important food item (i.e. *Calanus spp.*) to the biomass of the zooplankton samples, we multiplied developmental stage counts with stage-specific weight estimates from the literature (Heath et al. 2000). Note that for the early developmental stages of *Calanus spp.*, from nauplii to stage IV, *C. finmarchicus* and *C. helgolandicus* were pooled together. And although *C. finmarchicus* is frequently cited as the most preferred species for cod larvae, traditionally there appears to have been put little effort into distinguishing *C. finmarchicus* from sister species *C. helgolandicus* (Heath & Lough 2007)–but for most practical comparisons they are identical, where for example differences in size and mass of lipid storage is more variable among geographical populations within the species' range than between the two species (Wilson et al. 2015). *C. finmarchicus* and *C. helgolandicus* (stages V, VI female and VI male) were identified into species based on the shape and teeth of the basipod of the fifth swimming leg (Marshall & Orr 1955, Fleminger & Hulseman 1977). Species of *Pseudocalanus* spp. and *Paracalanus* spp. were treated as one group (Paracalanus/Pseudocalanus).

Results

Oceanographic conditions

The physical conditions in the pelagic habitat experienced by eggs and larval stages, sampled across Skagerrak throughout winter and spring, showed little deviance from the typical pattern since 1988. This can be deduced from the principal components analysis where observations in 2011 does not occupy a distinct area in the diagram but are distributed more or less evenly around the average measurement (i.e. the centre of the diagram). However, there were a few measurements of unusually high oxygen and chlorophyll concentrations in the Norwegian coastal water in February 2011, along with colder temperatures than normal (Fig. 2A). On closer inspection, this low temperature in the Norwegian coastal water in February 2011 was not sustained for long, but the cold bliss could be measured in all depths down to 20 m. However, this mid-water-mass warmed up unusually fast this year, and ended up being warmer than normal in the subsequent summer (Fig. 2B, C). Temperature in the littoral zone in late spring, summer, and autumn however, did not deviate from the normal since 2009, neither in the measurements taken inshore of Torungen nor in the Oslofjord (Fig. 2D).

Drift, settlement and recruitment

Of all pelagic juveniles produced in the model domain 1.3% and 1.6% spent their “settlement window” in Norwegian Skagerrak coast nursery habitat in the 2011 and 2012 spawning seasons. However, 4.6% and 5.5% of all the modelled pelagic juveniles spent at least one of their settlement days in Norwegian Skagerrak nursery habitat, whereas 7.4% and 9.5% of all the individual propagules (integrated over all pelagic stages) spent at least one day in Norwegian Skagerrak nursery habitat; these percentages being for 2011 and 2012 respectively. In both years the bulk of the modelled settlement was distributed west of the

Oslofjord, yielding few settlers to the Hvaler archipelago and leaving the Oslofjord almost devoid of North Sea import. There was a clear regional maximum in modelled settlement within and outside the Grenlandfjords and Kragerø area in both years. In 2011 three lesser maxima were found outside Arendal, Kristiansand, and Mandal. In 2012, there were two lesser maxima, found south of Arendal and outside Mandal. The majority of larvae settling along the Norwegian Skagerrak coast in 2011 were spawned either west of the Viking bank, over the Ling bank, the Fisher banks, or north of Skagen. In 2012, the major sources of settling larvae were similar to 2011, although with a larger supply coming from north of Skagen, reflecting the high number of eggs released there that year (Fig. 3). Comparing the alongshore distribution of modelled settlement with alongshore spatial abundance of half-year-old cod in beach seine hauls, there was a significant positive correlation in 2011 ($r = 0.4$, $t = 7.95$, $p<0.001$). In 2012 however, there was no correlation between modelled settlement and observed abundance ($r = 0.1$, $t = 1.66$, $p = 0.09$). The highest relative difference in modelled settlement to observed abundance in autumn was found within and outside the Grenlandfjords in both years (large peak at $xi \approx 400$ in Fig. 4A, B). Moreover, of the 815 half-year-old cod screened for genetic origin in the 2011 beach seine hauls, 86% were classified as North Sea-like, in distinction to Norwegian coastal cod. There was no large-scale geographical trend in prevalence of North Sea genotype juveniles, besides a slightly lower percentage in the samples taken inside the Oslofjord. However, this was also the region with the lowest sample sizes screened for genetic origin (as reflected in the wide interval estimates for the proportions), as well as having the lowest abundance of juveniles in beach seine hauls. The highest densities of juvenile cod were found in the Kristiansand area, and here North Sea originating juveniles dominated (Fig. 4A). The annual mean abundance of half-year-old cod found in the Skagerrak division of the IBTS in autumn was significantly correlated with the mean abundance of half-year-old cod found in the annual beach seine survey along the

Norwegian Skagerrak coast ($r = 0.42$, $t = 2.1$, $df = 21$, $p < 0.05$, see figure 4C for average yearly abundance in the two nursery areas).

Copepod phenology and biomass

The phenology of our selected copepod species assemblage started with a peak in calanoid nauplii abundance on the 28th of February 2011 (87 552 ind/m^2), coinciding with the modelled end of the yolk sac stage of the earliest hatched larvae that year (i.e. upon reaching ≈ 5 mm). Further into the 2011-season the subsequent peaks of the later developmental stages of *Calanus spp.* closely followed the development of the cod larvae. The peak abundance of *Calanus spp.* copepodites was sampled on the 9th of June (3712 ind/m^2), which coincided with the start of the settlement period, as 23% of the total number of settlement days spent in the nursery habitat had already accumulated at this point. Afterfter the settlement period was over in 2011 (i.e. when all modelled juveniles had grown past 50 mm), there was a high abundance of *Oithona sp.* and Paracalanus/Pseudocalanus (87 552 ind/m^2 and 79 626 ind/m^2) present in the zooplankton of (Figure 5A). Despite the low numerical abundance of *Calanus spp.* copepodites compared to the higher numbers of *Oithona sp.* and Paracalanus/Pseudocalanus, *Calanus spp.* contribution to the overall biomass of the zooplankton outweighed all the other zooplankton species during spring and early summer of 2011; and of the two congeners *C. helgolandicus* and *C. finmarchicus* the latter was by far the dominant contributor to the overall biomass of the zooplankton (Figure 5B). In spring 2012 the succession of the zooplankton was more sporadic, and no peak in favoured food items coincided with the modelled settlement period. However, on 27th of August and 19th of September, both dates well beyond the settlement period in 2012, we found the highest abundance of Paracalanus/Pseudocalanus and *Oithona sp.* in the two-year zooplankton sampling record of 120 832 ind/m^2 and 119 296 ind/m^2 (Figure 5A).

Discussion

Here we presented a case study that covered all the relevant aspects of the drift, development, settlement, and food availability of North Sea and Skagerrak cod larvae during the most recent good year of recruitment (2011). We compared the oceanic conditions in Skagerrak in the winter and spring of 2011 with the normal the past three decades and found few systematic deviations. Neither was the temperature in the littoral zone in summer significantly different from the normal of the past decade. The modelled onshore drift of North Sea originating pelagic juveniles to the coast was also remarkably consistent between years. However, one thing that stood out in our analysis was the phenology of the important prey copepod species in 2011, where especially the succession of the developmental stages of *Calanus spp.* was close to the theoretical optimum for cod larvae. At a first glance, our data thus lends support to the notion that availability of food to larvae determines year class strength of cod in coastal Skagerrak, in distinction to physical variables as for example temperature and drifting routes. In the following sections we will try to generalise our findings to further capsulate the driving forces for recruitment of North Sea cod in Skagerrak nursery grounds.

Inter-annual consistency in drift and settlement patterns

The large scale flow pattern of water masses between the northern North Sea and Skagerrak is highly robust among years, and has been relatively unchanged since the beginning of the "modern" observational record, i.e. since the 1950s. We do note that there are alternative flow patterns, but these have been relatively uncommon the past decades because of the contemporary state of the North Atlantic Oscillation (Winther & Johannessen 2006, Hjøllo et al. 2009, Mathis et al. 2015). In detail, the majority of the upper water masses flowing through the North Sea and Skagerrak during spring is advected from the North Sea over the open northern boundary between Shetland and the Viking bank (Hjøllo et al. 2009), and the inflowing Atlantic water is extremely stable in temperature, ranging from 7 °C in February to 9 °C at end of May (Furnes et al. 1986). The usual wind direction over the North Sea in spring is westerly (i.e. wind coming from between south-southwest and north-northwest, Heath et al. 1999), which means that by Ekman drift the upper water masses of the northern North Sea is advected along the Norwegian trench and subsequently into Skagerrak (Furnes 1980, Furnes et al. 1986). Along the south-western slopes of the trench elevated densities of newly spawned cod eggs are found, released by the high densities of cod congregating along the slopes of the Trench (Fox et al. 2008). Most likely this happens over a fixed season every year with peaks of very little inter-annual variability, which is common for cod in these waters (Cushing 1990, Brander 1994). When entering the Skagerrak, this egg-enriched northern North Sea water mass gets wedged between the westwards flowing Norwegian coastal current and the intermittent West-Jutland coastal current. In the convergence zone of these three water masses a more or less continuous front is sustained, traversing almost the entire Skagerrak. Within this front high concentrations of cod larvae of all sizes is a typical feature in spring and early summer (Munk 2007, 2014). Although this front is present year-round, the half-life of the water masses contained within it is quite short. This is because of the intense mixing of the northern North Sea water with the fresher German bight water and the Baltic outflow. The resulting water mass of intermediate density created by this mixing subsequently has to float out of Skagerrak, and does so in a counter clock-wise motion, piling up along the Norwegian Skagerrak coast (Gustafsson & Stigebrandt 1996). Concurrent with the results from our dispersal model, field studies suggest that high abundances of drifting larvae are still present in the continuum of the frontal water mass flowing along the Norwegian Skagerrak coast (Munk et al. 1995, 1999). Furthermore, beach seine hauls performed throughout spring and summer along the Norwegian Skagerrak coast suggest a consistent settlement period between May to August, peaking in June with a similar magnitude among years (Johannessen *et al.* 2014), a time frame that is identical with our modelled settlement period. In light of earlier population genetic studies on larvae and juvenile cod Skagerrak (Knutsen et al. 2004, 2011, Øresland & Andre 2008), and given the high densities of mature cod found along the Norwegian Trench the past decade (Engelhard et al. 2014, Holmes 2014), we can thus safely conclude that a large portion of the North Sea originating juveniles repeatedly found in the Skagerrak nursery grounds follow the drift route sketched out above. However, we can also from the first part of our discussion agree that a high number of cod larvae drifting into Skagerrak from the North Sea is probably not an uncommon phenomena that in itself guarantee a great year for recruitment, since both years modelled here had almost equal import of North Sea settlers, but yielded very different year class strength.

In both of the years we ran the biophysical model there was a distinct maximum in predicted settlement outside the Grenlandfjords not reflected in the observed recruitment in that area, followed by minor peaks further down the coast. We note that ichtyoplankton surveys done in spring/summer in the Skagerrak have identified a high abundance of cod larvae outside the Grenlandfjords, with a minor peak further south (Munk et al. 1995, 1999). However, the high level of modelled settlement here may also be an artefact from the model. More specifically, in the deep gorge pointing into the Grenlandfjords, topographic steering of the coastal current onto the coast could be overrepresented compared to areas with smaller gorges actually present along the coast not represented well in the model. On the other hand, this may also be the kind of macro scale topographic structures that induces settlement by disrupting the continuity in flow of the coastal current, effectively creating pockets of retention. The Grenlandfjords have also been an area along the Norwegian Skagerrak coast that have historically had consistently high recruitment, but saw collapse in the 80s most likely due to changes in the zooplankton community as response to eutrophication

(Johannessen & Sollie 1994, Johannessen et al. 2012). Thus, although the settlement patterns predicted by our biophysical dispersal model compared fairly well with field observations, the relatively coarse resolution of our model compared to the detailed topography of the coast could bias the results.

Is there a critical period for cod larvae in Skagerrak?

In light of the acclaimed critical period hypothesis that we set out to test, where the theory suggest that year class strength of cod is determined in the period immediately following the time of first feeding–how does this compare with what we observed in the Skagerrak? As was discussed in the introduction a major difference to nursery habitat in more northern latitudes compared to southern nursery grounds may be the challenges related to metabolic activity and food availability during pelagic juvenile stage. The rationale was that as the phenology of the zooplankton usually ‘matures’ earlier and faster in the south, reducing the chance for larval cod to capitalise on their most favoured food item (i.e. *C. finmarchicus*)–and at the same time the higher temperatures increases the chance of starvation if the right food is lacking. To further ground our hypothesis we will briefly review the feeding ecology of cod larvae and the challenges they face in the first few months of development. When cod larvae are small several food items can fill the “feeding niche” that is mainly constrained by availability and the gape size of the larvae (i.e. the max size of prey a larva can ingest), whereas when the cod larvae grow larger they prefer the later stages of *C. finmarchicus* (Economou 1991, Munk 1997, Heath & Lough 2007). The first pelagic juveniles of the season observed along the Norwegian Skagerrak coast usually arrive in late April at a mean size of ≈ 3 cm (Johannessen *et al.* 2014), which compares well with our modelled progression of the settlement period, starting at 17th in 2011 and 14th of April in 2012. Now, the diet of newly settled larvae/juveniles smaller than 3 cm is exclusively pelagic; at 3 cm 75% is pelagic prey; at 5 cm

50% is still pelagic prey; but at 7 cm the transition to benthic feeding is almost total (Bastrikin et al. 2014). And as shown by Johannessen et al. (2014), the presence of *Calanus ssp.* during that early benthic phase makes a huge difference in condition and survival of the settled juveniles in Skagerrak nursing grounds. In our zooplankton record we observed a peak in biomass of *Calanus ssp.* and peak abundance of *C. finmarchicus* copepodites at the start of settlement period of 2011; this in contrast to the settlement period of 2012 when much lower biomass of preferred prey was found. Knowing that the energetic requirement of newly settled juveniles most likely skyrocket as response to the increasing summer temperatures in the littoral zone (estimated to 7.8°C, 12.7°C, 16.4°C, and 18.5°C from May through August when temperature peaks), we can safely argue that any variability in food availability during this period can prove fatal, as may have been the case in 2012 when few of the preferred *Calanus ssp.* copepodites were present. Thus, in the period from settlement until at least reaching ≈ 5 cm, when a sustainable range of benthic prey start being eatable/available to the settlers (Demain et al. 2011, Bastrikin et al. 2014), acquiring the proper pelagic prey is crucial. But at the same time, the abundance of *C. finmarchicus* in these waters usually peak in April and thus a deviation from the normal is needed for adequate availability to the recently settled cod in this critical period. A displacement in *C. finmarchicus* peak abundance can for example be caused by variability in environmental factors such as primary productivity or predation (Head et al. 2000), as well as more stochastic effects as for example advection (Aksnes et al. 1989, Salvanes et al. 1995). However, the most parsimonious explanation for the delayed peak in *C. finmarchicus* biomass in 2011 may be the lower than normal temperatures observed in the coastal water in winter and spring, given the mechanistic relationship that exists between water temperature and the phenology of *C. finmarchicus* (Kvile et al. 2014).

To conclude, our findings suggest that there indeed is a critical period that could determine year class strength of cod in Skagerrak. 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. It appears most probable that what determines the fate of the cod year class in Skagerrak, as in Lofoten, is that *missing factor*. However, in the case of Skagerrak nursing grounds, the *critical period* is not the start of larval development but at the end.

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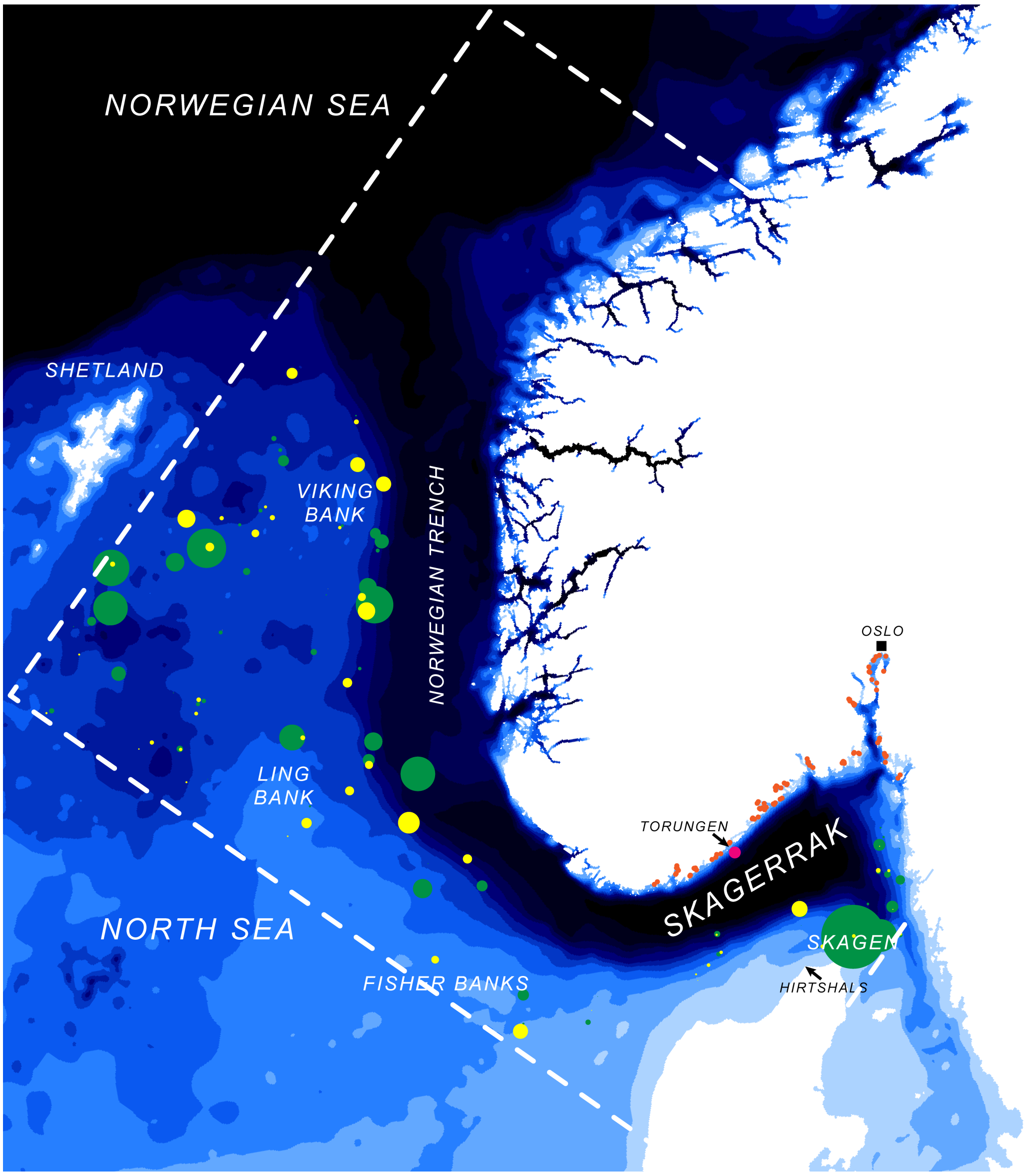

Figure 1. Bathymetry of Skagerrak and the North Sea. Yellow and green circles represent the spatial distribution and estimated egg production in 2011 and 2012, extrapolated from the ICES IBTS survey. Orange circles represent beach seine sampling locations for half-year-old cod in autumn, and the purple circle just south-east of Torungen represents the zooplankton sampling station.

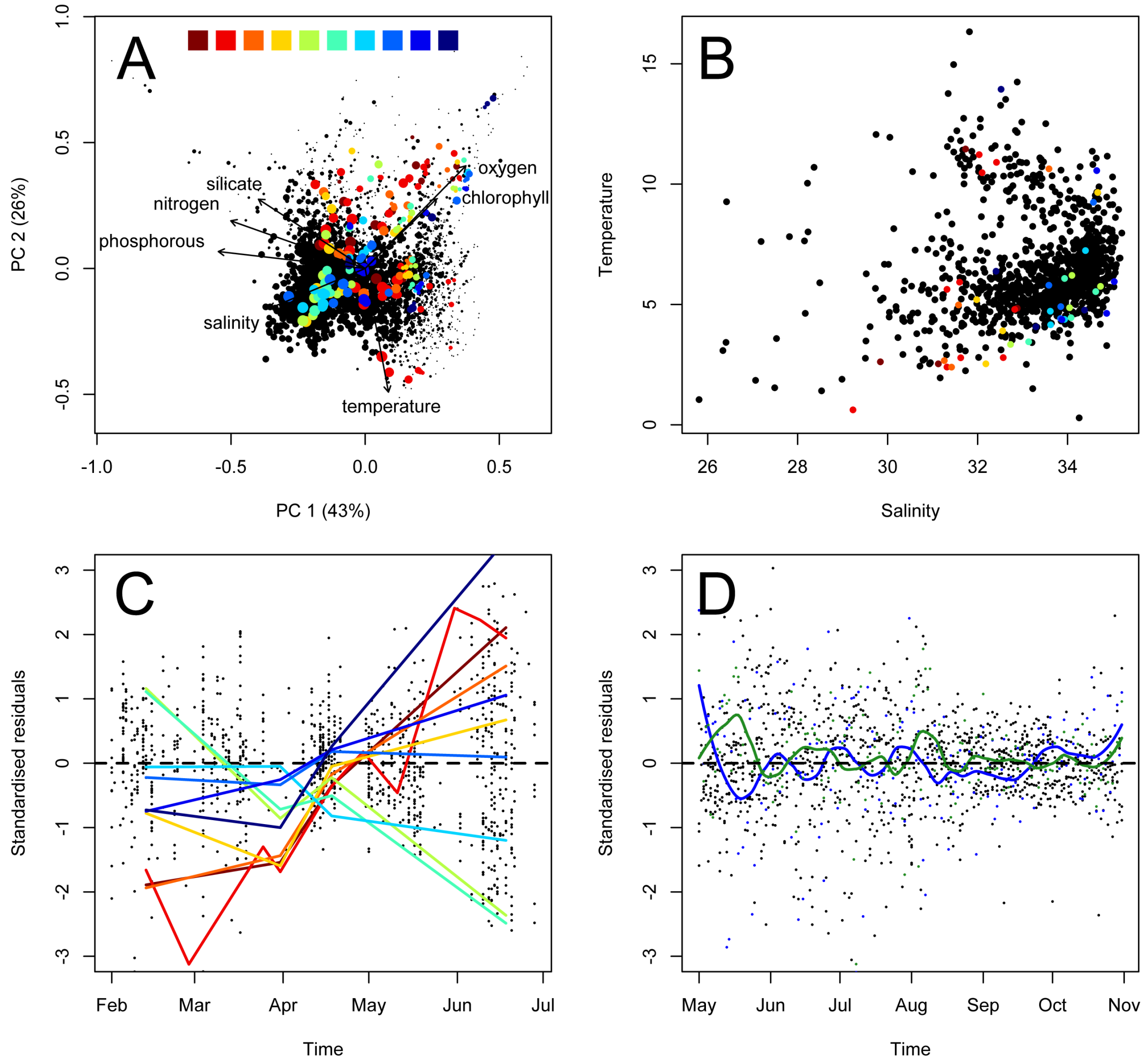

Figure 2. (A) Principal components analyses on environmental variables sampled bimonthly between February and May in years from 1988 to 2013 across the Torungen-Hirtshals transect. Highlighted in colours are the samples from spring 2011, where the sequence of coloured squares in the inset represents the geographical sequence of stations across the transect. Here red parts of the colour spectre represent samples from Norwegian coastal waters, greens the Skagerrak/northern North Sea water, and blues the southern North Sea water. (B) Physical characteristics of water masses sampled at 20 m across the transect, sampled between February and June. (C and D) Anomalies in temperature in the pelagic (20 m) and littoral zone (1 m), scaled to unit standard deviations. Colours in panel C represents

the same stations as in panel A. Green and blue points and lines in panel D are measurements taken in Flødevigen and mid Oslofjord in 2011, respectively.

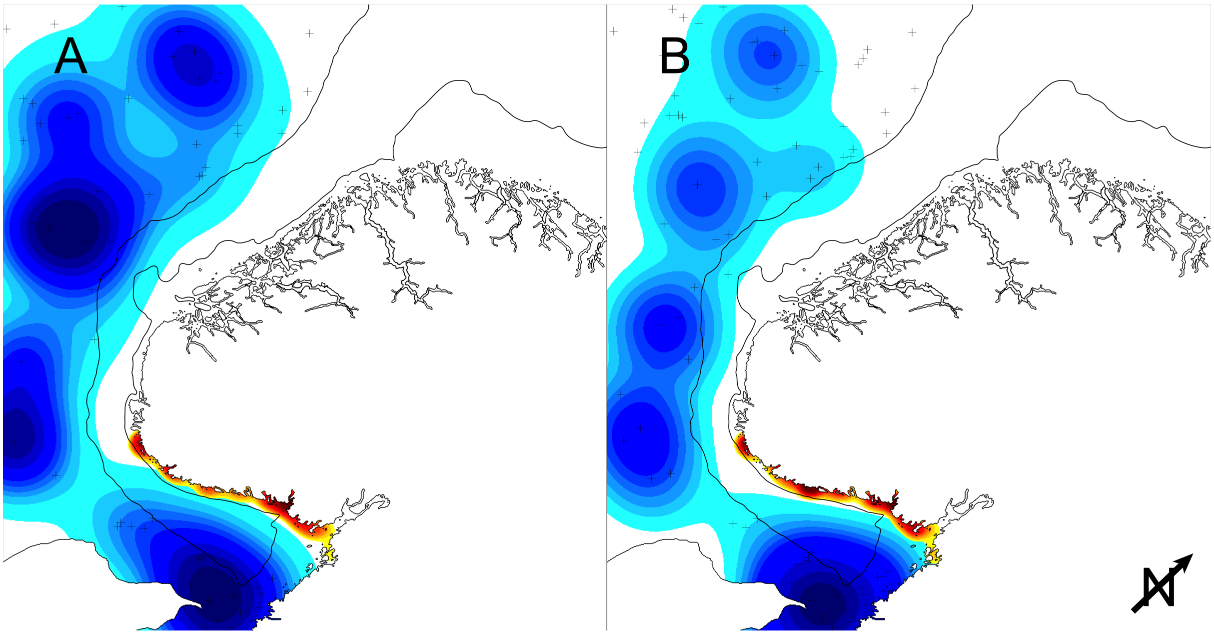

Figure 3. Density distributions of pelagic juvenile settlement days spent in Norwegian Skagerrak nursery habitat (warm colours) and starting positions of individual particle trajectories spending settlement days in Norwegian Skagerrak nursery habitat in 2011 (A) and 2012 (B).

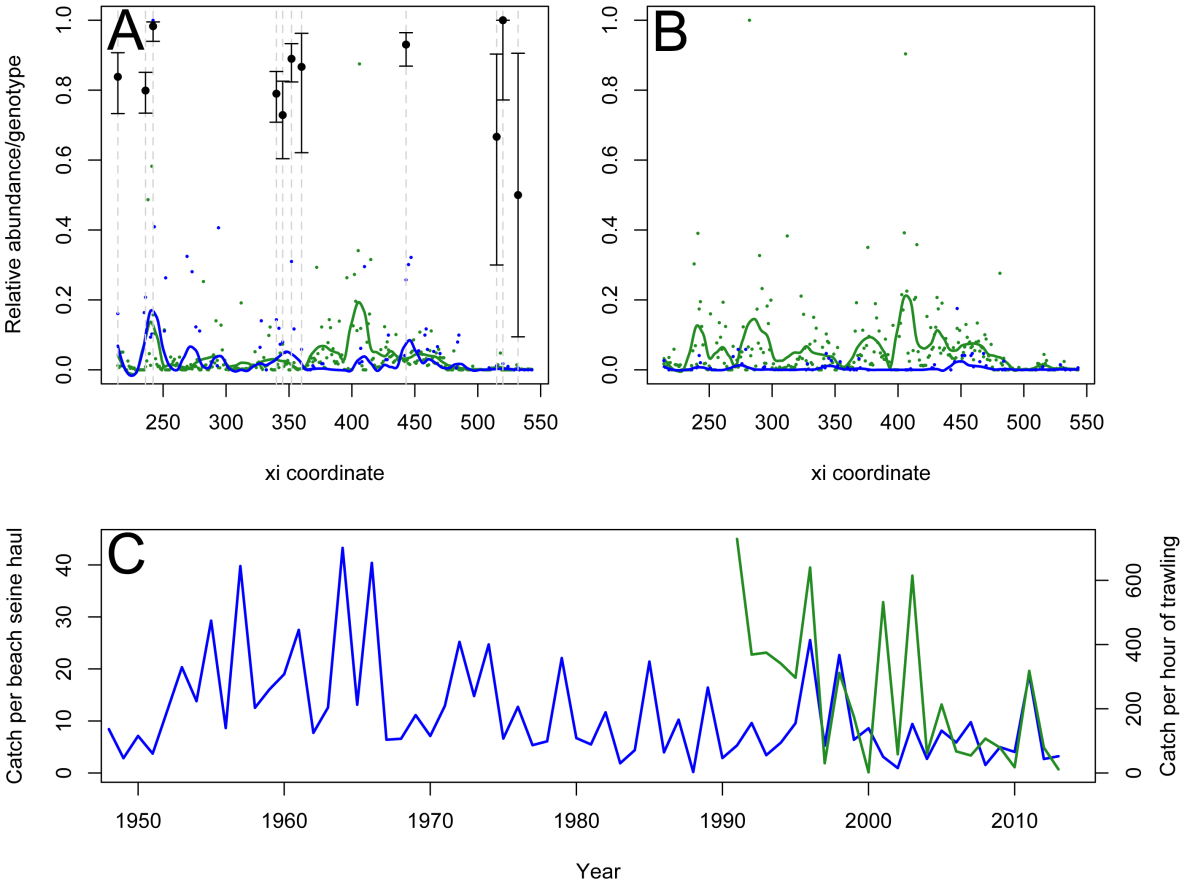

Figure 4. One-dimensional representation of the modelled settlement of pelagic juveniles on the Norwegian Skagerrak coast (green circles and smoothed lines), compared to sampled densities of half-year-old cod in beach seine hauls (blue circles and smoothed lines) of 2011 (A) and 2012 (B). The black circles and confidence intervals in panel A refers to the proportion of individuals sampled at a particular location of North Sea origin. (C) Average abundance of half-year-old cod caught in the annual beach seine survey along the Norwegian Skagerrak coast (blue line) and average number of half-year-old cod caught per hour of trawling in the Skagerrak division of the international bottom trawl survey (green line).

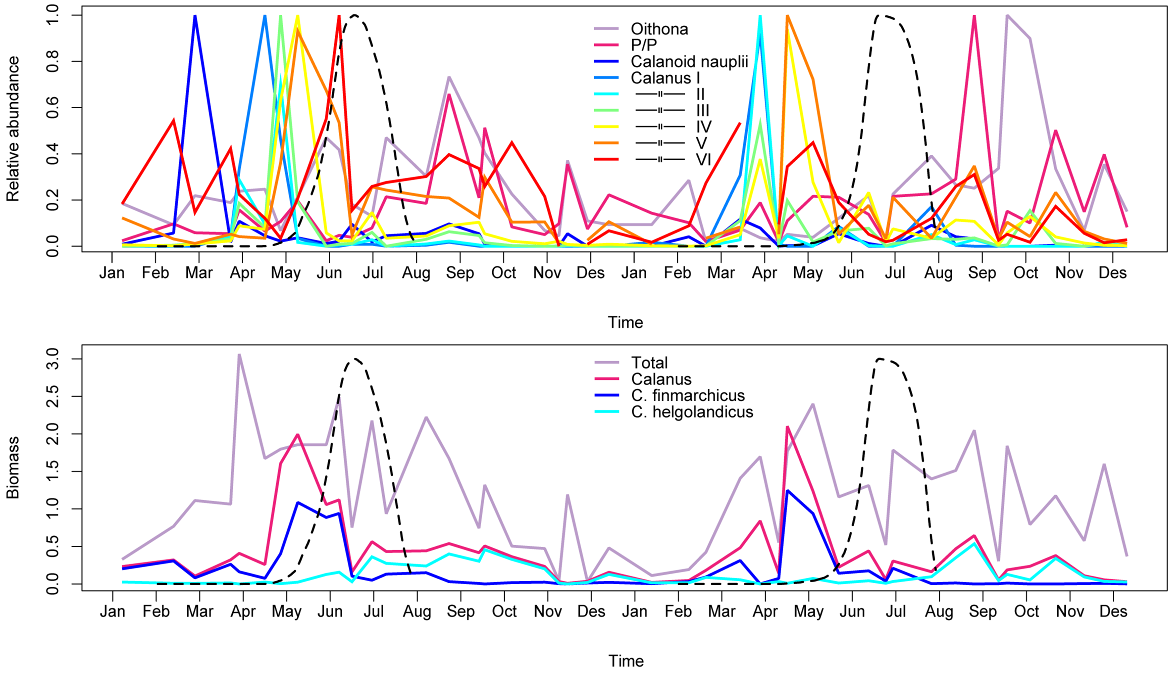

Figure 5. (A) Relative abundance of the three most favoured copepod species/groups throughout pelagic and early settlement stage of cod larvae, scaled by the peak abundance of each species/stage (see text for peak abundances), and modelled development of settlement phase (i.e. when larvae where between 25 mm and 49 mm, stapled curves). Note that all the developmental stages of *Calanus spp.* are represented, from nauplii to adults. (B) Total biomass of zooplankton samples and calculated total biomass of *Calanus spp* (integrated over all stages). Note that in biomass estimates only stages CV and CVI was separated down to species level between *C. finmarchicus* and *C. helgolandicus*.

Dynamics of coastal dispersal

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Abstract. The majority of the world's fished populations should be fished less to reduce the risk of depletion, and a widespread solution to safeguard against unsustainable harvesting is the use of marine reserves as management tools. In the coastal seascape of Skagerrak, a small branch of the North Sea, the local stock of Atlantic cod (*Gadus morhua*) suffer from unsustainable harvesting levels, where more than half of all deaths are fishing related. Genetic- as well as conventional tagging studies suggest that cod found in Skagerrak fjords constitute unique populations, with high proportions completing their entire life cycle within the boundaries of or in near proximity to the fjords. The current management regime does not account for the structured nature of the stock, and unique populations are thus at risk of local extinction, as already has occurred along the Swedish west coast. As spawning location is hypothesised to be the prime stock separating mechanism for coastal cod populations, the primary aim of this study was to delimit the hydrodynamical containment units that match the scale of the sub-stock structure in these waters. To address this question, we simulated ocean currents in the Skagerrak and the adjacent fjords using an ocean model with sufficiently high resolution, and by Lagrangian model drift experiments we quantified cod egg dispersal from all known Skagerrak spawning grounds. Our results suggest that the potential for egg retention within individual fjords is high, with low connectivity among fjords, as well as negligible import of eggs from more oceanic spawning areas into fjords. Our findings on the connectivity of the fjord cod stock are discussed in the context of the design of a provisional network of marine reserves.

Introduction

Over-exploitation characterise many marine populations in the world where more than 60% of the world's fished stocks should be fished less to reverse or avoid previous or on-going collapses (Worm et al. 2009). A proposed solution to safeguard against unsustainable harvesting, while at the same time replenish fished populations, is the use of no-take marine reserves as management tools (Gell & Roberts 2003, Fenberg et al. 2012, Baskett & Barnett 2015). The immediate observable positive effect of a marine reserve is higher densities of adults and juveniles within protected areas leading to a net dispersal from reserves to fished areas (termed "spillover"). For example, spillover from a spiny lobster (*Palinurus elephas*) reserve in the Baleares outside the Spanish coast sustained high catch rates 1.5 km into surrounding fishing grounds (Goñi et al. 2006). Despite closing 32% of the local fishing grounds, spiny lobster catches increased with over 10% within the management unit (Goñi et al. 2010). A second effect of a spatial fishing ban is the increased production and subsequent export of pelagic larvae from reserves (termed "recruitment effect"). Perhaps the best example where the recruitment effect has been observed in the wild was from protected reefs around the Keppel Islands in the Great Barrier Reef National park. Here 28% of reef area in the archipelago was protected by a network of reserves, and 83% and 55% of recruits of coral trout (*Plectropomus maculatus*) and stripey snapper (*Lutjanus carponotatus*) found in surrounding fished areas originated from the reserve network by larval dispersal (Harrison et al. 2012). Also, outside a 40 km^2 reserve in southern Africa abundance of sea bream (*Chrysoblephus laticeps*) doubled in the fished region surrounding the reserve, –an increase mainly credited to larval dispersal from the reserve (Kerwath et al. 2013).

In the Scandinavian coastal zone there is substantial harvest pressure on marine fish populations, exerting high levels of mortality which is likely to have played an important role in the collapse or even extinction of local populations of Atlantic cod (*Gadus morhua*) along the Skagerrak coast (Svedäng & Bardon 2003, Cardinale & Svedäng 2004). Although the cod fisheries of Skagerrak are all subject to restrictions, they are in practice 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% (Kleiven et al. 2016). Pilot studies testing marine reserves as management tools in Skagerrak have been performed on the Swedish coast since 1983 (Øresland & Ulmestrand 2013), and along the Norwegian coast a network of experimental partially protected areas (PPAs) has been in place since 2006 (Pettersen et al. 2009). Based on data collected before, and in four subsequent years after establishment of three experimental PPAs, size and densities of cod within the areas increased through the effect of banning all standing gear (Moland et al. 2013). Further studies on the effect of various protection schemes on cod, from partial to full protection through various gear restrictions indicated an additive-like response between the ban of specific gear types, which generally are associated with different user groups, and fishing mortality (Fernandez-Chacon et al. 2016). Besides the generally intense fishing pressure, a further complicating factor to the management of the coastal cod population in the 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 or 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 overfishing can be seen along the Swedish Skagerrak coast, where most local coastal cod populations have been wiped out, but with scattered recruitment in areas where local populations have somehow persisted (Svedäng & Svenson 2006). Even further increasing the biocomplexity of the stock is the large scale annual import of recruits from the

North Sea to Skagerrak through the anti-cyclonic North Sea-Skagerrak circulation cell (Otto et al. 1990, Knutsen et al. 2004, Stenseth et al. 2006). And in contrast to the local fjord populations, that complete their life cycle within the same fjord they were once spawned, at least parts of the North Sea originating recruits leave their coastal nursing grounds upon reaching maturity. It is likely that a homing mechanism allow them to return to spawn where they once were spawned, for example off northern Jutland or further west into the North Sea (Svedäng et al. 2007).

To prevent further depletion, or even extinction, of unique cod populations in the Skagerrak, the complex stock structure must be considered carefully in management planning. Considering the documented effect of PPAs in reducing mortality of cod, and the need to conserve the spatial heterogeneity in biocomplexity of the stock, a coastal-wide zoning network seems like the most parsimonious solution for conservation and restoration. Now, although a low connectivity among the fjord cod populations have been deduced from conventional tagging studies and the presence of a genetic population structure has been revealed, there is still a substantial knowledge gap on connectivity of eggs and larvae over ecological time, where stochastic processes are expected to dominate (Siegel et al. 2008). Under the overarching hypothesis that spawning location is the prime stock separating mechanism of cod in Skagerrak coastal waters (Svedäng et al. 2007), the primary focus in this study was to delimit the hydrodynamic containment units of pelagic eggs and larvae that match the scale of the sub-stock structure. For this purpose, we simulated the ocean currents of Skagerrak and its fjords over two consecutive spawning seasons using a state-of-the art ocean model, and by Lagrangian drift experiments we addressed the role of ocean/fjord physics in cod egg dispersal. Subsequently, based on the modelled flow of the upper water masses, we aimed to: (1) objectively delimit tentative spatial management units to fjord cod sub-populations; and (2) evaluate the significance of the identified spatial management units to the dispersal of eggs spawned within the management units. Finally, we discuss our findings on the connectivity of the fjord cod populations in the context of design of a provisional network of marine reserves.

Materials and methods

To validate the ocean model, we compared its physical output variables (salinity and temperature) with hydrographical data routinely collected (bi-monthly) in the Skagerrak or within adjacent fjords. In the absence of in situ current measurements and a direct validation of the dynamical properties of the model, we compared the density from the modelled and observed hydrographical profiles. As density variations is the main driver for currents in the Skagerrak and water exchanges with the fjords, validation of the modelled density field is a valuable tool for assessing the model performance. Since there was considerable variation in modelled physical attributes even on an hourly scale, a generalised additive model (GAM) was fitted to 24 'in silico' CTD profiles sampled (one per hour of the day) at the same day as the given field sample was done. A random intercept term was added to the GAMs (Wood 2006) giving the fitted models a favourable property: pick any random moment on the given day and with 95% probability the CTD profile would lie within the confidence interval of the GAMM. A total of 54 comparisons were made, distributed over 16 fixed stations (A-P in Fig. 1). Additionally, for stations E-P, hydrographical profiles were available going back to 1952, and for these stations the residuals between modelled and observed values were standardised by the long term standard deviation at the given station and depth. The circulation model used was the Regional Ocean Modelling System (ROMS, http://myroms.org), a free-surface, hydrostatic, primitive equation ocean model (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). Due to computational limitations, and to provide proper resolution of Skagerrak fjords, the bulk of Skagerrak was modelled within an 800-meter horizontal grid whereas coastal regions were forced separately within a 160-meter grid, all applying the results from the 800m-model along their open boundaries. A final 160-meter grid covering the entire Skagerrak was then established after the model simulation, where first the results from the 800-meter model was interpolated down to the large 160-meter grid, and subsequently the

160-meter sub-models were overlaid these results. The merged arrays of velocity fields and physical variables of Skagerrak thus covered a total area of 2552 × 1551 grid points (giving a total model area of approximately 408 km × 248 km), in 35 depth layers, and with a temporal resolution of one hour. The circulation model was forced over a time period of 2 × 70 days (from February 1st to May 1st) for two consecutive years (2011 and 2012), using daily averages of currents and hydrography along the open boundaries from a large-scale model covering the Nordic Seas (Lien et al. 2014), high-resolution wind fields (Weather Research and Forecasting model, WRF, using 3km horizontal resolution, see Skamarock et al. [2008]) and realistic freshwater discharge from all rivers in the model domain (provided by the Norwegian Water Resources and Energy Directorate, see Beldring et al. [2003]).

To identify tentative spatial management units in coastal Skagerrak we applied the INFOMAP algorithm to the connectivity matrix of the surface flow (Rosvall & Bergstrom 2008, Rossi et al. 2014, Ser-Giacomi et al. 2015). In practical terms, the method identifies areas of the surface flow that is well connected internally, and in general is more connected internally than externally with other areas. These spatially delimited units we henceforth refer to as ‘hydrodynamic provinces’, ‘fjord provinces’, or just ‘provinces’. In more detail, our connectivity matrix was a 16.278*16.278 matrix where each row and column of the matrix corresponds to the imports and exports to/from the N^{th} 1.6 km * 1.6 km * 20 m parcel/cube of water, where the grid of 16.278 parcels represents a discretisation of coastal Skagerrak upper water masses. Initially, 500 regularly spaced passive tracers were released within each parcel at each grid point of the model domain at 1 m, 5 m, 10 m, 15 m, and 20 m, yielding a total of 979.202 passive tracers per run (10*10 grid points per parcel * 5 different depths * 16.278 parcels; however, note that most parcels intersecting the coastal land topography would contain fewer particles initially). This procedure was then repeated 10 times for each of the two spawning seasons, where simulations were initiated at the beginning of every week of the simulation period. The integrated number of tracers released in one parcel that ended up within another after all simulations constitutes the weight that is given to two connections in the connectivity matrix. The INFOMAP algorithm then sends out random walkers within the empirically weighted network/connectivity matrix, and each time a 'walker' enters a new node in the network the next node it travels to is decided by the weight of the outgoing connections expressed as probabilities based on the weights in the connectivity matrix. The amount of time spent by a walker within a specific cluster of well-connected parcels is then what decides if it should be a cluster or not. This clustering is independent of scale, and the method stands out as completely objective as no parameters are set by the user to specify the size or number of clusters.

To evaluate the significance of the identified hydrodynamical provinces to cod population structure, we simulated egg drift from all known spawning sites in the Skagerrak based on national egg surveys (Espeland et al. 2013), spawned every 24 hours throughout the simulation period (Fig. 1). Here, the number of particles released from each spawning ground was equal, except the important spawning areas in Topdalsfjord, Tvedestrandfjord, Risørfjord, and inner Oslofjord (Espeland, personal communication), which each were provided double the number of eggs. To quantify the probability of egg leakage from hydrodynamic provinces, we fitted a binomial GAMMs to successes of being retained in a province, accounting for possible non-linear effects of drift/incubation duration, timing of spawning, and the random effect of which hydrodynamical province that eggs were spawned within. Advection of eggs in the horizontal plane was modeled using a fourth-order Runge-Kutta scheme with the velocity field arrays from the ocean model. Moreover, to capture the natural 'behavior' of cod eggs in the water column, an individual based model of vertical movement was included as a sub-routine within the particle-tracking model: at the initiation of each drift simulation, eggs were randomly assigned an individual buoyancy value measured in practical salinity units typical of coastal cod, between 28 and 32 (Ciannelli et al. 2010, Jung et al. 2012). Evaluated at each time step of ten minutes, the density of eggs was then calculated as a function of its pre-set salinity equivalent and its ‘in-silico’ temperature (Coombs et al. 1981). The egg was then pushed either upwards or downwards depending on the hydrostatic pressure acting on it. Egg incubation time was calculated as a function of temperature (Peterson et al. 2004). To account for vertical mixing experienced by eggs, a vertical perturbation component was added at each time step. This mixing coefficient was scaled directly to the wind field that was used to force the model, but at the same time attenuated by depth by exponential decay. If mixed into the transition layer and when situated below the upper mixing layer, a much smaller background-mixing coefficient was used. The mixing layer depth was calculated as the depth where the vertical gradient in water density was highest.

Results

The ROMS ocean model performed well overall when predicting density of water masses, where 90% of all density measurements were within 2 units outside the daily variation of the model. In general, deviations from the measured values were more frequent towards the surface, and the model tended to predict too heavy water in the upper 15 m (Fig. 2A). A large part of this bias could be traced to the comparisons from the coastal margin to the middle of Skagerrak, whereas fjordic comparisons showed little or no bias (Fig. 2B). When comparing the anomalies between observed density profiles and predicted values from the model divided by the long-term standard deviation at a given station and depth (i.e. the standardised residuals), 88% of all comparisons were within 1 standard deviation of the long term observations and 96% of comparisons where within 2 standard deviations (Fig. 2C, D). We note that there was no systematic bias in the ocean model's prediction of temperature, which might have biased the modelled egg incubation times if present.

The INFOMAP algorithm identified 31 hydrodynamic provinces in the surface-layer of Skagerrak fjords. All identified provinces were confined by fjords, in contrast to the single, large oceanic province representing the Skagerrak proper. The provinces identified by the algorithm were constant features between years, as the extent and number of provinces were almost identical in the 2011 and 2012 simulations of the surface flow. A single qualitative difference between the two years was a slight retraction of the extent of the outer Oslofjord province, and a corresponding intrusion of the Skagerrak province into the outer Oslofjord. The coherence ratio of the identified provinces, that is, the proportion of tracers uniformly released within a province that was retained, varied from 0.05 to 0.95, with an average around 0.34 (Fig. 3). Sixteen of the provinces contained one or more registered spawning grounds, while the big oceanic province representing the Skagerrak proper contained 109 spawning grounds. Fifteen of the provinces did not contain any registered spawning areas.

In total, 20% of all simulated cod eggs drifted out of the Skagerrak by means of transportation through the coastal current past the Naze (Lindesnes). The proportion of eggs that drifted out of the Skagerrak, spawned within fjord provinces or along the exposed coast respectively was 0.03 and 0.26. The distributions of the drifting distances were highly skewed, and the median dispersal distances of the two “spawning strategies”, i.e. either spawned in a fjordic province or along the exposed coastline were 2 km and 11 km, respectively (Fig. 4). Displayed in figure 5 is an example of the vertical distribution of eggs spawned from the Topdalsfjord (close to station A in figure 1) every night over one entire simulated spawning season. Moreover, the expected proportion of eggs that leaked from a randomly selected hydrodynamic province with documented spawning activity was 0.23 (95% CI, 0.05-0.63), given the mean incubation period of 24 days and being spawned in the middle of the modelled spawning period. Here, both timing of spawning and incubation period had a significant non-linear effect on probability of drifting out of the province, suggesting that drift duration and timing of spawning could be an important variable to the probability of retention. However, besides the high probability of retention at short drift durations (but note the wide confidence interval at short drift durations) and slightly elevated probabilities of export when spawned late in the season; the overall explanatory power of drift duration and timing of spawning was low, as reflected in the close to zero effect over large portions of the covariate-space (Fig. 6).

The ratio of eggs released from coastal spawning areas to fjord spawning areas (i.e. spawning areas within fjord provinces) were 2.3:1, where 5% of the eggs released in coastal areas were advected into fjord units and 15% of the eggs released in the fjord provinces was exported to coastal units. Oceanic/coastal Skagerrak thus received 39% more eggs than the fjords received from the Skagerrak. From a network perspective, direct connections among fjord provinces were few and only 7.5% of eggs spawned within the 30 fjord units were exchanged among fjord provinces. Here the strongest connection was by far from the inner to the outer Oslofjord, and this connection constituted 5.8% of the fjord released eggs alone, which left 1.5% that exchanged among the other units (Fig. 7). Twelve of the 15 provinces that did not contain any documented spawning grounds naturally acted as pure sinks, although the magnitude of import to these units was generally negligible, together less than 1.4% of total fjord egg production. Three of the 15 non-egg-producing provinces also did not receive any eggs from other provinces and were thus in every respect disconnected from the network. These unconnected provinces were found on the western side of the Oslofjord between Nøtterøy and Tjøme, between Hvasser and Tjøme (i.e. both in the Nøtterøy-Tjøme archipelago associated with the Færder area in the outer Oslofjord), and inside the Drammensfjord (see Fig. 3).

Discussion

The aims of this study was to: (1) delimit the hydrodynamic containment units of cod eggs in Skagerrak fjords; (2) evaluate the significance of our new-found retention zones to cod egg dispersal; (3) discuss the relevance of the hydrodynamic containment units to coastal cod population structure; and ultimately, (4) based on our findings, provide advice for the management of the fjord cod populations in the Skagerrak. Not unexpected, most, if not all Skagerrak fjords stood out as retention zones contrasted to the more open and exposed coastal seascape. In general, there was very low connectivity among the fjord provinces, although a few units had significant connections, for example from the inner to the outer Oslofjord province. In addition, there was very little import of eggs into fjord provinces from the coastal spawning grounds. Our results also suggest a clear difference in dispersal kernels of eggs spawned within the identified fjord provinces compared to coastally spawned eggs. Compared to field data describing the spatial scale of recruitment in these waters, our estimated dispersal kernel for fjord-province-spawned-eggs bears a striking resemblance; Rogers et al. (2014) detected significant spatial autocorrelation in recruitment strength out to a distance of at least 11.6 km (95% CI: 1.8 km – 27.4 km) in "sheltered" areas of the Skagerrak, which compares well with our identified fjord provinces where 80% of eggs spawned within were dispersed less than 12 km.

When synthesising the accumulated body of knowledge on the coastal/fjord cod population structure in Skagerrak with our modelling results, one can conceptually reduce this coastal/fjord cod-complex down to a meta-population model that has the following traits: (1) the stock has finite number of separate sub-populations that has very low immigration/emigration rates (Espeland et al. 2008, Rogers et al. 2014); (2) the probability of "rescue effects" is low due to limited exchange of recruits into- and among the fjord sub-populations; and (3) recruitment (i.e. survival of newly settled juveniles) appears stochastic in

Skagerrak nursery grounds (Fromentin et al. 2001), but that the environmental conditions and ultimately recruitment is correlated across the region due to geographical proximity (Lekve et al. 2002). The meta-population model roughly sketched out above has been thoroughly analysed in the literature, and given a certain set of parameters the outcome is known: if re-colonisation rate is lower than sub-population extinction rate, the only long-term equilibrium of the meta-population as a whole is extinction, and one of the solutions to reduce the risk if extinction is to reduce mortality within the sub-populations (Hanski 1991). In the wild, ecological extinction of several local cod populations has been observed, but we have yet to observe a single re-colonisation (Svedäng & Svenson 2006). Under the current management regime that has a minimum landing size as the only mortality-limiting measure, the annual survival is estimated to around 0.3. By for example removing one of the dominant gear types the survival within the sub-population is expected to increase to ≈0.5, and if all fishing is banned the survival is estimated to increase up towards 0.7 (Fernandez-Chacon et al. 2016, Kleiven et al. 2016). Thus within the identified provinces with existing spawning activity the message is clear: mortality should be lowered to reduce the risk of ecological extinction of sub-populations. On the other hand, within the 15 identified hydrodynamic provinces that had no registered spawning activity there are two options: (1) to fish as usual without compromising any local spawning populations on any dispersed coastal/fjord cod if present, as well as on the incoming North Sea recruits commonly observed along the coast (Knutsen et al. 2004, 2011, Stenseth et al. 2006); or (2) ban all fishing to increase the chance for re-colonisation and/or restoration. However, given the integrity of the hydrodynamic provinces these empty areas are not expected to receive much import from the outside. And because of the uncertain long-term effect of protecting areas without local production (i.e. whether local spawning will resume or not) conservation priority should be given to the identified provinces with local production already present. For the cod that inhabits the outer Oslofjord, our results are dichotomous, as our two years of simulation did not agree on whether it should be within a fjord province or not. The transient state of the outer Oslofjord as both oceanic or fjordic means that there can be one year of high import, while in other years it is more isolated and receives less recruits from outside. However, given the limited replicates of two spawning seasons, further studies should be performed to get an insight into the relative frequencies of these two outcomes, and until then caution should be made in the interpretation of this province. As for the general coastal population, that is, cod that inhabits -and spawns along the open and exposed coastal seascape, the direct effect of conservation is expected to be fuzzier. Our results suggest that the increased production most likely will be distributed over a larger area, and a substantial fraction will even drift out of the Skagerrak by the coastal current. However, due to the higher inherent connectivity of the general coastal stock, it is expected to be less prone to depletion/extinction. We thus suggest that conservation priority should be given to the areas where the risk of extinction is highest, namely within the identified fjord provinces that already has spawning activity.

Words of caution, no reserve is an Island

It is important to remember that processes happening outside a protected area will still affect even the best-designed network of reserves. For example, even the most extensive and well-planned network of marine reserves in the world, the Great Barrier Reef Marine Park, could not safeguard against the damage done to reefs by eutrophication caused by the land based sugar cane industry in Queensland state (Myers & Ambrose 2009). On that note, Johannessen et al. (2012) showed that eutrophication of the Skagerrak's coastal water mass caused a collapse in gadoid recruitment (including cod) in several fjords in the early 2000s by changing the composition of the zooplankton. The single most important food item of Atlantic cod larvae is the copepod *Calanus finmarchicus* (Economou 1991, Heath & Lough

2007), and the fate of larvae and newly settled juveniles is highly intertwined with the population dynamics of *C. finmarchicus* (Rothschild 1998, Sundby 2000, Beaugrand & Kirby 2010). At the fjord scale a self-sustained copepod community can exist to a varying degree (Bucklin et al. 2000), but the presence and persistence of *C. finmarchicus* is largely dependent on extrinsic factors such as exchange of fjord water masses with the costal water mass (Aksnes et al. 1989, Kaartvedt 1993, Salvanes et al. 1995), which again is governed by the variability in the density field of the coastal current (Aure et al. 1997). In short: the right types of zooplankton has to be present in high abundances for a stock recruitment relationship to arise (Olsen et al. 2011), which by all practical considerations is random in Skagerrak coastal waters due to the inherent stochasticity of underlying processes (i.e. advection of zooplankton). Moreover, under the scenario of a warmer future climate we predict the frequency of good years for recruitment of cod to be reduced in Skagerrak. The rationale is that a gradual increase in temperature will most likely speed up the seasonal phenology of *C. finmarchicus* leading to earlier peaks in abundance (Kvile et al. 2014), a peak that is already typically over before cod larvae have time to prey on them in these waters (Øresland & Andre 2008, Melle et al. 2014); in contrast to colder time periods where *C. finmarchicus* has been prolific even in summer at these latitudes (Cushing 1984, Rothschild 1998, Beaugrand et al. 2008). How the effects of a changing climate can be accounted for in management of the Skagerrak cod population is not straightforward, but reducing mortality will certainly increase the demographic width of the stock making it more resilient to environmental fluctuations (Cardinale & Svedäng 2004, Anderson et al. 2008). In a sense, this will allow the cod to realise their life history strategy, namely to endure unfavourable periods of low recruitment by their longevity and capitalise on the occasional good year with their high fecundity (Winemiller & Rose 1992). Thus, a word of caution: a high spawning stock biomass is not a guarantee of strong recruitment; it is only when the conditions are good for growth and survival of larvae (i.e. with the right types of zooplankton present) that strong recruitment can happen. However, the population still have to persist from one good year to the next, and as also was concluded in the previous paragraph, perhaps the only solution to bolster the resilience of the stock is simply to fish less.

Oceanographic sources of bias

Overall our ocean circulation model predicted the density field in the coastal water exceptionally well, with the vast majority of anomalies within one standard deviation of the long-term observations. However, there was a slight bias in predicted densities of upper water column of the coastal water masses. These water masses are of mixed origin, where the majority of freshwater content originates from local rivers along the Skagerrak coast and the Baltic outflow, mixed with the inbound North Sea water in the south-eastern corner of Skagerrak (Gustafsson & Stigebrandt 1996, Aure et al. 1998, Kristiansen & Aas 2015). Freshwater is by far the main defining variable to density in the coastal water, and the most logical source for this bias is not the model itself but the boundary conditions towards the Kattegat. The natural consequence of the model's positive density anomaly in the coastal current is that the eggs have a higher chance of floating towards the surface and being more prone to for example advection by wind. However, because the eggs largely obtain a sub-surface maximum due to the freshwater plume usually present inside the fjords (e.g. see figure 5), the impact of wind driven advection out of the fjords is expected to be small.

Conclusion

In this study, we have reviewed the connectivity of the coastal cod complex in the Skagerrak. As was concluded from our simulations and the subsequent enquiry, there was very low connectivity among the overfished fjord populations putting the relatively isolated and unique fjord sub-populations in high risk of extinction, as have already occurred in Swedish Skagerrak/Kattegat coastal areas. To hedge against further depletion of components in the fragmented stock structure, we recommend the implementation of no-take zones within many of the Skagerrak fjords as the next logical step for management. Through a combination of raised awareness and self-justice that usually comes with the implementation of reserves, the integrity of the stock can hopefully be ensured for future generations where traditional management has proven inadequate–as elegantly put by Agardy (1994): "*Marine protected areas ... provide the sociological anchor for averting the 'tragedy of the commons' and fostering a sense of stewardship for ocean resource and ocean space among the people who most rely on healthy, intact coastal systems*".

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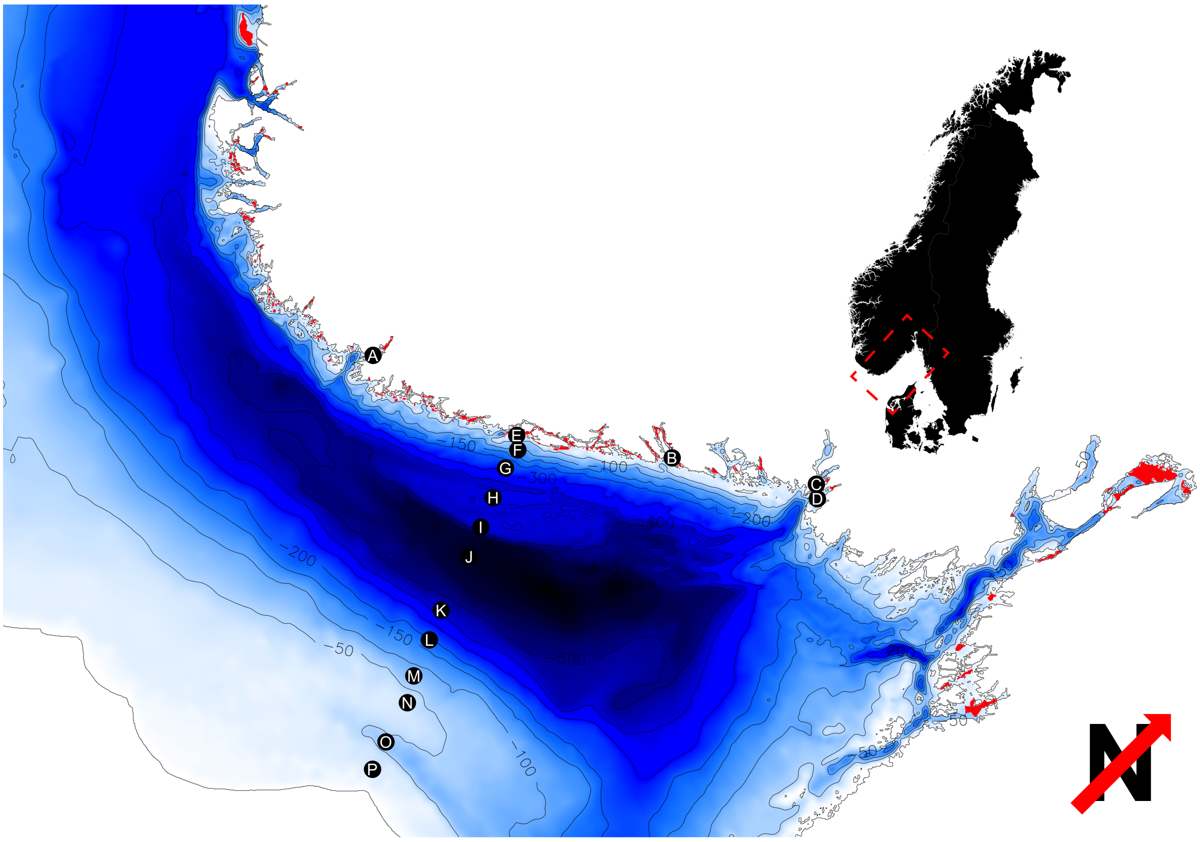


Figure 1. Bathymetry of the study area eqvivalent to the bottom topography of the ocean model. Marked in red are all registered spawning areas of cod along the Norwegian Skagerrak coast. Letters from A-P represents the fixed hydrological sampling stations where ocean model and field observations have been compared. Note that the map is rotated clockwise ≈45° from true north.

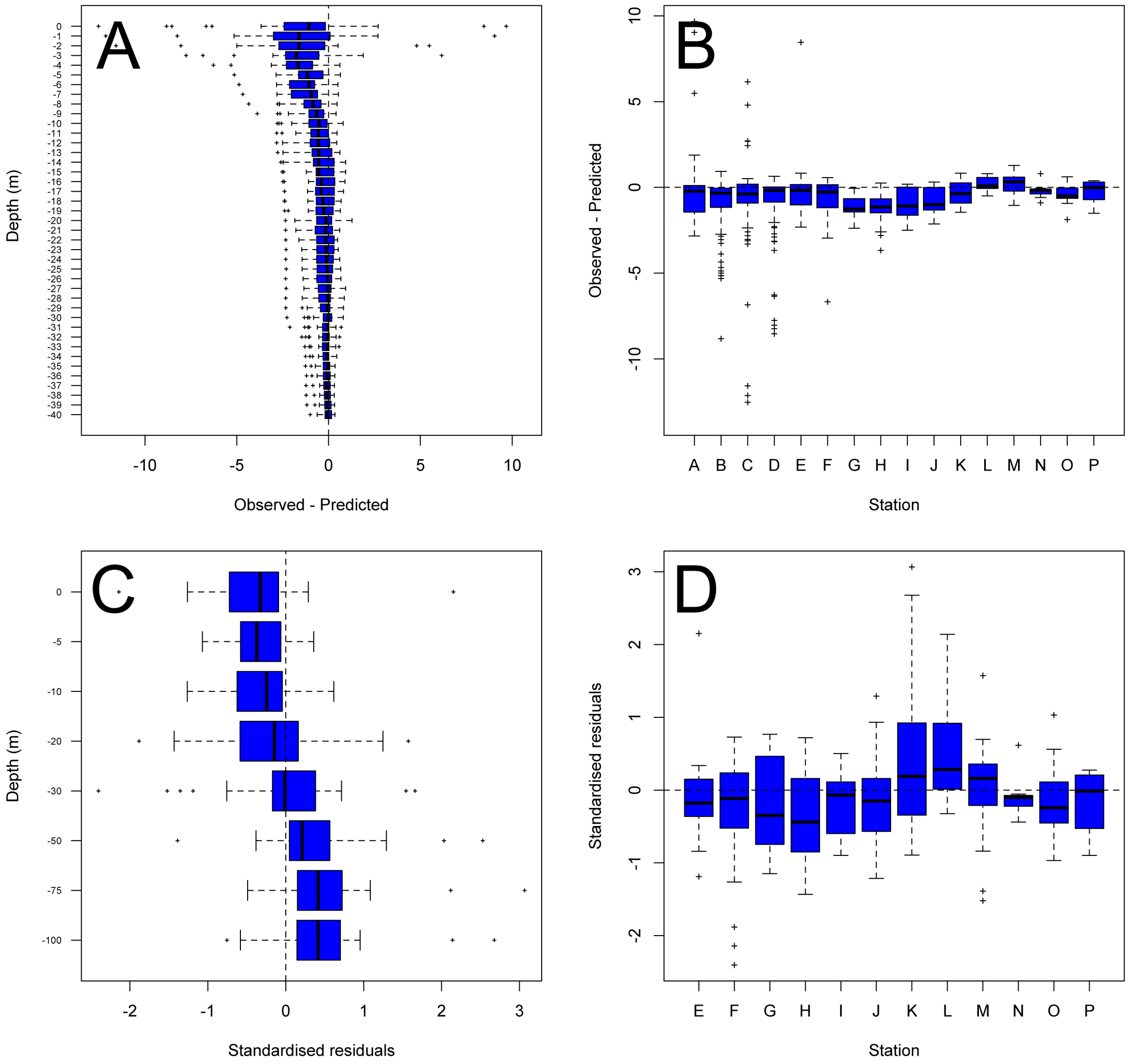


Figure 2. Boxplots of error residuals (observed – predicted vaules) of modelled and field-sampled density in upper water masses; classified by (A) one meter depth intervals, and (B) sampling station (where letters refer to the fixed sampling stations in figure 1). (C and D) Same as A and B but here residuals are divided by the long-term standard deviation at sampling station/depth. Note that fjord sampling sites (station A-D) were not covered by long-term sampling and is thus not included in panel C and D.

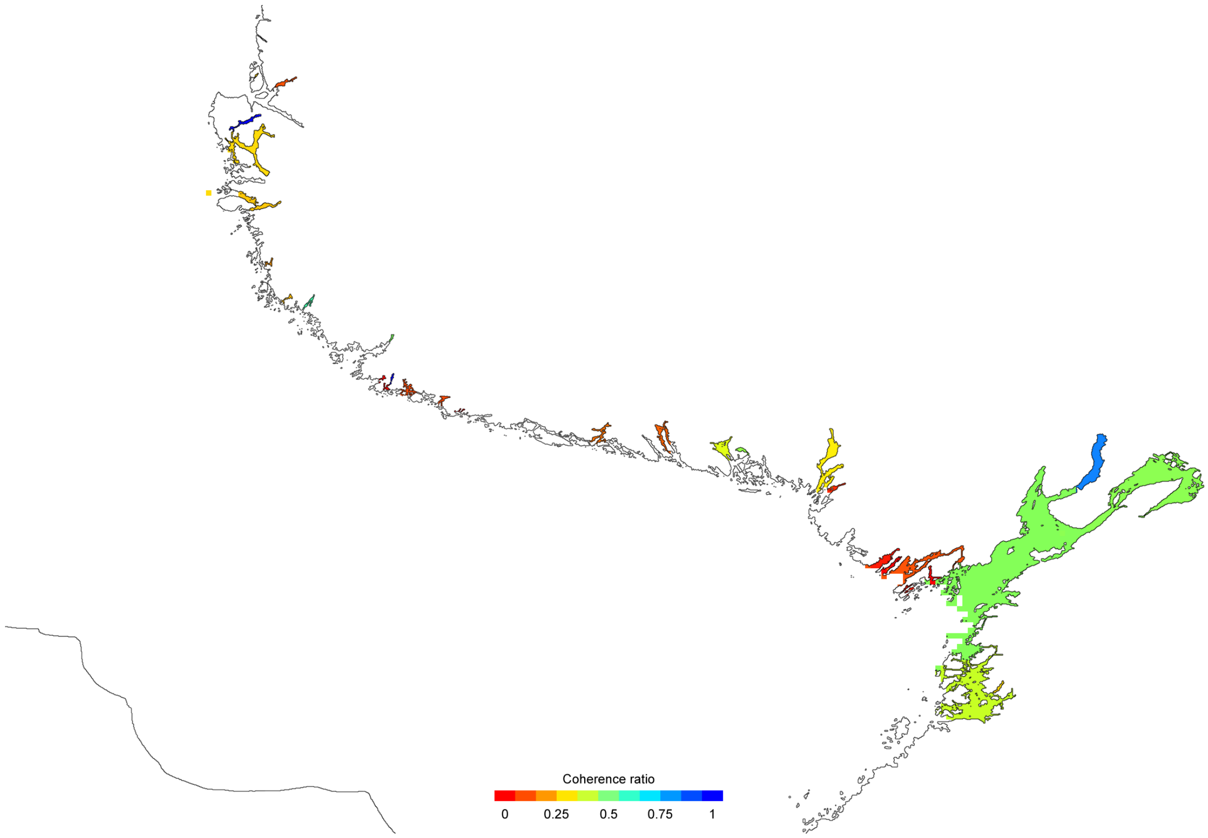
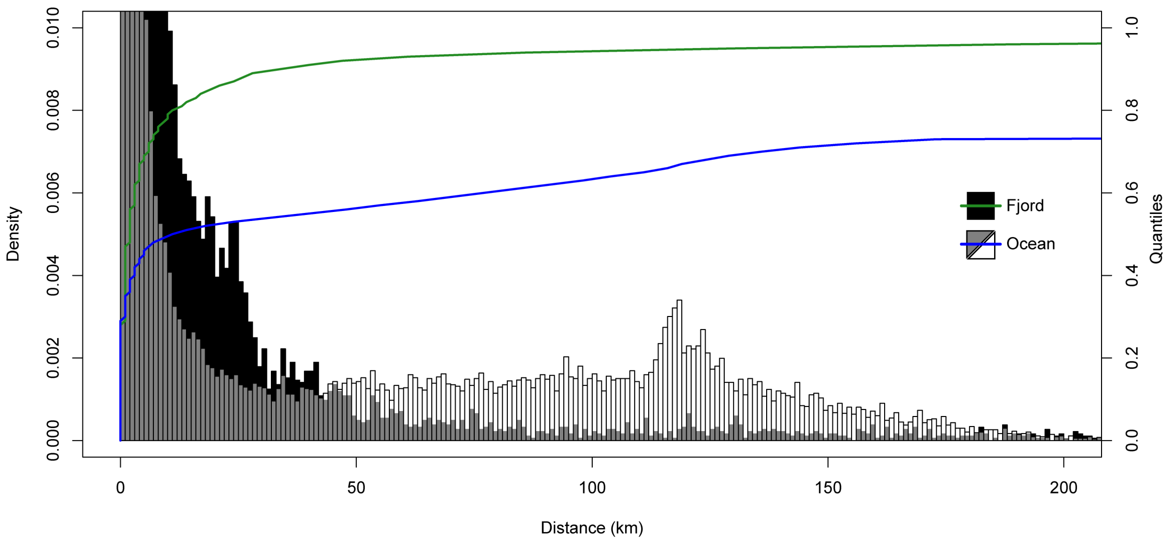


Figure 3. Hydrodynamic provinces identified by the INFOMAP algorithm, based on connectivity patterns in the upper water masses. Colours of provinces refer to the coherence ratio of each province, that is, the proportion of passive tracers initially released that is retained within the province.



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593 Figure 4. Density distribution of egg dispersal distances, spawned either within a fjord
594 province or in coastal spawning grounds (note that the left y-axis is depracitated for clarity).
595 Blue and green lines are the percentiles of egg dispersal distances (e.g. more than ≈90% of the
596 eggs released from fjord provinces drifted less than 25 km, whereas ≈70% of coastally
597 spawned eggs drifted less than 200 km).

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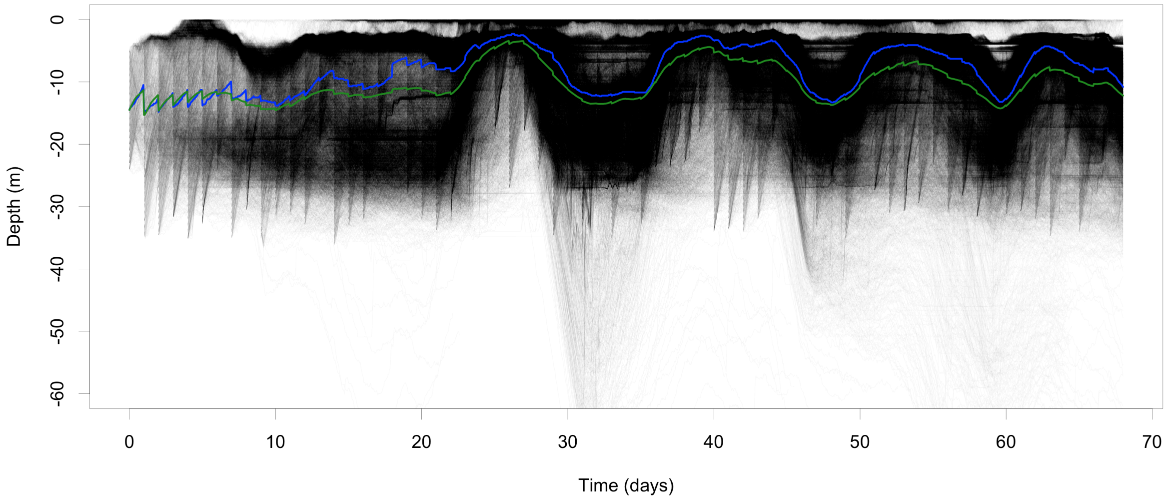

Figure 5. Vertical distribution of eggs spawned in Topdalsfjorden (the fjord marked with "A" in Figure 1) over the entire simulation period. Blue and green lines represents mean and median depth of eggs.

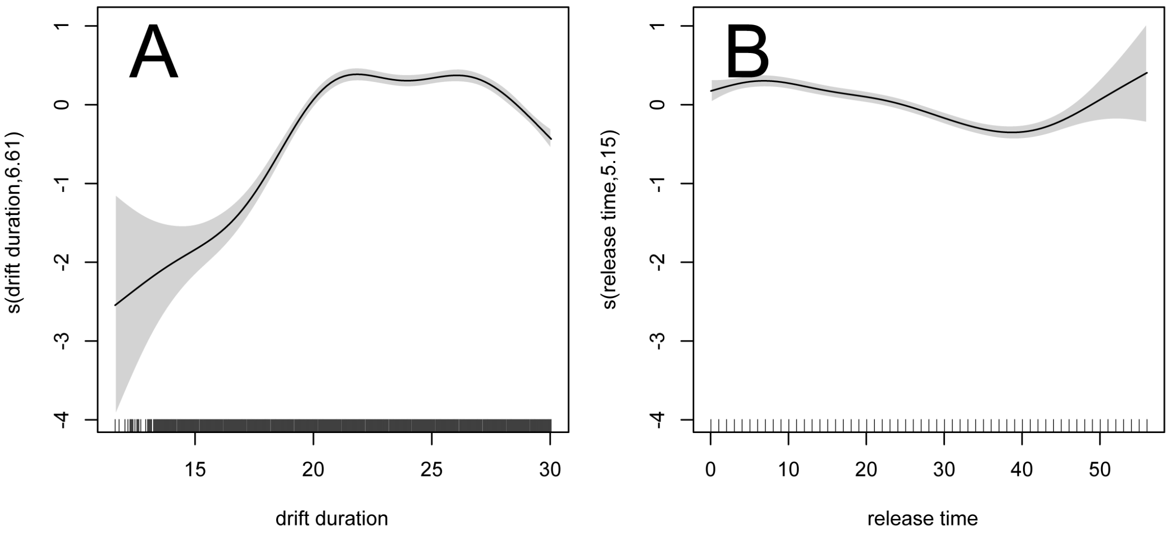

Figure 6. Non-linear effects of drifting/incubation duration (A) and timing of release (B) on estimated retention probability within hydrodynamic provinces (note that the y-axes are on log-odds scale, for probabilities values must be inverse-logit-transformed, which gives the same shape of response but expressed between 0 and 1).

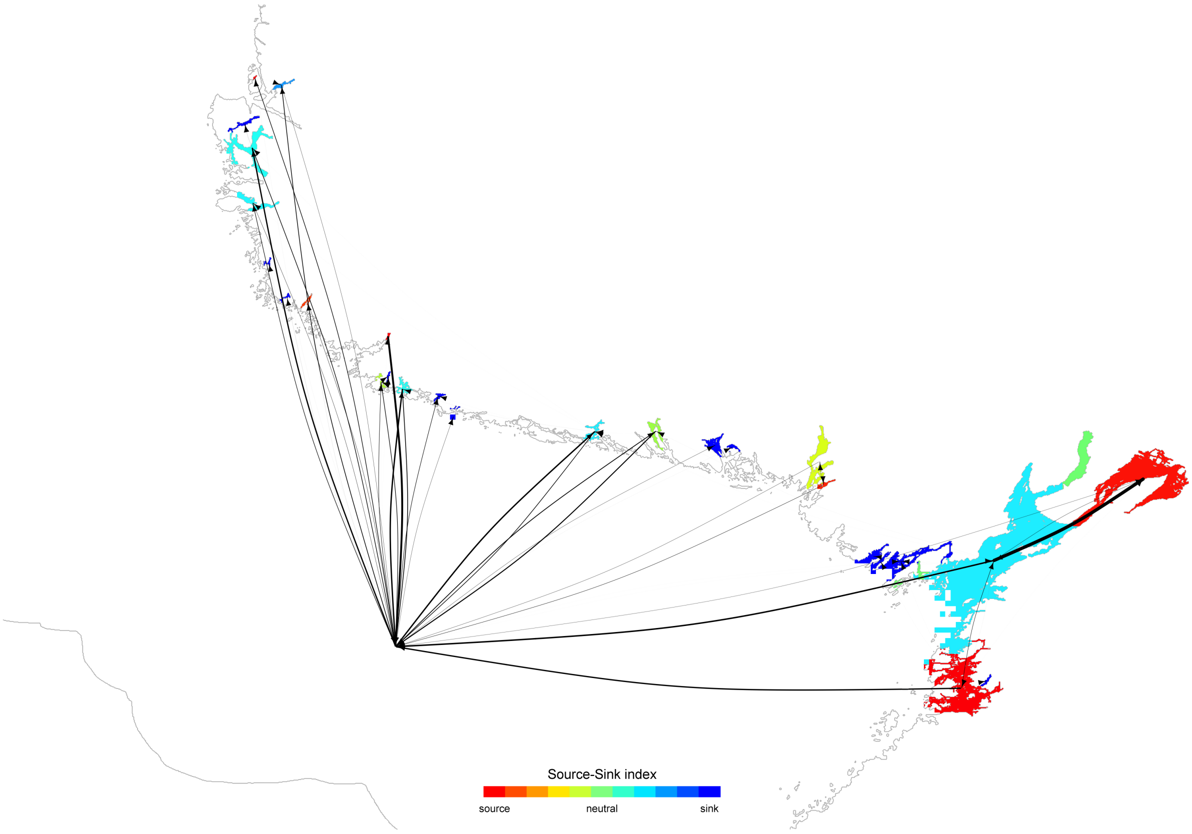

Figure 7. Network graph of the flow of eggs among provisional management units, where width of arrows represents the magnitude of transport. Also, the colour of each hydrodynamic province represent the source-sink index of the province, i.e. (import-export)/(import+export).