Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community

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Abstract: We describe dramatic shifts in the species composition of the marine fish community of the southern Gulf of St. Lawrence using a 35-year time series of catch rates in an annual bottom-trawl survey. We attempt to understand the causes of these changes using a traits-based approach that relates the similarity among species in their abundance trends to similarities in their ecological traits. We selected traits based on a priori beliefs of how each should reflect susceptibility to changes in a different external factor potentially affecting the community. We found evidence for an effect of ocean climate and top-down effects of fishing and seal predation, but not for bottom-up effects of prey availability on adult fishes. Mean body length in the community decreased dramatically in the 1990s. This reflected the removal of large-bodied fishes by fishing and sharp increases in the abundance of small fishes. The biomass of small fish was inversely correlated with an index of predation on those fish by larger fish, suggesting strong predator control of the abundance of small-bodied fishes. Our results suggest that changes in ocean climate combined with direct and indirect effects of harvesting can dramatically and rapidly alter the composition of marine fish communities.

Résumé : Nous décrivons des changements importants de composition spécifique dans les communautés de poissons marins du sud du golfe du Saint-Laurent à partir d'une série chronologique de 35 années de taux de captures dans des inventaires annuels au chalut de fond. Nous tentons de comprendre les causes de ces changements à l'aide d'une méthodologie basée sur les traits qui met en rapport les similarités des tendances d'abondance chez les espèces et les similarités de leurs traits écologiques. Nous avons choisi les traits d'après notre perception a priori de comment chaque trait devrait refléter la susceptibilité aux changements d'un facteur externe particulier qui affecte potentiellement la communauté. Nous trouvons des indications de l'existence d'un effet du climat océanique et d'effets descendants de la pêche et de la prédation par les phoques, mais non d'effets ascendants de la disponibilité des proies sur les poissons adultes. La longueur corporelle moyenne dans la communauté a diminué de façon importante durant les années 1990. Cela reflète le retrait des poissons de grande taille par la pêche et un accroissement marqué des petits poissons. Il existe une corrélation inverse entre la biomasse des petits poissons et un indice de prédation des gros poissons sur les petits, ce qui laisse croire à un important contrôle de l'abondance des poissons de petite taille par les prédateurs. Nos résultats indiquent que les changements dans le climat océanique combinés aux effets directs et indirects de la récolte peuvent modifier de façons importante et rapide la composition des communautés de poissons marins.

[Traduit par la Rédaction]

Introduction

There is increasing recognition of the need to consider fisheries in the context of the ecological communities and ecosystems in which they are prosecuted (e.g., Link 2002; Pikitch et al. 2004; Mangel and Levin 2005). Because of interspecific interactions, responses to harvesting may be more complex than those predicted by single-population models (e.g., Sih et al. 1985; Yodzis 2001; Bascompte et al. 2005). Furthermore, separating projected responses to harvesting (including top predator culling) from those caused by changes in climate (e.g., Bennett et al. 2004; Rose 2004) is crucial, because of these two effects, only the human activities related to harvesting can realistically be managed on the temporal and spatial scales that are relevant to stock and community dynamics. Retrospective analyses and modelling of exploited marine communities founded in multiple a priori hypotheses are necessary to understand such species and community responses (Hilborn and Mangel 1997).

Changes in the composition of marine fish communities have been reported for a number shelf ecosystems in recent years (e.g., Fogarty and Murawski 1998; Greenstreet et al. 1999; Choi et al. 2004). The top-down effects of fishing (e.g., Bianchi et al. 2000; Link and Garrison 2002; Frank et al. 2005) and effects of climate change (e.g., Perry et al. 2005; Poulard and Blanchard 2005) are often cited as principal causal factors. Quantitatively assessing the relative influence of these and other factors remains a particular challenge, though canonical multivariate analyses and approaches based on aggregate community properties (e.g., size composition, species richness, and diversity) have

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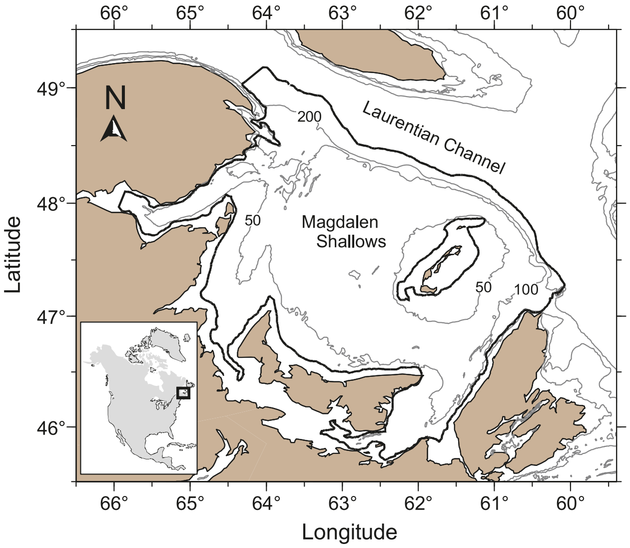
shown some promising results (e.g., Link et al. 2002; Blanchard et al. 2005; Worm et al. 2005).

In this paper, we describe profound changes from 1971 to 2005 in the species composition of the marine fish community in the southern Gulf of St. Lawrence (Northwest Atlantic, Canada; Fig. 1). We examine five competing hypotheses for the factors driving these changes: (*i*) direct top-down effects fishing; (*ii*) changes in predation by a marine-mammal top predator, the grey seal (*Halichoerus grypus*); (*iii*) climate variation; (*iv*) bottom-up effects on adult fishes of changes in the availability of their prey; and (*v*) changes in predation by marine fishes (i.e., release of small fish from predation as large fish are depleted by fishing, an indirect effect of fishing).

These hypotheses were selected based on observed changes in the underlying forcing factors and (or) their proposed importance in single species dynamics or other ecosystems. Overfishing has been implicated as the principal cause of the collapse of Atlantic cod (*Gadus morhua*) and other exploited groundfishes in the Northwest Atlantic (e.g., Myers et al. 1996; Sinclair and Murawski 1997). Fishing effort (and thus fishing mortality) in the southern Gulf was high throughout the 1970s and 1980s, rose to very high levels in the late 1980s and early 1990s, and has been at a low level since 1993 when a moratorium on directed fishing for cod was initiated (Fig. 2*a*). The abundance of grey seals in this and neighboring areas has been increasing exponentially for over three decades (Fig. 2*b*) (Bowen et al. 2003) and is correlated with high levels of natural mortality in the local cod population (Chouinard et al. 2005). Mean bottom-water temperatures cooled throughout the 1980s, resulting in a period of record-low temperatures in the early to mid-1990s (Fig. 2*c*) (Gilbert and Pettigrew 1997; Drinkwater and Gilbert 2004); comparable change in a neighboring area has been linked with apparent shifts in species distributions (Frank et al. 1996). Bottom-up effects of changes in prey availability have been observed in other systems (e.g, Beaugrand et al. 2003; Frederiksen et al. 2006) and may be important in our study area given observed long-term changes in the diet of southern Gulf cod (Hanson and Chouinard 2002). Finally, dramatic increases in the abundance of forage fishes in other ecosystems have been attributed to reduced predation following declines in the abundance of large piscivorous fishes (e.g., Daan et al. 2005; Frank et al. 2005; Ward and Myers 2005).

We examined the hypotheses for the causes of community change using a traits-based approach that relates the similarity between species in their population dynamics (i.e., their abundance trends) to the similarity in their ecological and functional traits. Analogous trait-based approaches have been used to successfully predict changes in species composition of a plant community during secondary succession (Shipley et al. 2006) and have been advocated as a promising avenue towards predictive community ecology (McGill et al. 2006). This approach is predicated on the idea that a given environment selects or filters for optimal states across a suite of traits, and species with trait combinations close to the optimum are favored (e.g., Keddy 1992). Changes in the environment (including modifications due to biological interactions and fishing) select for different trait values and lead to changes in the relative abundance of species. Synchronous changes in abundance of a group of species sharing certain traits (e.g., cold-water tolerance) therefore imply a common response to particular driving factors (e.g., changes in environmental temperatures).

Fig. 1. Southern Gulf of St. Lawrence bottom-trawl survey area (dark line) with 50, 100, and 200 m isobaths (grey lines). The survey covers depths from 15 to 350 m. The inset map shows the study location in North America.



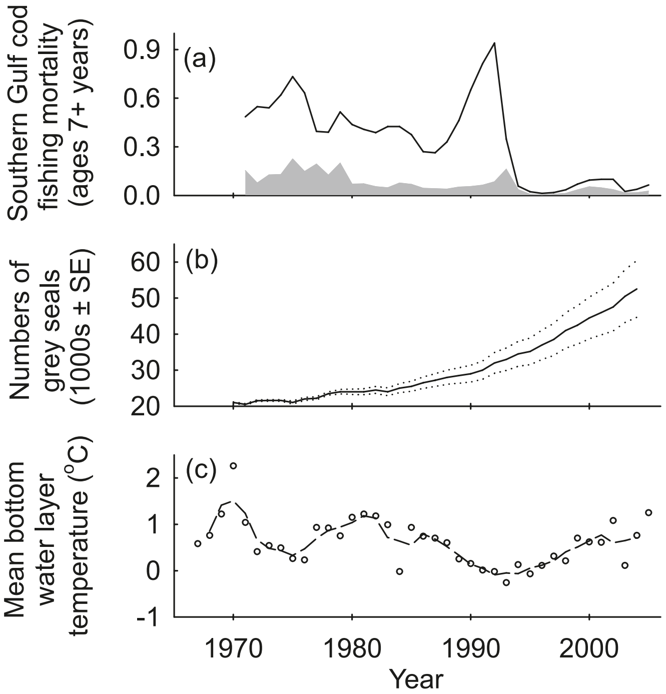
To examine our five competing hypotheses for the causes of fish community change in the southern Gulf of St. Lawrence, we attempted to select traits believed a priori to reflect susceptibility to the forcing factor underlying each hypothesis. We were able to identify an appropriate trait for four of the five hypotheses. These traits were (*i*) relative fishing mortality, reflecting direct fishing effects; (*ii*) an index of susceptibility to predation by grey seals; (*iii*) thermal preferences (as inferred from biogeographic distribution), believed to reflect susceptibility to climate variation; and (*iv*) diet composition, believed to reflect susceptibility to bottom-up effects of variation in prey availability. We were unable to identify a trait that unambiguously reflected susceptibility to changes in predation by marine fishes. Thus, instead of a traits-based approach, the fifth hypothesis was examined using the traditional approach of correlation, relating a response variable (biomass of small fish) to a potential forcing factor (an index of fish predation on small fish). These analyses provide evidence for effects of climate variation and top-down effects (i.e., consumer control) of fishing and predation on the composition of the marine fish community in the southern Gulf but fail to provide evidence of bottom-up effects of variation in prey availability on adult fishes (i.e., resource control).

Materials and methods

Changes in species composition of the fish community

Changes in species composition of the fish community in the southern Gulf of St. Lawrence were described based on catch rates (mean number of fish per standard tow) in a bottom-trawl survey conducted each September since 1971

Fig. 2. Temporal trends in three hypothesized causal factors for the changes in species composition in the southern Gulf of St. Lawrence. (*a*) Mobile (open area below line) and fixed-gear (shaded area) fishing mortality of adult Atlantic cod (*Gadus morhua*) in the southern Gulf (1971–2005; from Chouinard et al. 2006). Cod fishing mortality is correlated with total groundfish fishing effort in the ecosystem ($r = 0.89$ for mobile gear and $r = 0.74$ for fixed gear) and is therefore likely a good proxy for the fishing mortality of other species captured across all groundfish fisheries. (*b*) Abundance of grey seals (*Halichoerus grypus*) in the Gulf of St. Lawrence herd, 1970–2005 (from Hammill 2005). (*c*) Mean water temperature (○) and 3-year running average (—), 1967–2005, in the southern Gulf of St. Lawrence cold intermediate layer, the water layer that covers most of the bottom in the area.



(Fig. 1; see Hurlbut and Clay 1990 for details on survey methodology). A 19 mm trawl cod-end liner was used in all years to retain small fish. Where necessary, catch rates were adjusted for changes in gear, vessel, or survey protocol, as described by Benoît and Swain (2003) and Benoît (2006*b*). For each species *i* and year *j*, the standardized catch rate, c_{ij}, was then transformed by taking $[c_{ij} - \min(c_{i\cdot})]$ / $[\max(c_{i\cdot}) - \min(c_{i\cdot})]$, thereby reducing the values for each time series to the interval [0,1]. Only the 52 most abundant fish species were retained for analysis (Appendix A, Table A1). Owing to problems with taxonomic identification, six taxa were grouped at the level of genus or higher (Appendix A, Table A1; for explanation see Benoît and Swain 2003). These groups are nonetheless referred to commonly as "species" in the text for simplicity.

Temporal changes in species composition over the period 1971–2005 were summarized using a correspondence analysis (CA) of the $N \times Y$ catch rate matrix, $\mathbf{C}$ ($N = 52$ species, $Y = 35$ years). CA is a method of reduced-space ordination that is recommended when data contain a relatively large number of null values (Legendre and Legendre 1998). We used CA for two purposes. Species scores on the first CA eigenvector (CA-I) were used to sort species in a plot of $\mathbf{C}$, thereby highlighting the major pattern of temporal change in the community species composition. Secondly, a biplot of CA-I and CA-II was used to display changes in community trait composition (described below).

Species traits

Four traits were examined, each reflecting susceptibility to a forcing factor hypothesized to underlie the change in community composition. A separate matrix of species values, denoted $\mathbf{T}_t$, was created for each trait, *t*, as described below. The traits were exploitation level, susceptibility to predation by grey seals, biogeographic distribution, and diet.

Exploitation level was defined so as to reflect the average fishing mortality experienced by each species relative to their productivity. First, we calculated F_i, the 1971–2005 average relative fishing mortality for species *i*, adjusted by an index of productivity for that species:

$$(1) \qquad F_i = \frac{1}{35 \cdot m_i} \sum_{j=1971}^{2005} \frac{L_{ij} + D_{ij}}{B_{ij}}$$

where m_i is an estimate of the natural mortality rate for species *i*, L_{ij} is landed catch in year *j*, and D_{ij} and B_{ij} are annual estimates of total discarded catch and catchability-adjusted survey biomass, respectively. Catchability adjustments were based on length-dependent catchability models developed for a number of species and applied to species with generally similar body shapes and behaviour (see Appendix A, Table A1). Discarded catch was estimated using species-specific discard data collected by an at-sea fisheries observer program covering 5%–30% of commercial fishing trips since 1990 (see Benoît 2006*a* for details on the estimation). Natural mortality was included in the calculation because species with higher *m* tend to have higher production rates and can therefore sustain higher levels of fishing mortality (Beverton and Holt 1959). *m* was estimated based on an interspecific relationship between natural mortality rate and the Brody somatic growth coefficient, *K* ($m \approx 1.65K$; Charnov 1993). An estimate of *K* was available for 23 of the 35 species with nonzero fishery catches (Froese and Pauly 2007). For the remaining 12 species, *K*, which is known to be correlated with ultimate individual length (L_∞) from the von Bertalanffy growth equation, was estimated based on the maximum body length observed in the survey, $L_{\max}$. Based on the species for which we had an estimate for *K*, $K = 0.3140 - 0.0017\ L_{\max}$ ($R^2 = 0.36$, $n = 33$). Because of the large uncertainty in estimates of many of the quantities in eq. 1, we considered F_i to accurately reflect only order-of-magnitude differences in exploitation impacts. Thus, exploitation level was scored accordingly (Table 1), resulting in a semiquantitative ordinal trait.

A second trait examined was susceptibility to predation by grey seals. The grey seal is an important top predator of fishes in the community (Hammill and Stenson 2000). For each species *i*, we calculated S_i, an index of its susceptibility to predation by grey seals relative to its productivity:

Table 1. Exploitation level score as a function of relative fishing mortality, *F*.

Score	*F*	General characteristics of species occurring in the category
1	>0.5	Targeted species with landings >75% of quota determined by stock assessment or species commonly captured in large quantities as bycatch
0.67	0.05–0.5	Targeted species with landings 25%–75% of quota determined by stock assessment or species frequently captured as bycatch
0.33	0.0005–0.05	Some capture of the species was reported or estimated, but quantities were small relative to their biomass in the survey
0	∼0	Very few or no instances of capture reported

$$(2) \qquad S_i = d_i \left(\sum_{j=1990}^{2004} B_{ij}/15 \right)^{-1} m_i^{-1}$$

where m_i and B_{ij} are as defined above, and d_i is the proportion, by mass, of southern Gulf grey seal diets that are composed of species *i* from a study of digestive tract contents conducted over the 1990–2004 period (Hammill et al. 2007). Because of differential digestibility of prey items recovered from seals, imperfect characterization of spatial and seasonal differences in diet composition, and the uncertainties regarding m_i and B_i, S_i was transformed into a semi-quantitative trait scored as 0 (apparently not consumed), 0.5 (below median S_i), or 1 (above median S_i). Skates, which lack the bony parts used to infer seal diets, were scored as 1 based on observed consumption in other areas (Benoît and Bowen 1990). Other species not reported in seal diets observed in the southern Gulf but occurring in diets for neighbouring areas (also reported in Hammill et al. 2007) were scored as 0.5.

Biogeographic distribution was a third trait we examined and was expected a priori to reflect thermal preferenda and therefore the response to changes in temperature. It was composed of a set of three categories consisting of the proportions of the species' west Atlantic geographic range occurring in each of three zones: (1) Arctic–subarctic (north of 51°N), (2) boreal (between 44°N and 51°N), and (3) temperate (south of 44°N). These proportions were estimated based on a qualitative assessment of general accounts (Scott and Scott 1988; Brown et al. 1996; Colette and Klein-MacPhee 2002; Froese and Pauly 2007).

The fourth trait examined was diet. It was also composed of a set of categories consisting of the proportions of the diet by weight in each of eight prey groups: (1) fish eggs and larvae, (2) adult fish and squid, (3) marine worms, (4) shrimps and crabs, (5) plankton, (6) mollusks other than squid, (7) echinoderms, (8) other prey. Proportions were based on published data (Bowman et al. 2000; Hanson and Chouinard 2002; Savenkoff et al. 2004). Where size-specific data were available, the diet of an average-sized individual for the survey (generally adult fish) was used.

For the six taxa grouped to a level greater than species in the analysis (Appendix A, Table A1), the traits of the most common species in the group were used. Species trait values are presented graphically in Fig. 3.

Relating dissimilarity in abundance trends to species traits

Distance-based redundancy analysis (dbRDA; McArdle and Anderson 2001), a form of multivariate multiple regression, was used to assess the relative importance of each of the traits (explanatory variables), $\mathbf{T}_t$, in explaining differences among species in their time trends of survey abundance (response variables). dbRDA is performed directly on a distance or dissimilarity matrix, $\mathbf{D_C}$, a triangular matrix of pairwise measures of the dissimilarities in time trends between the species in **C** in our case. We calculated the dissimilarity in abundance trends using χ^2 distance. (Results were similar using another commonly used distance measure, Bray–Curtis dissimilarity).

The importance of each trait was first assessed individually in marginal tests. Then a forward selection procedure was used to find the suite of traits that best explained the dissimilarity among species in their abundance trends. Finally, the conditional (partial) significance and effect size of each of the selected traits was evaluated by testing the effect of one trait while controlling for effects of the others. Colinearity between traits was assessed using pairwise Mantel correlations (Legendre and Legendre 1998) of individual trait dissimilarity matrices, $\mathbf{D_T}$. The χ^2 distance was used to calculate $\mathbf{D_T}$ for the traits biogeographic distribution and diet, and absolute arithmetic difference was used for the other two traits.

Statistical significance in the dbRDA was assessed using 9999 unrestricted but simultaneous permutations of the rows and columns of $\mathbf{D_C}$ in the case of marginal tests and of the multivariate residual matrix in the case of conditional tests (Anderson 2003; Anderson and Legendre 1999). All dbRDAs were performed using the program DISTLM (Anderson 2003).

Time trends in the relative frequency of states for traits found to be important in the dbRDA were visualized by plotting trait state centroids on a biplot of the year scores from the first two CA eigenvectors. Trait centroids were calculated as the average position along the CA axes for all species having a particular trait state. For traits composed of multiple categories, centroids for each of the constituent categories were plotted based on the average position of all species along the CA axes weighted by their score for that category. Only traits found to be significant in the dbRDA were plotted.

The utility of the dbRDA is that it explicitly considers the interannual changes in abundance of all species. However, part of the variance it seeks to explain is short-term interannual variability, of which observation error is a non-negligible component (the average coefficient of variation for the abundance estimates in the survey is 46%). Thus, we also examined how well the traits explained the main pattern of change over time in the species composition of the community, summarized by CA-I. We used a general linear model (GLM) with the species scores on CA-I as the univariate response variable (N = 52) and the species traits as explanatory variables.

Testing traits as indicators of hypothesized causal effects

A key assumption of the traits-based analysis is that the correlation between a trait and $\mathbf{D_C}$ reflects the effect of the forcing factor thought to be associated with that trait. We were able to test this assumption for two of the traits, biogeographic distribution and seal predation, as follows.

We expected biogeographic distribution to reflect thermal preferences and thus responses to changes in climate. We predicted that if the climate signal could be "filtered" out of the time series of species abundances, then the relationship between abundance and trait matrices should weaken for biogeographic distribution but not for the other traits. To test this prediction, new time series of abundance were constructed for each species based on the residuals from the regression of abundance, $\mathbf{C}_{(i\cdot)}$, on the mean temperature in the cold intermediate layer (CIL: 30–150 m; –1 to 2 °C; Fig. 2*c*), the water layer that covers most of the bottom of the southern Gulf of St. Lawrence (Gilbert and Pettigrew 1997). The new abundance indices, controlled for the effect of changing climate, were again transformed to range over the interval [0,1]. The resulting $N \times Y$ residual abundance matrix, $\mathbf{R_{(CIL)}}$, was used to calculate a dissimilarity matrix, $\mathbf{D}_{\mathbf{R}_{(\mathrm{CIL})}}$, using the methods described previously. A Mantel test, based on ranks, was used to measure the respective $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D_C}$ and $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{CIL})}}$ correlations for each of the traits, t. Simultaneous bootstrapping (9999 iterations) of species in $\mathbf{C}$ and $\mathbf{R_{(CIL)}}$, followed by recalculation of $\mathbf{D_C}$ and $\mathbf{D}_{\mathbf{R}_{(\mathrm{CIL})}}$ and then the Mantel correlations was used to estimate the probability that the $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D_C}$ correlations were weaker than the $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{CIL})}}$ correlations. This was done by counting the number of paired bootstrap samples in which the Mantel correlation based on the residual abundance trends was greater than or equal to that based on the original trends. Because there are often delays between climatic changes and population responses (e.g., Stenseth et al. 2004), the cold intermediate layer temperature series was filtered from abundance trends using lags of 0 to 5 years, and the analysis was repeated for each case.

A similar analysis was conducted by filtering out the effect of seal predation based on the regression of $\mathbf{C}_{(i\cdot)}$ on grey seal abundance (Fig. 2*b*), lagging the seal index by 1 year, to produce the residual abundance matrix, $\mathbf{R_{(seal)}}$. The remainder of the analysis proceeded as described above. In this case, however, a decrease in correlation strength was predicted for the seal predation trait, but not the other traits. A similar analysis could not be conducted for exploitation level because reliable time series of fishing mortality were lacking for many species. The same was true for diet and time series of prey abundance. Furthermore, because this analysis tests for a decline in the association between traits and community dynamics, only traits showing a significant association in the dbRDA were tested.

Finally, a null distribution was also generated using 10 000 iterations in which an $\mathbf{R_{(random)}}$ matrix was created using randomly generated environmental series. The expectation for the null model is that $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{random})}}$ correlations would be stronger than $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D_C}$ correlations about 50% of the time.

Establishing absolute levels of removal by fisheries and seals

An important further step in evaluating the evidence for the hypothesized effects of fisheries and seals was to establish whether the absolute magnitude of fish removals by each of these two sources is sufficient to explain the changes observed in the community. Given the difficulties in quantitatively establishing the species composition of seal diets, we considered total annual removals of fish for the whole community. Annual grey seal consumption of fish prey, Q_j, was estimated using a mean annual individual consumption rate of 1.75 tonnes·seal^{-1} (calculated from Hammill and Stenson 2000) multiplied by the number of grey seals in the Gulf of St. Lawrence herd (Fig. 2*b*). Because there are seasonal movements between areas by seals in the Gulf herd (Harvey et al. 2008) and the neighboring Sable Island herd (Breed et al. 2006), estimated consumption of southern Gulf fish based on abundance of the Gulf herd alone is likely to be conservative given the much larger size of the Sable Island herd. Annual removals of fish by fisheries were summarized for landed (L_j) and discarded (D_j) catch by summing over species. Discarded catch was kept separate given that long-term survival of released fish is generally not well known (Davis 2002), though across all species and fisheries, we expect it to have been relatively low. The removals Q_j, L_j, and D_j were expressed as a percentage of catchability-adjusted fish standing stock biomass, B_j.

Top-down effects of fish predation

The final hypothesis, that the composition of the fish community is affected by changes in the amount of predation by piscivorous fishes, could not be evaluated using the traits-based approach. We could not identify a trait that unambiguously reflected susceptibility to predation by fishes. Thus, we used the more traditional approach of correlation, examining the relationship between relevant response and forcing factor variables.

We used the biomass of small-bodied fish (defined here as fish < 20 cm in length) as the response variable. This was estimated from catch rates (numbers) at length and length–weight data obtained for all fish species caught during the annual surveys. Catches were adjusted for catchability (see Appendix A, Table A1) and expanded from the area swept by a standard tow to the survey area.

The potential explanatory variable was an index of annual size-dependent piscivory (P_j) by the fish community (e.g., Duplisea 2005). P_j was calculated using an allometric relationship for total consumption combined with a correction for the proportion of fish in the diet of predators and size-dependent prey selectivities:

$$(3) \qquad P_j = 365 \sum_{i=1}^{N} \sum_{k=1}^{k_{\max_i}} A_{ijk}\ (0.01\ w_{ijk}^{0.75})\ \mathrm{PF}_{ik} \cdot C(<20)_{ik}$$

where A_{ijk} is the total catchability-adjusted abundance of fish predator species i in year j at length k, w_{ijk} is body weight at length k for species i in year j, PF_{ik} is the propor-

Table 2. Summary of the principal questions addressed in this paper, including in each case the type of analysis used, the response and explanatory variables involved, how statistical significance was assessed, and how the results are presented.

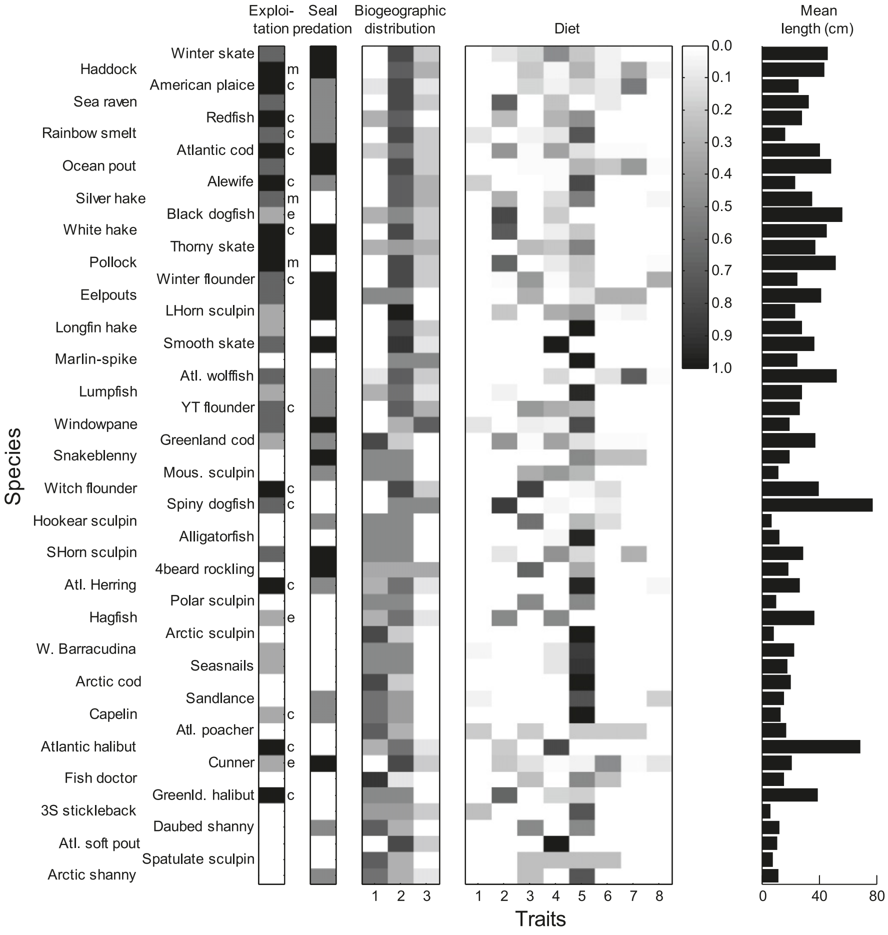
Analysis	Response variable	Explanatory variable	Statistical testing	Results presented
How has the species composition changed over time?				
CA	$\mathbf{C}$	—	—	1. Plot of standardized species abundance time series sorted by the first CA eigenvector (CA-I) (Fig. 4) 2. Ordination of years with respect to the first two CA eigenvectors (Fig. 5)
Which (*i*) traits or (*ii*) suite of traits are (is) related to interspecies differences in interannual changes in abundance?				
(*i*) dbRDA (marginal tests)	$\mathbf{D_C}$	$\mathbf{T}_t$	Permutation of the elements of $\mathbf{D_C}$	1. Effect size (explained variance, $R^2_{\mathbf{Y}\mid\mathbf{X}}$) and statistical significance (Table 3*a*) 2. Plot of trait values (Fig. 3) sorted in the same manner as the ordered species abundance time series (Fig. 4)
(*ii*) dbRDA (partial tests)	$\mathbf{D_C}$	$\mathbf{T}_t$	Permutation of the multivariate residual matrix	1. Plot of trait centroids in ordination of years (Fig. 5) 2. Cumulative effect size ($R^2_{\mathbf{Y}\mid\mathbf{X}}$) and individual statistical significance (Table 3*b*)
Which traits are related to the main pattern of change over time in species composition?				
GLM	CA-I species scores	$\mathbf{T}_t$	Parametric probability	Explained variance (R^2) and statistical significance presented in the text
How do the traits covary?				
Mantel correlation	$\mathbf{D}_{\mathbf{T}_t}$	—	Permutation of the elements of $\mathbf{D}_{\mathbf{T}_t}$	Table of pairwise Mantel correlation analysis results (Table 4) and plots of trait values (Fig. 3)
Does the correlation between a trait and the species dissimilarity matrix reflect the effect of the forcing factor thought to be associated with that trait?				
Mantel correlation	$\mathbf{D_C}$, $\mathbf{D}_{\mathbf{R}_f}$, $\mathbf{D}_{\mathbf{T}_t}$	Time series of f, as covariates to produce $\mathbf{R}_f$	Simultaneous bootstrapping of $\mathbf{C}$ and $\mathbf{R}$	Mantel correlation coefficients and the approximate probability that the $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D_C}$ correlations were weaker than the $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D_R}$ correlations (Table 5)
Are the estimated absolute levels of removal consistent with the effects of fishing and seal predation?				
—	B_j, L_j, D_j, Q_j	—	—	Plot of removals by fisheries and seals as a percentage of estimated fish biomass (Fig. 6)
Is there evidence that the composition of the fish community is affected by changes in the amount of predation by piscivorous fishes?				
Correlation	P_j (eq. 3), B_j (l<20 cm)	—	Parametric probability[a]	Plot of both time series (Fig. 7) along with correlation and associated p value

Note: The following notation is used in this table and in the text: CA and dbRDA denote correspondence analysis and distance-based redundancy analysis, respectively; $\mathbf{C}$ is the matrix of standardized annual species catch rates; $\mathbf{R}_f$ is the matrix of standardized residual annual species catch rates following regressions on the time series of forcing factor f (either the cold intermediate layer temperature or grey seal abundance); $\mathbf{T}_t$ is the species matrix for trait t; $\mathbf{D_C}$, $\mathbf{D}_{\mathbf{R}_f}$, and $\mathbf{D}_{\mathbf{T}_t}$ are, respectively, the species dissimilarity matrices based on the elements of $\mathbf{C}$, $\mathbf{R}_f$, and $\mathbf{T}_t$; B_j, L_j, D_j, and Q_j are, respectively, the total annual biomass, landings, discards, and grey seal consumption of marine fishes; GLM, general linear model.

[a] The probability of the data given the null hypothesis was based on degrees of freedom adjusted for autocorrelation.

tion of fish in the diet of species i at length k based on published accounts (Bowman et al. 2000; Hanson and Chouinard 2002; Savenkoff et al. 2004), and $C(<20)_{ik}$ is the fraction of the total fish consumption by species i of length k that is composed of fish prey less than 20 cm in length. The daily consumption rate (kg·individual^{-1}·day^{-1}) was estimated by the allometric relationship $0.01w^{0.75}$, based on the common exponent for metabolic rates (Brown et al. 2004) and a scaling parameter value used in multispecies virtual population analyses for North Sea cod (Magnússon 1995; ICES 1998). $C(<20)_{ik}$ was calculated using published linear relationships for minimum, average, and maximum prey sizes consumed as a function predator size (Scharf et al. 2000). For species without published relationships, we applied the relationships published for anatomically similar species: the cod relationships were used for other round fish, those for windowpane for the other flatfish, winter skate for the other skates, and spiny dogfish for black dogfish. Consumption was distributed among 1 cm prey size groups using one of two approaches: even distribution between the predicted minimum and maximum prey sizes or assuming the existence of a preferred prey size within the range of consumed prey. In the second approach, size preference was modeled using a normal distribution of consumption centered on the predicted mean prey size (with a standard deviation equal to one-sixth the difference between the maximum and minimum prey sizes). Both approaches produced similar temporal patterns in P_j, so results are pre-

Fig. 3. Biological traits of the southern Gulf of St. Lawrence marine fish species. Values for exploitation level, seal predation, biogeographic distribution, and diet are represented by shading (according to the inset bar), whereas a histogram is used to display mean body length. Species were sorted by species scores on the first correspondence analysis eigenvector (CA-I). Letters to the right of exploitation level indicate whether species were captured in a directed commercial fishery (c), sought in a mixed-species commercial fishery (m) directed principally at another species, or captured in a new or experimental commercial fishery (e). For the biogeographic distribution trait, the categories are as follows: 1, Arctic–subarctic; 2, boreal; 3, temperate. For diet, the categories are as follows: 1, fish eggs and larvae; 2, adult fish and squid; 3, marine worms; 4, shrimps and crabs; 5, invertebrate plankton; 6, mollusks other than squid; 7, echinoderms; 8, other prey. The mean length of species measured in the survey was added to the plot to highlight changes that have occurred in the size structure of the community.



sented here only for the approach assuming preferred prey sizes.

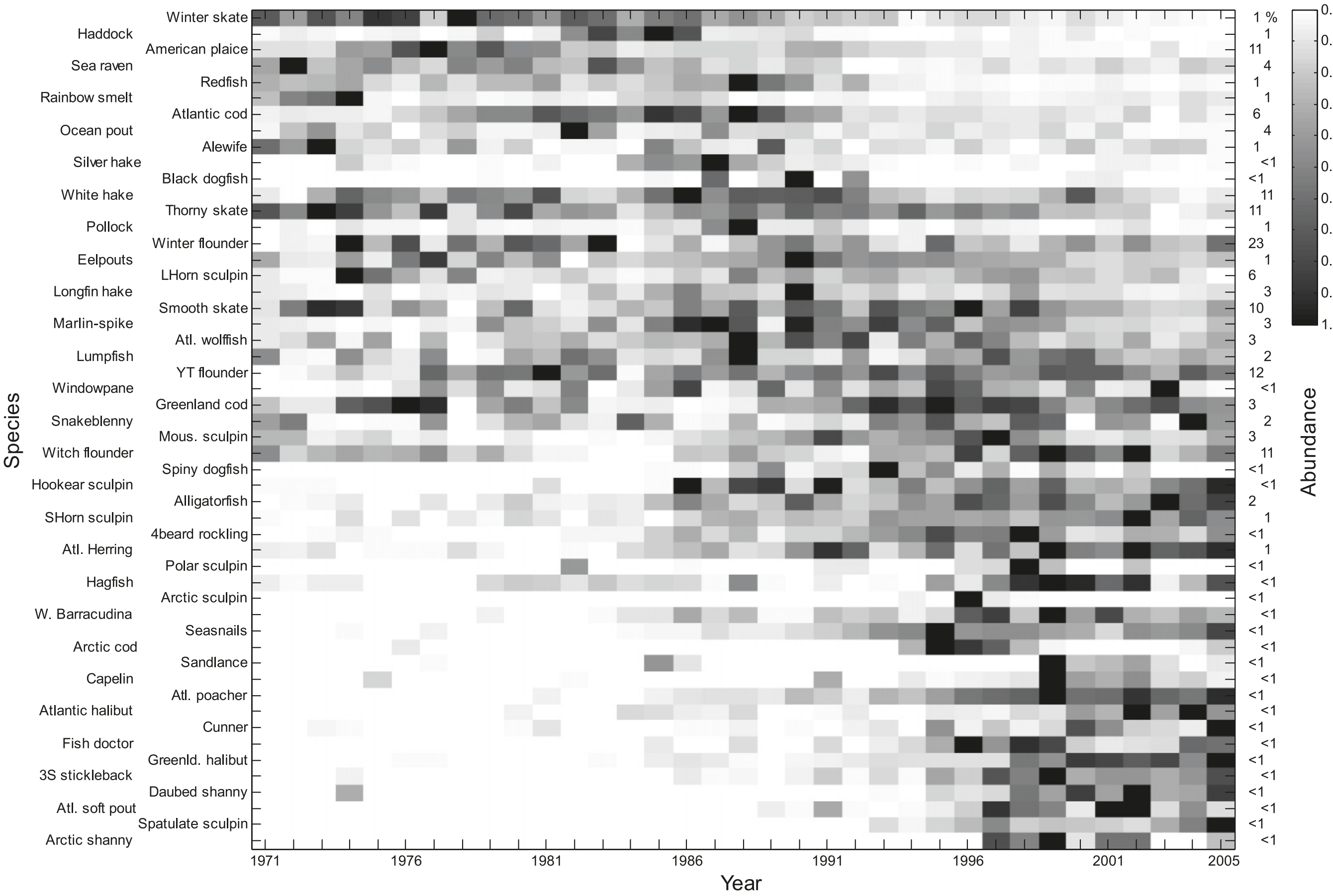
A summary is provided of the analyses described throughout the Methods section, including their inputs and outputs (Table 2).

Results

The first CA eigenvector (CA-I; 27% explained variance) summarized major time trends in species abundance (correlation with time, $r = 0.94$). Sorting the species in **C** by their scores on CA-I and plotting their abundance highlights clear and dramatic changes in the composition of the southern Gulf marine fish community that have occurred since monitoring began in 1971 (Fig. 4). The magnitude of change was considerable for most species (see numbers provided in Fig. 4). Some species declined sharply in abundance in the late 1970s and early 1980s and have remained at low levels since then (e.g., American plaice, winter skate); others increased sharply in abundance in the late 1970s or late 1980s but suffered rapid population collapses in the 1990s (e.g., Atlantic cod, redfish); still others increased dramatically in abundance in the mid- or late 1990s (e.g., Greenland halibut, daubed shanny).

In marginal dbRDA tests, temporal variability in community composition was significantly related to the traits exploitation level, biogeographic distribution, and seal predation, but not to diet (Table 3*a*). These relationships are visually apparent when comparing Figs. 3 and 4, in which species are sorted in the same order. Over time, the community has shifted from one dominated by boreal species that are heavily fished (or incidentally captured in fisheries at a high rate) and commonly occur in grey seal diets to one dominated by species that are rarely caught in fisheries, occur at more northerly latitudes, and tend to be less affected by seal predation (Fig. 5).

Fig. 4. Time series of abundance for 52 marine fish species (rows) in the southern Gulf of St. Lawrence, 1971–2005 (see Appendix A, Table A1 for scientific names). Abundance was transformed to range between 0 (lowest observed abundance, white) and 1 (highest observed, shaded black). Years with intermediate levels of abundance are shaded grey according to the bar on the right. The numbers immediately to the right of the plot are the minimum untransformed survey catch rate as a percentage of the maximum observed for each species, providing an indication of the magnitude of abundance change. As in Fig. 3, species are sorted by the species scores on CA-I to highlight the principal changes that have occurred in the community over time.



We found independent effects of the traits biogeographic distribution, exploitation level, and seal predation on the temporal variability in community composition using partial dbRDA (Table 3*b*). No significant relationships were found for diet in the partial analyses. Together, the three significant traits explained 25% of the multispecies abundance variation. However, intercorrelations among the traits (Table 4) limited somewhat the degree to which dissimilarity in abundance trends between species could be uniquely attributed to any one trait. By repeating the partial dbRDA with each trait in turn as the last-entered variable, we estimated that of the explained variation, 6% was uniquely attributable to biogeographic distribution, 5% to seal predation, and 4% to exploitation level, with the remaining 10% confounded among the three traits. In the univariate (GLM) analysis of long-term trends in species abundance, 55% of the variance in species scores on CA-I was explained by the three traits. The result for all three traits was statistically significant in marginal tests (in all cases, $p \leq 0.001$) and in conditional tests when entered as the last variable in the model (i.e., type III sums of squares; all $p < 0.05$).

The shift in community trait composition corresponds qualitatively with changes in the hypothesized forcing factors relevant to the traits. Much of the decline in abundance of the species most impacted by fisheries occurred during periods of high overall groundfish fishing mortality, particularly during the early 1990s (Fig. 2*a*). Likewise, the lack of recovery or continued decline of many of these species following large reductions in fishing effort in the early 1990s corresponds with dramatic increases in the abundance of grey seals in the ecosystem (Fig. 2*b*). Furthermore, the shift in the biogeographic origin of species coincides with changes in the mean bottom-water temperatures in the cold intermediate layer (Fig. 2*c*). The abundance of cooler-water species, particularly Arctic species, peaked during or shortly after the period of coldest water temperatures, declining somewhat subsequently as temperatures moderated (Figs. 3 and 4). Shorter-term temperature changes occurring during the 1970s do not appear to have led to comparable shifts in species composition (Fig. 5).

We found support for our assumption that the correlation between the trait biogeographic distribution and $\mathbf{D_C}$ reflects an effect of changing water temperatures. When the cold intermediate layer temperature series was filtered from $\mathbf{C}$ to

Table 3. Relationships between abundance trends and species traits in the southern Gulf of St. Lawrence marine fish community based on distance-based redundancy analysis (dbRDA).

Traits	Pseudo-*F*	*p*	$R^2_{\mathbf{Y}\mid\mathbf{X}}$
(*a*) Marginal tests.			
Biogeographic distribution	3.28	**<0.0001**	17.0
Seal predation	4.37	**0.0007**	8.1
Exploitation level	7.94	**<0.0001**	13.7
Diet	1.25	0.1092	18.9
(*b*) Conditional test, forward selection.			
1. Biogeographic distribution	3.28	**<0.0001**	17.0[a]
2. Seal predation	2.80	**0.0041**	21.7[a]
3. Exploitation level	1.81	**0.0431**	24.7[a]
4. Diet	1.02	0.4397	32.0[a]

Note: $R^2_{\mathbf{Y}\mid\mathbf{X}}$ is the percentage of the multivariate species-abundance dynamics (matrix **Y**) explained by the trait(s) (matrix **X**) and is the multivariate equivalent of the regression coefficient of determination. Analyses yielding a probability value smaller than 5% are interpreted as being statistically significant and are indicated in bold.

[a] Cumulative.

Table 4. Results of pairwise Mantel correlation analyses of species–trait dissimilarity matrices (*p*, based on 9999 permutations).

	Trait			
Trait	2	3	4	5
1. Exploitation level	<0.001	0.056	0.003	<0.001
2. Biogeographic distribution	—	0.794	0.030	0.011
3. Diet	—	—	0.077	<0.001
4. Seal predation	—	—	—	0.065
5. Mean body length	—	—	—	—

Note: Dissimilarities were calculated using the χ^2 distance for traits 2 and 3 and absolute arithmetic difference for the others.

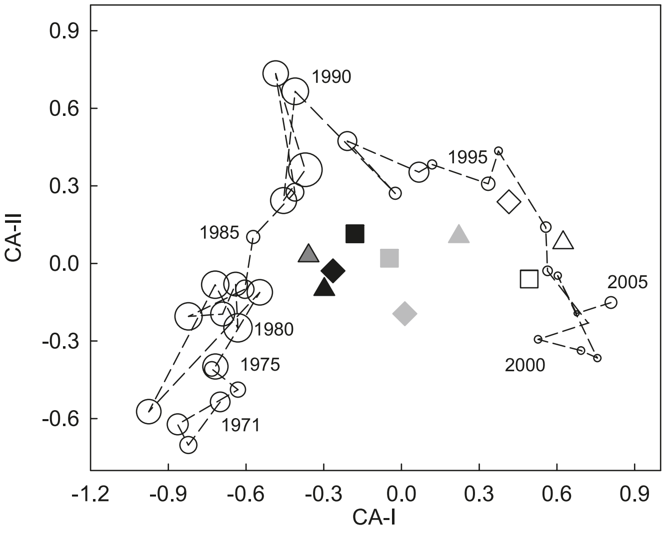


Fig. 5. Temporal trends in the species and trait composition of the southern Gulf of St. Lawrence marine fish community. The plot presents the ordination of years (circles) with respect to axes I and II of the correspondence analysis (CA) of fish species abundance in the southern Gulf (1971–2005). The axes explained 27.2% (λ_1 = 0.345) and 9.8% (λ_2 = 0.124) of the variability in abundance, respectively. The distance between years in the plot reflects their similarity in species composition. Trait centroids are plotted for the traits exploitation level (triangles: black, score =1 (high); dark grey, 0.67 (intermediate); light grey, 0.33 (low); open, 0 (no capture)), seal predation (diamonds: black, 1 (above median); grey, 0.5 (below median); open, 0 (no predation)), and biogeographic distribution (squares: black, temperate; grey, boreal; open, Arctic–subarctic). The survey-derived mean annual body length in the community is indicated by the size of the circle for each year (minimum 8 cm, maximum 24 cm). The proximity of trait centroids to a given year is an indication of the characteristics of the species dominating the community in that year (e.g., Arctic–subarctic species were a more important component of the community in the 2000s than in the 1970s).

produce $\mathbf{R}_{(\mathbf{CIL})}$, the resulting $\mathbf{D_T}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{CIL})}}$ Mantel correlations were weaker than the $\mathbf{D_T}$–$\mathbf{D_C}$ correlations (Table 5). This difference was observed for the temperature time series lagged by 0 to 3 years, though it was strongest and statistically significant (5% type I error level) for lags of 2 or 3 years. In contrast, yet also in line with prediction, there were no significant differences between $\mathbf{D_T}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{CIL})}}$ and $\mathbf{D_T}$–$\mathbf{D_C}$ correlations for the exploitation level and seal predation traits for any time lag. Results for the null model analysis were consistent with our expectation of equally strong $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{random})}}$ and $\mathbf{D}_{\mathbf{T}_t}$–$\mathbf{D_C}$ correlations (Table 5).

We also found support for the mechanism assumed to underlie the correlation between the seal predation trait and $\mathbf{D_C}$. When the grey seal abundance time series was filtered out of **C** to produce $\mathbf{R}_{(\mathbf{seal})}$, the $\mathbf{D_T}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{seal})}}$ Mantel correlation was considerably weaker than the $\mathbf{D_T}$–$\mathbf{D_C}$ correlation for the seal predation trait (Table 5). Furthermore, as predicted, a statistically significant difference was not observed for the biogeographic distribution trait. In contrast with our predictions though, we observed a $\mathbf{D_T}$–$\mathbf{D}_{\mathbf{R}_{(\mathrm{seal})}}$ correlation that was significantly weaker than its $\mathbf{D_T}$–$\mathbf{D_C}$ counterpart for the exploitation level trait, suggesting that the effects of exploitation and seal predation are somewhat confounded in our analyses. This confounding follows from a correlation between the traits believed to reflect susceptibility to fisheries and seal predation (Table 4) and a trade-off over time in the estimated removals by these two sources of mortality (Fig. 6). For the primary prey of seals, increased consumption by seals in the early to mid-1990s counteracted the sharp decline in fishery removals so that the total rate of removal due to fishing and seal predation remained roughly constant over the time series (Fig. 6*a*). This is less evident considering removals of all seal prey, though the contribution of seals to these removals generally increased over the series (Fig. 6*b*).

The estimated magnitude of combined removals by fishing and seals (~10% of total seal prey or ~25% primary prey biomass) supports these two sources of mortality as plausible causes of community change for seal prey species (Fig. 6). Likewise, for species captured by fisheries but not seals, an average of 37% (1971–1989) or 5% (1990–2005) of standing stock biomass was removed every year (figure not shown), levels of removal that make an effect of fishing plausible.

The changes in species composition were also accompanied by a change in community size structure, with particularly sharp declines in mean length during the 1990s

Table 5. Results of Mantel correlation analyses relating the dissimilarity matrices for three traits (biogeographic distribution, seal predation, and exploitation level) to the dissimilarity matrices based on (*i*) the original species–year matrix, and residual species–year matrices from (*ii*) the randomly generated environmental time series, (*iii*) the abundance of grey seals, and (*iv*) cold intermediate layer temperatures at various time lags.

	Species trait		
Filtered series	Biogeographic distribution	Seal predation	Exploitation
(*i*) None	0.16 (—)	0.12 (—)	0.15 (—)
(*ii*) Random series[a]	0.16 (0.474)	0.12 (0.501)	0.14 (0.546)
(*iii*) Seal abundance	0.11 (0.194)	0.01 (**0.011**)	0.03 (**0.027**)
(*iv*) Mean cold intermediate layer temperature[b]			
No lag	0.10 (0.088)	0.11 (0.511)	0.13 (0.390)
Lag 1 year	0.11 (0.099)	0.11 (0.532)	0.13 (0.363)
Lag 2 year	0.10 (**0.019**)	0.13 (0.626)	0.14 (0.446)
Lag 3 year	0.09 (**0.039**)	0.13 (0.660)	0.11 (0.332)
Lag 4 year	0.15 (0.325)	0.12 (0.319)	0.12 (0.235)
Lag 5 year	0.16 (0.452)	0.11 (0.300)	0.14 (0.445)

Note: Mantel correlation coefficients are presented along with, in parentheses, the approximate probability that the Mantel correlation with the residual species–year matrix is equal to or greater than that with the original matrix. Analyses yielding a probability smaller than 5% are indicated in bold.

[a] Mantel correlation values presented in (*ii*) are the mean for 10 000 simulations.

[b] Although time lags up to 10 years were initially analyzed, only those from 0–5 years are presented as all lags of 4 years or more produced similar results.

Fig. 6. Total annual fishery landings (grey), estimated fishery discards (open), and estimated grey seal consumption (black) as a percentage of fish standing stock biomass. The percentages in (*a*) are for only those species scored as 1 on the seal predation trait, based on the conservative assumption that 50% of total seal predation was concentrated on those species. Similarly, the percentages in (*b*) are for all seal fish prey (i.e., seal predation trait = [0.5,1]).

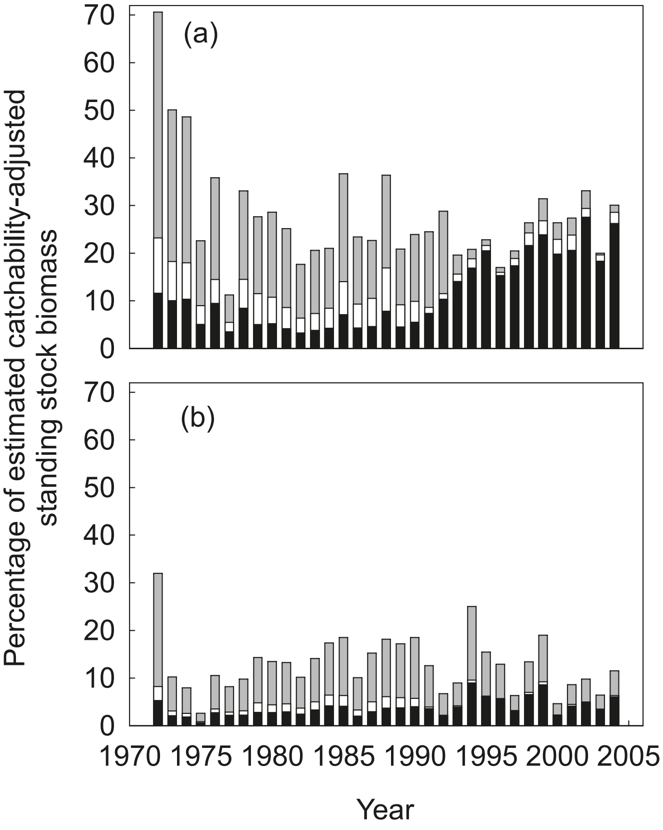
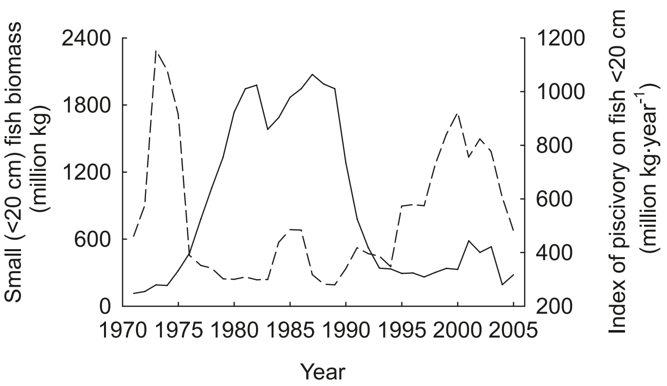


Fig. 7. Total annual biomass of fish <20 cm in length (broken line) and the index of potential predation by piscivorous fish on those small-bodied fish (solid line), 1971–2005. Both quantities are estimated using catchability-adjusted research survey catches and are presented as 3-year running averages.



(Fig. 5). These changes are characterized by both a decrease in abundance of many large-bodied species, particularly during the late 1980s, and an increase in smaller-bodied species during the 1990s (Figs. 3 and 4). We found opposite trends over time in total small fish biomass and in the index of predation on them by larger fish (Fig. 7; Spearman's correlation = –0.70, p = 0.012 based on degrees of freedom adjusted for autocorrelation following eqs. 1, 6, and 7 of Pyper and Peterman 1998). This result is consistent with a hypothesized effect of piscivory on community size structure. Size-dependent predation may not be the only cause of change, however, as many of the cooler-water species in the community are also smaller-bodied (Fig. 3). The correlation between the traits biogeographic distribution and body size (Table 4) suggests that changing water temperatures may have indirectly contributed to changes in size structure. However, only the patterns in size-dependent piscivory can explain the high biomass of small fishes during the early 1970s (Fig. 7).

Discussion

In this paper, we have adopted the view that the dynamics of an ecological community reflect changes over time in its environment, which selects for or against particular suites of functional traits and species tolerances (e.g., Keddy 1992). In our view, this traits-based approach has a number of advantages. First, the functional forms of species interactions and population responses to environmental forcing do not need to be specified (Shipley et al. 2006). This is advantageous, for example, when species population responses to external change are nonlinear (e.g., Mysterud et al. 2001; Stenseth et al. 2002). Second, by comparing the dynamics of numerous species with widely contrasting states across a suite of relevant traits, it may be possible to disentangle the responses to otherwise confounded multiple forcing factors. Third, a functional basis for expected responses of species to environmental change is the foundation of the approach. Functional models can also be used in traditional approaches, with the responses of individual species to forcing factors explicitly modeled; however, these traditional models become problematic as the number of species, and thus their interactions with each other and physical forcing factors, increase. However, despite these advantages, the traits-based approach remains essentially correlative. Thus, where possible, we attempted to strengthen our inference by examining the effect of filtering the underlying forcing factors from the time series of species abundance and by examining whether the effects of the hypothesized forcing factors (i.e., magnitude of fishery removals, seal consumption) were sufficient to have a substantial influence on community dynamics.

The traits-based approach also had a number of limitations in our case. First, only static (i.e., average) trait values could be used. This is a particular issue for the exploitation level trait because of changes in target species over time. However, because interspecific differences in exploitation rate generally exceeded intraspecific differences over time (results not shown), this trait was still a useful general measure of susceptibility to fishing. A second limitation was the use of semiquantitative traits. On one hand, the semiquantitative traits likely limited the variance in **C** explained in the dbRDA. On the other hand, some subjectivity in our choice of traits scoring may have influenced our results. Sensitivity to the scoring was, however, examined by repeating the dbRDA using traits that were scored more coarsely (e.g., reducing diet to four prey groups or seal predation to two levels). Results (not shown) were robust to these alternate scoring schemes. A third limitation was that it may not be possible to identify a trait that is unambiguously linked to a hypothesis of interest. In our study, this was the case for the hypothesized effect of predation by fishes. In the absence of a detailed food web of the southern Gulf community, susceptibility to predation by fishes could only be defined on the basis of body size. The problem is that body size in the community is also potentially affected by climate change (e.g., Blanchard et al. 2005), seal predation (e.g., Duplisea 2005), and the direct and indirect effects of fishing (e.g., Pope et al. 2006). The test of the hypothesized effect of predation by fishes was therefore necessarily ad hoc, though we again aimed to establish that both the magnitude and trend in predation were consistent with the inferred effects on the community. A final caveat with respect to our analysis is that it was focused largely on the dynamics of the adult and late juvenile stages (i.e., the size classes well sampled by the survey). This is particularly relevant to the hypothesis of bottom-up effects of changes in prey availability. Our analysis was based on the prey of adult fish, whereas bottom-up effects may be strongest at earlier life-history stages (e.g., Beaugrand et al. 2003).

Our analyses indicate that dramatic shifts in species composition of the fish community in the southern Gulf of St. Lawrence are related to the traits of these species. These traits, chosen to reflect susceptibility to particular forcing factors, allowed us to test four hypotheses for the causes of community change: direct fishing effects, climate change, changes in prey availability, and effects of a top predator, the grey seal. We found that three of these traits, the traits related to direct effects of fishing, climate change, and seal predation, could account for 25% of the interannual variability in the abundances of the 52 species in our analysis. The low percentage of variability explained by these traits may partly reflect observation error, an important component of the interannual variability in survey catch rates. Indeed we found that 55% of the variation in the species scores on CA-I, which summarized the main temporal trends in species composition, could be explained by these three traits.

Fishing is probably most often the factor implicated in marine fish community change (see the many examples in Hall 1999). This is not without cause given that mortality imposed by targeted fishing can be high, often exceeding that from natural sources (Stokes and Law 2000). Furthermore, incidentally captured (and discarded) sizes and species of fish often form a large proportion of total catches (e.g., Harrington et al. 2005). In the southern Gulf of St. Lawrence, every species that declined in abundance over the 35-year study period was susceptible to capture by fisheries. Much of this decline occurred during the late 1980s and early 1990s when fishing effort increased sharply. Declines were most pronounced for species with relatively high scores (0.67 and 1) on the exploitation level trait. These included both targeted species (e.g., Atlantic cod, redfish) and species that are incidentally caught and discarded (e.g., sea raven).

Exploited species that declined to low abundance in the 1990s have failed to recover despite very low levels of fishing for over a decade. This suggests a decline in the productivity of these populations (e.g., Shelton et al. 2006), possibly because of ecosystem change. The reduced productivity of Atlantic cod in the southern Gulf of St. Lawrence stems in large part from elevated natural mortality of adult cod (Sinclair 2001). Congruent trends between that mortality and grey seal abundance suggest the hypothesis that increasing predation by grey seals may contribute to the reduced productivity of this cod population (Chouinard et al. 2005). Our results are consistent with this hypothesis and suggest a broad impact of elevated seal predation on the fish community. Since the late 1980s, composition of the community has shifted towards species that are less impacted by grey seals.

Among the large-bodied species susceptible to capture by fisheries, only those consumed at a low rate or not at all by seals have increased in abundance since the mid-1980s (e.g., witch flounder and Greenland and Atlantic halibuts).

Although our analyses did identify independent effects of the traits exploitation level and seal predation, these two sources of mortality were largely confounded, perhaps partly as a result of the use of static trait values. Among their primary prey in particular, increased consumption by grey seals replaced reduced fishery removals in the 1990s, providing an explanation for the lack of recovery of these fishes despite severely reduced fishing activity. Furthermore, the estimated magnitude of fish removals by fishermen and seals, though subject to the catchability adjustments used, supports these two sources of mortality as plausible causes of community change. The additional impact of other top predators such as harbour porpoise (*Phocoena phocoena*) is unknown given a lack of data on their diet and abundance.

Most fishes with infrequent capture in fisheries and low predation rates by seals increased dramatically in abundance in the 1990s. With few exceptions (e.g., Atlantic halibut), increasing species were small-bodied. Increased abundance implies reduced mortality from other sources, increased recruitment, and (or) increased immigration from other areas. One explanation for the recent increases in these small-bodied fishes is a release from predation following the depletion of large fish by fisheries (e.g., Blanchard et al. 2005; Frank et al. 2005). This explanation is supported by the inverse relationship observed between the estimated biomass of small fish and the consumption of these fish by large fish. The relative ranges of estimated small fish biomass (300–2300 million kg) and their consumption by large fish (200–1100 million kg·year^{-1}), though contingent on the assumptions made in estimating them, further make this mechanism plausible.

Effects of fishing and predation by seals and large piscivorous fish on the composition of this fish community suggest strong consumer control of fish production. In this case, these top-down effects all appear to reflect direct or indirect impacts of harvesting. Reduced predation by overexploited large piscivorous fish in the 1990s is likely an indirect effect of fishing. Likewise, increased predation by grey seals in the 1990s may be an indirect effect of reduced harvests and population control activities since the 1970s (Zwanenburg and Bowen 1990). Indirect harvesting impacts have also been proposed to explain reduced recruitment success of southern Gulf cod as stocks of Atlantic herring and Atlantic mackerel (*Scomber scombrus*), potential predators of cod eggs and larvae, rebuilt in the 1980s following reductions in harvesting (Swain and Sinclair 2000).

Our analyses also identified a significant effect of climate on the composition of the southern Gulf of St. Lawrence fish community. This effect was largely independent of those of fishing and seal predation and was linked to variation in bottom water temperatures. Community composition shifted towards species with more northerly biogeographic distributions following the cooling of the cold intermediate layer in the late 1980s and early 1990s. This mirrors a similar shift in zooplankton community composition in the Labrador Sea following cooling conditions (Beaugrand et al. 2002). The southern Gulf fish community appears to have responded to changing thermal conditions within 3 years. The range of possible time lags associated with the community changes suggests that the mechanisms underlying them may have varied between species. These mechanisms include climate-driven shifts in distribution (e.g., Beaugrand et al. 2002; Perry et al. 2005), environmental influences on demographic rates (e.g., Attrill and Power 2002), and a combination of the two (e.g., McGowan et al. 1998). The sudden appearance of species such as polar sculpin and Arctic sculpin, coincident with the occurence of unusually cold water temperatures in the mid-1990s and their rapid disappearance as temperatures warmed, is consistent with a distributional shift. The same is true of the relationship observed between the broader-scale distribution of capelin in the Gulf and the spatial extent of cold water (Grégoire et al. 2004). For other species such as Atlantic and Greenland halibuts, increases in the abundance of juvenile individuals in the southern Gulf (Benoît et al. 2003) are consistent with possible climate-mediated increases in recruitment.

We found no evidence, however, for bottom-up effects of environmental change acting through the prey of adult fish. (The relatively high proportion of variation explained by diet in the dbRDA is a reflection of the large number of categories used for this trait.) However, we can not rule out the existence of prey-mediated increases in certain individual species or bottom-up effects of changes in preferred prey of juvenile fish. Furthermore, an assumption underlying our analyses, that changes in prey availability should have similar effects on species with similar diets, may be invalid given expected effects of interspecific competition (e.g., Duplisea and Blanchard 2005). We can only say that the other effects considered — fishing, seal predation, and climate change — explain more of the changes observed in the survey of the southern Gulf fish community.

Our analyses point to direct impacts on species productivity stemming from changes in environmental conditions and mortality due to key predators (fish, seals, and ultimately humans). Interactions between these causal factors, though not addressed in our analysis, have the potential to add complexity to community dynamics. For example, differential species responses to climate change may affect existing local trophic relationships (Edwards and Richardson 2004) and the population dynamics of those interacting species (Davis et al. 1998; Petchey et al. 1999). Also, the consequences of fishing are likely to depend on how species resilience and productivity are affected by climate change (e.g., Mora et al. 2007; Hsieh et al. 2006; Rose 2004) and top predators (e.g., Trzcinski et al. 2006). The potential for such interactive effects combined with our observed additive effects of multiple causes of community change underscore the need to adopt an ecosystem-based approach to management (Link 2002; Pikitch et al. 2004). However, given the suddenness of many of the changes observed here and elsewhere (Mullon et al. 2005), accelerating rates of climate change (Stainforth et al. 2005), and limited abilities to isolate direct, let alone indirect, effects of various drivers of community change, the effectiveness of both contemporary single-species and ecosystem-based fishery management is at risk of being “too little, too late”. In the face of such a situation, we agree with others (Botsford et al. 1997) that greater precaution in management is prescribed.

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Appendix A

Table A1 appears on the following pages.

Table A1. Common and scientific names of species included in the southern Gulf of St. Lawrence fish community analysis.

Class–Order–Family	Genus–species	Common name	*Q*
Myxini			
Myxiniformes			
Myxinidae	*Myxine glutinosa*	Atlantic hagfish	3
Chondrichthyes			
Rajiformes			
Rajidae	*Amblyraja radiata*	Thorny skate	5
	Leucoraja ocellata	Winter skate	5
	Malacoraja senta	Smooth skate	5
Squaliformes			
Etmopteridae	*Centroscyllium fabricii*	Black dogfish	4
Squalidae	*Squalus acanthias*	Spiny dogfish	4
Actinopterygii			
Aulopiformes			
Paralepididae	*Arctozenus risso*	White barracudina	3
Clupeiformes			
Clupidae	*Alosa pseudoharengus*	Alewife	6
	Clupea harengus	Atlantic herring	6
Gadiformes			
Gadidae	*Boreogadus saida*	Arctic cod	4
	Gadus morhua	Atlantic cod	1
	Gadus ogac	Greenland cod	3
	Melanogrammus aeglefinus	Haddock	2
	Pollachius virens	Pollock	4
Macrouridae	*Nezumia bairdii*	Marlin-spike	3
Merlucciidae	*Merluccius bilinearis*	Silver hake	4
Phycidae	*Enchelyopus cimbrius*	Fourbeard rockling	3
	Phycis chesteri	Longfin hake	4
	Urophycis tenuis	White hake	3
Gasterosteiformes			
Gasterosteidae	*Gasterosteus aculeatus*	Threespine stickleback	4
Salmoniformes			
Osmeridae	*Mallotus villosus*	Capelin	6
	Osmerus mordax mordax	Rainbow smelt	6
Perciformes			
Ammodytidae	*Ammodytes dubius*	Northern sand lance	7
Anarhichadidae	*Anarhichas lupus*	Atlantic wolffish	3
Labridae	*Tautogolabrus adspersus*	Cunner	3
Stichaeidae	*Leptoclinus maculatus*	Daubed shanny	3
	Lumpenus lampretaeformis	Snakeblenny	3
	Stichaeus punctatus	Arctic shanny	3
Zoarcidae	*Gymnelis viridis*	Fish doctor	3
	Lycodes sp.	Eelpouts	3
	Melanostigma atlanticum	Atlantic soft pout	3
	Zoarces americanus	Ocean pout	3
Pleuronectiformes			
Pleuronectidae	*Glyptocephalus cynoglossus*	Witch flounder	5
	Hippoglossoides platessoides	American plaice	5
	Hippoglossus hippoglossus	Atlantic halibut	5
	Limanda ferruginea	Yellowtail flounder	5
	Pseudopleuronectes americanus	Winter flounder	5
	Reinhardtius hippoglossoides	Greenland halibut	5
Scophthalmidae	*Scophthalmus aquosus*	Windowpane	5
Scorpaeniformes			
Agonidae	*Aspidophoroides monopterygius*, *Ulcina olrikii*	Alligatorfishes	3
	Leptagonus decagonus	Atlantic poacher	3

Table A1 (*concluded*).

Class–Order–Family	Genus–species	Common name	*Q*
Cottidae	*Artediellus* sp.	Hookear sculpins	3
	Icelus spatula	Spatulate sculpin	3
	Myoxocephalus octodecemspinosus	Longhorn sculpin	3
	Myoxocephalus scorpioides	Arctic sculpin	3
	Myoxocephalus scorpius	Shorthorn sculpin	3
	Triglops murrayi	Moustache sculpin	3
Cyclopteridae	*Cyclopterus lumpus*	Lumpfish	3
Liparidae	*Liparis* sp.	Seasnails	3
Hemitripteridae	*Hemitripterus americanus*	Sea raven	3
Psychrolutidae	*Cottunculus microps*	Polar sculpin	3
Scorpaenidae	*Sebastes* sp.	Redfish	4

Note: *Q* refers to the taxa- and length-dependent catchability corrections applied to the survey catches for each species to obtain estimates of the absolute abundance. Five of these models, based on species or species groups, were presented in Harley and Myers (2001): (1) Atlantic cod, (2) haddock, (3) demersal gadoids–roundfish, (4) pelagic gadoids, and (5) flatfish. Using stock assessment data for southern Gulf Atlantic herring, we fitted a similar model to apply to the (6) pelagic fishes (unpublished analyses). Finally, a length-aggregated correction for northern sand lance (7) was obtained from Sparholt (1990).

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