



Original Article

Local recruitment of Atlantic cod and putative source spawning areas in a coastal seascape

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Increased knowledge on connectivity is crucial to our understanding of the population dynamics, genetic structure, and biogeography of many coastal species. In coastal marine populations, the main factor for structuring is thought to be the degree of isolation and confinement, limiting genetic exchange between populations. However, many offshore populations use the coastal areas as nursery grounds, but venture back to natal spawning grounds as adults. Therefore, increased knowledge on the connectivity between coastal and offshore populations is crucial to ensure correct assessment of coastal living resources. Here, we combine genetic assignment data of Atlantic cod recruits sampled in 2017 and 2018 (as 0- and 1-group cod, respectively) in outer Oslofjord (eastern Skagerrak) with a biophysical model for the Skagerrak region over the time period from spawning to settlement in 2017. We located the most probable spawning locations of Atlantic cod recruits by “back-tracking” larval drift trajectories and found putative source areas on both sides of the outer Oslofjord, as well as potential upstream sources in the North Sea and Kattegat. Findings are discussed with regards to suitable management strategies and potential for restoration of coastal cod populations.

Keywords: connectivity, ecotypes, fisheries management, *Gadus morhua*, seascape genetics.

Introduction

Since the “gadoid outburst” ended in the mid-1980s (Cushing, 1984), Atlantic cod (*Gadus morhua*) has undergone a significant reduction across its range, reaching a historically low biomass in the 1990s. Over-exploitation exacerbated by a changing ocean climate to a warmer state, has left several cod stocks depleted (Myers *et al.*, 1996; Cardinale and Svedäng, 2004; Drinkwater, 2005). Despite measures to reduce fishing mortality, several stocks have shown little or no recovery during the past decade (Hutchings and Reynolds, 2004), with some exceptions such as the Barents Sea cod (Kjesbu *et al.*, 2014).

In eastern Skagerrak, abundance of cod and other demersal fish species > 30 cm, has declined dramatically since the 1970s

(Svedäng, 2003). Despite good levels of recruitment to nurseries along the Skagerrak coast in some years (Aglen *et al.*, 2016), the overall trend is declining (ICES, 2021). It is not known why these years of strong recruitment do not seem to replenish local populations in the long term (ICES, 2021). The occasional high abundance of young fish in the absence of older individuals suggests that these juveniles originate from upstream spawning grounds in the North Sea and Skagerrak (Svädeng, 2003). Mortality (fishing and natural) is presently too high for many of the juveniles to reach older ages (Olsen and Moland, 2011; Fernández-Chacón *et al.*, 2015). This is corroborated by recent modelling of population genetics data from the same system, which pointed to high fishing mortality and high fishing gear selectivity as mechanisms likely to reproduce the empirical levels of genetic differentiation (Spies *et al.*, 2018). Alternatively,

or in addition, cod may return to their extant population of origin upon reaching maturity (Svedäng *et al.*, 2007; André *et al.*, 2016).

Along the Norwegian Skagerrak coast, the Atlantic cod is known to exhibit population structure on both small and large spatial scales (Hutchinson *et al.*, 2001; Knutsen *et al.*, 2003; Jorde *et al.*, 2007; Barth *et al.*, 2017, 2019; Dahle *et al.*, 2018). More recently, population genetic studies have revealed that in coastal areas, Atlantic cod is present in two genetically distinct ecotypes, which appear to co-exist during a large part of their life cycle (Knutsen *et al.*, 2018). These ecotypes are usually referred to as a “fjord” type, and a “North Sea” type, and display differences in relation to growth trajectories (Knutsen *et al.*, 2018; Jørgensen *et al.*, 2020), metabolic rates (Chung *et al.*, 2021), and habitat selection (Knutsen *et al.*, 2018). Where the “fjord” type is usually thought to be highly stationary and dominating in the inner parts of the fjord, the “North Sea” type is known to dominate the outer parts and in the open waters (Knutsen *et al.*, 2018; Jorde *et al.*, 2018a). Recent work suggest that the co-existing ecotypes possess innate differences in feeding and movement ecologies and may, thus, fill different functional roles in the coastal marine ecosystem (Kristensen *et al.*, 2021). Three large chromosomal inversions have been described as polymorphic within both fjord and offshore cod on the Norwegian Skagerrak coast (Sodeland *et al.*, 2016). These inversions have been identified on both sides of the Atlantic Ocean (Bradbury *et al.*, 2010, 2014), and SNPs within these inversions have been linked to temperature (Bradbury *et al.*, 2010), as well as salinity and oxygen (Berg *et al.*, 2015).

To implement a successful management regime and restoration of cod populations in the Skagerrak, it is important to gain knowledge on connectivity in the two ecotypes and identify spawning grounds that could be important for successful recruitment. Along the Norwegian Skagerrak coast, there is potential for major transport of eggs and larvae of cod from the North Sea, some years more than others (Knutsen *et al.*, 2004; Stenseth *et al.*, 2006). The population structuring that has been documented is likely a result of resident local behavioural units or populations with spawning aggregations in fjords and coastal lagoons (Jorde *et al.*, 2007; Knutsen *et al.*, 2011). Cod eggs are spawned directly into the free water masses, which in theory would disperse eggs (and later larvae) widely with the prevailing currents. And although the specific gravity of pelagic eggs (slightly buoyant in typical “Atlantic” water masses of ≈ 34 psu) might be a possible retention mechanism by giving the eggs a subsurface maximum when the surface layer is less saline (Ciannelli *et al.*, 2010), there are to date no evidence for active behaviour driving retention during the larval stage. The degree to which settled juveniles stay and recruit to the local adult population, and whether such populations are mostly self-recruiting is not known. However, the relatively stable co-existence of at least two distinct ecotypes indicate that several populations use the convoluted Skagerrak coastline for spawning, as nursery, and for longer term (> 1 year) residence (Rogers *et al.*, 2014; Barth *et al.*, 2017; Knutsen *et al.*, 2018; Villegas-Ríos *et al.*, 2021).

When studying population connectivity, one of the biggest challenges has been the uncertainties regarding the physical oceanography, especially in coastal environments. Pelagic eggs and larvae hold the potential to be transported far away from original spawning sites, and local currents can retain them at the coastal sites (Ciannelli *et al.*, 2010). Combining genetic data with a biophysical model of ocean drift, also referred to as “multidisciplinary seascape genetics,” provides an approach that could reveal new insights into the processes that affect connectivity between offshore and coastal populations, which could be crucial for implementing new and better strategies for fisheries management and marine conservation networks (Selkoe *et al.*, 2008).

Here, we utilized an abundant cohort of young-of-the-year (YOY) cod observed as recently settled 0-group juveniles in summer and autumn of 2017, and as highly stationary 1-group juveniles in spring 2018, to make inference regarding likely sources of recruits to nursery areas in the outer Oslofjord seascape located in the north-eastern parts of Skagerrak. Genetic assignment of individuals sampled as 0- or 1-group juveniles was combined with a nested hydrodynamic model simulating drift of early pelagic cod stages from potential sources both in the North Sea and the Oslofjord, during spring and summer 2017. By “back-tracking” larval drift trajectories from observed juvenile cod sampled in autumn and following summer, the aim of this study was to gain insight into which population of origin is the most probable source of recruits contributing to replenishment of coastal cod populations found inhabiting the outer Oslofjord region. Using particle backtracking, we evaluated the likely area of origin for individuals that genetically assigned to the “North Sea” type, and tested if those assigned to the “fjord” type were indeed likely to originate from local, proximal spawning populations. We discuss our findings in light of population connectivity and its implications for restoration of depleted local spawning populations.

Material and methods

Study area

This study was conducted in the outer Oslofjord, a section of coastal Skagerrak in Southeast Norway. Here, recently designated national parks, Færder and Ytre Hvaler National Park (hereafter, referred to as “West” and “East,” respectively), cover mainland coastlines and archipelagoes along the western and eastern shores of the Oslofjord (Figure 1). Both the national parks are high in biodiversity and cover diverse nature types, which consists of several eelgrass beds, kelp forests, soft-bottom areas, and shell–sand beaches. It is a highly populated region, and the area is affected by long-term fishing pressure, from both commercial and recreational fisheries. Both sampling areas hold the status as national parks, but there is no protection of fish *per se*. Until recently, the only regulation for cod within the 12 nm limit (thus, including our study area) was a minimum size limit of 40 cm. Since June 2019, a ban on recreational capture of cod has been implemented in the wider inner Skagerrak area, from Telemark to the Swedish border, including seasonal closure of known coastal spawning sites (from January to April). Bottom trawling for northern shrimp (*Pandalus borealis*) remains the last economically viable fishery in inner Skagerrak, and all suitable areas deeper than 60 m are subject to bottom trawling, including the national parks, with the exception of a ban in limited areas known to harbour *Lophelia* cold water corals. Sorting grids are mandatory in the bottom trawl fishery for shrimp, but additional legal capture of cod and other groundfish is common through the use of a “retention bag” mounted above the grid—retaining above legal-size fish but allowing the escape of sub-legal fish by means of mesh size. The study area is in general a topographically complex region, with several forcing mechanisms on multiple scales. The Oslofjord proper is dominated by tidal forces and freshwater input from the Glomma (East) and Drammenselva (West) rivers (see Figure 1), creating a net outward flow of the surface layer. The circulation in offshore areas in Skagerrak are strongly influenced by the prevailing wind field (Gustafsson and Stigebrandt, 1996), as well as freshwater input from the continental rivers of southern North Sea and the Baltic (Kristiansen and Aas, 2015). Additionally, there is occasional wind driven import of North Sea water, sweeping along the southern slopes of the Norwegian Trench into Skagerrak (Huserbråten *et al.*, 2018). In effect, these diverse forcing mechanisms together create

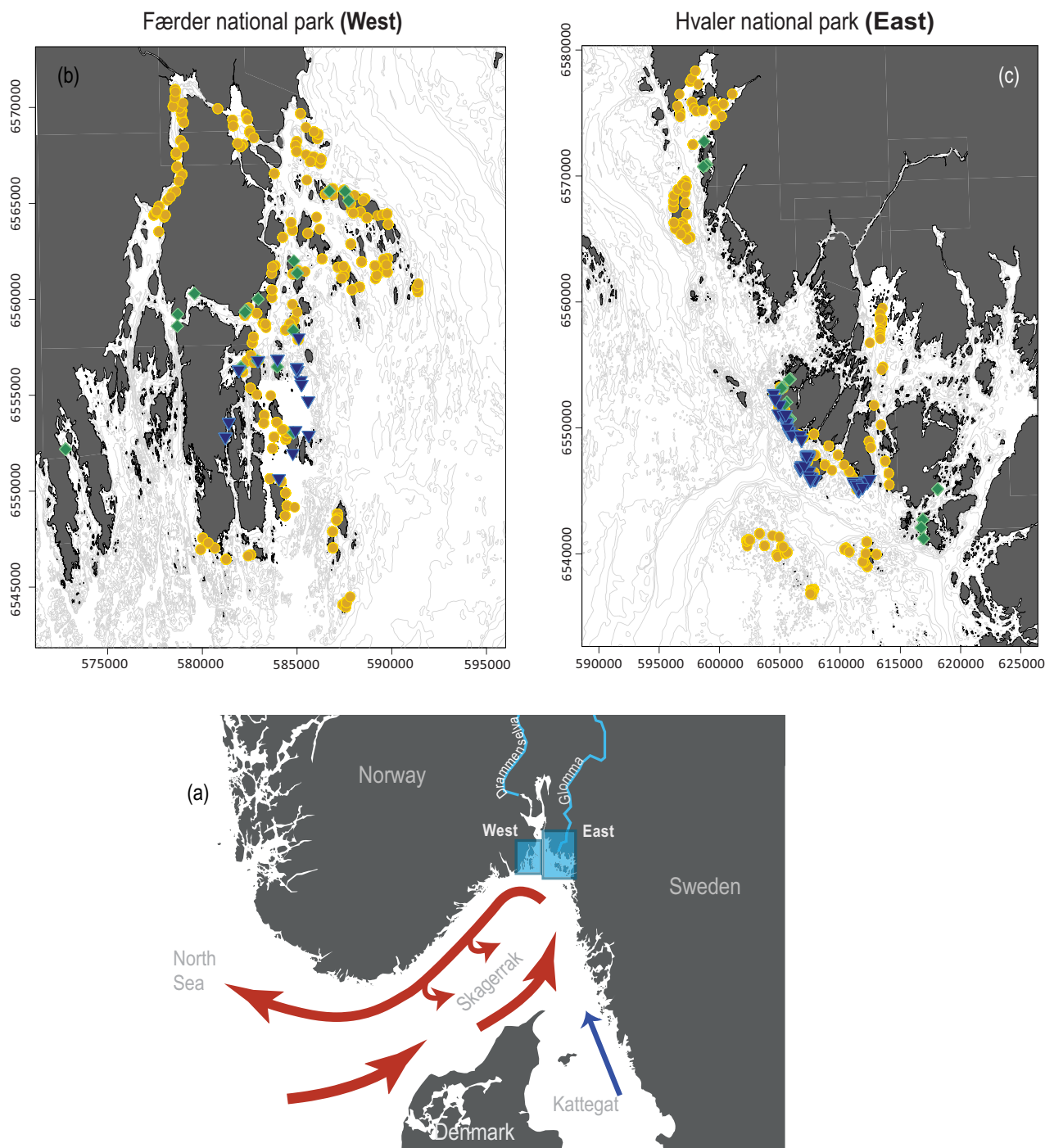


Figure 1. Map of study area (a) and sampling locations for the two national parks and adjacent areas located on the west (b) and east (c) side of outer Oslofjord. Triangles represent sampling sites from July to August 2017 (blue, pot-traps). Sampling performed in September and October 2017 are shown as diamond squares (green, beach seine). Circles represent sampling sites from May 2018 (yellow, fyke-nets). Main currents in Skagerrak are displayed as red (North Atlantic current) and blue arrow (Baltic current).

a cyclonic (anti-clockwise) circulation pattern, with peak current velocities along the coastal boundary (Figure 1).

Sampling and sampling methods

To obtain maximum spatial and temporal coverage of the 2017 coastal Atlantic cod cohort we employed three modes of sampling.

During July and August, YOY cod (hereafter, referred to as “0-group”) was sampled with the help of two local wrasse fishers on the eastern and western side of the opening of outer Oslofjord, respectively. Sampling was performed using wrasse traps placed in groups of five to six traps on each sampling site located close to shore, no deeper than 7–8 m, to keep any fish from getting damaged by pressure differences (Figure 1). On the east side, sampling

was performed during nighttime until morning the next day (2:00–12:00) for 5 d. On the west side, sampling was performed during daytime (09:00–15:00) for 2 d. All 0-group cod caught as bycatch was measured to the nearest cm, and fin-clipped for genetic analysis before being released back into the sea. Tissue samples were stored in 99% ethanol for further DNA extraction.

In September and October, we utilized the beach seine survey conducted annually since 1919, with several fixed stations in the outer Oslofjord and 15 additional stations added specifically for the purpose of this study (Figure 1). The beach seine covers an area of up to 700 m² per haul and is used in suitable nearshore habitats (<15 m depth). In each haul, all fish were counted and identified to species. All cod was measured to nearest mm. In addition, for this survey, all 0-group cod were collected and frozen whole on-board within 30 min of sampling. In September, individuals ranging from 5 to 15 cm are assumed to be 0-group cod, and >15 cm is classified as young and older adults.

Sampling of fully recruited subadult cod (hereafter referred to as “1-group”) from the 2017 cohort was performed during 1st–8th May of 2018 using fyke-nets with 55 cm openings and 18 mm cod end mesh size. Sampling was performed during daytime (08:00–18:00) and fyke-nets were soaked for approximately 24 h before being hauled and moved to a new site. All sites were chosen at random but located close to the coastline of mainland and skerries, with a maximum depth of 6–7 m (Figure 1). All fish were counted and identified to species level and measured to nearest cm (fork length, FL) before being released back into the ocean. All Atlantic cod captured was fin-clipped for genetic analysis, and tissue samples were stored in 99% ethanol until further DNA extraction. In May 2018, all cod \leq 30 cm were considered 1-group recruits from the 2017 cohort.

DNA extraction and genotyping

A total of 1096 cod tissue samples from 0-group and 1-group cod catches from 2017 to 2018 were genotyped for the present study. Fin-clips were stored at 4°C in pure ethanol prior to DNA extraction. DNA was extracted from all samples using the E.Z.N.A. tissue kit (Omega Bio-tek), following manufacturers protocol for tissue DNA extraction. A sub sample of 15–20 samples for each 96-well-plate was quality-verified and quantified using Qubit assays (ThermoFisher) before genotyping. The SNPs used in this study were previously specially developed to distinguish among individuals from coastal and North Sea ecotypes (see Jorde *et al.*, 2018a). Originally, 27 SNPs were used to discriminate between populations, however, one SNP (Gdist_68504_1675) was discarded due to repeated failure. In this paper, all analysis were, therefore, limited to 26 SNPs. Genotyping of the 26 SNPs was done on a MassARRAY platform (Sequenom Inc.) at the IMR laboratory in Bergen, Norway.

Population genetics—assignment of individuals

As genetic reference for the fish sampled in outer Oslofjord, we used two previously sampled and genotyped sets of individuals from the Norwegian Skagerrak coast and from the North Sea (see Jorde *et al.*, 2018a), representing a “fjord” reference and a “North Sea” reference, respectively. Genetic assignment was computed using the Bayesian assignment method using the GeneClass2 software (Piry *et al.*, 2004). Individuals that had a score lower than 80% ($n = 46$)

and <20 loci ($n = 28$) were omitted from further analysis, resulting in 1022 individuals being scored successfully.

Statistical analyses

Estimates of genetic differentiation (F_{ST} : Weir and Cockerham) and a heterogeneity test (exact G-test) for general structure in the data were performed using GENEPOP 4.7 on the web (Raymond and Rousset, 1995). Pairwise F_{ST} estimates between samples collected from the east and west side of the Oslofjord were calculated for all fjord individuals and North Sea individuals separately (Supplementary Tables S1 and S2). Correlation between geographic and genetic distances was computed using pairwise comparisons of individuals (\hat{a} statistic; Rousset, 2000) using GENEPOP 4.2 on the web. For each data set, a Mantel test with 10000 permutations was used to test for significance of geographic and genetic distance between all fjord individuals from the sampling locations, under the null hypothesis of independence between genotype and geographical location (Rousset, 2008). Geographic distances between individuals represent linear geographic distances in km. Our data was divided into individuals from “East” and “West” and tested separately, before then testing all individuals from both locations combined. (note: five individuals of “fjord” cod sampled in July on the west side of the fjord was grouped together with samples from September due to low sample size).

Ocean model and Lagrangian particle advection scheme

The hydrodynamic models used to represent the ocean currents in the study area was based on the Regional Ocean Modeling System (ROMS, <http://myroms.org>), a free-surface, hydrostatic, primitive equation ocean general circulation model (Shchepetkin and McWilliams, 2005; Haidvogel *et al.*, 2008). The large-scale ROMS model, used to simulate potential upstream imports from the North Sea and Kattegat, was run with a horizontal resolution of 4 km x 4 km in an orthogonal, curvilinear grid covering parts of the North Atlantic and all the Nordic and Barents seas over the time period 1960–2017 (Lien *et al.*, 2013, as applied in e.g. Lien *et al.*, 2014). The small-scale ROMS model, used to simulate local cod spawning in the Oslofjord, was run with a horizontal resolution of 160 m x 160 m, and was forced using hourly values of currents and hydrography along the open boundaries from a larger-scale model covering the whole Norwegian coast (Albretsen, 2011), high-resolution wind fields (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 model the advection of particles in the horizontal plane we applied the fourth order Runge–Kutta scheme LADIM (Ådlandsvik, 2021) coupled with the velocity fields from the ROMS models. Here, particles were released randomly across the North Sea, Skagerrak, Kattegat, and Oslofjord in areas shallower than 200 m, every day from the 1st to 31st of March 2017 (see Brander, 1994 and Heath *et al.*, 2008 for review of spawning times in the North Sea). In total, 1240000 particles were released in the two model domains (620000 in each of the two domains) and were allowed to drift until the 20th of July, as settlement period of cod in this area has been found to last from start of June–mid-July (see Johannessen, 2014, but also Huserbråten *et al.*, 2018 for modelled drift period), giving a drift period of 62–141 d. Due to the vast (and largely unknown parameter space) with regards to the vertical movement of cod larvae in this

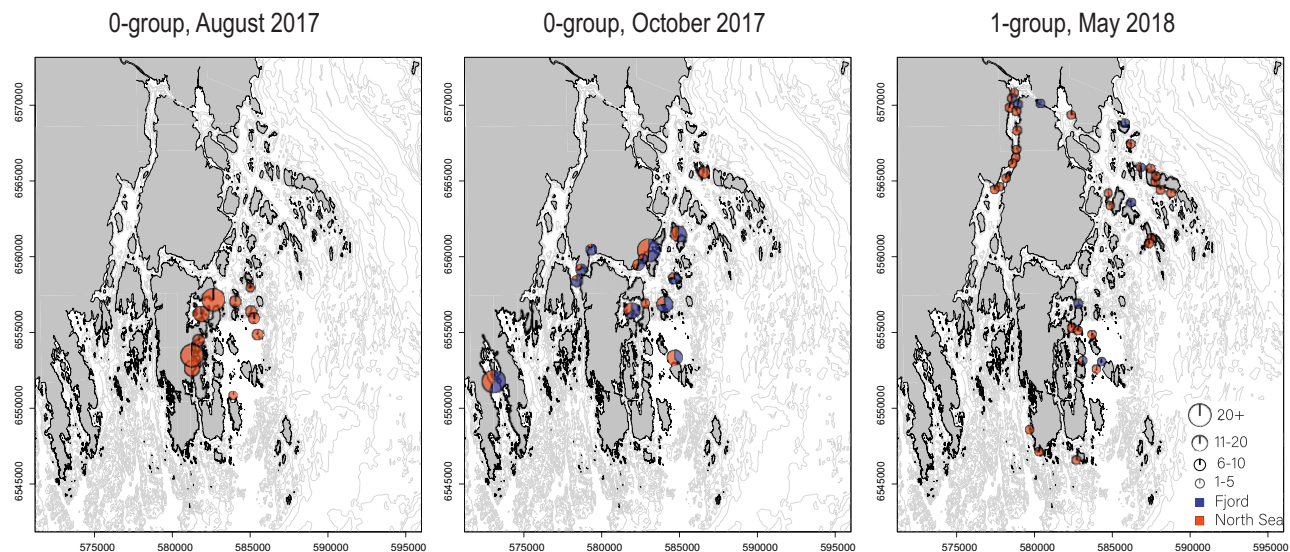


Figure 2. Spatial genetic assignment of the two ecotypes and their distribution in the western sampling site. Red colour on pie chart displays the number of cod assigned to the North Sea reference, while blue colour displays the number of cod assigned to the “fjord” reference. Sample size is represented by size of pie chart (explained by legend in the right corner).

hydrographically complex environment, we applied a conservative approach to egg and larval vertical behaviour. Thus, the particles drifted at a fixed depth, uniformly distributed between 1 and 20 m throughout the simulations. Based on a previous study on cod larvae at drift in the greater North Sea area (Huserbråten *et al.*, 2018), this simplification of vertical behaviour (from more “realistic” to fixed drift depth) did not affect their predicted settlement areas significantly.

To locate the most probable source sites (i.e. spawning locations) of cod in the two model domains we “back-tracked” larval drift trajectories from observed 0-group/1-group cod in autumn to the most probable spawning locations in spring (see method applied in Huserbråten *et al.*, 2019). More specifically, an objective search algorithm identified drift trajectories (evaluated from all random particle release locations) that intersected the 0-group/1-group sampled locations, within the settlement phase 1st of June–20th July. This exercise was performed separately for all observations within each of the three sub-domains Færder (I), Ytre Hvaler (II), and Krokstad-/Kurefjord and Rauer Island (III). Here, all sampling sites with successful captures of “fjord”-assigned ecotype within the sub-domain were combined as one common sink, with a 1600 m radius buffer around the capture points (i.e. within ten grid points of the hydrodynamic model). Due to the coarser resolution of the large-scale model we used the entire outer Oslofjord area as settlement area when locating/“back-tracking” the North Sea/Kattegat source sites. The intersection of drift trajectories with the observed 0-group/1-group was, thus, interpreted as an indication of spawning at a given release point, and also confirmed that transport from the given area was physically feasible within the pelagic timeframe. Subsequently we fitted a 2D Generalized Additive Model (GAM) to the successful/unsuccessful drift intersection of a given release location with the identified settlement areas, with x and y coordinates of release point as covariates, as implemented in R-package “MGCV” (Wood and Wood, 2007).

Results

Assignment and size distribution of the two ecotypes

A total of 1022 individuals, representing 0-group and 1-group juvenile cod sampled in summer and autumn 2017 (0-group cod) and spring 2018 (1-group cod), respectively, were successfully genotyped and had an assignment score above 80% and >20 SNPs producing a valid genotype. Assignment tests showed that overall, there was a slightly higher proportion of cod assigned to the “North Sea” reference ($n = 530$) compared to the “fjord” reference ($n = 492$) in our data. The spatial distribution of genetically assigned individuals showed that both ecotypes seem to recruit to overlapping locations in the national parks, with no apparent distinction in habitat preference (Figures 2 and 3).

Sampling of 0-group cod performed in July and August 2017 aboard wrasse fisher vessels caught a considerably higher proportion of individuals assigned to the “North Sea” reference (98%) in both National parks. Mean size (cm \pm SD) of sampled 0-group cod was 9.37 ± 1.48 and 10.1 ± 1.43 , in July and August, respectively. (Figure 4, upper panels, Table 1).

Sampling conducted in September and October showed a higher abundance of 0-group cod assigned to the “fjord” reference in both National parks (Figure 4, middle panels, Table 1). On the West side, 57% of the 0-group cod caught in the beach seine was assigned to the fjord reference, and 43% to the North Sea reference. On the East side, the proportion of “fjord” cod was even higher (84%) with only 16% of the beach seine samples assigned to the “North Sea” ecotype. Mean size (cm \pm SD) of sampled 0-group cod in September was 8.2 ± 1.39 .

In May 2018, a total of 96 cod considered older than 1 year (14 to ≤ 30 cm FL) were caught, ranging in size from 14 to 30 cm, mean 21.7 ± 4.2 SD. Overall, there was a higher proportion of individuals assigned to the “North Sea” reference (65%). Body size, on average, was larger for 1-group cod assigned to “North Sea” than those assigned to “fjord” on the east side of the fjord (Figure 4, lower left

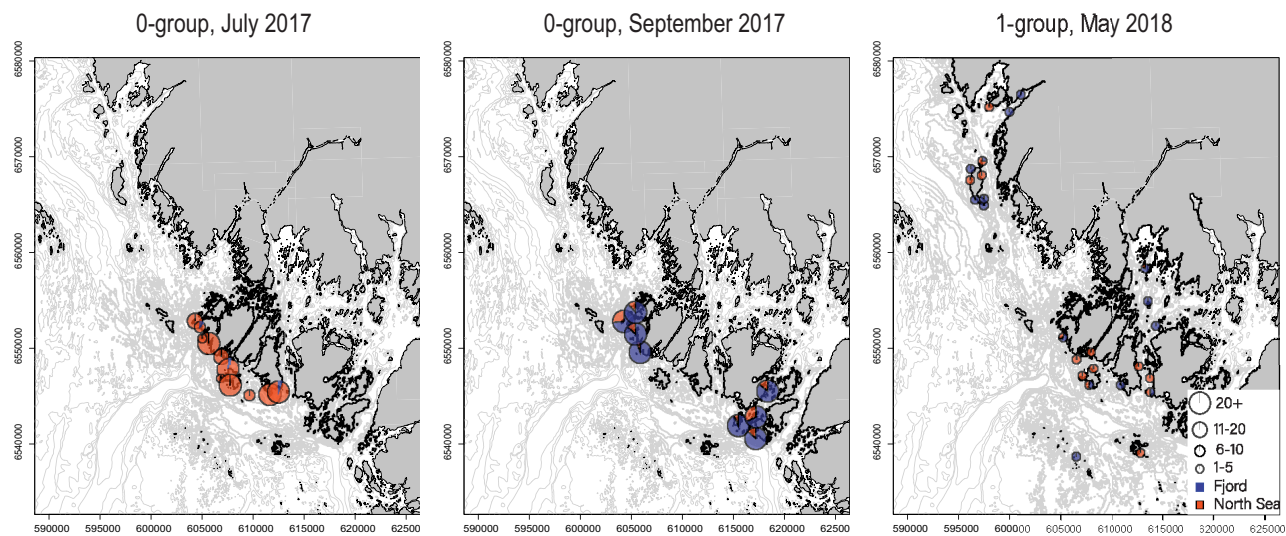


Figure 3. Spatial genetic assignment of the two ecotypes and their distribution in the eastern sampling site. Red colour on pie chart displays the number of cod assigned to the North Sea reference, while blue colour displays the number of cod assigned to the “fjord” reference. Sample size is represented by size of pie chart (explained by legend in the right corner).

panel), whereas the average size of both ecotypes was similar in samples from the west side (Figure 4, lower right panel). In May 2018, 14 and 19 larger cod (>30 cm) were sampled and assigned to the “fjord” (mean 39.6 cm \pm 6.63 SD, range 32–54 cm) and “North Sea” reference (mean 37.7 cm \pm 3.9 SD, range 31–50 cm), respectively.

Connectivity

Results from the large-scale biophysical model pointed to three likely source areas for long distance transport of eggs and larvae imported to nursery areas in outer Oslofjord, from the North Sea (Fladen ground and Fisher banks) and Kattegat (Figure 5). Fladen ground, a shallow bank located in the northern North Sea, was the potential source located furthest away from Skagerrak, and had a maximum probability of 3% of delivering recruits settling in the outer Oslofjord. Fisher bank, a sand bank located off the west coast of Denmark, was the most probable source of origin for transport of cod eggs and larvae from the North Sea into the outer Oslofjord region, with recruits spawned there having a maximum probability of 5% of settling in the outer Oslofjord. In addition, Kattegat also stands out as a potential source of recruits, with particles released along the coastal stretch between Halmstad and Gothenburg having up to 5% chance of settling in the outer Oslofjord. Interestingly, the model also suggested a high probability (up to 50%) of local sources of recruits from the north-eastern Skagerrak and the Oslofjord proper.

Results from the high-resolution, small-scale biophysical model suggested three possible sources of origin of local “fjord” cod; with one putative spawning area on the western side of the Oslofjord, and two on the eastern side. Here, the spawning area on the western side had a maximum probability of 5.3% of supplying larval recruits to the western sampling sites (Figure 6, box “I”); the eastern spawning area a maximum probability of 0.5% of supplying larval recruits to the eastern sampling sites (Figure 6, box “II”); and the north-eastern spawning area a 0.7% maximum chance of recruiting to the north-eastern sampling area (Figure 6, box “III”).

Population genetic structure

The 26 loci used for this study were chosen to segregate between the two cod ecotypes, and the results clearly illustrate that both ecotypes were present in both east and west side of the fjord (Supplementary Figure S1). Overall, we found no significant genetic differentiation for the “fjord” ecotype between the east and west side of the fjord ($F_{ST} = 0.0012$, $p > 0.1$). For the “North Sea” ecotype, genetic differentiation between the east and west side of the fjord was low, but significant ($F_{ST} = 0.0017$, $p = 0.027$). The pairwise F_{ST} showed overall higher differentiation for the “fjord” ecotype (Supplementary Table S1) compared to the “North Sea” ecotype (Supplementary Table S2), but only one comparison came out significant after FDR correction (Supplementary Table S1). The relationship between genetic differentiation and geographical distance was assessed between all “fjord” individuals both within sampling location and between sampling locations. No significance was found between genetic and geographic distances of assessed “fjord” individuals, whether measured among “fjord” individuals in the east (Mantel test: $p = 0.355$), or in the west ($p = 0.303$).

Discussion

Although the larger size component in coastal cod populations in eastern Skagerrak has declined dramatically, some years show a strong recruitment signal. As samples collected during such pulses of strong recruitment have been dominated by “North Sea” assigned individuals, it has been suggested that recruits originate mostly from offshore spawning grounds (Knutsen *et al.*, 2004; Stenseth *et al.*, 2006). These offshore originating individuals are hypothesized to migrate back to natal spawning grounds upon reaching maturity (e.g. Svedäng *et al.*, 2007). By utilizing one such year of strong recruitment (2017), we combined genetic data from recruits settled throughout the outer Oslo fjord seascape with a biophysical model of ocean drift to investigate which putative spawning locations were the most likely to contribute to successful recruitment into the area. Considering the apparent absence of older, mature cod in eastern coastal Skagerrak our null hypothesis assumed that cod recruits—

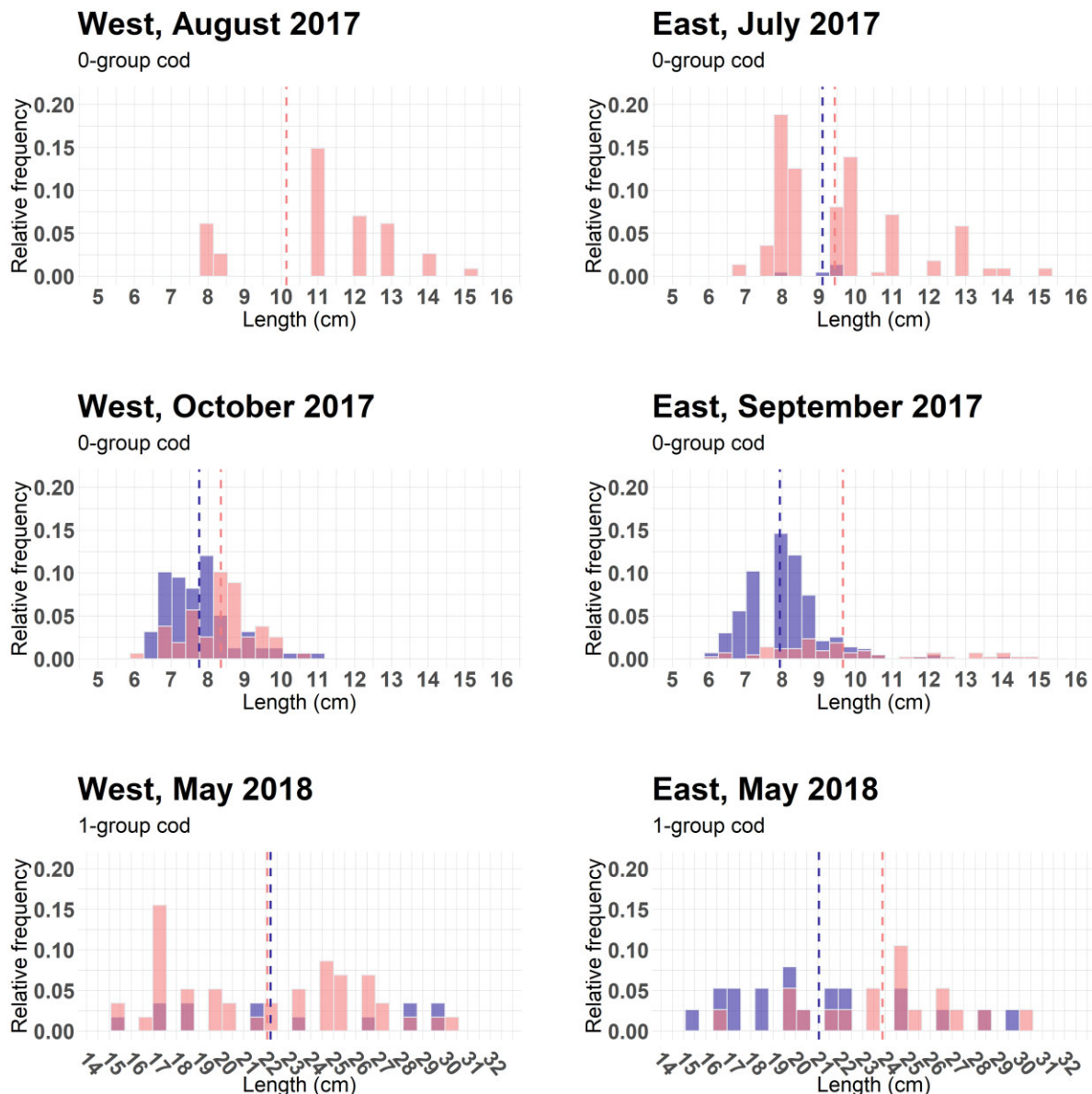


Figure 4. Relative frequency histogram showing length distribution of 2017 YOY “fjord” cod (blue) and “North Sea” cod (red) sampled on the west and east side of outer Oslofjord in 2017 (0-group) and 2018 (1-group). (Purple colour represents overlap in distributions). Average length is shown as dotted bars for both ecotypes. Relative frequency is displayed on the y-axis and length (cm) is displayed on the x-axis. Notice the different scaling of the x-axis in relation to whether 0- or 1-group cod are displayed.

irrespective of genetic assignment, settling into nursery habitat in the outer Oslofjord seascape—would have equal probability of originating from any putative source area in the biophysical models.

Genetic assignment of 0- and 1-group cod sampled in this study provided evidence that both ecotypes of Atlantic cod deliver viable recruits to areas in the outer Oslofjord seascape in eastern Skagerrak, which supports findings reported in earlier genetic studies (Munk *et al.*, 1999; Knutsen *et al.*, 2004, 2018; Stenseth *et al.*, 2006). Our results indicate that coastal cod in outer Oslo fjord harbor a mix of both ecotypes, at least during their first year of life. Previous studies (e.g. Jorde *et al.*, 2007) have found significant population structure on finer scales between coastal cod populations along the Norwegian Skagerrak coast, however, these studies were conducted prior to any knowledge on the chromosomal inversions (Sodeland

et al., 2016) and, thus, on the two ecotypes. Some genetic markers used for these studies (e.g. Jorde *et al.*, 2007) have been shown to be positioned inside the chromosomal inversions, that we now know to differ between the ecotypes. Thus, the former observed population structure of coastal cod could potentially be due to the different proportions of the two ecotypes in the sample.

High resolution back-tracking of larval dispersal trajectories in the Oslofjord suggested three spatially distinct spawning areas for “fjord” cod within or adjacent to the areas sampled for this study (cf. Figure 6). Proper fjord cod are known to be highly stationary and can live their whole life inside a fjord and populations are assumed to be mostly self-recruiting (Rogers *et al.*, 2014). Spawning site fidelity as well as retention of eggs and larvae have been proposed as mechanisms contributing to the observed population

Table 1. Sample overview of 0-group cod collected in 2017, and 1-group individuals collected in 2018, assigned to “fjord” and North Sea ecotype from the two national parks located on the west and east side of outer Oslofjord.

Year	Month	Life stage	Sampling gear	Sample size	Assigned to	
					North Sea	Fjord
Færder national park (west)						
2017	August	0-group	Pot trap	114	114	0
2017	September	0-group	Beach seine	158	68	90
2018	May	1-group	Fyke-net	58	44	14
Hvaler national park (east)						
2017	July	0-group	Pot trap	223	218	5
2017	September	0-group	Beach seine	431	68	363
2018	May	1-group	Fyke-net	38	18	20
Total				1 022	530	492

structure in Atlantic cod (Espeland *et al.*, 2007; Ciannelli *et al.*, 2010; Skjæraasen *et al.*, 2011). However, based on the genetic markers used in this study, cod from the North Sea proper could not be distinguished from the “North Sea” ecotype found along coastal Skagerrak. Thus, in reality, the locally sampled “North Sea” type could also potentially have been spawned in nearby coastal areas (Barth *et al.*, 2017; Jorde *et al.*, 2018a; Barth *et al.*, 2019); which also had the overall the highest success rate in our large-scale model (cf. Figure 6).

The large-scale hydrodynamic model pointed out three potential (long range) source areas that credibly could supply recruits to the outer Oslofjord (cf. Figure 5). First, the Fisher bank in the southern North Sea was suggested as the most probable source of long-range supply in our study area, which also holds a known spawning ground for cod (Munk *et al.*, 2009). Although no known investigations have been performed to reveal genetic composition of cod spawning on the Fisher Bank, it is assumed to be primarily used by “North Sea” ecotype cod. Second, the Fladen ground located outside the southwest coast of Norway, south-east to the Viking bank, was also suggested as a potential source of recruits albeit with slightly lower probability. While there is significant genetic heterogeneity also within the North Sea cod stock (Heath *et al.*, 2014); for the purpose of this study, no “fjord” ecotype cod is believed to be spawning in the northern North Sea (i.e. Fladen ground and Viking Bank). Previous drift-modelling studies have shown that larval drift from Viking bank and Dogger bank into Skagerrak (and possibly also to the coastal regions) could be of the same magnitude (Romagnoni *et al.*, 2020). Note that Dogger Bank did not come out as a likely source in our simulations; however, these dissimilarities are more likely to arise due to inter-annual variations in the surface layer drift patterns of the southern North Sea (e.g. Mathis *et al.*, 2015) rather than differences in modelling approaches. Third, Kattegat was also highlighted as a potential source of recruits in our large-scale model. Cod in the southern Kattegat is genetically quite similar to the coastal “fjord” cod ecotype and may well contribute to recruitment on the Skagerrak coast (Jonsson *et al.*, 2016; Barth *et al.*, 2017). While the realized connectivity between Kattegat and outer Oslofjord is largely unknown, there is certainly a potential for eggs and larvae to be transported northward with the Baltic outflow, before settling into nursery habitat in the outer Oslofjord. Yet, although a Kattegat source seems probable in our model, the limitations of the SNPs used for this study did not allow us to investigate the Kattegat–Oslofjord connectivity link any further. Moreover, the passive behaviour of the particles in the model is probably

a simplification of reality—at the same time there is no consensus on cod larval vertical movement/behaviour (due to little real-life data) making the implementation of a more “realistic” model an educated guess at best. Most of the advection will happen at the early phases (i.e. in egg and pre-flexion larval stages) when particles are more passive, and less advection is expected when pelagic juveniles start seeking to the bottom in summer. However, a sensitivity analysis on modelled vertical behaviour was done in an earlier paper (Huserbråten *et al.* 2018), which concluded that a more “realistic” model did not necessarily give significantly different drift outcome than fixed drift depths.

Overall, our sampling design was successful in obtaining a wide spatial coverage of the 2017 Atlantic cod cohort settling into nursery areas in the outer Oslofjord; however, the results showed some peculiar temporal patterns. For example, sampling performed in late summer (July and August) were dominated by cod assigned to the “North Sea”; yet, when sampling in September and October, the catches were dominated by cod assigned to “fjord” reference. This change of dominating ecotype in our data may reflect a period of high inflow of North Sea waters into Skagerrak (Knutsen *et al.*, 2004; Stenseth *et al.*, 2006), and/or different pulses of benthic recruits settling at different times (e.g. as showed also in Johannessen, 2014). More specifically, if considering batch spawning during an extended spawning season in larger cod, the temporal differences in assignment ratios could be due to different batches of recruits having reached different sub-areas (habitats) in the seascape at different times. Moreover, as different gear was used for the late summer (wrasse traps) and early fall (beach seine) sampling, this result also could be an artefact of juvenile cod reaching the size at which they were vulnerable to fishing gear at different times. Also, the different gear target different habitats in the seascape and it is likely that there is unknown and unobserved heterogeneity in habitat specificity of settling recruits operating at finer scale. Nevertheless, our results show that both ecotypes of cod are present in the system as 0-group cod, and both ecotypes are thus contributing recruits into the coastal population in this area.

Our results showed that both ecotypes are present in the outer Oslofjord as 1-group individuals. However, they both seem to disappear from the area after reaching 3 years of age, which could be due to migration or mortality, or both (Kleiven *et al.*, 2016; Kristensen *et al.*, 2021). Individuals larger than 30 cm were rare in both ecotypes. We suggest two possible explanations for the observed truncated size/age structure, which are not mutually exclusive. First, while the “fjord” ecotype is known to be rather stationary (as dis-

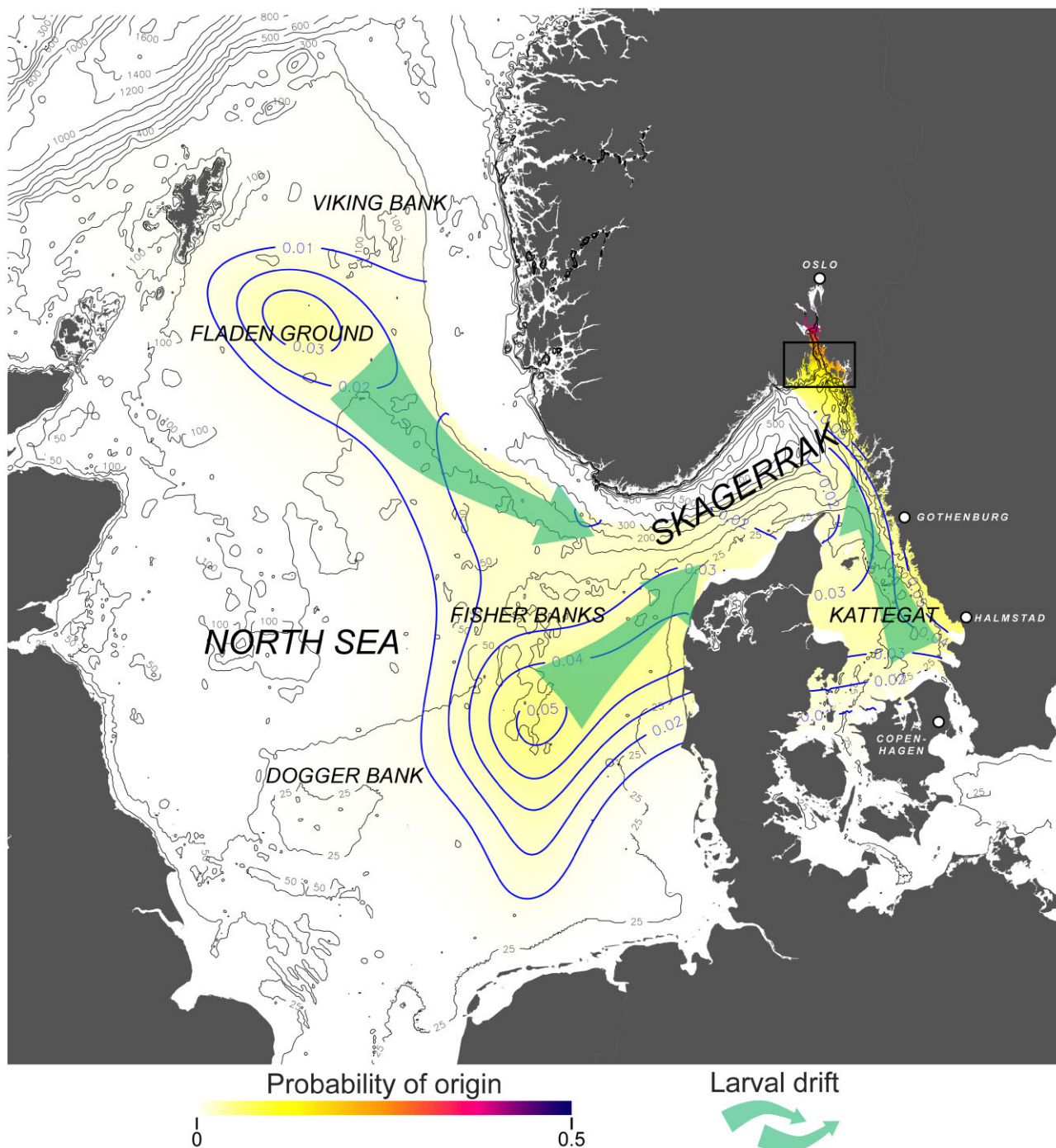


Figure 5. Predicted Atlantic cod source locations (spawning sites) of cod larvae settling into the outer Oslofjord in 2017, based on the large-scale hydrodynamical model. Green arrows represent the idealized drift routes from probability “hotspots” over Fisher Banks, Kattegat, and Fladen Ground, and black box represents the focal area and designated sink of recruits (the outer Oslofjord).

cussed previously), it is hypothesized that the “North Sea” ecotype uses coastal Skagerrak as nursery grounds, before eventually migrating back to natal spawning grounds in the North Sea (Pihl and Ulmestrand, 1993; André *et al.*, 2016). Second, the presence of juveniles but absence of older fish indicate that total mortality is high, and point to excessive fishing mortality with reduction of mean age and size, known as a common hallmark of overfishing (Pauly *et al.*, 2005; Francis *et al.*, 2007). Overfishing by removal of larger indi-

viduals not only reduces reproductive potential of the population, it also makes them more vulnerable to environmental fluctuations, by increasing recruitment variability (Hutchings and Reynolds, 2004; Berkeley *et al.*, 2004; Hsieh *et al.*, 2006). Bottom trawling in the area (mainly targeting northern shrimp, *P. borealis*) remove sessile benthic fauna and alter habitats, and is known to affect demersal fish both directly and indirectly (Dayton *et al.*, 1995; Preciado *et al.*, 2019). The “North Sea” ecotype is overrepresented in

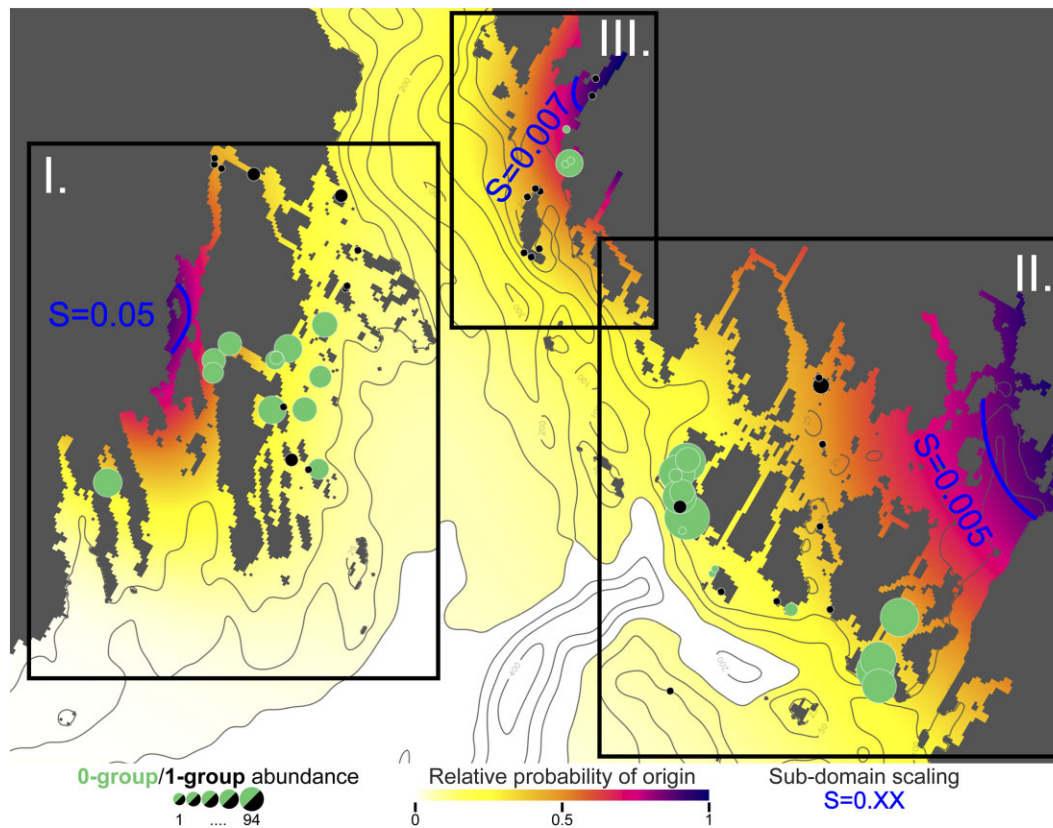


Figure 6. Predicted source locations (spawning sites) of “fjord” ecotype settling inside the Oslofjord, predicted from the small-scale hydrodynamical model. Note that the coloured gradients within sub-areas denoted by roman numerals must be scaled by: (I.) 0.053, (II.) 0.005, and (III.) 0.007; meaning that peak probability of recruitment to the sampled sites within the three sub-areas are: (I.) 5%, (II.) 0.5%, and (III.) 0.7%, with low end probabilities approaching zero. Also, plotted is the location and abundance of the 2017 cod cohort assigned to “fjord” origin, sampled as 0-group recruits during summer and autumn 2017 (green circles), and as 1-group juveniles ($\leq 30\text{ cm}$) in spring 2018 (black circles).

samples collected from shrimp trawlers in coastal Skagerrak (Jorde *et al.*, 2018b). In addition to overfishing, cod living in the species southern distribution range is facing several other challenges, as eutrophication, increasing temperature, and ocean acidification (Fretitas *et al.*, 2015; Havenhand *et al.*, 2019; Riera *et al.*, 2020). Thus, improved management is crucial for the protection and restoration of the species. Marine protected areas (MPAs) are valuable tools for management and small-scale application have demonstrated utility for coastal cod in Skagerrak by means of population, size, and survival increase (Moland *et al.*, 2013; Fernández-Chacón *et al.*, 2015; 2021). MPA networks can be designed according to home range size and ontogenetic movement patterns of target species and have the possibility to increase productivity and improve resilience of the ecosystem (Fenberg *et al.*, 2012; Roberts *et al.*, 2017). Our results point to three areas of interest located inside the study area, which would be good candidates for inclusion in a region-wide zoning scheme in outer Oslofjord. Protection of these areas could benefit the coastal cod population by providing suitable nursery habitat for juveniles, and with implementation of appropriately designed and scaled no-take zones might also increase abundance of larger individuals of both ecotypes, indirectly also increasing robustness of adjacent oceanic sub-stocks (i.e. North Sea and Kattegat).

In conclusion, results reported in this paper shows that both ecotypes of Atlantic cod are present in the outer Oslofjord seascape, both as 0-group and 1-group individuals. Genetic results combined with the oceanographic simulations does not rule out the occur-

rence of remnant local spawning/spawning migrations to coastal sites inside both sampling areas, as known to occur historically throughout the Oslofjord and other Skagerrak fjords. Verification of suggested local spawning areas and implementation of MPAs in the seascape studied herein could promote restoration of both ecotypes in the coastal cod mixture by increasing abundance and size distribution of protected individuals.

Data availability

The data underlying this article are available in the Dryad Digital Repository, at <https://doi.org/10.5061/dryad.nzs7h44sr>.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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