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Transport of North Sea cod larvae into the Skagerrak coastal populations

Halvor Knutsen[1,2], Carl André[3], Per Erik Jorde[1,2], Morten D. Skogen[4], Emma Thuróczy[3] and Nils Chr. Stenseth[1,2*]

[1]*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1050 Blindern, N-0316 Oslo, Norway*
[2]*Flødevigen Marine Research Station, Institute of Marine Research, N-4817 His, Norway*
[3]*Department of Marine Ecology, Göteborg University, Tjärnö Marine Biological Laboratory, S-452 96 Strömstad, Sweden*
[4]*Institute of Marine Research, N-5817 Bergen, Norway*

The Atlantic cod (*Gadus morhua*) is economically one of the world's most important marine species—a species presently suffering from heavy overexploitation throughout its range of distribution. Although not fully understood, the Atlantic cod is believed to be structured into populations in a rather complex manner, whereby both highly migratory and more confined ocean-spawning stocks coexist with stationary coastal populations. Owing to the complex population structure, little is presently known about how overexploitation of offshore stocks may affect other segments of the species. Here, we use microsatellite DNA analyses of coastal and offshore cod in combination with oceanographic modelling to investigate the population structure of Atlantic cod in the North Sea–Skagerrak area and evaluate the potential for larval transport into coastal populations. Our results suggest an extensive but temporally variable drift of offshore cod larvae into coastal populations. In a year (2001) with high inflow of North Sea waters into the Skagerrak we find that juvenile cod caught along the Skagerrak coast are predominantly of North Sea origin, whereas in a year (2000) with low inflow juveniles appear to be of local origin. These findings indicate that offshore cod may influence coastal cod populations over large distances.

Keywords: Atlantic cod; *Gadus morhua*; larval drift; local populations; genetic differentiation; microsatellite DNA

1. INTRODUCTION

Recent molecular genetic analyses have demonstrated that the coexistence of multiple populations within a species is a common phenomenon (Avise 2000). Many marine fishes of great commercial value, including the Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*), are characterized by large offshore spawning populations and smaller aggregations confined to coastal waters (Danielssen 1969; McQuinn 1997; Svedäng 2003). Information on the interconnectivity of offshore and coastal populations is scarce, however, and, in the absence of conclusive information, offshore and coastal fish populations are typically managed separately (ICES 2003).

Solving the issue of the interconnectivity of populations in the marine environment requires that populations can be delineated and that interactions among populations are characterized over all life stages. Continuous water masses facilitate the dispersal of adult individuals and pelagic eggs and larvae by passive drift. While traditional methods employing artificial marks (e.g. tagging) may be well suited to studying migratory behaviour in adults, such techniques can rarely be applied to the egg and larval stages. Indirect methods, using genetic polymorphisms, may therefore improve knowledge of population structure beyond that which is feasible with traditional approaches (Shaklee & Bentzen 1998). Population genetic analyses are also comparatively cheap and do not require extensive fieldwork. However, genetic differentiation requires a sufficient time and degree of isolation and is weak in many marine species (Ward *et al.* 1994; McQuinn 1997; Waples 1998). Hence, population substructure may go unnoticed.

In the Atlantic cod, genetically distinct offshore populations have been detected off both Canada (Ruzzante *et al.* 2001) and Iceland (Jónsdóttir *et al.* 2001). In these areas, gyre-like water-circulation systems are believed to be an important force preventing intermixing and thus maintaining population structure (Ruzzante *et al.* 1999, 2001). Genetic differences have also been uncovered between offshore and coastal populations (reviewed in Ruzzante *et al.* (1999)), in areas where offshore cod undergo systematic feeding migrations to coastal areas (Rose 1993), and among coastal cod populations (Ruzzante *et al.* 2000; Pogson & Fevolden 2003; Knutsen *et al.* 2003). Hence, genetic methods appear well suited to delineating the complexities of the population structure in Atlantic cod, especially when genetic data can be combined with information on oceanographic features (Ruzzante *et al.* 1999).

We have recently used microsatellite DNA techniques to demonstrate the existence of local populations along the coast of Skagerrak on the scale of local fjords (Knutsen *et al.* 2003; see also Mork *et al.* 1984). A long-standing question is whether and how the coastal cod in the Skagerrak are influenced by ocean-spawning cod in the nearby North Sea (Hjort & Dahl 1899; Dahl & Dannevig 1906). The North Sea harbours a commercially important cod

* Author for correspondence (n.c.stenseth@bio.uio.no).

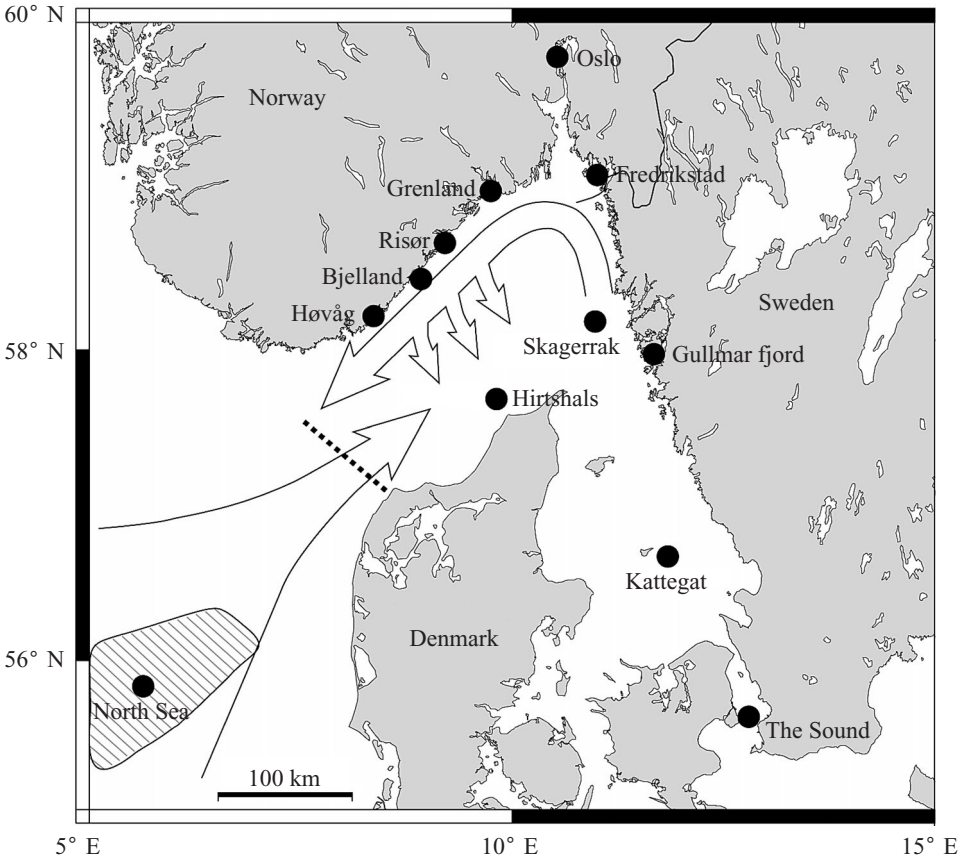

Figure 1. The study area indicating the locations of genetic sampling (black circles), offshore spawning sites (shaded area) and the predominant ocean currents into and out of Skagerrak (arrows). The flow of North Sea waters into Skagerrak is modelled through the transect indicated with a dotted line at the entrance to Skagerrak.

stock (probably consisting of several populations; Hutchinson *et al.* 2001, 2003) that has been severely overexploited for many years and is on the decline (ICES 2003). Forced by the North Atlantic circulation flowing on both sides of the British Isles, water masses from the North Sea flow into Skagerrak, make a counterclockwise loop and pass along the coasts (Danielssen *et al*. 1997; cf. figure 1). Because cod larvae stay in the water column for some weeks after hatching, North Sea cod larvae are probably exposed to this ocean current for at least a month (about March–April). Despite the obvious potential for larval drift, it remains unclear to what extent coastal populations influence each other ecologically and genetically, and how coastal populations relate to the larger offshore North Sea cod stock (Munk *et al*. 1999).

In this paper we compare, in an effort to elucidate the origin of coastal juvenile cod, spawning cod from the North Sea with larvae and juvenile cod from various locations in coastal Skagerrak by means of microsatellite DNA analyses. Our results demonstrate that larvae of North Sea origin can be found deep inside the Skagerrak and that the occurrence of such larvae varied between the two sample years (2000 and 2001). Using oceanographic modelling to estimate the flow of water masses from the North Sea into the Skagerrak for the two years, we find a congruent pattern whereby larval drift, as inferred from the genetic data, appears to be stronger when the inflow of North Sea waters is high. The ecological consequences of the observed larval drift are addressed in a forthcoming paper.

2. MATERIAL AND METHODS

(a) *Samples for genetic analyses*

Samples of mature cod for genetic analyses were collected during the spawning period (late January to early April in the years 2000–2002; cf. table 1) with either trawling or gill nets, at or near presumed spawning grounds, with assistance from local fishermen. We sampled *ca*. 100 adult fishes from each of 10 locations around the Skagerrak coast and one location in the North Sea (figure 1). All sampled cod were aged by otolith readings, sexed, weighed, measured and assigned a sexual maturity index (according to Fotland *et al.* (2000)). The samples were presumed to reflect locally spawning cod, and the percentage of mature individuals in the samples averaged 79% (range of 38.5–100%; table 1). Some of these samples were analysed by Knutsen *et al.* (2003); this study includes five additional adult coastal and offshore samples and seven samples of juvenile cod from coastal Skagerrak (cf. table 1). The juvenile cod were sampled in 2000 (three localities) and in 2001 (four localities) and consist in part of newly hatched pelagic larvae and in part of older (less than 6 months) bottom-settled '0 group' cod. Pelagic larvae were sampled during April 2000 by trawling, whereas the settled 0 group were sampled in June–September 2000 and 2001 by a beach seine, as part of an ongoing coastal cod monitoring programme (Gjøsæter *et al.* 2004).

Table 1. Samples for genetic analyses.

location	sample size	mature spawners (%)	date	coordinates	life-history stage
Høvåg[a]	100	81.1	Feb.–Mar. 2000	58.2° N, 8.32° E	adults
Høvåg 01	100	—	June 2001	58.2° N, 8.32° E	bottom-settled 0 group
Bjelland[a]	92	46.7	Feb. 2000	58.4° N, 8.90° E	adults
Risør[a]	101	57.5	Feb.–Mar. 2000	58.7° N, 9.35° E	adults
Risør 01	100	—	June 2001	58.7° N, 9.35° E	bottom-settled 0 group
Grenland[a]	100	64.0	Apr. 2000; Jan. 2001	59.5° N, 9.65° E	adults
Oslo[a]	109	68.8	Feb. 2001	59.8° N, 10.56° E	adults
Fredrikstad[a]	109	38.5	Jan.–Mar. 2000	59.2° N, 10.96° E	adults
Fredrikstad 00	99	—	Sept. 2000	59.2° N, 10.82° E	bottom-settled 0 group
Fredrikstad 01	100	—	Sept.–Oct. 2001	59.2° N, 10.82° E	bottom-settled 0 group
Gullmar fjord	72	100[b]	Jan.–Mar. 2000	58.3° N, 11.50° E	adults
Gullmar fjord 00	106	—	Apr. 2000	58.3° N, 11.50° E	pelagic larvae
Gullmar fjord 01	82	—	Aug. 2001	58.3° N, 11.50° E	bottom-settled 0 group
Kattegat	135	100	Jan.–Feb. 2000/2001	56.7° N, 11.80° E	adults
The Sound	99	100	Feb. 2000	55.8° N, 12.83° E	adults
Hirtshals	101	95	Feb. 2000/2001	57.7° N, 9.78° E	adults
North Sea	100	100	Mar. 2002	55.6° N, 5.85° E	adults
Skagerrak 00	96	—	Apr. 2000	58.1° N, 10.95° E	pelagic larvae

[a] Samples analysed in Knutsen *et al.* (2003).
[b] Twenty-one individuals were not examined for maturity.

(b) *Genetic analysis*

Genomic DNA was isolated from muscle tissue using a commercial extraction kit (Qiagen, Inc.). Eight microsatellite loci, already known to be highly polymorphic in the sampling area (Knutsen *et al.* 2003; Nielsen *et al.* 2003), were amplified from extracted DNA with PCR and screened for genetic variability following slightly modified published protocols: Gmo2 and Gmo132 (Brooker *et al.* 1994); Gmo19, Gmo34, Gmo35, Gmo36 and Gmo37 (Miller *et al.* 2000); and Tch13 (O'Reilly *et al.* 2000). Microsatellite DNA was separated and detected on ALFexpress II automatic DNA analysers (Amersham Pharmacia Biotech). Care was taken to avoid misclassification of alleles and genotypes, and we screened a large number of individuals using different manufactures of *Taq*-polymerase and PCR amplification buffers and different PCR conditions to reduce short-allele dominance. For one locus (Gmo35) all individuals were amplified and screened at least twice to eliminate erroneous classification of heterozygotes caused by reduced amplification of the longer allele under some PCR conditions.

(c) *Statistical analysis*

Deviations from Hardy–Weinberg genotype proportions were characterized by F_{IS} and tested separately for deficiencies and excesses of heterozygotes, using one-sided exact tests in the software GENEPOP (v. 3.1d; Raymond & Rousset 1995). When testing the hypothesis of genome-wide Hardy–Weinberg equilibrium we combined single-locus tests using the procedure of Fisher (1950), i.e. we summed twice the negative logarithm of each single-locus' p-value and evaluated the sum against the theoretical χ^2 distribution for d.f. = 16 (i.e. twice the number of loci). When evaluating deviations from Hardy–Weinberg proportions over multiple locations, we used two different approaches. First, we applied the sequential Bonferroni method (Rice 1989) and adjusted the alpha level for each test (location). Second, we tested the overall hypothesis of no heterozygote deficiency in coastal Skagerrak by applying Fisher's summation method over locations.

Because the level of genetic differentiation in Atlantic cod is low, we used multiple approaches to investigate spatial and temporal genetic structure. First, differentiation among locations was quantified by F_{ST} (using the estimator θ of Weir & Cockerham (1984)) and tested for allele-frequency heterogeneity using an exact test (Raymond & Rousset 1995). We tested the joint null hypothesis of no differentiation at any locus using Fisher's summation procedure on the single-locus tests, as recommended by Ryman & Jorde (2001). Second, we calculated pairwise the F_{ST} between the North Sea sample and each of the adult and juvenile samples. For the purpose of presentation, we averaged these pairwise values for the Skagerrak adult (excluding Kattegat and The Sound, which are outside Skagerrak proper) and juvenile samples from 2000 and 2001 separately. The null hypothesis of no genetic differentiation between the North Sea and Skagerrak was tested by permutating individuals, using the software GENETIX 4.01 (Belkhir *et al.* 2002). A total of 10 000 replicate permutations of the North Sea and each of the Skagerrak samples at a time were generated and new pairwise F_{ST} values between them were calculated and compared with the observed value for that locality. The proportion of times, out of 10 000 replicates, that the value for the permutated samples was smaller than the observed value was taken as the probability of the observed F_{ST} being larger than zero. Similarly, the averaged F_{ST} values were tested by averaging the permutated values for the relevant locations and comparing against the observed averages. This procedure was carried out for each locus separately and for all loci simultaneously. Third, we performed an assignment test with a Bayesian approach using the software

GENECLASS and the option 'self-classification of reference data' (Cornuet *et al.* 1999). In this test, which was carried out for the adult Skagerrak samples and the sample from the North Sea, each individual fish was assigned to its most likely geographical origin on the basis of its multi-locus genotype, using the leave-one-out procedure. We used a similar method to assign juveniles to adult source populations using the North Sea and the adult Skagerrak samples (Kattegat and The Sound excluded) as baseline populations and the seven juvenile samples as 'unknown samples', using the software option 'assignation of unknown data using reference'.

(d) *Modelling of the ocean current from the North Sea into Skagerrak*

We applied a numerical model (the NORWECOM model; Skogen & Søiland 1998) to estimate ocean-current patterns and strength in the study area, because this information is not available directly. The NORWegian ECOlogical Model system is a coupled physical, chemical and biological model that can be used to study primary production and the dispersion of particles such as fish larvae or pollution. The circulation model is based on the three-dimensional primitive-equation time-dependent wind and density driven Princeton Ocean Model (Blumberg & Mellor 1987). In the present study a nested version of the model was used with a coarse (20 km × 20 km) grid on an extended North Sea area, and a fine (4 km × 4 km) mesh in the Skagerrak–Kattegat area. The forcing variables are 6 h hindcast atmospheric pressure fields and wind stress from the Norwegian Meteorological Institute, four tidal constituents at the lateral boundaries and freshwater runoff. To account for a lack of data on the surface heat fluxes, a relaxation-toward-climatology method is used for temperature in the surface layer.

From the modelled current fields the inflow of water to the Skagerrak across the transect indicated in figure 1 was calculated on monthly and daily bases. The ocean current was modelled for the period where cod egg and larvae are in the pelagic phase (from March throughout April) in the two years for which we have genetic data on juvenile cod (i.e. 2000 and 2001).

3. RESULTS

(a) *Genotype distribution*

Samples generally conformed to Hardy–Weinberg genotype proportions, although there was a tendency towards heterozygote deficiency in several samples, significantly so at Fredrikstad (both adults and juveniles from 2000) and Gullmar fjord (both adults and juveniles) and for all samples considered jointly (cf. table 2). The significances at particular locations do not remain, however, if we apply table-wide Bonferroni corrections.

(b) *Population structure of adult cod*

North Sea cod were found to be significantly differentiated genetically from the adult populations of coastal Skagerrak, although weakly so. The pairwise F_{ST} values between each location and the North Sea, averaged over eight loci, are: Høvåg 0.0040, Bjelland 0.0018, Risør –0.0005, Grenland 0.0041, Oslo 0.0001, Fredrikstad 0.0025, Gullmar fjord 0.0022, Kattegat 0.0019 and The Sound 0.0013 (0.0020 ($p < 0.001$) on average for the seven locations from Skagerrak proper; see table 3 for locus-specific values). As reported previously (Knutsen *et al.* 2003), a low but significant level of differentiation is also present among adult coastal Skagerrak populations (average $F_{ST} = 0.0022$, $p \ll 0.0001$) indicating population substructure within Skagerrak. This geographical substructuring of adult cod is reflected in the assignment tests, which give the highest assignment to the site of capture for all adult samples (figure 2). The sample from Hirtshals is very similar genetically to the one from the North Sea (pairwise $F_{ST} = -0.0018$; n.s.); it is thus likely that the Hirtshals sample represents an eastern segment of the North Sea population, rather than a coastal Skagerrak population.

(c) *Origin of juvenile cod*

The juvenile samples displayed different patterns in each of the two years of the investigation (figure 3): in 2001 all juvenile samples showed highest assignment to the North Sea adults, and none of the four estimates of pairwise F_{ST} for these juveniles was different from zero (average $F_{ST} = -0.0005$ over the four 2001 juvenile versus North Sea pairs; table 3). The 2001 juveniles are also all significantly different from their corresponding adult coastal cod populations (average $F_{ST} = 0.0045$, $p < 0.001$ for each 2001 juvenile versus adult sample from the same location) and appear to constitute a homogenous group, as no genetic differentiation among them appears to be present (the average pairwise $F_{ST} = -0.0001$ among the 2001 juvenile samples). In the year 2000, conversely, one of the juvenile samples showed highest assignment to the adult sample from the same location (Fredrikstad) and the other two (Gullmar fjord and offshore Skagerrak) showed highest assignment to other adult Skagerrak samples. These 2000 juvenile samples were all significantly distinct from the North Sea adults (average $F_{ST} = 0.0024$, $p < 0.001$ for each group of 2000 juveniles versus North Sea). This contrasting pattern for the two juvenile cohorts is consistent across loci: for the 2001 juveniles all but one locus (Gmo132) display a negative F_{ST} estimate, indicating no differentiation, whereas for the 2000 juveniles all but one locus (Gmo34) display a positive F_{ST} estimate, significantly so at four loci (table 3).

4. DISCUSSION

Most of the North Sea water masses flow through the Skagerrak basin (Danielssen *et al.* 1997) and pass close to the coast (figure 1). The strength of this current varies extensively with time, however (cf. figure 4). In particular, the oceanographic model indicated that the water flux from the North Sea was high early in March 2000 but subsequently dropped to a low level for more than a month during the period in which larval drift ought to be most extensive (Brander 1994). In 2001, conversely, the influx of North Sea water increased in mid-March and reached a high level during the first half of April (figure 4). The potential for drift of pelagic cod eggs and larvae from the North Sea to the Skagerrak coast should therefore have been higher in 2001 than in the preceding year, a prediction that is consistent with our genetic findings indicating cod larvae of predominantly North Sea origin in 2001. Further support for the notion of elevated larval drift in 2001 derives from observations of considerably higher numbers of 0 group cod along the eastern (Swedish) Skagerrak coast in 2001 than in 2000 (Svedäng

Table 2. Summary statistics on deviations from Hardy–Weinberg genotype proportions within samples.
(F_{IS} represents the deviation averaged over loci (with positive values indicating heterozygote deficiencies). Significant p-values for individual samples (after Bonferroni correction) are given in bold and italic, and loci deviating significantly in either direction are superscripted in italic: $^{*}p < 0.05$; $^{**}p < 0.01$. Average p-values were calculated with Fisher's method using uncorrected p-values for individual samples.)

sample	average F_{IS}	heterozygote excess p-value	heterozygote deficiency p-value
juveniles from 2000			
Skagerrak 00	0.016	0.92	$0.05^{Gmo37*Gmo132*}$
Gullmar fjord 00	0.008	0.87	$\boldsymbol{0.00}^{Gmo34**Gmo132**}$
Fredrikstad 00	–0.011	$0.26^{Gmo36*Gmo37*}$	$\boldsymbol{0.01}^{Gmo2**Gmo132*}$
average	0.004	0.70	$< \boldsymbol{0.0001}$
juveniles from 2001			
Høvåg 01	0.014	0.77	$0.06^{Gmo37**}$
Risør 01	–0.005	0.58	0.79
Fredrikstad 01	0.016	0.86	0.24
Gullmar fjord 01	0.032	0.85^{Gmo19*}	$0.02^{Gmo34*Gmo35*Gmo132**}$
average	0.014	0.97	$\boldsymbol{0.03}$
adults			
Høvåg	–0.004	0.88	0.08^{Gmo34*}
Bjelland	0.031	0.90	$0.08^{Gmo132*Gmo19**}$
Risør	0.002	0.69	0.33^{Gmo19*}
Grenland	0.007	0.96	0.08^{Gmo34*}
Oslo	–0.004	$0.51^{Gmo132*}$	0.14
Fredrikstad	0.040	1.00	$0.02^{Gmo19**}$
Gullmar fjord	0.022	0.76	$0.05^{Gmo35**Gmo19*}$
Kattegat	0.029	0.93	$0.06^{Gmo37*Gmo132*}$
The Sound	–0.007	0.81	$0.27^{Gmo132*}$
Hirtshals	0.001	0.22^{Tch13*}	$0.10^{Gmo19**Gmo35*}$
North Sea	0.004	0.80^{Gmo36*}	0.16
average	0.011	~1.00	$< \boldsymbol{0.0001}$

Table 3. Average pairwise F_{ST} values between the North Sea sample and adult and juvenile Skagerrak samples.
(Adult Skagerrak samples are from Høvåg, Bjelland, Risør, Grenland, Oslo, Fredrikstad and Gullmar fjord. See table 1 for details on samples; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.)

		Skagerrak juveniles versus North Sea	
locus	Skagerrak adults versus North Sea	2000	2001
Gmo2	0.0044**	0.0047**	–0.0014
Gmo19	0.0003	0.0003	–0.0009
Gmo34	–0.0024	–0.0019	–0.0036
Gmo35	–0.0005	0.0013	–0.0027
Gmo36	0.0071**	0.0005	–0.0011
Gmo37	0.0022**	0.0071***	–0.0012
Gmo132	0.0028**	0.0034**	0.0056***
Tch13	0.0009	0.0018*	–0.0003
average	0.0020***	0.0024***	–0.0005

2003). Elevated numbers of the 2001 cohort were also observed along the Norwegian Skagerrak coast in November 2001 (J. Gjøsæter, unpublished data).

An alternative to larval drift as an explanation for the high genetic similarity between cod larvae in Skagerrak and adult North Sea cod is that a segment of the North Sea cod population ventures to spawn along the Skagerrak coast. This scenario appears unlikely, however, as tagging studies of adult cod indicate little or no migration from the North Sea to the Norwegian Skagerrak coast (Danielssen 1969). However, there appears to be frequent migration of adult cod between Hirtshals and the North Sea (Danielssen 1969), explaining the lack of any obvious genetic differentiation between these two locations.

Cod in the North Sea and adjacent areas are probably structured into several populations (Hutchinson *et al.* 2003), and one cannot rule out the possibility that larvae from different populations dominate the currents reaching Skagerrak in different years. Ocean currents change rapidly, and less than two weeks is sufficient for the water

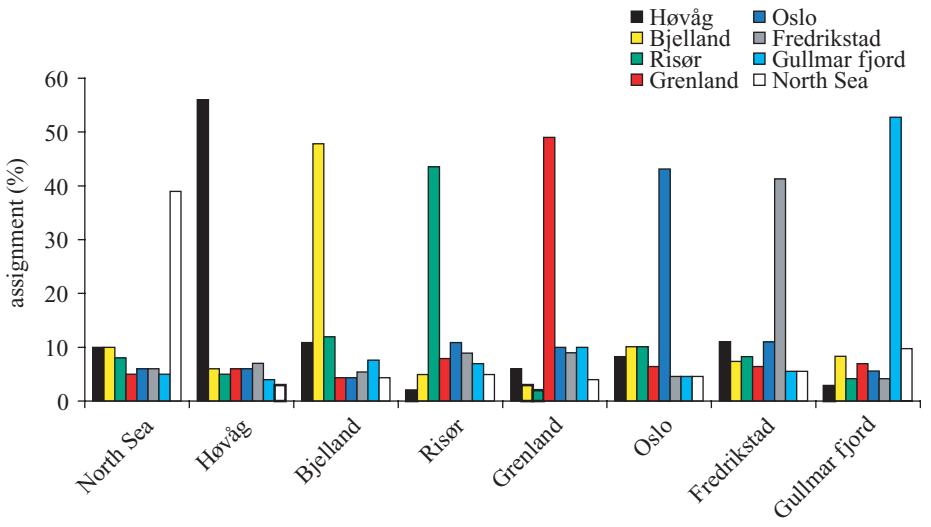

Figure 2. Assignment of sampled individual adult cod to their most likely geographical origin, among the sampled locations, based on their multilocus genotype.

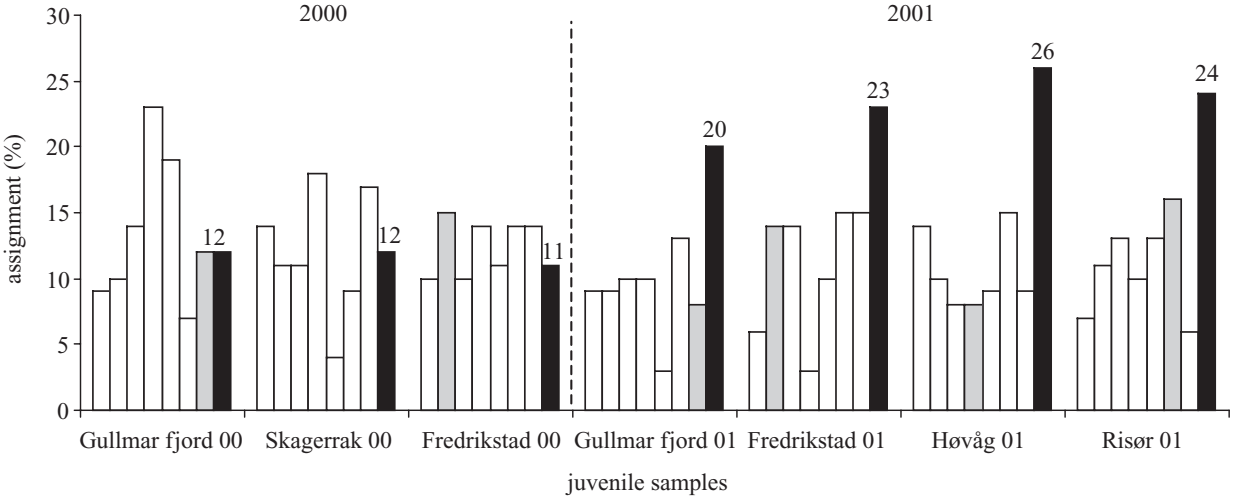

Figure 3. Assignment of juvenile cod to the North Sea (black bars) and Skagerrak locations. Grey bars represent the percentage assignment to the local adult population, and open bars represent the percentage assignments to other Skagerrak locations. (Note that the sample from offshore Skagerrak has no adult counterpart.)

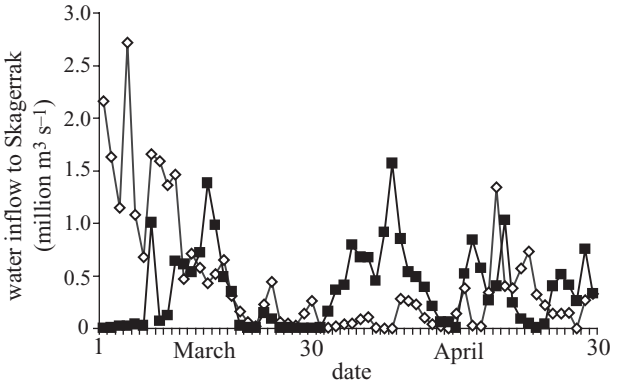

Figure 4. Water transport (inflow) from the North Sea into Skagerrak (modelled over the transect shown in figure 1) from the beginning of March until the end of April in the years 2000 (open diamonds) and 2001 (filled squares).

masses to reach the entire Skagerrak basin (D. S. Danielssen, personal communication). However, the main concentrations of cod larvae in the North Sea, in the German Bight and Dogger bank (Munk *et al.* 2002), are closely situated to our North Sea sample location (cf. figure 1), which is thus the more likely source of larvae reaching Skagerrak.

Because we detect North Sea larvae at such distant locations as Høvåg and Gullmar fjord, it appears that the influx of cod larvae from the North Sea affects coastal cod throughout Skagerrak. This is expected considering the circulation of the current and its closeness to the coast. The widespread larval drift provides an obvious explanation for the observed high degree of genetic similarity among coastal cod populations in Skagerrak. While we presently do not know the fate of the North Sea larvae along the Skagerrak coast, the fact that many of them were collected as bottom-settled 0 group fishes (cf. table 1) suggests that they have or may become part of the local

coastal populations. This gene-flow scenario can explain the low level of genetic differentiation within Skagerrak, the apparent lack of any geographical pattern within Skagerrak (Knutsen *et al.* 2003) and the high genetic similarity between Skagerrak populations and North Sea cod. An alternative scenario, so far unsubstantiated, is that North Sea cod use coastal areas in Skagerrak as nursery areas and return to the North Sea to spawn (cf. Pihl & Ulmestrand 1993).

Deficiencies of heterozygotes at some coastal sites in Skagerrak are consistent with the mixing of locally produced cod with cod originating in the North Sea. Because the deviations from the Hardy–Weinberg proportions are not limited to any specific locus or loci (cf. table 2), alternative explanations, such as the presence of null alleles, are less likely. The use of the highly conservative Bonferroni corrections obscures the overall tendency towards systematically low *p*-values in our samples (cf. table 2). Given that the null hypothesis represents panmixia, the alternative hypothesis is that there is larval drift and intermixture of offshore and coastal cod throughout Skagerrak. This justifies our application of single-sided tests and consideration of a joint hypothesis, using Fisher's summation procedure, over all Skagerrak localities.

Based on results from genetic analysis and oceanographic modelling, we conclude that cod larvae are passively transported from open-ocean spawning areas in the North Sea into coastal Skagerrak, where their presence as 0 group cod is detected. It is a common observation in marine fishes that local populations tend to be genetically quite similar over appreciable distances (summarized in Ward *et al.* 1994), and this suggests that passive larval drift in the ocean currents as we find for the Atlantic cod may be a general phenomenon for marine species that have pelagic larval stages (but see, for example, Taylor & Hellberg (2003) for a counter-example). Hence, care must be exercised when attempting to elucidate adult migration patterns from genetic data in these species, as patterns of genetic similarities may largely reflect gene flow at the egg and larval stages. On the ecological side, inflow of larvae may have important rescue effects on populations with poor or temporally variable local recruitment (Palumbi 2003), including the eastern Skagerrak coastal cod populations (Svedäng 2003). At present, the North Sea cod population is severely overexploited (Cook *et al.* 1997; ICES 2003), and a fishing moratorium is being discussed (ICES 2003). Our findings suggest that protecting the North Sea cod population is also likely to have important effects on the species outside the North Sea.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.