



Habitat effects on population connectivity in a coastal seascape

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ABSTRACT: Knowing how population connectivity varies across heterogeneous habitats can provide insight into the mechanisms underlying population structuring, and ultimately help to inform conservation and management actions. We studied whether the spatial extent of connectivity in coastal Atlantic cod *Gadus morhua* varied with coastal topography, hypothesizing that connectivity during all life stages would be greater among open, exposed habitats compared to sheltered, fjord-like habitats. We tested this hypothesis using (1) an extensive mark-recapture data set to analyze movements of age 1+ cod along a gradient from inshore (sheltered) to offshore (exposed) habitats, and (2) an analysis of demographic dependence (recruitment synchrony) among exposed versus sheltered areas using a 93 yr spatially explicit time series of juvenile (age-0) abundance. We found that habitat did have a significant effect on both the scale of recruitment synchrony and movement distances, both of which were greater in exposed regions relative to sheltered. However, even in open habitats, tagged cod were highly sedentary, and connectivity among regions due to movement of age 1+ individuals was exceptionally low. Thus, despite likely differences among habitats in dispersal of egg and larval stages, older cod were highly site-attached regardless of habitat. These results highlight how physical habitat interacts with behavior to determine the scale of population structuring in marine fishes.

KEY WORDS: Migration · Population structure · Skagerrak coast · Southern Norway · Synchrony · Connectivity · Dispersal

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INTRODUCTION

Population spatial structure emerges from a set of processes determining the connectivity and isolation of population subunits over space and time (reviewed by Ciannelli et al. 2013). Dispersal of individuals over space will tend to erode genetic structure and synchronize population dynamics, whereas natal homing and small home-ranges will promote genetic differentiation, local adaptation, and demographic independence among subpopulations. A wealth of terrestrial studies have shown that the spatial scale of these processes is often linked to landscape features

which may, for instance, facilitate movement or determine the direction of dispersal (Manel et al. 2003, Baguette & Van Dyke 2007). As in terrestrial landscapes, marine seascapes are heterogeneous environments, and the spatial scale of connectivity processes may vary depending on seascape features (e.g. Banks et al. 2007). Therefore, characterizing patterns of connectivity, and how they vary across a seascape, can provide important information for understanding population spatial structure in marine environments and the mechanisms that underlie it.

Marine fish populations were long thought to be demographically open and genetically homogeneous

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over broad expanses (Hjort & Dahl 1900, reviewed in Hauser & Carvalho 2008). This was largely due to the wide dispersal potential of pelagic eggs and larvae in oceanic currents and frequently-observed migrations in older fish. However, genetic and demographic structure is increasingly being documented at relatively fine spatial scales (Conover et al. 2006, Jorde et al. 2007, Hauser & Carvalho 2008, Knutsen et al. 2011). The mechanisms used to explain such population structure in marine environments include the retention of eggs and larvae in currents or eddies (Sponaugle et al. 2002, Morgan et al. 2009, Ciannelli et al. 2010), high mortality of dispersing individuals (KoeHN et al. 1980), and the homing of larval and mature fish to natal habitats (Jones et al. 1999, Thorrold et al. 2001). While the scale of larval dispersal has often been the focus of studies on marine population connectivity, adult behavior can also be a crucial factor (Frisk et al. 2014). It is therefore the combination of processes acting on early life stages as well as the behavior of older individuals which ultimately determines the spatial scale of population structuring and the degree of connectivity between sub-areas or regions.

Coastal ecosystems are dynamic and heterogeneous environments, often characterized by complex topography and currents. Such physical habitat features may result in spatial differences in larval or adult dispersal distances, and subsequent differences in the scale of population structuring. Recent studies of Atlantic cod *Gadus morhua* along the Norwegian Skagerrak coast suggest that coastal topography may be linked to population spatial structure. Genetic studies of coastal cod sampled in small fjords have documented population structure at a scale down to approximately 30 km (Knutsen et al. 2003, Jorde et al. 2007), where the pattern most likely arises from individuals sampled in sheltered locations far inside the fjords (Knutsen et al. 2011). Differences in coastal cod life-history traits have been observed at a similar spatial scale, indicative of local adaptations (Olsen et al. 2008). In contrast, genetic structure is less evident in more open continental shelf habitats (i.e. outside fjords) influenced by a strong coastal current (Knutsen et al. 2004, 2011). Together, these studies suggest that the spatial scale of population structuring and connectivity may vary among open and sheltered coastal areas.

While genetic tools can provide valuable information regarding population spatial structure, genetic signals become eroded at even very low levels of connectivity, equivalent to the exchange of only a few individuals per generation (Hauser & Carvalho

2008). Ecologically relevant structure may thus go undetected using only genetic tools, necessitating alternative approaches to study connectivity and population spatial structure. For instance, tracking of individuals can indicate the degree of connectivity among sub-areas, common garden studies can detect local adaptations which may go unnoticed by genetic tools (Hutchings et al. 2007), and demographic analysis can indicate whether (sub-) populations display demographic independence, which is generally considered to occur when fewer than 10% of individuals are exchanged between sub-areas (Hastings 1993). However, such approaches are often challenging in marine environments due to the difficulty of observing individual organisms and the lack of demographic data on appropriate spatial or temporal scales.

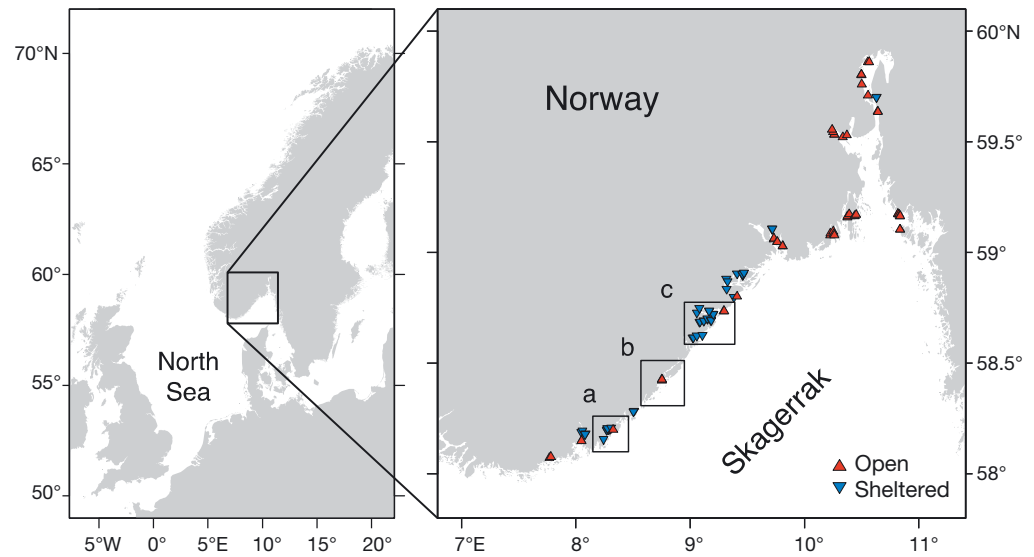
Here, we analyze the movements of individuals together with spatial patterns in recruitment dynamics to draw inferences about connectivity along the Skagerrak coast during multiple life stages of Atlantic cod. We hypothesize that coastal topography plays an important role in determining the spatial scale of connectivity in coastal cod populations. We expect that populations inside fjords will be structured at a finer scale than those in outer coastal areas, and that this will be reflected in the recruitment dynamics and in the behavior of older life stages. We first analyze a 93 yr time series of juvenile cod abundance sampled along ~250 km of the coastline to compare the spatial scale of recruitment synchrony among open versus sheltered areas. We then compare these results to the spatial patterns of juvenile and adult movements using an extensive mark-recapture study of cod tagged along a gradient from sheltered to open habitats in 3 separate regions of the Norwegian Skagerrak coast. This allows us to examine differences in movement strategies among cod found inside versus outside of fjords, as well as to detect connectivity to offshore areas such as the North Sea. Finally, we put these results in the context of recent population genetics findings to draw general conclusions about patterns of connectivity and scales of population structuring in complex coastal habitats.

MATERIALS AND METHODS

Study area and species

The Atlantic cod *Gadus morhua* is an ecologically important harvested species found in coastal and offshore shelf habitats in the North Atlantic. It is a highly

Fig. 1. Study area. Locations of beach seine stations used in the Atlantic cod recruitment analysis are indicated by triangles and colored according to their degree of exposure to the open Skagerrak. Regions where tagging of individuals took place are indicated by (a) Lillesand, (b) Arendal, and (c) Risør



fecund batch-spawner with pelagic eggs and larvae (Kjesbu 1989). In the coastal Skagerrak (Fig. 1), the larvae metamorphose into juveniles and settle in near-shore nursery areas during May and June. Growth is about 10 to 15 cm yr⁻¹ and maturity sets in at an age of 2 to 4 yr and a body length of 30 to 50 cm (Dannevig 1954, Olsen et al. 2008). Spawning has been documented in some fjords, particularly in sheltered areas away from the Norwegian Coastal Current (Knutsen et al. 2010), but comprehensive knowledge of spawning locations is lacking. Coastal cod in the Skagerrak experience considerable harvest pressure from both commercial and recreational fishers, and few individuals survive past age 5 (Julliard et al. 2001).

Long-term beach seine survey

Since 1919, an annual beach seine survey has been conducted to study variability in juvenile cod abundance on the Norwegian Skagerrak coast (see Stenseth et al. 1999 for a detailed description). The survey initially included 66 sampling stations between the southern tip of Norway and Kragerø, and since 1936 has extended north to Oslo Fjord and east to the Swedish border (Fig. 1). Stations are distributed from sheltered locations far inside fjords to exposed areas on the open Skagerrak coast. The survey is carried out in September to October of each year and primarily captures half-year old cod (hereafter referred to as 'age-0' or 'recruits'). The abundance of age-0 cod in autumn will reflect the reproductive output of spawners, the probability of larvae drifting to and settling at a particular site, and survival through the first summer.

Spatial scale of recruitment synchrony

Spatial coherence in age-0 variability could arise if juveniles come from a common pool of spawners, if eggs and larvae from multiple pools of spawners are mixed prior to settling in demersal habitats, or if exposure to common environmental conditions has spatially similar effects on spawning or early-life survival. To calculate the spatial coherence in the variability of age-0 cod abundance, we calculated the Pearson's correlation coefficient in log-transformed age-0 catches for each pair of stations. A constant of 1 was added to all catches to avoid taking the log of zero counts. Log-transformation has the effect of reducing the influence of extreme high catches on correlation coefficients. However, because catches were sometimes zero, often low (e.g. <10 ind.), and occasionally very high (max. catch = 934 ind.), we also calculated correlations assuming a bivariate Poisson log-normal distribution (Engen et al. 2008), which may be more appropriate for overdispersed count data (O'Hara & Kotze 2010). We selected only those stations which were sampled at least 50% of the years since 1919 ($n = 95$), and correlations were only calculated for pairs of stations which overlapped in their temporal coverage by at least 20 yr.

We quantified the rate at which correlations in age-0 abundance decreased with increasing geographic distance by fitting an exponential decay model:

$$\rho(d) = \rho_r + \rho_0 e^{-\left(\frac{d}{v}\right)}$$

where $\rho(d)$ is the pairwise correlation at distance d , ρ_r is the asymptotic correlation, or background regional

correlation in recruitment, and $\rho_r + \rho_0$ is the estimated correlation at zero distance. The parameter v describes the rate at which correlations decrease with distance, and is referred to as the e-folding scale (Bjørnstad et al. 1999). Specifically, v estimates the distance at which the pairwise correlation between time series is reduced to $\sim 37\%$ (e^{-1}) of that at zero distance, relative to the background regional level of correlation. This model was modified from that of Myers et al. (1997) and Bjørnstad et al. (1999) by including an additional term (ρ_r) such that the correlation at maximum distance is not assumed to be zero.

To test our hypothesis that the spatial scale of recruitment synchrony would be greater for cod in open habitats outside fjords, we classified stations according to their degree of exposure to the open sea, and fit models separately to sheltered versus exposed stations in order to compare estimates of v . A second set of models were fit to first-differenced log-transformed data in order to remove long-term trends from the survey data. Models were fit using non-linear least squares in R (R Development Core Team 2011), with pairwise correlations weighted by the number of overlapping years used to calculate each correlation. Bivariate Poisson log-normal distributions were estimated using the function 'bipoi-logMLE' in the 'poilog' package in R. A cost-distance function, implemented using the 'gdistance' package in R, was used to calculate the shortest distance over water between stations.

Mark-recapture-recovery study

From 2005 to 2010, a mark-recapture-recovery study was conducted along the southern part of the Norwegian Skagerrak coast. Cod were captured in fyke nets between April and June and individually marked with an external T-bar anchor tag (TBA-2, Hallprint). A total of 9518 individual cod were tagged and released. Tagged individuals ranged from 15 to 93 cm in total length (mean = 40 cm), corresponding to ages 1 and older. All cod were captured in shallow water (1 to 5 m depth) and released at the exact point of capture immediately after being tagged and measured. Earlier studies have evaluated T-bar tagging mortality and tag loss in Atlantic cod, and found similar short-term mortalities between tagged and untagged cod (control group), while annual tag loss could be in the range of 10 to 20% (Bratley & Cadigan 2004, Cadigan & Bratley 2006). In our study, recaptures consisted of

live recaptures by researchers and by local eel fishers who were paid to report and release cod caught in their fyke nets as bycatch, and dead recoveries which were reported by recreational and commercial fishers. To encourage the reporting of marked fish, tags were printed with a return address and reward (either 50 or 500 Norwegian kroner). When available, the date, location, and length at recapture were recorded. When exact latitude and longitude were unavailable, an approximate latitude and longitude were assigned based on the description of the area.

Tagging effort was focused in 3 sections of coastline with differing structure and bathymetry nearby the towns of Lillesand, Arendal, and Risør (Fig. 1). Within each region, tagging effort was well-distributed along a gradient from the innermost habitats of fjords to outer islands, which are exposed to the open sea (Fig. 2). Previous work has suggested that cod eggs are largely retained within fjords by inward-flowing currents and shallow sills, promoting the maintenance of local population structure (Ciannelli et al. 2010). The fjords near Lillesand and Risør have such sills, whereas Arendal does not and is more appropriately described as a bay, partially protected from the Skagerrak by coastal islands.

Statistical modeling of movement patterns

Generalized additive models (GAMs) were used to determine whether there were spatial patterns in movement distances, or whether there were other ecological factors associated with movement distances. For each region, the distance (calculated as the shortest distance over water) between tagging location and final recapture location was natural log-transformed and modeled as a bivariate smooth function of the latitude and longitude of tagging. Additional terms considered were the number of days between tagging and recapture (DaysBtw), the month of tagging (fMonthT) and of recapture (fMonthR), and the total length at tagging (Length). Thin plate regression splines were used for each term except month, which was modeled as a factor. Models were restricted to include only individuals with at least 30 d at liberty. Model selection proceeded by comparing the generalized cross validation (GCV) scores of competing models, with a lower GCV indicating lower prediction error and thus a stronger model. All GAMs were implemented in the 'mgcv' library in R (Wood 2006).

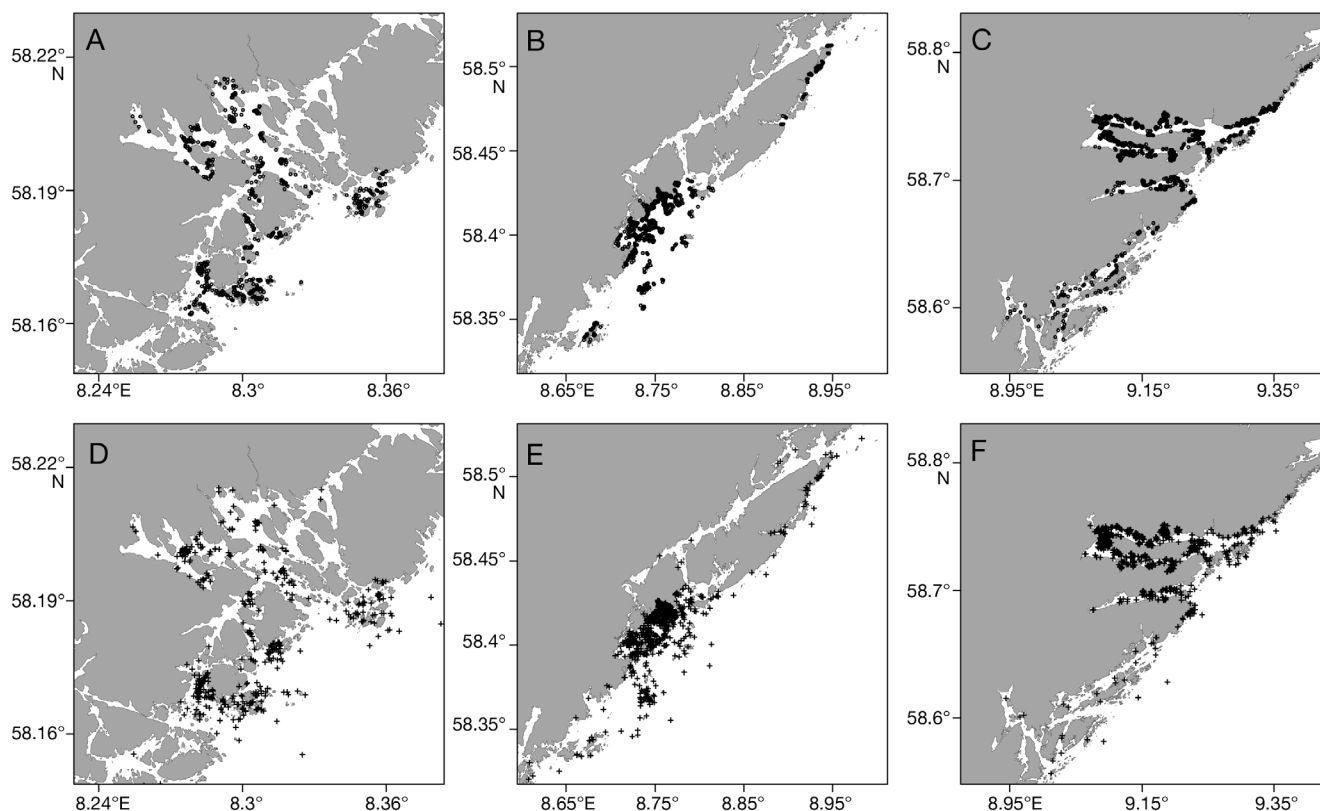


Fig. 2. (A–C) Tagging locations of Atlantic cod and (D–F) final recapture locations within the regions Lillesand (A,D), Arendal (B,E), and Risør (C,F)

RESULTS

Spatial scale of covariation in recruitment

Temporal variation in the abundance of age-0 cod was correlated among all regions of the Norwegian Skagerrak coast (Fig. 3). Correlations were highest among nearby stations, and declined with increasing distance. This decline occurred rapidly when comparing among stations inside fjords, with correlations remaining above background regional levels only for stations less than ~25 km apart. This corresponds to roughly the scale of a single fjord. In contrast, stations on the outer coast showed a coarser spatial structuring, with elevated recruitment synchrony up to distances of approximately 75 km. Accordingly, v was estimated to be 3 times larger in exposed versus sheltered areas ($v = 33.7$ and 11.6 km, respectively, based on analysis of log-transformed count data). ($\rho_0 + \rho_r$) and ρ_r were not significantly different between sheltered and exposed

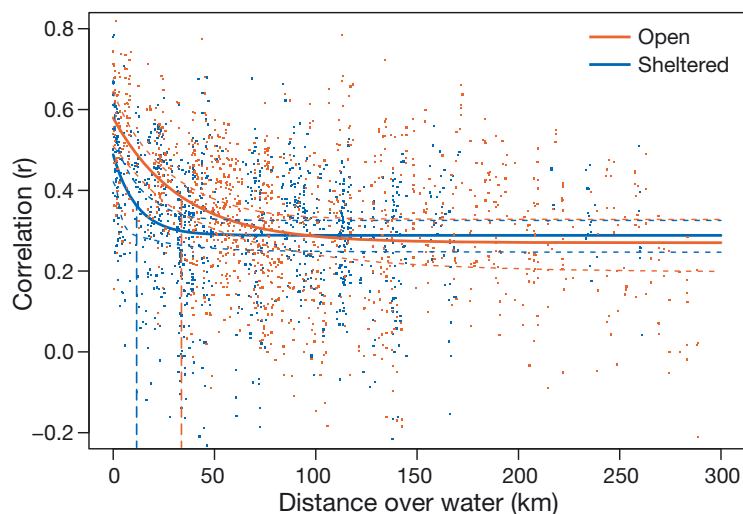


Fig. 3. Pairwise correlations among time-series of log(age-0 abundance) of Atlantic cod for 95 stations along the Norwegian Skagerrak coast. Solid lines show the fitted exponential decay model for stations in sheltered (dark blue) and open (light orange) areas, along with bootstrapped 95% confidence intervals (dashed lines). Vertical dashed lines indicate the e-folding scale (v), estimated to be 11.6 km (95% CI = 1.8–27.4) for stations in sheltered areas, and 33.7 km (95% CI = 20.3–57.9) for stations on the outer coast. Confidence intervals are based on 10000 bootstrap replicates (Bjørnstad et al. 1999)

Table 1. Mark-recapture experiment on Atlantic cod carried out from 2005 to 2010 in 3 regions along the Norwegian Skagerrak coast. Final recapture locations are given for cod tagged in the 3 primary study regions. For recapture locations outside the study regions, SW indicates coastal areas to the southwest of Lillesand, and NE indicates coastal areas to the northeast of Risør. Offshore recaptures include those in the Skagerrak near Norway, Denmark and Sweden, and in the North Sea

Tagging region	No. marked	No. re-captured	Median distance (km)	Moved >20 km	Recapture location					
					Within study regions			Coastal Skagerrak		Offshore
					Lillesand	Arendal	Risør	SW	NE	
Lillesand	1663	646	0.26	13	631	4	0	4	1	6
Arendal	3883	1309	0.38	36	1	1274	6	11	4	13
Risør	3972	1347	0.37	20	0	9	1328	1	3	6

stations. Analysis of first-differenced data gave nearly identical results ($v = 36.9$ km for exposed areas and 11.4 km for sheltered areas). Results from the bivariate Poisson log-normal model agreed with the analysis of log-transformed counts ($v = 32.0$ km for exposed areas and 10.8 km for sheltered areas).

Movement patterns of age 1+ cod

Out of a total of 9518 fish that were tagged and released, 3302 (35%) were recaptured at least once during the duration of the study (Table 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m511p153_supp.pdf). Of these, 715 were recaptured multiple times. Only the final recapture occasion (dead or alive) was considered for subsequent analyses of movement patterns. The median number

of days between tagging and final recapture was 115 (range: 2 to 1588). Final recaptures were primarily made by recreational (45%) and professional (42%) fishers, with a smaller proportion (13%) made by researchers. Recaptures were well distributed throughout the 3 study regions, from the most sheltered areas to the outer coast and offshore (Fig. 2). The majority of recaptures occurred in summer, likely reflecting increased fishing effort during this time (especially by recreational fishers on holiday) but recaptures were reported during all months of the year (Fig. S1 in the Supplement).

The vast majority of individuals were recaptured in close proximity to their tagging location (Fig. 4B,C). Considering all recaptured individuals, 81% were caught within 1 km of where they were tagged and released. Of those at liberty for a minimum of 1 yr ($n = 681$), 71% were recaptured within 1 km of their

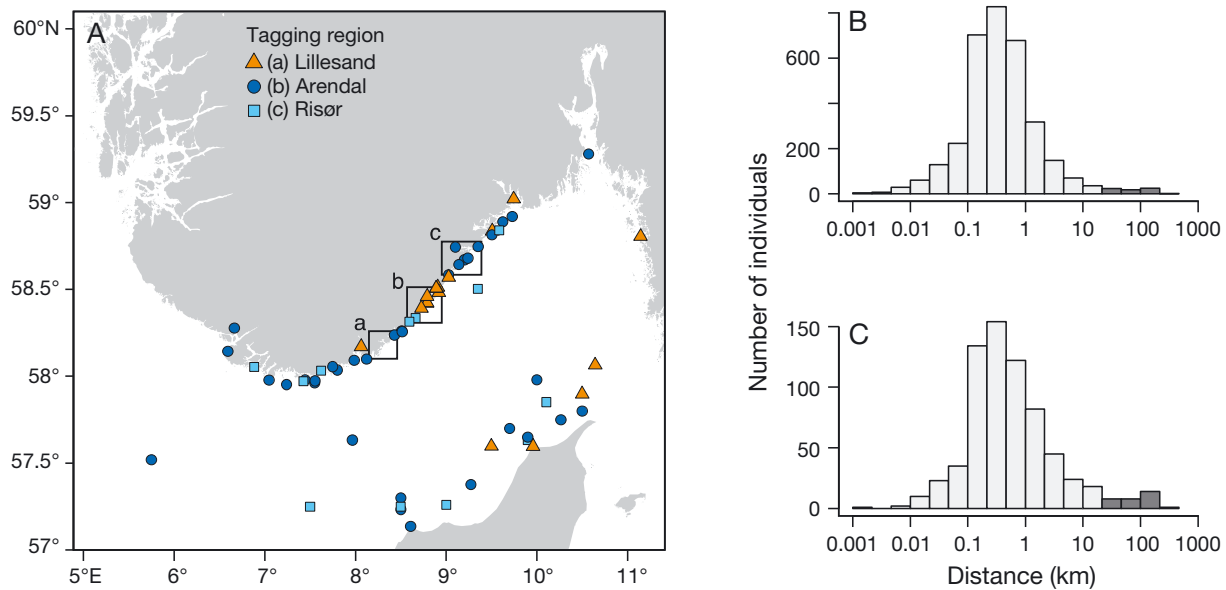


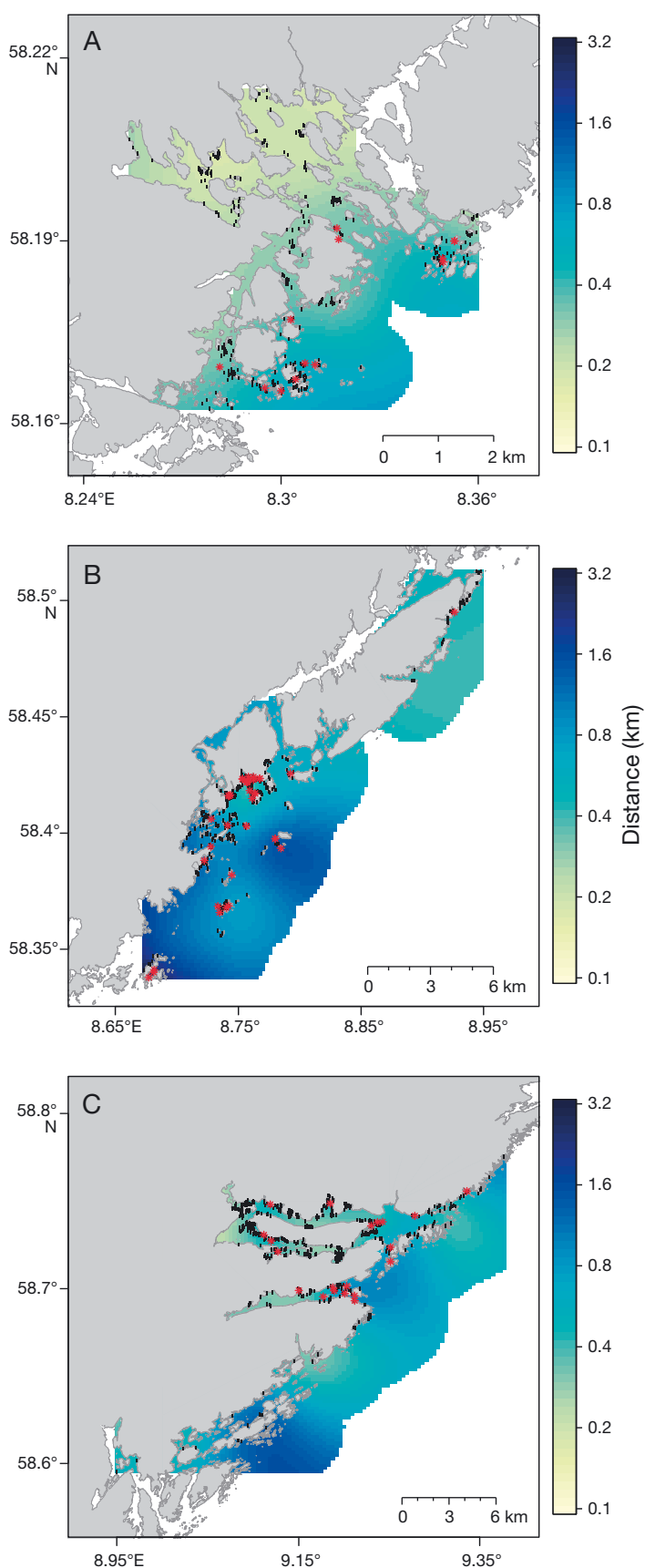
Fig. 4. (A) Recapture locations of long-distance dispersers (Atlantic cod recaptured >20 km from tagging location). Symbols indicate the region where tagged. The distribution of distances between tagging and final recapture locations are shown for (B) all recaptured individuals and (C) individuals with at least 1 yr at liberty. Long-distance dispersers (dark bars) represented only 2% of all recaptures

tagging location. Almost all (98 %) of the documented movements occurred within fjords or regions (Table 1). Forty-four individuals were captured elsewhere along the Skagerrak coast, and 25 were caught far offshore, either towards the Danish coast or in the North Sea proper (Table 1, Fig. 4A). Assuming a recapture rate of 35 % and similar mortality rates between stationary and non-stationary fish, we estimate that approximately 2 % of the cod present in the coastal Skagerrak region in April to June exhibited long-distance dispersal, defined as movements >20 km. This is an underestimate if the probability of a tagged fish being recaptured and reported was lower in regions outside the study area, or if mortality was higher among dispersing fish.

Within-region differences in movement patterns were indicated by GAMs. The best model of the distance between tagging and recapture locations for each region, according to GCV scores, included a bivariate smooth term for latitude/longitude where tagged, the month of recapture, and a smooth or linear term for the number of days between tagging and recapture (Table S2 in the Supplement). Length at tagging was also included as a linear term in the final models for Arendal and Risør, indicating a slight increase in $\log(\text{distance})$ with larger body size (Fig. S2 in the Supplement). The final models explained between 13.1 and 22.3 % of the variance in $\log(\text{distance})$.

All 3 regions demonstrated clear spatial patterns in the distance between tagging and recapture locations, with the distance being generally greater for fish tagged in exposed areas rather than in more sheltered areas (Fig. 5). This gradient was clearest for the Lillesand region, with fish tagged in the inner parts of the fjord showing the shortest movement distances within any of the regions. The onshore/offshore gradient was least clear in Arendal and the predicted movement distances were on average higher than in the other 2 regions, with cod tagged around some offshore islands showing the greatest movement distances. These spatial patterns did not change when fish recaptured less than 1 yr after tagging were excluded.

Fig. 5. For regions (A) Lillesand, (B) Arendal, and (C) Risør, colors show the fitted generalized additive model (GAM) prediction surface based on the latitude and longitude of the location of tagging Atlantic cod, indicating spatial patterns in the distance between tagging and recapture locations. Symbols indicate the tagging locations of fish recaptured at least 30 d later, with red stars indicating the fish which were recaptured >20 km away. Predicted distances are given for median values of the other covariates (length = 470 mm, days at liberty = 115, month of recapture = July)



The inclusion of month and days at liberty in the final models suggests temporal patterns in movement. In all regions, movement distance increased with the number of days between tagging and recapture (Fig. S2). However, when only recaptures with at least 1 yr at liberty were included in the model ($n = 89, 243, \text{ and } 348$ for Lillesand, Arendal, and Risør, respectively), time at liberty became insignificant for both Risør and Arendal. In general, the fish recaptured in winter months (Dec to Mar) were recaptured further from where they were tagged than fish recaptured during the rest of the year (Fig. S3 in the Supplement), indicating seasonal changes in behavior or spatio-temporal changes in recapture effort. However, by including the month term in our models we accounted for such variation when estimating the spatial patterns in movement.

DISCUSSION

The spatial structuring of marine fish populations has long been the subject of scientific investigation and speculation (e.g. Hjort & Dahl 1900), as it determines at which geographic level local adaptations may evolve, the spatial extent of population impacts caused by local or regional disturbances, and the appropriate spatial scale for management plans. Recent evidence of an erosion of population structure in some marine fishes (Hutchinson 2008), as well as of the importance of maintaining population diversity and local adaptations for fisheries sustainability (Schindler et al. 2010), emphasize the need to correctly characterize population units and the degree of connectivity between those units. With increasing frequency, marine fishes are being described as metapopulations, consisting of several subpopulations mixing to an intermediate degree, rather than larger panmictic units or multiple independent populations (Kritzer & Sale 2004). Our study indicates that Skagerrak coastal cod fall in the continuum between a metapopulation and multiple independent populations, and that the degree of connectivity likely differs depending on seascape features. While cod in inner fjord areas appear to consist of independent populations, with local recruitment dynamics and highly site-attached adults, cod in exposed areas of the coast likely have greater connectivity over longer distances due to dispersing early life stages. Thus, we find evidence that the population structure on the coast is complex, and cannot easily be described by any single conceptual model of population spatial structure.

Based on the analysis of recruitment time series, the spatial scale of recruitment synchrony clearly differed between exposed (i.e. open) and sheltered regions of the coast, with exposed areas showing elevated correlations in recruitment up to a distance of ~75 km (Fig. 3). This matches our prediction of higher rates of egg and larval dispersal among open areas, which would act to homogenize the recruitment dynamics along the coastline. Strong coastal currents along the Skagerrak coast in spring may, on average, transport early life stages along the entire coast over ca. 1 wk (cf. Danielssen et al. 1997). In contrast, when comparing among sheltered areas, correlations in recruitment decreased rapidly with distance, remaining above background levels essentially only for stations sampled within a single fjord. An analysis of egg buoyancy and circulation patterns within fjords found that eggs are concentrated in inward-flowing currents, acting as a retention mechanism for eggs spawned locally within fjords (Ciannelli et al. 2010). Tagging studies on recently settled age-0 cod also indicate that this early life stage is very stationary (Grant & Brown 1998, Olsen et al. 2004). Our recruitment analysis provides further support for the hypothesis that dispersal among the inner fjord areas is low, and that local spawning populations are largely self-recruiting.

Spatial correlation in recruitment can also be caused by spatial correlation in factors which affect recruitment (Myers et al. 1997), such as zooplankton quality or quantity (Beaugrand et al. 2003). Because average correlations were above zero for all distances, even up to ~280 km, this suggests some common environmental influence on recruitment all along the Skagerrak coast, including exposed and sheltered areas. Indeed, Fromentin et al. (1998) found a low-frequency signal in recruitment that was common to all regions, and not spatially-structured, suggesting a common extrinsic factor such as climate (i.e. a Moran effect; Moran 1953). However, when the long-term trend was removed from our data by first-differencing, and year-to-year variation compared, the spatial patterns remained the same. This demonstrates that similarity in long-term trends is not driving the distance-decay patterns we observed. Environmental conditions could still play a role if conditions are more homogeneous along the outer coast than among fjords, which could result in the different distance-decay patterns found. The higher correlations among nearby areas (within single fjords, and across exposed regions) thus likely contain a signal of both locally correlated environmental conditions and the dispersal of eggs and larvae. Fully quantifying the rela-

tive contributions of shared environmental conditions and dispersal to the correlation patterns found will require substantial advances in particle-tracking methods or genetic tools such as parentage analysis. However, both indicate important differences in the spatial scale of factors influencing populations in sheltered versus exposed regions.

While both genetics and recruitment data suggest differences in early life-stage dispersal among exposed and sheltered parts of the coastline, the tagging experiment did not show corresponding strong differences in the scales of movement at older life stages. Although cod in the more exposed parts of the coastline were, on average, recaptured slightly further from their point of tagging than cod in the most sheltered fjords, the differences were slight in ecological terms. This raises questions about the ultimate fate and behavior of individuals dispersed as eggs or larvae. In other cod populations, such as the Northeast Arctic cod, long-distance dispersal of larvae is matched by migrations of older age classes back to natal spawning grounds (Robichaud & Rose 2004). We did not find evidence for consistent natal migrations, either to offshore spawning grounds (e.g. in the North Sea), or along-shore to other coastal spawning grounds. This indicates that any cod of non-local origin are either small in number relative to locally-spawned individuals, or do not demonstrate natal homing behavior and rather carry out their life cycle close to where they settle as juveniles. Only a few immigrants per generation is sufficient to prevent differentiation at neutral genetic markers; thus connectivity among the coastal areas and with offshore stocks may still be very low despite the lack of a clear genetic signal. Determining the fate of early life stage dispersers remains the biggest challenge for characterizing cod population spatial structure in exposed coastal areas.

The limited spatial movements of Skagerrak coastal cod documented herein are remarkable among cod populations. During all months of the year, cod were recaptured, on average, within 2 km of where they were tagged. Acoustic telemetry studies in the same area found cod home ranges of less than 80 ha, confirming that Skagerrak coastal cod exhibit extraordinary sedentary behavior (Espeland et al. 2007, Olsen et al. 2012). In other cod stocks classified as sedentary, typical movement distances are an order of magnitude longer (10 to 20 km) (Robichaud & Rose 2004), which is still a strong contrast to the >1000 km migrations made by Northeast Arctic cod to their spawning grounds each winter. Such remarkable variation in movement illustrates the ability of cod to utilize different physical and behavioral mechanisms

to maintain population persistence, and is also likely linked to the spatial scale of population structuring. The extreme sedentary behavior observed in the coastal Skagerrak suggests that cod in this region, particularly in sheltered fjord areas, may exhibit population spatial structure at a finer scale than elsewhere in its range.

While long-distance movements were rare, a small proportion (~2%) of individuals were detected to have moved over 20 km. These few long-distance dispersers are indicative of population heterogeneity, and could either be individuals of non-local origin or local cod exhibiting a divergent 'straying' type of behavior. Such divergent movements are common in natural populations of mobile organisms and may represent bold individuals that risk movement across potentially hazardous habitats for potential fitness advantages such as increased growth rate (Fraser et al. 2001). On a population level, even rare long-distance dispersal may influence processes such as gene flow, and ultimately be important for meta-population dynamics by reducing the occurrence of local extinctions.

The prevalence of long-distance movements may be underestimated due to spatial biases in recapture effort and reporting. Recapture effort by researchers was focused within the 3 study areas; total recapture effort therefore may have been lower outside the study areas relative to inside. However, only a minor fraction (13%) of the total recaptures were made by researchers, and evidence from other studies suggests that fishing rates by commercial and recreational fishermen were likely to be relatively high elsewhere along the Norwegian Skagerrak coast, as well as offshore in the Skagerrak, Kattegat, and North Sea. Previous tagging studies in the eastern Skagerrak and Kattegat have reported recapture and reporting rates by commercial fishers ranging from 20 to 66% depending on region and year (Robichaud & Rose 2004, Svedäng et al. 2007). There is no reason to believe that reporting rates for the current study should have been lower. Therefore, the very low number of reported recaptures in the Eastern Skagerrak, Kattegat, and North Sea (Table 1, Fig. 4) indicates that migrations of coastal cod to these regions must be rare. Spatial variation in recapture effort could also bias the comparison of sheltered versus protected areas. For instance, if no recapture effort occurred in sheltered regions, only the fish moving out of these areas would be detected. While we cannot quantify the effort, the spatial distribution of recapture locations (Fig. 2) suggests that recapture effort was well distributed throughout the 3 regions.

Further knowledge of connectivity processes in marine fishes and how they are shaped by seascape features will help to guide conservation and management of marine resources, a highly relevant topic today given the growing human impacts on coastal ecosystems. Marine reserves are increasingly being implemented to aid in the conservation and recovery of exploited populations; however, the effectiveness of marine reserves depends critically on the spatial scale of processes such as larval and adult dispersal (Botsford et al. 2003, Kritzer & Sale 2004, Grüss et al. 2011). In 2012, Norway's first no-take marine reserve was established in the Tvedestrand fjord between our Arendal and Risør study sites, spanning 1.5 km² of the inner fjord habitat and including a major cod spawning and nursery area (Ciannelli et al. 2010). Marine reserves are generally not considered for highly migratory species such as Atlantic cod, but what we now know about movement and dispersal of Skagerrak coastal cod suggests that even a relatively small reserve could be an effective conservation tool in this region, protecting sedentary adults from harvest (see also Moland et al. 2013). However, any spill-over benefits to fishers outside the reserve will depend on relative dispersal rates of eggs and larvae into and out of the reserve (Botsford et al. 2003), which likely vary among inshore versus exposed areas. Reserve placement within the coastal seascape will therefore be critical for its success, depending on the stated (conservation and/or fisheries) goals.

Identifying the spatial scale of population structuring is critical for the successful monitoring, management, and conservation of marine fishes. Current fisheries management strategies are often criticized for not considering population units at an appropriate biological scale (Hutchinson 2008, Reiss et al. 2009). Our results emphasize how the processes underlying spatial population structuring can differ across space, as well as through a life-cycle, resulting in a complex spatial population structure mapped on a heterogeneous seascape. Such spatial complexity is certainly not unique to this system, and calls for the development of management strategies that are either adapted to, or robust to uncertainties in population spatial structure.

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