ICES Journal of Marine Science

ICES Journal of Marine Science (2018), doi:10.1093/icesjms/fsy080

Who is fishing on what stock: population-of-origin of individual cod (*Gadus morhua*) in commercial and recreational fisheries

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Jorde, P. E., Kleiven, A. R., Sodeland, M., Olsen, E. M., Ferter, K., Jentoft, S., and Knutsen, H. Who is fishing on what stock: population-of-origin of individual cod (*Gadus morhua*) in commercial and recreational fisheries. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsy080.

Received 14 December 2017; revised 1 June 2018; accepted 4 June 2018.

Atlantic cod (*Gadus morhua*) in Skagerrak are structured into distinct ecotypes or stock components that have been severely depleted over the past decades. To improve our understanding of how local commercial and recreational fisheries influence cod stocks, we investigated whether these user groups target different stock components of cod. Cod were sampled from the recreational rod and line fishery and from commercial shrimp trawlers catching cod as by-catch. Based on a large set of single nucleotide polymorphisms (SNPs), we defined a subset of 27 semi-diagnostic SNPs designed to discriminate between two cod stock components: "inner fjord" cod and "North Sea" cod, designated by their dominant habitat preferences. Genetic assignments of fishery-caught cod indicated that 4% of individuals caught by shrimp trawlers belonged to the inner fjord cod component and 96% to the North Sea, whereas among cod caught by recreational fishers, the estimated percentages were 11.8 and 88.2%, respectively. Our findings confirm the existence of two sympatric cod stock components in coastal Skagerrak, indicating that existing management units are biologically inappropriate and should be reconsidered. Furthermore, more attention should be given to recreational angling to reduce fishing mortality on the depleted inner fjord cod component.

Keywords: fishery management, *Gadus morhua*, genetic stock identification, recreational fisheries, shrimp trawl.

Introduction

Conflicts surrounding fishery resources have a long history (Charles, 1992). In recent years, there have been an increasing number of disagreements between recreational and commercial fisheries as resources are getting scarce and more regulated (Kearney, 2001; Kearney, 2002; Sutinen and Johnston, 2003; Momtaz and Gladstone, 2008; Borch, 2010; Ngoc and Flaaten, 2010; Crowe *et al.*, 2013). Recent studies suggest that recreational fisheries have a significant impact on fish stocks (Coleman *et al.*, 2004; Cooke and Cowx, 2004; Lewin *et al.*, 2006; Kleiven *et al.*, 2012, 2016; Hyder *et al.*, 2018), indicating a biologically relevant resource conflict between commercial and recreational fishers.

Atlantic cod (*Gadus morhua*) is a popular target species for both commercial and recreational fishers in the North Atlantic (Sparrevohn and Storr-Paulsen, 2012; Strehlow *et al.*, 2012; Anonymous, 2013; Brownscombe *et al.*, 2014; Kleiven *et al.*, 2016). In Norway, management recognizes four distinct stocks: (1) the oceanic Northeast Arctic cod, (2) coastal cod north of 62°N, (3) coastal cod south of 62°N, and (4) a North Sea/Skagerrak stock. Outside the 12-nautical mile (nm) territorial line, North Sea cod are managed in collaboration with the European Union. However, inside the 12-nm line, cod are viewed as coastal cod and managed as Norwegian stock. While North Sea cod are managed by quotas, coastal cod are managed by only

technical regulations (Minimum landing size [MLS = 40 cm], mesh size, etc.). Hence, commercial vessels face different management regulations, depending on distance from shore. In addition, recreational fishing mostly takes place well inside the 12-nm line.

Capture-mark-recapture studies in coastal Skagerrak have estimated an annual fishing mortality for Atlantic cod of 50% or higher (Olsen and Moland, 2011), accounting for almost 100% of the total mortality of larger mature cod in some years (Fernández-Chacón *et al.*, 2015). Along the Norwegian and Swedish Skagerrak coasts, abundances have declined, especially in recent decades (Svedäng and Bardon, 2003; Olsen *et al.*, 2009; Johannessen, 2014; Roney *et al.*, 2016). This decline is now emerging as a resource-conflict among stakeholders. The Directorate of Fisheries in Norway has advised the Ministry of Fisheries and Coastal Affairs to take several management actions to rebuild the coastal cod stock.

The Skagerrak region is the most densely populated area in Norway and the southern coast is a popular summer vacation area. Recreational fishing along the Norwegian Skagerrak coast appears to dominate the catches of cod within the sheltered coastline, and a mark-recapture study by Kleiven *et al.* (2016) found that recreational fishers were responsible for 72% of the total near-shore cod catches in Aust-Agder county. Angling accounted for 83% of the total recreational catches, with peak catches from June to August.

Shrimp trawling is one of the most important commercial fisheries on the Skagerrak coast and has been criticized for by-catching large quantities of cod, including cod smaller than the MLS. A total of 143 shrimp trawlers (50% of which are smaller than 11 m) are registered in Norwegian Skagerrak and 57 in our coastal study area (municipalities from Risør to Kristiansand; E. Grimsrud, Fiskerlaget Sør, pers. comm.). Trawlers landed 1500 tons of shrimp worth 72 million Norwegian kroner (ca. €8 mill) in 2012 (NDF, 2015). Even though the main target is shrimp, it is a mixed fishery in which a diversity of species, including cod, are caught and landed. By-catch is regulated as a maximum species-specific level proportional to the shrimp catch and allows up to 5% of cod in the total catch by weight (NDF, 2016). Discards are banned in Norway, and all catch must be landed, including fish under the MLS (Gullestad *et al.*, 2015). Moreover, in 2012, total cod landings from the local shrimp trawl vessels in this region were 63 tons. In the same year, official landings of cod by commercial fishers using passive gear were 76 tons.

In the present study, we established that cod in the Skagerrak belonged to two genetically divergent groups or lineages (Sodeland *et al.*, 2016; Barth *et al.*, 2017) that occur in sympatry in coastal waters (Knutsen *et al.*, 2018). One lineage is closely related to cod in the North Sea and possibly represents offspring from North Sea spawning grounds carried into the Skagerrak coast by ocean currents (Stenseth *et al.*, 2006). The other genetic lineage resembles cod in the southern Kattegat and western Baltic Sea (Barth *et al.*, 2017). The two lineages differ in the frequencies of a large number of genes throughout the genome (this study; Knutsen *et al.*, 2018, Supplementary Figure S1), including genes residing in putative chromosome inversions (Sodeland *et al.*, 2016). The two lineages co-exist in coastal waters as juveniles and adults, but display different proportions in inner fjords and outer coastal areas, with the North Sea type dominating the latter (Knutsen *et al.*, 2018). In the present study, we refer to the two genetic lineages of coastal cod as "inner fjord" and "North Sea" cod and treat them as distinct cod stock components.

This complex spatial ecology indicates potential for a mismatch between management and biological units, in which neighbouring or co-existing stock components may be overlooked (Kuparinen *et al.*, 2015; Roney *et al.*, 2016). Cod fisheries in coastal Skagerrak are likely to include both stocks, because of the co-existing genetic lineages. The basic tool for characterizing mixed-stock fisheries is genetic screenings (e.g. Milner *et al.*, 1985). Mixed-stock analyses (MSA) rely on the genetic characterization of putative source populations and on statistical analysis to estimate mixture proportions or to assign individuals to population of origin. Recent advances in genomics have greatly expanded the power of MSA by supplying a large number of polymorphic genetic markers.

The main objective of the present study was to quantify how the two cod stock components were harvested by recreational and commercial fishers, to aid in solving resource conflicts between these two fisheries, and to improve management of coastal cod. Because the fisheries targeting cod in Skagerrak are poorly documented, we collected catch information from both the recreational rod and line (angling) and the commercial trawl fishery to quantify catches of the cod stock components in these fisheries.

Material and methods

Study area and fishery

The study area covered the Norwegian Skagerrak from Kristiansand in the west to Risør in the east, about 120 km of coastline (Figure 1). The coastline consists of several smaller fjords stretching up to 20 km inland and a large archipelago between the mainland and the 300–700 m deep Norwegian trench. Coastal municipalities in this region have a resident population of nearly 172 000 inhabitants (Statistics Norway), among whom recreational fishing is popular (Hallenstvedt and Wulff, 2004), but catch-effort levels are unknown (Kleiven *et al.*, 2016). Recreational catches of cod peak during the influx of summer tourists (Kleiven *et al.*, 2016).

Sampling

Sampling consisted of three separate efforts: (1) sampling of baseline populations for assigning fishery samples to stock component or population of origin, (2) sampling of the recreational fishery, and (3) sampling of the commercial (shrimp trawl) fishery.

Population baseline sampling

Population samples were collected from the innermost and outer coastal regions of three fjords, near the shrimp trawling areas and extending from Topdalsfjord near Kristiansand (KR) in the west to Søndeledfjord near Risør (RI) in the east (Figure 1). We collected young-of-the-year cod for at least 3 years (Supplementary Table S1) and froze the fish whole in the field during an ongoing beach-seine monitoring program (Olsen *et al.*, 2009). Multiple years were used to assure representative sampling of the spawning population(s). Juvenile young-of-the-year cod were used because they are stationary (Olsen *et al.*, 2004) and because of logistic difficulties of sampling reasonable numbers of local spawners. Samples collected from the innermost part of the fjords represented inner fjord cod. Samples of adult cod were collected at two North Sea localities (Figure 1; Table 2), caught by commercial, off-shore fishers and frozen whole on board. We found no genetic substructure within the North Sea, nor among fjords and therefore pooled these samples to obtain two baseline samples: a

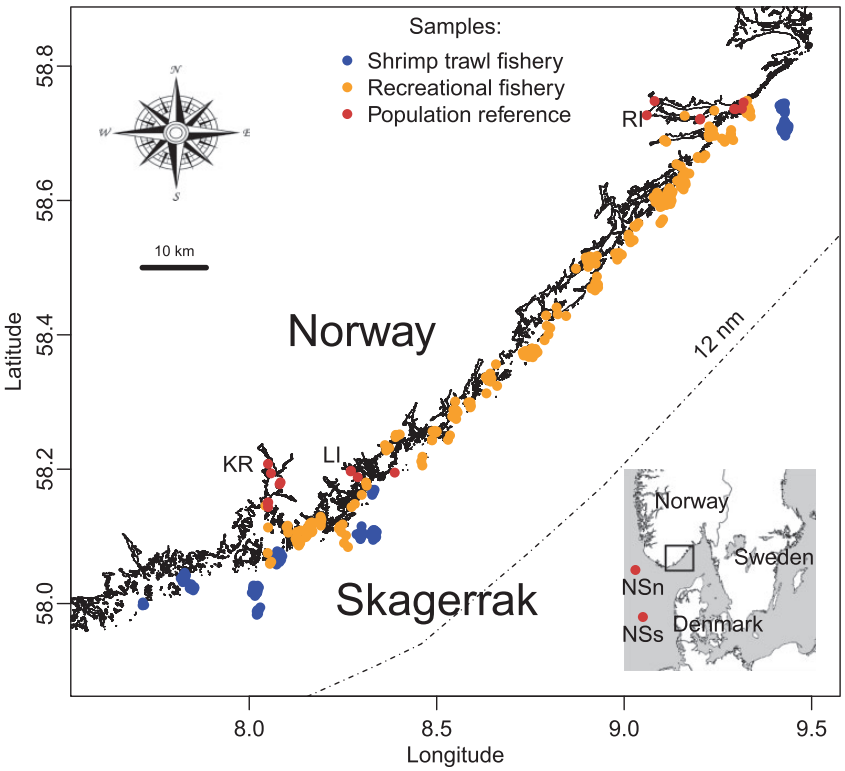

Figure 1. Map of the study area including trawling areas in which cod was collected from shrimp trawls (*blue dots*) and recreational fishing interviews with landed cod (*yellow dots*). *Red dots* indicate population samples for assessment of population structure and for genetic assignments of individual cod from the fisheries. *Dotted line*: the 12-nm territorial limit, inside of which cod are defined as "coastal cod" in the current management. Location abbreviations: KR = Kristiansand, LI = Lillesand, RI = Risør, which are harbours for the three commercial trawlers, NSn and NSs = North Sea north and south, respectively.

"North Sea" sample ($n = 91$) and an "inner fjord" sample ($n = 143$). Allele frequencies in the two pooled samples differed at 1069 of 5758 single nucleotide polymorphisms (SNPs) ($P < 0.05$, exact G-tests, GENEPOP 4.2.1; Rousset, 2008). We used these two pooled samples as a population baseline for the MSA of the cod fishery. The two pooled baseline samples have been used in other studies (Sodeland *et al.*, 2016; Knutsen *et al.*, 2018). An additional population sample from the outer coastal region was added to characterize population structure and the occurrence of stock components throughout the study area and to evaluate the accuracy of genetic assignments of individuals to population of origin.

Recreational sampling

We focused on angling from April to August 2012, using a roving creel survey by boat, because most recreational catches are reported by anglers in summer (Kleiven *et al.*, 2016). This period has high participation in recreational fisheries. Five survey routes were designed to represent the study area (Table 1). The survey was conducted each month during one sampling session on week days and weekends. The starting point of the survey route and the driving direction were randomly chosen at the beginning of a sampling session. Recreational fishing boats that are actively angling were approached, and fishers were interviewed about catch and effort, and GPS position and depth was recorded. All landings and releases were recorded. The GPS position and depth at time of interview was used as a proxy for fishing area, even though fishers may have covered large areas during a fishing trip. Cod were measured for length, otoliths were extracted for aging, and tissue samples were collected for DNA analyses.

Table 1. Monthly numbers of cod collected by three commercial shrimp trawlers, and by recreational fishers (including number of interviews).

	Commercial			Recreational	
	RI	LI	KR	# interviews	# cod
January	0	0	0	0	0
February	0	0	20	0	0
March	20	20	0	0	0
April	0	0	0	27	39
May	21	20	18	63	95
June	28	0	0	43	36
July	0	0	20	106	94
August	0	20	0	120	82
September	0	0	0	0	0
October	18	20	20	0	0
November	12	0	0	0	0
December	0	20	20	0	0
Total	99	100	98	359	346

Sample location designated by nearby cities (RI = Risør, LI = Lillesand, KR = Kristiansand).

Table 2. Samples of cod for genetic analyses.

		Number genotyped		
	Sample sites	**SNP-schip**	**Sequenom**	**Sum**
Fishery samples:				
Commercial (KR +LI +RI)	98 + 100 + 99	38 + 40 + 40	60 + 60 + 50	288
Recreational (all coast)	346	0	346	346
Population samples:				
Inner fjords (KR +LI +RI)[a]	48 + 48 + 48	48 + 47[b] + 48	48	143
North Sea (NSs +NSn)[a]	43 + 48	43 + 48[b]	48	91
Outer fjords (KR +LI +RI)[c]	48 + 48 + 48	48 + 48 + 48	0	144

The two fishery samples included cod from the commercial shrimp-trawl (3 subsamples: Table 1) and the recreational fisheries (continuously sampled over the study area: plotted in Figure 1). The baseline population samples for genetic assignments consisted of the inner fjord (3 subsamples) and the North Sea (2 subsamples: Supplementary Table S1). Also given are sample sizes, numbers genotyped on each of the two genotyping platforms (Illumina 12k SNP-chip and/or 40-plex Sequenom), and the total number of genotyped individuals. Subsets of individuals were scored on both platforms (marked with a[b]) for evaluation.

[a]Used as baseline samples in GENECLASS assignments.

[b]Duplicated on the Sequenom 40-plex platform (95 individuals).

[c]Used for evaluating precision of assignments.

Commercial sampling

Three coastal trawlers were selected to represent the commercial shrimp fishery and the crew were recruited to sample cod caught as by-catch (trawling areas in Figure 1). Crew members were instructed in collection procedures to secure accurate landing data and well-preserved cod samples for later DNA extraction and measurements on frozen fish. Trawlers, with 1–2 persons per boat, fish mainly within the 12-nm line. The crew of each trawler was asked to collect 100 cod through five sampling events throughout 2012 and to record date and fishing area of the sample. Fishers were instructed to collect the first 20 cod landed and freeze the cod whole at their landing destination. Length and weight measurements, and otolith and DNA samples for genetic analyses were taken later from frozen specimens. Age was estimated from otolith growth zones (Rollefsen, 1933).

Total catch of the inner fjord cod component in the shrimp fishery was estimated from official landing statistics collected by the fishers' trade organization "Skagerakfisk". The estimate was taken as the official reported catches multiplied by the proportion of inner fjord cod estimated from the MSA analyses of the trawl catch. We estimated catches under MLS based on the length distribution in the shrimp trawl samples because few cod under the MLS were registered in the official landing statistics (Jørn Lian, pers. comm.). The mean weight of cod in the shrimp trawl sample was used to estimate the total weight of landed inner fjord cod over MLS and of landed or discarded inner fjord cod under MLS in the region's shrimp trawl fishery. Individual trawlers were used as the primary sampling unit, and sampling event as a secondary sampling unit to calculate stratified mean length and age (and standard errors, SE) in the commercial fishery. In the recreational fishery, individual cod was used as the primary sampling unit, and means and SE were calculated over all individuals, because cod observations were distributed among many boats.

Genetic analyses

A fin-clip from frozen fish was taken for genetic analysis and stored at 4°C in pure ethanol prior to DNA extraction. Genomic DNA was extracted using the E.Z.N.A. Tissue DNA Isolation Kit (Omega Bio-Tek, www.omegabiotek.com). Population baseline samples and a subset from the commercial trawls (118 fish) were genotyped with an Illumina 12k SNP chip (Table 2; Sodeland *et al.*, 2016), yielding 9187 SNPs that were polymorphic in the present material. Several hundreds of these SNPs were in strong linkage disequilibrium, either because of close physical distance along a chromosome or because they were positioned within large chromosomal rearrangements that suppressed recombination (Berg *et al.*, 2016; Sodeland *et al.*, 2016; Barth *et al.*, 2017).

One of the pair of linked SNPs was excluded from the 9187 set to obtain a representative set of high-quality SNPs throughout the genome. We excluded the lowest ranked SNP (i.e. the SNP with the lowest F_{ST} among population samples) in each pair showing composite linkage disequilibrium (CLD; Gao *et al.*, 2008) >0.1, starting with the highest ranked SNPs. Finally, the SNPs were filtered with the GenABEL R-package (Aulchenko *et al.* 2010) to retain those with a call rate >95%. This resulted in a panel of 5758 SNPs considered to be statistically independent of one another and usable for population screenings. Population structure of coastal cod was characterized at the individual and sample levels using the population baseline samples (Table 2). First, we compared individual cod without regards to sampling locality by statistically clustering genotypes from the 5758 unlinked SNPs with the model-based approach in STRUCTURE 2.3.4 (Pritchard *et al.*, 2000) with the correlated allele frequencies model (Falush *et al.*, 2003), and by principal component analysis (PCA) in the R-package ADEGENET 2.0.1 (Jombart, 2008). Second, levels of genetic divergence were quantified with Wright's *F*-statistics within and among sample localities, using the AMOVA routine in ARELEQUIN 3.5 (Excoffier *et al.*, 2005). Data were formatted with *PGDspider* 2.1.0.3 (Lischer and Excoffier, 2012).

Design of diagnostic markers

For routine screenings of the commercial and recreational samples, we developed a small panel of 40 SNPs that captured the main genetic divergence pattern in the population baseline samples to minimize cost and effort. Design of this sub-selection of diagnostic SNPs followed the recommendations of Wilkinson *et al.* (2011). We first ranked the 9187 SNPs by their G_{ST} values among population samples and filtered the ranked SNPs by linkage disequilibrium, eliminating SNPs with a CLD > 0.5 to a higher ranked SNP. A Sequenom MassARRAY system multiplex containing the 40 highest ranked SNPs was used for genotyping,

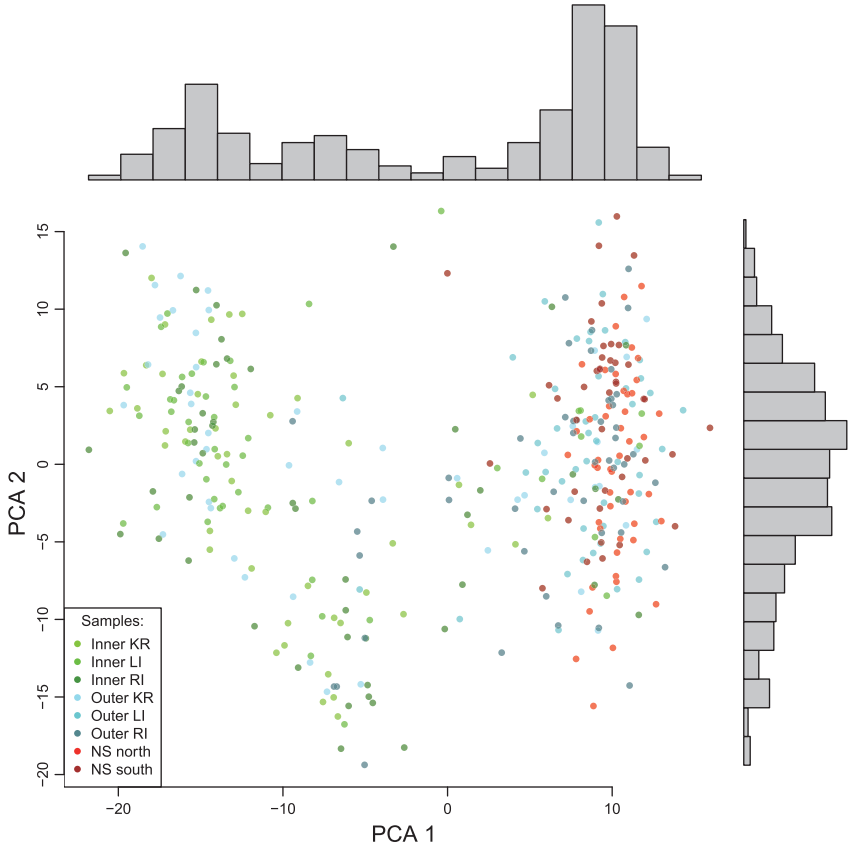

Figure 2. PCA clustering of population samples for determination of cod population structure in the study area. Central panel: scatterplot of individual PCA values of the first two axes; marginal panels: histogram of first (top panel) and second (right panel) axis values. Calculated from the 5857 SNP panel with function *dudi.pca* in the *adegenet* package. See Supplementary Table S1, for sample data and abbreviations.

resulting in 29 successfully scored SNPs (Supplementary Table S2). As quality control, a subset of 95 individuals from the population samples, originally genotyped with the Illumina 12k SNP-chip, was re-genotyped with the 29 SNPs to check for genotyping errors. This quality control identified the loss of heterozygotes for two of the 29 SNPs. These two were eliminated from further analyses. Evaluations of the precision of the assignments from this small panel were made with the outer fjord sample. These assignments revealed that genotypes 7 of 139 outer-fjord individuals differed between the 27-SNP and 5758 SNP-panels (Table 3) indicating an assignment error rate of 7/139 = 5.0% for the 27-SNP panel, under the assumption that the 5758-SNP panel resulted in correct assignments of the 139 individuals. Hence, the assignment precision of the restricted 27-SNP panel is estimated to be 95%, justifying its use in classifying coastal cod into stock components in the present study.

Mixed-stock analysis

Genetic assignments of the commercial and recreational catches to baseline populations were conducted with the 27 diagnostic SNPs, using GENECLASS2 2.0.g (Piry *et al.*, 2004) with the Bayesian method of Rannala and Mountain (1997). The precision of assignments based on these 27 SNPs was evaluated using the outer fjord samples (Table 2), by comparing with the assignments of the same individuals with the 5758-SNP panel. The number of outer-fjord individuals that assigned differently between the two SNP panels was interpreted as the error rate in the 27-SNP panel.

Table 3. Comparison of GENECLASS2 assignments for the 27 and 5758 SNP panels of outer fjord cod samples (KR+LI+RI outer: Table 2).

	5758 SNP panel	
27 SNP panel	**North Sea**	**Inner fjord**
North Sea	45	4
Inner fjord	3	87

Five individuals had score <80% with the 27 SNP panel and were excluded. Note that 7 of 139 fish were assigned to a different stock component with the 27 SNP panel.

Assignments for the evaluation of errors and for the fishery catches used a lower limit on GENECLASS likelihood ratio of 80%. Individuals failing this limit were excluded from the analyses. Estimated proportions and associated uncertainties of the two stock components in the fisheries were also estimated with ONCOR (Kalinowski *et al.*, 2007) and gsi_sim software (Anderson EC *et al.*, 2008). For ONCOR, we ran mixture analyses separately for commercial and recreational samples using 10 000 bootstrap replicates to compute 95% confidence intervals. We repeated the mixture analysis with gsi_sim using a default number of MCMC burn-ins (5000) and sweeps (25 000).

Results

In total, 359 interviews of recreational boats (712 fishers) were conducted from April to August 2012 (Table 1), in which 116

boats had cod on board at the time of interview. The number of landed fish ($n = 2238$) included mackerel (*Scomber scombrus*) with 60% of fish landings, followed by cod (17%), saithe (*Pallachius virens*; 16%), and pollock (*Pollachius pollachius*; 4%). Release rate of cod was 55%. The main reason for releasing cod was "too small". For the commercial fishery, 297 cod were sampled from the three shrimp trawlers throughout 2012 (Table 1).

Genetic population structure

Analyses of the 5758-SNP genotypes among the population samples revealed two major groups of cod along PCA axis-1 that largely coincided with their geographic origin (Figure 2). The left-hand cluster included individuals exclusively from the coast and mostly from the inner fjords (*green dots*). Cod from all three inner fjords clustered together in the PCA plot, indicating no apparent genetic subdivision among fjords. The right-hand cluster included all North Sea cod (*red dots*) and a substantial fraction of coastal cod, mostly from outer fjord localities (*blue dots*). A similar pattern appeared in the STRUCTURE analysis, which yielded the least negative ln P(K|Data) values with $K = 2$ populations (Supplementary Table S3). The assignment plot (Figure 3) indicated genetically homogeneous samples from the North Sea, and largely homogeneous inner fjord samples with some individuals with high to moderate affinity to the North Sea. Outer coastal samples were more heterogeneous, consisting of a mixture of individuals of different affinities, in agreement with the PCA clustering pattern and with previous findings for cod populations along the Norwegian Skagerrak coast (Sodeland *et al.*, 2016; Barth *et al.*, 2017; Knutsen *et al.*, 2018).

The analysis of genotypic frequencies among inner fjord and North Sea samples (Supplementary Table S1) with AMOVA revealed moderate but highly significant genetic differences between the North Sea and the inner fjords (Table 4; average over 5758 SNP loci: $F_{ST} = 0.0064$; $P < 0.0005$), while no significant differences were detected among sample localities within the North Sea or among the three fjords ($F_{ST} = 0.0000$; $P = 0.3809$), nor among sample years ($F_{ST} = 0.0002$; $P = 0.1119$).

A slight, but significant, deficit of heterozygotes within samples ($F_{IS} = 0.0029$; $P = 0.0014$) may indicate mixing among populations (Wahlund effect). The consequences of such mixture in the baseline sample(s) for the subsequent genetic assignments of fishery cod were evaluated in two steps. First, we used gsi_sim to carry out a self-assignment estimate of the two baseline samples. The result indicated that 22 of the 143 cod from the inner fjord assigned to the North Sea and, conversely, that 3 of 91 cod from the North Sea assigned to the inner fjord (Supplementary Table S4). Second, we removed these 25 individuals from the baseline and re-ran the gsi_sim mixture analysis of the fishery samples (see next section).

Genetic assignment of commercial and recreational cod

Of the 643 fish from the fisheries (Table 1), 634 were analysed genetically (Table 2). Three individuals had poor DNA quality and yielded no genotypes, leaving 345 from the recreational fishery and 286 from the commercial trawl fishery. A total of 24 individuals (3.8% of the total samples; 15 recreational and 9 commercial) were unassigned with the 27-SNP panel with a cut-off score of 80% in GENECLASS2 and were removed from further consideration. Of the remaining 607 cod, 557 assigned to the pooled North Sea baseline sample and 50 to the inner fjord component (Table 5). Among cod from commercial trawlers, 96% assigned to the North Sea, whereas 11 of 277 (4%) fish assigned to the inner fjord component. Cod caught by recreational fishers also assigned mostly to the North Sea (88.2%), but the fraction

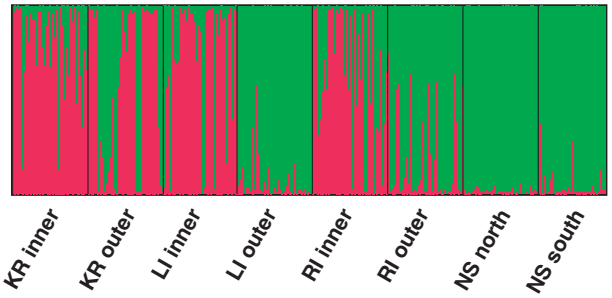

Figure 3. Graphical presentation of STRUCTURE analysis of 5758 unlinked SNP genotypes in the population samples. The panel represents individual probabilities (coloured vertical columns) of belonging to one of two (green or red) pre-assumed populations; K = 2 populations having the greatest statistical support (*cf.* Supplementary Table S3). See Supplementary Table S1 for sample abbreviations.

Table 4. Characterization of genetic diversity within and among the North Sea and inner fjord baseline samples, based on 5758 SNPs.

Variance component	Fixation index estimates	(95% CI)	*P*
Within total:			
Between baseline samples	$F_{ST} = 0.0064$	(0.0059–0.0069)	<0.0005
Among individuals	$F_{IT} = 0.0093$	(0.0071–0.0114)	<0.0005
Within baseline samples:			
Among localities	$F_{ST} = 0.0000$	(−0.0002–0.0003)	0.3809
Among years	$F_{ST} = 0.0002$	(−0.0001–0.0005)	0.1119
Among individuals	$F_{IS} = 0.0029$	(0.0007–0.0050)	0.0014

Analysis of molecular variation (AMOVA) was carried out for the total baseline material (*upper part*) and within the North Sea and the inner fjord samples (*bottom part*). The table shows estimates of fixation indices and *CI*, along with *P*-values for the null hypotheses of $F = 0$ (calculated by bootstrapping in 5000 replicates).

Table 5. Statistical assignment of commercial and recreational caught cod to the North Sea and inner fjord baseline samples based on 27 diagnostic SNPs.

	Assigned to			
Source	**North Sea**	**Inner fjord**	**Sum assigned**	**Unassigned**
Commercial	266	11	277	9
Recreational	291	39	330	15
Sum	557	50	607	24

Results are presented for the GENECLASS2 analyses, and fish with a score <80% were left unassigned. Contingency Chi-square test of the null-hypothesis of equal proportions of fish assigned to the two stock components in the two fisheries, $X^2_{df=1} = 12.268$, $P = 0.0005$.

assigned to the fjord component (39 of 330 cod, 11.8%) was significantly larger than the proportion in samples from commercial fishers (contingency $X^2_{df=1} = 12.268$, $P = 0.0005$; Table 5). Assuming a binomial distribution, these estimates imply standard deviations of $\sqrt{[(0.04 \times 0.96)/277]} = 0.0118$ (1.2%) and $\sqrt{[(0.118 \times 0.882)/330]} = 0.0178$ (1.8%), for the commercial ($n = 277$) and recreational fishery ($n = 330$) samples, respectively. The results from the ONCOR and gsi_sim analyses were similar (Supplementary Tables S5 and S6): the scaled likelihoods calculated by gsi_sim assigned 3.5% (SD = 1.1%) of the commercial catch to the inner fjord stock component, whereas in the recreational fishery 11.4% (SD = 1.8%) assigned to this component. The corresponding proportions with ONCOR were 3.3% (confidence interval (*CI*) range 1.2–5.6%) and 11.3% (*CI* range 7.8–14.9%). Estimated proportions of the two stock components in the fisheries did not change appreciably after excluding admixed fish from the population baseline: with gsi_sim the proportion of the inner fjord component was slightly reduced, to 3.1% in the commercial catch and to 10.5% for the recreational fishery.

No significant differences in the proportions of catches assigned to the two stock components appeared among the three trawl samples (contingency $X^2_{df=2} = 1.599$, $P = 0.450$; data not shown). Nor did the proportions of the two stock components differ during the year (among months: $X^2_{df=8} = 9.799$, $P = 0.279$: data not shown).

Fishery statistics

Thirty-one percent of the trawl-caught cod were under MLS (40 cm), as compared to 24% in the recreational fishery. Mean weight of cod above MLS collected from the shrimp trawlers was 1.74 kg [standard error (SE) 0.09]. We estimated that the total official landing of "inner fjord" cod above MLS by shrimp trawlers for the study area were 2.5 tons (4% of 63 tons) or 1400 individuals in 2012, by assuming that samples from the three shrimp trawlers represented the regional fleet and that landed cod above MLS were representative of the official landed catch. Mean weight of cod under MLS was 0.34 kg (SE 0.02), implying a total catch of 150 kg (440 individuals) inner fjord cod under MLS. These estimates by extrapolations from a small number of fishers are uncertain and should be considered only tentatively.

Discussion

We detected significant genetic heterogeneity among cod inside the Norwegian 12-nm limit in the Skagerrak, which are defined by present management as "coastal cod". In particular, we confirm differentiation into two major groups or stock components that have also been reported elsewhere in the Skagerrak (Barth *et al.*, 2017; Knutsen *et al.*, 2018). It remains unclear whether this pattern is maintained by selective differences between oceanic and fjord environments, by barriers to interbreeding, or by a combination of mechanisms (Bierne *et al.*, 2011; Sodeland *et al.*, 2016). However, a tentative conclusion of partial isolation between North Sea and inner fjord populations may be drawn on the basis of finding that more than 1000 of the 5758 unlinked SNPs were statistically significant. These differences are unlikely to be maintained by divergent selection alone.

GENECLASS2 estimates indicate that the proportion of the fjord component is small (4%) in the commercial trawl catches and in the recreational angling fishery (11.8%), but is significantly larger than in the commercial catches. Estimates from other software and with cleaned baseline samples yielded similar, but slightly smaller estimates (3.1–3.5% and 10.5–11.4%, respectively). These various analyses yielded small uncertainties with standard deviations of the order of 1%, no doubt due to our choice of discriminatory SNPs for genotyping.

The different mixed-stock proportions between the two fisheries is likely to reflect different habitat preferences of the two ecotypes. Differences between fisheries also reflect a tendency for commercial trawlers to exploit more off-shore areas compared to recreational fishers. As we found no significant differences in stock component proportions among trawlers, nor during the season, we conclude that the two fisheries consistently target different cod stock components in Skagerrak.

The results of our study indicate that the current management strategy for coastal cod in Skagerrak suffers from an inaccurate geographic scale for stocks or management units (e.g. Kerr *et al.*, 2014), and the results reported here do not suggest any easy solution. In particular, the coexistence of two or more stock components or populations of cod along the coast complicates the identification of management units in coastal waters. One clear implication of our findings is that there is no scientific evidence for today's management regime based on the 12 nm boundary, as the cod stock inside this limit is heterogeneous and represents a mixture of cod of different origins. Recent studies inside this boundary have also reported fine-scaled spatial structure in productivity-related traits such as growth and maturation (Olsen *et al.*, 2008; Kuparinen *et al.*, 2015; Roney *et al.*, 2016), suggesting that coastal cod may show important fitness components for the environment they inhabit. Hence, eradication of coastal populations through local overfishing, habitat intrusion or destruction, or other impacts could have wider negative consequences for populations, which may already be stressed due to climate change (Rogers *et al.*, 2011; Freitas *et al.*, 2016). Portfolio effects deriving from intraspecific biodiversity, such as stock, life-history, and genetic diversities, are important for overall productivity and associated long-term yields (Anderson CNK *et al.*, 2008; Schindler *et al.*, 2010). Harvests that lead to loss of these diversities are likely to negatively impact human communities that depend on these ecosystem services (Zhou *et al.*, 2010). Thus, it is of high importance to maintain as much as possible of the intraspecific biodiversity of coastal cod, including fjord and North Sea components in the coastal zone.

The current knowledge about total catches of fjord cod in the recreational fisheries is limited. The total impact of fjord cod from recreational fisheries is therefore unknown. However, recreational fisheries dominate the cod catches in inshore areas (Kleiven *et al.*, 2016). Here, we show that recreational fisheries capture a significantly larger proportion of fjord cod than do shrimp trawlers. We therefore advise increased attention on the management of recreational fisheries to reduce fishing mortality on the fjord cod component. At the same time, there is a need to collect data on recreational harvest to strengthen the current knowledge of the cod fishery, and their impacts, along the Skagerrak coast.

The large percentage of undersized fish (31%) in the shrimp trawl fishery can add substantially to the overall fishing mortality when these fish are discarded and when discard mortality is high.

We added cod under MLS to the total catch to estimate stock components due to the discard ban in Norway. However, it is unclear whether all discards are reported. The shrimp fishery may under-report discards, as few cod under MLS are officially registered in the landing statistics. Discard mortality is influenced by several factors including, but not limited to, towing duration, catch composition, individual fish injuries, fish size, and time on the deck (Davis, 2002). Humborstad *et al.* (2009) found that discard mortality of Danish seine caught cod was mainly linked to air exposure with 75% mortality at 10 min on deck. However, no data are available on the discard mortality of cod in the Norwegian shrimp trawl fishery. For cod caught and released by anglers, Ferter *et al.* (2015a) showed that lethal and sub-lethal impacts are limited when the cod are caught and released following best practice guidelines. Moreover, released cod have a high survival potential even when caught from great water depth as long as they manage to submerge and are otherwise not substantially injured (Ferter *et al.*, 2015b). It is therefore reasonable to expect that release mortality might be lower for recreational anglers than in the shrimp trawl fishery.

Other commercial and recreational fisheries, such as gillnet and trap fisheries, were not examined in the present study, but may have significant impact on the inner fjord cod stock component. The method developed here should be suitable to investigate these other fisheries in the same area in a cost-efficient manner. Future research should aim to cover all commercial and recreational fisheries to estimate the total impact of various fisheries on fjord cod. The results of these studies would be of special interest to management to formulate effective fishery regulations to promote sustainable harvests of fjord cod populations.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgement

We wish to thank Torbjørn Ertzeid Opsahl, Marine Dedeken and Enrique Blanco Gonzales for the assistance in collecting recreational fishing data, Hanne Sannæs and Kristil Kindem Sundaasen for lab assistance, and the editor Stewart Grant and two anonymous reviewers for valuable comments. The volunteer data collection from the four commercial fishing boats was highly appreciated. 12k SNP chip genotypes for the study were provided by the Norwegian Cod SNP Consortium (CSC). The work has been supported by the Norwegian Research Council (project no. 216410/O10), Aust Agder Knowledge Foundation (www.aaukf.no), Sørlandet Knowledge Foundation (www.skf.no) and the European Regional Development Fund (Interreg IVa, "MarGen" project).

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Handling editor: W. Stewart Grant