

## ORIGINAL ARTICLE

# Spatio-temporal variations in demersal fish assemblages and diversity in the northern Gulf of St. Lawrence (Canada)

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Biodiversity; community structure; ecosystem; groundfish; multivariate analysis.

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**Abstract**

Species diversity is generally considered one of the key factors of ecosystem resilience in response to anthropogenic pressures, including fishing. In this context, the spatial and temporal changes in demersal fish assemblages and species diversity were investigated in the northern Gulf of St. Lawrence (Canada), over a 20-year period (1990–2010). Data were obtained from the summer research survey conducted by the Department of Fisheries and Oceans, and include commercial and non-commercial species. The study covers the period of groundfish fishery collapse, the moratorium period, and the post-moratorium period, and reflects various modifications in management. Multivariate statistical methods revealed two communities. A coastal community corresponds to strata located above 200 m depth and a deeper community located in the deep channels. Interannual differences in the composition of fish assemblages were observed and are mainly due to the changes in the relative biomass of some dominant species. Three diversity indices (Shannon–Wiener, Simpson's Index of Diversity and Motomura's constant) indicate a slight but significant increase of the diversity over time. This trend is due to the increase of the relative biomass of low-rank species, which may have been favoured by the prohibition of groundfish trawling after 1997 in that region. The geographical distribution of the Shannon–Wiener index also shows temporal dynamics reflecting the biomass distribution of dominant demersal species.

**Introduction**

Since the middle of the 20th century, profound changes in marine biodiversity and assemblage structure have occurred (Ward & Myers 2005; Oguz & Gilbert 2007; Barausse *et al.* 2011). Several factors are considered to have driven those changes, such as exploitation, pollution, habitat loss induced by anthropogenic activities, and recent warming of the climate system (Jennings & Kaiser 1998; Gray *et al.* 2005; Poulard & Blanchard 2005; Rochet *et al.* 2010). Fishing is regarded as the primary factor affecting ocean environments. Fishing changes the characteristics of the exploited species, for example by reducing biomass, changing the density and spatial distribution, and decreasing the average size of individuals, or the age

of sexual maturity. The United Nations Food and Agriculture Organization (FAO) estimates that one-third of world fish stocks are overexploited (Food & Agriculture Organisation (F.A.O.) 2009). Several stocks are now in a collapsed state (Myers & Worm 2003); Canada is not an exception. In the Canadian Atlantic, a general decline of groundfish stocks was noticed starting in the 1970s (Zwanenburg 2000), the most obvious example being the cod stocks (*Gadus morhua*) in Canadian Atlantic (Hutchings 1996; Myers *et al.* 1996a,b), which have experienced a series of moratoria since 1992. In fact, most Atlantic Canadian groundfish fisheries were affected; in 1995, 24 of 50 stocks were closed to direct fishing (Brêthes 1998).

Fishing indirectly affects the community structure and the global functioning of ecosystems (Jennings & Kaiser

1998; Shears & Babcock 2003; Gray *et al.* 2005; Genner *et al.* 2010). Several studies demonstrated the loss of diversity in the marine environment arising from the exploitation of fish populations. Following the intensification of fishing activities occurring within the past 50 years, changes in the trophic structure of demersal fish communities have been documented, specifically the replacement of long-lived species by smaller short-lived species (Piet & Jennings 2005; Dään *et al.* 2005; Genner *et al.* 2010). Changes in size, abundance and biomass have been described, especially by Greenstreet & Hall (1996), Sainsbury *et al.* (1997) and Haedrich & Barnes (1997). In the Gulf of Thailand, the extensive changes in the demersal fish communities were linked to the rapid expansion of the trawl fishing industry after 1960 (Pauly 1988; Christensen 1998). Pauly *et al.* (1998) found that the mean trophic level of the world landings was decreasing from year to year. Essington *et al.* (2006) observed that this decline in the mean trophic level could be induced by the expansion of the exploitation of species at low trophic levels. Revising both landings and scientific survey data in several world ecosystems, Branch *et al.* (2010) have shown that fisheries overexploited most trophic levels, which could have intensified fisheries collapses. That might have been the case for Atlantic Canadian fisheries.

Changes in the size structures of species in the systems were particularly explored. Hutchings & Myers (1994) noted that overfishing not only caused the decline of cod (*Gadus morhua*) off Newfoundland and Labrador, but also led to the disappearance of large individuals and a decrease in the weight of the spawners. Zwanenburg (2000) observed that the average weight of demersal species exploited in Nova Scotia has dropped dramatically, by 51% on the East Coast and 41% on the West Coast. In addition, in both regions a reduction in the size structure of species was observed. Similar effects of fishing have also been demonstrated in Australia (Sainsbury *et al.* 1999), the North Sea (Svedäng 2003) and the China Sea (Xu & Jin 2005). From an analysis of data collected in different areas of the world, Bianchi *et al.* (2000) have shown the relationship between fishing activity, the disappearance of large fish and the decrease of species diversity (richness and evenness). The same observation was made in the North Sea by Greenstreet & Hall (1996), Greenstreet *et al.* (1999), Svedäng (2003) and Genner *et al.* (2010).

The Gulf of St. Lawrence is an ecosystem historically intensively exploited. Between the 1960s and the mid-1980s, fish stocks were affected by an increase in fishing. The landings of the fisheries in the Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization (NAFO), division 4RST) during that period testify to the high fishing activity in this inland sea. Indeed, recorded catches of demersal fish fluctuated between 150,000 and 280,000

tons. In the northern Gulf, cod landings peaked at 106,000 tons in 1983, and those of redfish (*Sebastes* spp.) at 78,000 tonnes in 1992 (DFO 2011a,b, 2012a). That period was followed by a decline, since the stock of cod in the northern Gulf was closed to direct fishing in 1994, and that of redfish in 1995 (DFO 2011a, 2012a). That situation became a serious concern, prompting the Committee on the status of Endangered Wildlife in Canada (COSEWIC 2010) to recommend changing the classification of the cod population in the northern Gulf of St. Lawrence (Laurentian North unit) to endangered.

Various hypotheses have been proposed to explain this decline, including over-exploitation (Myers & Hutchings 1996; Myers *et al.* 1997; Sinclair & Murawski 1997), adverse environmental conditions (Dutil *et al.* 1998, 1999), errors in stock assessment, and poor fishing practices (Walters & Maguire 1996). Despite a significant reduction in fishing effort, no significant signs of recovery have been observed. This lack of recovery may be due to several causes, still under study. Predation on pre-recruits by herring, which population is no longer controlled by cod, was suggested (Collie *et al.* 2013). Savenkoff *et al.* (2007) have shown that intense exploitation modified the trophic structure of the northern Gulf of St. Lawrence, as top predators switched from large-bodied demersal fishes, such as cod, to marine mammals. This situation may have induced a new stable state resulting in an ecological lock, as observed in the Maine (USA) kelp forest (Steneck *et al.* 2013).

Fisheries in the Gulf of St. Lawrence have changed significantly since the mid-80 s. Fishing in the Gulf has undergone profound changes, with a decrease in mean trophic levels in the landings, the size at maturity and the average size of individuals (Fréchet 2005). Significant changes have taken place particularly during the 1990s. The introduction of the separator grate 'Nordmore' in northern prawn fishing (*Pandalus borealis*) significantly reduced the bycatch of juvenile fish. Until 1994 (the year of introduction of the moratorium on directed fishing), cod fishing was essentially a winter trawl practice. Since the reopening of the directed fishing industry in 1997, fishing activity has been conducted exclusively by fixed gears (longlines and gill nets) in the summer.

In the Gulf of St. Lawrence, though the effect of fishing on major commercial species is well documented, the effect on fish communities is poorly known. One study has described the structure of demersal fish assemblages in the northern Gulf (Chouinard & Dutil 2011). That study considers a short period of time (2004–2008) and does not have the intention of understanding spatio-temporal variations, or the various changes in fishing activity and management measures.

This paper aims at analysing the structure and diversity of the demersal fish community over two decades (1990–

2010) in the northern Gulf of St. Lawrence. It highlights the changes that might have occurred in parallel with the known changes in fishing practise and management.

**Material and Methods**

**Study area**

The study area covers 103,812 km<sup>2</sup> in the northern Gulf of St. Lawrence (North-West Atlantic Fisheries Organization, NAFO, divisions 4RS) (Fig. 1). The region is physically and topographically heterogeneous (Koutitonsky & Bugden 1991). It consists of four distinct areas: a shallow shelf (<100 m) off Newfoundland’s west coast, a shelf on Quebec’s North Shore characterized by its uneven bottom, the Laurentian Channel, which extends from Cabot Strait to the centre of the Gulf and can reach 500 m in depth, and the Esquiman Channel, which connects the Laurentian Channel to the Strait of Belle Isle to the north, with an average depth of about 200 m.

**Data sources**

The data used were obtained from the summer research bottom trawl surveys in NAFO divisions 4RS, conducted every year by the Department of Fisheries and Oceans, Canada. Surveys take place in August using a stratified-random survey design. The study covers the period from 1990 to 2010. During that period, the annual mean number of hauls was 145 (min. 89, max. 202), taken each year over 34 strata. Strata surface ranges from 555.64 to 6976.42 km<sup>2</sup>, for a total area sampled of 96,564 km<sup>2</sup>.

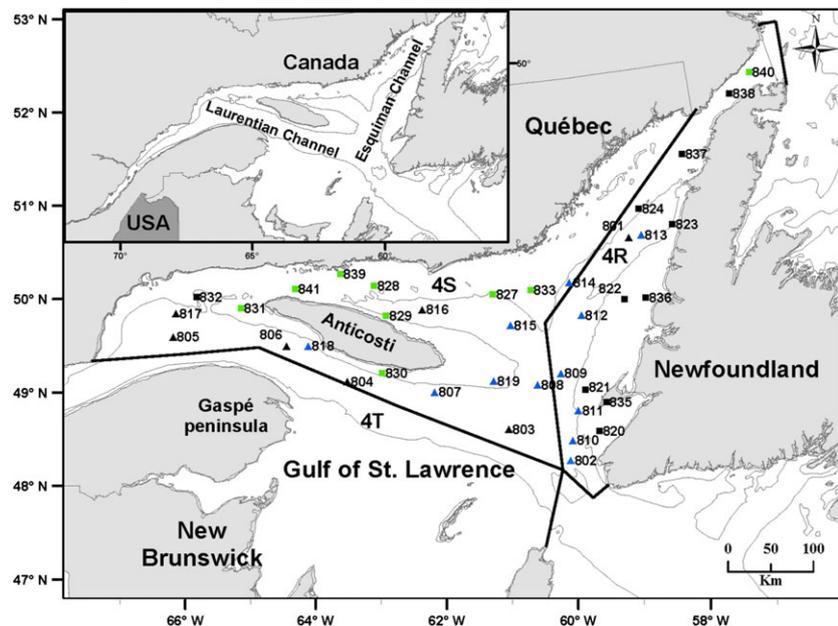
Number of hauls is proportional to stratum surface, in order to provide unbiased estimates of population abundance over time (Gagnon 1991).

From 1990 to 2003, the survey was conducted with the RV *Alfred Needler* using a URI trawl with a 19-mm liner in the cod-end (24-min tows). Since 2004, the survey has been conducted with the RV *Teleost* equipped with a Campelen 1800 trawl with a 13-mm liner (15-min tows). The URI trawl data were converted to Campelen trawl data based on comparative fishing experiments held in 2004 and 2005. For each species, a correction was made taking into account the effects on catchability of fish size, depth, diurnal cycle, and tandem vessel/trawl (Bourdages *et al.* 2007).

Research bottom trawl surveys aim at estimating the abundance in number and biomass of four main commercial species (Atlantic cod, Greenland halibut, redfish and Northern shrimp), though other species were also identified, counted and weighed. The quality of identification of the non-commercial species has fluctuated from year to year, with an improvement in the recent period. To avoid bias caused by misidentification, groupings were made according to the lowest accurate identification in all tows. A total of 117 species or species groups were recorded in all tows from 1990 to 2010, and were grouped into 70 taxa, which were used in the analysis.

**Structure of fish assemblages**

To analyse the spatio-temporal structure of fish assemblages, the stratum was used as the sampling unit in order to limit biases caused by small-scale random variations.



**Fig. 1.** The study area in the Gulf of St Lawrence (Northwest Atlantic Fisheries Organization divisions 4R and 4S). Number represent sampling strata considered. The grey line indicates the 200 m isobath. Symbols of strata are the same as the results shown in Fig. 2.

The data from all hauls from the same stratum were grouped in a single series of species biomass, considered in this study to be a representative sample of the population.

Multivariate ordination methods were applied to investigate the demersal fish community structure. The data were square-root transformed to reduce the influence of the dominant species and to support the importance of the rare ones (Somerfield & Clarke 1997; J rgensen *et al.* 2005). The similarity among strata was calculated using the Bray–Curtis index (Bray & Curtis 1957; Field *et al.* 1982). This is generally considered an excellent similarity measure as it preserves the ecological distance among the studied communities (Clarke & Warwick 1994). A cluster analysis was applied to define groups of strata. The observed differences among groups were tested *a posteriori* using an analysis of similarity randomization test (ANOSIM). Finally, a non-metric multidimensional scaling (nMDS) was performed, using the groups observed in the cluster analysis, in order to visualize the spatio-temporal structure of fish assemblages. Additionally, a SIMPER (similarity percentage) analysis was performed (Clarke 1993; Clarke & Warwick 1994) to quantify the percentage of contribution of each species to the average similarity/dissimilarity between groups. Species showing ratios of average similarity or dissimilarity to standard deviation ( $r > 1.5$ ) were considered to be typical (in similarity analyses) or discriminatory (in dissimilarity analyses) (Clarke & Warwick 1994). Sometimes the samples contain individuals who differ widely in their size or activity within the system, as is the case in this study. It was therefore considered preferable to make the calculations from biomasses, instead of numbers (Legendre & Legendre 1998; Magurran *et al.* 2011). Statistical analyses (nMDS, SIMPER, ANOSIM) were all performed using the PRIMER package (release 6.0) (Clarke & Gorley 2006). Following the results of the analysis of the spatial structure of assemblages, the temporal variation of each assemblage was studied using the same approach. The ordination method allowed the identification of separate periods, and the difference between those periods were tested *a posteriori* using the ANOSIM technique.

In addition to multivariate ordination methods,  $k$ -dominance curves were constructed. The graphical representation of cumulative frequency distributions of abundance and biomass in descending order of species was performed according to the periods identified in the temporal analysis. This method was developed by Lamshead *et al.* (1983) and provides a diagnosis of the ecological state of the community along a continuum from unstressed to grossly stressed. The diagnosis depends on the value of the  $w$ -statistic, based on the relative position of the two  $k$ -dominance curves (Lamshead *et al.* 1983)

for biomass and abundance (Clarke & Warwick 1994; Clarke & Gorley 2006). Comparison of those curves may show whether communities are dominated by small individuals or by individuals with high body mass. Moreover, the  $k$ -dominance curves offer the advantage of showing the relative dominance of rare *versus* common species (Lamshead *et al.* 1983).

### Diversity indices

To investigate the diversity of demersal fish in the northern Gulf, the sampling unit was the haul. Three indices of species diversity were used. The Shannon–Wiener index ( $H'$ ), which takes into account information on both species richness and the distribution of individuals among species, was calculated as:

$$H = - \sum_{i=1}^S P_i \log_2(P_i)$$

where  $S$  is the number of species per haul 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).

It is recognized that the Shannon–Wiener index ( $H'$ ) may be influenced by sampling effort and sample size. It is also sensitive to rare species (M rigot *et al.* 2007). Therefore, the Simpson's Index of Diversity (SID) was also used. This index is less sensitive to sampling effort (Niklitschek *et al.* 2010) but more sensitive to dominant species. SID is estimated as:

$$\text{SID} = 1 - \sum_{i=1}^S (P_i)^2$$

where  $S$  is the number of species per haul and  $P_i$  is the proportion of individuals in a haul. SID varies between 0 and 1 and is a function of species richness (Simpson 1949).

The Motomura constant was calculated in addition to the two previous indices (Daget 1979). It corresponds to the anti-logarithm of the slope of the regression between the log of the biomass and the species ranks:

$$m = 10^{(-a)}$$

where  $m$  is the Motomura constant, which takes values between 0 and 1, and  $a$  is the slope of the regression line. That constant was calculated for each period previously identified, and an analysis of covariance (ANCOVA) was used to compare the periods.

The Shannon–Wiener index was mapped to visualize possible spatial variations between periods. Cokriging was used to spatially interpolate values, using the depth as

co-variate. The ArcGis Geostatistical analyst extension (ArcGIS, ESRI Corporation, Redlands CA, USA) was used.

## Results

### Spatial structure of assemblages

The ordination analyses reveal a spatial structure of fish assemblages over the entire time period from 1990 to 2010 (Fig. 2). Two units appear at 25% similarity. One corresponds to the strata shallower than 200 m depth (Group A) and the other to strata deeper than 200 m (Group B). The average group similarity (Table 1) is the same for the two groups (~ 66%), suggesting a similar number of constant species. Species that contribute mainly to Group A (the shallow assemblage) are Atlantic cod (*Gadus morhua*), with 38.53% of total contribution, American plaice (*Hippoglossoides platessoides*), with 15.06%, and Thorny skate (*Amblyraja radiata*), with 5.61% (Table 1). Species that contribute most to the total percentage of similarity in Group B (deep strata) are redfish (*Sebastes* spp.), with 32.09%, Greenland halibut (*Reinhardtius hippoglossoides*), with 14.08%, Thorny skate (*Amblyraja radiata*), with 7.25%, Witch flounder (*Glyptocephanus cynoglossus*), with 5.83%, and White hake (*Urophycis tenuis*), with 5.13% (Table 1). The difference between these two groups is confirmed by ANOSIM ( $R = 0.830$ ,  $P < 0.001$ ). More than 50% of dissimilarities between the two groups can be attributed to four species: redfish, Atlantic cod, Greenland halibut, and American plaice.

At a threshold of 40% similarity, those two groups are divided into subsets. For the coastal group (A), the strata

located in the eastern part of the Gulf along Newfoundland (sub-group A<sub>1</sub>) tend to isolate themselves from the strata north of Anticosti Island (sub-group A<sub>2</sub>). For the deep group (B), a sub-group is formed by all strata located mainly in the Laurentian Channel (sub-group B<sub>1</sub>), while another sub-group is formed by the strata located essentially in the Esquiman Channel (sub-group B<sub>2</sub>). ANOSIM confirms a significant difference between those sub-groups (global  $R_{A_1-A_2} = 0.635$ ,  $R_{B_1-B_2} = 0.514$ ,  $P < 0.001$ ). Species that discriminate the two coastal sub-groups (shallow strata, A<sub>1</sub>–A<sub>2</sub>) are Atlantic cod, American plaice, redfish and Thorny skate, with more than a 50% contribution to dissimilarity. Those species are more abundant in sub-group A<sub>1</sub>. For the two deep sub-groups (deep strata, B<sub>1</sub>–B<sub>2</sub>) the discriminating species are Greenland halibut, redfish, Atlantic cod, and Black dogfish, with a 53.91% contribution to dissimilarity. Greenland halibut and Black dogfish are abundant in sub-group B<sub>1</sub>, while redfish and Atlantic cod are abundant in the sub-group B<sub>2</sub>.

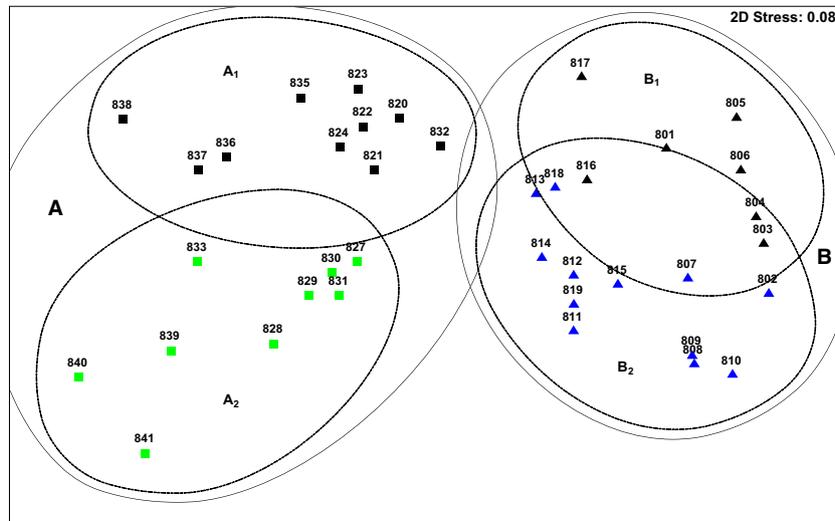
### Temporal variation of assemblage structure

At the scale of the entire northern Gulf of St. Lawrence (4RS, all assemblage combined), a temporal structure of communities emerges from the MDS analysis (Fig. 3). Three separate periods appear at 75% of similarity (Fig. 3A): 1990–1994, corresponding to pre-collapse period, 1995–2003, corresponding to the moratorium period, and the recent period, 2004–2010. ANOSIM indicates that the difference between those periods is significant ( $R = 0.906$ ,  $P < 0.001$ ).

**Table 1.** Percentage contributions of species (>2%) to the average similarity of assemblage, identified by SIMPER analysis.

Scientific name	Common name	Coastal assemblage (<200 m)	Deeper assemblage (>200 m)
<i>Myxine glutinosa</i>	Atlantic hagfish	–	4.19 <sup>a</sup>
<i>Amblyraja radiata</i>	Thorny skate	5.61 <sup>a</sup>	7.25 <sup>a</sup>
<i>Malacoraja senta</i>	Smooth skate	1.32	4.98 <sup>a</sup>
<i>Gadus morhua</i>	Atlantic cod	38.53 <sup>a</sup>	5.27
<i>Gadus ogac</i>	Greenland cod	1.02	–
<i>Urophycis tenuis</i>	White hake	–	5.13 <sup>a</sup>
<i>Nezumia bairdi</i>	Marlin-spike	–	1.22
<i>Anarhichas lupus</i>	Striped wolffish	3.61	–
<i>Eumesogrammus praecisus</i>	Snake blenny	2.06	–
<i>Lycodes</i> sp.	Eelpout ns.	2.01 <sup>a</sup>	–
<i>Sebastes</i> sp.	Redfish	4.39	32.09 <sup>a</sup>
<i>Myoxocephalus scorpius</i>	Shorthorn sculpin	2.66 <sup>a</sup>	–
<i>Hippoglossoides platessoides</i>	American plaice	15.06 <sup>a</sup>	3.35 <sup>a</sup>
<i>Glyptocephanus cynoglossus</i>	Witch flounder	2.4	5.83 <sup>a</sup>
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	2.27	14.68 <sup>a</sup>
<i>Hippoglossus hippoglossus</i>	Atlantic halibut	1.29	3.02 <sup>a</sup>
Average similarity by group		65.97%	66.06%

<sup>a</sup>Species characterizing the two assemblages (Sim/SD > 1.5).



**Fig. 2.** Result of multidimensional scaling ordination showing the spatial structure of demersal fish assemblage in northern Gulf of St. Lawrence. Dashed line represents 40% of similarity, solid line 25%. A: coastal assemblage (<200 m); B: deeper assemblage (>200 m).

At the scale of coastal assemblages (shallow strata <200 m), three periods are also observed at 74% similarity (Fig. 3B), 1990–1992, 1993–2003 (the year 2002 remaining isolated), and the recent period 2004–2010. The difference between these periods was verified by ANOSIM ( $R = 0.933$ ,  $P < 0.001$ ). Species that contribute mainly to the period 1990–1992 were Atlantic cod, with a total contribution of 43.41%, and American plaice, with a total contribution of 14.82% (Table 2). Those species also contributed to the period of 1993–2003, with contributions of 35.09 and 20.44%, respectively (Table 2). For the recent period (2004–2010), a decrease in the total contribution of those two species (28.20 and 13.36% respectively) was observed, along with an increase of the contribution of Greenland halibut (*R. hippoglossoides*) and the appearance of other species such as Shorthorn sculpin (*Myoxocephalus scorpius*) and lumpfish (*Cyclopterus lumpus*) (Table 2).

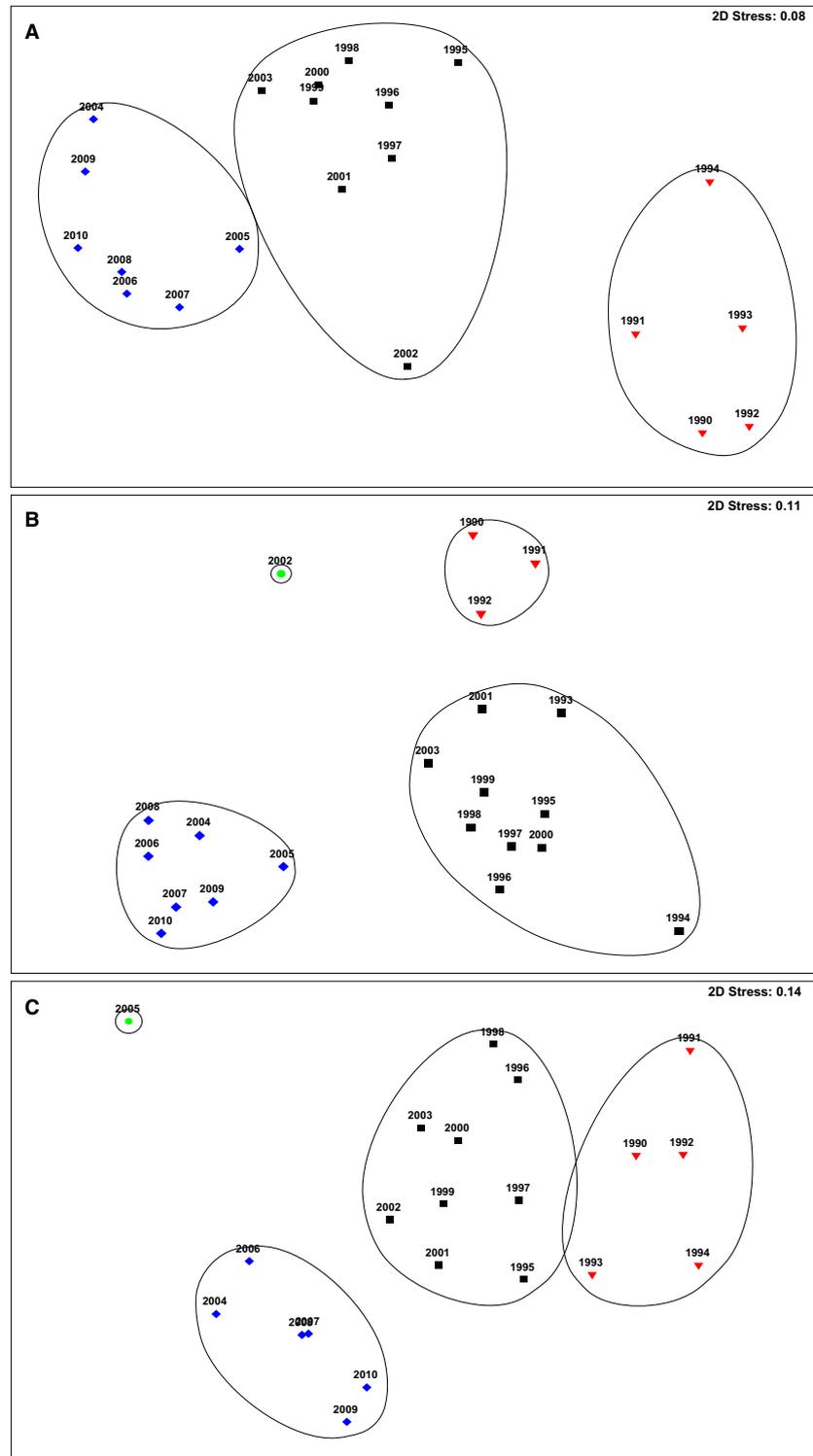
At the scale of deeper assemblages (deep strata >200 m), the temporal pattern was close to the pattern observed for the entire northern Gulf (Fig. 3C). Three distinct periods appeared at 68% similarity: 1990–1994, 1995–2003, and 2004–2010, the year 2005 being isolated. The ANOSIM showed a significant difference between those periods (global  $R = 0.86$ ,  $P < 0.001$ ). The species that contributed the most to the similarity in the three periods are Redfish, Atlantic cod, Greenland halibut and Black dogfish (*Centroscyllium fabricii*) (Table 3). Those four species together accounted for 34.33, 31.17, and 32.05% similarity for the periods 1990–1994, 1995–2003 and 2004–2010, respectively (Table 3). An increase was observed in the total contribution of Greenland halibut (and Atlantic halibut *Hippoglossus hippoglossus*), and a decrease in that of redfish and Black dogfish over these

periods. However, the contribution of Atlantic cod remained relatively stable over time. It is worth noting that those dominant species are traditionally targeted by fishers in the Gulf of St. Lawrence.

To draw the  $k$ -dominance curves, data were grouped for each period defined by the temporal analysis: 1990–1994, 1995–2003 and 2004–2010. For the period from 1990 to 1994 (Fig. 4A) the distribution curve of species abundance was higher than the distribution of biomass, indicating a predominance of individuals of low body mass ( $W$ -statistic,  $W = -0.005$ ), which may be associated with the pressure of fishing in the northern Gulf reducing the abundance of the largest individuals. In the period of 1995–2003 (Fig. 4B), there was an inversion of biomass distribution which was more prominent than the distribution of abundance of dominant species ( $W$ -statistic,  $W = 0.019$ ). This is related to growth of the individuals present without the addition of new individuals. The inversion may be associated with the introduction of moratoriums from 1994 to 1996 and in 2003, as well as a reduced total allowable catch since 1997. In the recent period of 2004–2010 (Fig. 4C), the trend was similar to the pre-collapse period of 1990–1994 ( $W$ -statistic,  $W = -0.006$ ). This may be related to the addition of recruited small individuals of key species and the effect of fishing pressure.

### Diversity

A gradual increase in the mean Shannon–Wiener diversity index was observed between periods, from the oldest to the most recent: 1990–1994 ( $H' = 1.103 \pm 0.063$ ), 1995–2003 ( $H' = 1.366 \pm 0.057$ ) and 2004–2010 ( $H' = 1.676 \pm 0.044$ ). The same trend was observed for the



**Fig. 3.** Two-dimensional multi-dimensional scaling plot of temporal structure of demersal fish assemblage in northern Gulf of St. Lawrence. A: entire northern Gulf; B: coastal assemblage; C: deeper assemblage. Solid line represents respectively 75%, 74% and 68% of similarity.

mean Simpson's Index of Diversity: 1990–1994 ( $SID = 0.384 \pm 0.006$ ), 1995–2003 ( $SID = 0.469 \pm 0.005$ ) and 2004–2010 ( $SID = 0.529 \pm 0.006$ ). The temporal variation of both indices was significant (ANOVA,

$P < 0.0001$ ). For the same periods, the Motomura constant ( $m$ ) showed a relative increase in diversity through time. Values of the Motomura constant were 0.864, 0.871 and 0.888 for the periods 1990–1994, 1995–2003 and

**Table 2.** Percentage contributions of species (>2%) to the average similarity of coastal assemblage (<200 m), identified by SIMPER analysis. The year 2002 was excluded.

Scientific name	Common name	1990–1992	1993–2003	2004–2010
<i>Amblyraja radiata</i>	Thorny skate	7.97 <sup>a</sup>	7.28 <sup>a</sup>	5.58 <sup>a</sup>
<i>Malacoraja senta</i>	Smooth skate	–	1.48	–
<i>Gadus morhua</i>	Atlantic cod	43.41 <sup>a</sup>	35.09 <sup>a</sup>	28.20 <sup>a</sup>
<i>Gadus ogac</i>	Greenland cod	–	0.58	1.29
<i>Melanogrammus aeglefinus</i>	Haddock	1.46	–	0.27
<i>Anarhichas lupus</i>	Striped wolffish	3.9	6.18 <sup>a</sup>	4.89 <sup>a</sup>
<i>Eumesogrammus praecisus</i>	Snake blenny	–	1.31	1.65
<i>Lycodes</i> sp.	Eelpout ns.	–	–	2.52 <sup>a</sup>
<i>Sebastes</i> sp.	Redfish	11.7	5.14	4.41
<i>Myoxocephalus scorpius</i>	Shorthorn sculpin	–	0.5	4.41 <sup>a</sup>
<i>Cyclopterus lumpus</i>	Lumpfish	–	1.30 <sup>a</sup>	1.66
<i>Hippoglossoides platessoides</i>	American plaice	14.82 <sup>a</sup>	20.44 <sup>a</sup>	13.36 <sup>a</sup>
<i>Glyptocephanus cynoglossus</i>	Witch flounder	5.23 <sup>a</sup>	4.79	3.41
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	2.97 <sup>a</sup>	4.91	4.74 <sup>a</sup>
<i>Hippoglossus hippoglossus</i>	Atlantic halibut	0.14	0.49	2.13
Average similarity by period		83.71%	82.19%	86.26%

<sup>a</sup>Species characterizing the periods of coastal assemblages (Sim/SD > 5).

**Table 3.** Percentage contributions of species (>2%) to the average similarity of deeper assemblage (>200 m), identified by SIMPER analysis. The year 2005 was excluded.

Scientific name	Common name	1990–1994	1995–2003	2004–2010
<i>Myxine glutinosa</i>	Atlantic hagfish	2.59 <sup>a</sup>	4.67 <sup>a</sup>	2.14 <sup>a</sup>
<i>Centroscyllium fabricii</i>	Black dogfish	5.06 <sup>a</sup>	4.95	3.31
<i>Amblyraja radiata</i>	Thorny skate	3.71 <sup>a</sup>	4.26 <sup>a</sup>	4.52 <sup>a</sup>
<i>Malacoraja senta</i>	Smooth skate	4.65 <sup>a</sup>	3.79	2.13 <sup>a</sup>
<i>Gadus morhua</i>	Atlantic cod	7.5 <sup>a</sup>	8.35	7.99 <sup>a</sup>
<i>Phycis chesteri</i>	Longfin hake	2.66 <sup>a</sup>	3.23 <sup>a</sup>	2.82
<i>Urophycis tenuis</i>	White hake	3.26 <sup>a</sup>	3.51 <sup>a</sup>	2.33 <sup>a</sup>
<i>Enchelyopus cimbrius</i>	Fourbeard rockling	1.69 <sup>a</sup>	1.92 <sup>a</sup>	–
<i>Nezumia bairdi</i>	Marlin-spike	4.14 <sup>a</sup>	2.24 <sup>a</sup>	1.70 <sup>a</sup>
<i>Anarhichas lupus</i>	Striped wolffish	2.17 <sup>a</sup>	1.35	1.44
<i>Sebastes</i> sp.	Redfish	17.38 <sup>a</sup>	9.75 <sup>a</sup>	9.6
<i>Hippoglossoides platessoides</i>	American plaice	2.80 <sup>a</sup>	2.93 <sup>a</sup>	3.10 <sup>a</sup>
<i>Glyptocephanus cynoglossus</i>	Witch flounder	1.89 <sup>a</sup>	2.09 <sup>a</sup>	2.07 <sup>a</sup>
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	4.39 <sup>a</sup>	8.12 <sup>a</sup>	11.15 <sup>a</sup>
<i>Hippoglossus hippoglossus</i>	Atlantic halibut	2.96	4.15 <sup>a</sup>	5.44
Average similarity by period		76.52%	77.39%	78.98%

<sup>a</sup>Species characterizing the periods of deeper assemblages (Sim/SD > 5).

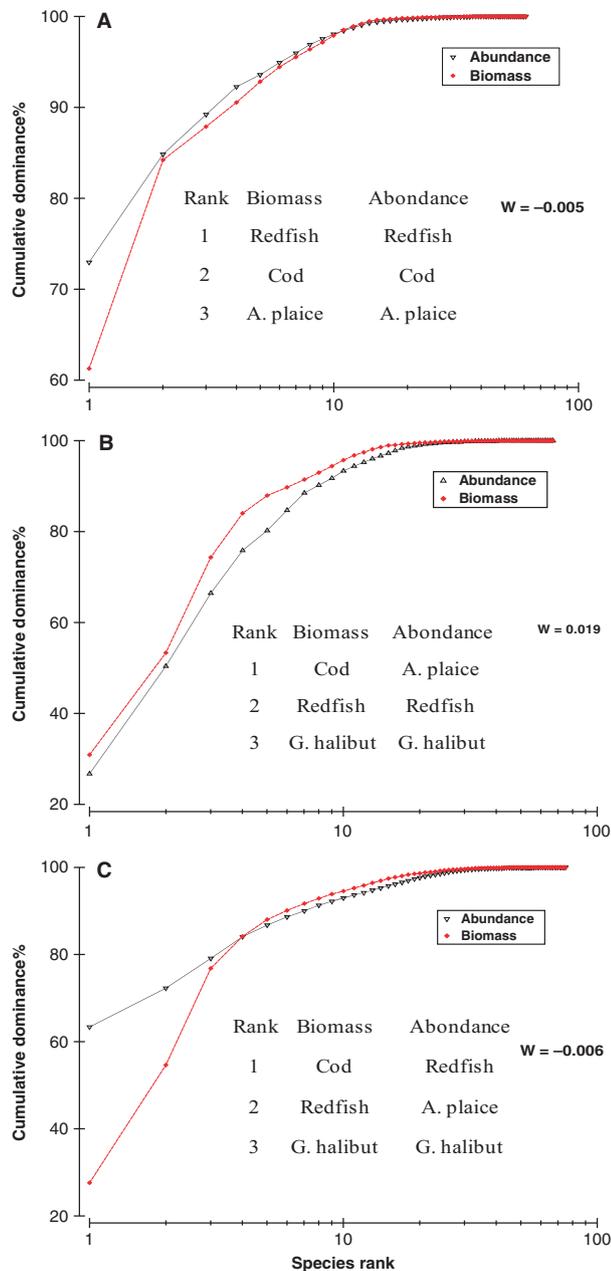
2004–2010, respectively. The difference between periods was small, but nonetheless significant (ANCOVA,  $P < 0.0001$ ). A gradual increase in the relative biomass of secondary species, unlike dominant species, was observed over the periods (Fig. 5).

The spatial distribution of the Shannon–Wiener index varied throughout the periods. In the period of 1990–1994, diversity showed a spatial heterogeneity with a hot-spot ( $H' > 2$ ) observed northwest of Anticosti Island (Fig. 6). Other small diversity hotspots were scattered along the west coast of Newfoundland and along the northern side of the Laurentian Channel. For the period

of 1995–2003, the repartition of diversity is more homogeneous, with higher values ( $H' > 1.5$ ) around Anticosti Island (Fig. 6). Finally, in the recent period (2004–2010), the area of higher values expanded around Anticosti Island ( $H' > 1.5$ ) and on the western side of the region (Fig. 6).

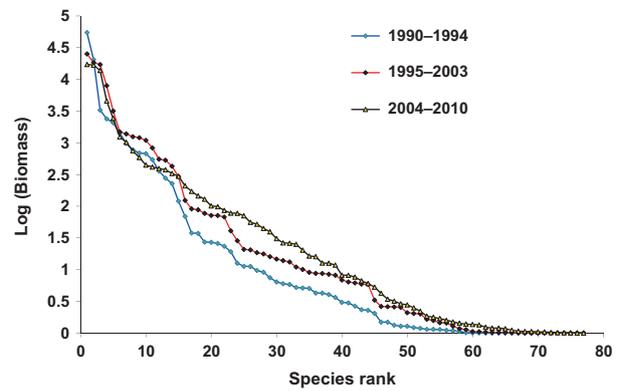
## Discussion

Two well defined communities were revealed by statistical analysis (Fig. 2). The coastal community corresponds to strata located above 200 m in depth. It is characterized



**Fig. 4.** K-dominance curves of demersal fish assemblages in the northern Gulf of St. Lawrence by period. A: 1990–1994; B: 1995–2003; C: 2004–2010. Species with the highest ranks are listed.

mainly by eelpout (*Lycodes* sp.), Shorthorn sculpin (*Myoxocephalus scorpius*), Striped wolfish (*Anarhichas lupus*) and Snake blenny (*Eumesogrammus praecisus*) (Table 1). A deeper community is located in channels of the Gulf of St. Lawrence, and the characteristic species are Atlantic hagfish (*Myxine glutinosa*), and White hake (*Urophycis tenuis*). A third group of species is common to both assemblages: Atlantic cod (*Gadus morhua*),

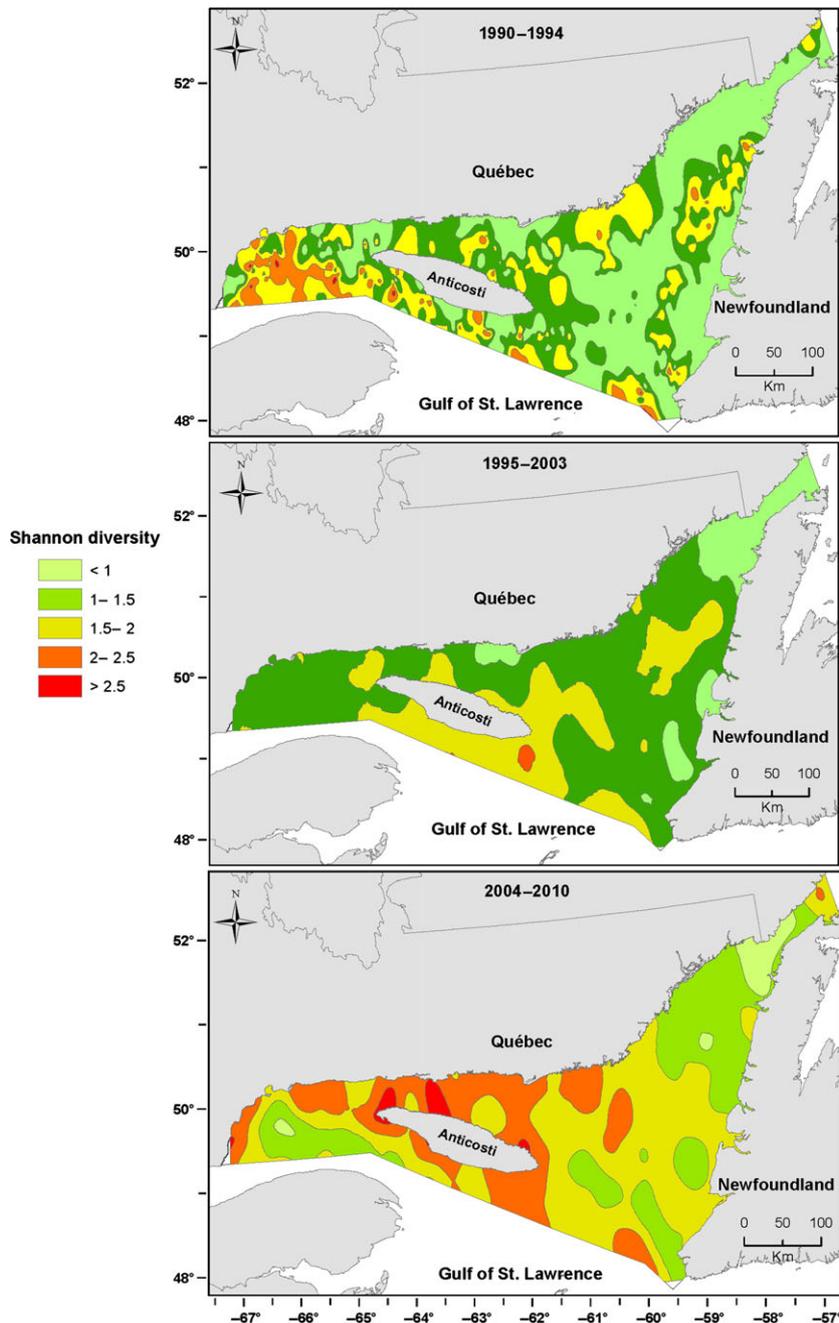


**Fig. 5.** Rank frequencies distribution of demersal fish based on log biomass, according to periods defined by the temporal analysis of demersal structure of assemblages in the northern Gulf of St. Lawrence.

redfish (*Sebastes* spp.), Greenland halibut (*Reinhardtius hippoglossoides*) and American plaice (*Hippoglossoides platessoides*). These species are widely distributed and traditionally fished in the Gulf of St. Lawrence.

A global spatial structure emerges from the ordination analyses, and temporal changes are mainly due to changes in the relative dominance of species. That structure is similar to that already observed both in the southern and northern Gulf of St. Lawrence by Koeller & Legresley (1981), Bosman *et al.* (2011) and Chouinard & Dutil (2011). It is common for the assemblages of demersal fishes in the North Atlantic. This spatial structure is described with the same characteristic species as on the Grand Banks of Newfoundland by Overholtz & Tyler (1985), Mahon & Smith (1989) and Gomes *et al.* (1995). It is also found in the Northeast Atlantic (Gomes *et al.* 2001). According to those studies, the common species between the two assemblages were considered ubiquitous species by Koeller & Legresley (1981), which seems appropriate for the Gulf of St. Lawrence.

In the northern Gulf of St. Lawrence, demersal fish communities appear to be structured according to depth. Distribution of demersal fishes linked to bathymetric gradients has often been observed by different authors in the North Atlantic (Mahon *et al.* 1998; Gomes *et al.* 2001; Sousa *et al.* 2005; Ross & Quattrini 2009), in the Mediterranean Sea (Gaertner *et al.* 1998, 2005; Colloca *et al.* 2003), Southeastern Australia (Connell & Lincoln-Smith 1999), the China Sea (Jin 2004), and the Southern and Southeastern Asia (Garces *et al.* 2006). However, it is difficult to identify the factor responsible for the spatial structure of communities along the bathymetric gradient. Many authors have demonstrated that several environmental variables are linked to the bathymetric gradient, such as temperature, salinity, oxygen concentration, and



**Fig. 6.** Geographical distribution of Shannon-Wiener diversity index ( $H'$ ) according to periods defined by temporal analysis of demersal structure of assemblages in northern Gulf of St. Lawrence.

sediment (Auster *et al.* 1995; Swain & Benoit 2006; Ordines & Massuti 2009). In the northern Gulf of St. Lawrence, those environmental variables also influence community structure, as has been observed by Chouinard & Dutil (2011).

Multivariate analyses show temporal changes of demersal assemblages across the northern Gulf of St. Lawrence. Three periods were identified: the pre-collapse period (1990-1994), which includes the first moratorium on directed fishing for cod; the period from 1995 to 2003,

which also includes three moratoria (1995, 1996 and 2003); and the recent period from 2004 to 2010 (Fig. 3A). The high level of similarity observed is linked to the species common in all three periods: Atlantic cod, redfish, American plaice and Greenland halibut. At the level of the deeper assemblages ( $>200$  m), the same temporal structure and dominant species were observed (Table 3, Fig. 3C), unlike the coastal assemblage ( $<200$  m), where small differences appear (Table 2, Fig. 3B). As already observed in the Yellow Sea (Xu & Jin

2005), the relative variations in biomass of a few dominant species are responsible for the structural changes between the different time periods. Namely cod, redfish, Greenland halibut and American plaice accounted for 10–40% of the total dissimilarity. In fact, the biomass of cod and redfish has declined dramatically during the period analysed, while the Greenland halibut showed a significant increase (Tables 2 and 3). According to these results, the coastal assemblage appears more affected by fishing than the deeper one. The variations in abundance of a few dominant species in the community's structure is also shown by *k*-dominance curves (Fig. 4). In the period of 1990–1994, communities are dominated by individuals of small body size. This may be linked to fishing pressure, which is known primarily to affect the largest individuals and to induce a shrinkage of the fish size structure (Hutchings & Myers 1994). An inversion of biomass distribution of dominant species was observed (Fig. 4B) in the period of 1995–2003, which may be related to the growth of the individuals present without the addition of recruits. This was observed for the Atlantic cod, for which an increase in the mean individual weight was also noted (Fréchet *et al.* 2009). This growth was allowed by management measures imposed by the Department of Fisheries and Oceans (DFO), and was especially assisted by the moratorium on directed fishing. A trend similar to the pre-collapse period of 1990–1994 was observed in the recent period (Fig. 4C). This may be related to the addition of recruits of small individuals for key species, such as redfish, especially in 2004 (DFO 2010). The change of fishing gear, in 2004, may induce an overestimation of fish of small body size in the recent period compared with the previous periods. Indeed, in the intercalibration process between gears, a size effect was observed for cod and American plaice, but not for redfish and Greenland halibut (Bourdages *et al.* 2007). In the *k*-dominance curves of the 2004–2010 period (Fig. 4C), the position of the curve of abundance is induced by redfish, first rank, and American plaice second rank, and Greenland halibut. It seems, then, that gear change has a minimal effect on the picture provided by the *k*-dominance curves.

All diversity indices, Shannon–Wiener, Simpson's index and Motomura, point to a slight but significant increase in diversity through time. The biomass-ranks curves indicate that this increase is mainly due to a biomass increase of secondary species (ranks >10), whereas the biomass of dominant species remain fairly stable. These species form a heterogeneous group which includes species of some commercial importance (*e.g.* Angler fish, *Lophius americanus*, Spotted wolffish, *Anarhicas minor*, or Spinytail skate, *Bathyrāja spinicauda*), as well as those of non-commercial importance (*e.g.* *Lycodes* sp.). As these species used to be common bycatches in trawl fishing,

their relative biomass increase could be related to the reduction of activity in that sector after 1997 in the northern Gulf.

The trends of the geographical distribution of diversity appear consistent with the geographical distribution of the main demersal species. During the first period (1990–1994), species such as cod, Greenland halibut, lumpfish (*Cyclopterus lumpus*), Witch flounder, Smooth and Thorny skates were the most abundant west of Anticosti Island (Archambault *et al.* 2013), in correlation with the observed hotspots of diversity. During the period of 1995–2003, cod and redfish stocks showed a contraction toward the eastern side of this area (DFO 2011a; Fréchet *et al.* 2009; Tamdrari *et al.* 2010; Archambault *et al.* 2013), while other species showed a more homogeneous distribution in agreement with the distribution of the diversity. In the recent period (2004–2010), the north-westward shift of the diversity hotspots can be attributed to warmer conditions (Tamdrari *et al.* 2012), as well as average recruitment of species that were dominant in the system of the northern Gulf of St. Lawrence such as cod, Witch flounder and Greenland halibut (DFO 2011a,c, 2012a,b).

It is important while interpreting the results to consider limitations linked to diversity indices. Indeed, these indices ( $H'$ ,  $SID$ ,  $m$ ) do not take into account the size frequency distribution of the species studied. Juvenile and mature fish do not occupy the same trophic level and should probably be considered different 'species'. The same index values may also correspond to different structures, as is observed in our study. In addition, an increase of the index value, reflecting in this study a narrowing biomass structure, is not necessarily a sign of improvement of the ecosystem of northern Gulf of St. Lawrence.

Despite these limitations, the present study reflects the dynamic structure of the demersal fish community. It shows that the composition of fish communities and their related diversity is stable neither in time nor space. This is important in a context where biodiversity maps are commonly used for the delineation of marine protected areas, and introduces new information that will allow a better understanding of the northern Gulf ecosystem and help to enhance its management and protection.

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