



Local cod (*Gadus morhua*) revealed by egg surveys and population genetic analysis after longstanding depletion on the Swedish Skagerrak coast

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Dramatic and persistent reductions in Atlantic cod (*Gadus morhua*) are common in many coastal areas. While offshore cod stocks still were abundant and productive, the Swedish west coast showed signs of diminishing adult cod abundance at the beginning of the 1980s, where the local cod component was considered to be extirpated. To survey the present cod spawning activity and stock composition, we initiated egg trawling over two consecutive years (203 hauls in total) in combination with population genetic analyses (425 individually genotyped eggs). Here, we provide evidence of cod spawning at the Swedish Skagerrak coast, suggesting recolonization or that local cod has recovered from a nearly depleted state. Early stage eggs were found inside fjords too far to have been transported by oceanic drift from offshore spawning areas. The cod eggs were genetically similar in early to late life-stages and cluster mainly with the local adult cod, indicating that eggs and adults belong to the same genetic unit. The cod eggs were genetically differentiated from adult North Sea cod, and, to a lesser degree, also from the Kattegat and Öresund cod, i.e. indicating a possible recovery of local coastal stock. The patterns of the genetic structure in the inshore areas are, however, difficult to fully disentangle, as Atlantic cod in the North Sea-Skagerrak area seem to be a mixture of co-existing forms: local cod completing their entire life cycle in fjords and sheltered areas, and oceanic populations showing homing behaviours. The egg abundances are considerably lower compared with what is found in similar studies along the Norwegian Skagerrak coast. Nevertheless, the discovery of locally spawning cod along the Swedish west coast—although at low biomasses—is an encouraging finding that highlights the needs for endurance in protective measures and of detailed surveys to secure intraspecific biodiversity and ecosystem services.

Keywords: conservation, egg abundance, fisheries management, genetic population structure, recruitment, spawning.

Introduction

Fish productivity remains low in many parts of the world in comparison to historical levels, although some previously depleted fish stocks show encouraging signs of recovery due to protective measures (Costello *et al.*, 2016). Even when recovery occurs, the pace is slow, especially in cases of prolonged overexploitation of already collapsed fish stocks (Neubauer *et al.*, 2013). The decline in many Atlantic cod (*Gadus morhua*) stocks is illustrative in this sense. Albeit some depleted stocks show some degree of recovery such as in Canadian waters (Rose and Rowe, 2015) and in the northern North Sea (ICES, 2017), these upturns have seldom been fast nor complete. Lack of revival of adult cod abundance is known from, for instance, Scottish inshore areas (Thurstan and Roberts, 2010), the Swedish west coast (Bartolino *et al.*, 2012), and in the southern North Sea (ICES, 2017). The reasons behind this rather slow recovery remain unclear, and there may be several possible explanations, such as changes in trophic structure, decline in individual growth due to size selective mortality (e.g. Sinclair *et al.*, 2002), Allee effects (Hutchings, 2014; Kuparinen *et al.*, 2014), and/or changes in population structure due to the loss of subpopulation components (Lilly *et al.*, 2008).

How marine fish populations arise and how they are connected through time and space to other population units is central to fish population ecology (Sinclair and Solemdal, 1988) and the prospects of recoveries. Studies indicate that natal homing and barriers to dispersal such as hydrographic features between spawning sites are essential population structuring factors (Svedäng *et al.*, 2007; André *et al.*, 2016; Bonanomi *et al.*, 2016; Jonsson *et al.*, 2016; Zemeckis *et al.*, 2017). Studies in the North Sea region suggest that sea currents connect cod population units by transporting propagules (i.e. eggs and larvae) from spawning grounds to nursery areas (Stenseth *et al.*, 2006; Heath *et al.*, 2008; Munk *et al.*, 2009; Jonsson *et al.*, 2016). Albeit mixing of eggs, larvae and juveniles from various population units may occur, genetic differentiation of populations appears to persist over time (Knutsen *et al.*, 2004, 2011; André *et al.*, 2016; Barth *et al.*, 2017; Knutsen *et al.*, 2018). Erosion of sub-population structure could hence imply losses of spawning sites, migration routes, and, eventually, reduced fish production, and thus may be of particular significance for stock recovery (Smedbol and Stephenson, 2001).

Where past local populations of Atlantic cod have entirely disappeared, it has been found difficult or impossible to predict the time needed for re-colonization (Hutchings, 2000; Rose *et al.*, 2011). Naturally, it is essential in studies on recovery potential and colonization processes, to first conclude whether local spawning still occurs or if the population has disappeared altogether. If spawning occurs on a regular basis, it is also an issue whether the spawning fish represent remnants of former populations or are immigrants from further afield.

The cod stocks along the Swedish west coast have become successively depleted, and in some places, probably even extirpated since the 1970s, as indicated by the deteriorated cod fisheries in these areas over the past decades (Svedäng, 2003; Svedäng and Bardon, 2003). The decline is profound, lasting and so far, no recovery has been identified (Sköld *et al.*, 2011; Bartolino *et al.*, 2012). This reduction has been attributed to an erosion of local stock structures (Svedäng, 2003). In support of such a local population structure, cod spawning activity has been documented throughout the Skagerrak and Kattegat (Figure 1; Hallbäck *et al.*, 1974; Jacobsson, 1982; Hagström *et al.*, 1990; Svedäng and Bardon, 2003; Knutsen *et al.*, 2004; Espeland *et al.*, 2007; Knutsen

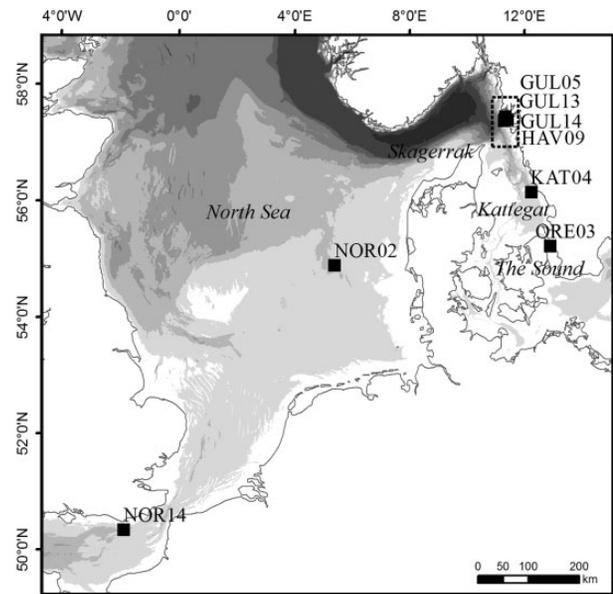


Figure 1. Map of the North Sea, Skagerrak, Kattegat, and Öresund. The inserted box on the Swedish west coast frames the combined study areas in 2013 and 2014 show in Figure 2.

et al., 2007; Vitale *et al.*, 2008; Börjesson *et al.*, 2013). There is historical evidence of cod spawning along the Swedish Skagerrak and Kattegat coasts, based on interviews with fishers and from fishers' private logbooks, which coincides with reports on higher stock productivity (Svedäng *et al.*, 2004). According to official statistics, inshore county cod landings (i.e. reported cod fishing in the county of Bohuslän inside the archipelago) between the 1920s and 1960s amounted 400–600 tonnes annually, whereas the coastal cod fishing declined step by step until it vanished in late 1990s due to increasingly poor catches (Svedäng, 2003; Svedäng *et al.*, 2004). These earlier landing records constitute a floor regarding potential yields in the Swedish Skagerrak inshore because the official landings report neither included subsistence nor recreational fishing catches. The total cod landings in 1999 in all kinds of fisheries except for trawl fishery, including both inshore areas and the “near offshore”, amounted to ~70 tonnes, which is only ~15% of the official historical landings.

In spite of the much-reduced local cod stocks along the Swedish Skagerrak coast, juvenile abundance has been high in some years relative to the near absence of adult cod most of the time (Pihl and Ulmestrand 1993; Svedäng, 2003; Svedäng and Svenson, 2006). This paradox has led to the suggestion that juvenile cod found along the eastern Skagerrak coast may have been passively transported from offshore spawning areas (Munk *et al.*, 1999; Svedäng, 2003; Cardinale and Svedäng, 2004). The unexpected low abundance of adult cod led to the hypothesis of return migration of juvenile and maturing fish to distant spawning areas (Pihl and Ulmestrand, 1993), which has been supported by recent tagging studies (Svedäng *et al.*, 2007; André *et al.*, 2016) and the genetic assignment of strong year classes of juvenile cod along both the Norwegian and Swedish Skagerrak coast to North Sea cod populations (Knutsen *et al.*, 2004; André *et al.*, 2016; Knutsen *et al.*, 2018). Another potentially important element shaping the population structure of Atlantic cod are observed differences in the genomic architecture (such as chromosomal rearrangements,

see Berg *et al.*, 2016; Kirubakaran *et al.*, 2016; Sodeland *et al.*, 2016), which may enable local adaptations, and create barriers to gene flow among populations (Barth *et al.*, 2017). Barth *et al.* corroborated the clear separation between the North Sea and Kattegat cod population units demonstrated in previous studies (e.g. André *et al.*, 2016), but also showed that cod in eastern Skagerrak fjords (Gullmarfjord and Idefjord) cluster genetically with both the North Sea and Kattegat cod. Indeed, where spawning cod may still exist on the Swedish Skagerrak coast, they do

not form a population unit separate from the North Sea or Kattegat spawning cod, but rather a mechanical mixture of these two components. Barth *et al.* (2017) suggested that either the former local cod stocks are extirpated in the area or have never existed.

Here, we investigate whether cod spawning activity still occurs along the Swedish Skagerrak coast (Figures 1 and 2), which, if so, would inform us concerning the prospects of a future recovery. We studied the spawning activity by estimating the abundance of

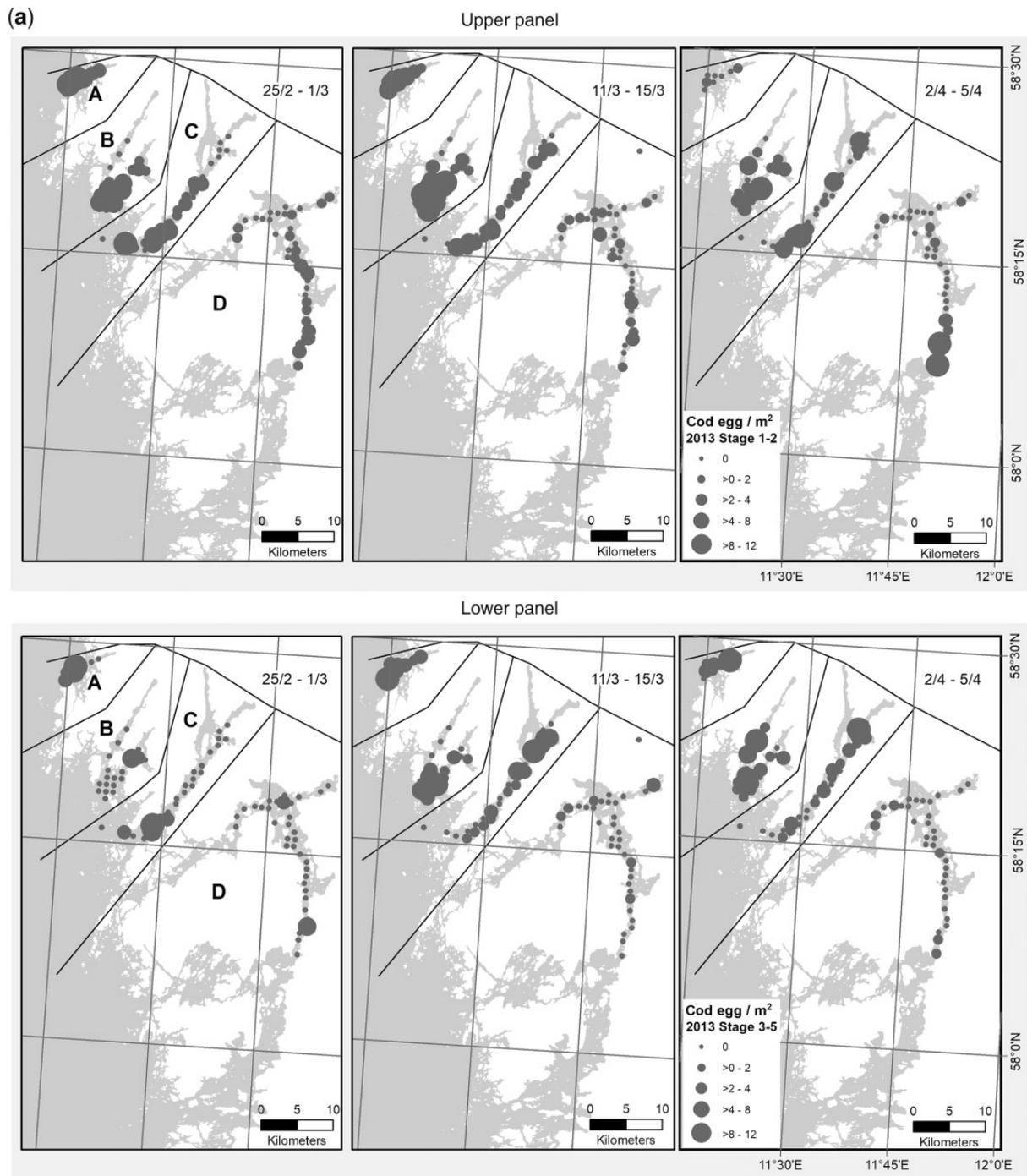


Figure 2. Catch-per-unit-effort (no. m^{-2}) of potential cod eggs in different developmental stages and survey in (a) 2013 and (b) 2014 on the Swedish Skagerrak coast. Areas A–F identify the different studied coastal areas. Point size indicates quantity of cod eggs per station.

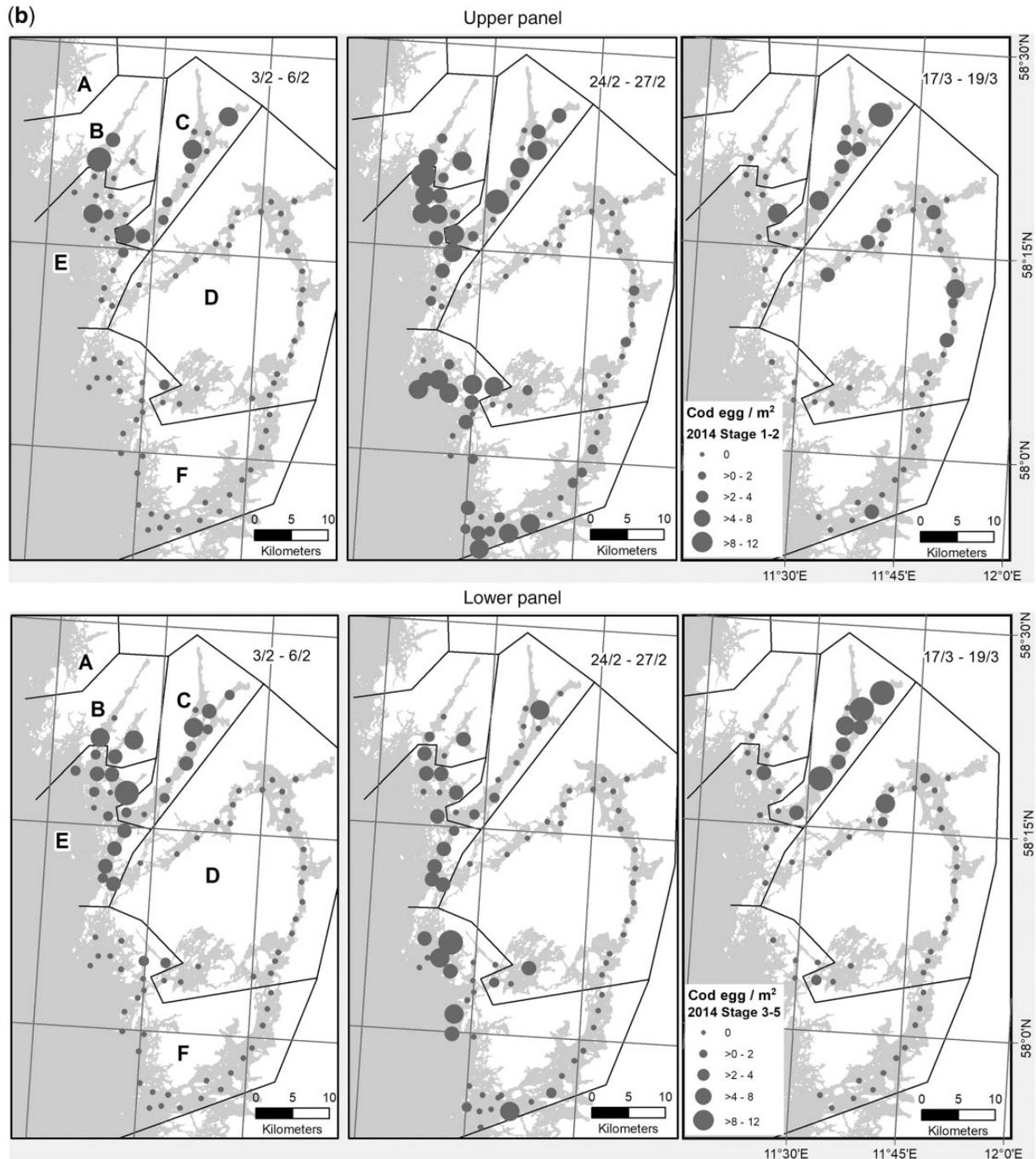


Figure 2. Continued.

early life stage cod eggs, which are 0–4 days old (stage I–Ib), or six days old (stage II), respectively (Geffen *et al.*, 2006). For such short periods of time, only limited horizontal transportation of the eggs in the order of a few up to 20 km may be assumed to have taken place since oviposition, depending on where in the water column the eggs are deposited (Arneborg, 2004; Pacariz *et al.*, 2014; Espeland *et al.*, 2015; Jonsson *et al.*, 2016). In other words, by estimating egg abundances across a geographic area, it is possible to identify spawning sites or “hot spots” (e.g. Bui *et al.*, 2011). Secondly, using a panel of SNP markers, we assessed the genetic clustering of these early-stage cod eggs in comparison to

reference populations of spawning adult cod (André *et al.*, 2016; Barth *et al.*, 2017) to investigate the origin of the observed cod eggs on the Swedish Skagerrak coast.

Material and methods

Egg surveys

We carried out fish egg surveys in the Swedish Skagerrak during two consecutive years. In 2013, we investigated egg abundance with vertical tows in four fjords: Bottnafjord, Brofjord, Gullmarfjord, and Havstensfjord (Figure 2a; Table 1). As to cover

Table 1. Total number of cod eggs in early stages (I–II) per area and survey in 2013 and 2014.

ID	Locality	Survey occasion and date		
		1	2	3
Year of sampling: 2013		25 Feb–1 March	11–15 March	2–5 April
2013A	Bottnafjord	1	31	2
2013B	Brofjord	27	91	28
2013C	Gullmarfjord	5	48	25
2013D	Havstensfjord	19	17	16
	Sum	52	187	71
Year of sampling: 2014		2–6 Feb	24–27 Feb	17–19 March
2014B	Brofjord inshore	2	6	0
2014C	Gullmarfjord	3	24	7
2014D	Orust inshore	0	3	7
2014E	Coastal Gullmarfjord & Brofjord	1	24	2
2014F	Inshore Tjörn & coastal Tjörn and Orust	0	37	1
	Sum	6	94	17

peak spawning activity, the survey was repeated three times all together in February, March, and April (Table 1; Supplementary Table S1). The tows were conducted at 71, 81, and 83 stations on the three sampling occasions, arranged by square grids covering the target areas. Some stations varied between surveys due to changes in ice cover. Fish eggs were sampled with vertical tows using a WP2 (Ø 1 m, mesh size 500 µm). The vertical speed of the net was 0.5 m s⁻¹. The tows were usually made from the bottom (down to a maximum 50 m depth) to the surface, meaning that at all sites except in some parts of the Gullmarfjord, the tows covered the whole water column. Each survey included several days of sampling.

In 2014, the egg survey was partly moved to the south, omitting the Bottnafjord area and extending the investigation by including the inshore of Hakefjord and Koljefjord, and more exposed areas west of the islands of Orust and Tjörn close to the offshore (Figure 2b; Table 1). The survey was repeated three times during February–March (Supplementary Table S1), including 85, 83, and 62 stations respectively. The number of stations varied due to weather conditions with high wind speed restricting the number of stations close to the open offshore.

Egg sorting

We analysed all water samples within 24 h and all detected gadoid eggs within the size interval of Ø 1.2–1.6 mm were staged according to Thompson and Riley (1981). Subsequently, we preserved the eggs in 96% ethanol for genetic analyses of individual eggs.

Atlantic cod egg abundance

Atlantic cod egg abundance per square metre was calculated as the number of eggs per haul divided by the surface area of the net (0.785 m²). Mean egg abundance was estimated as the mean number of eggs per tow and locality, by pooling all eggs identified as Atlantic cod (using species specific DNA marker, see below) per locality and sampling occasion, divided by the number of valid egg tows. Because not all gadoid eggs were included in the analysis in 2013 due to resource limitations, and due to the fact that some eggs with a gadoid appearance turned out to have been damaged, some underestimation of the total number of cod eggs may have occurred. Therefore, to compensate for this possible reduction, the proportion of Atlantic cod eggs per locality and

sampling occasion was estimated. This proportion was hence multiplied by the number of non-analysed gadoid eggs to determine the total number of potential cod eggs. Finally, we calculated the catch-per-unit-effort (CPUE) of eggs in different stages as the potential number of cod eggs divided by the number of hauls per locality. Both the total CPUE for all cod eggs, as well as the CPUE for cod eggs in early stages (i.e. I–II), were estimated.

Egg species identification and genotyping

DNA was extracted from the ethanol-preserved eggs in 96-well format using a modification of the salt extraction protocol (Aljanabi and Martinez, 1997). A species-specific marker for Atlantic cod was used for proper identification of cod eggs (Taylor *et al.*, 2002). Furthermore, the identified cod eggs were genotyped individually, using a set of 25 diagnostic SNP loci selected from previous studies: 13 loci identified by Heath *et al.* (2014) to study population structure in the North Sea area, and 12 loci from Berg *et al.* (2015), based on the ability to discriminate between the Kattegat and North Sea cod (Supplementary Table S2). SNP genotyping of eggs was done using KASPar assays (LGC, UK).

Genetic comparison of cod eggs relative to adult spawning populations

To determine the likely origin of the cod eggs collected in the Swedish Skagerrak, we assessed the genetic similarity of individual eggs relative to adjacent source populations. As such, we included samples of adult cod at spawning from the two major spawning units in the North Sea and Kattegat/Öresund (see Barth *et al.*, 2017), as well as adult cod from putative local spawning aggregations in eastern Skagerrak fjords (Figure 1; Table 2). The samples were mainly obtained from scientific surveys but also from commercial and recreational fishing. For these adult reference populations, we used already generated genotype data (12 K Illumina SNP-chip) obtained from Berg *et al.* (2015) [eastern North Sea (NOR02), Kattegat (KAT04), and Öresund (ORE03)], Barth *et al.* (2017) [Gullmarfjord 2005 (GUL05) and Havstensfjord (HAV09)]. Genotype data for Gullmarfjord 2013 (GUL13) and Gullmarfjord 2014 (GUL14) were obtained using the same method as described in Barth *et al.* (2017). The reference sample from the southern North Sea (NOR14) was genotyped together

Table 2. Sample information for adult reference populations.

Sample ID	Locality	Stage (% spawning)	Date	Lat	Long	n
NOR02	North Sea	Adult (100)	Mar 2002	55.57	05.85	42
NOR14	Eastbourne	Adult (n/a)	Mar 2014	50.61	00.33	8
GUL05	Gullmarfjord	Adult (100)	Mar 2005	58.24	11.36	47
GUL13	Gullmarfjord	Adult (100)	Apr 2013	58.17	11.30	20
GUL14	Gullmarfjord	Adult (100)	Jan-Mar 2014	58.18	11.32	28
HAV09	Havstensfjord	Adult (100)	Mar 2009	58.18	11.43	12
KAT04	Kattegat	Adult (96)	Feb 2004	56.90	12.15	48
ORE03	Öresund	Adult (100)	Mar 2003	55.95	12.70	48
					Total	253

Table 3. Genetic sample information for cod eggs.

ID	Egg sampling locality	Stage I–II	Stage III–V	n
2013A	Bottnafjord	28	40	68
2013B	Brofjord	54	63	117
2013C	Gullmarfjord	33	50	83
2013D	Havstensfjord	9	8	17
2014B	Brofjord inshore	4	5	9
2014C	Gullmarfjord	22	19	41
2014D	Orust inshore	4	4	8
2014E	Coastal Gullmarfjord and Brofjord	23	13	36
2014F	Coastal Tjörn and Orust; inshore Tjörn	31	15	46
	Total	207	218	425

Sample ID, number and stage of individually genotyped eggs collected in 2013 and 2014 at different sampling sites (Figure 2).

with the cod eggs using KASPar assays, thus enabling control for genotyping consistency among genotyping platforms. In total, we used genotype data for 25 SNP loci in 948 individuals. We filtered the data on genotyping success including only individuals that were successfully genotyped for at least 20 loci. The final dataset consisted of 425 cod eggs and 253 adult individuals genotyped for 20–25 loci. The egg data were pooled over the three sampling occasions per year, and over nearby sampling sites, resulting in four pooled samples (locations) in 2013 and five in 2014 (see Tables 2 and 3 for details).

Genetic clustering of cod eggs and adults was assessed using principal component analysis (PCA) by applying the function `smartpca` included in the software EIGENSOFT v6.0.1 (Patterson et al., 2006; Price et al., 2006). We used “`lsqproject`” to correct for missing data. Separation of clusters was tested with ANOVA in R v3.3.3 (R Core Team, 2017). Population differentiation (F_{ST}) among all eight adult and nine egg samples were also estimated using Genepop 4.2, with exact tests of statistical significance. False discovery rate (FDR) (Benjamini and Hochberg, 1995) was used to correct for multiple testing.

Results

Cod egg surveys

Atlantic cod eggs in early developmental stages (stages I–II), were found at all localities in both years (Table 4; Supplementary Table S3). The density of eggs was unevenly distributed, both within as well as among localities (Figure 2a and b). The CPUE of eggs in stages I–II at the different coastal localities varied between the years (Table 4). In 2013, the highest CPUE was observed in the Bottnafjord and Brofjord, whereas in 2014, the CPUE was

higher in the Gullmarfjord. Egg densities at a comparable level were also found in 2014 west of the large islands of Orust and Tjörn, in the vicinity of the outer skerries close to the offshore. In both years, the highest densities within the localities occurred at closely situated sampling sites (Figure 2). Eggs in later developmental stages were often found in close vicinity to where eggs in early stages of development had been collected. This progression of egg developmental stages up to the larval stage over the sampling period occurred in both years (Table 4).

Genetic assessment of locally spawned eggs

PCA based on 25 SNPs showed a scattered distribution of both adults and eggs (Figure 3a). There was, however, a clear separation between the North Sea and the Kattegat/Öresund adult reference samples (Figure 3b). The first principal component (PC) axis explains 11.2% of the total genetic variation and is defined by a significant separation among the three adult reference groups [North Sea (NOR02) vs. Kattegat/Öresund (KAT04, ORE03) ANOVA, $F_{1, 138} = 284$, $p < 0.001$; North Sea vs. Gullmarfjord/Havstensfjord (GUL05/GUL13/GUL14/HAV) ANOVA, $F_{1, 149} = 78.9$, $p < 0.001$; and Kattegat/Öresund vs. Gullmarfjord/Havstensfjord ANOVA, $F_{1, 203} = 49.5$, $p < 0.001$; Figure 3a and b; for mean PCA scores see Figure 3j]. The adult Skagerrak fjord samples (HAV09, GUL05, GUL13, and GUL14) show no significant differentiation among each other, except for the comparison between the Gullmarfjord samples GUL05 with GUL14 (ANOVA, $F_{1, 75} = 8.3$, $p < 0.01$; Figure 3c and j). Pairwise estimates of F_{ST} also show a strong differentiation among the adult reference samples (e.g. NOR02 vs. KAT04 $F_{ST} = 0.182$; for all pairwise F_{ST} values see Table 5).

The PCA analysis did not detect any differentiation between egg samples and young (stage 1–2) and older (stage 3–4 and larvae) egg samples were not differentiated (Figure 3g–i). Egg year classes, 2013 vs. 2014 (Figure 3e and f) were not separated either, but the combined egg sample was significantly separated along PC1 from all three adult reference groups, the North Sea, Kattegat/Öresund, and the adult Skagerrak fjord samples (ANOVA $F_{1, 466} = 212$, $p < 0.001$; $F_{1, 520} = 39.3$, $p < 0.001$; and $F_{1, 531} = 10.6$, $p < 0.01$) (Figure 3j). Likewise, all pairwise F_{ST} estimates between the North Sea and the different egg samples were relatively high and statistically significant (Table 5). Inspecting the separate pairwise F_{ST} comparisons in more detail (Table 5), we find, however, that the egg samples were not differentiated from the two adult Skagerrak samples collected furthest inside the fjord system (adult Gullmarfjord 2005 and Havstensfjord), and to a varying degree to the two Gullmarfjord samples collected

Table 4. The development of cod eggs over time in 2013 and 2014 at the studied localities.

ID	Year, locality and egg stages Year of sampling: 2013	Survey 1 No. m ⁻²	Survey 2 No. m ⁻²	Survey 3 No. m ⁻²
2013A	Bottnafjord			
	Stage I–II	3.4 ± 1.9	4.9 ± 2.7	0.32 ± 0.59
	Stage III–IV	1.1 ± 1.4	2.7 ± 1.6	2.0 ± 2.2
2013B	Brofjord			
	Stage I–II	2.4 ± 1.9	5.3 ± 4.8	2.0 ± 1.9
	Stage III–IV	0.20 ± 0.64	1.7 ± 1.8	1.9 ± 2.1
2013C	Gullmarfjord			
	Stage I–II	1.6 ± 2.0	2.3 ± 2.1	1.2 ± 1.8
	Stage III–IV	0.35 ± 0.90	1.3 ± 1.9	1.0 ± 1.5
2013D	Havstenfjord			
	Stage I–II	0.62 ± 0.85	0.72 ± 1.0	0.49 ± 1.3
	Stage III–IV	0.09 ± 0.42	0.15 ± 0.42	0.15 ± 0.40
2014B	Brofjord inshore			
	Stage I–II	0.74 ± 1.2	2.4 ± 1.5	0.0
	Stage III–IV	2.3 ± 1.7	0.87 ± 1.1	0.0
2014C	Gullmarfjord			
	Stage I–II	0.43 ± 0.56	2.8 ± 3.0	1.1 ± 1.3
	Stage III–IV	0.90 ± 1.3	0.58 ± 1.2	1.7 ± 1.2
2014D	Orust inshore			
	Stage I–II	0.0	0.18 ± 0.48	0.42 ± 0.78
	Stage III–IV	0.0	0.14 ± 0.50	0.15 ± 0.52
2014E	Coastal Gullmarfjord & Brofjord			
	Stage I–II	0.15 ± 0.42	2.9 ± 2.6	0.32 ± 0.41
	Stage III–IV	1.4 ± 1.7	1.5 ± 0.99	0.16 ± 0.45
2014F	Inshore Tjörn & coastal Tjörn and Orust			
	Stage I–II	0.009 ± 0.05	1.8 ± 1.6	0.08 ± 0.33
	Stage III–IV	0.018 ± 0.07	0.86 ± 1.8	0.0
	Stage V and larvae	0.0	0.082 ± 0.32	0.0

CPUE (\pm SD) of estimated potential Atlantic cod eggs per square metre (eggs m⁻²) by developmental stages per locality and survey occasion in 2013 and 2014, respectively. CPUE is estimated as the total observed number of potentially Atlantic cod eggs divide by the number of hauls per locality and sampling occasion.

closer to the fjord mouth, and even more strongly differentiated to Kattegat and Öresund adult samples (Table 5).

Discussion

Evidence of local cod spawning on the Swedish Skagerrak coast

By combining egg survey data and genetic analyses, this study reveals that local spawning of Atlantic cod on the Swedish Skagerrak coast is a wide-spread and regular phenomenon, although the present spawning activity is low (c.f. Espeland *et al.*, 2007). Previous investigations have indicated that the cod stocks along the Swedish west coast could be depleted or even extirpated (Svedäng, 2003; Svedäng and Bardon, 2003; Bartolino *et al.*, 2012). Indeed, the very existence of such local populations has been a matter of debate for several decades (e.g. Pihl and Ulmestrand, 1993; Barth *et al.*, 2017). In contrast, we find here evidence of a homogenous, separate coastal population. Yet, its origin cannot be determined with certainty albeit present observations suggest it existed before the stock decline in the late

1970s (Svedäng and Bardon, 2003) rather than formed recently, since the egg samples suggest a closer connection to the Kattegat stock in spite of the present stronger influence from the North Sea population components (André *et al.*, 2016; Barth *et al.*, 2017). These new insights thus give us a better understanding of the current cod population structure on the Swedish Skagerrak coast and how subpopulations may have been formed and are maintained.

These results are highly important for an ecosystem fisheries management (c.f. Long *et al.*, 2015; Bryhn *et al.*, 2017) that needs to take the presence of local spawning into account in future planning. However, patterns of the genetic structure are difficult to disentangle, as Atlantic cod in the North Sea—Skagerrak—Kattegat area seem to be a mixture of co-existing resident local forms, completing their entire life cycle in fjords or sheltered areas, and oceanic populations (Knutsen *et al.*, 2011, 2018; Barth *et al.*, 2017).

A key element of the population dynamics of cod in coastal Skagerrak has been the continued and unfaltering level of recruitment of juvenile cod, in spite of the prevailing low adult cod

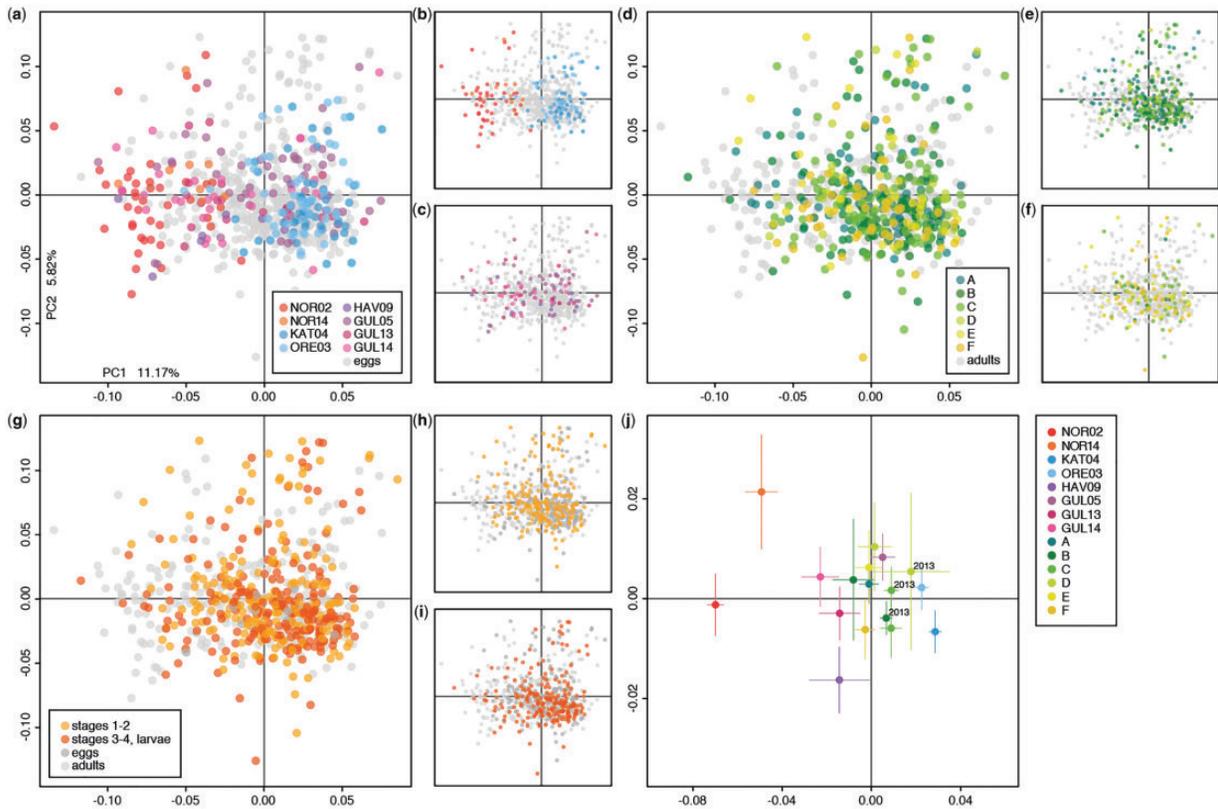


Figure 3. PCA (a–i). Principal component analysis (PCA) highlighting different groupings: (a–c) adult Atlantic cod, (a) all adult individuals, (b) adult reference samples from adjacent populations in the North Sea and Kattegat/Öresund, (c) adult fjord samples, (d–i) Atlantic cod eggs, (d) all eggs sorted according to sampling location, (e) 2013 egg samples, (f) 2014 egg samples, (g) all eggs sorted according to developmental stages, (h) stage 1–2 eggs, (i) stage 3–4 eggs and larvae, (j) PCA mean scores for each sampling location including standard error.

abundance in the Swedish Skagerrak inshore over the last three decades (Pihl and Ulmestrand, 1993; Svedäng, 2003; Cardinale and Svedäng, 2004; Svedäng and Svenson, 2006; Bartolino *et al.*, 2012). This over time steady supply of juveniles, has been credibly linked to the transportation of propagules (eggs and larvae) from offshore spawning aggregations/populations in the Kattegat and the North Sea into the Skagerrak inshore using a combination of statistical modelling (Spies *et al.*, 2018), oceanographic modelling (Jonsson *et al.*, 2016) and genetic studies (Knutsen *et al.*, 2004; Stenseth *et al.*, 2006; Barth *et al.*, 2017). Since this inflow of recruits into the coastal Skagerrak stocks has never transformed into a high abundance of adult cod (Svedäng, 2003; Svedäng and Svenson, 2006; Bartolino *et al.*, 2012), it has been hypothesized that the currently low abundance of adult cod in the eastern Skagerrak is due to return migrations to natal areas in the North Sea and Kattegat (Pihl and Ulmestrand, 1993; Svedäng, 2003). Indeed, such migratory behaviours have been corroborated in tagging and genetic studies (Svedäng *et al.*, 2007; André *et al.*, 2016).

Conclusively, the explanation of the difference between former rich and productive cod stocks at the Swedish Skagerrak coast and the current depleted state has been limited to speculations that local spawning cod may have strongly contributed to the previous adult cod abundance (e.g. Svedäng, 2003). Since this study provides pieces of evidence suggesting that local cod spawning still is a regular event on the Swedish Skagerrak coast, the discrepancy between past and present productivity may hence be seen as

partly resolved. The widespread occurrence of local spawning cod is the likely reason why the former abundance of adult cod was considerably higher when those local aggregations were more productive.

The field surveys

Cod eggs in early developmental stages were found in all localities and both years. Cod eggs at stages I–II are 0–6 days old at the ambient water temperatures (Geffen *et al.*, 2006). It may, therefore, seem reasonable to assume that only limited horizontal transport of the eggs, at ~1–4 km per day, can have taken place since oviposition (Jonsson *et al.*, 2016, Table 6; see also Arneborg, 2004; Knutsen *et al.*, 2007; Espeland *et al.*, 2015; Øresland and Ulmestrand, 2013), strongly indicating local spawning activity. The dispersal distance depends, however, not only on the duration in the water mass but also on whether the eggs are located below or above the halocline (Pacariz *et al.*, 2014; Espeland *et al.*, 2015; Jonsson *et al.*, 2016). Estimates of the average turnover time in the sill fjord Gullmarfjord is 16–26 days for the water above the halocline, and 40 days for the intermediate water below the halocline (Arneborg, 2004). In the nearby Brofjord, which is sheltered by small islands and skerries, the water exchange below the halocline at 16 m depth has been observed to be very slow in the summer period (Øresland and Ulmestrand, 2013). However, experiments with drifters demonstrated relatively fast movements

Table 5. Genetic differentiation (pairwise F_{ST}) among cod eggs collected in Skagerrak in 2013 and 2014 and putative source populations of adult cod—see map in Figure 1.

	NOR02	NOR14	GUL05	GUL13	GUL14	HAV09	KAT04	ORE03	2013A	2013B	2013C	2013D	2014B	2014C	2014D	2014E	2014F
NOR02	—																
NOR14	0.0704	—															
GUL05	0.1169	0.1023	—														
GUL13	0.0689	0.0548	0.0082	—													
GUL14	0.0489	0.0452	0.0198	−0.0086	—												
HAV09	0.0771	0.0966	−0.0051	−0.0119	0.0058	—											
KAT04	0.1820	0.1740	0.0115	0.0371	0.0608	0.0266	—										
ORE03	0.1638	0.1582	0.0011	0.0338	0.0543	0.0121	0.0005	—									
2013A	0.1053	0.0984	−0.0017	0.0019	0.0123	−0.0031	0.0193	0.0093	—								
2013B	0.1336	0.1207	−0.0005	0.0103	0.0281	−0.0019	0.0106	0.0043	0.0019	—							
2013C	0.1382	0.1273	−0.0016	0.0103	0.0320	−0.0058	0.0134	0.0023	0.0008	−0.0009	—						
2013D	0.1134	0.1183	−0.0091	−0.0033	0.0047	−0.0066	0.0127	0.0021	−0.0161	−0.0067	−0.0074	—					
2014B	0.1036	0.0872	−0.0042	0.0109	0.0058	0.0043	0.0425	0.0248	−0.0019	0.0209	0.0172	0.0011	—				
2014C	0.1514	0.1310	0.0010	0.0160	0.0344	−0.0010	0.0130	0.0074	0.0051	0.0013	−0.0031	−0.0026	0.0133	—			
2014D	0.1450	0.1154	−0.0030	0.0179	0.0302	0.0086	−0.0020	−0.0093	0.0007	−0.0064	0.0019	−0.0119	0.0221	0.0179	—		
2014E	0.1140	0.0938	−0.0081	0.0039	0.0144	−0.0084	0.0205	0.0067	−0.0032	−0.0009	−0.0028	−0.0116	0.0055	0.0012	−0.0005	—	
2014F	0.1054	0.0795	−0.0002	−0.0021	0.0071	−0.0045	0.0252	0.0197	−0.0005	0.0013	0.0090	−0.0066	−0.0019	0.0075	0.0080	0.0006	—

Bold values are significant after FDR correction.

of large water masses in the surface layers, which also was reflected in a varying halocline depth. In the present study, we made no records of the vertical distribution of cod eggs, and it, therefore, remains uncertain how far eggs may have drifted, and consequently if some eggs could have been transported and dispersed from some spawning locations outside the area of investigation. Nevertheless, modelled drift distances and water turnover rates for the fjord water masses are consistent with local spawning activity. In comparison, Myksvoll *et al.* (2011) and Myksvoll *et al.* (2014) showed high retention of cod eggs inside a Norwegian fjord and negligible transport from coastal areas into fjords.

The observed gradual development of the eggs to the larval stage over the sampling period is also consistent with local spawning activity. In other words, if the eggs had originated from spawning sites outside the investigated coastal areas, it is unlikely that these would have reached the Swedish Skagerrak coast in a seasonal succession of developmental stages, i.e. from very early stages (eggs with just 0–4 cells), and thereafter continuously up to the larval stage. In comparison, sexual mature plaice (*Pleuronectes platessa*), seldomly occur at the Swedish Skagerrak coast and have a very low local spawning activity. Hence, most plaice eggs are presumably transported from offshore spawning sites to the Swedish coast (Ulmestrand, 1992; Ulrich *et al.*, 2013). Indeed, all plaice eggs were at the same late developmental stages throughout the study (i.e. stage III–V, Supplementary Table S4).

Also, our results give a possibility to assess the present local population status (c.f. Bartolino *et al.*, 2012; Bryhn *et al.*, 2017). The observed maximal egg densities, including both years, varied between 0.18 and 5.3 stage I–II cod eggs m^{-2} between studied areas (Table 4). This range of cod abundance was considerably lower compared with what has been found in similar studies at the Norwegian Skagerrak coast (e.g. Espeland *et al.*, 2007). However, an unbiased, quantitative comparison is not possible as the reported densities by Espeland *et al.* reflected only stage I cod egg by metre vertical haul, and was not normalized for the opening area of the VP2 dip-net. This discrepancy between areas is consistent with the present depleted status of cod on the Swedish part of the Skagerrak coast (c.f. Bartolino *et al.*, 2012). The highest densities in this study were recorded from sampling stations in Bottnafjord and Brofjord, suggesting somewhat larger spawning aggregations in these two areas.

Genetic analysis of the egg samples

The rather small set of SNP loci used were selected to detect differentiation between the two major spawning units North Sea and Kattegat, with limited power to delineate more subtle population structure. For example, the recent findings of a western Skagerrak fjord type associated with chromosomal rearrangements observed by Barth *et al.* (2017), is unlikely to be detectable in the present study.

As expected, the PCA separated the adult reference samples in one North Sea cluster and one Kattegat cluster (Figure 3b and j). The adult fjord samples clustered in between, with the Gullmarfjord 2005 sample closer to the Kattegat and the other fjord samples closer to the North Sea (Figure 3c and j). Using a much larger set of ~6000 loci, Barth *et al.* showed that individual adults from the Gullmarfjord seem to belong to either of the North Sea or the Kattegat cluster, but as a group showed intermediate clustering (Figures 3b and S3a3 in Barth *et al.*, 2017).

They concluded that the Gullmarfjord cod might be a mechanical mix of the North Sea and Kattegat/Öresund cod rather than a distinct fjord population. Here we demonstrate that local spawning occurs inside the fjords, and that the eggs, although showing a somewhat scattered clustering, clearly group with the adult 2005 Gullmarfjord cod collected deep inside the fjord, indicating that adult individuals and eggs belong to the same genetic unit(s), adding evidence for the existence of a fjord population (Figure 3j and Table 5). The eggs are differentiated from adult cod collected in the eastern North Sea and the English Channel, and, to a lesser degree, also from the Kattegat and Öresund cod. The closer similarity to the Kattegat than the North Sea is consistent with a recent egg dispersal model by Jonsson *et al.* (2016) indicating that the Swedish Skagerrak coast may have stronger connectivity with the Kattegat than the North Sea. This similarity between the Swedish Skagerrak coast and the Kattegat, in spite of the fact that juvenile cod in the Skagerrak inshore, at present, seem to originate from the North Sea rather than the Kattegat due to the depletion of the Kattegat stock (André *et al.*, 2016; Barth *et al.*, 2017), might reflect a historically stronger genetic influence from the Kattegat cod.

Finally, our results with a more dichotomous clustering of adults compared with eggs may reflect a selection or sorting process, where a weak local population producing eggs is swamped by immigration of drifting juveniles and swimming adults from an adjacent population, e.g. the North Sea (c.f. André *et al.*, 2016).

Conclusions

The occurrence of locally spawned cod eggs suggests that spawning on the Swedish Skagerrak coast, in fact, takes place. The higher degree of genetic similarity between coastal cod eggs and the Kattegat/Öresund cod compared with the North Sea cod further suggests close connectivity between different populations in the region. These eggs could belong either to a coastal subpopulation that is a remnant stock of a once much larger cod population (e.g. Svedäng and Bardon, 2003) or to a newly formed subpopulation that is now successfully inhabiting the coastal ecosystems along the Swedish Skagerrak coast. In either case, the discovery of locally spawned cod eggs in an area where Atlantic cod were believed to be extirpated due to the overfishing is encouraging news. However, as the fish productivity of the Skagerrak coastal area is far from restored, the present unsatisfactorily situation hints that the stock is still struggling to overcome thresholds.

Supplementary data

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

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