

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 imminent depletion/collapse, 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 the 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 on the Swedish west coast. As spawning location is hypothesised to be the prime stock separating mechanism for cod, 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 & Burnett 2015). The immediate observable positive effect of a marine reserve is dispersal of adults and juveniles from reserves to fished areas (termed "spillover"). For example, spillover from a spiny lobster (*Palinurus elephas*) reserve in the Balears 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*), respectively, found in surrounding fished areas originated from the reserve network by larval dispersal (Harrison et al. 2012). Also, outside a 40 km² 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 eradication 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 somehow have escaped the onslaught (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 Skagen or further westward 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 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 these 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

112 within the management units. Finally, we discuss our findings on the connectivity of the fjord
113 cod populations in the context of design of a provisional network of marine reserves.
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Materials and methods

To validate the ocean model, we compared its physical output variables (salinity and temperature) with hydrographical data routinely collected in the Skagerrak or within adjacent fjords. In the absence of in situ current measurements and a direct validation of the dynamical properties, we calculated the density from the modelled and observed hydrographical profiles. As the density variations is a 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 (citation needed?). 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 (Fig. 1). 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 firstly the results from the 800-meter model were interpolated down to the large 160-meter grid and secondly, 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 $408 \text{ km} \times 248 \text{ km}$), 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; an in-depth theoretical and practical description of the application of the method can be read in Ser-Giacomi et al. 2015, and a case study on connectivity in the Mediterranean can be read in Rossi et al. 2014). 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 is 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} $1.6 \text{ km} \times 1.6 \text{ km} \times 20 \text{ m}$ 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 (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, which each were provided two times 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, one tenth of the mixing coefficient above the pycnocline 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). There was no systematic bias in prediction of temperature, and 95% of the observations were within 2 units outside the daily variation of the model.

The INFOMAP algorithm identified 31 hydrodynamic provinces in the surface-layer of the 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 provinces into the outer Oslofjord. The coherence ratio of the identified provinces, that is, the proportion of tracers uniformly released within the 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. The proportion of eggs that drifted out of the Skagerrak spawned within hydrodynamic provinces and along the exposed coast

was 0.03 and 0.26 respectively. 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 (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 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 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 (i.e. together less than 1.5% of total fjord egg production). Three of the 15 non-egg-producing provinces also did not receive any eggs from other provinces and were in every respect disconnected from the network. These unconnected provinces were found on the eastern side of the Oslofjord between

251 Nøtterøy and Tjøme, between Hvasser and Tjøme (i.e. both in the Nøtterøy-Tjøme
252 archipelago associated with the Færder area in the outer Oslofjord), and inside the
253 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 in contrast to the more open and exposed coastal seascape. In general, there was very low connectivity among the fjord provinces, although some 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 distances of eggs spawned within the identified fjord provinces compared to coastally spawned eggs. Compared to field data describing the spatial scale of recruitment, our estimated dispersal kernel for fjord-province-spawned-eggs bears a striking resemblance to empirical work. 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 coincides with our identified fjord provinces where 80% of eggs were dispersed less than 12 km. The observed similarities are compelling evidence of a spatial structuring of fjord population recruitment, a structure that is also present in neutral genetic markers on the same scale (Knutsen et al. 2011).

When synthesising the accumulated body of knowledge on the coastal/fjord cod population structure in Skagerrak with our modelling results, one can conceptually reduce our system down to a meta-population model with a finite number of separate sub-populations. If we for the moment omit the North Sea stock, since it does not appear to interbreed with the coastal populations (Svedäng et al. 2007), our conceptual meta-population has very low

immigration/emigration rates (Espeland et al. 2008, Rogers et al. 2014), and based on our simulations, the probability of rescue effects is low due to limited exchange of recruits into and among the fjord sub-populations. For simplicity, we can assume similar mortality rates in the sub-populations, and that they all experience more or less stochastic recruitment, but that the environmental conditions and ultimately the recruitment is correlated across the region due to geographical proximity (Lekve et al. 2002). The meta-population model roughly sketched out above has probably been analysed hundreds of times, and given a certain set of parameters the outcome is known. From the annals of ecology we can read that 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 avoid this 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). Within the framework of our conceptual model of the system, the only parameter that we can manage for is fishing mortality. Under the current management regime that involves a minimum landing size as the sole limiting measure, we have an annual survival of around 0.3. By 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).

To summarise the implications of our conceptual model: within the identified provinces with existing production the message is clear, mortality should be lowered to prevent the further ecological extinction of sub-populations that have already been observed along the Swedish coast. Moreover, in our simulations we identified 15 hydrodynamic provinces inside which no spawning activity has been registered in national surveys. When considering the large-scale import of recruits from the North Sea commonly observed along

the coast, these empty provinces might be areas that can be fished without compromising any local populations. Thus, in the case of the identified provinces without local production there are two options: (1) fishing as usual on the random dispersers from other sub-populations and incoming North Sea component, if present; or (2) ban of all fishing to increase the chance for re-colonisation. However, given the integrity of the hydrodynamic provinces, these empty provinces are not expected to receive much import from the outside, and may even be unsuitable cod habitat altogether. However, because of the uncertain long-term effect of protecting areas without local production (i.e. whether local spawning will resume or not), it is common sense that 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, since our two years of simulation did not agree on whether it should be a fjord province or not. The implications are that this area has a transient state as coastal and fjordic, meaning that you can have one year of high import from outside (i.e. as was obviously the case in the 2012 simulation), while being more self-sufficient and isolated in another. However, given the limited replicates of two spawning periods, 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.

Furthermore, 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, as our results suggest that the increased production most likely will be distributed over a larger area, or even drift out of the Skagerrak by means of the coastal current. However, due to these characteristics, the general coastal stock is also less prone to depletion/extinction, and we suggest that conservation priority should be given to the areas where the risk of extinction is highest, namely within the identified fjord provinces. Having identified priority areas for conservation, it will be up to local decision makers to decide the

measures they want to take to ensure the well-being of their local populations, where any change in gear restriction will most likely help.

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 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* (Heath & Lough 2007), and the fate of larvae and newly settled juveniles is highly intertwined with the population dynamics of *C. finmarchicus* (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 coastal water mass (Kaartvedt 1993), 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 (Rothschild 1998, Olsen et al. 2011), which is largely a stochastic process in these waters. Under the scenario of a warmer future climate we predict the frequency of good years for recruitment of cod to be reduced in these waters. The rationale is that a gradual increase in temperature will most likely even further speed up the spring bloom of the phytoplankton as well as the succession of *C. finmarchicus* developmental stages, which already typically is

over before cod larvae have time to prey on them in these waters (Øresland & Andre 2008, Melle et al. 2014). How the effects of a changing climate can be accounted for in management of the Skagerrak cod population is unclear, 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 what it is adapted for, namely to endure long periods of low recruitment by its longevity and capitalise on the occasional good year with its 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 ensure the resilience of the stock is simply to fish less.

Oceanographic sources of bias

Our ocean circulation model tended to overestimate the density of the upper water column, from the coastal margin and towards the middle of Skagerrak. The water masses that are sampled in these stations are of mixed origin, where the major freshwater content originates from local rivers along the Skagerrak coast in addition to the Baltic outflow, mixed with the inbound North Sea water in the south-eastern corner of Skagerrak (Gustafsson & Stigebrandt 1996, Aure et al. 1998). Freshwater is by far the main defining variable to density in these water masses, 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, compared to

previous studies that has modelled vertical distribution of cod eggs (e.g. Röhrs et al. 2014), at least qualitatively, little difference can be observed in the vertical distribution.

Conclusion

In this study, we have thoroughly reviewed the connectivity of coastal Atlantic cod populations in the Skagerrak. As was concluded from our simulations and the subsequent enquiry, there was 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*”.

396 **Bibliography**

- 397 Agardy MT (1994) Advances in marine conservation: the role of marine protected areas.
398 Trends Ecol Evol 9:267–70
- 399 Anderson CNK, Hsieh C, Sandin S a, Hewitt R, Hollowed A, Beddington J, May RM,
400 Sugihara G (2008) Why fishing magnifies fluctuations in fish abundance. Nature
401 452:835–9
- 402 Aure J, Danielssen D, Svendsen E (1998) The origin of Skagerrak coastal water off Arendal
403 in relation to variations in nutrient concentrations. ICES J Mar Sci J du Cons 55:610–619
- 404 Aure J, Molvær J, Stigebrandt A (1997) Observations of inshore water exchange forced by a
405 fluctuating offshore density field. Mar Pollut Bull 33:112–119
- 406 Beaugrand G, Kirby RR (2010) Climate, plankton and cod. Glob Chang Biol 16:1268–1280
- 407 Beldring S, Engeland K, Roald L a., Sælthun NR, Voksø a. (2003) Estimation of parameters
408 in a distributed precipitation-runoff model for Norway. Hydrol Earth Syst Sci 7:304–316
- 409 Bucklin A, Kaartvedt S, Guarnieri M, Goswami U (2000) Population genetics of drifting
410 (Calanus spp.) and resident (Acartia clausi) plankton in Norwegian fjords. J Plankton
411 Res 22:1237–1251
- 412 Cardinale M, Svedäng H (2004) Modelling recruitment and abundance of Atlantic cod, Gadus
413 morhua, in the eastern Skagerrak-Kattegat (North Sea): Evidence of severe depletion due
414 to a prolonged period of high fishing pressure. Fish Res 69:263–282
- 415 Ciannelli L, Knutsen H, Olsen EM, Espeland SH, Asplin L, Jelmert A, Knutsen JA, Stenseth
416 NC (2010) Small-scale genetic structure in a marine population in relation to water
417 circulation and egg characteristics. Ecology 91:2918–2930
- 418 Coombs SH, Harding D, Nichols JH, Fosh CA (1981) The vertical distribution and buoyancy
419 of eggs of plaice (Pleuronectes platessa L.) in the southern North Sea. Ices C
420 1981/G84:133–139

421 Espeland SH, Albretsen J, Nedreaas K, Sannæs H, Bodvin T, Moy F (2013) Kartlegging av
 422 gytefelt (In Norwegian). *Fisk og Havet*:1–45

423 Espeland SH, Olsen EM, Knutsen H, Gjøsæter J, Danielssen D, Stenseth NC (2008) New
 424 perspectives on fish movement: Kernel and GAM smoothers applied to a century of
 425 tagging data on coastal Atlantic cod. *Mar Ecol Prog Ser* 372:231–241

426 Fernandez-Chacon A, Moland E, Espeland SH, Kleiven AR, Olsen EM (2016) Causes of
 427 mortality in depleted populations of Atlantic cod estimated from multi-event modelling
 428 of mark-recapture and recovery data. *Can J Fish Aquat Sci* 53:1689–1699

429 Gell FR, Roberts CM (2003) Benefits beyond boundaries: The fishery effects of marine
 430 reserves. *Trends Ecol Evol* 18:448–455

431 Goñi R, Hilborn R, Díaz D, Mallol S, Adlerstein S (2010) Net contribution of spillover from a
 432 marine reserve to fishery catches. *Mar Ecol Prog Ser* 400:233–243

433 Goñi R, Quetglas A, Reñones O (2006) Spillover of spiny lobsters *Palinurus elephas* from a
 434 marine reserve to an adjoining fishery. *Mar Ecol Prog Ser* 308:207–219

435 Gustafsson B, Stigebrandt A (1996) Dynamics of the freshwater-influenced surface layers in
 436 the Skagerrak. *J Sea Res* 35:39–53

437 Haidvogel DB, Arango H, Budgell WP, Cornuelle BD, Curchitser E, Lorenzo E Di, Fennel K,
 438 Geyer WR, Hermann AJ, Lanerolle L, Levin J, McWilliams JC, Miller AJ, Moore AM,
 439 Powell TM, Shchepetkin AF, Sherwood CR, Signell RP, Warner JC, Wilkin J (2008)
 440 Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of
 441 the Regional Ocean Modeling System. *J Comput Phys* 227:3595–3624

442 Hanski I (1991) Single-Species Metapopulation Dynamics: Concepts, Models and
 443 Observations. *Biol J Linn Soc* 42:17–38

444 Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim
 445 KA, Herwerden L Van, Planes S, Srinivasan M, Berumen ML, Jones GP (2012) Larval

446 export from marine reserves and the recruitment benefit for fish and fisheries. *Curr Biol*
447 22:1023–1028

448 Heath MR, Lough RG (2007) A synthesis of large-scale patterns in the planktonic prey of
449 larval and juvenile cod (*Gadus morhua*). *Fish Oceanogr* 16:169–185

450 Hutchinson WF, Oosterhout C van, Rogers SI, Carvalho GR (2003) Temporal analysis of
451 archived samples indicates marked genetic changes in declining North Sea cod (*Gadus*
452 *morhua*). *Proc Biol Sci* 270:2125–2132

453 Johannessen T, Dahl E, Falkenhaug T, Naustvoll LJ (2012) Concurrent recruitment failure in
454 gadoids and changes in the plankton community along the Norwegian Skagerrak coast
455 after 2002. *ICES J Mar Sci* 69:795–801

456 Jung KM, Folkvord A, Kjesbu OS, Agnalt AL, Thorsen A, Sundby S (2012) Egg buoyancy
457 variability in local populations of Atlantic cod (*Gadus morhua*). *Mar Biol* 159:1969–
458 1980

459 Kaartvedt S (1993) DRIFTING AND RESIDENT PLANKTON. *Bull Mar Sci* 53:154–159

460 Kerwath SE, Winker H, Götz A, Attwood CG (2013) Marine protected area improves yield
461 without disadvantaging fishers. *Nat Commun* 4:2347

462 Kleiven AR, Fernandez-Chacon A, Nordahl J-H, Moland E, Espeland SH, Knutsen H, Olsen
463 EM (2016) Harvest Pressure on Coastal Atlantic Cod (*Gadus morhua*) from Recreational
464 Fishing Relative to Commercial Fishing Assessed from Tag-Recovery Data. *PLoS One*
465 11:e0149595

466 Knutsen H, André C, Jorde PE, Skogen MD, Thuróczy E, Stenseth NC (2004) Transport of
467 North Sea cod larvae into the Skagerrak coastal populations. *Proc Biol Sci* 271:1337–
468 1344

469 Knutsen H, Jorde PE, André C, Stenseth NC (2003) Fine-scaled geographical population
470 structuring in a highly mobile marine species: The Atlantic cod. *Mol Ecol* 12:385–394

471 Knutsen H, Olsen EM, Jorde PE, Espeland SH, Andr?? C, Stenseth NC (2011) Are low but
 472 statistically significant levels of genetic differentiation in marine fishes “biologically
 473 meaningful”? A case study of coastal Atlantic cod. *Mol Ecol* 20:768–783
 474 Lekve K, Ottersen G, Stenseth NC, Gjøsæter J (2002) Length Dynamics in Juvenile Coastal
 475 Skagerrak Cod : Effects of Biotic and Abiotic Processes. *Ecology* 86:1676–1688
 476 Lien VS, Gusdal Y, Vikebø FB (2014) Along-shelf hydrographic anomalies in the Nordic
 477 Seas (1960-2011): Locally generated or advective signals? *Ocean Dyn* 64:1047–1059
 478 Melle W, Runge J, Head E, Plourde S, Castellani C, Licandro P, Pierson J, Jonasdottir S,
 479 Johnson C, Broms C, Debes H, Falkenhaug T, Gaard E, Gislason A, Heath M, Niehoff
 480 B, Nielsen TG, Pepin P, Stenevik EK, Chust G (2014) The North Atlantic Ocean as
 481 habitat for *Calanus finmarchicus*: Environmental factors and life history traits. *Prog*
 482 *Oceanogr* 129:244–284
 483 Moland E, Olsen EM, Knutsen H, Garrigou P, Espeland SH, Kleiven AR, André C, Knutsen
 484 JA, Kleiven R, B PRS, Andre C (2013) Lobster and cod benefit from small-scale
 485 northern marine protected areas: inference from an empirical before-after control-impact
 486 study. *Proc Biol Sci* 280:20122679
 487 Myers M, Ambrose R (2009) Differences in benthic cover inside and outside marine protected
 488 areas on the Great Barrier Reef: influence of protection or disturbance history? *Aquat*
 489 *Conserv Mar Freshw Ecosyst* 19:736–747
 490 Olsen EM, Ottersen G, Llope M, Chan K, Beaugrand G, Stenseth NC (2011) Spawning stock
 491 and recruitment in North Sea cod shaped by food and climate. *Proc Biol Sci* 278:504–
 492 510
 493 Øresland V, Andre C (2008) Larval group differentiation in Atlantic cod (*Gadus morhua*)
 494 inside and outside the Gullmar Fjord. *Fish Res* 90:9–16
 495 Øresland V, Ulmestrand M (2013) Marine Science. *ICES J Mar Sci* 70:532–539

496 Otto L, Zimmerman JTF, Furnes GK, Mork M, Saetre R, Becker G (1990) Review of the
 497 physical oceanography of the North Sea. *Netherlands J Sea Res* 26:161–238
 498 Peterson RH, Martin-Robichaud DJ, Harmon P (2004) Influence of incubation temperature on
 499 body movements of Atlantic cod (*Gadus morhua* L.) embryos and on size at hatch.
 500 *Aquac Res* 35:453–457
 501 Rogers LA, Olsen EM, Knutsen H, Stenseth NC (2014) Habitat effects on population
 502 connectivity in a coastal seascape. *Mar Ecol Prog Ser* 511:153–163
 503 Röhrs J, Christensen KH, Vikebø F, Sundby S, Saetra Ø, Broström G (2014) Wave-induced
 504 transport and vertical mixing of pelagic eggs and larvae. *Limnol Oceanogr* 59:1213–
 505 1227
 506 Rossi V, Ser-Giacomi E, López C, Hernández-García E (2014) Hydrodynamic provinces and
 507 oceanic connectivity from a transport network help designing marine reserves. *Geophys*
 508 *Res Lett* 41:2883–2891
 509 Rosvall M, Bergstrom CT (2008) Maps of random walks on complex networks reveal
 510 community structure. *Proc Natl Acad Sci U S A* 105:1118–23
 511 Rothschild BJ (1998) Year class strengths of zooplankton in the North Sea and their relation
 512 to cod and herring abundance. *J Plankton Res* 20:1721
 513 Ser-Giacomi E, Rossi V, López C, Hernández-García E (2015) Flow networks: A
 514 characterization of geophysical fluid transport. *Chaos An Interdiscip J Nonlinear Sci*
 515 25:36404
 516 Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a
 517 split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean*
 518 *Model* 9:347–404
 519 Siegel D a, Mitarai S, Costello CJ, Gaines SD, Kendall BE, Warner RR, Winters KB (2008)
 520 The stochastic nature of larval connectivity among nearshore marine populations. *Proc*

521 Natl Acad Sci U S A 105:8974–8979
 522 Skamarock WC, Klemp JB, Dudhi J, Gill DO, Barker DM, Duda MG, Huang X-Y, Wang W,
 523 Powers JG (2008) A Description of the Advanced Research WRF Version 3. Tech
 524 Rep:113
 525 Stenseth NC, Jorde PE, Chan K-S, Hansen E, Knutsen H, Andre C, Skogen MD, Lekve K
 526 (2006) Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. Proc
 527 R Soc B Biol Sci 273:1085–1092
 528 Sundby S (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection
 529 of copepod populations. Sarsia 85:277–298
 530 Svedäng H, Bardon G (2003) Spatial and temporal aspects of the decline in cod (*Gadus*
 531 *morhua* L.) abundance in the Kattegat and eastern Skagerrak. ICES J Mar Sci 60:32–37
 532 Svedäng H, Righton D, Jonsson P (2007) Migratory behaviour of Atlantic cod *Gadus morhua*:
 533 natal homing is the prime stock-separating mechanism. Mar Ecol Prog Ser 345:1–12
 534 Svedäng H, Svenson a. (2006) Cod *Gadus morhua* L. populations as behavioural units:
 535 inference from time series on juvenile abundance in the eastern Skagerrak. J Fish Biol
 536 69:151–164
 537 Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American
 538 fishes: implications for population regulation Patterns of Life-History Diversification in
 539 North American Fishes: Implications for Population Regulation. Can J Fish Aquat
 540 49:2196–2218
 541 Wood SN (2006) Low-rank scale-invariant tensor product smooths for generalized additive
 542 mixed models. Biometrics 62:392
 543 Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA,
 544 Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PM, McClanahan TR, Minto C,
 545 Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R, Zeller D (2009)

546 Rebuilding global fisheries. *Science* 325:578–585

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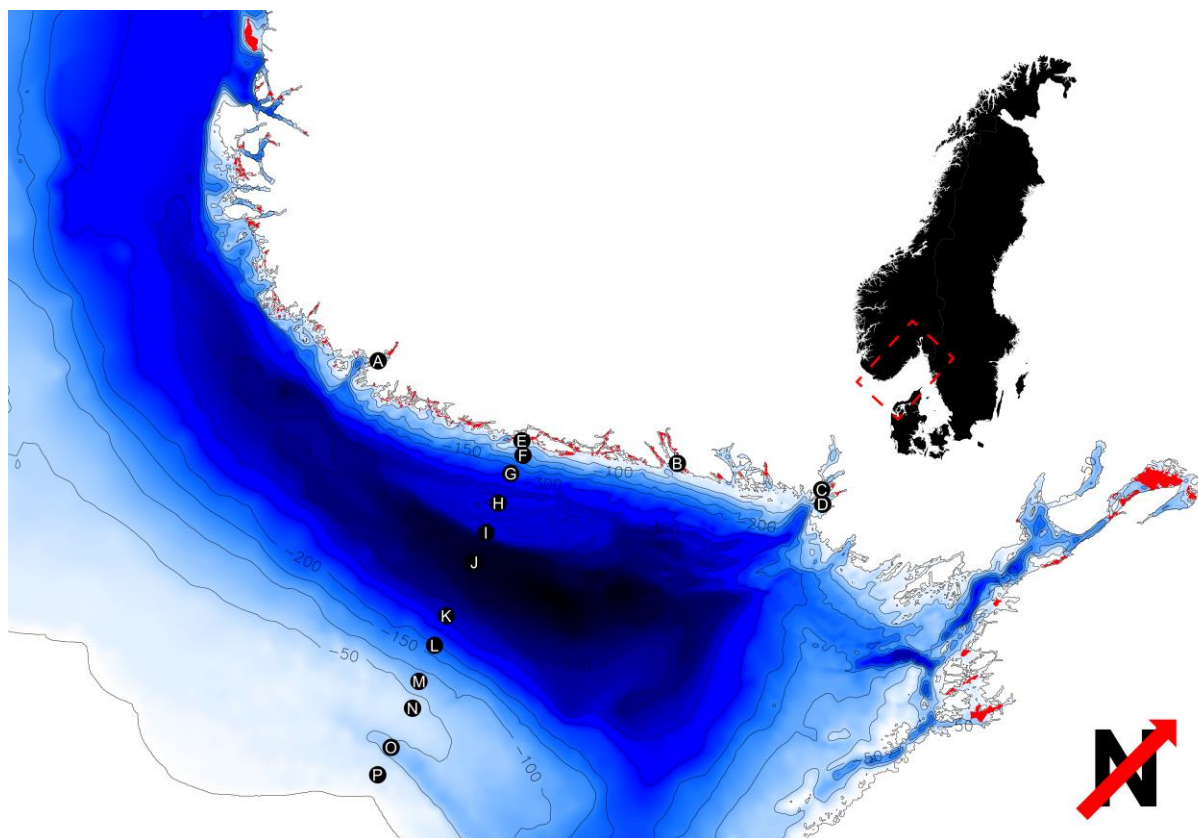


Figure 1. Bathymetry of the study area equivalent to the bottom topography of the ocean model. Marked in red are all registered spawning areas of cod along the Norwegian Skagerrak coast. Letters from A-P represents the fixed hydrological sampling stations where ocean model and field observations have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

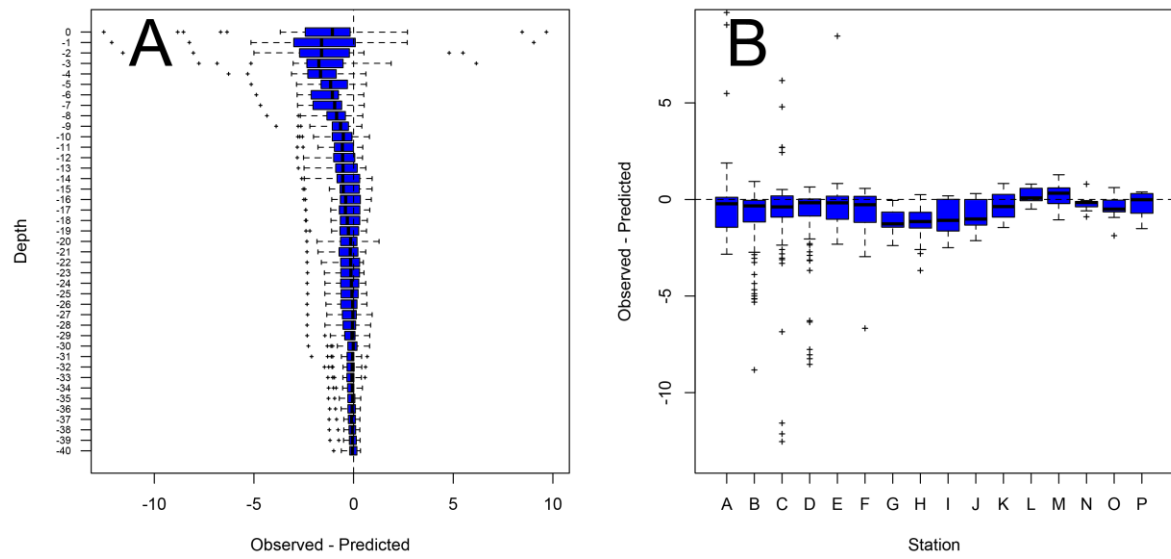


Figure 2. Boxplots of error residuals (observed – predicted vaules) of modelled and field-sampled density in upper water masses; classified by (A) one meter depth intervals, and (B) sampling station (where letters refer to the fixed sampling stations in figure 1).

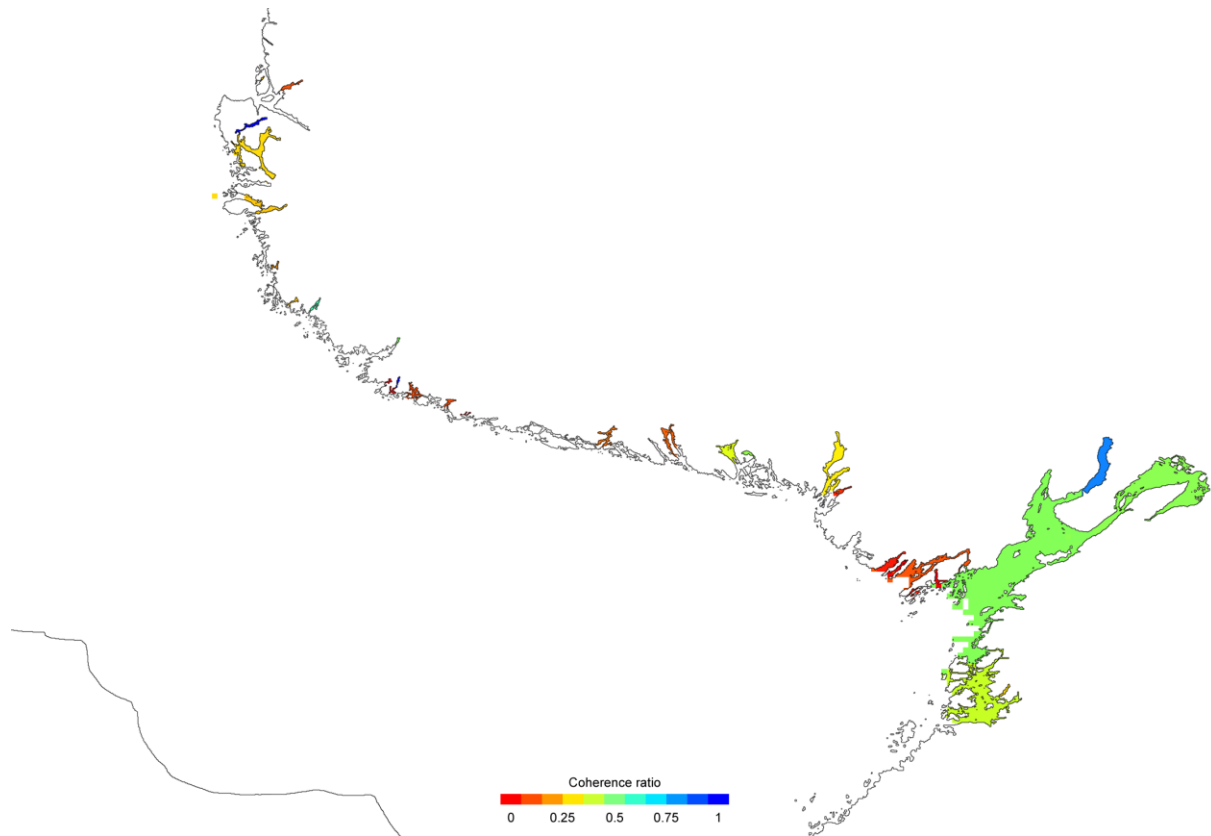


Figure 3. Hydrodynamic provinces identified by the INFOMAP algorithm, based on connectivity patterns in the upper water masses. Colours of provinces refer to the coherence ratio of each province, that is, the proportion of passive tracers initially released that is retained within the province.

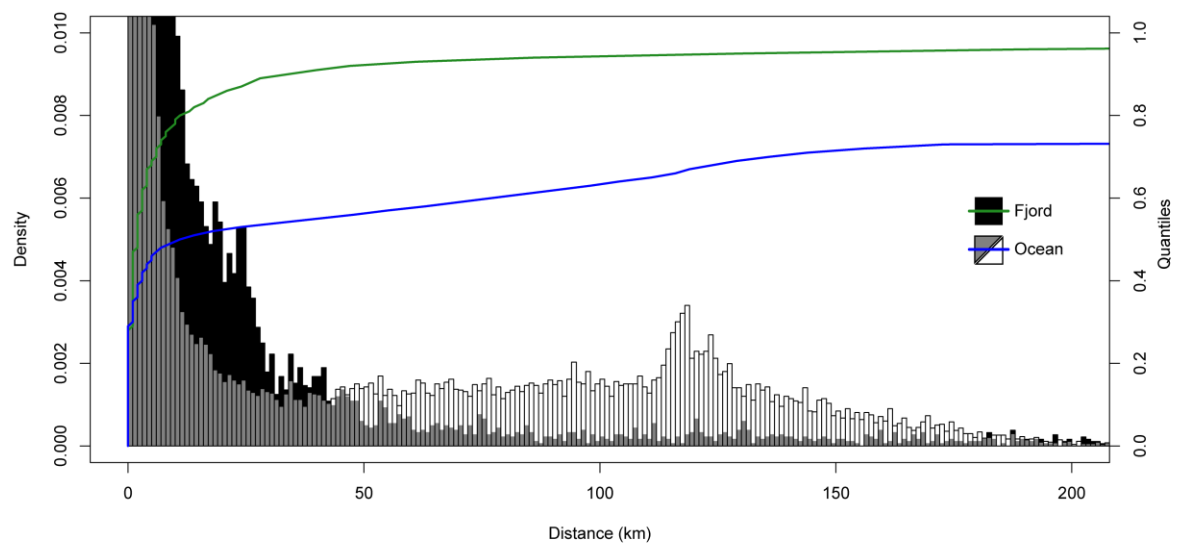
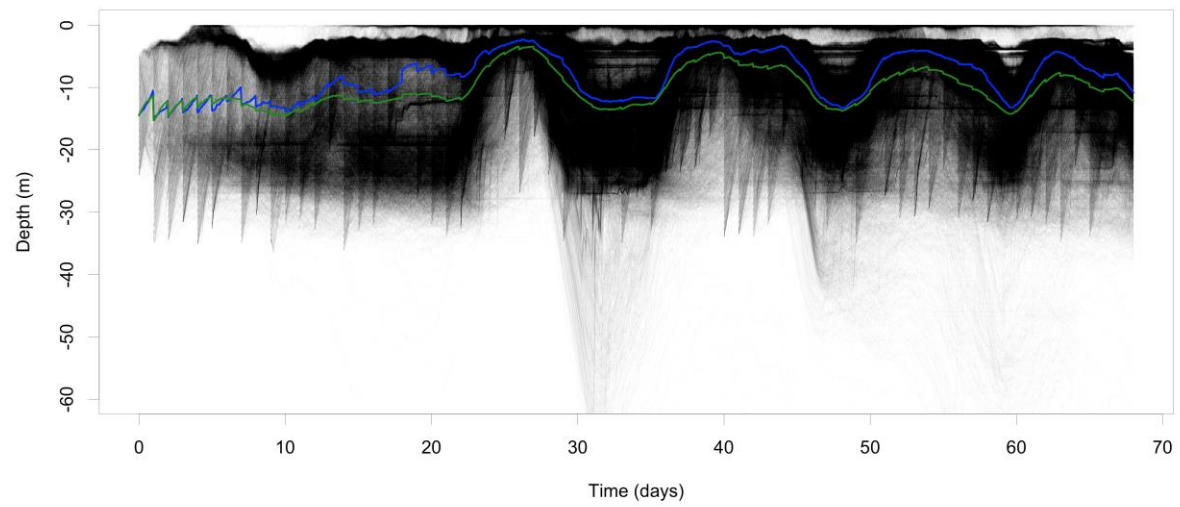


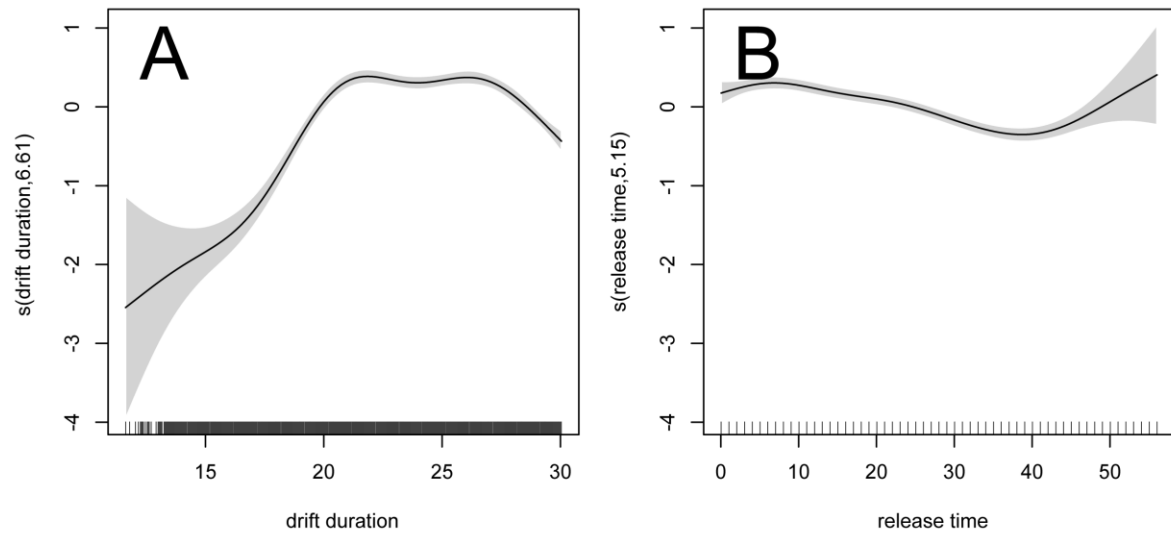
Figure 4. Density distribution of egg dispersal distances, spawned either within a fjord province or in coastal spawning grounds. Blue and green lines are the quantiles of egg dispersal distances.



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

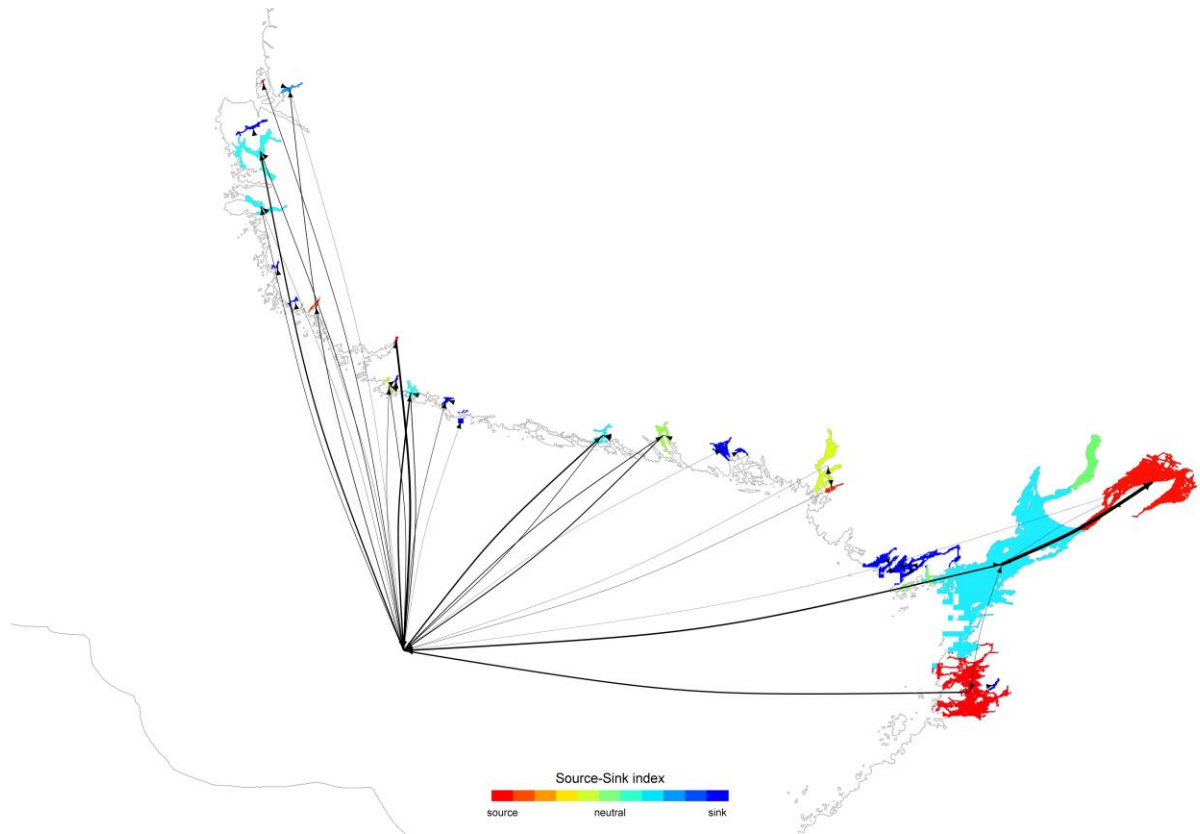
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578 Figure 6. Non-linear effects of drifting/incubation duration (A) and timing of release (B) on
 579 estimated retention probability within hydrodynamic provinces (note that the y-axes are on
 580 log-odds scale).

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582

583 Figure 7. Network graph of the flow of eggs among provisional management units, where
 584 width of arrows represents the magnitude of transport. Also, the colour of each hydrodynamic
 585 province represent the source-sink index of the province.