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The effect of area closures on the demersal fish community off the east coast of Iceland

Andrzej Jaworski, Jon Solmundsson, and
Stefan Aki Ragnarsson

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The effect of reduced fishing effort on the demersal fish community, following area closures in 1993, was analysed for two protected areas off the east coast of Iceland, Digranesflak and Breiddalsgrunn. The data were collected using a standardized bottom trawl during groundfish surveys in the period 1985–2004. The aspects of the fish community that were analysed included abundance by size class, mean size, species richness, diversity, and composition. The analysis was conducted for closed areas and adjacent reference (fished) areas, as well as for periods before and after the closure (and also after the re-opening in Breiddalsgrunn), using an ANOVA model and planned comparisons. The closure had a favourable impact on abundance of haddock (*Melanogrammus aeglefinus*) and small long rough dab (*Hippoglossoides platessoides*) in Digranesflak, and on exploitable sizes of haddock and cod (*Gadus morhua*) in Breiddalsgrunn. The mean size of haddock increased considerably within the protected areas relative to the reference areas: by 16 cm in Digranesflak and by 10 cm in Breiddalsgrunn. Species richness, diversity, and composition varied over the study period and between areas, but no effect of area closure was found. The observed changes in the fish community in Breiddalsgrunn were reversed within 7 years of the re-opening of the area to fishing. The possible causes for the observed patterns of response to area closures are discussed.

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Keywords: abundance, closed areas, fish community, fishing effort, mean size, species diversity, species richness.

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A. Jaworski, J. Solmundsson, and S. A. Ragnarsson: Marine Research Institute, Skulagata 4, PO Box 1390, 121 Reykjavík, Iceland. Correspondence to A. Jaworski: tel: +354 575 2000; fax: +354 575 2001; e-mail: andrzej@hafro.is.

Introduction

There is a rapidly growing interest in marine protected areas (MPAs) as a tool for fishery management and ecosystem conservation. There is also much debate on their effectiveness. Although many authors recognize the limitations of MPAs, most agree that they can serve as an important supplement to other measures (Browman and Stergiou, 2004; Hilborn *et al.*, 2004).

Evaluation of the effectiveness of MPAs plays a crucial role in their management and re-design, as well as in the designation of new ones. The expected benefits resulting from the establishment of reserves and fishery closures most often include preservation or recovery of habitats, protection of biodiversity and ecosystem structure, and among fishery benefits, increases of spawning stock size, biomass, body size, and reproductive output of exploited species (Gell and Roberts, 2002; Jones, 2002). Several studies have been done worldwide, mostly in tropical waters, but also in some temperate waters (North Sea, Mediterranean Sea, Canada, and New Zealand), to demonstrate these benefits (see reviews in Jennings, 2001; Gell and Roberts, 2002; Jones, 2002; Halpern, 2003). However, the quantity of sound scientific evidence is rather limited (Willis *et al.*, 2003).

A common approach in evaluation studies is to contrast areas or periods subject to different intensities of fishing (Piet and Rijnsdorp, 1998; Frank *et al.*, 2000; Gell and Roberts, 2002; Ferraris *et al.*, 2005). Piet and Rijnsdorp (1998) studied the effect of the reduction in trawling effort within a protected area in the southeastern North Sea (the so-called “plaice box”), following its closure, on the size distribution and species composition in the demersal fish assemblage. They found that the overall size structure of commercially exploited fish species was affected by the

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reduction in trawling effort, whereas that of non-target species remained unaffected. Pastoors *et al.* (2000) evaluated the effect of the "plaice box" in a wider context by considering natural and anthropogenic factors that affect recruitment, such as natural mortality and discard mortality. In contrast to their expectations, those authors observed a decrease in yield and spawning biomass, which they attributed to changes in growth and natural mortality. Frank *et al.* (2000) evaluated the effectiveness of an area closure off Nova Scotia on recruitment, survival, and distribution of juvenile haddock (*Melanogrammus aeglefinus*). Their evaluation revealed that the management objective of reducing juvenile mortality by the area closure was not fully met. Fisher and Frank (2002) found significant changes in the finfish community composition in that area after the implementation of the closure. Jennings (2001) considered the factors that influence population recovery following area closures (such as initial population size, the intrinsic rate of population increase, and the degree of compensation or depensation in the spawner/recruit relationship), described patterns of recovery, and suggested how recovery rates could be predicted. Ferraris *et al.* (2005) proposed a statistical approach based on multivariate analysis and general linear models to study the impact of changes in the status of a reef reserve in New Caledonia at the fish assemblage level.

Area closures are one of the tools used for managing Icelandic fisheries and have long been implemented on the Icelandic continental shelf (Anon., 1973). Other management measures include setting total allowable catches (TACs) based on a system of Individual Transferable Quotas (ITQ), seasonal closures, short-time closures, and selectivity measures including mesh size regulations and the mandatory use of sorting devices on gears to prevent catches of juvenile fish in the shrimp and groundfish fisheries.

The first protected areas in Icelandic waters were established in the early 1970s (Anon., 1973), either to protect spawning grounds (off the southwest coast) or nursery areas for juveniles (off the north and east coast) of the most important demersal stock, cod (*Gadus morhua*). A wide range of protected areas have been established since then, also aiming at other stocks such as redfish (*Sebastes marinus*), haddock, and saithe (*Pollachius virens*). Today, they form a network of protected areas. Some are subject to temporary or seasonal closures, and others are permanently closed. In certain areas, the use of certain gear types is banned or limited. The number of areas, their size and location, and the restrictions imposed have varied over the past three decades, being subject to numerous modifications or revisions (Anon., 1973). Although they have been in effect for some time, hardly any evidence is available that demonstrates their effectiveness at protecting fishery resources.

This paper is an attempt to assess biological implications following the establishment of closed areas off East Iceland more than a decade ago, with a focus on two, for which sufficient data were available. The management objective behind the imposition of these permanent closures was to protect undersized fish (mainly cod 3–4 years old, some 40–55 cm long) that previously had been protected through some consecutive short-term closures (Kristinsson *et al.*, 2005).

The main question addressed here is whether the area closures have had any effect on the structure of the demersal fish community. The analysed aspects include changes in abundance by size class, mean body size, species richness, diversity, and composition. In addition to the description of observed changes in the fish community, an attempt is made to relate them directly to changes in fishing effort, either to those enforced by the imposition of area closures, or to those following the relaxation of restrictions.

Methods

Two protected areas off the eastern coast of Iceland were selected to study the effect of reduced fishing effort on the fish community: Digranesflak and Breiddalsgrunn (P1 and P2; Figure 1). The other three areas: "Off the northeast coast" (P3), Langanesgrunn (P4), and Glettinganesgrunn (P5) could not be studied owing to there being insufficient data. Area P3 was closed in the early 1970s and no data were available before the closure, while the spatial

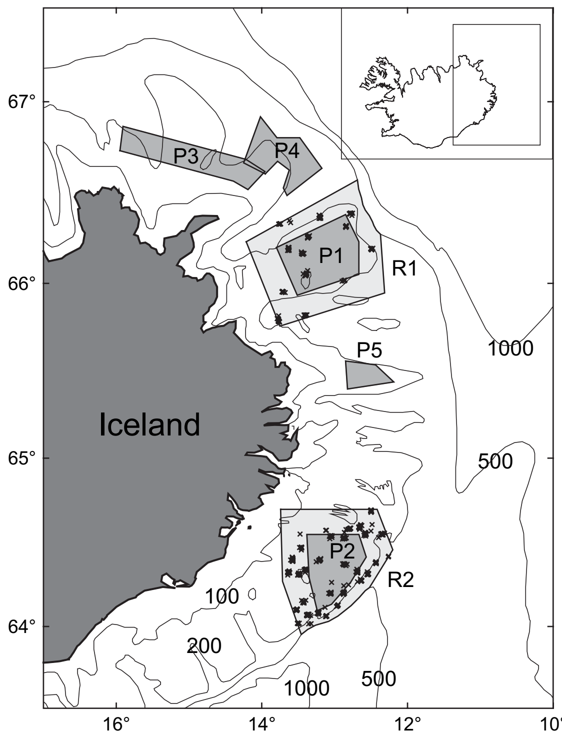

Figure 1. Main protected areas (P1–P5) off the east coast of Iceland. Areas P1 and P2 and the adjacent reference areas (R1 and R2) are the subjects of the current study. The sampling stations within these areas are shown.

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distribution of sampling stations in Langanesgrunn and Glettinganesgrunn was uneven and inadequate for the purpose of this study. In addition to the selected areas P1 and P2, two reference/control areas, R1 and R2 (Figure 1), surrounding the former, were delineated on the basis primarily of bathymetry (areas with depths similar to those in the protected areas were prioritized), distribution of fishing effort, and allocation of sampling stations. A summary of the areas studied is given in Table 1. Stations from the reference areas tended to be located in deeper water than the protected areas (Table 1). Only stations with bottom depths ≤300 m were selected for the analysis (all samples in the protected areas and 86% of samples in the reference areas).

For each of the two protected areas, a ban on bottom and pelagic trawls as well as on longlines was imposed in 1993 (Table 1). However, some restrictions had already been imposed in 1992 (a ban on trawls in Digranesflak), and a number of small modifications and exemptions were made to the general ban during the post-closure period. For Digranesflak, two periods were distinguished, before and after the closure, of length 8 and 11 years, respectively. For Breiddalsgrunn, another period was distinguished following the re-opening of the area to fishing. The three time periods for that area were 8, 4, and 7 years, respectively.

The Icelandic Groundfish Survey (IceGFS) has been conducted by the Marine Research Institute in Icelandic waters on an annual basis in March since 1985. Area-based stratified sampling is used in the survey. Samples are taken with a standardized bottom trawl with the following main specifications: headline 32 m, fishing line 19 m, bobbin footrope 18 m, weighing 4.0–4.2 t, bridles 64 and 82 m (depending on depth), and otter boards 1.7–2.0 t; mesh size in the front section 135 mm, in the belly 80 mm, in the extension piece 135 mm, in the codend 155 mm, and in the codend cover 40 mm; vertical opening approximately 2–3 m; and average distance between wing ends 17 m. The trawl is towed over the bottom at a standard speed of approximately 3.8 knots. Towing distance is about 4 nautical miles. A more detailed description of the survey design and specification of the gear can be found in Palsson *et al.* (1989, 1997). Some minor changes have been made in the survey design since 1985, but they are not considered to have had a significant effect on survey results (Palsson *et al.*, 1997).

For the present study, the data collected during the IceGFS during the period 1985–2004 were used. These data included time, position, bottom depth, and bottom temperature for individual hauls, fish species, and their numbers at length. Fish species classified as demersal, bathydemersal, or benthopelagic (according to species characteristics in FishBase; Froese and Pauly, 2004) were considered to form the demersal community, and were consequently selected for the analysis. Although redfish are classified as pelagic and deepwater redfish (*Sebastes mentella*) as bathypelagic, both occurred in considerable numbers in the samples and were therefore also included in the analysis. Other pelagic and bathypelagic species, which were occasionally found in the samples, were excluded. The analysis of the effect of area closure on abundance and mean size was carried out individually for the seven most abundant species for each area and, in addition, for commercially important species as a whole (Table 2). Only a few species from the category non-commercial species were measured in the early years of the IceGFS. Therefore, this category could not be analysed aggregated in a similar manner as commercial species.

In the analysis of the effect of area closure on the abundance, a two-way ANOVA model was used with two main factors: "area" and "period", and data were

Table 1. Summary of protected (P1 and P2) and reference (R1 and R2) areas under study. *n* is the number of samples.

			Depth* (m)		Period					
					Before closure		After closure		After re-opening	
Protected area	Area symbol	Area (km^2)	Range	Mean	Years	*n*	Years	*n*	Years	*n*
Digranesflak	P1	1 621	83–182	139	1985–1993†	45	1993–2004‡,§	56		
	R1	3 205	140–278	205		61		79		
Breiddalsgrunn	P2	1 397	123–220	150	1985–1993‖	48	1993–1997¶	21	1997–2004**	39
	R2	3 080	79–299	189		184		80		136

*Depth at the stations selected for the study (where depth ≤300 m).
†A larger part of area P1 (1069 km^2) was closed to trawling in 1992. In 1993, the area was extended and a ban on longlines added.
‡A slight change was made to the shape of area P1 in 2000. A large part of area R1 was closed to trawling in 2000, with the exception of trawls with a sorting grid.
§Area still protected.
‖A series of changes in the shape of area P2 was made during 1993.
¶Exemption from the ban was granted in 1997–1998 for trawls with a sorting grid. The ban was completely lifted in 1998.
**A small area (520 km^2) within areas P2 and R2 was closed to bottom trawling from 2000 to 2002.

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Table 2. Demersal commercial and non-commercial species present in the samples taken in protected areas P1 and P2, and in reference areas R1 and R2. Species are listed in each category from the most to the least abundant.

Commercial species ($n = 21$)		Non-commercial species ($n = 35$)	
Scientific name	Common name	Scientific name	Common name
*Melanogrammus aeglefinus**,†	Haddock	*Sebastes viviparus**,†	Norway haddock
*Gadus morhua**,†	Cod	*Lycodes vahli**,†	Vahl's eelpout
*Hippoglossoides platessoides**,†	Long rough dab	*Lumpenus lampretaeformis**,†	Snake blenny
*Sebastes marinus**,†	Redfish	*Triglops murrayi**,†	Moustache sculpin
*Anarhichas lupus**,†	Atlantic wolffish	*Enchelyopus* (=*Rhinonemus*) *cimbrius**,†	Fourbearded rockling
*Pollachius virens**,†	Saithe	*Trisopterus esmarkii**,†	Norway pout
Amblyraja (=*Raja*) *radiata**,†	Starry ray	*Merlangius merlangus**,†	Whiting
*Brosme brosme**,†	Tusk	*Leptagonus decagonus**,†	Atlantic poacher
*Microstomus kitt**,†	Lemon sole	*Argentina silus*†	Greater argentine
*Anarhichas minor**,†	Spotted wolffish	*Anarhichas denticulatus**,†	Jelly cat
*Cyclopterus lumpus**,†	Lumpsucker	*Artediellus atlanticus**,†	Atlantic hookear sculpin
*Pleuronectes platessa**,†	Plaice	*Lycodes esmarkii**,†	Esmark's eelpout
*Sebastes mentella**,†	Deepwater redfish	*Cottunculus microps**,†	Polar sculpin
*Hippoglossus hippoglossus**,†	Halibut	*Gaidropsarus* (=*Onogadus*) *argentatus**,†	Arctic rockling
*Reinhardtius hippoglossoides**,†	Greenland halibut	*Icelus bicornis**,†	Twohorn sculpin
Molva molva†	Ling	*Careproctus reinhardti**,†	Longfin snailfish
*Glyptocephalus cynoglossus**,†	Witch	*Leptoclinus maculatus**,†	Spotted snake blenny
Lophius piscatorius†	Monkfish	*Squalus acanthias*†	Dogfish
*Limanda limanda**,†	Dab	*Boreogadus saida**,†	Polar cod
Molva dipterygia†	Blue ling	*Gymnelus retrodorsalis**,†	Aurora pout
Lepidorhombus whiffiagonis†	Megrim	*Gaidropsarus vulgaris*†	Threebearded rockling
		*Lycodes eudipleurostictus**,†	Doubleline eelpout
		*Lycodes reticulatus**	Arctic eelpout
		Dipturus (=*Raja*) *batis**,†	Blue skate
		Eutrigla gurnardus†	Grey gurnard
		Liparis montagui†	Montagui's seasnail
		*Lycodes pallidus**	Pale eelpout
		Ciliata septentrionalis†	Northern rockling
		*Coryphaenoides rupestris**	Roundnose grenadier
		*Liparis fabricii**	Gelatinous snailfish
		Lycenchelys muraena†	—
		*Lycodes rossi**	Threespot eelpout
		*Macrourus berglax**	Roughhead grenadier
		Phycis blennoides†	Greater forkbeard
		Leucoraja (=*Raja*) *fullonica*†	Shagreen ray

*Species recorded in Digranesflak (areas P1 and R1).
†Species recorded in Breiddalsgrunn (areas P2 and R2).

expressed as number of fish per tow. As the abundance data were not normally distributed, they were log-transformed [$\ln(n+1)$] to achieve normality before statistical analyses were performed. Depth and temperature were included in the model as linear covariates to account for the observed dependence of fish abundance on these two variables. To further reduce the magnitude of error variance, "year" was added into the model as a nested factor (within "period"). The factor "area" had two levels: *protected* and *reference*, while the factor "period" had two or three levels: *before closure* and *after closure* (in Digranesflak) or, additionally, *after re-opening* (in Breiddalsgrunn). The interaction between "area" and "period" was considered to result mainly from the changes in the status of the protected area (closure or re-opening). The ANOVA analysis was carried out separately for each 10-cm size class. Size classes containing few individuals (typically near the bounds of size ranges) were combined to form classes that contained at least ten individuals. The groups corresponding to the levels of the two main effects ("area" and "period") or their interaction were of different size (i.e. the design was unbalanced). Unless indicated otherwise, differences between groups were estimated from standardized effects that sum to zero (MathSoft, 1998).

Similarly, a two-way ANOVA model, with depth, temperature, and year (nested within "period") as covariables,

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was used to determine the effect of area closure on mean size of fish, species richness, and diversity. Species richness was expressed as number of species per tow. Species diversity was measured by Simpson's reciprocal index and a Shannon−Wiener index, and calculated for each tow. The analyses of mean size, species richness, and diversity were conducted with non-transformed data, because these measures showed no marked departure from normality.

The results were summarized to show changes in the difference between the protected and reference areas throughout the time periods. These changes were tested in planned comparisons for unequal sample sizes (Sokal and Rohlf, 1981), by applying appropriate contrasts to four groups (2 areas × 2 periods, in Digranesflak) or six groups (2 areas × 3 periods, in Breiddalsgrunn). With two areas and two periods (in Digranesflak), testing of the change in the difference between the protected and reference areas was equivalent to testing of the interaction between the main effects of area and period (Zolman, 1993). With two areas and three periods (in Breiddalsgrunn), the test of the interaction provided an overall test of significance of changes (in the difference between the protected and reference areas) over time, whereas planned comparisons were used explicitly to test significance of changes between two consecutive periods: (i) before and after the closure; (ii) before and after the re-opening. The analyses of species richness and diversity were extended beyond the interaction of area and period to consider the main effects. Any differences found in the statistical analyses were considered as significant when $p < 0.05$.

When analysing the effect of area closure on species richness, frequency of occurrence (i.e. proportion of tows in which a species occurred) was examined for individual species to find which of them were most affected, and how, by area closure. The changes in frequency of occurrence were examined within and outside the protected areas.

Changes in the fish community were compared with changes in fishing effort in the protected and reference areas. Data on effort (in number of tows per km^2 per year) by otter trawlers, and also by shrimp trawlers, were available for the period 1991−2003, which covered part of the period before closure and the whole period after closure (also after the re-opening in Breiddalsgrunn).

Results

Digranesflak

The temperature in Digranesflak was consistently higher inside the protected area than in the deeper waters of the reference area (on average by 0.5°C), and showed an increasing trend in the two areas throughout the study period. Fish abundance, mean size, species richness, and diversity measures varied from year to year and depended on depth and to a lesser degree on temperature (not shown). All three covariables included in the ANOVA model (year, depth, and temperature) were significant in most cases.

In the whole area (areas P1 and R1 combined), 43 species were recorded (Table 2). Among the most abundant species, some were more abundant within the protected area (redfish, Atlantic wolffish, haddock, and saithe), and others were more common in the reference area (long rough dab and starry ray; Figure 2a−g). The differences in abundance between the two areas were in general size-specific. For example, the greater abundance of haddock in the protected area was more pronounced in smaller fish (Figures 2e and 3a−f). As a result, the mean size of haddock was smaller in the protected area than in the reference area (Table 3). Also, long rough dab, cod, Atlantic wolffish, saithe, and the aggregate category of commercial species were smaller inside the protected area.

After the closure, the difference in abundance between the protected and reference areas increased markedly for haddock (especially at sizes 30−60 cm long; Figures 2e and 3a−f) and small long rough dab (<20 cm; Figure 2a). For redfish, Atlantic wolffish, and saithe, this increase was not significant or significant only for a single size class (20−30 cm), while the abundance of cod and starry ray in the protected area in relation to the reference area was unaffected by the closure (Figures 2b−d, f, g and 3g−o). The large increase in abundance of medium-sized haddock following the closure (larger than in small fish) was reflected in the mean size in the protected area compared with the reference area being smaller by 17 cm before but only by 1 cm after the closure (Table 3). Alternatively, the mean size within the protected area increased by 20 cm, compared with an increase of only 4 cm in the reference area.

The difference in the mean number of species per tow between the two areas showed no significant changes after the closure (Table 4, Figure 4a). This difference for the whole period (i.e. the main effect of area) was also not significant. The only difference observed was between the time periods for the whole area (i.e. for the main effect of period). The mean number of species per tow increased over the whole area by one.

Frequency of occurrence of several fish species, e.g. tusk, saithe, lumpsucker, and Atlantic poacher, in the protected area changed markedly relative to the reference area over the study period (Figure 5a). Tusk and saithe occurred more frequently inside the protected area, and this difference increased considerably in the post-closure period. Lumpsucker were also more frequent in the protected area, but this difference decreased in the post-closure period. Atlantic poacher were more frequently found outside the protected area, and this difference increased considerably after the area closure.

The fish community in the protected area consisted predominantly of four species: long rough dab, cod, redfish, and Atlantic wolffish (Figure 6a). The reference area was dominated by two species: long rough dab (which

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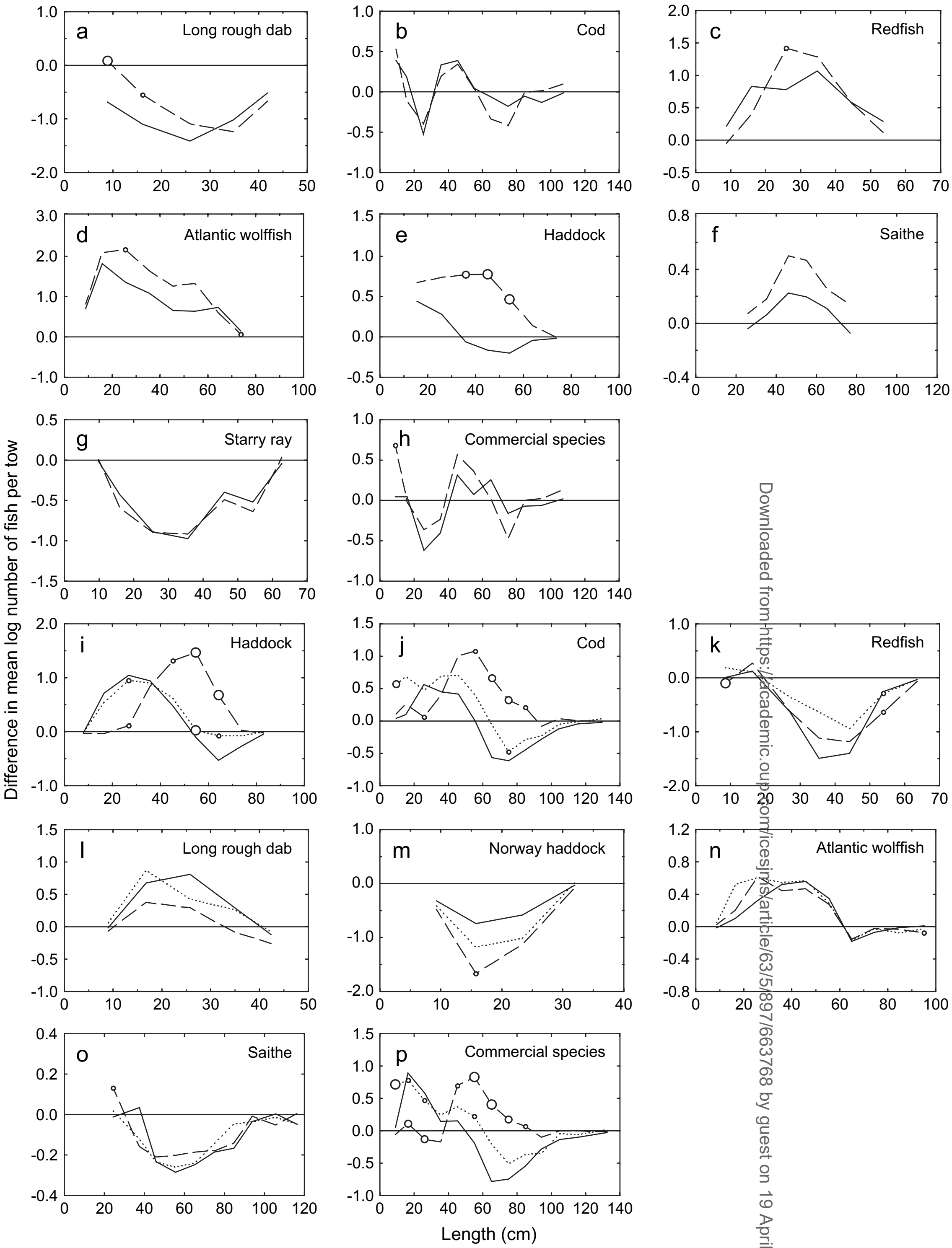

Figure 2. Difference in the mean log numbers (observed values) of fish per tow between the protected and reference areas for the seven most abundant species and the aggregate category of commercial species in Digranesflak (a–h) and Breiddalsgrunn (i–p) in the different periods: before the closure (solid line), after the closure (dashed line), and after the re-opening in Breiddalsgrunn (dotted line). The circles denote statistically significant changes within size classes; big circles, $p < 0.001$; medium-sized circles, $p < 0.01$; and small circles, $p < 0.05$. Note the different scales on the y-axes.

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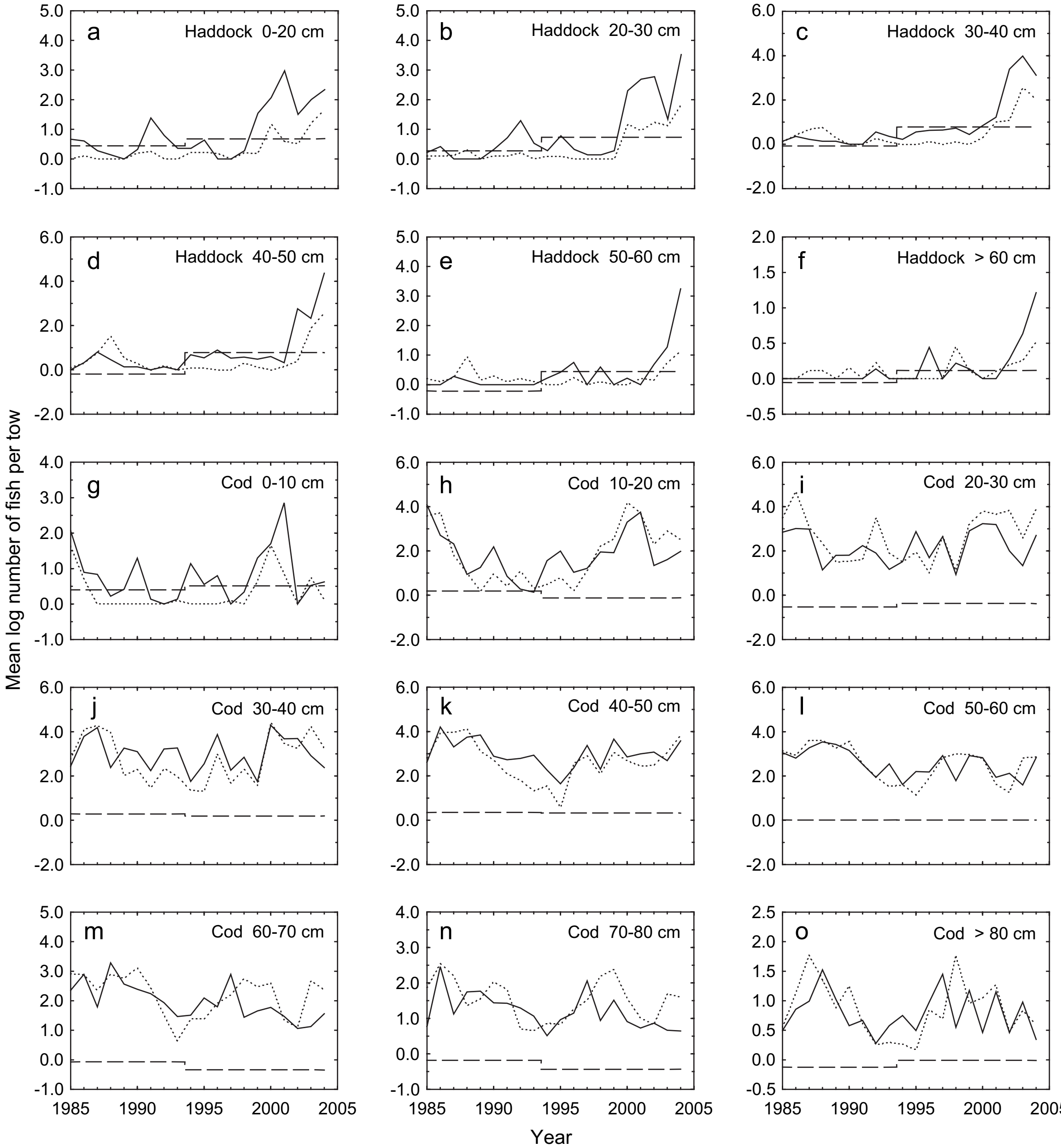

Figure 3. Interannual variability in the mean log number of haddock (a–f) and cod (g–o) per tow by size class in Digranesflak, in the protected area (solid line) and in the reference area (dotted line). The dashed line shows the mean difference between the two areas for the two selected periods: before and after the closure. Note the different scales on the *y*-axes.

constituted, in number, roughly half the fish community) and cod (Figure 6b). The difference in species diversity (in both indices) between the two areas showed no significant changes after the closure (Table 4, Figure 4b, c). However, diversity was greater in the protected area over the whole period. No period effect was detected for species diversity over the whole area, although there was a considerable increase in the proportion of haddock from 2002 on (Figure 6a, b).

Breiddalsgrunn

The temperature in Breiddalsgrunn was higher than in Digranesflak (on average by 2.6°C). It showed less difference between the protected and reference areas when compared to Digranesflak, but the interannual variability was high (not shown). Similar to the situation in Digranesflak, year, depth, and temperature were in most cases significant covariables in the ANOVA model.

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Table 3. Difference in mean fish length between the protected and reference areas in the different periods estimated from the ANOVA model. The significance of changes between periods is indicated as follows: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and n.s. = not significant. Overall means for the areas (with s.d. in parenthesis) are also shown.

				Difference in mean length (cm)		
Protected area	Fish species/category	Number of fish	Mean length (cm)	Before closure	After closure	After re-opening
Digranesflak	Long rough dab	103 610	26.9 (6.9)	−1.2	−2.6***	–
	Cod	62 376	43.5 (16.1)	−9.8	−7.9***	–
	Redfish	29 489	24.3 (8.3)	1.4	1.0*	–
	Atlantic wolffish	19 034	31.6 (14.4)	−7.4	−10.4***	–
	Haddock	11 280	34.3 (12.4)	−17.4	−1.1***	–
	Saithe	6 073	50.0 (5.9)	−2.0	−2.0 n.s.	–
	Starry ray	3 966	40.0 (13.4)	−0.5	1.9*	–
	Commercial species	239 147	32.7 (13.9)	−6.6	−6.4 n.s.	–
Breiddalsgrunn	Haddock	272 808	38.0 (11.5)	−5.6	4.0***	−0.1***
	Cod	100 418	56.4 (15.0)	−3.4	−2.4 n.s.	−2.3 n.s.
	Redfish	65 695	35.2 (5.7)	−4.0	−1.3***	−2.0 n.s.
	Long rough dab	37 228	28.4 (6.6)	−0.8	0.0***	−0.8***
	Norway haddock	16 591	16.7 (4.3)	1.7	0.3***	−1.0 n.s.
	Atlantic wolffish	13 190	45.4 (15.7)	−1.4	−1.7 n.s.	−2.0 n.s.
	Saithe	9 613	53.0 (11.5)	10.9	−9.7***	8.2***
	Commercial species	514 613	41.1 (14.4)	−4.0	5.5***	−0.3***

The number of species recorded in the whole area (areas P2 and R2 combined) was higher ($n = 50$) than in Digranesflak (Table 2). The fish community in Breiddalsgrunn generally consisted of larger fish than that in Digranesflak (Table 3). This difference in mean size for redfish, cod, and Atlantic wolffish was as large as 11–14 cm.

As in Digranesflak, the abundance of the more common species in Breiddalsgrunn differed between the protected area and the adjacent reference area. Haddock, long rough dab, and Atlantic wolffish were in general more abundant inside the protected area (Figures 2i–o and 7a–f). Redfish, Norway haddock, and saithe were more common in the reference area. Cod, redfish, long rough dab, and Atlantic wolffish were smaller inside the protected area than in the reference area (Table 3).

The difference in abundance of haddock between the protected and reference areas varied along the size range and between the three time periods (Figures 2i and 7a–f). It decreased in small classes following the closure, and increased after the re-opening (significantly in size

Table 4. Difference in diversity measures between areas and periods estimated from the ANOVA model. The significance of difference between periods or between areas is indicated as follows: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and n.s. = not significant. Overall means for the areas (with s.d. in parenthesis) are also shown.

			Difference between protected and reference areas				Difference between periods‡	
Diversity measure	Protected area	Mean per tow	Before closure	After closure	After re-opening	All periods†	After closure	After re-opening
Species richness	Digranesflak	11.0 (2.1)	0.1	0.2 n.s.	–	0.2 n.s.	0.9***	–
	Breiddalsgrunn	11.2 (1.8)	−0.3	−1.2 n.s.	−0.5 n.s.	−0.8***	1.1***	−0.2 n.s.
Simpson's reciprocal index (D^{-1})	Digranesflak	2.65 (0.83)	0.37	0.43 n.s.	–	0.40*	−0.17 n.s.	–
	Breiddalsgrunn	3.00 (1.21)	−0.43	−0.46 n.s.	−0.47 n.s.	−0.45***	0.13*	−0.92 n.s.
Shannon–Wiener index (H)	Digranesflak	1.22 (0.28)	0.15	0.19 n.s.	–	0.17**	−0.01 n.s.	–
	Breiddalsgrunn	1.31 (1.39)	−0.17	−0.21 n.s.	−0.15 n.s.	−0.17***	0.11***	−0.28*

†Significance refers to the difference between the two areas for the whole study period (main effect of area).
‡Significance refers to the difference between periods for the combined areas (main effect of period).

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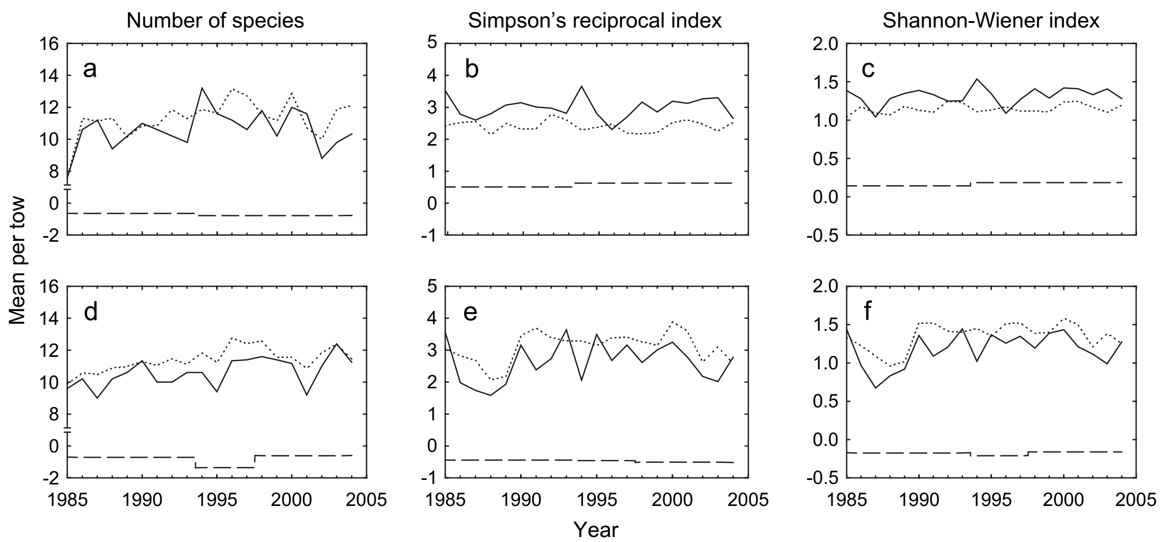

Figure 4. Interannual variability in the mean number of species (a, d), Simpson's reciprocal index (b, e) and the Shannon−Wiener index (c, f) per tow in Digranesflak (a−c) and Breiddalsgrunn (d−f), in the protected area (solid line) and reference area (dotted line). The dashed line shows the mean difference between the protected and reference areas for the selected periods: before and after the closure (in Digranesflak), or before the closure, after the closure, and after the re-opening (in Breiddalsgrunn).

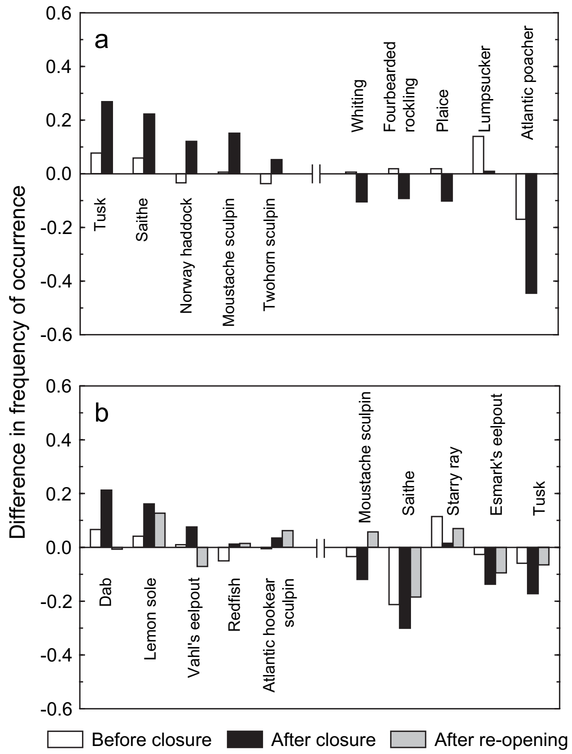

Figure 5. Difference in frequency of occurrence of some species between the protected and reference areas in (a) Digranesflak and (b) Breiddalsgrunn during different periods. For each of the two areas, ten species are shown for which this difference changed most after the closure.

class 20−30 cm). In contrast, the difference between the two areas for larger haddock increased after the closure (mainly in the size classes 40−70 cm), and decreased after the re-opening. Changes were similar for cod (Figures 2j and 7g−q), although the reversed effect following the re-opening of the protected area was less pronounced than in haddock. The largest increase in abundance following the closure was observed for cod 50−90 cm long. The abundance of small cod declined after the closure, and increased after the re-opening (particularly the smallest size class, ≤10 cm long). The shift in the effect of closure or re-opening across the size range was observed, for both haddock and cod, at a length of 30−40 cm (Figures 2i, j and 7c, j).

The observed changes in abundance and size structure of haddock were reflected in changes in mean size (Table 3). This was initially smaller (by 6 cm), but after the closure larger (by 4 cm), in the protected area than in the reference area (alternatively, the mean size within the protected area increased by 4 cm and decreased by 6 cm in the reference area). After the re-opening, the mean size was nearly equal in both areas. The greatest changes in mean size over time (opposite to those for haddock) were observed for saithe (Table 3).

The difference in the mean number of species per tow between the two areas showed no significant changes over time (Table 4, Figure 4d). Over the whole period, the average number of species per tow was higher outside the protected area (by 0.8). For the whole area, an increase by one species was noted after the closure, but no change was observed after the re-opening.

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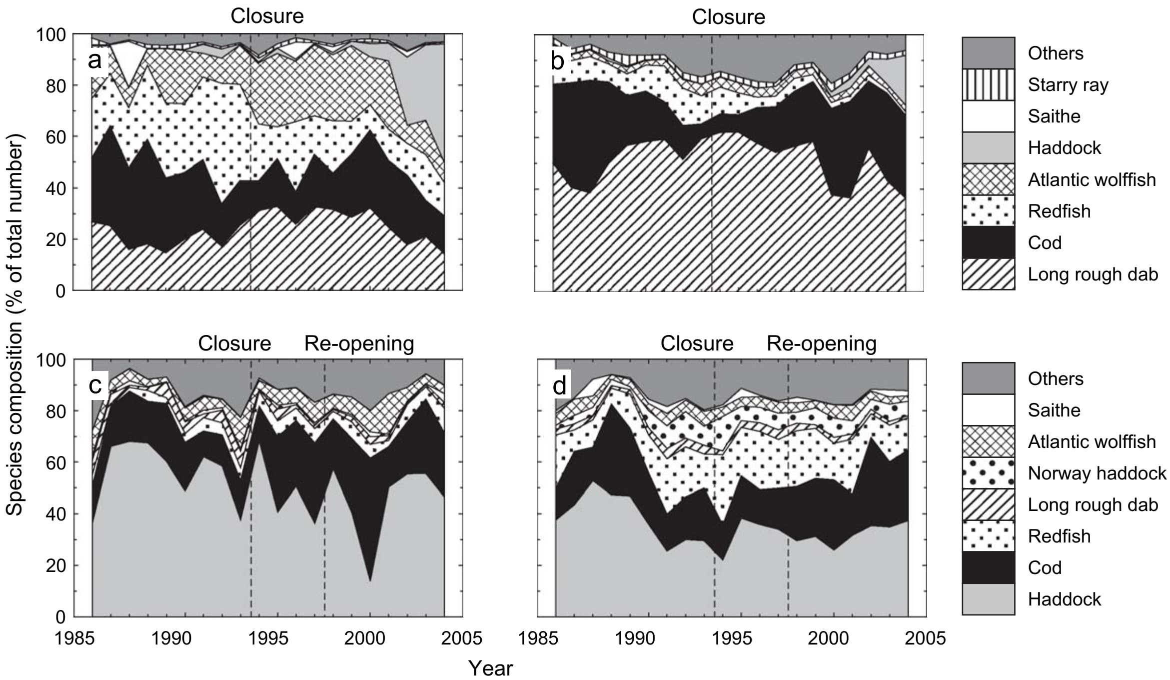

Figure 6. Species composition in (a, b) Digranesflak and (c, d) Breiddalsgrunn, in the protected (left) and reference areas (right). The vertical dashed lines show major changes in the status of protected areas (see Table 1).

Among the species for which the greatest changes in frequency of occurrence following the closure were observed were dab, lemon sole, Esmark's eelpout, and tusk (Figure 5b). While dab and lemon sole were more frequently encountered in the protected area, Esmark's eelpout and tusk were found more frequently in the reference area. These differences increased after the closure. The trends that were observed following the area closure were reversed in most species after the re-opening of the area.

The most common species in the two areas, particularly in the protected area, was haddock (Figure 6c, d). The difference in species diversity (in both indices), and similarly as for the mean number of species, did not change significantly over time (Table 4, Figure 4e, f). However, the diversity was lower in the protected area over the whole period. It increased in the whole area after the closure. The Shannon−Wiener index decreased in the whole area after the re-opening. The observed low species diversity in the period 1986−1989 (Figure 4e, f) matched the period of great dominance of haddock and cod in the survey catch (Figure 6c, d).

Fishing effort

The overall fishing effort by otter trawlers was considerably higher in Breiddalsgrunn than in Digranesflak (Figures 8 and 9). It was particularly intense on the shelf edge, and showed relatively small changes in spatial distribution over time. However, a substantial reduction in fishing effort following the closure was observed within the two closed areas. The small amount of effort deployed in the protected areas after the closure was difficult to explain. The re-opening of the protected area in Breiddalsgrunn resulted in an increase in fishing pressure inside the area, to levels observed in the pre-closure period. There was also some reduction in fishing effort in the reference areas following the closure of the protected areas. The fishing pressure in the reference area of Digranesflak increased considerably after 1999, and in Breiddalsgrunn after the re-opening of the protected area. In addition to otter trawling, there was also some shrimp trawling, but it was conducted almost entirely outside the protected areas (not shown).

Discussion

The observed effects of reduced fishing effort following area closures on fish abundance and mean size differed between the two study areas and varied across species and size ranges. The expected increase in abundance was generally evident in haddock and small size classes of long rough dab in Digranesflak, and in exploitable size classes of haddock and cod in Breiddalsgrunn. The results from Digranesflak may suggest that indirect fishing mortality (such as discards) had been substantial before the closure, and was considerably reduced after the closure. However, no estimates of indirect fishing mortality in the area were available for the study period. Small size classes of cod and haddock in Breiddalsgrunn were adversely affected by the closure, as

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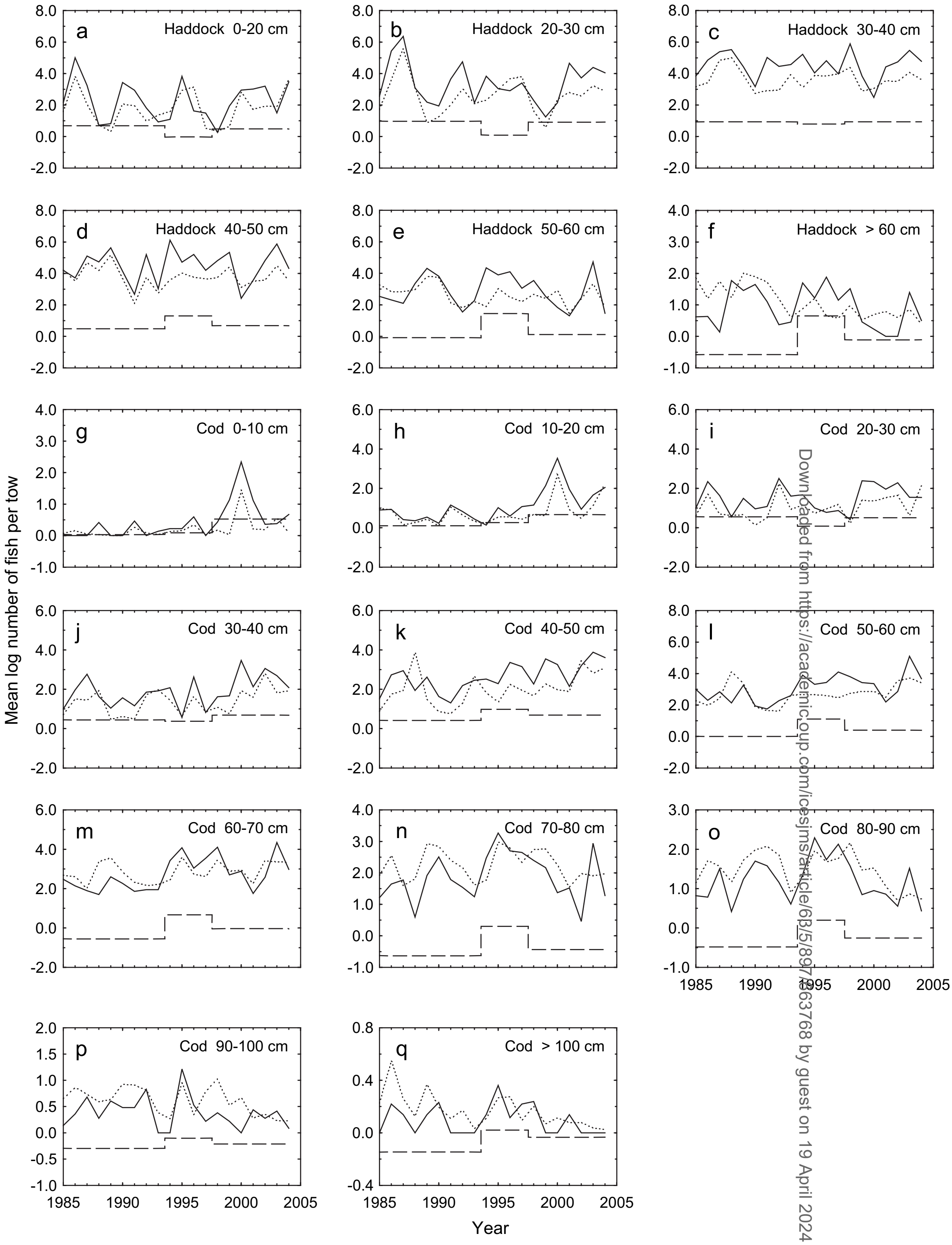

Figure 7. Interannual variability in the mean log number of haddock (a—f) and cod (g—q) per tow by size class in Breiddalsgrunn, in the protected area (solid line) and in the reference area (dotted line). The dashed line shows the mean difference between the two areas for the three selected periods: before and after the closure, and after the re-opening. Note the different scales on the y-axes.

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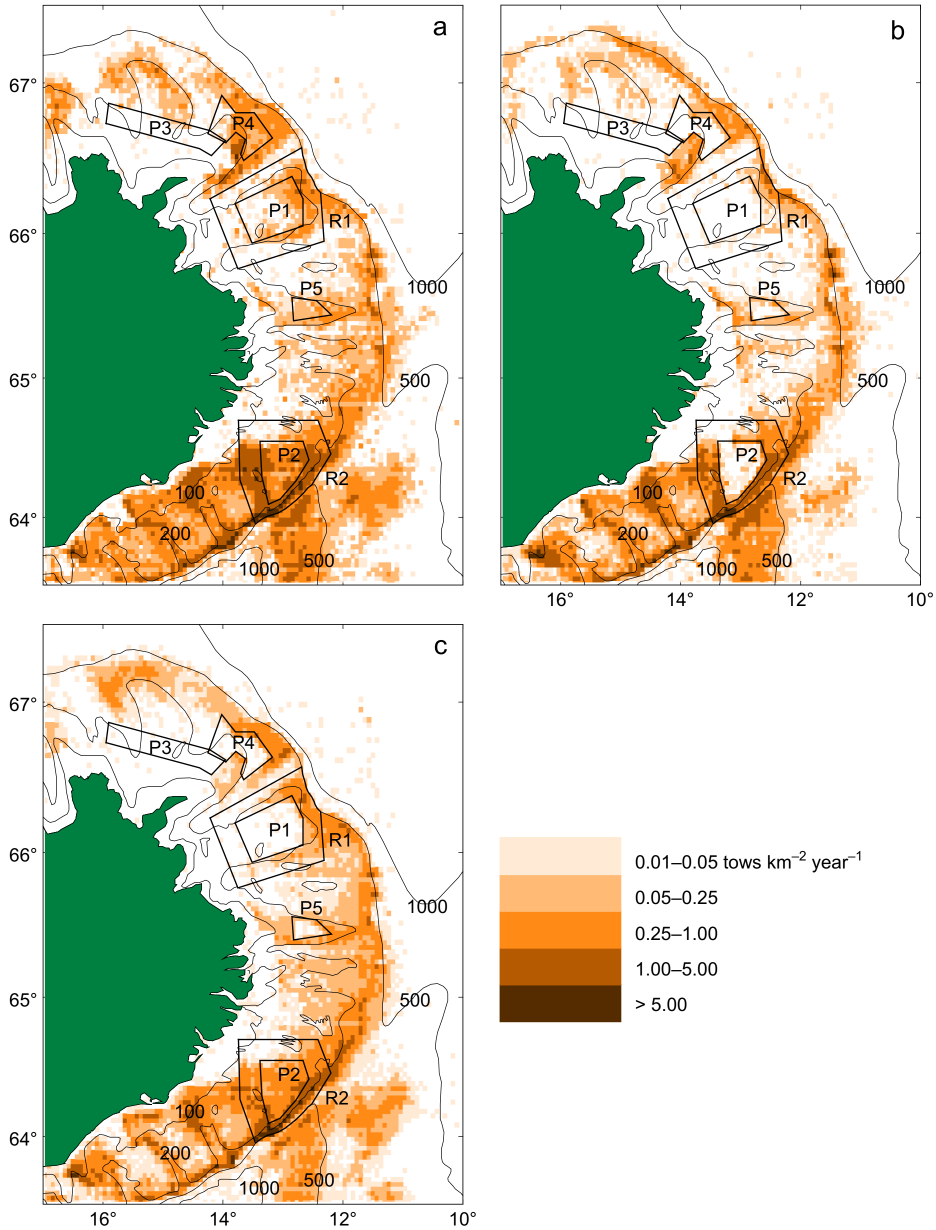

Figure 8. Distribution of otter trawl effort off the east coast of Iceland in three periods: (a) 1991–1993 (before the closure), (b) 1993–1997 (after the closure), and (c) 1997–2003 (continued closure in Digranesflak, and after the re-opening in Breiddalsgrunn). The spatial resolution is set to $2' \times 4'$.

shown by the trends in abundance across the size range and in the time-series. This effect may have been a consequence of greater predation by the then more abundant cod.

The example of Breiddalsgrunn demonstrates that the observed effects of area closure (particularly on the abundance and size structure of haddock and cod) were reversed by the re-opening of the area to fishing (within 7 years). We could not find any examples in the literature of reversed changes in fish communities following the re-opening of formerly closed areas. Ferraris *et al.* (2005) studied the impact of the removal of reserve status based on data from two surveys, towards the end of a total ban and 2 years after partial opening, but they made no reference to the pre-closure period.

The area closures appeared to have had no appreciable effect on species richness, diversity, or composition. The

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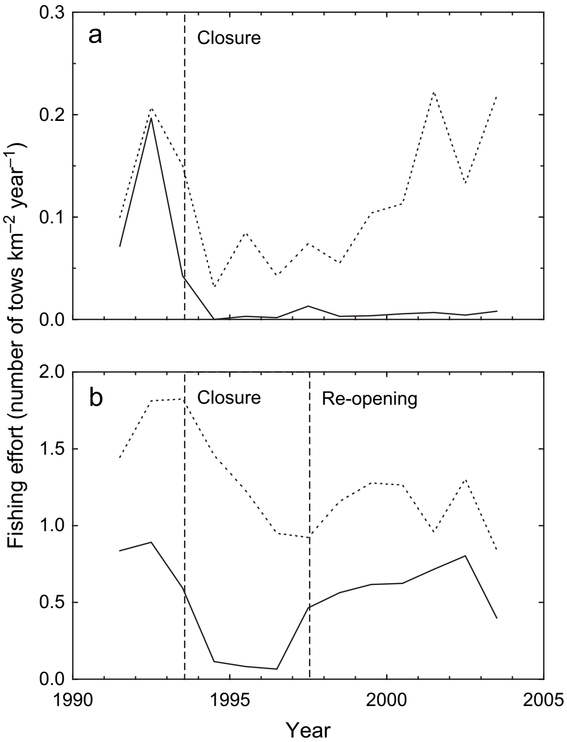

Figure 9. Otter trawl effort in (a) Digranesflak and (b) Breiddalsgrunn in the period 1991–2003, separately for the protected (solid line) and reference areas (dotted line). The vertical dashed lines show major changes in the status of the protected areas (see Table 1). Note the different scales on the *y*-axes.

observed overall increase in species richness over time (roughly by one species per tow) may have resulted from improved species identification rather than from real changes in the community. Regardless of the cause, the observed increase in species richness was the main effect of period, whereas the interaction between area and period appeared to have had no effect on the mean number of species present in the survey catch. Nevertheless, some species appeared to be affected by the closure, either benefiting or being adversely affected by it. Piet and Rijnsdorp (1998) also observed a general increase in species richness both within and outside the "plaice box" (higher outside), which they attributed to an influx of species from the south. Changes in the finfish community after implementation of a closure on the Scotian Shelf reported by Fisher and Frank (2002) were more apparent from multivariate analyses than from the comparison of univariate diversity measures before and after the closure. Those authors attributed the changes to shifts in the relative abundance of the component species, rather than to major shifts in species composition.

A number of factors in addition to changes in fishing effort may have played a role in the observed pattern of recovery, so need to be identified. The most likely ones are: (i) differences in habitat characteristics between protected and fished areas; (ii) length of recovery period (i.e. time for a population to rebuild); (iii) relocation pattern of fishing effort after the closure; and (iv) transfer of fish ("spill-over") from protected to fished areas.

To analyse the effect of area closures, we contrasted protected areas with adjacent reference areas. Ideally, the two areas should in each case be comparable in terms of habitat characteristics, but in the present study, this condition was only partly fulfilled. While the protected areas were on the continental shelf, the reference areas were generally deeper and located partly on the shelf edge, where temperature and bottom type may differ from those on the shelf. Nevertheless, the observed high densities of a number of species in the reference areas shows that the latter cannot be classified explicitly as marginal habitat. Frank *et al.* (2000) analysed trends in recruitment, survival, and distribution of haddock juveniles in ecologically similar control and impact areas. They tested (*t*-test) whether the mean difference between "control" and "impact" was different before and after the closure. The approach of Ferraris *et al.* (2005) accounted for habitat-related spatial variability; in their models, the habitat factor explained a substantial part of density variations. Piet and Rijnsdorp (1998) selected data for their analysis from a narrow range of depths and additionally included depth in their ANOVA model as a covariate. The depth range in the present study was greater. Including depth, temperature, and year in the model considerably reduced the unexplained variability and increased the power of the statistical tests, agreeing with the suggestions given by Ferraris *et al.* (2005) for modelling densities when testing the impact of area closures.

The time periods after the closure in the two studied areas differed in duration. In Digranesflak, initially there was no clear effect on the abundance of haddock in the period after the closure, but the effect became more apparent towards the end of the study period (after 5–9 years, depending on size class). In contrast, changes in Breiddalsgrunn could be observed within just 4 years of the closure. Effects of closure have frequently been detected within 5 years (in some cases even within 1–3 years) after the establishment of protected areas (Gell and Roberts, 2002). The fish populations in the present study should be considered as "slow response" species, for which, in general, longer study periods are required to detect any effects. The quick response to closure in Breiddalsgrunn may be explained by the high fish densities resulting from better habitat suitability in the area (a so-called "hot spot"; Jennings, 2001) relative to other areas. This, in turn, can be explained by the fact that Breiddalsgrunn (and the surrounding area) is located in one of the most productive of Icelandic marine regions (Astthorsson and Vilhjalmsson, 2002).

The main management objective of establishing protected areas off the east coast of Iceland was to protect cod 3–4 years old. It seems that this goal was met in Breiddalsgrunn, where a significant reduction in fishing effort benefited cod >40 cm. In Digranesflak, fishing effort was

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about 10 times lower than in Breiddalsgrunn, so no apparent effects of the closure on cod were observed. This suggests that a substantial reduction in fishing effort within a protected area is necessary to detect changes in a fish community. Similarly, when contrasting a protected area with an adjacent control area, it may not be possible to detect any changes unless the contrast in fishing pressure between the two areas is great.

The distribution of fishing effort was spatially similar over time, which under normal management reflects both the patchiness of fishing grounds and the availability of target species (Dinmore *et al.*, 2003). It was difficult to relate the observed changes in fishing effort, or its distribution, in the reference areas to changes in the status of the protected areas. For example, the overall reduction of fishing effort inside the closed areas after the closure was accompanied by some reduction in effort in the non-restricted areas, although the opposite could have been expected. This is most likely attributable to a 42% reduction in the national TAC of cod between 1992 and 1995 (Anon., 2005). Moreover, the fishing vessels showed no clear tendency to cluster along the borders of the closed areas. Such relocation of effort (sometimes called ‘‘fishing-the-line’’) is a typical response of fishing fleets to area closures (Rijnsdorp *et al.*, 2001) and has been explained by better catches in the boundary area, where spill-over effects first become apparent (Gell and Roberts, 2002).

In the present study, we frequently observed the same pattern of changes in the protected areas and the adjacent reference areas after the closure, the changes being more marked inside the protected areas. This could perhaps be attributed to a spill-over effect. It is likely that some transfer of fish between protected and fished areas takes place and will thus affect recovery. This transfer occurs through: (i) random movement, (ii) density-dependent movements, (iii) directed movements (migrations), and (iv) ontogenetic habitat shifts (Gell and Roberts, 2002). The transfer rate depends on many factors, some discussed by Jennings (2001). Gains in abundance are greater when transfer rates are low, so area closures are considered to be most effective for more sedentary species (Jennings, 2001; Hilborn *et al.*, 2004) and to provide, in general, little protection to highly migratory species, even in large areas (Stefansson and Rosenberg, 2005). Our results show that species with great mobility, such as cod and haddock, may benefit from area closures. Many species, such as cod (Hutchings, 1996) and other groundfish, show density-dependent habitat use. As abundance in the protected area increases, such species may emigrate from the protected area to surrounding fishing grounds, where intraspecific competition may be less and habitat more suitable (Shepherd and Litvak, 2004), slowing the apparent rate of recovery (Jennings, 2001). Knowing patterns of fish movement between protected and fished areas seems crucial in evaluation studies of protected areas. Such information can be derived from tagging experiments.

Besides data quality, distribution of sampling stations is of great importance in evaluation studies of marine protected areas. Our study was based on groundfish survey data that were not collected specifically for such studies. As a consequence, the sampling stations were not located as would have been most appropriate for our purpose. In Digranesflak, most stations in the reference area were located where the fishing effort by otter trawlers has been low during at least the past 13 years. This shortcoming is likely to have reduced the ability of the model used to detect potential effects of the closure in this area.

The present study shows that the fish community has been affected by the imposition of closed areas. However, such changes are generally difficult to detect and may be masked by a number of factors. Therefore, extensive and representative data are required to conduct effective evaluation of the impacts of closures on fish communities. Ideally, rigorous survey designs should be implemented before reserve establishment (Willis *et al.*, 2003). It is likely that more comprehensive studies of all important factors related to the fishery within a regulatory area (catch and effort data, other scientific data such as migrations, recruitment, growth rate, mortality, and feeding patterns) will be needed to provide better diagnostics of this management tool.

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