# Groundfish species diversity and assemblage structure in Icelandic waters during a period of rapid warming (1996-2007)

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**Research project for the degree of MSc (90 ECTS units)**
**Supervisor: Guðrún Marteinsdóttir**
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**UNIVERSITY OF ICELAND** FACULTY OF SCIENCE
DEPARTMENT OF BIOLOGY

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**September 2008**

# Fjölbreytileiki og samfélagsgerð botnfiska á Íslandsmiðum á árunum 1996-2007

**Lilja Stefánsdóttir**

I declare that this thesis is supported by my research work, written by myself ad has not as a part or as a whole been published before due to higher educational degree.

Hér með lýsi ég yfir að ritgerð þessi er byggð á mínum eigin athugunum, er samin af mér og að hún hafi hvorki að hluta né í heild verið lögð fram til hærri prófgráðu.

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Lilja Stefánsdóttir

Abstract

Elevated oceanic temperatures have been predicted to lead to a poleward shift in the latitudinal distribution ranges of fish species. Different responses of species to rising temperatures might lead to changes in  assemblage structure and local species richness. Changes in abundance and distribution due to oceanographic variability have been documented for several species in Icelandic waters. The aim of this study was to analyze spatial and temporal trends in diversity and assemblage structure of groundfish in Icelandic waters during a period of rapid warming, and to identify the effects of environmental factors on these trends.

The assemblage structure and diversity of groundfish in Icelandic waters was examined using data from the annual autumn (October) groundfish survey conducted by the Marine Research Institute (MRI) in Iceland in 1996-2007. The survey is a stratified systematic survey where the same stations are repeated annually. We used hierarchical cluster analysis (HCA) to define assemblages in two time periods and canonical correspondence analysis (CCA) to explore the relationships between the assemblages and temperature, depth, latitude, longitude and year. We further used two estimates of diversity, species richness and the Shannon index. Relationships between diversity and depth, temperature, primary production, location and year, were examined using generalized additive models (GAMs).

Four major species assemblages were identified; those with deep-southwest, deep-north, shelf-south and shelf-widespread distributions. Assemblages in the hydrographically stable deep waters north of the country were consistent between periods, whereas species living in the more variable shallow waters underwent a change in assemblage structure during 1996-2007. For this period of generally increasing sea temperature, the CCA also revealed a shift towards species

representative of warmer temperatures. Diversity was shown to be highly variable both temporally and spatially, and also to vary with depth and temperature. Species richness increased with temperature and time southwest of the country, but decreased northeast of the country. In some areas where species richness was high, Shannon index was low. This suggests that although these areas contain numerous species, just a small number of those are in high abundance, while the rest are represented by relatively few individuals.

# Ágrip

Hlýnandi loftslag undanfarinna ára hefur valdið breytingum á útbreiðslu fiskitegunda á norðurhveli jarðar. Ólík svörun tegunda við hækkandi hita getur leitt til breytinga á samfélagsgerð og staðbundnum tegundafjölda. Í kjölfar breytinga á sjávarhita hafa verið skráðar breytingar á stofnstærð og útbreiðslu nokkurra fiskitegunda á Íslandsmiðum. Markmið þessarar rannsóknar voru að kanna breytingar á útbreiðslu, fjölbreytileika og samfélagsgerð botnfiska á Íslandsmiðum á hlýnunarskeiði og hvaða umhverfisþættir ráða þeim.

Í rannsókninni voru notuð gögn Hafrannsóknastofnunarinnar úr árlegum (1996-2007) stofnmælingum botnfiska að hausti (október). Í stofnmælingunni eru sömu stöðvar endurteknar ár hvert. Klasagreining (hierarchical cluster analysis) var notuð til að skilgreina samfélög fiska á tveimur tímabilum og fjölþáttagreiningin CCA (canonical correspondence analysis) til að kanna tengsl milli samfélaga og hitastigs, dýpis, breiddar- og lengdargráðu og ára. Einnig voru notaðir tveir fjölbreytileikastuðlar; fjöldi tegunda og Shannon index. Tengsl fjölbreytileika og hitastigs, dýpis, frumframleiðslu, staðsetningar og ára voru könnuð með GAM líkönum (generalized additive models).

Fjögur meginsamfélög með útbreiðslu í suðvestur-djúpi, norður-djúpi, suður landgrunni og með víða útbreiðslu á landgrunni voru greind með klasagreiningu. Samfélög í köldum sjó djúpt norður af landinu voru óbreytt á rannsóknartímanum, en samfélagsgerð tegunda í breytilegri hlýsjó yfir landgrunninu sýndu meiri breytingar á sama tímabili. Fjölþáttagreining sýndi líka fram á aukið vægi hlýsjávartegunda á þessu hlýnunarskeiði. Í ljós kom að fjölbreytileiki var mismunandi eftir árum og staðsetningu, auk þess sem hann breyttist með dýpi og hitastigi. Tegundafjöldi jókst með hitastigi og tíma suður og vestur af landinu, en minnkaði fyrir norðan og austan

land. Á sumum svæðum þar sem fjöldi tegunda var mikill var Shannon index lágur.

Þetta gefur til kynna að þrátt fyrir að margar tegundir séu á þessum svæðum, þá er

einstaklingsfjöldi flestra þeirra lítill.

## Acknowledgments

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# Distribution of fish assemblages in Icelandic waters in relation to environmental factors in the years 1996-2007

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Abstract

Elevated oceanic temperatures have been predicted to lead to a poleward shift in the
latitudinal ranges of fish species. Different responses by individual species to
changes in water temperature may disrupt assemblage structure. The assemblage
structure of groundfish in Icelandic waters was examined for a period of rapid
warming (1996-2007) using autumn survey data. We used hierarchical cluster
analysis (HCA) to define assemblages in two time periods and canonical
correspondence analysis (CCA) to explore the relationships between the assemblages
and temperature, depth, latitude, longitude and year. Four major species assemblages
were identified; those with deep-southwest, deep-north, shelf-south and shelf-
widespread distributions. Assemblages in the hydrographically stable deep waters
north of the country were consistent between periods, whereas species living in the
more variable shallow waters underwent a change in assemblage structure during
1996-2007. For this period of generally increasing sea temperature, the CCA also
revealed a shift towards species representative of warmer temperatures. Depth was
the single environmental factor that had greatest effects on assemblage structure in
the CCA. Changes in groundfish assemblage structure were observed for both
exploited and unexploited species.

## Introduction

Temperature affects the distribution, abundance and survival of fish species through its influence on life history traits such as behavior, growth and reproduction (Attrill and Power 2002, Roessig *et al.* 2004, Perry *et al.* 2005, Pörtner and Knust 2007). Concurrent with the recent warming of the climate system (Levitus *et al.* 2002, Salinger 2005), ocean temperatures have been rising worldwide (IPCC 2007). Elevated oceanic temperatures have been predicted to lead to a poleward shift in the latitudinal ranges of fish species (Parmesan and Yohe 2003). Species have also shown shifts in depth distribution, probably to exploit the colder water at greater depths (Perry *et al.* 2005, Dulvy *et al.* 2008). Different responses by individual species to changes in water temperature may alter community structure and disrupt species interactions (Walther *et al.* 2002, Pörtner and Knust 2007).

A study from the U.S. Pacific coast suggests that exploited fish species have shown a more distinct distributional shift in response to environmental change than unexploited species (Hsieh *et al.* 2008). In the North Atlantic Ocean, warming-related changes in geographic ranges have occurred in both commercially exploited species and species that are not targeted by fisheries (Brander *et al.* 2003). In general, temperate species have increased in abundance and expanded their distributions northward, while cold-water species have been more stable or have decreased in abundance (Brander *et al.* 2003, Parmesan and Yohe 2003, Perry *et al.* 2005).

The distributional limits of many North Atlantic fish species occur within the waters around Iceland (Björnsson and Pálsson 2004, Ástþórsson *et al.* 2007). These waters are influenced by relatively warm and saline Atlantic water that predominates in the southwest and cold water masses of lower salinity in the northeast. Frontal

regions are formed where these water masses meet (Malmberg and Valdimarsson 2003). The location of these fronts varies from year to year due to variable inflow of Atlantic water. The hydrography of the waters over the continental shelf north of Iceland is also highly variable due to changes in the relative influence of Atlantic, Arctic and Polar water masses (Malmberg and Valdimarsson 2003, Jónsson and Valdimarsson 2005). Since 1999, inflow of warm Atlantic water has been noted farther north and east of Iceland, compared to the preceding years, resulting in higher bottom temperatures (Anon. 2008). Although the hydrography of the shelf areas in the south and west are more stable, sea temperature and salinity have been rising during the period 1996-2007 (Anon. 2008).

Changes in abundance and distribution due to oceanographic variability have been documented for several species inhabiting Icelandic waters. Associated with a warm period in the late 1920s and the 1930s, feeding and spawning grounds of cod (*Gadus morhua*) and herring (*Clupea harengus*) increased in size and extended to the north and east of Iceland (Vilhjálmsson 1997). Numerous species that had previously been rare or absent in Icelandic waters also became more common (Vilhjálmsson 1997). During a cold period in the 1960s, the Atlanto-Scandian herring stock disappeared from Icelandic waters (Jakobsson and Östvedt 1999). The Icelandic cod stock was also in low abundance during that period, although that was due to the combined effects of environmental change and overexploitation (Vilhjálmsson 1997). In recent years, changes in distribution coinciding with rising sea temperatures have been noted for a number of fish species in Icelandic waters. In general, warm-water species have increased in abundance and the distribution of cold-water species has shifted farther north (Vilhjálmsson 1997, Björnsson and Jónsson 2004, Björnsson and Pálsson 2004, Ástþórsson *et al.* 2007, Sólmundsson *et*

*al.* 2007). Recent shifts in the distribution of Icelandic summer spawning herring have also been related to the warming (Guðmundsdóttir and Sigurðsson 2004).

The main objective of this study was to describe changes in distribution and composition of groundfish communities in Icelandic waters, in relation to environmental parameters. Previous studies have been mainly based on commercially exploited fish species and so less is known about responses of unexploited species or fish communities to environmental fluctuations. By studying a single commercial species, the potential effects of environmental change may be masked by the effects of fishing, whereas by analyzing the fish community as a whole, these effects may become more evident.

## Materials and methods

**Data**

Data on fish assemblages and distribution were obtained from the annual (1996-2007) autumn (October) groundfish survey conducted by the Marine Research Institute (MRI), Iceland. The survey is a stratified systematic survey where the same stations are repeated annually (Björnsson *et al.* 2007), and standardized fishing methods are employed i.e. tows are taken with a bottom trawl at 3.8 knots for 3 nautical miles. The stations are situated across the Icelandic continental shelf and part of the continental slope, at depths from 20 to 1500 m. Data collected during the survey are therefore representative of most groundfish habitats in Icelandic waters. At each station, all fish species were identified, counted and total length was measured. In addition, geographic location, depth, and in most cases bottom temperature, were recorded. Most pelagic and semi-pelagic species were included in the analyses, although in some cases they may not have been sampled effectively by bottom-trawling. Capelin (*Mallotus villosus*) were excluded due to inconsistent sampling through the study period. Lanternfishes (*Myctophidae*) were also excluded due to uncertainty in species identification. Barracudinas (*Paralepididae*) were combined at the family level.

**Cluster analysis**

Hierarchical cluster analysis (HCA) was used to define species assemblages. In order to investigate the influence of rising sea temperatures and increased inflow of Atlantic water during the study period, HCA was performed for two separate time periods, 1996-1998 and 1999-2007. Only those stations that were sampled at least 10 times in the 12 year period were included, resulting in a total of 308 stations (Fig. 1).
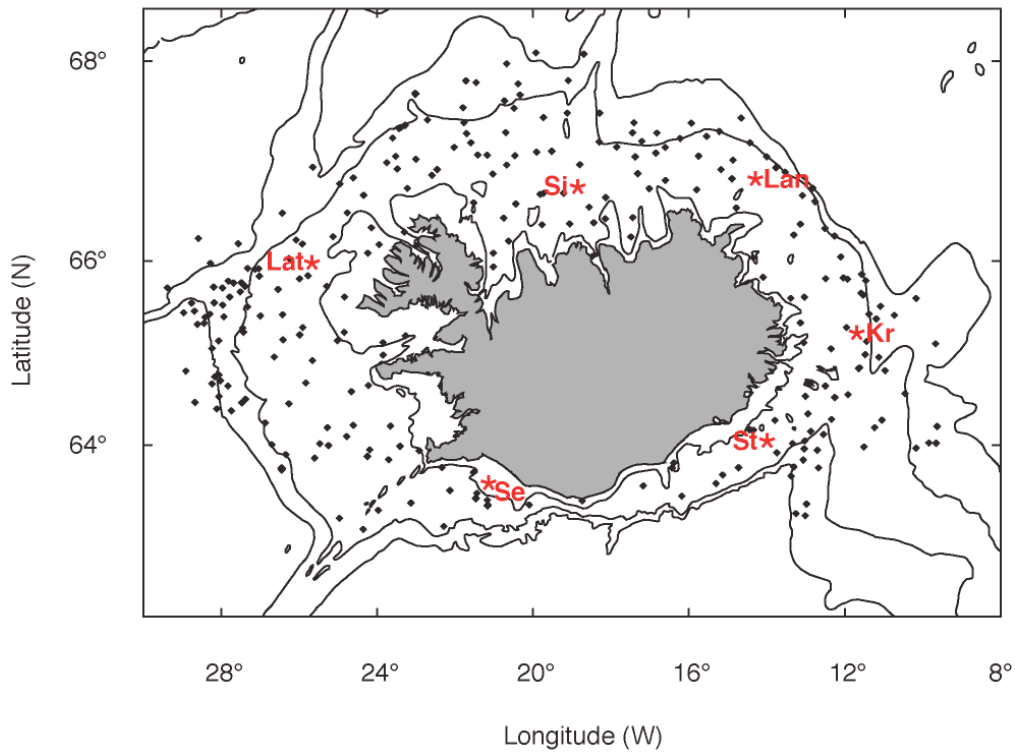
Fig. 1. Distribution of sampling stations in the autumn groundfish survey used in the study. Depth contours for 100, 500 and 1000 m are shown. Also shown are locations of stations for temperature measurements: St=Stokksnes, Se=Selvogsbanki, Lat=Látrabjarg, Si=Siglunes, Lan=Langanes, Kr=Krossanes (See Fig. 4).

HCA was based on a Bray-Curtis dissimilarity matrix and Ward's method was chosen to minimize the variance within clusters. For each time period, all species that were represented by on average >500 individuals per year, or >5% of the sum of individuals in the stations they were present at were included in the analyses. All species that were represented by on average <10 individuals per year were excluded.

## CCA

Canonical correspondence analysis (CCA) (ter Braak 1986, ter Braak and Verdonschot 1995) was used to identify species assemblages and their relationships with environmental variables. CCA is a constrained ordination technique that can be used to provide a simultaneous ordination of species, sites and environmental variables. With this technique, ordination axes are constrained to be linear

combinations of the environmental variables used in the analysis.

Species included in the CCA were chosen with the same criteria as HCA. The (continuous) environmental variables included in the CCA were location (latitude and longitude), depth and bottom temperature, while the categorical variable year was entered as a dummy variable (Legendre and Legendre 1998). All data from 1999 were excluded due to missing temperature measurements. Only stations that had complete environmental data for at least 9 of the 11 years were included, resulting in a total of 264 stations.

A forward stepwise selection procedure (ter Braak and Verdonschot 1995) was used to select and rank the important explanatory variables using permutation tests, with the variables entered into the model in the order: depth, latitude, temperature, longitude and year. All variables significantly contributed to the amount of variation (inertia) explained in a partial CCA and were therefore included in the final model.

The results of the CCA are presented in the form of an ordination diagram containing points for species categories, indicating their optimal distribution, and the continuous explanatory variables (latitude, longitude, depth and bottom temperature) plotted as arrows pointing in the direction of the most rapid change. The length of a vector is proportional to the correlation between ordination and the given explanatory variable (ter Braak 1986). The categorical variable 'year' is represented by centroids of the samples belonging to each category.

Abundance data were $\log_e(x+1)$ transformed prior to CCA and HCA in order to reduce the effects of dominant species. CCA and HCA were performed using the Community Ecology Package "vegan" in R (Oksanen 2005).

Results

**Cluster analysis**

A total of 69 and 76 species in 1996-1998 and 1999-2007 respectively, were included in the HCA of the species abundance data (Appendix 1). Four clusters were identified in both time periods (Fig. 2). In general, the species featuring in each of the four clusters were derived from i) deep areas southwest of Iceland (DSW), ii) deep areas in the north (DN), iii) shelf areas in the south (SS) and iv) species having a widespread-shelf (WS) distribution (Appendix 1).

In both time periods, the DSW assemblage was separated as a distinct group from the remaining species at a higher level of dissimilarity (Fig. 2). It included species living in the relatively warm waters west, southwest and south of Iceland, i.e. grenadier species, North Atlantic codling, Baird's smooth head, black scabbardfish, spiny eel, black dogfish, great lanternshark and some less common deep-water species (see Appendix 1 for latin species names). Five additional species were included in this assemblage during the 1999-2007 period. These were doitre blacksmelt, Bean's sawtoothed eel, longnose velvet dogfish, slender codling and spearnose chimaera.

The DN assemblage was very stable through the study period. It consisted of two subgroups with distributions at different depths. The deeper subgroup included Greenland halibut, Arctic sculpin, Atlantic poacher, sea tadpole and various eelpout species. The shallower subgroup included spotted wolffish, thorny skate, lumpsucker, Atlantic hookear sculpin and moustache sculpin.

The SS and WS assemblages were inconsistent between the two time periods. The WS assemblage included important commercial species such as cod, haddock, herring, golden redfish, blue whiting and wolffish, as well as long rough dab,
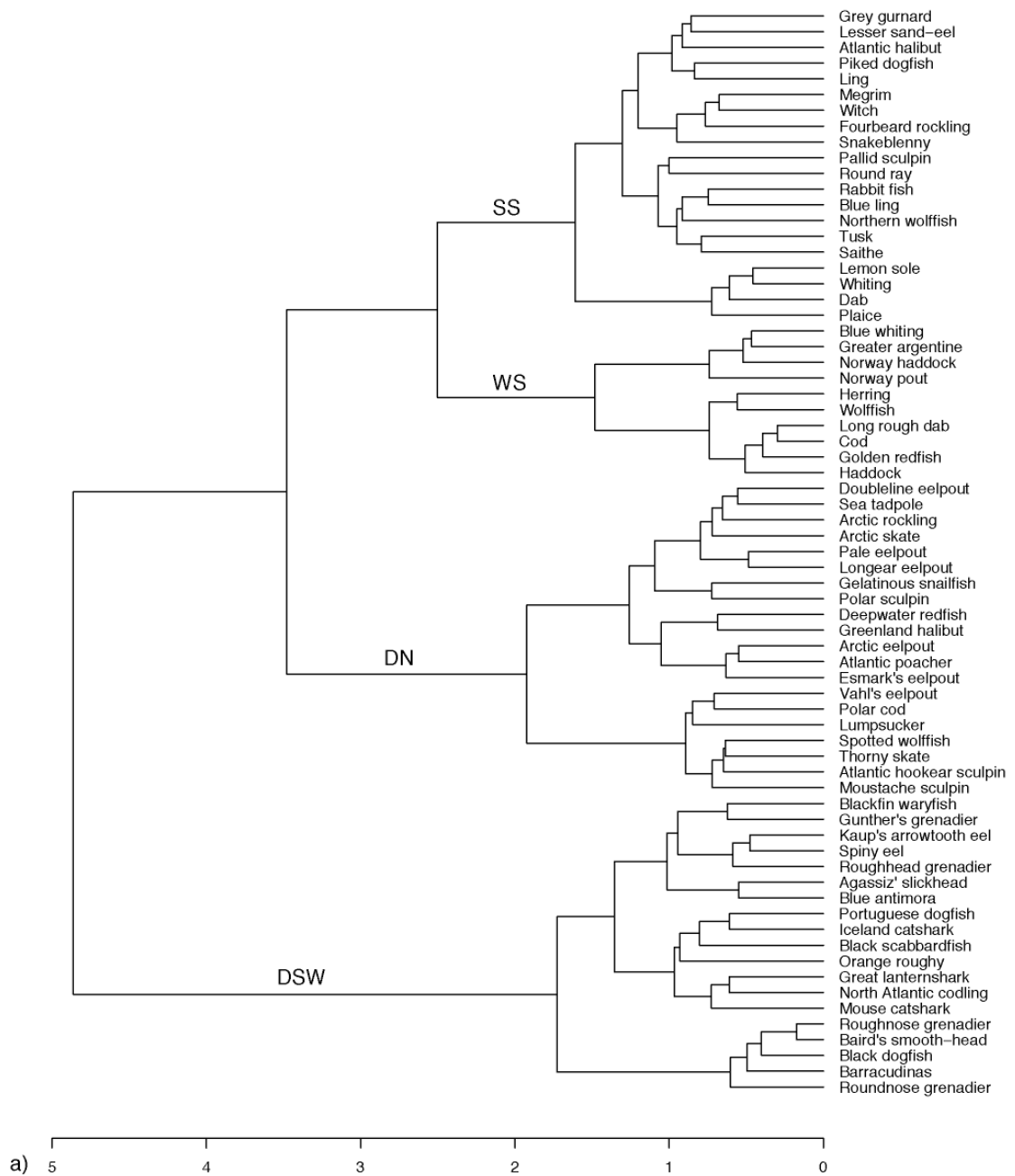
Fig 2. Hierarchical cluster analysis of species abundances (based on Spearman rank correlation matrix and Ward's method) for a) 1996-1998 and b) 1999-2007. Abundance data were $\log_e(x+1)$ transformed prior to analysis. See appendix 1 for Latin species names.

Norway pout, Norway haddock and greater argentine. The majority of these species are found in relatively high abundance across the Icelandic continental shelf.

The SS assemblage included species living in relatively shallow waters or near the slope areas southwest, south and southeast of the country, i.e. tusk, witch, grey gurnard, rabbit fish and some other less common species. In the later time period,

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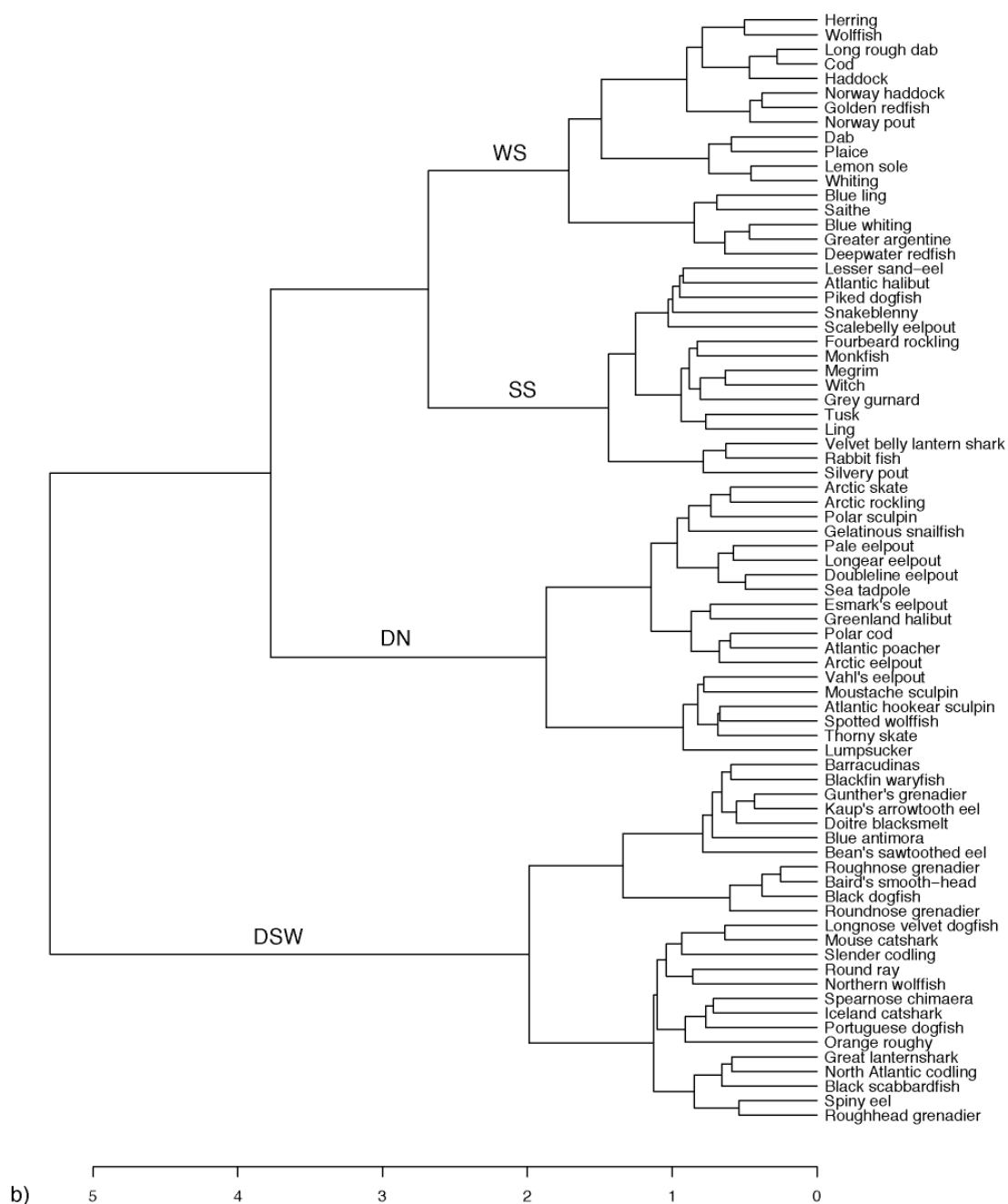
Fig 2. *(continued)*

this assemblage included some southerly species that had gradually become more common, e.g. monkfish, velvet belly lantern shark and silvery pout.

Some species consistently clustered together at low dissimilarities, but were found as parts of different assemblages in the two time periods. As an example, whiting, lemon sole, plaice and dab formed a group that belonged to the SS

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assemblage in 1996-1998 but the WS assemblage in 1999-2007. This shift from the SS to the WS assemblage was also observed for saithe and blue ling.

According to the cluster analysis, northern wolffish and round ray moved from the SS assemblage in the earlier time period to the DSW assemblage in the later time period. Deepwater redfish was clustered within the DN assemblage in 1996-1998 but with the WS assemblage in 1999-2007.

**CCA**

A total of 69 species were included in the CCA. The CCA ordination explained 26% of the total variation in the abundance data and the first two canonical (constrained) axes accounted for 87% of the constrained variation.

The same assemblages as in the HCA could be identified in the CCA diagram (Fig. 3). Fish assemblage structure was most significantly affected by depth. A group of species positively correlated with the depth and longitude axes was almost identical to the DSW assemblage in the cluster analysis. Another group that was positively correlated with the depth and latitude axes, and negatively correlated with the temperature axis, consisted of the same species as the DN assemblage. Species belonging to the WS assemblage in the HCA were scattered around the center of the CCA diagram. Their distribution was situated at the center of the range of the environmental factors. The shallower group of the DN assemblage (spotted wolffish, moustache sculpin, lumpsucker and Vahl's eelpout) was situated more closely to the WS assemblage than indicated by the HCA. The SS and WS assemblages overlapped somewhat in the CCA, and included those species which moved from the SS to the WS assemblage in the HCA. Species which moved from the SS to the DSW assemblage in the cluster analysis (round ray and northern wolffish) were located

Fig. 3. CCA ordination diagrams for 69 species in the autumn groundfish survey. The arrows indicate the explanatory variables (latitude °N, longitude °W, depth m, and bottom temperature °C), with the arrowheads indicating the increase in gradient. Years represent centroids for that categorical variable. Data points indicate scores of species categories in ordination space.

between the DSW and SS/WS assemblages in the CCA diagram.

There was a gradual movement of 'year' centroids towards higher temperatures during the first years of the study, i.e. associated with a general increase in temperature during 1996–2003, whereas since 2004 temperatures have been relatively high and stable. 'Year' centroids also moved towards warm-water species belonging to the WS and SS assemblages, many of whose relative abundance has been increasing with rising sea temperature.

Discussion

A clear groundfish assemblage structure was observed in the study. In the cluster analysis, four major assemblages were identified, separating species with deep-southwest (DSW), deep-north (DN), south-shelf (SS) and widespread-shelf (WS) distributions. Assemblages in the hydrographically stable deep waters north of Iceland were consistent between periods, whereas species living in the more variable shallow waters have shown a change in assemblage structure between 1996 and 2007. Furthermore, a greater number of southerly species were included in the SS and DSW assemblages in the later time period. In previous similar studies, the overall pattern has been consistency through time (Overholtz and Tyler 1985, Gabriel 1992, Gomes *et al.* 1992, Fossheim *et al.* 2006), although some changes were found due to e.g. environmental change or fisheries.

For this period of generally increasing sea temperature (see Fig. 4), the CCA also revealed a shift towards species representative of warmer temperatures. Conversely, there has not been a noticeable increase in temperature in deep waters at the Siglunes section north of Iceland (Fig. 4), which may explain the observed stability in the DN assemblage. The survey data used in these analyses have the advantage of good spatial and depth coverage, but the survey was initiated in 1996 and so data are lacking for the period prior to the recent warming. Despite this, many changes in groundfish assemblage structure were observed during the study period.

In the cluster analysis, whiting, lemon sole, plaice and dab moved from the SS assemblage to the WS assemblage in the later time period. Whiting and lemon sole have extended their distribution on the Icelandic shelf (Valdimarsson *et al.* 2005, Björnsson *et al.* 2007) and thus probably benefited from the increased inflow of warm Atlantic water. On the other hand, dab and plaice have decreased in abundance
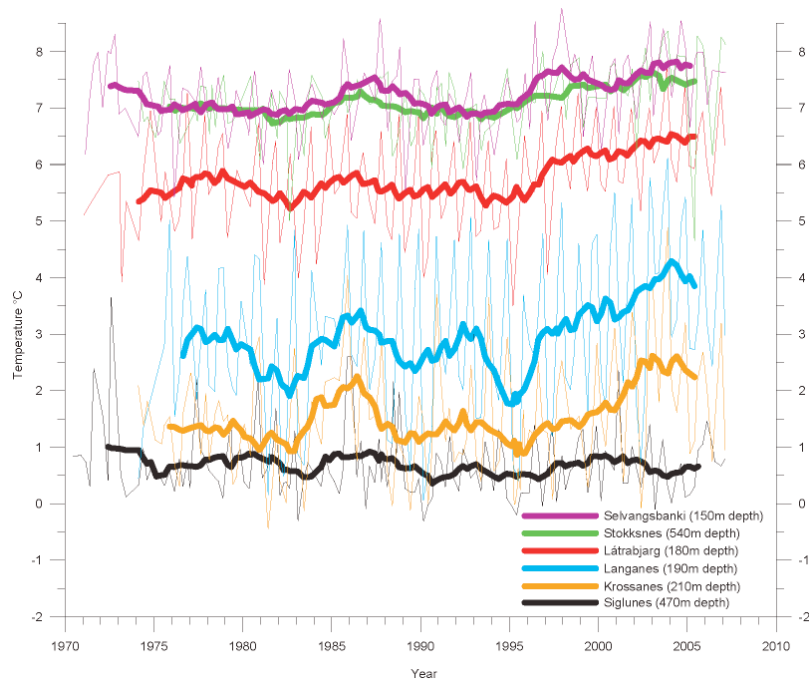
Fig. 4. Near-bottom temperature measurements at selected stations on the Icelandic shelf (see Fig. 1 for location of stations). Average for 50-100m depth interval above bottom (thin lines) and approximately 3 year running mean (thick lines). Figure from Anon. 2007.

on the Icelandic shelf, especially south of the country (Björnsson *et al.* 2007), which may explain this assemblage shift.

Five more species were included in the DSW assemblage in the warmer time period, all living at the northern border of their distribution ranges in Icelandic waters (Jónsson and Pálsson 2006). However, this does not necessarily indicate that those species were not present between 1996 and 1998, but rather that they were not present in high enough abundance to be included in the analyses due to the selection method used. Monkfish is an example of a species living in Icelandic waters at the northern boundary of its distribution range, and changes in its distribution have been recently documented. The stock size has increased and the species has extended its spatial distribution along the continental shelf west of Iceland, to the northwest and north (Sólmundsson *et al.* 2007). Pelagic monkfish larvae might disperse from monkfish spawning areas at the Rockall Plateau and northwest of the Hebrides to

Iceland (Hislop *et al.* 2001), so any increase in abundance of monkfish in Icelandic waters might be due to increased inflow of Atlantic water from that area (Hátún *et al.* 2005), rather than resulting from higher temperatures alone. This might be true for other species as well. Haddock and saithe are other examples of commercial species in Icelandic waters that have shown extensions in their distributional range and increased abundance during the recent warming (Valdimarsson *et al.* 2005). For saithe, this was observed as a shift from the SS assemblage to the WS assemblage. It should be noted that saithe has a patchy distribution all around the country and occasional large hauls could have notable effects on the assemblage which it clusters with (Björnsson *et al.* 2007). Deepwater redfish was clustered within the DN assemblage in the earlier period, but with the WS assemblage in the later period. These results should be interpreted with caution since the stations used in the analysis did not cover the main distributional range of this species in Icelandic waters.

Depth was the single environmental factor that had the greatest effect on assemblage structure in the CCA. In many studies on groundfish assemblage structure, depth has been an important structuring environmental factor (Overholtz and Tyler 1985, Gabriel 1992, Gomes *et al.* 1992, Francis *et al.* 2002, Magnussen 2002). This may be seen simply as assemblage boundaries following depth contours or by using ordination methods such as CCA. Fossheim *et al.* (2006) used CCA to examine fish assemblage structure in the Barents Sea and found temperature to be the most important structuring environmental factor. The study covered a narrower depth range than the present study, so less depth structure should be expected. Depth might also serve as a proxy for other factors such as temperature, light, pressure and bottom type.

This study reflects assemblage structure in the autumn only. Different factors might influence assemblage structure in other seasons and many species exploit different water masses at different times of the year. For example, cod generally spawn in relatively warm waters south and west of Iceland in spring and migrate to feeding grounds in colder waters north and east of the country later in the year (Jónsson 1996). Many species also show ontogenetic shifts in distribution, meaning that different life history stages could cluster within different assemblages. For example, juvenile cod tend to remain in cold waters north and northeast of Iceland, while adults move into deeper and warmer water (Sæmundsson 2005). Differences in year class strength could therefore have an effect on what assemblage the given species clusters with. It should be noted that this study cannot determine whether the assemblages represent species that interact with each other as a whole, or just a group of spatially and temporally co-occurring species. Some species interactions are well known, such as trophic interactions. As an example, Greenland halibut in Icelandic waters feed mainly on capelin and eelpouts, as well as some invertebrates (Sólmundsson 2007). Capelin was not included in this study, but Greenland halibut and eelpout species clustered within the same DN assemblage.

Fishing, although not included as an explanatory factor in the present study, is likely to affect community structure (Overholtz and Tyler 1985, Gabriel 1992). In this study, temporal changes in groundfish assemblage structure were observed for exploited, as well as unexploited species. A comparison of fished and non-fished areas east of Iceland indicated that fishing affects the abundance of some groundfish species, as well as body size of individuals (Jaworski *et al.* 2006). Many areas of the Icelandic continental shelf are heavily fished, with highest demersal fishing activity occurring off the south, southwest and northwest coasts (Ragnarsson and

Steingrímsson 2003). Any changes in assemblage structure are therefore likely to be due to the combined effects of environmental factors and fishing. The areas exposed to lowest relative fishing effort, i.e. north of the country and in deeper water, are generally also the areas with the most stable temperatures. This might make it difficult to distinguish between effects of environmental change and fishing on groundfish assemblages in Icelandic waters.

In conclusion, by applying hierarchical cluster analysis and canonical correspondence analysis to autumn groundfish survey data, we were able to distinguish four species assemblages in Icelandic waters. These assemblages were mostly related to depth. Most notably, during a period of generally increasing sea temperature a shift toward species representative of warmer temperatures was observed. This suggests that if warming continues, it will likely lead to further changes in the composition, abundance and distribution of fish species within Icelandic waters. Given the additional pressure of fishing activity on many species in Icelandic waters, continued monitoring and future management action will be necessary.

References:

Anon. (2007). Þættir úr vistfræði sjávar 2006 / Environmental conditions in Icelandic waters 2006. Hafrannsóknastofnunin Fjölrit 130.

Anon. (2008). Þættir úr vistfræði sjávar 2007 / Environmental conditions in Icelandic waters 2007. Hafrannsóknastofnunin Fjölrit 139.

Ástþórsson ÓS, Gíslason Á, Jónsson S. (2007). Climate variability and the Icelandic marine ecosystem. Deep-Sea Research II 54,2456-2477.

Attrill MJ, Power M. (2002). Climatic influence on a marine fish assemblage. Nature 417,275-278.

Björnsson H, Jónsson E. (2004). Estimation of hidden mortality of Icelandic haddock caused by fisheries. ICES CM FF:24.

Björnsson H, Pálsson ÓK. (2004). Distribution patterns and dynamics of fish stocks under recent climate change in Icelandic waters. ICES CM K:30.

Björnsson H, Sólmundsson J, Kristinsson K, Steinarsson BÆ, Hjörleifsson E, Jónsson E, Pálsson J, Pálsson ÓK, Bogason V. (2007). Stofnmæling botnfiska á Íslandsmiðum (SMB) 1985-2006 og Stofnmæling botnfiska að haustlagi (SMH) 1996-2006 / The Icelandic groundfish surveys in March 1985-2006 and in October 1996-2006. Hafrannsóknastofnunin Fjölrit 131 *(in Icelandic)*.

Brander K, Blom G, Borges MF, Erzini K, Henderson G, MacKenzie BR, Mendes H, Ribeiro J, Santos AMP, Toresen R. (2003). Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? ICES Marine Science Symposia 219,261-270.

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology 45,1029 - 1039.

Fossheim M, Nilssen EM, Aschan M. (2006). Fish assemblages in the Barents Sea. Marine Biology Research 2.

Francis MP, Hurst RJ, McArdle BH, Bagley NW, Anderson OF. (2002). New Zealand demersal fish assemblages. Environmental Biology of Fishes 65,215-234.

Gabriel WL. (1992). Persistance of Demersal Fish Assemblages Between Cape Hatteras and Nova Scotia, Northwest Atlantic. J. Northw. Atl. Fish. Sci. 14.

Gomes MC, Haedrich RL, Rice JC. (1992). Biogeography of Groundfish Assemblages on the Grand Bank. J. Northw. Atl. Fish. Sci. 14,13-27.

Guðmundsdóttir A, Sigurðsson T. (2004). Veiðar og úrbreiðsla íslensku sumargotssíldarinnar að haust-og vetrarlagi árin 1978-2003 (The autumn and winter fishery and distribution of the Icelandic summer spawning herring during 1978-2003). Hafrannsóknastofnunin Fjölrit 104.

Hátún H, Sando AB, Drange H, Hansen B, Valdimarsson H. (2005). Influence of the Atlantic Subpolar Gyre on the Thermohaline Circulation. Science 309,1841-1844.

Hiddink JG, ter Hofstede R. (2008). Climate induced increases in species richness of marine fishes. Global Change Biology 14,453-460.

Hislop JR, Gallego A, Heath MR, Kennedy FM, Reeves SA, Wright PJ. (2001). A synthesis of the early life history of the anglerfish, Lophius piscatorius (Linnaeus, 1758) in northern British waters. ICES Journal of Marine Science 58,70-86.

Hsieh C, Reiss CS, Hewitt RP, Sugihara G. (2008). Spatial analysis shows that fishing enhances the climate sensitivity of marine fishes. Can. J. Fish. Aquat. Sci. 65,947-961.

IPCC (2007). Climate change 2007; Fourth Assessment Report. Cambridge Univ. Press, Cambridge, UK.

Jakobsson J, Östvedt OJ. (1999). A review of joint investigations on the distribution of herring in the Norwegian and Icelandic Seas 1950-1970. Rit Fiskideildar 16,209-238.

Jaworski A, Sólmundsson J, Ragnarsson SÁ. (2006). The effect of area closure on the demersal fish community off the east coast of Iceland. ICES Journal of Marine Science 63,897-911.

Jónsson G, Pálsson J. (2006). Íslenskir fiskar. (Vaka-Helgafell, Reyjavik).

Jónsson J. (1996). Tagging of cod (*Gadus morhua*) in Icelandic waters 1948-1986. Rit Fiskideildar 14, 5-82.

Jónsson S, Valdimarsson H. (2005). Recent developments in oceanographic research in Icelandic waters. In Iceland - Modern processes and past environments. Caseldine C, Russell A, Harðardóttir J, Knudsen O, eds. (Elsevier, Amst.). pp 79-92.

Legendre P, Legendre L. (1998). Numerical ecology, 2nd English edn. (Elsevier Science, Amsterdam).

Levitus S, Antonov JI, Boyer TP, Stephens C. (2000). Warming of the World Ocean. Science 287,2225-2229.

Magnussen, E. (2002). Demersal fish assemblages of Faroe Bank: species composition, distribution, biomass spectrum and diversity. Mar Eol Prog Ser 238, 211-225.

Malmberg S-A, Valdimarsson H. (2003). Hydrographic conditions in Icelandic waters, 1990-1999. ICES Marine Science Symposia 219,50-60.

Oksanen J. (2005). Multivariate Analysis of Ecological Communities in R: vegan tutorial.

Overholtz WJ, Tyler AV. (1985). Long-term responses of the demersal fish assemblages of Georges Bank. Fishery bulletin 83,507-520.

Parmesan C, Yohe G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421,37-42.

Perry AL, Low PJ, Ellis JR, Reynolds, J.D. (2005). Climate change and distribution shifts in marine fishes. Science 308,1912-1915.

Pörtner HO, Knust R. (2007). Climate change affects marine fishes through the oxygen limitation to thermal tolerance. Science 315,95-97.

Ragnarsson SÁ, Steingrímsson SA. (2003). Spatial distribution of otter trawl effort in Icelandic waters: comparison of measures of effort and implications for bentic community effects of trawling activities. ICES Journal of Marine Science 60,1200-1215.

Roessig JM, Woodley CM, Cech JJJ, Hansen LJ. (2004). Effects of global climate change on marine and estuarine fishes and fisheries. Reviews in Fish Biology and Fisheries 14,251-275.

Sæmundsson K. (2005) Geographical distribution and dispersal of juvenile Icelandic cod (*Gadus morhua*). MSc thesis, University of Iceland. 117 pp.

Salinger MJ. (2005). Climate variability and change: past, present and future - An overview. Climatic Change 70,9-29.

Sólmundsson J, Jónsson E, Björnsson H. (2007). Recent changes in the distribution and abundance of monkfish (*Lophius piscatorius*) in Icelandic waters. ICES CM K:02,16.

ter Braak CJF. (1986). Canonical correspondance analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67,1167-1179.

ter Braak CJF, Verdonschot PFM. (1995). Canonical correspondance analysis and related multivariate methods in aquatic ecology. Aquatic sciences 57,255-289.

Valdimarsson H, Björnsson H, Guðmundsson K. (2005). Breytingar á ástandi sjávar á Íslandsmiðum og áhrif þeirra á lífríkið (Climate variability in Icelandic waters and effects on marine biota). Hafrannsoknastofnunin Fjölrit 116,23-28.

Vilhjálmsson H. (1997). Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century. Rit Fiskideildar 13,9-29.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. (2002). Ecological responses to recent climate change. Nature 416,389-395.

Appendix 1. Species included in the analyses. Common names are cited in the text. Also shown are the assemblages the species clustered with in the two time periods (1996-1998 and 1999-2007), DSW = deep-southwest assemblage, DN = deep-north assemblage, SS = south-shelf assemblage, WS = widespread-shelf assemblage.

| English common name | Icelandic name | Latin name | Cluster 96-98 | Cluster 99-07 |
|---|---|---|---|---|
| Agassiz' slickhead | berhaus | *Alepocephalus agassizii* | DSW | |
| Arctic eelpout | blettamjóri | *Lycodes reticulatus* | | DN |
| Arctic rockling | (rauða) sævesla | *Onogadus argentatus* | | DN |
| Arctic skate | skjótta skata | *Amblyraja hyperborea* | | DN |
| Atlantic halibut | lúða | *Hippoglossus hippoglossus* | | SS |
| Atlantic hookear sculpin | krækill | *Artediellus atlanticus* | | DN |
| Atlantic poacher | áttstrendingur | *Leptagonus decagonus* | | DN |
| Baird's smooth-head | gjölnir | *Alepocephalus bairdii* | | DSW |
| Barracudinas | geirsílaætt | *Paralepididae* family | | DSW |
| Bean's sawtoothed eel | trjónuáll | *Serrivomer beani* | | DSW |
| Black dogfish | svartháfur | *Centroscyllium fabricii* | | DSW |
| Black scabbardfish | stinglax | *Aphanopus carbo* | | DSW |
| Blackfin waryfish | uggi | *Scopelosaurus lepidus* | | DSW |
| Blue antimora | fjólumóri | *Antimora rostrata* | | DSW |
| Blue ling | blálanga | *Molva dypterygia* | SS | WS |
| Blue whiting | kolmunni | *Micromesistius poutassou* | | WS |
| Cod | þorskur | *Gadus morhua* | | WS |
| Dab | sandkoli | *Limanda limanda* | SS | WS |
| Deepwater redfish | djúpkarfi | *Sebastes mentella* | DN | WS |
| Doitre blacksmelt | skjár/blálax | *Bathylagus euryops* | | DSW |
| Doubleline eelpout | tvírákamjóri | *Lycodes eudipleurostictus* | | DN |
| Esmark's eelpout | dílamjóri | *Lycodes esmarki* | | DN |
| Fourbeard rockling | blákjafta | *Enchelyopus cimbrius* | | SS |
| Gelatinous snailfish | dökki sogfiskur | *Liparis fabricii* | | DN |
| Golden redfish | karfi/gullkarfi | *Sebastes marinus* | | WS |
| Great lanternshark | dökkháfur | *Etmopterus princeps* | | DSW |
| Greater argentine | gulllax | *Argentina silus* | | WS |
| Greenland halibut | grálúða | *Reinhardtius hippoglossoides* | | DN |
| Grey gurnard | urrari | *Eutrigla gurnardus* | | SS |
| Günther's grenadier | ingólfshali | *Coryphaenoides guentheri* | | DSW |
| Haddock | ýsa | *Melanogrammus aeglefinus* | | WS |
| Herring | síld | *Clupea harengus* | | WS |
| Iceland catshark | gíslaháfur | *Apristurus laurussonii* | | DSW |
| Kaup's arrowtooth eel | djúpáll | *Synaphobranchus kaupi* | | DSW |
| Lemon sole | þykkvalúra | *Microstomus kitt* | SS | WS |
| Lesser sand-eel | marsíli | *Ammodytes marinus* | | SS |
| Ling | langa | *Molva molva* | | SS |
| Long rough dab | skrápflúra | *Hippoglossoides platessoides* | | WS |
| Longear eelpout | hálfberi mjóri | *Lycodes seminudus* | | DN |
| Longnose velvet dogfish | þorsteinsháfur | *Centroscymnus crepidater* | | DSW |
| Lumpsucker | hrognkelsi | *Cyclopterus lumpus* | | DN |
| Megrim | stórkjafta | *Lepidorhombus whiffiagonis* | | SS |
| Monkfish | skötuselur | *Lophius piscatorius* | | SS |
| Mouse catshark | jensensháfur | *Galeus murinus* | | DSW |
| Moustache sculpin | þrömmungur | *Triglops murrayi* | | DN |
| North Atlantic codling | bláriddari | *Lepidion eques* | | DSW |
| Northern wolffish | blágóma | *Anarhichas denticulatus* | SS | DSW |

| | | | | | |
|---|---|---|---|---|---|
| Norway haddock | litli karfi | *Sebastes viviparus* | | WS | |
| Norway pout | spærlingur | *Trisopterus esmarki* | | WS | |
| Orange roughy | búrfiskur | *Hoplostethus atlanticus* | | | DSW |
| Pale eelpout | fölvi mjóri | *Lycodes pallidus* | | DN | |
| Pallid sculpin | tómasarhnýtill | *Cottunculus thomsonii* | SS | | |
| Piked dogfish | háfur | *Squalus acanthias* | | SS | |
| Plaice | skarkoli | *Pleuronectes platessa* | SS | | WS |
| Polar cod | ískóð | *Boreogadus saida* | | DN | |
| Polar sculpin | marhnýtill | *Cottunculus microps* | | DN | |
| Portuguese dogfish | gljáháfur | *Centroscymnus coelolepis* | | | DSW |
| Rabbit fish | geirnyt | *Chimaera monstrosa* | | SS | |
| Roughhead grenadier | snarphali | *Macrourus berglax* | | | DSW |
| Roughnose grenadier | langhalabróðir | *Trachyrhynchus murrayi* | | | DSW |
| Round ray | pólskata | *Rajella fyllae* | SS | | DSW |
| Roundnose grenadier | slétti langhali | *Coryphaenoides rupestris* | | | DSW |
| Saithe | ufsi | *Pollachius virens* | SS | | WS |
| Scalebelly eelpout | nafnlausi mjóri | *Lycodes squamiventer* | | | SS |
| Sea tadpole | hveljusogfiskur | *Careproctus reinhardti* | | DN | |
| Silvery pout | silfurkóð | *Gadiculus argenteus thori* | | | SS |
| Snakeblenny | stóri mjóni | *Lumpenus lampretaeformis* | | SS | |
| Spearnose chimaera | trjónufiskur | *Rhinochimaera atlantica* | | | DSW |
| Spiny eel | broddabakur | *Notacanthus chemnitzii* | | DSW | |
| Slender codling | silfurþvari | *Halargyreus johnsonii* | | | DSW |
| Spotted wolffish | hlýri | *Anarhichas minor* | | DN | |
| Thorny skate | tindaskata | *Amblyraja radiata* | | DN | |
| Tusk | keila | *Brosme brosme* | | SS | |
| Vahl's eelpout | litli mjóri | *Lycodes vahli* | | DN | |
| Velvet belly lantern shark | loðháfur | *Etmopterus spinax* | | | SS |
| Whiting | lýsa | *Merlangius merlangus* | SS | | WS |
| Witch | langlúra | *Glyptocephalus cynoglossus* | | SS | |
| Wolffish | steinbítur | *Anarhichas lupus* | | WS | |

# Groundfish diversity in Icelandic waters during a period of rapid warming (1996-2007)

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Abstract

Species richness generally decreases from low to high latitudes. For marine fishes at high latitudes, rising sea temperatures might lead to local increases in species richness through latitudinal distribution range shifts. We used autumn groundfish survey data to examine groundfish diversity in Icelandic waters in 1996-2007, a period of rapid warming. We used two estimates of diversity: species richness and the Shannon index (H'). Relationships between diversity and depth, temperature, primary production, location and year were examined using generalized additive models (GAMs). Analyses were performed for two study areas which differ greatly in hydrographical characteristics. Diversity was found to be highly variable both temporally and spatially, and also to vary with depth and temperature. Species richness increased with temperature and time south and west of the country, but decreased in the north and east. In some areas where species richness was high, H' was low. This suggests that although these areas contain numerous species, just a small number of those are in high abundance, while the rest are represented by relatively few individuals.

## Introduction

Biodiversity is believed to affect ecosystem functioning and stability (Loreau *et al.* 2001, Hooper *et al.* 2005, Worm *et al.* 2006). Higher diversity is likely to increase an ecosystem's capacity to withstand and recover from perturbations (Worm *et al.* 2006). This may be especially important for fish communities exposed to climatic changes and/or the impacts of fishing.

Diversity is usually measured as the number of species present in a given area (species richness), often weighted by some measure of abundance. Species richness generally decreases from low to high latitudes, and this is believed to be linked to temperature (Willig *et al.* 2003). This pattern has been observed for marine fishes in many regions (McClatchie *et al.* 1997, Grey 2001, Macpherson 2002, Rose 2005, Sousa *et al.* 2006, Tolimieri 2007). For marine fishes at high latitudes, rising sea temperature might lead to local increases in species richness through latitudinal range shifts (Hiddink and ter Hofstede 2008). This has been observed in some areas of the North-Atlantic, with increased abundance of species at the northern boundary of their distributional range (Poulard and Blanchard 2005, Hiddink and ter Hofstede 2008). Patterns of species richness with depth are more complex (Grey 2001, Sousa *et al.* 2006) and latitudinal gradients in species richness are probably not as profound at greater depths (McClatchie *et al.* 1997, Rose 2005, Tolimieri 2007).

In recent years, oceanic temperature around Iceland has been rising. Relatively warm and saline Atlantic water predominates southwest of the country, but since 1999 inflow of this water mass has been noted farther north and east of Iceland (Anon. 2008b). The hydrography of the waters over the continental shelf north of Iceland is highly variable due to changes in the relative influences of the Atlantic, Arctic and Polar water masses, and the recent changes have led to elevated sea

temperature and salinity in the area (Malmberg and Valdimarsson 2003, Jónsson and Valdimarsson 2005, Anon. 2008b). Mean annual productivity is higher in the Atlantic water than in the more variable waters north and east of the country. The distribution of many marine organisms reflects these regional differences in the water masses (Gíslason and Ástþórsson 2004).

The distributional limits of many North Atlantic fish species are found in Icelandic waters (Björnsson and Pálsson 2004, Ástþórsson *et al.* 2007). Associated with a warm period in the late 1920s and the 1930s, numerous southerly species that had previously been rare or absent in Icelandic waters became more common, and northerly species such as cod (*Gadus morhua*) and capelin (*Mallotus villosus*) shifted farther north (Vilhjálmsson 1997). In recent years, increases in the abundance and/or distribution of several species such as monkfish (*Lophius piscatorius*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*) have been associated with the warming of Icelandic waters (Valdimarsson *et al.* 2005, Sólmundsson *et al.* 2007).

The aim of this study is to analyze spatial and temporal trends in the diversity of groundfish communities in Icelandic waters in the period 1996-2007. Effects of depth and temperature on diversity will be analyzed for two areas, which differ greatly in temperature due to prevailing currents. More specifically, we test whether species richness and diversity have increased with increased flow of warm Atlantic water onto the Icelandic continental shelf.

## Materials and methods

**Data**

Data on fish distribution and species composition were obtained from the annual autumn groundfish survey 1996-2007, conducted in October by the Marine Research Institute (MRI). The survey covers the area of the Icelandic continental shelf and slope, at depths from 20 to 1500 m. It is a stratified systematic survey where the same stations are repeated annually (Björnsson *et al.* 2007). Standardized fishing methods are employed where tows are taken with a small-meshed bottom trawl at 3.8 knots for 3 nautical miles. At each station, all fish were identified to the species level and counted, length was measured, geographic location, depth, and in most cases bottom temperature, were recorded. Most pelagic and semi-pelagic species were included in the analysis, although in some cases they may not have been sampled effectively with the gear used. Capelin was excluded due to an inconsistency in registration and lanternfishes (*Myctophidae*) due to uncertain species identifications. Barracudinas (*Paralepididae*) were combined at the family level. Only stations that had complete environmental data for at least 10 of the 12 years were included, leaving a total of 264 stations (Fig. 1).

Annual primary production was entered as average chlorophyll *a* concentration (mg m$^{-3}$) in March-October at each location on a 9 × 9 km grid, estimated from satellite pigment images (data from SeaWIFS[1]). However, chlorophyll *a* concentration was not available for 1996-1997 and so average values for the available years (1998-2007) were used.

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[1]      http://oceancolor.gsfc.nasa.gov/SeaWiFS/
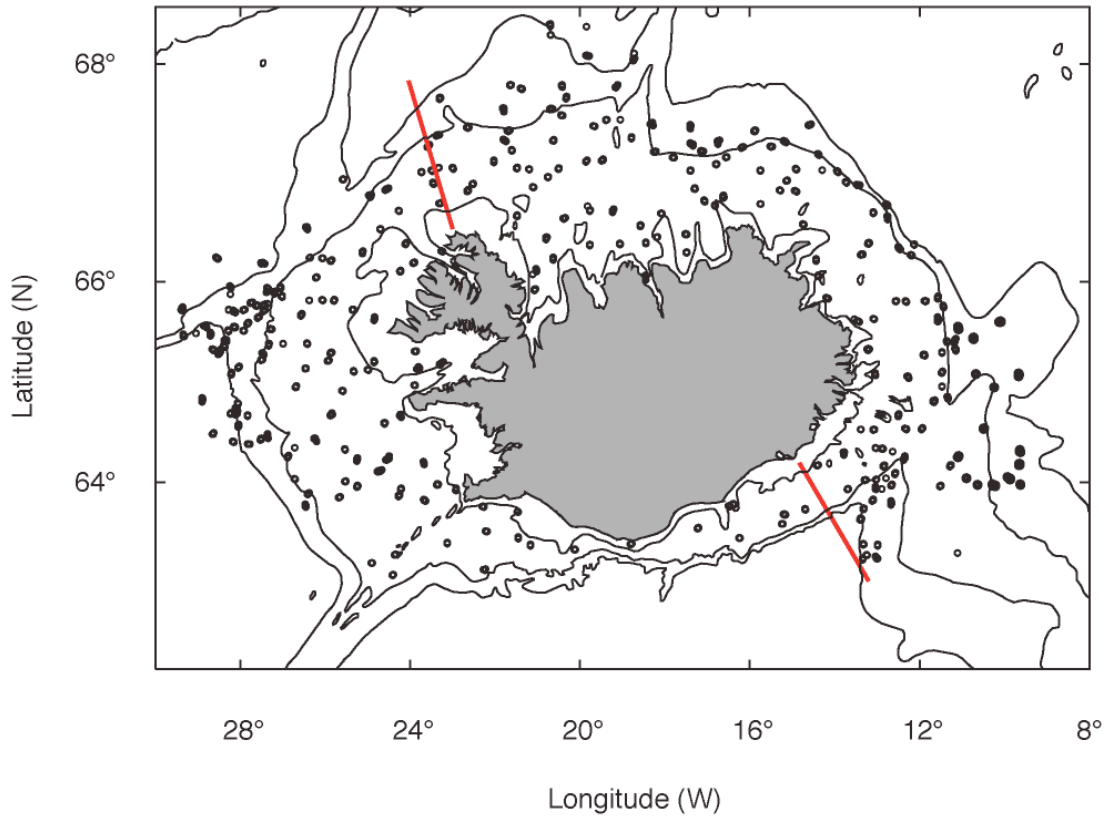
Fig. 1. Distribution of sampling stations in the autumn groundfish survey. Only stations that had complete data for at least 10 of 12 years (1996-2007) were included (264 stations). Depth contours for 100, 500 and 1000 m are shown and the red lines indicate the division between the NE and SW areas.

**Diversity indices**

In order to select an appropriate measure of diversity, four indices which capture different aspects of diversity were calculated:

i) species richness is one of the most commonly used indicators of species diversity. In this study it was expressed as the number of species per tow.

ii) Shannon index (H'), which takes into account information on both species richness and the distribution of individuals among species, was calculated as:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where $S$ is the number of species per tow and $p_i$ is the proportion of individuals in a tow belonging to species $i$. H' takes values between 0 and ln $S$ ($H_{max}$) (Zar 1999).

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iii) Shannon evenness index (E) expresses diversity as a proportion of the maximum

possible diversity (Zar 1999) and was calculated as:

$$E = H' / H_{max}$$

iv) Simpson's reciprocal index ($D^{-1}$) takes into account information on both species

richness and the distribution of individuals among species, but puts greater weight on

dominant species than H' (Mouillot and Depretre 1999). The index was calculated as

$D^{-1}$ where D is:

$$D = \sum_{i=1}^{S} p_i^2$$

(Simpson 1949). $D^{-1}$ takes values between 0 (lowest diversity) and 1 (highest

diversity).

The Shannon index was found to be highly correlated with the evenness index

and Simpson's reciprocal index (Table 1). Therefore, only species richness and the

Shannon index (H') were used in further analyses.

Table 1: Spearman rank correlations among diversity indices: species richness, H' (Shannon index), $D^{-1}$ (Simpson reciprocal index) and E (Shannon evenness).

|  | Sp. richness | H' | $D^{-1}$ | E |
|---|---|---|---|---|
| Sp. richness | 1 | | | |
| H' | 0.12 | 1 | | |
| $D^{-1}$ | -0.01 | 0.96 | 1 | |
| E | -0.22 | 0.91 | 0.94 | 1 |

**Spatial analysis**

Geographical distribution of species richness and H' were mapped by spatially

interpolating the data using a kriging method (Kalzuny *et al.* 1998). Fitting of the

variogram model parameters was done by eye. Kriging was performed with the

statistical program S-PLUS using the *geo* library package from the Marine Research

Institute in Iceland (Anon 1996).

## GAMs

Generalized additive models (GAMs) were used to examine the effects of year, depth, bottom temperature, location (bivariate function of latitude and longitude) and estimates of primary production at each station, on species diversity.

GAMs are nonparametric generalizations of multiple linear regression that are not restricted to specific functional relationships or underlying statistical distributions of the data. Each predictor is included in the model as a non-parametric smoothing function (Hastie and Tibshirani 1990). The GAMs were constructed using version 1.3-29 of the *mgcv* library in the statistical package R, where GCV optimization selects the degrees of freedom for each term automatically (Wood and Augustin 2002). Model terms were selected using backward model selection via generalized cross-validation scores. The diversity indices were normally distributed, so the identity link function was used. The starting model was:

$$g(species\ richness\ /\ H') = \beta_0 + year + s(latitude \times longitude) + s(temperature) +$$
$$s(depth) + s(log(chlorophyll\ a))$$

where $g(\mu)$ is the identity link function, $\beta_0$ is the intercept and s is a spline smoother. Model validation involved checking the statistical assumption of normality of residuals. GAMs were also constructed separately for two study areas: north and east (NE) and south and west (SW) of Iceland (Fig. 1). These two areas were chosen to accentuate the different hydrographical characteristics of the relatively warm Atlantic water predominant in the south and west of Iceland, and the colder water

masses in the north and east (Malmberg and Valdimarsson 2003, Ástþórsson *et al.* 2007). All data collected in 1999 were excluded from the GAMs due to missing temperature measurements.

## Results

**Species richness**

A total of 159 species were included in the analyses (Appendix 1), ranging from 1 to 24 species per station. Only a few species were found to be relatively widespread in Icelandic waters, occurring at 30-70% of stations, while the rest had more restricted distributions (Table 2). The most widespread species were not necessarily the most abundant ones; only six of the ten most widespread species belong to the top ten most abundant ones (Table 2).

Table 2: The ten most widespread and abundant species in the autumn groundfish surveys 1996-2007. For the ten most widespread species the average proportions of stations at which they were caught and standard deviation are given. For the ten most abundant species the average number of individuals per year and standard deviation are given. See Appendix 1 for Latin species names.

| Most widespread species | % of stations | SD | Most abundant species | Average abundance | SD |
|---|---|---|---|---|---|
| Long rough dab | 66.7 | 2.0 | Haddock | 82 132 | 32 967 |
| Cod | 65.1 | 3.3 | Blue whiting | 41 933 | 17 586 |
| Golden redfish | 59.4 | 2.4 | Norway pout | 40 847 | 30 171 |
| Thorny skate | 55.0 | 3.4 | Golden redfish | 39 485 | 17 113 |
| Haddock | 46.1 | 3.8 | Roundnose grenadier | 26 413 | 6 137 |
| Greenland halibut | 39.0 | 2.3 | Long rough dab | 15 501 | 3 259 |
| Blue whiting | 36.7 | 8.9 | Deepwater redfish | 12 120 | 4 249 |
| Norway haddock | 36.4 | 6.9 | Norway haddock | 12 110 | 3 245 |
| Wolffish | 35.9 | 1.9 | Cod | 10 151 | 2 213 |
| Herring | 31.7 | 2.8 | Whiting | 9 437 | 4 244 |

Species richness varied spatially in Icelandic waters in the study period (Fig. 2). High diversity was observed on the continental slope west of the country and in shallow waters in the southwest, as well as on the northern continental shelf. In comparison to the later years, species richness tended to be high and evenly distributed across the study area in 1996. A notable increase in species richness was seen in the southwest and in deep water west of Iceland in the years 2002-2007. For

all years other than 1996, the deep waters north and east of the country contained the fewest species. In some years, low species richness was also noticed in coastal areas north and east of the country (Fig. 2).

All predictors in the GAM model, with the exception of primary production, had a significant effect on species richness and therefore were included in the final model (Table 3). The model for all stations explained 43.6% of the total deviance. The models for the NE and SW areas explained 40.5% and 38.6% of the total deviance, respectively.

Temperature did not have a statistically significant effect on species richness in the NE area, but including it in the model nevertheless gave a better model fit. Species richness was predicted to show a slight decline with temperature when all stations were combined (Fig. 3a). In the SW area, species richness increased with temperature, reaching a peak at approximately 4-6°C (Fig. 3c).

The effect of depth was similar for all models. Species richness increased with depth to approximately 400 m, then decreased thereafter, except for a smaller peak at about 900 m in the NE area (Fig. 3d,e,f). This is consistent with the spatial distribution of species richness, with relatively high values observed on the continental shelf towards the 500 m depth contour (Fig. 2).

For the whole area, species richness decreased from 1996 to 2000, but increased again in 2002 to a similar level as that observed in 1996. Since then it has been relatively stable. (Table 3 and Fig. 3g). Species richness in the NE area was high in 1996 but significantly lower in most years between 1997 and 2007 (Table 3 and Fig. 3h). In the SW area, species richness increased with time and when compared to the reference year of 1996, it was significantly higher from 2001 onwards (Table 3 and Fig. 3i).
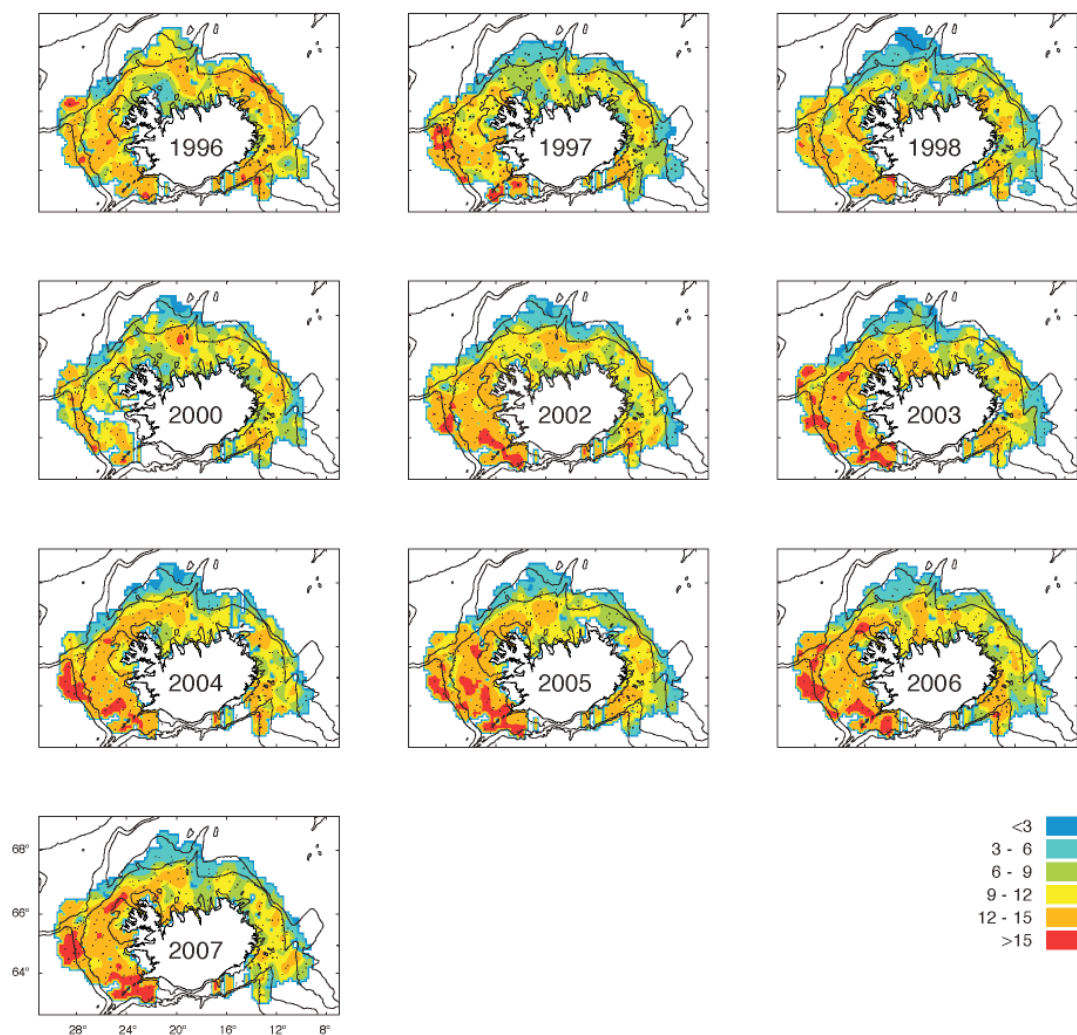
Fig 2. Geographical distribution of species richness during the autumn groundfish surveys 1996-2007. Depth contours for 100, 500 and 1000 m are shown. Temperature data were missing from 1999 so that year was excluded from the analyses. No figure available for 2001.

Table 3. Results of GAM models predicting species richness in the autumn groundfish surveys. P-values for smoothed terms and parameter estimates are shown, along with standard errors and p-values for the categorical term year. Significant effects are indicated at the 0.001***, 0.01** and 0.05* levels.

Species richness

**All stations - deviance explained = 43.6%**

| Model term | Coefficient | Std.error | p |
|---|---|---|---|
| Intercept | 11,64 | 0,18 | $< 2 \times 10^{-16}$ *** |
| year(1997) | -0,72 | 0,24 | 0,0028 ** |
| year(1998) | -0,95 | 0,24 | $9.84 \times 10^{-5}$ *** |
| year(2000) | -0,68 | 0,25 | 0,0078 ** |
| year(2001) | 0,43 | 0,26 | 0,0982 |
| year(2002) | 0,00 | 0,25 | 0,9986 |
| year(2003) | 0,50 | 0,25 | 0,0458 * |
| year(2004) | 0,14 | 0,24 | 0,5755 |
| year(2005) | 0,25 | 0,24 | 0,3047 |
| year(2006) | 0,60 | 0,24 | 0,0135 * |
| year(2007) | 0,14 | 0,24 | 0,5757 |

| Model term | edf | p |
|---|---|---|
| s(temp) | 3,98 | 0,00468 ** |
| s(depth) | 6,55 | $< 2 \times 10^{-16}$ *** |
| s(lon,lat) | 27,96 | $< 2 \times 10^{-16}$ *** |

**NE area - deviance explained = 40.5%**

| Model term | Coefficient | Std.error | p |
|---|---|---|---|
| Intercept | 11,19 | 0,21 | $< 2 \times 10^{-16}$ *** |
| year(1997) | -1,74 | 0,28 | $8.16 \times 10^{-10}$ *** |
| year(1998) | -1,80 | 0,29 | $3.37 \times 10^{-10}$ *** |
| year(2000) | -0,87 | 0,29 | 0,0027 ** |
| year(2001) | -0,35 | 0,31 | 0,2617 |
| year(2002) | -0,67 | 0,31 | 0,0297 * |
| year(2003) | -0,56 | 0,30 | 0,0633 |
| year(2004) | -0,97 | 0,28 | 0,0006 *** |
| year(2005) | -1,04 | 0,29 | 0,0003 *** |
| year(2006) | -0,76 | 0,28 | 0,0067 ** |
| year(2007) | -1,36 | 0,29 | $2.16 \times 10^{-6}$ *** |

| Model term | edf | p |
|---|---|---|
| s(temp) | 3,70 | 0,0938 |
| s(depth) | 7,61 | $2.71 \times 10^{-14}$ *** |
| s(lon,lat) | 27,34 | $< 2 \times 10^{-16}$ *** |

**SW area - deviance explained = 38.6%**

| Model term | Coefficient | Std.error | p |
|---|---|---|---|
| Intercept | 12,20 | 0,27 | $< 2 \times 10^{-16}$ *** |
| year(1997) | 0,44 | 0,37 | 0,2419 |
| year(1998) | 0,02 | 0,38 | 0,9549 |
| year(2000) | -0,63 | 0,41 | 0,1217 |
| year(2001) | 1,42 | 0,38 | 0,0002 *** |
| year(2002) | 1,06 | 0,37 | 0,0047 ** |
| year(2003) | 1,92 | 0,38 | $6.76 \times 10^{-7}$ *** |
| year(2004) | 1,42 | 0,38 | 0,0002 *** |
| year(2005) | 1,81 | 0,37 | $1.09 \times 10^{-6}$ *** |
| year(2006) | 2,22 | 0,37 | $4.14 \times 10^{-9}$ *** |
| year(2007) | 1,99 | 0,37 | $1.23 \times 10^{-7}$ *** |

| Model term | edf | p |
|---|---|---|
| s(temp) | 2,59 | $3.63 \times 10^{-5}$ *** |
| s(depth) | 6,47 | $4.71 \times 10^{-9}$ *** |
| s(lon,lat) | 27,26 | $< 2 \times 10^{-16}$ *** |
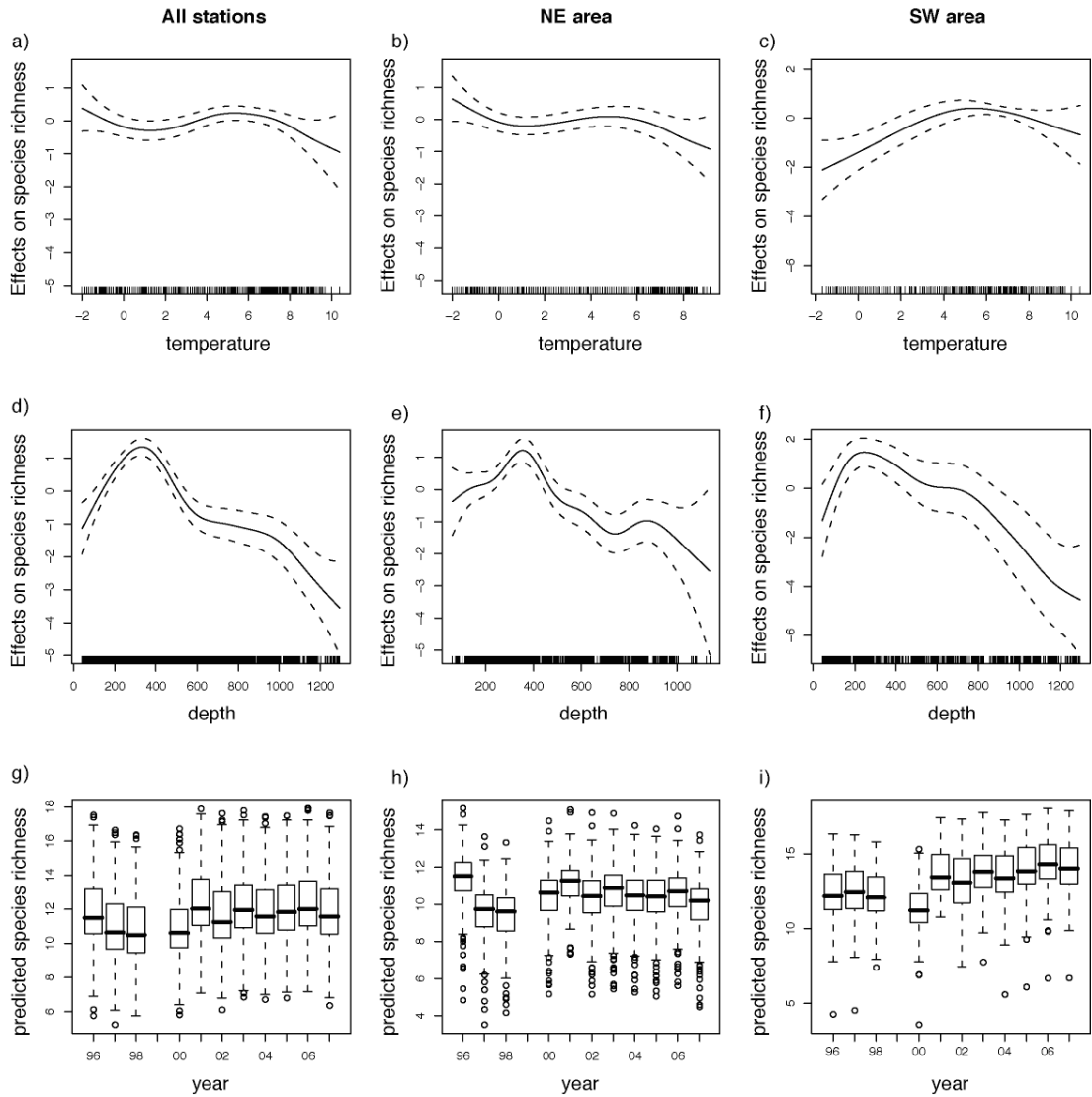
Fig 3. Predictions from a GAM model examining the effects of temperature, depth and year on species richness in Icelandic waters. Conditional effects of smooth terms and 95% confidence intervals (dashed lines) are shown for the effects of temperature (a-c) and depth (d-f) for all stations combined (a,d), the NE area (b,e) and SW area (c,f). The y-axis is scaled to zero and reflects the relative importance of the covariate. The rugplot on the x-axis represents the number of observations. Interannual variation in the predicted species richness is shown for g) all stations, h) the NE area and i) the SW area. Each box shows the median (bold horizontal line) value and the 25 and 75 percentiles (upper and lower limit of the box respectively). The dashed vertical line indicates 1.5 times the interquartile range of the data, with points representing extreme values.

**Shannon index**

The Shannon index (H') ranged from 0–2.44 per station. High values were
observed north of Iceland in 1996, but H' was lower in all the following years (Fig.
4). H' was generally evenly distributed in Icelandic waters, except perhaps in deep
waters southeast of the country, where low values were observed. H' "hot spots"
were observed at depths of 400-500 m in the Denmark Strait north-west of Iceland in
most years (Fig. 4). After 1996, H' was relatively stable in Icelandic waters.
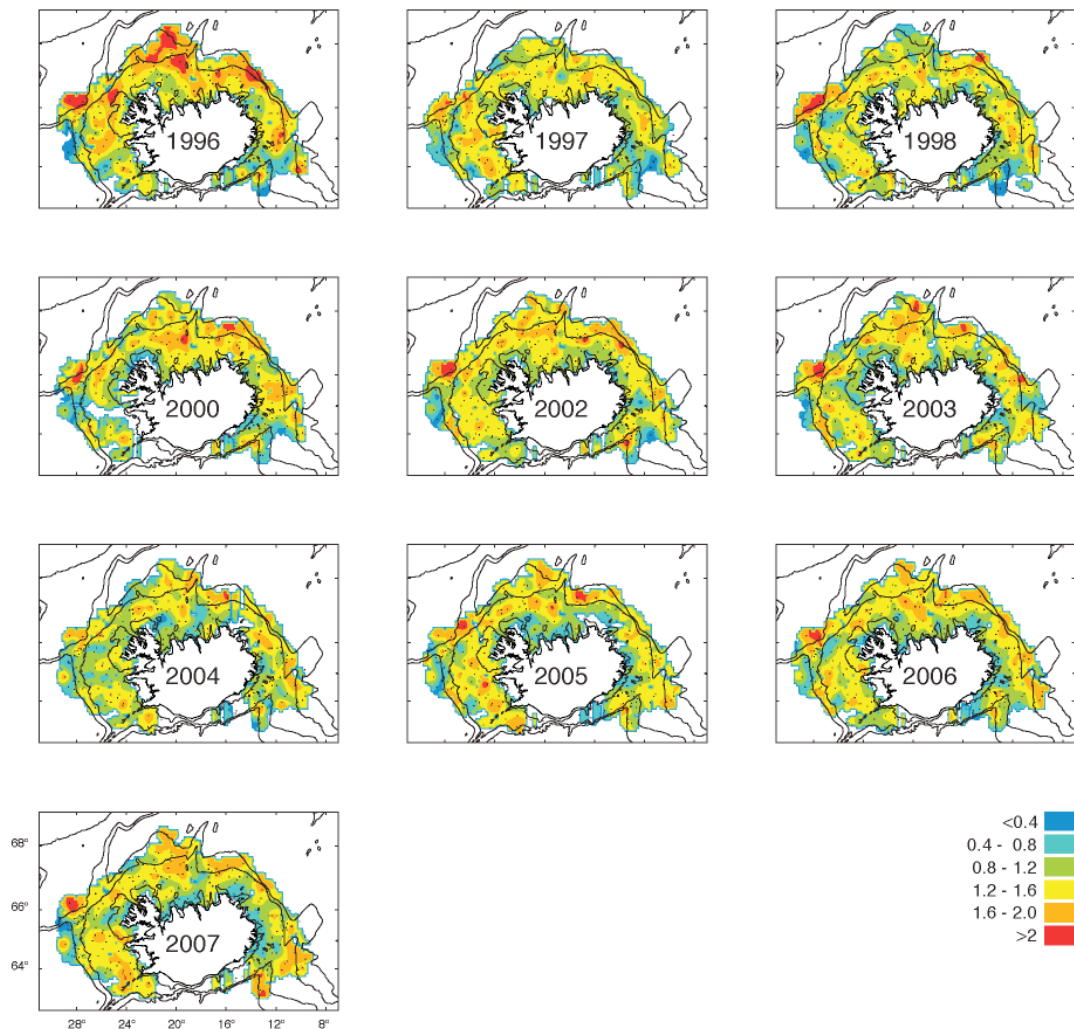


Fig 4. Geographical distribution of Shannon index during the autumn groundfish surveys 1996-
2007. Depth contours for 100, 500 and 1000 m are shown. Temperature data were missing from
1999 so that year was excluded from the analyses. No figure available for 2001.

Table 4. Results of GAM models predicting Shannon index in the autumn groundfish surveys. P-values for smoothed terms and parameter estimates are shown, along with standard errors and p-values for the categorical term year. Significant effects are indicated at the 0.001***, 0.01** and 0.05* levels.

H

**All stations - deviance explained = 26%**

| Model term | Coefficient | Std.error | p |
|---|---|---|---|
| Intercept | 1,30 | 0,03 | $< 2 \times 10^{-16}$ *** |
| year(1997) | -0,12 | 0,04 | 0,0030 ** |
| year(1998) | -0,13 | 0,04 | 0,0008 *** |
| year(2000) | -0,06 | 0,04 | 0,1447 |
| year(2001) | -0,04 | 0,04 | 0,3064 |
| year(2002) | -0,01 | 0,04 | 0,7919 |
| year(2003) | -0,06 | 0,04 | 0,1334 |
| year(2004) | -0,17 | 0,04 | $3.3 \times 10^{-5}$ *** |
| year(2005) | -0,12 | 0,04 | 0,0035 ** |
| year(2006) | -0,09 | 0,04 | 0,0294 * |
| year(2007) | -0,10 | 0,04 | 0,0155 * |

| Model term | edf | p |
|---|---|---|
| s(temp) | 5,00 | $1.32 \times 10^{-6}$ *** |
| s(depth) | 8,52 | $< 2 \times 10^{-16}$ *** |
| s(lon,lat) | 24,69 | $< 2 \times 10^{-16}$ *** |

**NE area - deviance explained = 30.8%**

| Model term | Coefficient | Std.error | p |
|---|---|---|---|
| Intercept | 1,41 | 0,04 | $< 2 \times 10^{-16}$ *** |
| year(1997) | -0,24 | 0,05 | $1.78 \times 10^{-6}$ *** |
| year(1998) | -0,24 | 0,05 | $1.99 \times 10^{-6}$ *** |
| year(2000) | -0,08 | 0,05 | 0,0964 |
| year(2001) | -0,10 | 0,06 | 0,0667 |
| year(2002) | -0,07 | 0,05 | 0,2029 |
| year(2003) | -0,14 | 0,05 | 0,0086 ** |
| year(2004) | -0,25 | 0,05 | $5.53 \times 10^{-7}$ *** |
| year(2005) | -0,22 | 0,05 | $7.93 \times 10^{-6}$ *** |
| year(2006) | -0,13 | 0,05 | 0,0087 ** |
| year(2007) | -0,18 | 0,05 | 0,0005 *** |

| Model term | edf | p |
|---|---|---|
| s(temp) | 6,824 | 0,041 * |
| s(depth) | 5,65 | $6.57 \times 10^{-15}$ *** |
| s(lon,lat) | 26,52 | $< 2 \times 10^{-16}$ *** |

**SW area - deviance explained = 35.9%**

| Model term | Coefficient | Std.error | p |
|---|---|---|---|
| Intercept | 1,16 | 0,01 | $< 2 \times 10^{-16}$ *** |

| Model term | edf | p |
|---|---|---|
| s(temp) | 5,97 | $6.48 \times 10^{-12}$ *** |
| s(depth) | 8,30 | $< 2 \times 10^{-16}$ *** |
| s(lon,lat) | 21,57 | $1.17 \times 10^{-12}$ *** |
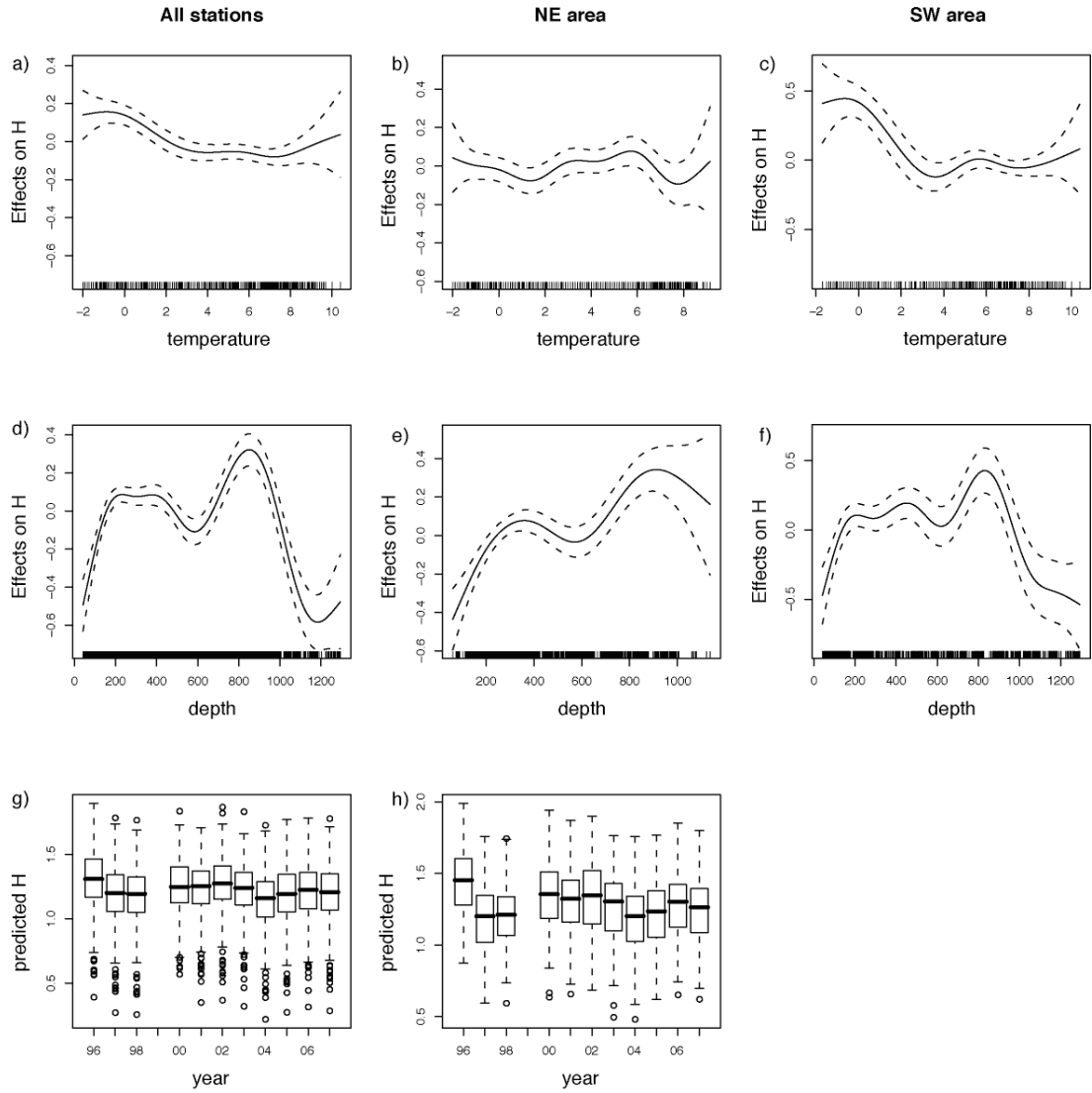
Fig 5. Predictions from a GAM model examining the effects of temperature, depth and year on the Shannon index (H') in Icelandic waters. Conditional effects of smooth terms and 95% confidence intervals (dashed lines) are shown for the effects of temperature (a-c) and depth (d-f) for all stations combined (a,d), the NE area (b,e) and SW area (c,f). The y-axis is scaled to zero and reflects the relative importance of the covariate. The rugplot on the x-axis represents the number of observations. Interannual variation in the predicted species richness is shown for g) all stations and h) the NE area. Each box shows the median (bold horizontal line) value and the 25 and 75 percentiles (upper and lower limit of the box respectively). The dashed vertical line indicates 1.5 times the interquartile range of the data, with points representing extreme values. Year did not have a significant effect on Shannon index in the SW area and was not included in the model.

All predictors in the GAM model, with the exception of primary production, had a significant effect on H' when all stations were included (Table 4). This model explained 26% of the total deviance. When GAMs were constructed for the two areas separately, there was no significant effect of year in the SW area (Table 4). The separate area models explained a higher percentage of the total deviance than the model for all stations: 30.8% and 35.9% for the NE and SW areas, respectively.

For all stations combined and the NE area, H' showed little variation with temperature (Fig. 5a,b). In the SW area, H' decreased at temperatures between -2°C and approximately 3°C and was rather stable at higher temperatures (Fig. 5c).

The effect of depth on H' was similar in all models, with H' increasing to a small peak at 200-500 m, decreasing until 600 m and then rising to highest values at depths of approximately 900 m (Fig. 5d,e,f). In the models for all stations and for the SW area, H' decreased rapidly at depths >900 m (Fig. 5d,f). A lack of data at depths beyond 900 m meant that the presence of such a trend in the NW area could not be confirmed (Fig. 5e).

H' was generally stable through time, except that it was significantly higher in 1996 than in 1997-1998 and 2004-2007 (Table 4 and Fig. 5g). Like species richness, H' in the NE area was highest in 1996 and significantly lower in other years, with the exception of 2000-2002 (Table 4 and Fig. 5h).

Discussion

The diversity of groundfish species in Icelandic waters was found to vary both temporally and spatially, as well as with depth and temperature. The diversity indices used (species richness and the Shannon index, H') illustrated different features of groundfish diversity in Icelandic waters. Species richness did increase during the study period, but H' was relatively stable through time.

Areas of high species richness were found mainly southwest of Iceland and in deep water west of the country, while areas of lower richness were observed in the colder waters north and east of the country. In general, this supports the findings of other studies which have examined gradients in species richness with temperature and latitude (McClatchie *et al.* 1997, Macpherson 2002, Willig *et al.* 2003, Rose 2005, Sousa *et al.* 2006, Tolimieri 2007, Hiddink and ter Hofstede 2008).

The prediction of spatial patterns in species richness and H' by the kriging method and GAMs were mostly consistent. Species richness was low in deep waters in the north and east, seen in the GAMs as a decrease at depths of >400 m. H' was generally evenly distributed in Icelandic waters, but H' 'hot spots' were revealed in small areas on the slope north and west of the country. That was reflected in the GAMs by a peak at about 900 m depth. However, there were some inconsistencies between the two methods used in the study. The high species richness in the deep water west of the country was not observed in the GAMs, but instead species richness was predicted to decrease at depths >800 m in the SW area. A potential explanation for this discrepancy is that the partial effects of depth and temperature were analyzed for all years combined in the GAMs, and due to this averaging effect the GAMs could be unable to capture all the variation revealed by the kriging method.

Results for all stations combined were not consistent with those for the two different areas. This shows that when analyzing data sampled across a spatially heterogeneous environment, variation in responses could be overseen. To illustrate this point, species richness in the NE area appeared to decrease with temperature but increase in the SW area. These contrasting trends were also observed in H', for which a notably higher proportion of the deviance was explained when areas were analyzed separately, compared to the model where all stations were combined. Species richness increased west of Iceland through the study period, but was more stable east of the country. Latitudinal gradients of species diversity are likely to be quite complex in Icelandic waters due to the prevalent hydrographic conditions, which are characterized by temperatures in the west being generally higher than those at the same latitudes in the east (Malmberg and Valdimarsson 2003).

According to the GAMs, species richness decreased with depth after about 400 m, which supports the findings of other studies such as Rose (2005) and Tolimieri (2007). However, many studies have found species richness to increase with depth (McClatchie *et al.* 1997, Grey 2001, Sousa *et al.* 2006). Depth related gradients of species richness are complex and are clearly not as consistent as latitudinal gradients in species diversity (Grey 1994, Grey 2001, Sousa *et al.* 2006). Depth gradients may be affected by depth preferences of local dominant species, where high abundance of one species may lead to low species richness in that depth zone (Tolimieri 2007).

Species richness and the Shannon index (H') were both relatively high north of the country in 1996. With the exception of 1996, H' was rather stable across the years. Species richness on the other hand increased notably in the SW area after 2002. Concurrent with the recent rise in sea temperature, numerous species that were previously rare or absent in Icelandic waters have been recorded, most of them

southerly species. In 1996-2005, twenty-two newly occurring species were found in Icelandic waters, with many of them recorded more than once (Ástþórsson and Pálsson 2006). Only one of these species was included in our study: the humpback anglerfish (*Melanocetus johnsonii*, see Appendix 1), caught at deep stations west of the country in 2004, 2005 and 2007. It was first recorded in Icelandic waters in 1996, but is more commonly found in more southerly locations in the North Atlantic (Ástþórsson and Pálsson 2006).

The increased species diversity in the SW area observed in this study may be better explained by the extended distribution of common 'warm water species' such as monkfish, saithe (*Pollachius virens*), whiting (*Merlangius merlangus*) and ling (*Molva molva*). Changes in the distribution of these species have been consistent with the increased inflow of Atlantic water onto the Icelandic shelf (see Appendix 1, Valdimarsson *et al.* 2005, Björnsson *et al.* 2007, Sólmundsson *et al.* 2007). Elsewhere in the Northeast Atlantic, 'southerly' species have expanded their distributional range northwards, coinciding with rising sea temperatures (Brander *et al.* 2003, Poulard and Blanchard 2005, Hiddink and ter Hofstede 2008). In the North Sea, such an expansion in small southerly species has led to an increase in local species richness (Hiddink and ter Hofstede 2008).

The notably high species diversity in the NE area in 1996, compared to the following years, suggests that significant changes may have taken place in this ecosystem. The high diversity in 1996 was caused mainly by the extended distribution of several small-bodied northerly species, such as arctic rockling (*Onogadus argentatus*), gelatinous snailfish (*Liparis fabrici*), moustache sculpin (*Triglops murrayi*), Atlantic poacher (*Leptagonus decagonus*) and a few eelpout species (*Lycodes vahli*, *Lycodes pallidus*, *Lycodes reticulates*). In Icelandic waters,

similarly as in the North Sea (Hiddink and ter Hofstede 2008), recent decreases in distributional ranges, possibly due to higher temperatures, have been observed for some 'northerly' species such as spotted wolffish (*Anarhichas minor*), Greenland halibut (*Reinhardtius hippoglossoides*) and long rough dab (*Hippoglossoides platessoides*) (Björnsson *et al.* 2007). These changes may have contributed to the decreased diversity observed in the NE area during the study period. However, since these are commercially exploited species, fishing may also have played a role in these observed changes. Fishing may not affect species richness directly, but rather by altering the proportional abundances of species and thus the evenness of the community (Bianchi *et al.* 2000).

In northern Icelandic waters, the year 1995 was characterized by exceptionally low temperatures (Anon. 2008b). Commercial cold-water species such as northern shrimp (*Pandalus borealis*) and capelin were found in high abundance in that and the following year (Anon. 2008a). Since 1997, the abundance of these species has significantly decreased, and in this study we have shown that the distributional ranges of several non-commercial species has also decreased. This suggests that some large-scale processes, such as oceanographic variability, may have been involved. Species for which a reduction in distributional range has been observed in the North Sea are those of larger body sizes, with boundaries of their northern range occurring at higher latitudes, e.g. wolffish (*Anarhichas lupus*), spurdog (*Squalus acanthias*) and ling (Hiddink and ter Hostede 2008). A latitudinal shift in the distribution of ling appears to have occurred over the last few years since its distribution has decreased in the North Sea but increased in Icelandic waters (Valdimarsson *et al.* 2005, Hiddink and ter Hofstede 2008).

With the exception of 1996, H' did not really show much temporal variation, and

the effect of year was not significant in the SW area. At the same time, species richness increased in the SW area and this suggests that the two diversity measures are capturing different aspects of the groundfish diversity. In some areas where species richness was high, H' was found to be low. This suggests that although these areas contain numerous species, just a small number of those are in high abundance, while the rest are represented by relatively few individuals. Some of the most abundant species included in this study have relatively limited distributions, so where they occur they are likely to be found in high abundance. This could lead to low H' values in those areas. In contrast, H' was high in deep water north of the country, but species richness was usually low. This could indicate that few species are present in those areas, but that they exist in similar abundances. In other areas, high H' was concurrent with high species richness. This was for example the case in a relatively small area west of the country, shown by a species richness and H' 'hot spot' throughout the study period.

Primary production has been suggested as an explanatory factor for latitudinal patterns of species diversity (Willig *et al.* 2003). When included in our GAM models, it did not explain a statistically significant part of the deviation in species richness or H'. However, areas of high species richness observed in our study, such as the warm Atlantic water southwest of Iceland and the frontal areas in the northwest and southeast, are areas known for high productivity (Ástþórsson *et al.* 2007). The species richness and H' 'hot spot' west of the country is in a frontal area in the Denmark Strait (Macrander *et al.* 2007). Similarly, McClatchie *et al.* (1997) found demersal fish diversity 'hot spots' in New Zealand waters in frontal areas known for high primary production. Measurements for chlorophyll *a* at each station were not available in this study, but instead estimated concentrations over the whole

summer for gridded data (9 × 9 km) were used. This is temporally a rather coarse estimate of primary production, which may explain why it was not significant in our statistical models. The absence of statistical significance may also be because primary production does not affect Icelandic groundfish directly, but rather their prey species or species further down the food web that are often mobile themselves. Furthermore, primary production in surface layers at each station could have more effect on fish species in other stations, depending on the strength and direction of water currents.

In conclusion, we have shown that groundfish diversity varies spatially and temporally in Icelandic water. The different trends detected between the northern and southern areas illustrate the importance of performing analyses at the most appropriate scale. When examining biological variation in Icelandic waters, analyses should be performed with sufficient spatial resolution that the extensive heterogeneity in the environmental characteristics, which effect biological parameters such as species richness and diversity, can be accounted for. What might be of greater importance for the functioning of ecosystems than simply the number of species present, are the functional characteristics of the species and species interactions (Grey 2001, Hooper *et al.* 2005). Further insight into the "functional diversity" of Icelandic waters, e.g. patterns of species dominance and food web interactions, might give more insight into the effects of ocenographical variability on the fish community.

References:

Anon. (1996). Manual for geo Splus programs. (Marine Research Institute, Reykjavik).

Anon. (2008a). Nytjastofnar sjávar 2007/2008. Aflahorfur fiskveiðiárið 2008/2009. (State of Marine Stocks in Icelandic Waters 2007/2008. Prospects for the Quota Year 2008/2009.) Hafrannsóknastofnunin, fjölrit 138.

Anon. (2008b). Þættir úr vistfræði sjávar 2007. (Environmental conditions in Icelandic waters 2007.) Hafrannsóknastofnunin, fjölrit 139.

Ástþórsson ÓS, Gíslason Á, Jónsson S. (2007). Climate variability and the Icelandic marine ecosystem. Deep-Sea Research II 54,2456-2477.

Ástþórsson ÓS, Pálsson J. (2006). New fish records and records of rare southern species in Icelandic waters in the warm period 1996-2005. ICES CM C:20.

Bianchi G, Gislason H, Graham K, Hill L, Jin X, Koranteng K, Manickchand-Heileman S, Paya I, Sainsbury K, Sanchez F, Zwanenburg K. (2000). Impact of fishing on size composition and diversity of demersal fish communities. ICES Journal of Marine Science 57,558-571.

Björnsson H, Pálsson ÓK. (2004). Distribution patterns and dynamics of fish stocks under recent climate change in Icelandic waters. ICES CM K:30.

Björnsson H, Sólmundsson J, Kristinsson K, Steinarsson BÆ, Hjörleifsson E, Jónsson E, Pálsson J, Pálsson ÓK, Bogason V. (2007). Stofnmæling botnfiska á Íslandsmiðum (SMB) 1985-2006 og Stofnmæling botnfiska að haustlagi (SMH) 1996-2006. (The Icelandic groundfish surveys in March 1985-2006 and in October 1996-2006.) Hafrannsóknastofnunin, fjölrit 131.

Brander K, Blom G, Borges MF, Erzini K, Henderson G, MacKenzie BR, Mendes H, Ribeiro J, Santos AMP, Toresen R. (2003). Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? ICES Marine Science Symposia 219,261-270.

Gíslason Á, Ástþórsson ÓS. (2004). Distribution pattern of zooplankton around Iceland in spring. Sarsia 20,85-94.

Grey JS. (1994). Is deep-sea diversity really so high? Species diversity of the Norwegian continental shelf. Marine.Ecology Progress Series 112, 205-209.

Grey JS. (2001). Marine diversity: the paradigms in patterns of species richness examined. Scientia Marina 65, 41-56.

Hastie TJ, Tibshirani RJ. (1990). Generalized Additive Models. (Chapman & Hall, London).

Hiddink JG, ter Hofstede R. (2008). Climate induced increases in species richness of marine fishes. Global Change Biology 14,453-460.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S and others. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75,3-35.

Jónsson S, Valdimarsson H. (2005). Recent developments in oceanographic research in Icelandic waters. In Iceland - Modern processes and past environments. Caseldine C, Russell A, Harðardóttir J, Knudsen O, eds. (Elsevier, Amst.). pp 79-92.

Kaluzny SP, Vega SC, Cardoso TP, Shelly AA. (1998). S+ Spatial Stats. (Springer-Verlag, New York). pp xvi + 327.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA. (2001). Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science 294,804-808.

Macpherson E. (2002). Large-scale species-richness gradients in the Atlantic Ocean. Proceedings of the Royal Society B 269,1715-1720.

Macrander A, Kase RH, Send U, Valdimarsson H, Jónsson S. (2007). Spatial and temporal structure of the Denmark Strait Overflow revealed by acoustic observations. Ocean Dynamics 57,75–89.

Malmberg S-A, Valdimarsson H. (2003). Hydrographic conditions in Icelandic waters, 1990-1999. ICES Marine Science Symposia 219,50-60.

McClatchie S, Millar RB, Webster F, Lester PJ, Hurst R, Bagley N. (1997). Demersal fish community diversity off New Zealand: Is it related to depth, latitude and regional surface phytoplankton? Deep-Sea Research I 44,647-667.

Mouillot D, Lepretre A. (1999). A comparison of species diversity estimators. Population Ecology 41,203-215.

Poulard J-C, Blanchard F. (2005). The impact of climate change on the fish community structure of the eastern continental shel of the Bay of Biscay. ICES Journal of Marine Science 62,1436-1443.

Rose GA. (2005). On distributional responses of North Atlantic fish to climate change. ICES Journal of Marine Science 62,1360-1374.

Simpson EH. (1949). Measurement of diversity. Nature 163,688.

Sólmundsson J, Jónsson E, Björnsson H. (2007). Recent changes in the distribution and abundance of monkfish (*Lophius piscatorius*) in Icelandic waters. ICES CM K:02,16.

Sousa P, Azevedo M, Gomes MC. (2006). Species-richness patterns in space, depth, and time (1989-1999) of the Portuguese fauna sampled by bottom trawl. Aquatic Living Resources 19,93-103.

Tolimieri N. (2007). Patterns in species richness, species density, and evenness in groundfish assemblages on the continental slope of the U.S. Pacific coast. Environmental Biology of Fishes 78,241-256.

Valdimarsson H, Björnsson H, Guðmundsson K. (2005). Breytingar á ástandi sjávar á Íslandsmiðum og áhrif þeirra á lífríkið (Climate variability in Icelandic waters and effects on marine biota). Hafrannsóknastofnunin Fjölrit 116,23-28.

Vilhjálmsson H. (1997). Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century. Rit Fiskideildar 13,9-29.

Willig MR, Kaufman DM, Stevens RD. (2003). Latitudinal Gradients of Biodiversity: Patterns, Process, Scale and Synthesis. Annual Review of Ecology, Evolution and Systematics 34,273-309.

Wood SN, Augustin NH. (2002). GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecological Modelling 157,157-177.

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR and others. (2006). Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science 314,787 - 790.

Zar JH. (1999). Biostatical Analysis. (Prentice Hall International, inc.).

# Appendix 1

Species included in the analysis. Common Icelandic and English names are given as well as Latin names. Also given, for each year, are proportions (%) of stations used in the analysis at which the species were caught.

| | | | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Myxini** | | | | | | | | | | | | | | |
| Myxiniformes | | | | | | | | | | | | | | |
| *Myxine jespersenae* | slímáll | Jespersen's hagfish | 0.4 | | | | | | | 0.3 | | 0.3 | 0.6 | 0.3 |
| **Monorhina** | | | | | | | | | | | | | | |
| Petromyzoniformes | | | | | | | | | | | | | | |
| *Petromyzon marinus* | sæsteinsuga | Sea lamprey | | 0.3 | 0.3 | | | | 0.3 | 0.3 | 0.7 | | 0.6 | 1.3 |
| **Condrichtyes** | | | | | | | | | | | | | | |
| Chimaeriformes | | | | | | | | | | | | | | |
| *Chimaera monstrosa* | geirnyt | Rabbit fish | 2.7 | 4.9 | 4.1 | 3.9 | 3.9 | 4.2 | 3.9 | 3.6 | 1.3 | 3.2 | 3.6 | 4.9 |
| *Hydrolagus affinis* | stuttnefur | Smalleyed rabbitfish | | 0.3 | | 0.7 | | 0.6 | 0.6 | 0.6 | 0.7 | | | 0.3 |
| *Hydrolagus pallidus* | hvítnefur | | | | | | | | | | | | 0.3 | |
| *Harriotta raleighana* | langnefur | Narrownose chimaera | 1.1 | 1.0 | 0.3 | 1.0 | 0.6 | 0.6 | 0.6 | 1.0 | 1.3 | 0.3 | | 0.6 |
| *Rhinochimaera atlantica* | trjónufiskur | Spearnose chimaera | 1.9 | 2.4 | 0.3 | 3.3 | 2.6 | 4.2 | 1.9 | 1.6 | 1.3 | 3.3 | 3.9 | 1.9 |
| Carcharhiniformes | | | | | | | | | | | | | | |
| *Apristurus laurussonii* | Gíslaháfur | Iceland catshark | 4.2 | 4.2 | 5.1 | 3.9 | 2.9 | 3.9 | 4.9 | 2.9 | 1.3 | 2.9 | 3.2 | 3.6 |
| *Apristurus aphyodes* | Mattaháfur | | | | | | | | | | | | | 0.3 |
| *Galeus murinus* | Jensensháfur | Mouse catshark | 3.0 | 3.8 | 1.7 | 2.9 | 1.9 | 4.9 | 4.2 | 3.2 | 3.9 | 5.9 | 4.2 | 4.2 |
| Squaliformes | | | | | | | | | | | | | | |
| *Centroscyllium fabricii* | svartháfur | Black dogfish | 15.1 | 16.0 | 17.0 | 16.1 | 13.6 | 16.3 | 15.0 | 15.3 | 14.1 | 14.7 | 15.3 | 15.0 |
| *Etmopterus princeps* | dökkháfur | Great lanternshark | 8.3 | 7.6 | 6.8 | 7.9 | 6.2 | 8.2 | 8.2 | 7.1 | 5.2 | 5.5 | 9.1 | 6.2 |
| *Etmopterus spinax* | loðháfur | Velvet belly lantern shark | 1.9 | 2.1 | 1.7 | 2.9 | 1.6 | 2.3 | 2.6 | 2.3 | 2.3 | 3.6 | 3.9 | 4.2 |
| *Centroscymnus coelolepis* | gljáháfur | Portuguese dogfish | 5.7 | 6.2 | 3.7 | 3.9 | 1.9 | 5.6 | 2.9 | 2.9 | 1.3 | 2.3 | 0.6 | 0.3 |
| *Centroscymnus crepidater* | Þorsteinsháfur | Longnose velvet dogfish | 1.9 | 1.7 | 3.4 | 2.9 | 3.6 | 1.6 | 3.3 | 2.9 | 3.9 | 1.6 | 4.9 | 1.3 |
| *Somniosus microcephalus* | hákarl | Greenland shark | | | 0.7 | | | | | 0.3 | | | 0.6 | |
| *Lepidorhinus squamosus* | rauðháfur | Leafscale gulper shark | 0.8 | 0.3 | | 0.7 | | 1.3 | 1.0 | 1.0 | 0.3 | 0.6 | 0.6 | 0.3 |
| *Deania calceus* | flatnefur | Birdbeak dogfish | 1.1 | 1.0 | 0.7 | 1.0 | 0.6 | 1.3 | 0.6 | 1.0 | 0.3 | | 0.3 | |
| *Squalus acanthias* | háfur | Piked dogfish | 3.8 | 2.8 | 2.7 | 3.3 | 2.9 | 2.0 | 2.3 | 1.0 | 1.6 | 1.9 | 1.6 | 1.0 |

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| (Appendix 1 cont.) | | | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hexanchiformes | | | | | | | | | | | | | | |
| *Hexanchus griseus* | brandháfur | Bluntnose sixgill shark | | | | 1.4 | 0.3 | | | | | | | |
| Rajiformes | | | | | | | | | | | | | | |
| *Bathyraja spinacauda* | maríuskata | Spinetail ray | 0.4 | 2.4 | 1.7 | | 1.6 | 1.6 | 1.6 | 1.0 | 1.6 | 1.0 | 1.3 | 2.3 |
| *Amblyraja hyperborea* | skjótta skata | Arctic skate | 7.2 | 7.6 | 8.2 | 8.2 | 10.7 | 10.1 | 10.5 | 10.1 | 11.8 | 9.4 | 13.0 | 10.7 |
| *Amblyraja radiata* | tindaskata | Thorny skate | 56.8 | 60.4 | 56.1 | 54.8 | 52.9 | 48.4 | 52.3 | 54.9 | 56.1 | 59.0 | 57.1 | 51.5 |
| *Dipturus batis* | skata | Blue skate | 0.8 | | 2.4 | 1.3 | 1.0 | 0.3 | 0.6 | 1.0 | 0.3 | 1.0 | 1.6 | 1.3 |
| *Raja lintea* | hvítaskata | Sailray | | | | | | | | | | | 0.6 | |
| *Rajella bathyphila* | djúpskata | Deepwater ray | | | | | 0.3 | | | 0.3 | | 0.3 | | |
| *Rajella fyllae* | pólskata | Round ray | 3.8 | 0.7 | 1.4 | 0.7 | 3.2 | 5.2 | 5.9 | 3.2 | 3.9 | 4.2 | 5.8 | 5.5 |
| **Actinopterygii** | | | | | | | | | | | | | | |
| Albuliformes | | | | | | | | | | | | | | |
| *Notacanthus chemnitzii* | broddabakur | Spiny eel | 12.9 | 16.7 | 16.3 | 13.1 | 14.0 | 14.7 | 12.7 | 12.7 | 12.5 | 11.7 | 13.3 | 12.0 |
| *Polyacanthonotus rissoanus* | fjölbroddabakur | Smallmouth spiny eel | 1.1 | 0.3 | | | | | 0.6 | | 0.7 | | 1.3 | |
| Anguiliformes | | | | | | | | | | | | | | |
| *Synaphobranchus kaupi* | djúpáll | Kaup's arrowtooth eel | 7.9 | 6.9 | 7.8 | 6.6 | 5.5 | 7.5 | 7.8 | 7.8 | 9.2 | 9.4 | 9.4 | 10.1 |
| *Nessorhampus ingolfianus* | nefáll | Duckbill oceanic eel | | | | | | | | 0.3 | | | 0.3 | |
| *Nemichthys scolopaceus* | álsnípa | Slender snipe eel | 1.9 | 1.0 | | 0.3 | 1.0 | | 1.3 | 0.6 | | 1.6 | 0.6 | 0.3 |
| *Serrivomer beani* | trjónuáll | Bean's sawtoothed eel | 3.0 | 2.1 | 0.7 | 1.0 | 1.6 | 2.9 | 2.0 | 4.5 | 6.6 | 4.6 | 5.2 | 5.9 |
| Clupeiformes | | | | | | | | | | | | | | |
| *Clupea harengus* | síld | Herring | 28.8 | 29.5 | 35.4 | 33.8 | 34.1 | 34.3 | 30.1 | 33.4 | 32.5 | 26.7 | 28.6 | 32.9 |
| Osmeriformes | | | | | | | | | | | | | | |
| *Argentina silus* | gulllax | Greater argentine | 23.1 | 25.7 | 30.9 | 28.8 | 25.0 | 34.0 | 31.4 | 29.9 | 28.5 | 30.3 | 29.2 | 34.8 |
| *Nasenia groenlandica* | Grænlandsnaggur | Greenland argentine | | 0.3 | 0.3 | | | | | | 1.0 | | 0.3 | |
| *Bathylagus euryops* | skjár | Doitre blacksmelt | 2.3 | 2.8 | 5.1 | 2.3 | 1.6 | 1.6 | 3.6 | 7.5 | 9.8 | 4.2 | 7.5 | 6.5 |
| *Alepocephalus agassizii* | berhaus | Agassiz' slickhead | 2.3 | 1.7 | 2.7 | 1.3 | 1.9 | 2.6 | 2.0 | 1.3 | 1.6 | 1.3 | 1.6 | 2.3 |
| *Alepocephalus bairdii* | gjölnir | Baird's smooth-head | 8.7 | 10.1 | 9.5 | 9.2 | 8.8 | 9.5 | 10.1 | 8.8 | 8.5 | 9.1 | 9.1 | 9.4 |
| *Bajacalifornia megalops* | slétthaus | Bigeye smooth-head | | 0.3 | | 0.7 | | | | | | | 0.3 | 0.3 |
| *Rouleina attrita* | mjúkhaus | Softskin smooth-head | | | | | | | | | 0.7 | | | 0.3 |
| *Xenodermichthys copei* | bersnati | Bluntsnout smooth-head | 0.4 | 1.7 | | | 0.6 | 2.3 | 0.3 | 1.3 | 1.0 | 0.6 | 0.3 | 2.3 |
| *Holtbyrnia anomala* | græðisangi | Bighead searsid | | | | 0.7 | | 1.6 | 1.0 | 1.0 | 1.0 | 1.0 | 1.6 | 1.0 |
| *Holtbyrnia macrops* | marangi | Bigeye searsid | | | | | | 0.3 | | | | | 0.3 | |

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| (Appendix 1 cont.) | | | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Maulisia mauli* | njarðarangi | Maul's searsid | | | | 0.3 | 0.3 | | | | | | | |
| *Normichthys operosus* | sæangi | Multipore searsid | | 0.3 | | | | 0.3 | | | | | | |
| *Searsia koefoedi* | ægisangi | Koefoed's searsid | | | | | | 0.3 | | 0.3 | | 1.0 | | |
| Stomiiformes | | | | | | | | | | | | | | |
| *Polyipnus polli* | orðufiskur | | | | | | | | | | | | | 0.3 |
| *Gonostoma bathyphilum* | ránarstirnir | Spark anglemouth | | | | | | | | | | | 0.6 | 0.3 |
| Astronesthidae | meitaætt | | | | | | | | | | 1.0 | | | |
| *Astronesthes gemmifer* | stjarnmeiti | Snaggletooth | | | | | | | | | 0.3 | | | |
| *Borostomias antarticus* | broddatanni | Large-eye snaggletooth | 1.1 | 0.3 | 1.0 | 0.3 | | 0.3 | 0.3 | 1.0 | 1.6 | 0.6 | 2.9 | 4.2 |
| *Stomias boa ferox* | marsnákur | | 0.8 | | | | | | | 0.3 | 1.3 | | 1.0 | 1.0 |
| *Chaulious sloani* | Slóans-gelgja | Sloane's viperfish | 4.2 | 1.4 | 0.3 | 0.3 | | 0.6 | 2.0 | 4.5 | 2.0 | 0.6 | 1.6 | 1.0 |
| *Melanostomias bartonbeani* | þráðskeggur | Scaleless black dragonfish | | | | | | | | | 0.3 | | | |
| *Malacosteus niger* | kolbíldur | Stoplight loosejaw | 0.8 | | | | | 0.6 | 0.6 | 0.3 | 2.0 | 1.3 | 1.0 | 2.3 |
| Melanostomiidae | kolskeggjaætt | | | | 0.3 | | | | | | 0.7 | | | |
| Aulopiformes | | | | | | | | | | | | | | |
| *Scopelosaurus lepidus* | uggi | Blackfin waryfish | 3.8 | 6.6 | 2.7 | 4.3 | 1.6 | 3.3 | 4.6 | 3.9 | 7.9 | 5.5 | 7.1 | 6.8 |
| Paralepididae | geirsílaætt | Barracudinas | 10.2 | 14.2 | 10.2 | 9.2 | 9.4 | 9.8 | 11.8 | 12.3 | 10.5 | 9.4 | 11.4 | 7.5 |
| Lampridiformes | | | | | | | | | | | | | | |
| *Trachipterus articus* | vogmær | Deal fish | | | | | | | | | 0.3 | | 0.6 | 0.3 |
| Ophidiiformes | | | | | | | | | | | | | | |
| Carapidae | sníkjaætt | | | | | 0.3 | | | | | | | 0.3 | |
| *Cataetyx laticeps* | flathaus | | 0.4 | | | | | 0.3 | 0.3 | 0.3 | | | | |
| Gadiformes | | | | | | | | | | | | | | |
| *Trachyrhynchus murrayi* | langhalabróðir | Roughnose grenadier | 9.5 | 10.4 | 9.2 | 8.5 | 7.5 | 9.1 | 8.8 | 8.8 | 8.5 | 8.8 | 9.4 | 7.2 |
| *Coryphaenoides rupestris* | slétti langhali | Roundnose grenadier | 11.4 | 12.1 | 12.2 | 11.8 | 12.3 | 12.7 | 13.1 | 12.3 | 13.1 | 12.7 | 12.7 | 12.0 |
| *Coryphaenoides guentheri* | ingólfshali | Günther's grenadier | | 3.8 | 3.7 | 2.0 | 3.9 | 4.6 | 6.2 | 7.8 | 8.5 | 6.8 | 8.4 | 5.9 |
| *Macrourus berglax* | snarphali | Roughhead grenadier | 11.4 | 10.1 | 10.5 | 9.5 | 9.1 | 11.8 | 7.8 | 7.8 | 6.6 | 7.8 | 9.1 | 5.5 |
| *Hollowsnout grenadier* | trjónuhali | Coelorinchus coelorhincus | | | | | | | | | | | | 0.3 |
| *Antimora rostrata* | fjólumóri | Blue antimora | 4.2 | 4.5 | 4.4 | 2.9 | 2.6 | 5.2 | 4.2 | 6.2 | 5.2 | 4.2 | 5.2 | 3.3 |
| *Halargyreus johnsonii* | silfurþvari | Slender codling | | | 1.0 | | 0.3 | 1.0 | 1.3 | 1.6 | 1.3 | 2.3 | 1.3 | 1.0 |
| *Lepidon eques* | bláriddari | North Atlantic codling | 6.8 | 8.7 | 7.8 | 8.5 | 7.8 | 8.8 | 9.5 | 9.1 | 10.8 | 9.4 | 11.0 | 9.8 |
| *Onogadus argentatus* | (rauða) sævesla | Arctic rockling | 21.6 | 12.5 | 13.3 | 10.5 | 17.2 | 19.3 | 13.7 | 12.7 | 9.8 | 11.1 | 17.5 | 11.1 |

| (Appendix 1 cont.) | | | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gaidrosarus vulgaris* | bletta | Three-bearded rockling | 0.4 | | | | | | | | | | | |
| *Enchelyopus cimbrius* | blákjafta | Fourbeard rockling | 6.1 | 4.9 | 3.7 | 4.9 | 4.5 | 4.6 | 4.9 | 4.5 | 5.6 | 6.8 | 3.9 | 4.9 |
| *Phycis blennoides* | litla brosma | Greater forkbeard | 1.5 | 1.0 | | 1.0 | 0.3 | | | 0.3 | | 0.3 | 0.6 | 1.9 |
| *Brosme brosme* | keila | Tusk | 16.7 | 12.8 | 9.9 | 11.1 | 8.4 | 14.7 | 14.4 | 14.9 | 16.4 | 14.7 | 18.8 | 21.2 |
| *Molva dypterygia* | blálanga | Blue ling | 18.6 | 15.3 | 15.6 | 20.0 | 15.9 | 19.3 | 18.9 | 20.4 | 18.7 | 22.8 | 24.3 | 22.5 |
| *Molva molva* | langa | Ling | 5.7 | 3.5 | 3.7 | 5.2 | 2.6 | 3.3 | 4.2 | 6.5 | 9.8 | 11.4 | 7.8 | 14.3 |
| *Boreogadus saida* | ískóð | Polar cod | 9.8 | 24.6 | 16.3 | 9.2 | 19.5 | 23.2 | 19.6 | 8.1 | 2.6 | 15.3 | 12.3 | 12.7 |
| *Gadiculus argenteus thori* | silfurkóð | Silvery pout | | 0.3 | | 0.7 | 0.3 | 1.3 | 0.6 | 0.6 | 1.6 | 1.9 | 1.3 | 1.0 |
| *Gadus morhua* | þorskur | Cod | 68.2 | 61.8 | 63.9 | 64.6 | 61.0 | 63.1 | 64.4 | 70.1 | 69.2 | 69.7 | 63.3 | 61.6 |
| *Melanogrammus aeglefinus* | ýsa | Haddock | 42.4 | 38.9 | 44.6 | 45.9 | 43.2 | 46.1 | 44.4 | 52.9 | 48.2 | 49.2 | 47.1 | 49.8 |
| *Merlangius merlangus* | lýsa | Whiting | 14.4 | 16.7 | 17.0 | 15.7 | 12.7 | 20.0 | 17.3 | 29.2 | 35.7 | 33.9 | 28.2 | 29.3 |
| *Micromesistius poutassou* | kolmunni | Blue whiting | 29.2 | 25.7 | 29.6 | 30.8 | 33.1 | 39.5 | 46.1 | 54.5 | 48.2 | 35.2 | 38.0 | 30.3 |
| *Pollachius virens* | ufsi | Saithe | 18.6 | 16.3 | 19.0 | 17.4 | 20.8 | 25.2 | 26.5 | 38.6 | 41.3 | 42.0 | 39.0 | 40.1 |
| *Trisopterus esmarki* | spærlingur | Norway pout | 14.0 | 15.3 | 20.1 | 22.0 | 20.8 | 21.9 | 20.0 | 34.4 | 31.5 | 25.4 | 23.0 | 28.0 |
| Lophiiformes | | | | | | | | | | | | | | |
| *Lophius piscatorius* | skötuselur | Monkfish | 2.3 | 2.4 | 2.4 | 3.3 | 1.3 | 2.3 | 2.3 | 3.6 | 11.1 | 6.2 | 6.5 | 9.1 |
| *Melanocetus johnsonii* | svartdjöfull | Humpback anglerfish | | | | | | | | | 0.3 | 0.3 | | 0.3 |
| *Chaenophryne draco* | drekahyrna | Smooth dreamer | | | | | | | 0.3 | 0.3 | 0.3 | | | |
| *Chaenophryne longiceps* | slétthyrna | Can-opener smoothdream | 1.1 | 0.3 | | | 0.3 | | 0.3 | | | | 0.3 | |
| *Ceratias holboelli* | sædjöfull | Krøyer's deep sea angler fish | | 0.3 | 0.7 | | | | 0.3 | 0.3 | 0.7 | 0.6 | | 0.3 |
| *Cryptopsaras couesii* | surtur | Triplewart seadevil | | | | | | 0.3 | | 0.3 | 0.3 | 0.3 | | 0.3 |
| *Linophryne lucifer* | surtla | | | | | | | | | | | | | 0.3 |
| *Linophryne coronata* | surtlusystir | | | | | | | | 0.3 | | | | | 0.3 |
| *Himantolophus groenlandicus* | lúsífer | Atlantic footballfish | | | | | | | | | | 0.3 | | |
| Stefanoberyciformes | | | | | | | | | | | | | | |
| Melamphaidae | serklingaætt | | | | | | 0.3 | | | | | | | |
| *Poromitra crassiceps* | kambhaus | Crested bigscale | | | | | | | 0.3 | | | | | |
| *Scopelogadus beanii* | kistufiskur | | | 0.7 | 0.7 | | | 2.0 | 0.3 | 1.3 | 3.6 | 1.0 | 2.3 | 2.6 |
| *Rondeletia loricata* | rauðskoltur | Redmouth whalefish | | | | | | | | | | | 0.3 | |
| *Anaplogaster cornuta* | bjúgtanni | Common fangtooth | | 0.3 | 0.7 | | 0.3 | 0.3 | 0.6 | 0.6 | 0.7 | 1.0 | 0.6 | 0.3 |
| *Hoplostethus atlanticus* | búrfiskur | Orange roughy | 0.8 | 1.0 | 0.7 | 1.0 | 0.6 | 1.0 | 0.6 | 1.3 | 1.0 | 0.6 | 0.6 | 0.6 |
| *Entelurus aequoreus* | stóra sænál | Snake pipefish | | | | | | | | | | 0.6 | 0.6 | |

| (Appendix 1 cont.) | | | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Helicolenus dactylopterus* | svartgóma | Blackbelly rosefish | | | 0.3 | 0.3 | 0.3 | | 1.0 | 1.9 | 0.7 | 1.0 | 2.6 | 2.6 |
| *Sebastes marinus* | gullkarfi | Golden redfish | 64.8 | 60.8 | 59.9 | 59.3 | 55.8 | 57.8 | 56.2 | 61.7 | 59.0 | 59.6 | 58.4 | 59.0 |
| *Sebastes mentella* | djúpkarfi | Deepwater redfish | 30.7 | 27.8 | 28.9 | 28.5 | 32.5 | 31.7 | 33.7 | 25.3 | 28.2 | 24.1 | 28.9 | 21.8 |
| *Sebastes viviparus* | litli karfi | Norway haddock | 30.7 | 28.1 | 29.9 | 30.8 | 31.2 | 35.6 | 33.3 | 42.9 | 38.4 | 44.0 | 42.5 | 49.2 |
| *Eutrigla gurnardus* | urrari | Grey gurnard | 4.2 | 3.1 | 3.1 | 4.3 | 3.2 | 3.6 | 5.2 | 3.9 | 4.9 | 5.5 | 5.5 | 6.8 |
| *Artediellus atlanticus* | krækill | Atlantic hookear sculpin | 18.9 | 14.9 | 16.7 | 15.7 | 20.8 | 18.6 | 15.7 | 14.9 | 12.5 | 16.3 | 14.0 | 14.3 |
| *Icelus bicornis* | fuðriskill | Twohorn sculpin | 0.8 | | | | | 0.3 | | | | | | |
| *Myoxocephalus scorpius* | marhnútur | Shorthorn sculpin | 0.4 | | | | | 0.3 | | | 0.3 | 0.3 | | |
| *Triglops murrayi* | þrömmungur | Moustache sculpin | 18.2 | 14.2 | 12.2 | 12.1 | 12.0 | 12.4 | 11.4 | 8.1 | 6.9 | 8.5 | 8.4 | 11.1 |
| *Leptagonus decagonus* | áttstrendingur | Atlantic poacher | 17.4 | 10.1 | 8.2 | 5.9 | 16.2 | 16.7 | 17.3 | 10.7 | 8.8 | 12.7 | 9.7 | 6.8 |
| *Cottunculus microps* | marhnýtill | Polar sculpin | 14.4 | 2.8 | 1.0 | 2.6 | 12.3 | 11.8 | 10.5 | 3.6 | 2.3 | 6.8 | 7.1 | 5.9 |
| *Cottunculus thomsonii* | tómasarhnýtill | Pallid sculpin | 1.1 | 1.7 | 3.1 | 1.3 | 1.0 | 2.6 | 0.6 | 1.6 | 1.0 | 0.6 | 2.9 | 0.3 |
| *Cyclopterus lumpus* | hrognkelsi | Lumpsucker | 12.1 | 14.6 | 10.5 | 7.5 | 8.1 | 10.8 | 12.1 | 8.4 | 11.1 | 15.0 | 14.0 | 12.0 |
| *Careproctus micropus* | litli hveljusogfiskur | | 0.8 | | | | | | | | | | | |
| *Careproctus reinhardti* | hveljusogfiskur | Sea tadpole | 17.4 | 12.8 | 10.2 | 9.5 | 18.5 | 22.9 | 18.9 | 16.2 | 14.4 | 13.3 | 16.2 | 13.3 |
| *Liparis fabricii* | dökki sogfiskur | Gelatinous snailfish | 7.6 | 0.3 | 0.3 | 1.3 | 4.5 | 5.9 | 3.9 | 3.6 | 6.2 | 3.2 | 1.9 | 3.9 |
| *Liparis liparis* | stóri sogfiskur | Striped seasnail | | | | 0.3 | 0.3 | | | | | | | |
| *Paraliparis bathybius* | úthafssogfiskur | Black seasnail | 0.8 | 1.4 | 0.7 | 0.3 | | | 1.3 | 0.6 | 1.0 | 0.6 | 0.3 | 0.6 |
| *Paraliparis copei* | djúphafssogfiskur | Blacksnout seasnail | | | | | | | | | | | 1.0 | |
| *Rhodichthys regina* | rósafiskur | Threadfin seasnail | 1.5 | | | | 0.3 | 0.6 | 0.6 | 1.0 | 0.6 | 1.3 | 1.6 | 0.6 |
| Perciformes | | | | | | | | | | | | | | |
| *Trachurus trachurus* | brynstirtla | Atlantic horse mackerel | | 0.3 | 1.0 | | | | | | 0.3 | | 0.6 | |
| *Platyberyx opalescens* | ennisfiskur | | 0.8 | 0.7 | | | | 0.3 | | 0.6 | | | | |
| *Gymnelus retrodorsalis* | guli brandáll | Aurora unernak | 0.4 | | | | 0.3 | | | | | 0.3 | 0.3 | |
| *Lycenchelys kolthoffi* | blettaálbrosma | Checkered wolf eel | 0.8 | | | | | | | | 0.3 | 0.3 | | 0.3 |
| *Lycenchelys muraena* | álbrosma | Moray wolf eel | | 0.3 | | | | | | | | | | |
| *Lycodes esmarki* | dílamjóri | Esmark's eelpout | 22.0 | 19.1 | 18.4 | 16.7 | 19.2 | 16.0 | 15.4 | 14.3 | 14.4 | 13.3 | 14.0 | 13.7 |
| *Lycodes eudipleurostictus* | tvírákamjóri | Doubleline eelpout | 17.4 | 14.2 | 11.6 | 13.4 | 17.5 | 19.3 | 17.6 | 13.6 | 16.7 | 14.7 | 16.2 | 15.6 |
| *Lycodes vahli* | litli mjóri | Vahl's eelpout | 26.5 | 19.1 | 19.4 | 22.0 | 23.7 | 18.3 | 15.7 | 10.1 | 9.2 | 17.3 | 11.0 | 9.4 |
| *Lycodes frigidus* | bleikmjóri | Glacial eelpout | | | | | | | | | | 0.3 | 0.6 | |
| *Lycodes pallidus* | fölvi mjóri | Pale eelpout | 11.4 | 4.2 | 5.8 | 5.2 | 10.4 | 13.7 | 11.8 | 6.5 | 9.2 | 4.6 | 11.0 | 8.8 |
| *Lycodes reticulatus* | blettamjóri | Arctic eelpout | 13.6 | 10.1 | 9.2 | 8.2 | 11.4 | 6.9 | 6.5 | 5.2 | 4.3 | 6.2 | 7.1 | 6.8 |
| *Lycodes seminudus* | hálfberi mjóri | Longear eelpout | 13.3 | 10.1 | 11.2 | 7.9 | 10.7 | 13.1 | 12.1 | 8.1 | 10.5 | 10.4 | 7.1 | 9.4 |

| (Appendix 1 cont.) | | | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lycodes squamiventer* | nafnlausi mjóri | Scalebelly eelpout | 2.6 | 1.4 | 2.0 | 0.7 | 1.3 | 2.0 | 2.0 | 1.3 | | 1.9 | 2.3 | 0.6 |
| *Lycodes adolfi* | Grænlandsmjóri | Adolf's eelpout | | | | | | | | | | | | 0.3 |
| *Leptoclinus maculatus* | flekkjamjóni | Daubed shanny | 1.1 | 1.0 | 2.7 | 0.7 | 1.3 | 1.6 | 0.6 | | | | 0.6 | 1.3 |
| *Lumpenus lampretaeformis* | stóri mjóni | Snakeblenny | 1.5 | 2.4 | 5.8 | 5.9 | 3.2 | 2.6 | 2.0 | 2.3 | 1.3 | 0.6 | 1.3 | 0.6 |
| *Anarhichas denticulatus* | blágóma | Northern wolffish | 9.5 | 13.9 | 6.5 | 9.2 | 7.5 | 10.5 | 7.2 | 8.4 | 3.3 | 6.2 | 8.1 | 6.8 |
| *Anarhichas lupus* | steinbítur | Wolffish | 37.9 | 33.7 | 34.3 | 38.4 | 34.4 | 38.2 | 35.6 | 37.0 | 36.1 | 36.2 | 36.7 | 32.6 |
| *Anarhichas minor* | hlýri | Spotted wolffish | 31.8 | 24.6 | 25.8 | 27.9 | 24.0 | 27.1 | 25.5 | 24.3 | 23.9 | 23.1 | 25.0 | 16.3 |
| *Chiasomodon niger* | gleypir | Black swallower | | | 0.3 | | 0.3 | 0.3 | | 1.0 | 0.3 | | 0.3 | |
| *Ammodytes marinus* | marsíli | Lesser sand-eel | 1.9 | 1.0 | 1.7 | 2.9 | 2.6 | 2.6 | 2.9 | 0.3 | | 0.6 | 1.0 | 0.6 |
| *Ammodytes tobianus* | sandsíli | Small sandeel | | 1.0 | 0.3 | | | 0.3 | 0.3 | 0.3 | | | | |
| *Hyperoplus lanceolatus* | trönusíli | Great sandeel | | | | | | 0.3 | 0.6 | | | | | |
| *Callionymus maculatus* | flekkjaglitnir | | 0.8 | 0.3 | 0.3 | | 0.6 | 0.3 | 1.0 | 0.6 | | | | |
| *Callionymus lyra* | skrautglitnir | Dragonet | | | | | | | | | | | | 0.3 |
| *Nesiarchus nasutus* | nasi | Black gemfish | | | | | | | | | | | 0.3 | |
| *Aphanopus carbo* | stinglax | Black scabbardfish | 2.3 | 2.8 | 5.1 | 3.9 | 2.6 | 4.6 | 2.9 | 4.9 | 3.9 | 3.6 | 7.5 | 7.8 |
| *Lepidopus caudatus* | marbendill | Silver scabbardfish | | | | | | | | | | | | 0.3 |
| *Centrolophus niger* | Svarthveðnir | Blackfish | | | | | | | | 2.3 | 0.3 | 0.6 | 0.3 | |
| *Schedophilus medusophagus* | Bretahveðnir | Cornish blackfish | | | | | | | | | 0.7 | | | 1.3 |
| Pleuronectiformes | | | | | | | | | | | | | | |
| *Lepidorhombus whiffiagonis* | stórkjafta | Megrim | 7.2 | 4.9 | 4.4 | 5.2 | 7.1 | 6.2 | 7.5 | 8.8 | 8.2 | 9.4 | 8.1 | 10.1 |
| *Hippoglossoides platessoides* | skrápflúra | Long rough dab | 69.7 | 67.7 | 66.3 | 65.6 | 66.2 | 68.0 | 69.9 | 67.2 | 64.6 | 66.4 | 66.2 | 62.5 |
| *Hippoglossus hippoglossus* | lúða | Atlantic halibut | 3.0 | 2.8 | 4.4 | 5.6 | 3.6 | 3.3 | 3.3 | 4.9 | 2.9 | 4.2 | 4.2 | 2.9 |
| *Reinhardtius hippoglossoides* | grálúða | Greenland halibut | 40.1 | 42.0 | 41.8 | 41.6 | 38.3 | 39.5 | 39.5 | 39.6 | 35.4 | 36.5 | 38.0 | 35.5 |
| *Glyptocephalus cynoglossus* | langlúra | Witch | 15.9 | 12.1 | 12.9 | 15.7 | 10.1 | 11.8 | 17.3 | 16.9 | 14.7 | 18.2 | 16.9 | 20.5 |
| *Limanda limanda* | sandkoli | Dab | 9.8 | 7.6 | 6.1 | 9.5 | 8.1 | 7.8 | 9.1 | 8.1 | 7.2 | 7.2 | 8.1 | 9.4 |
| *Microstomus kitt* | þykkvalúra | Lemon sole | 25.0 | 22.2 | 21.8 | 22.9 | 20.8 | 24.2 | 24.2 | 26.3 | 24.6 | 25.4 | 26.0 | 26.1 |
| *Pleuronectes platessa* | skarkoli | Plaice | 14.4 | 12.1 | 11.2 | 11.5 | 11.7 | 11.4 | 12.7 | 15.3 | 12.5 | 14.0 | 13.3 | 11.4 |