

# Cod at drift in the North Sea

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*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 clear 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 north 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

57 circulation pattern of water masses in the North Sea, where several more or less defined  
58 currents effectively divide the North Sea in two. The first division is made by the Fair Isle  
59 current that enters the North Sea between Orkney and Shetland, and this current transports  
60 coastal water originating from west of the British Isles into the North Sea. Its path continues  
61 south past the Scottish coast, and before reaching 57°N it turns east in an anti-clockwise  
62 fashion, while deflecting parts of its mass south along the English coast (in some sources  
63 referred to as the ‘Fulton drift’, e.g. in Franz et al. 1991) and onto the shallower  
64 central/southern North Sea plateau. The second barrier is the East Shetland current, which  
65 transports Atlantic water into the North Sea in a southern direction along the eastern side of  
66 Shetland. Upon reaching 58°N, the East Shetland current also turns east and aligns with the  
67 Fair Isle current in a double-entrainment, and together they form an anti-clockwise gyre over  
68 the Fladen ground. A branch of this double Fair Isle/East Shetland current (together referred  
69 to as the ‘Dooley current’) turns around the Ling bank and into Skagerrak, although with  
70 diminished strength (Svendsen et al. 1991, Turrell et al. 1996). This double barrier not only  
71 splits the North Sea cod stock in two, it also roughly demarcates the southern limit above  
72 which *C. finmarchicus* is usually found in large numbers in spring, while being a rare guest  
73 south of it (Fransz et al. 1991)—and since the cod fishery in the North Sea collapsed in the  
74 time period 1980s-1990s, catches of cod have been steadily high north-east of these currents,  
75 while dismally low to the south (Engelhard et al. 2014, Holmes 2014). Even further  
76 separating the northern and southern North Sea is a an unnamed current traversing the  
77 northern plateau along the diagonal between Shetland and the southern slope of the  
78 Norwegian Trench (hereby referred to as the ‘traverse’ current) transporting relatively cold,  
79 saline water into the Norwegian Trench (Ljøen & Sætre 1987, Svendsen et al. 1991).  
80 Moreover, sweeping along the open northern boundary to the Norwegian Sea and into the  
81 Norwegian Trench (a current referred to as the Continental Slope Jet) we find the main inflow

82 of Atlantic water to the North Sea (Winther & Johannessen 2006, Hjøllø et al. 2009).  
83 However, the majority of this inflowing Atlantic water gets retroflected and eject underneath  
84 the Norwegian coastal current on the eastern side of the Trench before reaching 59°N (Furnes  
85 et al. 1986). Although little is known of how the flow is organised in the conjunction were the  
86 traverse current, the double Fair Isle/East Shetland current, and the Atlantic inflow in the  
87 Norwegian Trench meet, we do know that the outflowing northern North Sea water gets  
88 topographically steered in a south-eastern and eastern direction along the western and  
89 southern slopes of the Norwegian Trench and into the Skagerrak (Furnes et al. 1986). And  
90 here, south of Norway within the more or less permanent front between the westward  
91 propagating, low saline Norwegian coastal current, a continuation of the Baltic current, the  
92 eastward flowing northern North Sea and Atlantic water, and the West-Jutlantic coastal  
93 current carrying coastal water from the southern North Sea, high abundances of cod larvae are  
94 found (Munk 2007, 2014). Now, the origin of these larvae is not known for certain, but peak  
95 abundances are found in water-masses typical of the northern North Sea in terms of salinity  
96 and temperature and also in respect to the assemblage of copepod species present. However,  
97 to date there have been no high-resolution drift studies addressing the dispersal of early  
98 pelagic stages of cod in the highly advective northern North Sea, hence little is known about  
99 the prevalent drift pathways taken by eggs and larvae spawned there, as well as potential  
100 nursery grounds they may settle in. Thus here we aim to: (1) describe the dispersal of pelagic  
101 offspring of cod spawned in the north-eastern North Sea; (2) quantify the potential for  
102 settlement to the various nursing grounds available to pelagic juveniles in drift; and (3)  
103 describe the oceanographic features that gives structure to this complex circulation system.  
104 Given the contemporary north-eastern modal distribution of the North Sea cod SSB, where  
105 most of the mature fish and newly spawned eggs are found along the western slopes of the  
106 Norwegian Trench (Fox et al. 2008), we predict that the eggs spawned in the highly advective

107 northern North Sea have a high dispersal potential. In light of our findings we will round off  
108 with a discussion on the potential reasons why the north-eastern North Sea cod is seemingly  
109 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:  $F = 5.4 \times L^3 - 13000$  (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 2<sup>nd</sup> to May 9<sup>th</sup> (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  $1 \text{ W/m}^2$ , downwards if above the isolume of  $10 \text{ W/m}^2$ , 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  $2 \times 180$  days (from February 1<sup>st</sup> to August 1<sup>st</sup>) 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  $880 \times 850$  grid points, giving a total model area of approximately  $704 \text{ km} \times 680 \text{ km}$  (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,  $\approx 50\%$  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  $\approx 5$  mm) of the larvae in the model was similar in the two years of simulation, in 2011 the mean date was March 29<sup>th</sup> (95%CI: March 2<sup>nd</sup> – April 26<sup>th</sup>), and in 2012 March 28<sup>th</sup> (95%CI: February 28<sup>th</sup> – April 22<sup>nd</sup>). 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 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 less than 0.5 Sv ( $1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$ ) to more than 1.8 Sv, but averaged around 1 Sv. The daily average transport responded

247 significantly to the daily NAO, but had a maximum correlation with the 5-day filtered NAO  
248 ( $\text{cor}_{\text{SV} - \text{NAO } 5} = 0.36$ ,  $p < 0.001$ , Figure 6). In 2012 however, the relationship between the daily  
249 NAO and the northern North Sea outflow was not significant ( $\text{cor}_{\text{SV} - \text{NAO}} = 0.14$ ,  $p = 0.09$ ).  
250 From the temperature vs. salinity profiles systematically sampling the modelled water masses  
251 occupying the Norwegian Trench, it was clear that Atlantic water in its undiluted form (with a  
252 salinity around 35 and temperature of 8-9°C in spring) does not intrude further than the  
253 saddle-point north of transect D, west of Stavanger (Figure 6, and see Figure 1).  
254

## 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, Hjøllø 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

305 overwintering ground of *C. finmarchicus* in the region is situated in the Faroe-Shetland  
306 channel (Heath & Jonasdottir 1999), and the overwintering copepodites' least variable entry  
307 point to the highly productive Norwegian coastal current is through the mouth of the  
308 Norwegian Trench (Gallego et al. 1999, Harms et al. 2000). Here, most of the inflowing, *C.*  
309 *finmarchicus* enriched Atlantic water gets retroflected and eject underneath the Norwegian  
310 coastal current on the eastern side of the channel before 59°N (Heath et al. 1999). This agrees  
311 well with our ocean model, where Atlantic water in its undiluted form did not intrude beyond  
312 the Trench saddle point at  $\approx 58^\circ\text{N}$ , as also pointed out by Furnes et al. (1986). Moreover, after  
313 the brief visit in the Trench mouth, the continuing Continental Slope Jet aligns with the  
314 Norwegian coastal current, and at  $\approx 63^\circ\text{N}$  (outside Svinøy) the highest abundances of *C.*  
315 *finmarchicus* throughout the northern hemisphere is found (Melle et al. 2014). Spawning at a  
316 location that ensures eggs and larvae are being entrained in this *C. finmarchicus* highway of  
317 the Nordic Seas seems to be a successful spawning strategy for the North Sea gadoids. For  
318 example, the main spawning grounds used by the North Sea saithe (*Pollachius virens*) is to  
319 release their eggs over the far northern, deep end of the North Sea/European continental shelf  
320 (Bjørke & Sætre 1994). Most of the saithe eggs and larvae spawned there subsequently follow  
321 the same short-circuit pathway across the Norwegian Trench that we sketched out for the cod  
322 eggs spawned north and east of the Viking bank (see figure 3B). The comparably vast SSB of  
323 North Sea saithe since the 1990s of between 100.000 and 300.000 tonnes bears witness to the  
324 recruitment potential that lies in this spawning strategy, even in the seemingly unfavourable  
325 climatic period since the start of the 90s (ICES 2015). In fact, when looking at catch data of  
326 North Sea cod aggregated into their respective north-eastern and south-western genetic units,  
327 the Viking spawning biomass has remained at its present level for at least 30 years, while the  
328 southern and north-western stocks drastically declined (Holmes 2014). It thus appears that  
329 despite the declining trends in the 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 the projected offset caused by human emission of green house gasses, predictions for the future ocean-climate and ecosystem state across the North Atlantic and Nordic Seas looks grim for the spring spawning gadoids in the North Sea, 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 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 south of Norway 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 a “continuum” of settlement habitat from the Northern North Sea/Skagerrak circulation cell and beyond 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

380 the western Norwegian coast or gets advected further along the Norwegian Sea shelf. We also  
381 showed and discussed how large-scale climatic forcing may enhance the export of eggs and  
382 larvae spawned over the northern North Sea in winters of high NAO, by increasing the flow-  
383 through of the northern North Sea circulation cell. The consequential north and eastern  
384 extension of North Sea cod nursery habitat we consider beneficial to survival of the settling  
385 juveniles, considering the marginalisation of the North Sea as nursery habitat for recently  
386 settled juvenile cod compared to historical conditions. Although the particle-tracking  
387 algorithm had its weaknesses, the main patterns compare well with observations in the wild.  
388 However, further field studies have to be performed to confirm our hypothesis of the north-  
389 eastern extension of the North Sea cod nursery grounds.

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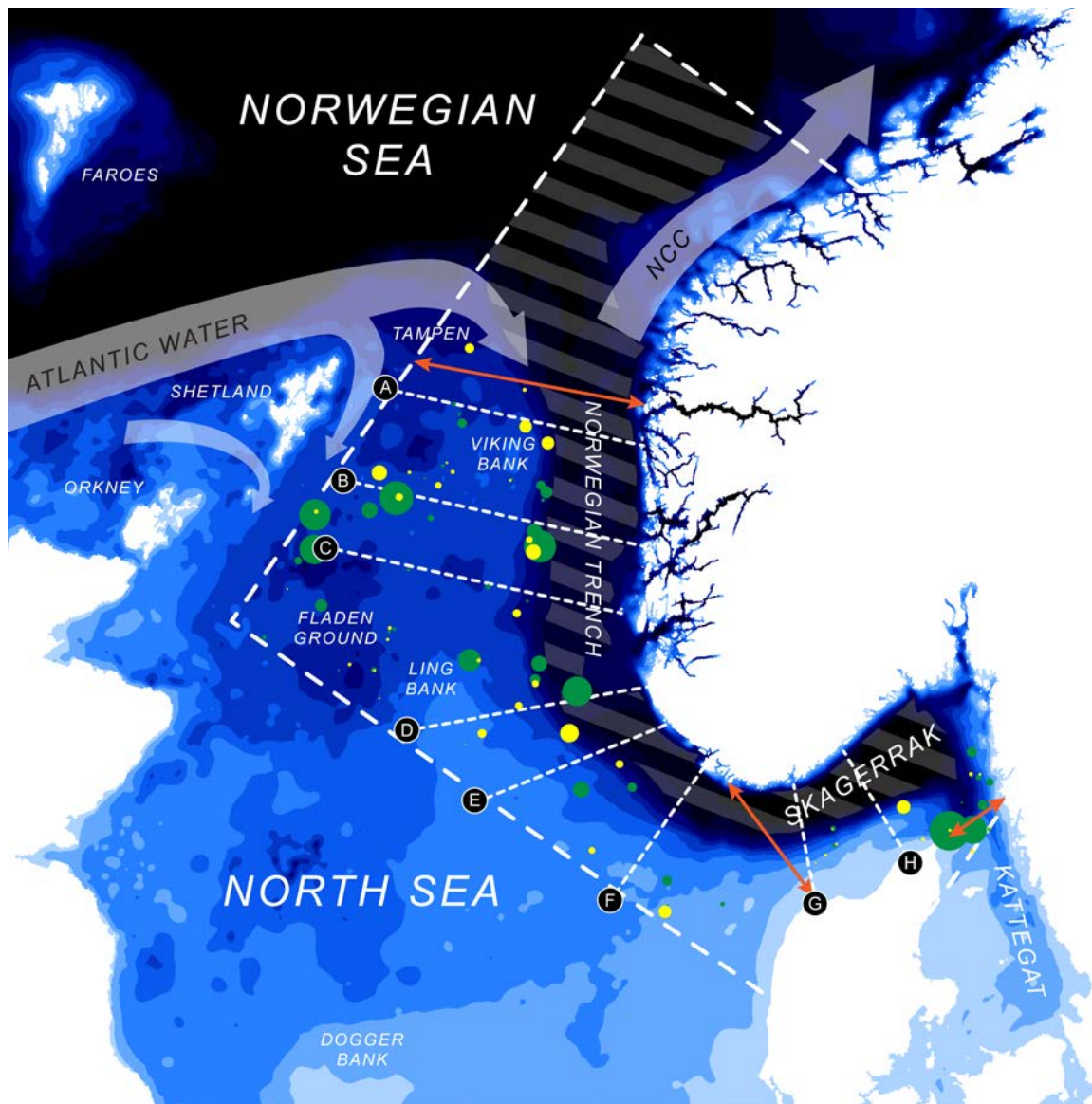
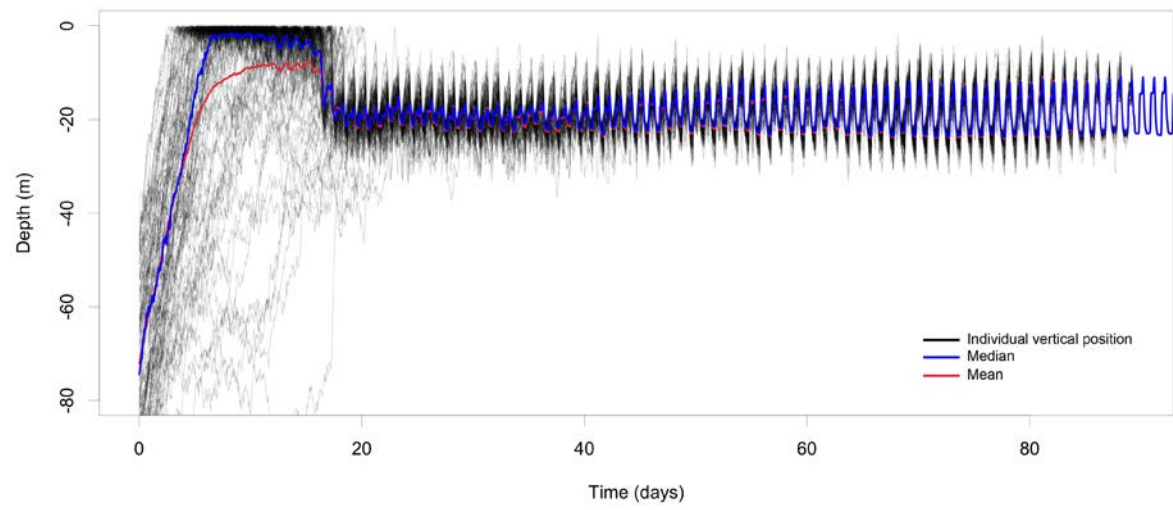


Figure 1. Bathymetry of the study area. White arrows represent the main inflow routes of Atlantic water, and the only outflow of North Sea water masses through the Norwegian coastal current. Yellow and green circles represent the spatial distribution and estimated egg production in 2011 and 2012, extrapolated 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 unsuitable settlement habitat for settling pelagic juveniles. Staped box represents the boundaries of the circulation model.



543

544 Figure 2. Vertical distribution of 100 eggs, larvae, and pelagic juveniles. Blue line represents

545 the median depth, while red represents mean depth.

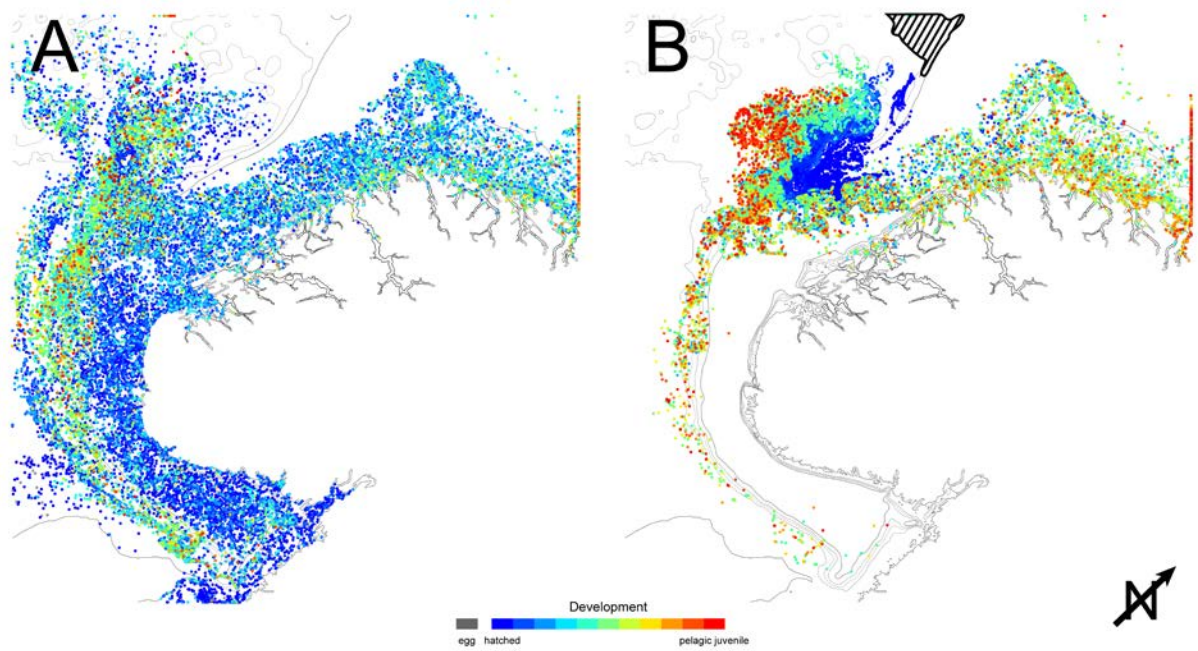


Figure 3. Comparison of flow dynamics of eggs spawned south and north of the Viking bank. Here panel A represents the drift of cod eggs and larvae spawned along the Norwegian Trench as suggested by recent surveys (ICES 2015). For illustrative purposes, panel B represents drift of eggs released over Tampen 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 1<sup>st</sup> 2011 and run until April 22<sup>nd</sup> 2011.

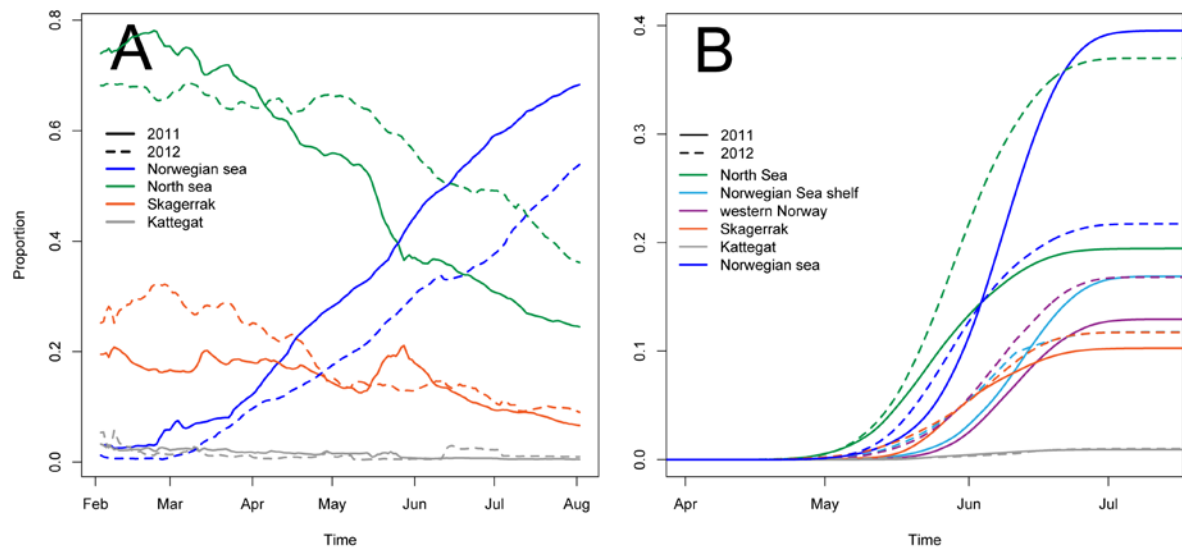


Figure 4 (A) Proportion of eggs and larvae spawned in the northern North Sea and Skagerrak situated in the North Sea, Skagerrak, Kattegat, or Norwegian Sea through the simulation period. (B) Proportion of days spent over the possible nursery habitats within our model domain by larvae ready to settle, between 25 and 35 mm in body size (see spatial distribution of settlement days in figure 5).



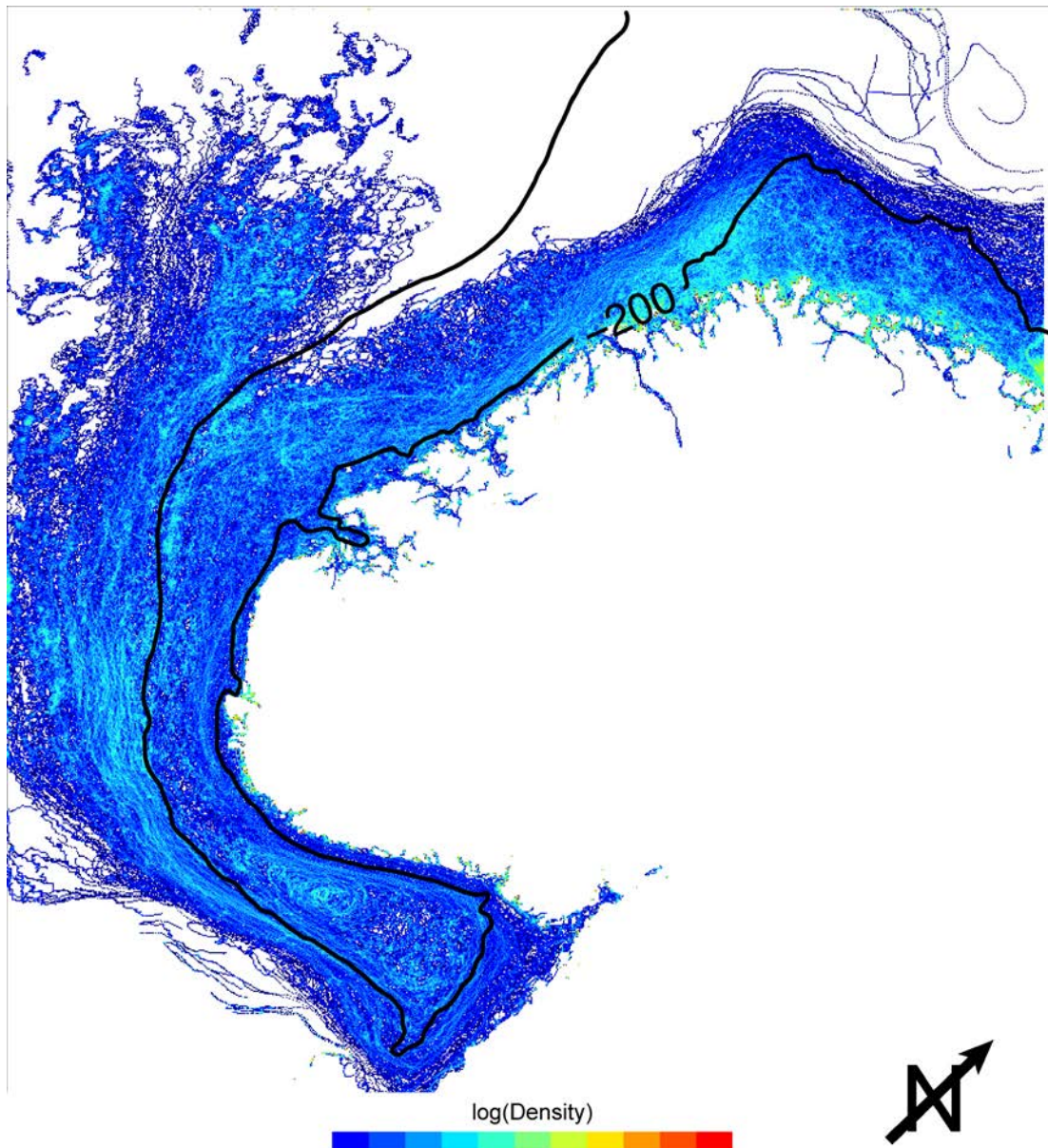
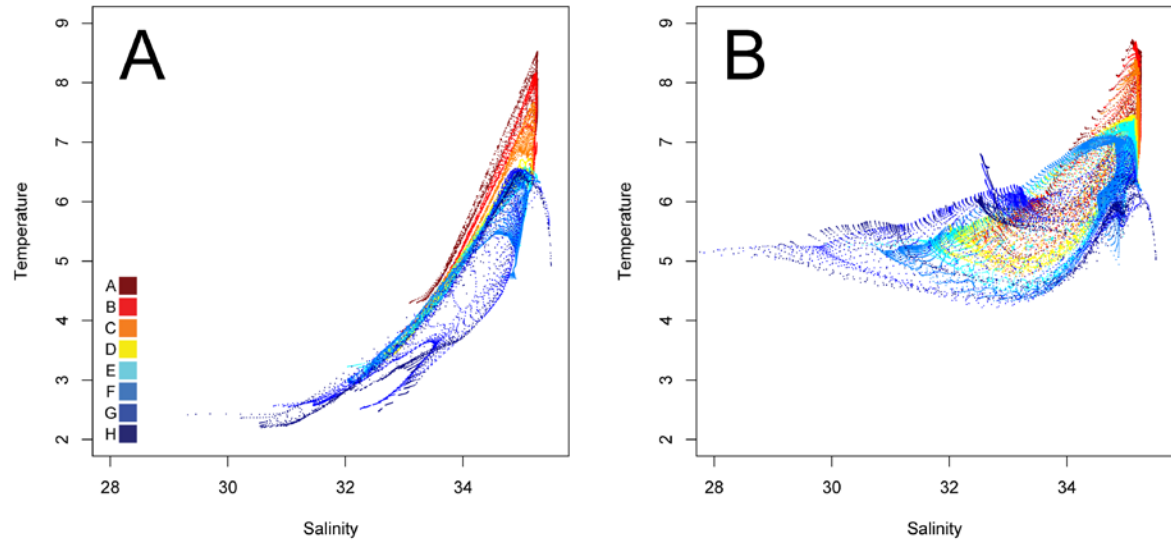


Figure 5. Spatial distribution of accumulated settlement days for pelagic juveniles spawned in the north-eastern North Sea and Skagerrak in 2011 (see figure 4 for summary of the proportion of settlement days spent in the different oceans/areas).



566

567 Figure 6. Monthly average salinity and temperature extracted from ocean model in all depths

568 at transects A-H in figure 1. Panel A represents average values for March 2011, and B is for

569 April 2011.



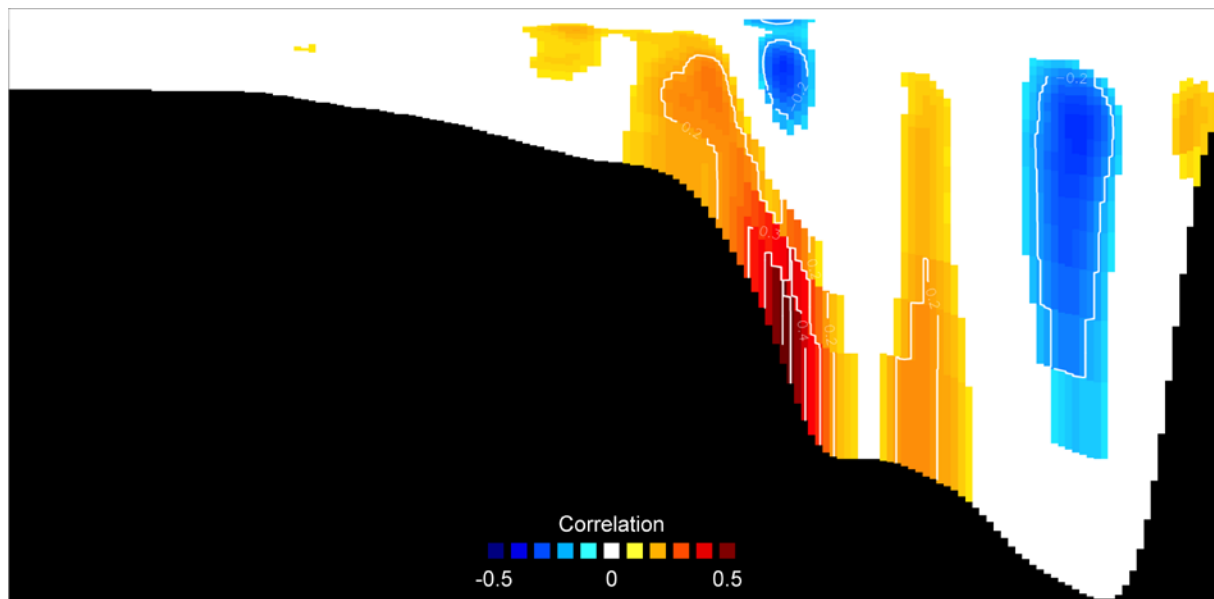
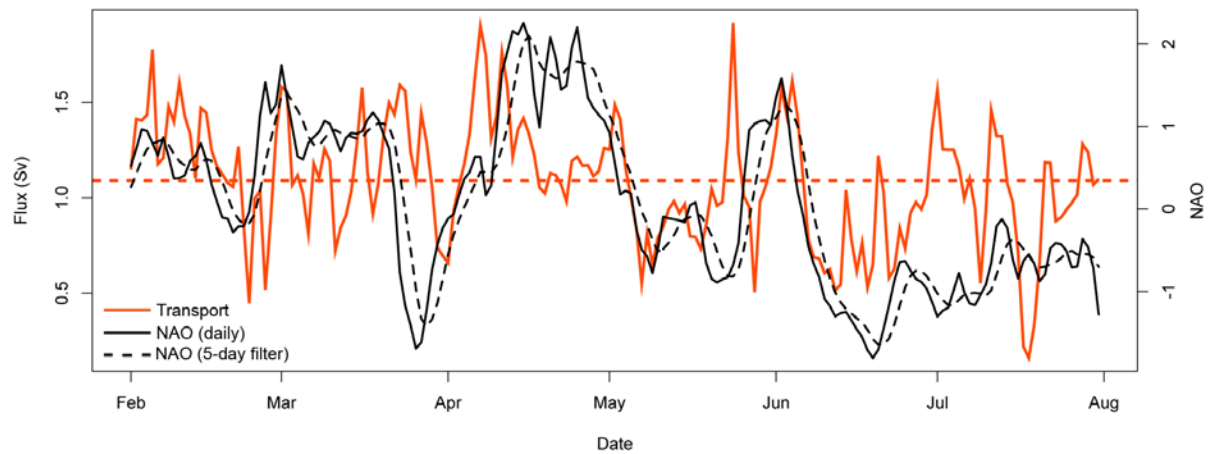


Figure 7. Cross-section of currents across the Norwegian Trench (at transect “F” in figure 1) correlated with the 5-day running average of NAO. Coloured areas of the cross-section identifies areas with a significant correlation between currents and NAO (white numbers and isolines indicates strength of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



577

578 Figure 8. Daily transport estimates of water masses leaving the northern/central North Sea and  
 579 entering Skagerrak (orange line, transport estimates based on same cross-section as figure 7,  
 580 at transect “F” in figure 1), the daily NAO (solid line, with the 5-day running average of NAO  
 581 used in figure 7, stapled line).