

## Original Article

# Connectivity among offshore feeding areas and nearshore spawning grounds; implications for management of migratory fish

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Knowing movement and structure of fish populations is a prerequisite for effective spatial fisheries management. The study evaluates migration patterns and connectivity of two groups of cod (*Gadus morhua*) associated with offshore feeding and nursery grounds. This was achieved by investigating (i) migration pathways of cod tagged at the feeding areas, (ii) immigration of cod to the areas based on mark-recapture data covering a period of two decades, and (iii) depth and temperature data from data storage tags (DSTs). Despite undertaking long-distance migrations after attaining sexual maturity, the cod aggregations in the two study areas appear to be largely separated from each other. This conclusion is supported by DSTs, indicating that mature fish associated with the two areas occupy different thermal-bathymetric niches. Low levels of connectivity suggest that effective spatial management in the two study areas would preserve fish of different origin. For the highly migratory adults, however, spatial management would need to focus on migration pathways and the areas where the fish are particularly vulnerable to fishing.

**Keywords:** cod *Gadus morhua*, migration, population structure, spatial fishery management, tagging.

## Introduction

Fish populations typically exhibit a high degree of spatial structure, and contain stock components that may differ with respect to various biological and behavioural factors and levels of interconnectivity (Hilborn *et al.*, 2003; Robichaud and Rose, 2004; Metcalfe, 2006; Ruzzante *et al.*, 2006; McAdam *et al.*, 2012). The spatial structure is generally thought to be determined at early life stages, and shaped by oceanographic processes and behaviour such as natal homing to spawning grounds (Heath *et al.*, 2008; Svedäng *et al.*, 2010; Bonanomi *et al.*, 2016). In fisheries management, it is important to take this variability into account in order to avoid overfishing of vulnerable stock components and preserve diversity within populations (Hutchinson, 2008; Ying *et al.*, 2011; Zemeckis *et al.*, 2014). Spatial closures, such as marine-protected areas (MPAs), have been put forward as a promising tool for conserving marine biodiversity and fish stocks (Jennings, 2001; Gell and Roberts, 2003; Roberts *et al.*, 2005), although they are not the

cure-all for fishery-management problems, and in the case of migratory fish cannot be relied upon as a sole solution (Hilborn *et al.*, 2004; Kaiser, 2005).

Different types of MPAs and seasonal closures are widely used as management tools for fish in temperate-boreal waters, such as for the commercially and ecologically important Atlantic cod (*Gadus morhua*) (Jaworski *et al.*, 2006; Le Bris *et al.*, 2013; Sherwood and Grabowski, 2016). Cod populations from different regions are known to consist of spatially segregated subpopulations or spawning components, in some cases with low levels of interconnectivity (Ruzzante *et al.*, 2000; Smedbol and Stephenson, 2001; Harrald *et al.*, 2010; Neat *et al.*, 2014; Zemeckis *et al.*, 2014). This metapopulation structure (Smedbol and Wroblewski, 2002) means that distant MPAs may preserve different subpopulations. However, the rate of transfer of fish between MPAs and fishing grounds will ultimately affect the efficacy of the MPAs as a management tool. Knowledge on fish migration

is therefore essential, both at the planning state of the MPAs and when evaluating their effectiveness (Horwood *et al.*, 1998; Kaiser, 2005).

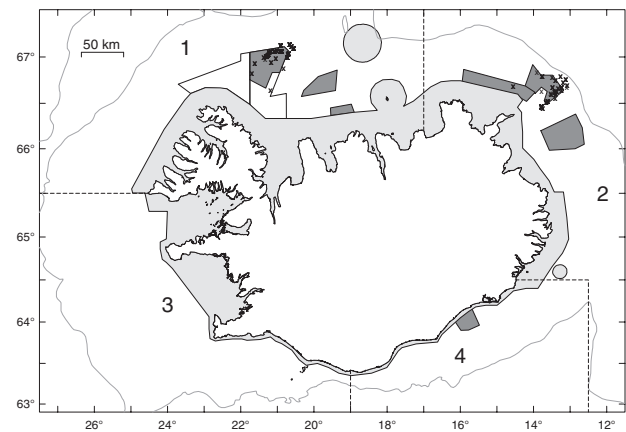
The groundfish fisheries in Icelandic waters are managed using a combination of measures, including various types of spatial closures (Jaworski *et al.*, 2006; Schopka *et al.*, 2010). Although permanent spatial closures have been established in different areas in order to reduce fishing mortality of young cod, their aim has not been to protect population diversity. In fact, the cod fishery is managed on a single-stock basis with total allowable catch limits set annually for the whole population (Marine Research Institute, 2016). Cod spawn at numerous locations around Iceland, and in recent years, studies have focused on biological variation in spawning components based on tagging studies (Pálsson and Thorsteinsson, 2003; Grabowski *et al.*, 2011; Sólmundsson *et al.*, 2015), otolith characteristics (Jónsdóttir *et al.*, 2006; Petursdóttir *et al.*, 2006), genetic variation (Pampoulie *et al.*, 2006, 2012; Eiríksson and Arnason, 2013), and morphology (McAdam *et al.*, 2012). The main spawning grounds are located in the south and southwest (Jónsson, 1996; Jónsson and Pálsson, 2013) from where eggs and larvae are considered to drift clockwise via the Irminger Current that flows north along the west coast. Part of that current branches in variable strength into North Icelandic waters (Jónsson and Valdimarsson, 2005). A freshwater-induced coastal current (Valdimarsson and Malmberg, 1999) further enhances the drift of larvae from spawning grounds to nursery areas.

The distribution of adult cod and larvae from the main spawning grounds is in accordance with the model of denatant migrations and dispersal (Harden-Jones, 1968). At the feeding areas, cod from spatially segregated spawning grounds are considered to mix with each other and concentrations of more stationary immature fish (Jónsson, 1996; Schopka *et al.*, 2010). However, it is not well known how thoroughly juvenile and adult fish from different spawning grounds are intermixed at the feeding areas. This knowledge is crucial for spatial fisheries management, whether it is no-take MPAs, spatial zoning of fleet access, or spatially explicit catch quotas (Rassweiler *et al.*, 2012). With this in mind, the study was aimed at evaluating distribution patterns and connectivity of two groups of cod that utilize distant offshore areas as nursery and feeding grounds. This was achieved by (i) investigating the distribution of recaptures of cod tagged within the feeding areas, (ii) evaluating immigration of cod from other areas, and (iii) analysing depth and temperature data from data storage tags (DSTs).

## Material and methods

### Emigration from feeding areas

Cod were tagged in surveys on RV Bjarni Saemundsson studying fish communities in offshore MPAs northwest and northeast of Iceland (Jaworski *et al.*, 2010). These waters are known to be nursery areas for cod and feeding areas for adults (Jónsson and Pálsson, 2013), but there is no information suggesting spawning in these areas. Fish were tagged inside or within 10 km outside the MPAs' boundaries (Figure 1); in the northwest area (NW-T) during 10–20 August 2004 (2153 cod tagged) and in the northeast area (NE-T) during 6–15 July 2005 (940 cod tagged). Fish for tagging were sampled using an otter trawl with a 40 mm mesh size in the codend. Tow duration was 15–70 min in 2004 (mean 45 min) and 20–38 min in 2005 (mean 31 min). Cod were immediately



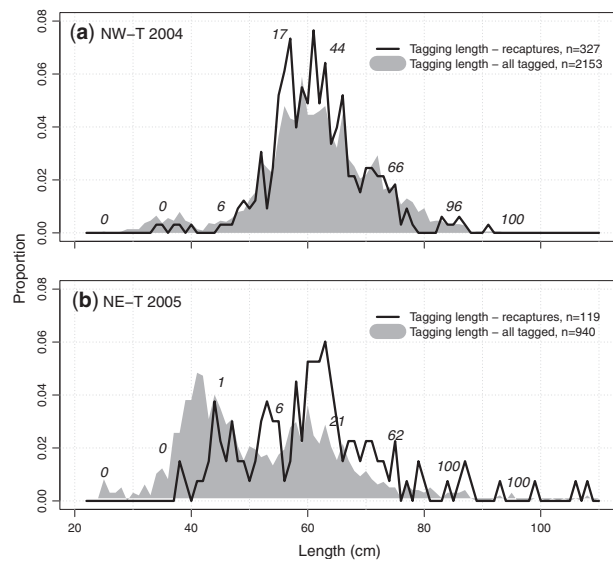
**Figure 1.** Cod tagging locations in area NW-T in August 2004, and area NE-T in July 2005 (black crosses). Dark-grey polygons indicate areas permanently closed to otter trawl, pelagic trawl and longline since 1993. The open (white) areas are either open seasonally or were re-opened in the study period. The light-grey areas have been permanently closed for otter trawl since 1976. Broken lines delineate Regions 1–4. The 500-m depth contours are shown as grey solid lines.

transferred into a basin with running seawater. Fish showing signs of weakness were removed but individuals considered to be viable were tagged 5–90 min later, measured for total length to the nearest cm, and released through a short pipe leading downwards to the sea surface.

Most cod (90%) tagged in the NW-T were 48–80 cm long, whereas 46% of those tagged in the NE-T were below 48 cm. For recaptured cod, however, the length at tagging was similar between areas ( $M = 61.7$  cm,  $SD = 8.2$  for the NW-T, and  $M = 59.4$  cm,  $SD = 11.1$  for the NE-T) (Figure 2). All cod were tagged with conventional anchor tags attached with a tagging gun at the base of the first dorsal fin. Sexual maturity of cod at the tagging areas was determined from samples collected during tagging, with 504 cod examined in the NW-T, and 214 cod in the NE-T. Stage of maturation was recorded according to a 4-stage classification as; immature, ripening, spawning, and post spawning. In total, 94% of fish below 60 cm in length were immature, whereas 74% of fish larger than 70 cm were post-spawners, but no actively spawning cod were found.

Recaptures were divided between three time periods and two seasons, following Schopka *et al.* (2010). The time periods were the calendar year of tagging (Period 1), the calendar year following the year of tagging (Period 2), and subsequent years (Period 3). The main feeding season is defined as June–January, whereas the period February–May includes the spawning season and the period of migration to and from the spawning grounds (Jónsson, 1982, 1996; Pálsson and Thorsteinsson, 2003; Grabowski *et al.*, 2011). In this paper the latter period is referred to as “the spawning season”. The spatial distribution of recaptures was compared to the spatial distribution of fishing effort targeting cod, based on fishing logbooks for the main fishing gear (otter trawls, longlines, gillnets, demersal seines and handlines) used in 2005–2007.

To estimate statistically whether NW-T and NE-T cod had different spatial distributions in the years following tagging, Icelandic waters were divided into four regions within the 500-m isobath (Figure 1). The boundaries of the four regions were based



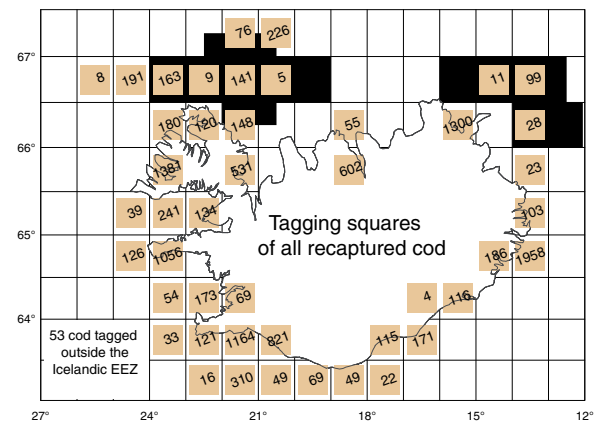
**Figure 2.** Relative length distribution of tagged cod (shaded area), and relative length distribution of recaptured cod at tagging (black line) in (a) NW-T 2004 and (b) NE-T 2005. The numbers above the shaded area indicate the percentage of sexually mature (post-spawning) fish for the corresponding 10-cm length intervals, according to samples collected during tagging.

on the definition of areas in the BORMICON multispecies model (Stefánsson and Pálsson, 1997). Spatial overlap in the recapture data was analysed using Chi-square tests. The observed numbers of recaptured cod from each tagging group (NW-T and NE-T) in each region/season were compared with the expected numbers assuming that the two tagging groups were thoroughly intermixed in the study area (Latour *et al.*, 2001). The null hypothesis is that there is no difference in spatial distribution between the two groups. Because there are two groups and four regions, the degrees of freedom were calculated as  $(2-1) \times (4-1) = 3$ , and  $\chi^2_{0.001, 3} = 16.3$  is used as a critical value.

### Immigration to feeding areas

The tag-recapture database at the Marine and Freshwater Research Institute was analysed for the years 1991–2010, with the purpose to locate original tagging sites of cod recaptured inside or adjacent to the MPAs in the northwest and northeast (“back tracking” from recapture to tagging). Tagging sites were grouped according to Icelandic statistical squares (0.5 degrees latitude  $\times$  1 degree longitude, hereafter called tagging squares) (Figure 3). In total, date and position of tagging for about 13 600 recaptured cod are available for this period, whereof about 12 500 include information on geographic coordinates or area of recapture. The tagging squares (45 in total) are distributed around Iceland, but most recaptures originate from nearshore waters (Figure 3).

Two “recapture areas” were defined, one including three MPAs in the northwest and nearby areas open to fishing (area NW-R), and the other including three MPAs in the northeast and nearby fishing areas (area NE-R) (Figure 3). The recapture areas were delimited by outlines of statistical squares overlapping the MPAs. The “back-track” approach is based on studying the number of recaptured cod from different tagging squares (Figure 3), and, therefore, affected by the number tagged in each square. To



**Figure 3.** Tagging squares (statistical squares) for all cod recaptured in Icelandic waters in 1991–2010, and the number of recaptures from each tagging square (only cod with known recapture location). Black polygons north of Iceland indicate the NW-R and NE-R “recapture areas”. EEZ = Exclusive Economic Zone.

account for this, the number of recaptures from each tagging square was scaled by the total number recaptured from the same square (excluding fish with unknown recapture location). The results are presented as number of recaptures per 100 total recaptures (%).

### Depth and temperature

Depth and temperature data were extracted from 16 returned DSTs (Table 1), produced by Star-Oddi and surgically implanted in the abdominal cavity of cod. Characteristics of the tags and tagging procedure are described on the website: [www.hafro.is/skrar/flokkar/merkingar\\_thorskur.pdf](http://www.hafro.is/skrar/flokkar/merkingar_thorskur.pdf) (accessed on 17 May 2017). The criteria for selecting DSTs were that they were either (i) recaptured within the recapture areas defined above (Figure 3), (ii) provided tidal locations (Thorsteinsson *et al.*, 2012) from within the recapture areas, and (iii) depth and temperature were measured for at least 5 months.

DSTs recaptured/positioned in the NW-R were retrieved from mature cod tagged on spawning grounds west and north of Iceland (west of 21°W). In contrast, DST tagged cod associated with the NE-R area originated from spawning grounds northeast or southeast of Iceland (east of 19°W). As a part of earlier studies, recaptured cod with DSTs were classified into “coastal” or “frontal” behavioural types (hereafter called frontal and coastal cod), based on their depth and temperature association outside the spawning season (Pálsson and Thorsteinsson, 2003; Pampoulie *et al.*, 2008; Grabowski *et al.*, 2011). Coastal cod show a clear seasonal change in temperature, with a maximum in September/October and a minimum in February/March, and reside mostly at depths less than 200 m. In contrast, frontal cod are generally found at depths greater than 200 m outside the spawning season, and tend to conduct frequent vertical migrations, often showing highly variable temperatures indicative of thermal fronts.

Daily depth and temperature data from the 16 DSTs were used to compare thermal-bathymetric “envelopes” of cod associated with the NW-R ( $n = 4$ ) and NE-R ( $n = 12$ ) areas, by plotting 50% and 95% bivariate kernel density distributions. The depth–

**Table 1.** Information on 16 data storage tags (DSTs) from cod associated with the NW-R or NE-R recapture areas.

ID	Ecotype	Data days	Tagging				Recapture				Tidal locations	
			$L_t$	Month	Year	Area	$L_r$	Month	Year	Area	Months	Area
3C1499	F	853	76	4	2005	W	–	8	2007	NW	2	NW
2C1492	F	778	76	4	2005	W	90	5	2007	W	11, 12, 1, 3, 4	NW
2C1493	C	190	74	4	2005	W	78	10	2005	NW		
1M1847	C	173	73	4	2002	NW	73	11	2002	NW		
1C0585	F	1108	99	4	2003	NE	111	9	2006	NE	11, 12, 1	NE
1C0605	F	682	78	4	2003	NE	90	3	2005	NE	2	NE
1C0611	F	1036	73	4	2003	NE	90	2	2006	NE		
1C0617	F	162	78	4	2003	NE	78	10	2003	NE		
1C0618	F	234	84	4	2003	NE	86	12	2003	NE		
1C0621	F	504	73	4	2003	NE	80	9	2004	NE		
2M1062	F	271	77	4	2002	NE	–	1	2003	NE		
1C1244	F	525	84	4	2004	SE	90	9	2005	NE	6, 9	NE
1M1761	F	176	77	4	2002	NE	86	1	2003	NE		
1C1225	C	927	87	4	2004	SE	101	11	2006	NE	2	NE
1M1082	C	423	66	4	2002	NE	–	11	2004	NE		
1M1091	C	201	78	4	2002	NE	–	11	2002	NE		

DST id, ecotype as classified by earlier studies (F = frontal, C = coastal), number of days where depth and temperature data were registered (Data days), total length at tagging ( $L_t$ ), month, year and area of tagging, total length at recapture ( $L_r$ ), month, year and area of recapture, and months where the fish were located in the NW-R or NE-R areas according to tidal locations.

**Table 2.** Temperature and depth at stations where cod were tagged in the NW-T and NE-T areas, and numbers tagged and recaptured by area.

Year	Tagging area	Bottom temperature (°C), mean (range)	Surface temperature (°C), mean (range)	Depth (m), mean (range)	No. tagged	No. recaptured	Percent (%) recaptured
2004	NW-T	4.2 (1.7–7.0)	8.8 (7.0–10.9)	191 (81–250)	2153	327	15.2
2005	NE-T	3.0 (2.0–3.6)	7.0 (5.8–8.4)	194 (128–230)	940	119	12.7
	Total				3093	446	14.4

temperature distributions need to be evaluated with the low sample size in mind. The maximum depth recorded on each calendar day was taken as indicative of the bottom depth where the fish resided, assuming that cod spend at least some time during every 24 h at or close to the seabed (Wright *et al.*, 2006; Le Bris *et al.*, 2013). Temperature at daily maximum depth was taken as indicative of near-bottom temperature.

The statistical program R version 3.1.3 (R Core Team, 2015) was used for statistical analyses and plotting. Terms regarding population structure are defined following Smedbol and Stephenson (2001), as described in Sólmundsson *et al.* (2015).

## Results

### Emigration from feeding areas

From a total of 3093 cod tagged in 2004 and 2005, a total of 446 (14.4%) were recaptured (Table 2). Relatively few (4%) of the smaller cod (20–45 cm) were recaptured but recaptures of 55–75 cm fish were 18%. Most fish (90%) were recaptured in the first 3 years after tagging. About 74% of the recaptured cod were caught by otter trawlers, 16% by longliners, and 10% by vessels using gillnets, handlines (jigs) or demersal seines.

Most cod tagged in the NW-T were recaptured off the western part of Iceland, west of 18°W in the north and west of 22°W in the south (Figure 4a–c). In the feeding season, most were distributed in offshore waters northwest of the country, whereas in the spawning season, cod were recaptured closer to the shore in the

southwest and west. In contrast, most cod tagged in the NE-T were recaptured in offshore waters northeast and east of Iceland in the feeding season, but in the spawning season, recaptures were more widely distributed (Figure 4a–c). A single NE-T cod was recaptured northeast of the Faroe Islands in May 2007. The spatial distribution of recaptures from the NW-T and NE-T areas matched reasonably well with the contemporary distribution of fishing intensity west and east of Iceland, respectively (Figure 4d–f).

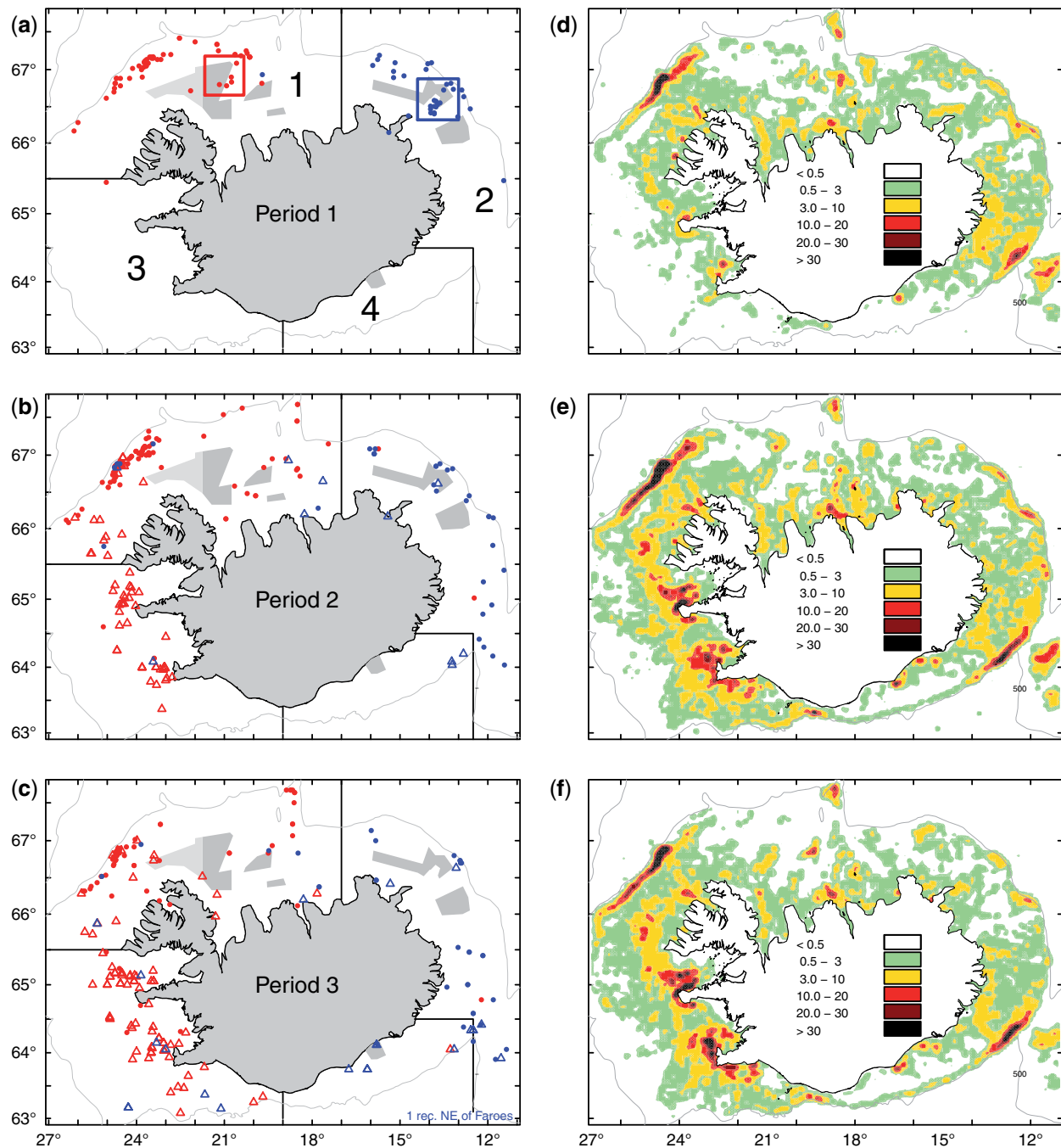
Seasonal migration patterns became clearly apparent by analysing temporal trends in minimum migration distance between tagging and recapture (Figure 5). Cod were consistently recaptured farther away from the tagging sites in the spawning season compared to the feeding season, for about 3 years after tagging. Seasonal migrations were less pronounced for the NE-T where the sample size was lower (Figure 5 and Table 2).

The observed numbers of recaptured cod from each tagging group (NW-T and NE-T) in each region/season indicates that the two groups were not thoroughly intermixed. For all seasons analysed, the calculated  $\chi^2$  statistics were greater than the critical value of 16.3 (Table 3). Therefore, the null hypothesis of uniform distribution of the two tagging groups was rejected ( $p < 0.001$ ).

### Immigration to feeding areas

Back tracking original tagging sites of cod recaptured within the specified recapture areas, revealed that most cod (134 out of 162)





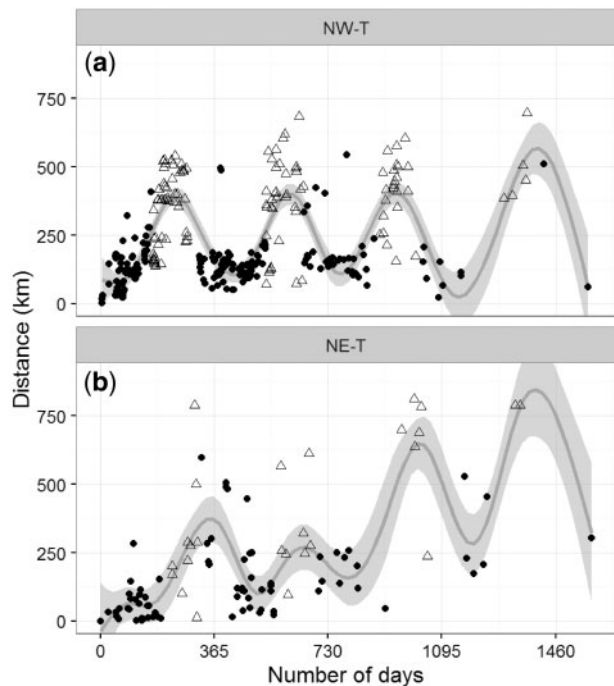
**Figure 4.** (a–c) Recapture locations of cod from the NW-T 2004 tagging (red) and the NE-T 2005 tagging (blue) by periods. (a) Calendar year of tagging, (b) calendar year after the year of tagging, and (c) subsequent years. Filled dots indicate recaptures during June–January (feeding season); open triangles during February–May (spawning season). Boxes show the tagging areas. The grey polygons denote MPAs in force during most of the recapture period (see Figure 1) and the lines show boundaries of regions 1–4 used for analysing the recapture data. (d–f) Spatial distribution of cod catch ( $t\ nmi^{-2}$ ) in (d) June to December 2005, (e) January to December 2006, and (f) January to December 2007 according to fishing logbooks.

recaptured in the NW-R were originally tagged northwest of Iceland (Figure 6a), in Region 1 (see Figure 1). The majority (113) of these fish were less than 65 cm at tagging (Table 4). Nineteen cod recaptured in the NW-R migrated from spawning grounds in the west and southwest (Region 3), whereof 14 were larger than 65 cm at tagging (Figure 6a and Table 4). In the NW-R,

only four cod were recaptured from extensive tagging studies in Region 2 northeast and east of Iceland (0–4% of recaptures from that area), and not a single cod from the central south or southeast coasts (Region 4). In addition to tagging studies at Iceland, five tags came from cod tagged off East Greenland (60–64°N, 37–46°W). They were 50–62 cm when tagged in

2007–2008, but 72–87 cm and 6–7 years old when recaptured in the NW-R in 2009–2010.

Most cod (126 out of 155) recaptured in the NE-R area originated from tagging sites in the northeast, including both large and small fish (Figure 6b and Table 4). In contrast to the NW-R, several large cod from spawning grounds off the south and south-eastern part of Iceland, east of 21°W, were recaptured in the NE-R, or up to 6% of fish from that area (Figure 6b). Thus, cod tagged off the south coast appear to migrate to the NE-R rather than the NW-R.

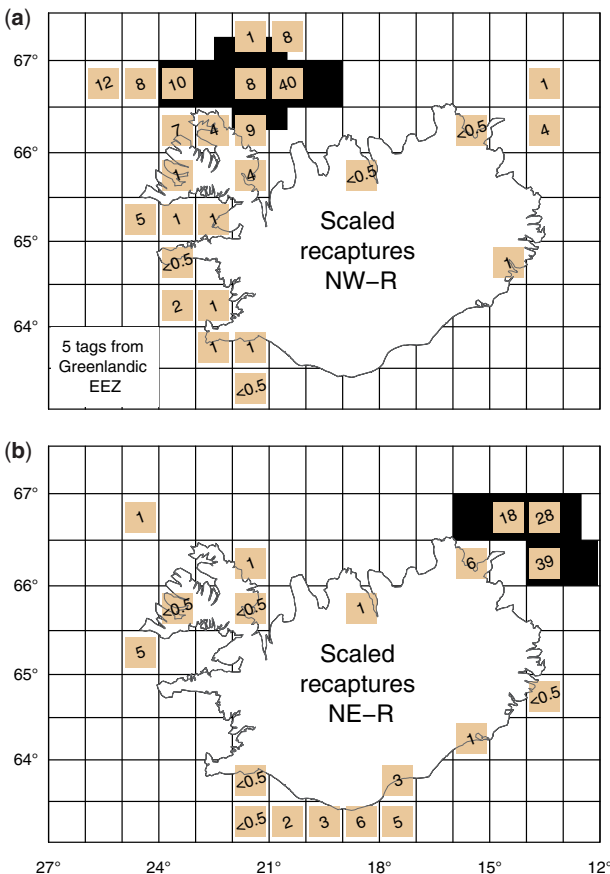


**Figure 5.** Minimum migration distance between locations of tagging and recapture, as a function of time from tagging, shown for cod tagged at (a) NW-T 2004 and (b) NE-T 2005. Black dots and open triangles indicate recaptures in the feeding (June–January) and spawning (February–May) periods, respectively. Trend lines are fitted using `stat_smooth` (method = “gam”, confidence level = 0.95) in the `ggplot2` package in R.

Furthermore, fish from only three (out of 17) tagging squares west of 22°W (Figure 3) were recaptured in the NE-R (Figure 6b).

### Depth and temperature

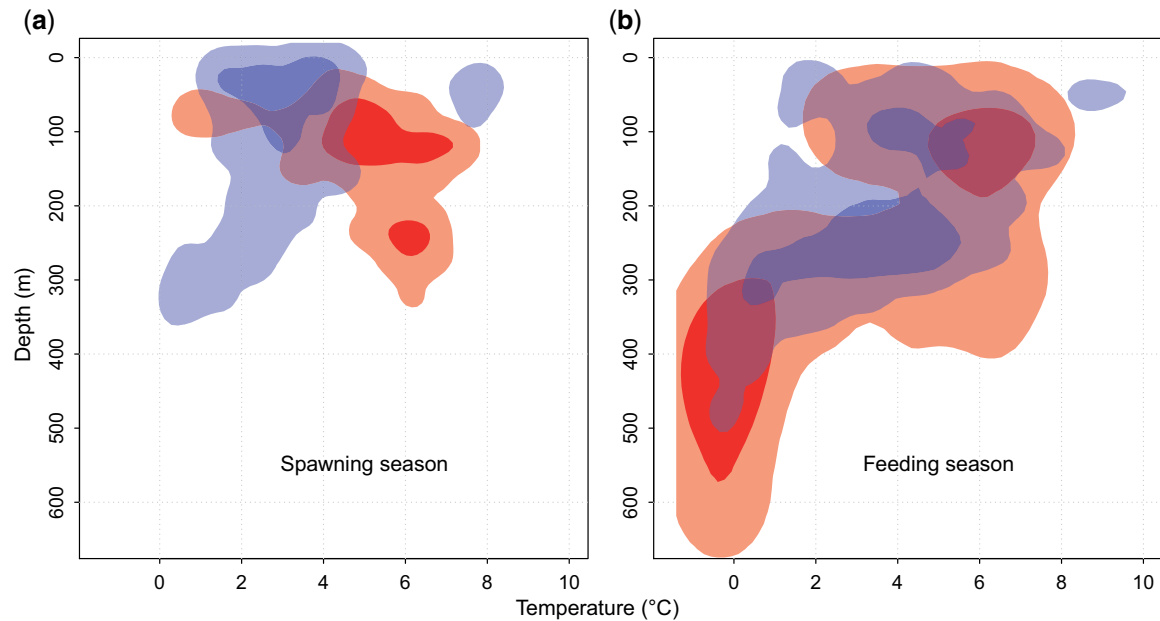
Cod associated with the two recapture areas occupied distinct thermal-bathymetric distributions during the spawning season.



**Figure 6.** Proportion (%) of all recaptures of cod from different tagging squares, recaptured in (a) the NW-R and (b) the NE-R recapture areas (black polygons). The total number of recaptures is shown in Figure 3.

**Table 3.** Observed/expected number of recaptures by tagging groups, regions and seasons, and corresponding  $\chi^2$  statistics.

Season	Group	Observed/expected by region			
		Region 1	Region 2	Region 3	Region 4
First spawning season	NW-T	20/20.5	0/1.7	38/33.3	0/2.6
	NE-T	4/3.5	2/0.3	1/5.7	3/0.4
	$\chi^2 = 33.7$				
Second feeding season	NW-T	92/73.9	2/19.4	3/2.2	0/1.5
	NE-T	7/25.1	24/6.6	0/0.8	2/0.5
	$\chi^2 = 85.9$				
Second and later spawning seasons	NW-T	16/14.0	0/2.3	60/52.1	1/8.6
	NE-T	2/4.0	3/0.7	7/14.9	10/2.4
	$\chi^2 = 47.2$				
Third and later feeding seasons	NW-T	57/41.3	1/15.8	5/3.3	0/2.6
	NE-T	6/21.7	23/8.2	0/1.7	4/1.4
	$\chi^2 = 67.9$				



**Figure 7.** Depth and temperature kernel density estimates in (a) the spawning season, and (b) the feeding season, based on data from DST-tagged cod associated with the NW-R (red, N = 4) and NE-R (blue, N = 16) areas. Dark and light colours show 50 and 95% kernel distributions, respectively.

**Table 4.** Number of cod recaptured in the NW-R and NE-R recapture areas, divided by length groups and area of tagging (Regions, see Figure 1).

Tagging area	Small (<65 cm)		Large (>64 cm)	
	NW-R	NE-R	NW-R	NE-R
Region 1	113	9	21	4
Region 2	3	63	1	63
Region 3	5	0	14	8
Region 4	0	1	0	7
E-Greenland	5	0	0	0

NW-R cod were mainly associated with bottom temperatures of 4–7 °C and depths around 100 m, while NE-R cod were found at 1–4 °C in shallower waters (Figure 7a). There were three notable exceptions; a NW-R cod (ID 1M1847) found in 1–2 °C and two NE-R cod (IDs 1C1244 and 1C1225) occupying temperatures of 7–8 °C.

In the feeding season, cod from the two recapture areas occupied a similar range of depth and temperature, except that the NE-R cod were rarely found at depths greater than 350 m (Figure 7b). The thermal-bathymetric feeding distribution of the NW-R cod clearly reflects behavioural differences between the two ecotypes, where two frontal cod were mainly found at depths of 300–550 m and temperatures at around 0 °C, but two coastal cod at 100–200 m and around 6 °C. Such prominent differences in behaviour were not observed for cod associated with the NE-R area, although two distinct 50% bivariate kernel density distributions emerged, with one group found at 200–300 m and 0–6 °C, but the other at around 100 m and 3–6 °C (Figure 7b).

**Discussion**

The study revealed distinct migration patterns of cod inhabiting two offshore feeding/nursery areas. Low connectivity, and association with different spawning grounds and environmental attributes, suggests that the areas are inhabited by segregated groups of fish. Although we cannot conclude whether the two groups are genetically/phenotypically distinct, this kind of spatial structure is of relevance for fisheries management (Metcalf, 2006; Hutchinson, 2008). In the long term, heavy or disproportionate fishing may reduce phenotypic, genetic or life-history diversity, which could reduce the ability of the population to withstand any additional pressure, e.g. due to environmental change (Audzijonyte et al., 2016).

Despite similar seasonal patterns in minimum migration distances between tagging and recapture sites, the spatial distribution and migratory routes of cod tagged in the two areas differed markedly. For the NW-T area, there was a strong connectivity to spawning grounds west of Iceland, whereas the NE-T area seems to be connected to several different spawning grounds around Iceland. Interestingly, the study suggests only a weak connection between both the NW-T and the NE-T areas and the main spawning grounds in the southwest (19°W–22°W). A study using otolith chemistry and length-at-age indicates a low contribution of the southwest spawning grounds to the feeding grounds northwest and east of Iceland (Jónsdóttir et al., 2007). Accordingly, findings from home-range analyses suggest the NW-T and NE-T areas are at the northern limit, or even outside of the SW spawning components’ feeding home range (Sólmundsson et al., 2015).

The clockwise currents from the south to the north and east of Iceland are conventionally referred to as a mechanism for larval transport within Icelandic waters (Astthorsson et al., 1994). However, the migrations of adults between spawning grounds off the central south coast and the NE area, and the lack of connection between the south coast and the NW area, suggest an

anticlockwise scenario for the central south spawning grounds, presuming denatant post-spawning migrations of cod with a linkage to drift of eggs and larvae (Harden-Jones, 1968). Connectivity between the south and the northeast areas could be promoted by larval advection by an intense eastward flow from the south and southeast shelf to the areas east of Iceland (Logemann *et al.*, 2013). However, more information is needed on larval dispersion and adult migrations to understand the interconnection between these areas.

Analysis of the DST data shows that the thermal-bathymetric “envelopes” of NW-R and NE-R cod differed in the spawning season, despite some variation observed for both areas. This is in line with the conventional tagging methods, where the two areas were found to be connected to different, but widely distributed spawning grounds. The data from the DSTs also show that both areas are inhabited/visited by both frontal and coastal cod, which is reflected in pronounced variation in thermal-bathymetric distributions in the feeding season. This variation was more apparent for fish associated with the NW-R, but we acknowledge that sample size was low. Coastal and frontal cod spawning northeast of Iceland appear to occupy relatively shallow waters throughout the year, as compared with their counterparts south and west of Iceland (Thorsteinsson *et al.*, 2012). Furthermore, there seems to be less difference in thermal-bathymetric distribution between the two ecotypes for the northeast spawners (Thorsteinsson *et al.*, 2012).

Feeding migrations of frontal cod to the outer parts of the continental shelf (400–800 m) could be underrepresented by conventional tagging methods, due to high vertical swimming activity and relatively low fishing pressure (Sólmundsson *et al.* 2015). Although these migrations are likely to be underestimated in this study, offshore tag recaptures indicate that frontal fish from the NW-T are likely to migrate to the slope areas northwest and north of Iceland, whereas NE-T frontal cod may forage in the deep waters in the northeast and east (see Figure 4b–c). In addition to behavioural differences, coastal and frontal cod display differences in genetic composition (Pampoulie *et al.*, 2008, 2015), morphology (McAdam *et al.*, 2012), and growth and condition (Jónsdóttir *et al.*, 2008). The two ecotypes provide an example of population variation that needs preservation from putative detrimental effects of disproportionate fishing (Jakobsdóttir *et al.*, 2011).

Most tagging studies investigate migration of fish from specific tagging sites (tag-recapture). This study also analysed original tagging sites of fish recaptured within certain areas (back-tracked recapture to tagging). Most cod recaptured in the NW-R originate from tagging squares different from those recaptured in the NE-R, in line with the migration pattern that emerged from the 2004–2005 tag-recapture study. Studying migration based on these alternative approaches, enabled the identification of consistent differences in migratory patterns between feeding and spawning grounds for the two groups of cod.

Although the tag-recapture and the back-track methods were largely consistent, there were some inconsistencies. These could partly be due to a potential bias of spatially variable fishing effort on the recapture data (Bolle *et al.*, 2005). Here, no attempt was made to standardize recapture data quantitatively by fishing effort data. The main aim was to estimate the relative distribution and mixing of the two tagging groups, for which recapture probabilities rely on the same distribution of fishing effort. As would be expected, the spatial distribution of recaptures corresponds well

with the distribution of fishing. Yet, a clear difference was observed between the two tagging areas. For the relatively heavily fished grounds southeast and east of Iceland, only three recaptures came from the NW-T area. On the other hand, relatively few tags from the NE-T, but a high number of tags from the NW-T, were recaptured in the main fishing areas west of Iceland. The back-track method is to a small extent influenced by heterogeneous fishing effort, but rather on the spatial distribution of tagging squares. The results were based on a standardized number of recaptures, but nonetheless they are less reliable for tagging squares with few recaptures, and in some areas, no tagging data were available.

The study investigated migration patterns of cod associated with MPAs in two offshore feeding and nursery areas. Low connectivity of fish from these areas shows that effective spatial management in the two areas is likely to protect immature fish of different origin. Other studies suggest that closures of this type and size may positively affect immature (Schopka *et al.*, 2010) and relatively sedentary cod (Sherwood and Grabowski, 2016). On the other hand, the MPAs are of little use *per se* in protecting highly migratory mature cod, for which spatial management would need to focus on migration pathways and areas where the fish are particularly vulnerable to fishing, e.g. the spawning grounds.

In recent decades, there have been large hydrographic changes in the waters north of Iceland, which have affected the whole ecosystem (Valdimarsson *et al.*, 2012). For a metapopulation faced with even stronger environmental forcing due to global atmospheric change, a higher degree of population diversity will increase the ability to cope with different conditions (Hilborn *et al.*, 2003; Klein *et al.*, 2016). The contrasting distribution patterns observed in the present study suggest that spatial management can supplement other measures in preserving population diversity of cod.

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## References

- Asthorsson, O. S., Gislason, A., and Gudmundsdottir, A. 1994. Distribution, abundance, and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions. ICES Marine Science Symposia, 198: 529–541.
- Audzijonyte, A., Fulton, E., Haddon, M., Helidoniotis, F., Hobday, A. J., Kuparinen, A., Morrongiello, J., *et al.* 2016. Trends and management implications of human-influenced life-history changes in marine ectotherms. Fish and Fisheries, 17: 1005–1028.
- Bolle, L. J., Hunter, E., Rijnsdorp, A. D., Pastoors, M. A., Metcalfe, J. D., and Reynolds, J. D. 2005. Do tagging experiments tell the truth? Using electronic tags to evaluate conventional tagging data. ICES Journal of Marine Science, 62: 236–246.
- Bonanomi, S., Therkildsen, N. O., Retzel, A., Hedeholm, R. B., Pedersen, M. W., Meldrup, D., Pampoulie, C., *et al.* 2016. Historical DNA documents long-distance natal homing in marine fish. Molecular Ecology, 25: 2727–2734.
- Eiríksson, G. M., and Árnason, E. 2013. Spatial and temporal micro-satellite variation in spawning Atlantic cod, *Gadus morhua*, around Iceland. Canadian Journal of Fisheries and Aquatic Sciences, 70: 1151–1158.



- Gell, F. R., and Roberts, C. M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution*, 18: 448–455.
- Grabowski, T. B., Thorsteinsson, V., McAdam, B. J., and Marteinsdóttir, G. 2011. Evidence of segregated spawning in a single marine fish stock: sympatric divergence of ecotypes in Icelandic cod? *PLoS ONE*, 6: e17528.
- Harden-Jones, F. R. 1968. *Fish migration*. Edward Arnold (Publishers) Ltd., London. 325 pp.
- Harrauld, M., Wright, P. J., and Neat, F. C. 2010. Substock variation in reproductive traits in North Sea cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 866–876.
- Heath, M. R., Kunzlik, P. A., Gallego, A., Holmes, S. J., and Wright, P. J. 2008. A model of meta-population dynamics for North Sea and West of Scotland cod—the dynamic consequences of natal fidelity. *Fisheries Research*, 93: 92–116.
- Hilborn, R., Quinn, T. P., Schindler, D. E., and Rogers, D. E. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America*, 100: 6564–6568.
- Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., et al. 2004. When can marine reserves improve fisheries management? *Ocean & Coastal Management*, 47: 197–205.
- Horwood, J. W., Nichols, J. H., and Milligan, S. 1998. Evaluation of closed areas for fish stock conservation. *Journal of Applied Ecology*, 35: 893–903.
- Hutchinson, W. F. 2008. The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. *Biology Letters*, 4: 693–695.
- Jakobsdóttir, K. B., Pardoe, H., Magnússon, Á., Björnsson, H., Pampoulie, C., Ruzzante, D. E., and Marteinsdóttir, G. 2011. Historical changes in genotypic frequencies at the *Pantophysin* locus in Atlantic cod (*Gadus morhua*) in Icelandic waters: evidence of fisheries-induced selection? *Evolutionary Applications*, 4: 562–573.
- Jaworski, A., Solmundsson, J., and Ragnarsson, S. A. 2006. The effect of area closures on the demersal fish community off the east coast of Iceland. *ICES Journal of Marine Science*, 63: 897–911.
- Jaworski, A., Solmundsson, J., and Ragnarsson, S. A. 2010. Fish assemblages inside and outside marine protected areas off northern Iceland: protection effects or environmental confounds? *Fisheries Research*, 102: 50–59.
- Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries*, 10: 209–231.
- Jónsdóttir, I. G., Campana, S. E., and Marteinsdóttir, G. 2006. Stock structure of Icelandic cod *Gadus morhua* L. based on otolith chemistry. *Journal of Fish Biology*, 69: 136–150.
- Jónsdóttir, I. G., Marteinsdóttir, G., and Campana, S. E. 2007. Contribution of different spawning components to the mixed stock fishery for cod in Icelandic waters. *ICES Journal of Marine Science*, 64: 1749–1759.
- Jónsdóttir, I. G., Marteinsdóttir, G., and Pampoulie, C. 2008. Relation of growth and condition with the *Pan I* locus in Atlantic cod (*Gadus morhua* L.) around Iceland. *Marine Biology*, 154: 867–874.
- Jónsson, E. 1982. A survey of spawning and reproduction of the Icelandic cod. *Rit Fiskideildar*, 6: 3–45.
- Jónsson, G., and Pálsson, J. 2013. *Íslenskir fiskar. Mál og menning*, Reykjavík. 493 pp.
- Jónsson, J. 1996. Tagging of cod in Icelandic waters 1948–1986. *Rit Fiskideildar*, 14: 7–82.
- Jónsson, S., and Valdimarsson, H. 2005. The flow of Atlantic water to the North Icelandic Shelf and its relation to the drift of cod larvae. *ICES Journal of Marine Science*, 62: 1350–1359.
- Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 1194–1199.
- Klein, E. S., Smith, S. L., and Kritzer, J. P. 2016. Effects of climate change on four New England groundfish species. *Reviews in Fish Biology and Fisheries*, doi:10.1007/s11160-016-9444-z.
- Latour, R. J., Hoenig, J. M., Olney, J. E., and Pollock, K. H. 2001. A simple test for nonmixing in multiyear tagging studies: application to striped bass tagged in the Rappahannock river, Virginia. *Transactions of the American Fisheries Society*, 130: 848–856.
- Le Bris, A., Fréchet, A., and Wroblewski, J. S. 2013. Supplementing electronic tagging with conventional tagging to redesign fishery closed areas. *Fisheries Research*, 148: 106–116.
- Logemann, K., Ólafsson, J., Snorrason, Á., Valdimarsson, H., and Marteinsdóttir, G. 2013. The circulation of Icelandic waters – a modelling study. *Ocean Science*, 9: 931–955.
- Marine Research Institute. 2016. State of marine stocks in Icelandic waters 2015/2016 and prospects for the quota year 2016/2017. *Marine Research in Iceland*, 185: 1–159.
- McAdam, B. J., Grabowski, T. B., and Marteinsdóttir, G. 2012. Identification of stock components using morphological markers. *Journal of Fish Biology*, 81: 1447–1462.
- Metcalfe, J. D. 2006. Fish population structuring in the North Sea: understanding processes and mechanisms from studies of the movements of adults. *Journal of Fish Biology*, 69: 48–65.
- Neat, F. C., Bendall, V., Berx, B., Wright, P. J., Cuaig, M., Townhill, B., Schön, P. J., et al. 2014. Movement of Atlantic cod around the British Isles: Implications for finer scale stock management. *Journal of Applied Ecology*, 51: 1564–1574.
- Pampoulie, C., Daniëlsdóttir, A. K., Thorsteinsson, V., Hjörleifsson, E., Marteinsdóttir, G., and Ruzzante, D. E. 2012. The composition of adult overwintering and juvenile aggregations of Atlantic cod (*Gadus morhua*) around Iceland using neutral and functional markers: a statistical challenge. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 307–320.
- Pampoulie, C., Jakobsdóttir, K. B., Marteinsdóttir, G., and Thorsteinsson, V. 2008. Are vertical behaviour patterns related to the *Pantophysin* locus in the Atlantic cod (*Gadus morhua* L.)? *Behavior Genetics*, 38: 76–81.
- Pampoulie, C., Ruzzante, D. E., Chosson, V., Jörundsdóttir, T. D., Taylor, L., Thorsteinsson, V., Daniëlsdóttir, A. K., et al. 2006. The genetic structure of Atlantic cod (*Gadus morhua*) around Iceland: insight from microsatellites, the *Pan I* locus, and tagging experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, 2674: 2660–2674.
- Pampoulie, C., Skirnisdóttir, S., Star, B., Jentoft, S., Jónsdóttir, I. G., Hjörleifsson, E., Thorsteinsson, V., et al. 2015. Rhodopsin gene polymorphism associated with divergent light environments in Atlantic cod. *Behavior Genetics*, 45: 236–244.
- Pálsson, Ó. K., and Thorsteinsson, V. 2003. Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 1409–1423.
- Petursdóttir, G., Beggs, G. A., and Marteinsdóttir, G. 2006. Discrimination between Icelandic cod (*Gadus morhua* L.) populations from adjacent spawning areas based on otolith growth and shape. *Fisheries Research*, 80: 182–189.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>.
- Rassweiler, A., Costello, C., and Siegel, D. A. 2012. Marine protected areas and the value of spatially optimized fishery management. *Proceedings of the National Academy of Sciences of the United States of America*, 109: 11884–11889.
- Roberts, C. M., Hawkins, J. P., and Gell, F. R. 2005. The role of marine reserves in achieving sustainable fisheries. *Philosophical*

- Transactions of the Royal Society B: Biological Sciences, 360: 123–132.
- Robichaud, D., and Rose, G. A. 2004. Migratory behaviour and range in Atlantic cod: Inference from a century of tagging. *Fish and Fisheries*, 5: 185–214.
- Ruzzante, D. E., Mariani, S., Bekkevold, D., Andre, C., Mosegaard, H., Clausen, L. A. W., Dahlgren, T. G., *et al.* 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proceedings of the Royal Society B: Biological Sciences*, 273: 1459–1464.
- Ruzzante, D. E., Wroblewski, J. S., Taggart, C. T., Smedbol, R. K., Cook, D., and Goddard, S. V. 2000. Bay-scale population structure in coastal Atlantic cod in Labrador and Newfoundland, Canada. *Journal of Fish Biology*, 56: 431–447.
- Schopka, S. A., Solmundsson, J., Ragnarsson, S. A., and Thorsteinsson, V. 2010. Using tagging experiments to evaluate the potential of closed areas in protecting migratory Atlantic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 67: 1024–1035.
- Sherwood, G. D., and Grabowski, J. H. 2016. A comparison of cod life-history parameters inside and outside of four year-round groundfish closed areas in New England, USA. *ICES Journal of Marine Science*, 73: 316–328.
- Smedbol, R. K., and Stephenson, R. 2001. The importance of managing within-species diversity in cod and herring fisheries of the north-western Atlantic. *Journal of Fish Biology*, 59: 109–128.
- Smedbol, R. K., and Wroblewski, J. S. 2002. Metapopulation theory and northern cod population structure: Interdependency of sub-populations in recovery of a groundfish population. *Fisheries Research*, 55: 161–174.
- Sólmundsson, J., Jónsdóttir, I. G., Björnsson, B., Ragnarsson, S. Á., Tómasson, G. G., and Thorsteinsson, V. 2015. Home ranges and spatial segregation of cod *Gadus morhua* spawning components. *Marine Ecology Progress Series*, 520: 217–233.
- Stefánsson, G., and Pálsson, Ó. K. 1997. Bormicon. A boreal migration and consumption model. *Hafrannsóknastofnunin Fjölrit*, 58: 223.
- Svedäng, H., André, C., Jonsson, P., Elfman, M., and Limburg, K. E. 2010. Migratory behaviour and otolith chemistry suggest fine-scale sub-population structure within a genetically homogenous Atlantic cod population. *Environmental Biology of Fishes*, 89: 383–397.
- Thorsteinsson, V., Pálsson, Ó. K., Tómasson, G. G., Jónsdóttir, I. G., and Pampoulie, C. 2012. Consistency in the behaviour types of the Atlantic cod: repeatability, timing of migration and geo-location. *Marine Ecology Progress Series*, 462: 251–260.
- Valdimarsson, H., Astthorsson, O. S., and Pálsson, J. 2012. Hydrographic variability in Icelandic waters during recent decades and related changes in distribution of some fish species. *ICES Journal of Marine Science*, 69: 816–825.
- Valdimarsson, H., and Malmberg, S.-A. 1999. Near-surface circulation in Icelandic waters derived from satellite tracked drifters. *Rit Fiskideildar*, 16: 23–39.
- Wright, P. J., Neat, F. C., Gibb, F. M., Gibb, I. M., and Thordarson, H. 2006. Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *Journal of Fish Biology*, 69: 181–199.
- Ying, Y., Chen, Y., Lin, L., and Gao, T. 2011. Risks of ignoring fish population spatial structure in fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 2101–2120.
- Zemeckis, D. R., Hoffman, W. S., Dean, M. J., Armstrong, M. P., and Cadrin, S. X. 2014. Spawning site fidelity by Atlantic cod (*Gadus morhua*) in the Gulf of Maine: implications for population structure and rebuilding. *ICES Journal of Marine Science*, 71: 1356–1365.

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