Using tagging experiments to evaluate the potential of closed areas in protecting migratory Atlantic cod (*Gadus morhua*)

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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.

About 5200 cod (*Gadus morhua*) were tagged on three fishing grounds and within two marine protected areas (MPAs) northwest of Iceland. Two of the fishing grounds were closed to otter trawling, and the third was open to all fishing gear. Tagged fish were divided into two size classes, below (small) and above (large) a reference length of 55 cm, and the following variables were estimated: (i) proportion of the recaptured small cod that did not reach the reference size, (ii) size increase from tagging to recapture, (iii) time at liberty, and (iv) spatial distribution of recaptures. For the small cod, the results suggest that not only protection status but also the distance to areas of intense fishing mainly account for differences in the variables among tagging areas. No differences were observed for the large cod among tagging areas. The results show that immature cod are relatively stationary, but perform seasonal migrations between feeding and spawning grounds after reaching maturity. The estimated distribution of tagged cod generally changed after standardizing the recapture data with fishing effort (catch per unit area). Our results suggest that area closures on nursery grounds can be useful in protecting immature cod, but the MPAs studied are of little use in protecting highly migratory adults.

Keywords: cod, fishing effort, *Gadus morhua*, migration, MPAs, nursery grounds, tagging.

Received 11 December 2008; accepted 17 November 2009; advance access publication 24 December 2009.

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Introduction

In recent years, permanent area closures or marine protected areas (MPAs) have received increasing attention as a tool in fishery management (Jennings, 2000; Rosenberg, 2001; Fisher and Frank, 2002; Gell and Roberts, 2003; Roberts *et al*., 2005), although their usefulness over other control measures is still being questioned (Kaiser, 2005; Jones, 2007). One concern regarding MPAs is that for fisheries managed by catch quotas, they may have the unwanted effect of increasing fishing effort in areas open to fishing (Horwood *et al*., 1998; Hilborn *et al*., 2004). This could even lead to a displacement of fishing activities to previously unexploited or lightly exploited areas (Kaiser, 2005). Nonetheless, protected areas can be an important conservation measure in quota-regulated fisheries by reducing direct and indirect fishing mortality of juvenile fish on nursery grounds, preventing disturbance of mating behaviour on spawning grounds, reducing bycatch of non-target species, and precluding damage to sensitive benthic habitats. For migratory fish stocks, MPAs are only considered beneficial when they are used in conjunction with other control measures, or cover most of the stocks' distributional areas (Stefansson and Rosenberg, 2006).

At present, there is limited evidence from empirical studies to verify the effectiveness of permanent area closures for migratory fish. Many commercially important fish species make long-distance migrations, and area closures may be of little effect if the fish migrate seasonally out of these areas (Horwood *et al*., 1998). Transfer rates of fish between MPAs and fishing grounds clearly affect their performance, and information on fish movements is essential, both in the initial planning of the MPAs, and when evaluating their effectiveness (Kaiser, 2005). Although there is good information on subtropical reef fish migrations from protected areas using various tagging methods (e.g. Zeller *et al*., 2003; Kaunda-Arara and Rose, 2004; Garla *et al*., 2006; Nemeth *et al*., 2007), there is a lack of data on migration of fish species inhabiting MPAs in temperate–boreal waters, such as the Atlantic cod (*Gadus morhua*).

Cod has long been one of the most important commercial species in the North Atlantic, and its migration patterns have been studied extensively (Robichaud and Rose, 2004). However, these studies have rarely been designed to investigate the effects of spatial closures, although some have related the observed migration patterns to optimal location, size, or conservation potential of protected areas (Cote *et al*., 2004; Gröger *et al*., 2007; Lindholm *et al*., 2007). Recently, marine reserves on cod feeding grounds have been proposed as a measure to reduce the potential evolutionary effects of fishing (Dunlop *et al*., 2009).

Temporarily, seasonally, and permanently closed areas to one or several fishing gear types have long been used as management tools in the cod fisheries in Icelandic waters, together with catch quotas, minimum landing sizes, and mesh-size and sorting-grid regulations (Jaworski *et al*., 2006). With the "Law of the Sea" from 1948, concerning the scientific conservation of the continental shelf fisheries, the Icelandic Ministry of Fisheries was given the authority to close fishing areas if considered necessary (Anon., 1948). Such closures were restricted to certain fishing gears, e.g. trawling in inshore waters, but other gears such as handlines (jigs), longlines, and gillnets were allowed.

Shortly after the extension of the exclusive economic zone to 200 nautical miles in 1975, the Marine Research Institute (MRI) became the authority in power to close areas temporarily for the protection of juvenile fish. This system of temporary closures has been in force since 1976 (Schopka, 2007). For example, areas are closed to fishing if the abundance of cod <55 cm in the commercial catch exceeds 25%. The temporary closures can be prolonged if required, with a regulation by law, in cases when temporary closures on the same fishing ground are frequent and persistent conditions of small fish in the catches prevail.

In summer 1993, ten permanently closed MPAs of a total of 12 700 km^2 were established on cod nursery grounds north and east of Iceland (Guijarro Garcia *et al.*, 2006; Schopka, 2007). These MPAs, closed year-round for all use of longlines and otter trawls, were located in areas where temporary closures and long-term regulation closures had been frequent in the preceding years. Their objective was to protect juvenile (mainly 3–4 year-old) cod to increase the long-term yield. From 1993 on, the number and the size of the MPAs on cod nursery grounds have been reduced, and in 2004 there were only six permanent MPAs with a total area of ~8000 km^2 (Guijarro Garcia *et al.*, 2006; Schopka, 2007).

Scientific information on the effectiveness of area closures in Icelandic waters is scarce. A case study analysing the effects of temporary closures northwest of Iceland concluded that the combination of the temporary-closure system and the subsequent closure of larger areas by a regulation could be a useful tool in reducing discards and protect juvenile cod (Kristinsson *et al.*, 2005). Jaworski *et al.* (2006) suggested that even species with great mobility such as cod and haddock (*Melanogrammus aeglefinus*) at fishable sizes could benefit from area closures located off the east coast of Iceland, but knowing patterns of fish movement between protected and fished areas would be basic in evaluating their effectiveness.

To investigate the potential of the MPAs established in 1993 to protect juvenile cod, tagging experiments were carried out in 1994 and 1995. The aim was to compare recapture rates of cod tagged within the protected areas to those from the nearby grounds with less or no restrictions on fishing and to estimate spatial distribution patterns of cod inhabiting these areas.

Material and methods

Tagging

In the period 20–27 July 1994, a cod tagging survey outside the 12-mile fishing limit off Northwest Iceland was carried out on board RV "Bjarni Saemundsson". In Djúpáll, where fishing was not restricted, 998 cod were tagged (Figure 1, Table 1). East of Djúpáll, in an area closed to otter trawling and longlining (MPA-1), 572 cod were tagged. This area was closed year-round in 1993, but has been open to a seasonal fishery (October–March) since 1997. East of MPA-1, in a protected area that has been permanently closed since 1993 (MPA-2), 999 cod were tagged.

During the period 13–21 June 1995, an effort was made to repeat the 1994 tagging experiment for comparative purposes, using the same vessel, fishing gear, and tagging methods. At that time, however, environmental conditions differed from the year before. Cod were hardly found in Djúpáll, and oceanic drift ice covered most of MPA-1. In MPA-2, 688 cod were tagged just before the area became covered with ice. As it was not possible to proceed with tagging in those regions, we decided to tag cod within the 12-mile limit in the fishing areas Ritur and Deild (Figure 1, Table 1). These areas are closed to trawling, but fishing by other gears is allowed. In all, 1039 cod were tagged in Ritur and a further 877 in Deild.

Fish for tagging were sampled using an otter trawl with a 40-mm mesh size in the codend. Tow duration ranged from 30 to 60 min. Cod were immediately transferred into a basin with running seawater. Cod that showed any signs of weakness were removed, but the most viable individuals were tagged 5–90 min later and released through a pipeline leading downwards to the sea surface. Two types of conventional tag were used. Floy

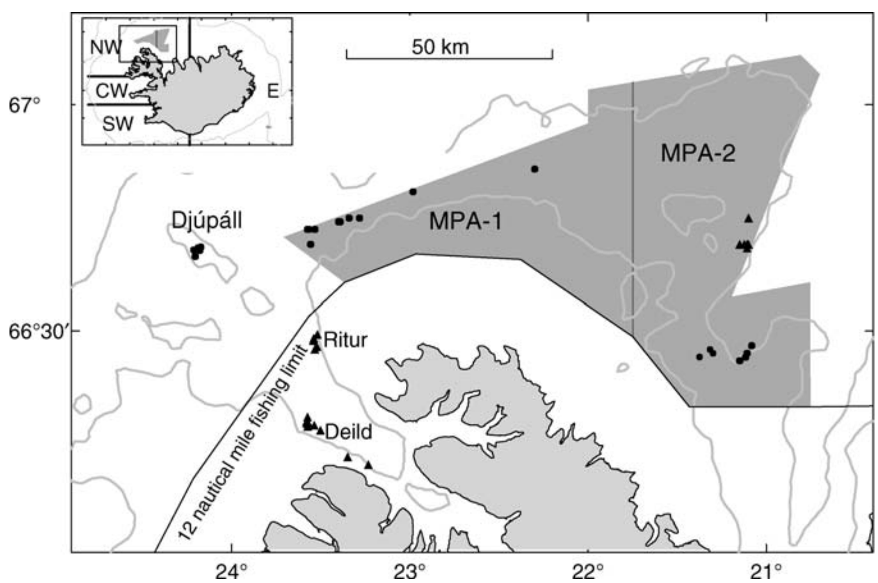

Figure 1. Tagging sites in 1994 (dots) and 1995 (triangles). The polygons denote the MPAs under study. Since 1997 MPA-1 has been open seasonally (October–March), whereas MPA-2 was unchanged until 2007. The 100- and 200-m depth contours are shown. The inset shows the division of Icelandic waters into areas.

Table 1. Temperature and depth by tagging area, and number of small and large cod tagged and recaptured by tag type and tagging area.

Year	Tagging area	Mean near-bottom temperature (°C)	Mean sea surface temperature (°C)	Mean depth (m)	Anchor tags: small cod/large cod			Alcathene tags: small cod/large cod		
					Number tagged	Number recaptured	% recaptured	Number tagged	Number recaptured	% recaptured
1994	Djúpáll	4.4	6.4	233	171/327	12/23	7.0/7.0	156/344	10/34	6.4/9.9
	MPA-1	3.5	7.3	138	215/77	38/19	17.7/24.7	140/140	9/21	6.4/15.0
	MPA-2	3.5	4.9	176	300/315	45/79	15.0/25.1	195/189	14/25	7.2/13.2
1995	MPA-2	2.7	3.3	208	413/87	67/20	16.2/23.0	158/30	11/3	7.0/10.0
	Deild	3.3	5.3	106	220/157	47/56	21.4/35.7	272/228	20/42	7.4/18.4
	Ritur	3.4	5.0	132	362/226	48/43	13.3/19.0	311/140	17/16	5.5/11.4
	All areas				1 681/1 189	257/240	15.3/20.2	1 232/1 071	81/141	6.6/13.2

anchor tags with an orange plastic tube and total length of 8 cm (Floy Tags and Manufacturing, Inc., Seattle, USA) were attached with a tagging gun through the flesh at the base of the first dorsal fin in such a way that the attachment was on one side of the interneural bones and the tag on the other. Alcathene tags, yellow and oval shaped (MRI; Jónsson, 1996), were fastened with a soft, braided nylon twine through the flesh ~2 cm in front of the first dorsal fin. All tags were imprinted with a unique identification number.

Recaptures

Returns of tags and data on release and recapture were facilitated by a special infrastructure at the MRI, which distributes envelopes with templates to be filled in and information leaflets. All recaptures were expected to come from the commercial fishery, and fishers were encouraged to return tags and otoliths from the recaptured fish to the MRI along with information on recapture location and date of capture, sex, and maturity of the fish. A reward was offered for each tag returned.

Areas, seasons, and periods

The waters around Iceland were divided into four areas within the 500-m isobath (Figure 1), based mainly on the locations of tagging areas and tag recaptures, but also on cod fishing areas and locations of the main spawning grounds.

The recaptures were divided between two seasons: the main feeding season is defined here as June–January, whereas the period February–May includes the main spawning season and the period of migration to and from the spawning grounds (Sæmundsson, 1926; Jónsson, 1996; Palsson and Thorsteinsson, 2003). In the following text, we refer to the latter season as the spawning season. In addition to season, recaptures were divided between three periods; the calendar year of tagging (Period 1), the calendar year after the year of tagging (Period 2), and subsequent years (Period 3).

Data analysis

Throughout the paper, we refer to cod 55+ cm and <55 cm at tagging as large and small cod, respectively. The 55-cm size limit was chosen because it is the reference length for cod in the present temporary-closure system in Icelandic waters (Schopka, 2007).

Analysis of recapture rates and length increase in small cod was based only on fish ranging from 40 to 54 cm when tagged, to increase comparability between tagging sites. The length increase in recaptured cod was estimated by comparing the length at the time of tagging with the length at recapture.

The spatial distribution of recaptures was compared both qualitatively and quantitatively with the spatial distribution of fishing effort by the main fishing gears used in the cod fishery in the years 1994–1998. These years were chosen because they represent the period when 95% of the recaptured cod were caught. From 1991 on, it has been mandatory to keep logbook data on fishing locations and catch for all gears, except for boats <10 GRT, for which logbook registration started in 1999. However, the landed catch and landing sites for small boats in the study period are available from the annual "Fishery Statistics" reports (e.g. Anon., 1999).

In the absence of suitable fishing effort data for some gears, we used total catch of cod (expressed as number of fish) in each area as a proxy for fishing effort to standardize the observed recaptures (R). Recaptures from all tagging within each year were combined, because of their small numbers. For the standardization, we used fishing logbook data when available, but otherwise we used landing data for each site. The catch, registered in terms of weight, was converted to numbers using mean weights of cod by gears and seasons in samples collected routinely by the MRI from the landed catch. We used an equation from Bayliff (1979), where the proportional distribution of tagged fish (P_{ij}) located in area i and period-season j is estimated from the number of recaptures (R_{ij}) weighted by the total catch (C_{ij}) and the size of the area (A_i), as follows:

$$P_{ij} = \frac{R_{ij}/(C_{ij}/A_i)}{\sum_{ij}(R_{ij}/(C_{ij}/A_i))}. \quad (1)$$

This method assumes that the probability of a tag recapture is related linearly to the catch. Tag reporting rate, catchability of cod, and patchiness in the spatial distribution of the catch in a given period-season are assumed to be equal between areas, and tag reporting rates from different gear types are assumed to be equal (Solmundsson *et al.*, 2005).

Results

Recapture rates

The total number of cod tagged was 5173, from which 719 (14%) were recaptured over the period 1994–2000 (Table 1). Overall, 53% of the recaptured cod were caught by otter trawlers, 18% by longliners, and 11, 10, and 5% by vessels using handlines, gillnets, and Danish seines, respectively (Table 2). The recapture rates of alcathene tags were considerably lower than those of anchor tags (Table 1), probably owing to a greater shedding of the alcathene tags. For that reason, comparison of recapture rates over time was based on fish tagged with anchor tags only.

Table 2. The percentage (%) of recaptured cod by type of fishing gear, estimated from a total of 632 tags where information on fishing gear was available.

Year	Tagging area	Otter trawl	Longline	Handline	Gillnet	Danish seine	Other
1994	Djúpáll	44.8	23.9	13.4	13.4	3.0	1.5
	MPA-1	73.3	8.0	5.3	10.7	1.3	1.3
	MPA-2	47.6	21.4	11.7	11.0	4.8	3.4
1995	MPA-2	62.5	16.7	10.4	5.2	5.2	0.0
	Deild	41.3	20.7	15.7	6.6	9.9	5.8
	Ritur	53.9	15.6	8.6	14.8	5.5	1.6
Total		52.7	18.0	11.1	10.3	5.4	2.5

Table 3. Recaptures (anchor tags only) of small cod (40–54 cm at tagging).

Year	Tagging area	Total number recaptured	Mean length at tagging (cm)	s.d.	Mean length at recapture (cm)	s.d.	Mean length increase (cm)	s.d.	Number of recaptures <55 cm	Number of recaptures 55+ cm	Percentage recaptured <55 cm
1994	Djúpáll	12	48.8	4.0	63.6	12.6	14.8	14.2	3	9	25.0
	MPA-1	26	50.9	2.8	67.1	12.3	16.2	12.6	4	22	15.4
	MPA-2	45	50.4	2.8	68.8	11.2	18.5	11.5	2	43	4.4
1995	MPA-2	53	45.5	4.1	69.8	12.4	24.3	12.0	5	48	9.4
	Deild	43	47.3	3.7	65.9	11.3	18.5	11.5	9	34	20.9
	Ritur	45	46.5	3.7	72.4	11.5	25.9	11.3	3	42	6.7

Length at tagging and recapture (mean and s.d.) by tagging area, and total numbers of recaptures by tagging area divided into groups according to the length at recapture (<55 or 55+ cm).

Recapture rates of small cod tagged with anchor tags ranged from 7% (Djúpáll) to 21% (Deild), and those of large cod from 7% (Djúpáll) to 36% (Deild; Table 1). The proportion of small cod (only those of 40–54 cm when tagged) that had not reached the reference length of 55 cm at recapture was lowest for cod tagged in MPA-2 in 1994 (4%), and highest in Djúpáll (25%; Table 3). However, as this proportion was relatively low in the Ritur fishing area (7%) but high in MPA-1 (15%), it does not seem to be related directly to the extent of protection at the tagging locations.

Length increase

No statistically significant differences were found among locations in the length increase in small cod from tagging to recapture in 1994 (one-way ANOVA; $F = 0.71$, $p = 0.40$; Table 3). On the other hand, such differences were significant for small cod tagged in 1995 ($F = 8.00$, $p = 0.005$), when length increase in MPA-2 and Ritur was greater than at Deild (results from multiple comparison tests are not shown). The length increase in the large cod between tagging and recapture did not differ significantly among sites in 1994 ($F = 1.03$, $p = 0.36$) or 1995 ($F = 1.08$, $p = 0.34$).

Time at liberty

For most tagging areas the recapture period lasted for 5 years, with the only exception of Djúpáll, where no fish was recaptured after 4 years. Most recaptured fish (78–94%, depending on tagging area) were caught in the first 3 years after tagging.

In Djúpáll and MPA-1 in 1994, most small cod were recaptured within 750 d of tagging, but in MPA-2 the recapture rate gradually increased and peaked 500–750 d after tagging (Figure 2). In 1995,

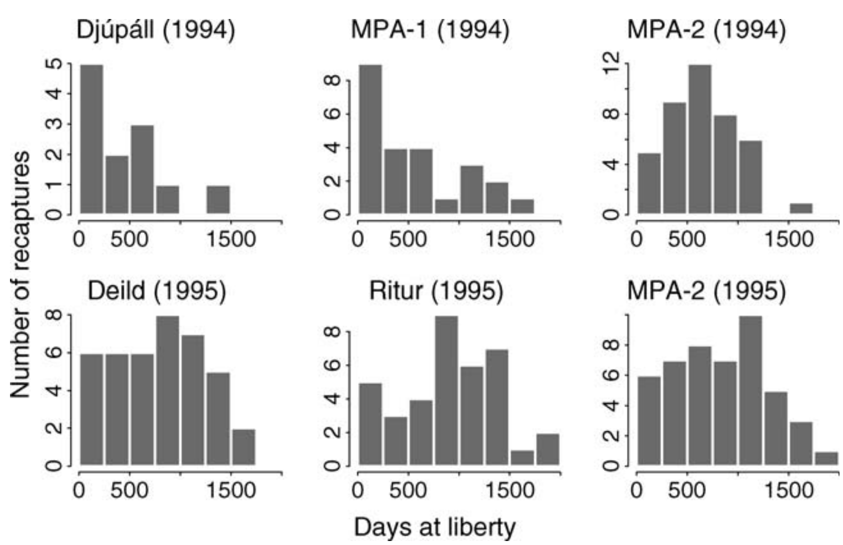

Figure 2. Days at liberty of small cod tagged with anchor tags (only those 40–54 cm at tagging) by tagging area.

the number of recaptures slowly increased with time at Ritur and in MPA-2, whereas at Deild the number of recaptures was more stable during the first 4 years.

Spatial distribution of recaptures

As distribution patterns did not appear to be influenced by tag type, analysis of cod migration was based on all recaptures. The spatial distribution of recaptures over time was similar for all sites and for both tagging years (Figures 3 and 4). Furthermore, no clear differences were found in the spatial distribution of cod from tagging sites located within and outside the MPAs.

During the first period, most cod were recaptured on the feeding grounds northwest of Iceland, mainly in areas near the continental slope, but also nearshore (Figures 3 and 4). Most of the cod tagged within the two MPAs were recaptured along the continental slope, whereas roughly half of all tags from the fishing areas Djúpáll, Deild, and Ritur were recaptured close to their original tagging sites. During the spawning season in the second period, the great majority of recaptures were from the southwest area, and with few exceptions they consisted of large cod (Figures 3 and 4). During the feeding season, on the other hand, most of the returns were from the northwest area. Although the majority of recaptures consisted of large cod, the proportion of small cod had increased. The distribution pattern of cod in Period 3 was similar to that in Period 2, although some individuals migrated longer distances to the southeast and northeast (Figures 3 and 4). Although most cod were found in the southwest during the spawning season, there was, nevertheless, a clear aggregation in the central-west area.

To explore the overall dispersal pattern of cod, the geographic positions of the recaptures (latitude) were plotted as a function of time from tagging (Figure 5). Clear seasonal and size-based migration patterns emerge. In general, the migration pattern of the large cod from tagging to the end of the third consecutive spawning season was consistent, i.e. the majority of recaptures were from the southwest area during the spawning season but from the northwest area during the feeding season (Figure 5a). Interestingly, the amplitude in the oscillation between peaks (feeding season) and troughs (spawning season) of the fitted trend line for the large cod became smaller with time. An increasing number of large cod recaptured in the central-west area accounts mainly for this trend.

Within the first two periods, relatively few small cod were recaptured in the central-west and southwest areas, and only a single cod that was still <55 cm at recapture (Figure 5b). In other words, most of the smaller fish apparently remained within the northwest area for about 2 years after tagging. However, in subsequent years, the recapture pattern of the small cod became similar to that of the large cod.

Accounting for fishing effort

The main fishing gear for cod in Icelandic waters is the otter trawl. During the study period, the major trawling grounds were located off the northwest and southeast coasts (Figure 6). Some trawling took place along the northern and western boundaries of the MPAs studied. Longlining for cod was mainly carried out along the west and southeast coasts, whereas the major part of the gillnet fishery was restricted to the southwest and south coasts. The Danish seine fishery was mainly confined to the relative shallow waters off the south and west coasts of Iceland (Figure 6).

In the feeding seasons of 1994–1998, cod catch per unit area was highest in the northwest, 1–3 times higher than in the central-west area and 2–5 times that of the southwest and east areas (Appendix). Fishing effort was displaced in the spawning season, when catch per unit area in the southwest and central-west areas (the main spawning grounds) was ~2–6 times higher than in the northwest and the east.

For each tagging survey, period, and season, the numbers of recaptures were standardized with the associated catch per unit area. The results indicate that 30 and 36% of the large cod tagged in 1994 and 1995, respectively, migrated to spawning areas off the southwest and west coasts in the spawning season following tagging, and 72 and 52% in the following spawning seasons (Table 4). Occurrence of large cod in the eastern area during spawning seasons was less pronounced (0–16%). The estimated percentage of small cod in the central-west and southwest spawning areas ranged from 12 to 18% in the first spawning season and from 43 to 54% in later years.

The percentage of large cod found in the northwest area during the feeding season was estimated at 93 and 95% in the first period, 46 and 62% in the second period, and 22 and 41% in the third period, for the 1994 and 1995 tagging experiments, respectively (Table 4). During the first period, all small cod were recaptured in the northwest area, whereas for the second and third periods the standardized recaptures indicate that 78–83% and 30–57% of the small cod, respectively, were in the northwest during the feeding season.

Discussion

The main goal of this study was to evaluate the potential of MPAs to protect juvenile cod, e.g. by evaluating whether undersized cod tagged within MPAs had a better chance than those on the fishing grounds to grow to a certain reference size (55 cm) before being recaptured. The proportion of small cod recaptured at sizes <55 cm was lower for MPA-2 than for most fished grounds, but also compared with MPA-1. Judging from the distribution of recaptures, the cause for this difference between the two MPAs is most likely the fact that MPA-1 is located closer to the heavily trawled areas near the continental slope northwest of Iceland.

The proportion of small cod recaptured smaller than the reference size differed between fishing areas as well. Low recapture rates of small cod from the tagging at Ritur compared with Deild may be due to less fishing effort by handlines and longlines in that area, presumably because it is located farther from the fishing villages in Northwest Iceland. This view is supported by the fact that a relatively high percentage of the cod from Deild was recaptured by small boats using these gears. This could also explain why the small cod in MPA-2 and Ritur were able to add more to their size than the small cod at Deild. On the other hand, the lack of difference in the length increase in the large cod among sites was probably due to the extensive migration conducted by adult cod, where fish from different tagging sites more or less utilized the same feeding and spawning areas. The results for adult cod are in accordance with a simulation study indicating that closed areas need to be much larger than at present to be effective as a management and conservation measure for migratory Icelandic cod (Stefansson and Rosenberg, 2005).

Among the factors that contribute to differences in length increase between sites and proportion of undersized fish recaptured, the most pertinent is the number of days at liberty. Although our analysis of time at liberty for small cod is based

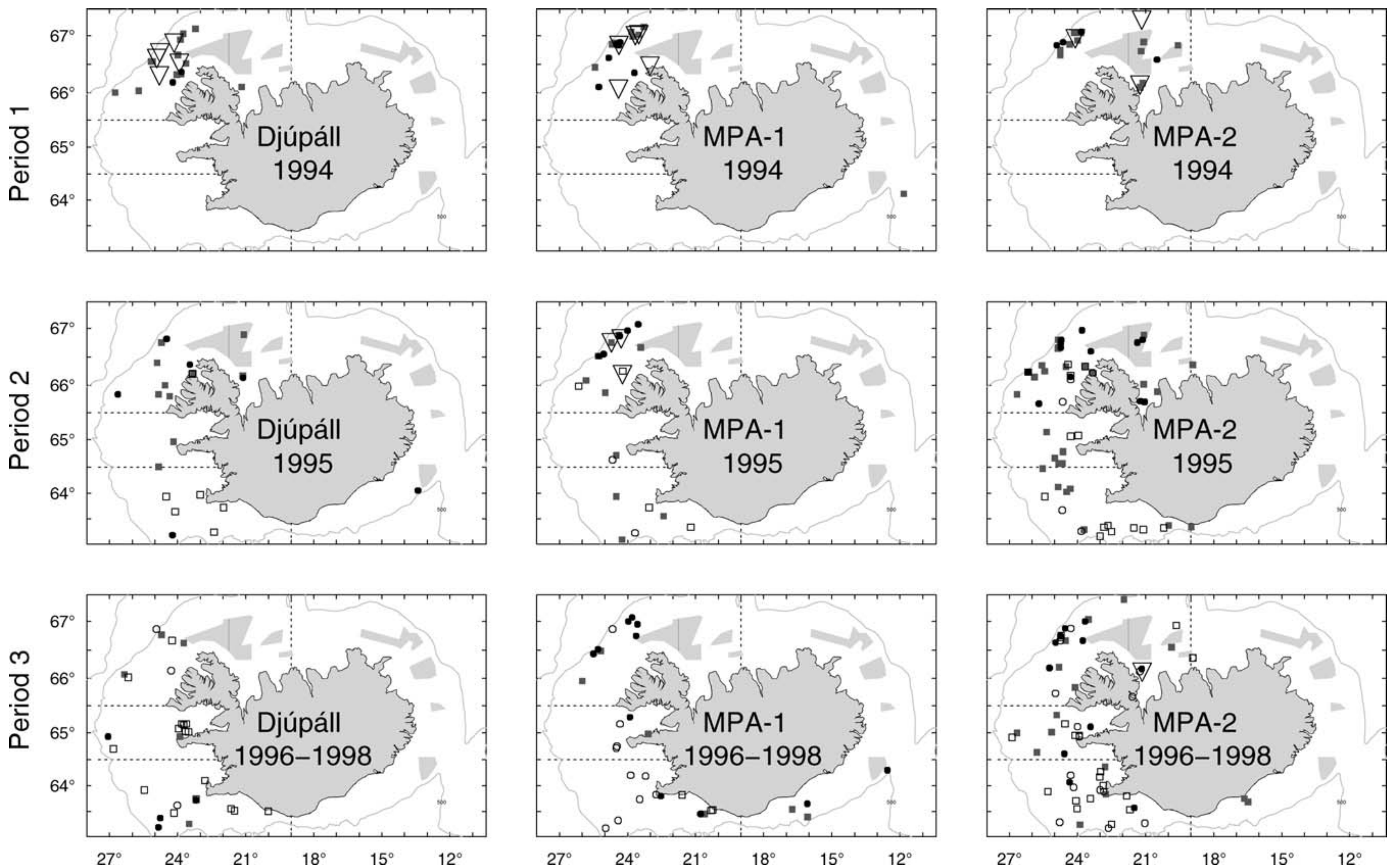

Figure 3. Recapture locations from the 1994 tagging experiments in Djúpáll, MPA-1, and MPA-2 (tagging locations are shown in Figure 1). Triangles indicate small cod recaptured <55 cm, dots indicate small cod recaptured 55+ cm, and boxes indicate large cod. Filled dots and boxes indicate recaptures during the months June–January (feeding season), and open dots and boxes indicate recaptures during the months February–May (spawning season). The dotted lines delimit the northwest, central-west, southwest, and east areas, and the polygons denote MPAs on cod nursery grounds in force during most of the recapture period. The 500-m depth contour is shown.

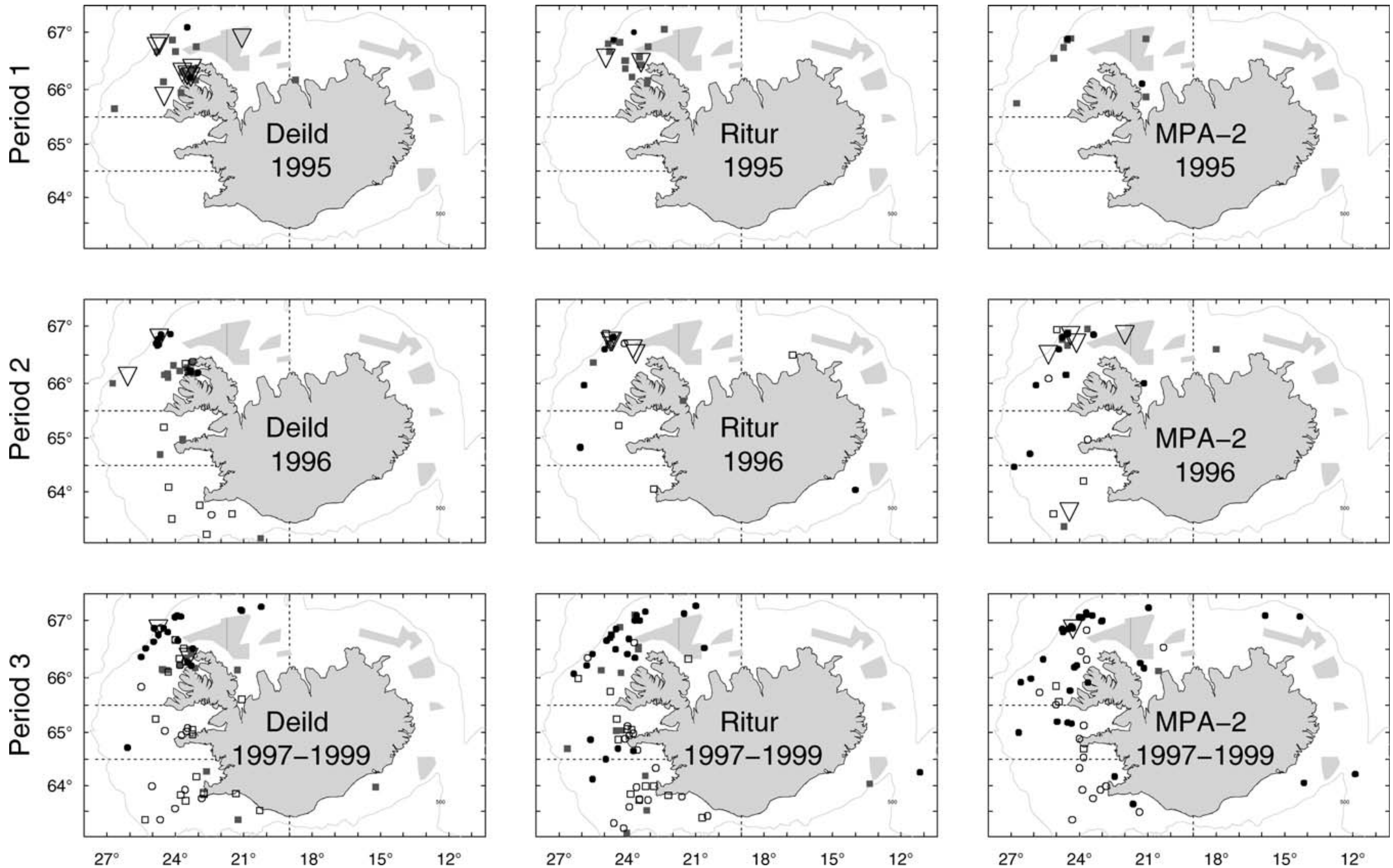

Figure 4. Recapture locations from the 1995 tagging experiments in Deild, Ritur, and MPA-2. For further information see legend of Figure 3.

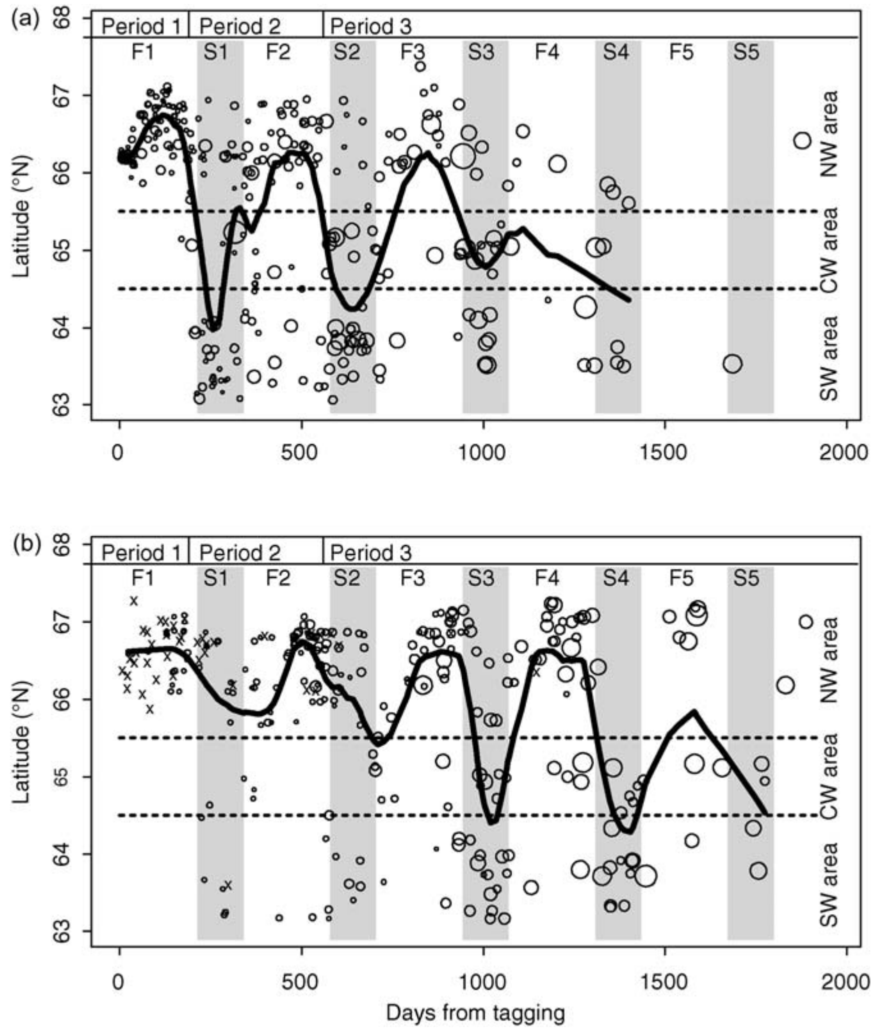

Figure 5. Changes in the latitudinal distribution of cod with time after tagging for (a) large cod, and (b) small cod, where fish measuring <55 cm at recapture are indicated by a cross, and fish measuring 55+ cm at recapture by circles. The size of the circles is proportional to the fish length at recapture, where the smallest and largest circles denote fish of 55 and 110 cm, respectively. The lines are fitted using a lowess scatterplot smoother in Splus. The spawning and migration period (February–May) is shaded; S1, first spawning season; F1, first feeding season, etc.

on a small sample size and therefore may have to be considered as a qualitative observation, it is of interest that it varied between tagging sites. In general, it seems that not only protection status, but also the distance to areas of intense fishing, mainly account for differences in time at liberty between tagging sites.

The overall recapture percentages in Djúpáll were lower than in other areas. This may seem surprising because this area was open for all fishing gears and located near heavily trawled grounds. A possible explanation could be that tagging-induced mortality was higher in that area because of the greater depth than at other tagging areas. This potential depth-related difference in short-term tagging mortality would make it difficult to estimate relative fishing mortality among tagging areas. For trawl catches taken at depths of 55–120 m off northern Norway, increasing catch depth had a generally negative effect on the viability of cod (Nøstvik and Pedersen, 1999). However, Brattey and Cadigan (2004) showed that high survival rates after tagging are possible for otter-trawled cod at capture depths down to ~200 m, but deeper waters were not studied.

An important goal of the study was to estimate the spatial distribution patterns of cod inhabiting fishing grounds and protected areas northwest of Iceland. Small cod rarely migrated long distances, but they later adopted spawning–feeding migrations similar to cod tagged at larger sizes. These results are in accordance with earlier studies on the general migration pattern of cod in Icelandic waters. Mature cod migrate between the main nursery and feeding grounds off the northwest and north coasts and the main spawning grounds in the south and west (Jónsson, 1996). Juvenile cod in Iceland tend to be resident in particular nursery areas, although variable environmental conditions may affect their distribution, most markedly between ages 3 and 4 (Sæmundsson, 2005). The large differences observed in environmental conditions between tagging cruises in 1994 and 1995 show that the areas northwest of Iceland are subject to severe environmental changes (see also Astthorsson *et al.*, 2007) that may affect cod distribution.

Out of 641 cod with accurate recapture location, only 10 were caught within the MPAs. This may seem to indicate that the cod

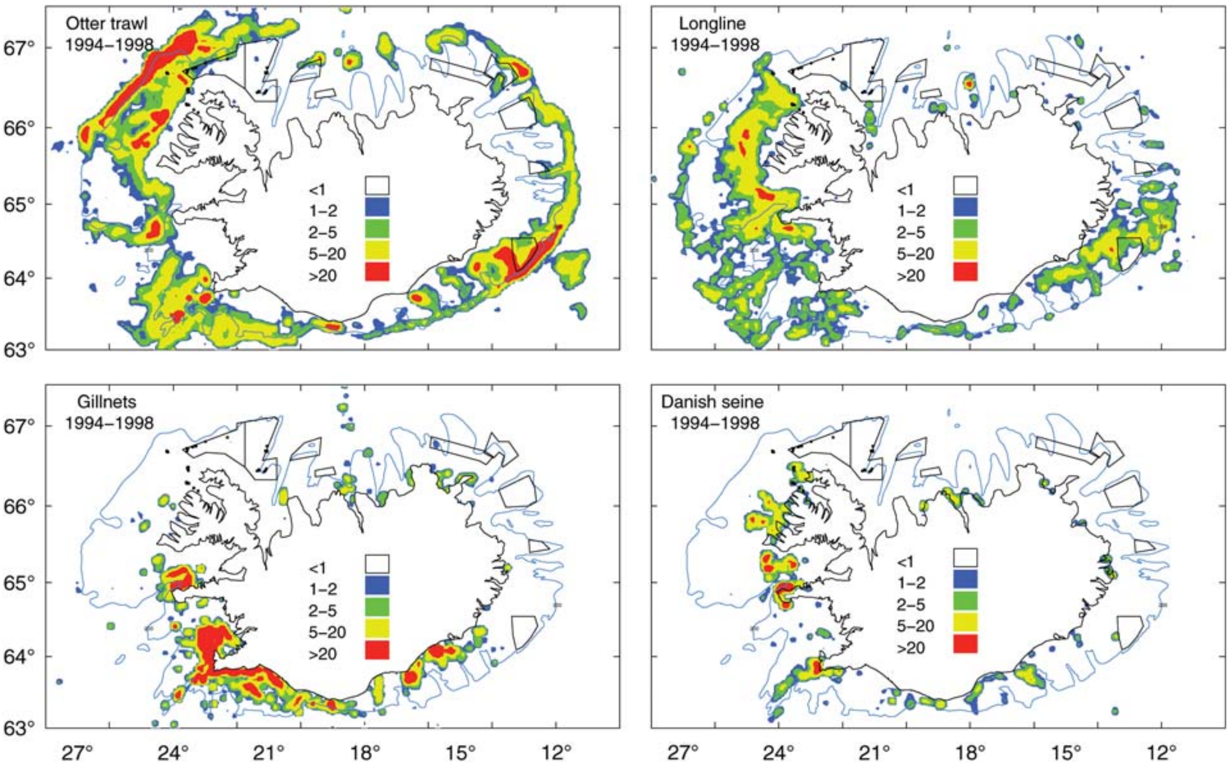

Figure 6. Spatial distribution of the commercial catch of cod (tonnes per square nautical mile) by vessels using otter trawls, longlines, gillnets, and Danish seines from August 1994 to December 1998, and locations of MPAs. Note that data from small boats using longlines are not presented.

are highly dispersed and mostly migrate out of the closed areas. However, the fishing effort within the protected areas is limited, so likewise is the probability of recapturing tagged fish. During the study period, only relatively small-scale handline fishing took place within the MPAs, and the overall effort was minor compared with the effort in adjacent areas targeted with otter trawls and longlines. This implies that the abundance of tagged cod that reside within the closures is much greater than the recapture data suggest. This limitation of the mark-recapture method makes it difficult to detect if resident components of cod exist within the MPAs. The migratory patterns of cod throughout its distributional range are known to range from long-distance migrations to mainly sedentary behaviour, and these two behavioural patterns may even exist within spatially defined populations (Robichaud and Rose, 2004; Lindholm *et al.*, 2007).

In the present study, we used total catch of cod per unit area for standardization of the observed recaptures. This method probably provides similar results to those based on some measure of fishing effort, but makes it more straightforward to combine fishing activities by vessels using different gear types. The standardization of recaptures had a pronounced effect in both spawning and feeding seasons, where spawning migrations to the southwest and fidelity to the northwest feeding area in the years following tagging were significantly downweighted, owing to the high catch taken in these areas/seasons. These results seem to support the common perception that, ideally, recaptures from conventional tagging studies need to be standardized with fishing effort, or otherwise the distribution of recaptures would mirror the distribution of fishing activities (Harden Jones, 1968; Bolle *et al.*, 2005). Although widely accepted, this procedure has been neglected by many tagging studies (but see, e.g. Bayliff, 1979; Lawson and Rose, 2000; Solmundsson *et al.*, 2005; Wright *et al.*, 2006; Armannsson *et al.*, 2007), usually because of a lack of adequate fishing effort or catch data. However, we acknowledge that the approach used for standardization is based on many assumptions and, for that reason, the estimates that are provided should be regarded as approximate.

Here, we have only dealt with one species, but the MPAs studied have the potential to reduce discarding of undersized fish of several species discarded in the Icelandic demersal fisheries (Pálsson *et al.*, 2007). They could also benefit fish species that are vulnerable to mesh penetration and other indirect impacts of trawling, e.g. haddock (Suuronen, 2005; Ingólfsson *et al.*, 2007). Furthermore, permanent area closures could protect or rehabilitate the three-dimensional structure of the benthic habitat, providing a shelter for juvenile demersal fish (Benaka, 1999).

We conclude that conventional tagging experiments can be used to evaluate the performance of area closures in protecting commercial fish species, by providing critical information on their movements and growth potential. The mark-recapture method, however, has several inherent limitations, and more advanced fishery-independent tag types, such as electronic data storage tags or acoustic transmitters (e.g. Bolle *et al.*, 2005; Thorsteinsson and Saemundsson, 2006; Lindholm *et al.*, 2007), should be used additionally to study the patterns of site fidelity and movement in protected areas. The results here suggest that area closures on nursery grounds can be a useful approach in protecting immature cod, but they are of little use in protecting highly migratory adults. For that purpose, the areas would have to be

Table 4. Distribution of recaptures from all releases in 1994 and 1995, shown for the two size classes of cod by period and season (see text).

			%*R* (*P*)			
Period	**Season**	***R***	**NW**	**CW**	**SW**	**E**
Large cod 1994						
1	F	34	97 (93)	0	0	3 (7)
2	S	25	32 (70)	8 (5)	60 (25)	0
2	F	51	61 (46)	16 (13)	20 (33)	4 (8)
3	S	36	11 (19)	31 (31)	56 (41)	3 (10)
3	F	27	41 (22)	22 (16)	22 (36)	15 (26)
Small cod 1994						
1	F	25	100 (100)	0	0	0
2	S	8	50 (83)	13 (6)	38 (12)	0
2	F	27	93 (83)	0	4 (7)	4 (10)
3	S	30	33 (48)	17 (14)	47 (29)	3 (10)
3	F	28	50 (30)	18 (14)	25 (43)	7 (14)
Large cod 1995						
1	F	58	98 (95)	0	0	2 (5)
2	S	17	35 (47)	12 (9)	47 (27)	6 (16)
2	F	24	79 (62)	8 (8)	8 (19)	4 (11)
3	S	32	31 (48)	25 (20)	44 (32)	0
3	F	30	67 (41)	10 (8)	17 (36)	7 (14)
Small cod 1995						
1	F	17	100 (100)	0	0	0
2	S	14	79 (88)	7 (5)	14 (7)	0
2	F	34	88 (78)	6 (7)	3 (8)	3 (8)
3	S	47	30 (46)	26 (21)	45 (33)	0
3	F	79	76 (57)	11 (11)	5 (13)	8 (19)

R, number of recaptures; %*R*, percentage distribution of recaptures; *P*, percentage standardized distribution of recaptures after weighing with catch per unit area; F, feeding season; S, spawning season. Deviations from a sum of 100% are due to rounding.

significantly larger than at present. However, we emphasize that MPAs only constitute one of the many management tools in the Icelandic cod fishery, and as such they can serve as a useful supplementary measure.

Acknowledgements

We thank the crew and researchers aboard RV "Bjarni Saemundsson" for cooperation in the tagging cruises, and Ólafur S. Astthorsson, Elena Guijarro Garcia, and two anonymous reviewers for improving earlier versions of this paper.

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Appendix

Estimated landings of cod in numbers (millions) by areas, years, seasons (F, fishing season; S, spawning season), and gears, 1994–1998, and total catch per km^2 in numbers (the unit used for standardizing the recaptures). Estimated size of areas: Northwest (NW) = 50 820 km^2, Central–west (CW) = 25 120 km^2, Southwest (SW) = 42 470 km^2, and East (E) = 90 440 km^2.

			Landings of cod per fishing gear						
Year	Season	Area	Longline	Gillnets	Handline	Danish seine	Otter trawl	Total catch	Catch area^{-1}
1994	F	NW	2.595	0.022	3.053	0.193	6.222	12.086	237.8
		CW	2.914	0.384	1.559	0.590	0.770	6.217	247.5
		SW	1.281	0.620	0.605	0.136	1.536	4.179	98.4
		E	1.606	0.188	1.552	0.147	4.809	8.301	91.8
1995	S	NW	1.040	0.002	0.143	0.008	0.434	1.627	32.0
		CW	1.588	0.329	0.795	0.203	0.100	3.015	120.0
		SW	1.202	1.462	0.765	0.238	3.424	7.091	167.0
		E	0.445	0.534	0.280	0.190	1.178	2.626	29.0
1995	F	NW	4.015	0.008	2.541	0.323	6.373	13.260	260.9
		CW	2.692	0.327	1.437	0.783	0.844	6.083	242.2
		SW	2.268	0.938	0.719	0.104	0.981	5.011	118.0
		E	2.470	0.353	1.466	0.124	3.821	8.235	91.1
1996	S	NW	1.748	0.004	0.166	0.031	1.274	3.224	63.4
		CW	1.182	0.279	0.638	0.298	0.260	2.656	105.7
		SW	0.858	1.993	0.667	0.366	2.377	6.261	147.4
		E	0.363	0.708	0.303	0.187	1.273	2.835	31.3
1996	F	NW	2.776	0.046	2.760	0.273	9.779	15.634	307.6
		CW	2.305	0.359	1.382	0.957	1.034	6.037	240.3
		SW	1.958	1.186	0.507	0.142	0.697	4.490	105.7
		E	2.769	0.558	1.107	0.277	3.893	8.603	95.1

Continued

Continued

Year	Season	Area	Landings of cod per fishing gear					Total catch	Catch area^{-1}
			Longline	Gillnets	Handline	Danish seine	Otter trawl		
1997	S	NW	1.016	0.000	0.367	0.029	2.485	3.898	76.7
		CW	1.494	0.523	0.774	0.242	0.660	3.694	147.0
		SW	0.645	2.395	0.733	0.597	2.362	6.732	158.5
		E	0.481	0.751	0.267	0.183	2.219	3.901	43.1
1997	F	NW	1.315	0.032	4.085	0.754	11.357	17.542	345.2
		CW	2.739	0.314	1.508	0.813	1.137	6.511	259.2
		SW	1.116	1.256	0.926	0.155	0.709	4.162	98.0
		E	1.985	0.533	1.284	0.219	5.371	9.393	103.9
1998	S	NW	1.300	0.047	0.427	0.111	2.791	4.676	92.0
		CW	1.437	0.941	0.337	0.658	0.271	3.644	145.1
		SW	1.084	2.459	0.798	0.568	4.020	8.929	210.2
		E	0.311	1.041	0.167	0.251	2.125	3.895	43.1
1998	F	NW	2.418	0.120	5.292	1.261	15.111	24.202	476.2
		CW	2.365	0.274	0.728	0.567	0.540	4.475	178.1
		SW	1.112	1.248	0.708	0.221	1.103	4.392	103.4
		E	2.886	0.416	1.259	0.181	8.876	13.618	150.6

doi:10.1093/icesjms/fsp281