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Changes in size-dependent mortality in the southern Gulf of St. Lawrence marine fish community

Variations de la mortalité liée à la taille dans la communauté de poissons marins du sud du golfe du Saint-Laurent

H.P. Benoît and D.P. Swain

Fisheries and Oceans Canada
Aquatic Resources Division, Gulf Region
Gulf Fisheries Centre
343 avenue université, P.O. Box 5030
Moncton, NB E1C 9B6

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ABSTRACT

In this document we review the evidence for size-dependent mortality in the marine fish community of the southern Gulf of St. Lawrence (sGSL), and consider the support for fishing and predation as likely causes for this mortality. This work was undertaken as a contribution to the October 2010 Zonal Advisory Process on the Impacts of Grey Seals on Fish Populations in Eastern Canada. The review is based on analyses of data from the annual bottom-trawl survey of the sGSL. Size-based indicators suggest that since the early 1990s, the survival rate of small fish in the ecosystem has improved considerably and the survival rate of the largest fish in the community has declined considerably. These size-related changes are largely consistent both within species and at the community level. The improved survival of small fish is consistent with release from predation by formerly abundant large groundfish. Declines in the abundance of larger fish appear to be related to fishing and predation by grey seals. The overall intensity of fishing on groundfish species has declined considerably since the early 1990s, and has been at a very low level for more than a decade. Decreases in the abundance of larger fish, coincident with a rapid increase in fishing intensity during the late 1980s and early 1990s, is consistent with a direct effect of fishing. Failure of those populations to recover despite the recent period of little fishing is not consistent with a direct fishing effect. Species that have failed to recover are all known grey seal prey. It is possible to calculate age or stage-dependent mortality rates for a small number of sGSL species. The rate of survival for juvenile skates, white hake and American plaice has improved, in some cases dramatically, over the past 20-30 years. In contrast, the rates of adult survival have declined over the same period. Because rates of fishing mortality also declined over this period, the worsening adult survival is concluded to be due to natural mortality.

RÉSUMÉ

Dans le présent document, nous examinons les preuves de la mortalité liée à la taille dans la communauté de poissons marins du sud du golfe du Saint-Laurent (SGSL), ainsi que les données à l'appui de l'hypothèse voulant que les activités de pêche et la prédation sont les causes probables de cette mortalité. Ces travaux ont été entrepris dans le cadre du Processus de consultation scientifique zonal d'octobre 2010 sur l'incidence du phoque gris sur les populations de poissons dans l'est du Canada. L'examen s'appuie sur l'analyse des données provenant du relevé annuel au chalut de fond du SGSL. Les indicateurs basés sur la taille suggèrent que depuis le début des années 1990, le taux de survie des petits poissons dans l'écosystème s'est considérablement amélioré, et le taux de survie des plus gros poissons dans la communauté a fortement diminué. Ces variations liées à la taille sont tout à fait constantes à la fois au sein des espèces et au niveau de la communauté. L'amélioration du taux de survie chez les petits poissons est en accord avec le fait que ceux-ci ne sont plus soumis à la prédation par les gros poissons de fond qui étaient auparavant abondants. La diminution du nombre de poissons plus gros semble être associée aux activités de pêche et à la prédation par les phoques gris. L'intensité globale de la pêche des espèces de poissons de fond a considérablement baissé depuis le début des années 1990, et elle se maintient à un niveau très bas depuis plus d'une décennie. Le déclin de l'abondance des poissons plus gros, qui a coïncidé avec l'augmentation rapide de l'intensité de la pêche à la fin des années 1980 et au début des années 1990, peut être considéré de façon cohérente comme une conséquence directe de la pêche. Le fait que ces populations ne parviennent pas à se rétablir, malgré la faible intensité des activités de pêche au cours des dernières années, ne peut toutefois pas être considéré de façon cohérente comme une conséquence directe de la pêche. Les espèces n'ayant pas réussi à se rétablir sont toutes des proies connues du phoque gris. Il est possible de calculer les taux de mortalité liée à l'âge ou au stade de développement pour un petit nombre d'espèces vivant dans le SGSL. Le taux de survie des raies, des merluches blanches et des plies canadiennes juvéniles s'est amélioré, considérablement dans certains cas, au cours des 20 à 30 dernières années. En revanche, le taux de survie chez les adultes a baissé au cours de la même période. Étant donné que le taux de mortalité liée à la pêche a également diminué au cours de cette période, on conclut que la détérioration du taux de survie chez les adultes est due à une mortalité naturelle.

INTRODUCTION

The natural mortality of adult southern Gulf of St. Lawrence (sGSL) Atlantic cod (*Gadus morhua*) has increased considerably concurrent with increases in the abundance of grey seals, *Halichoerus grypus*, suggesting a possible effect of predation by the seals (Chouinard et al. 2005; Swain et al. 2009b). Because grey seals are generalist predators, increases in natural mortality related to increased predation by an expanding NW Atlantic grey seal population should also be apparent for other important seal prey species, provided that this increase is not offset by decreases in mortality from other sources. Of course, grey seals are not the only agents of mortality that have undergone important changes over the past 40 years. Until the early 1990s there were large and intensive groundfish fisheries, which have since been reduced to very low levels. Cod and other formerly abundant large demersal fish, were once important predators of small demersal fish. In this paper we consider the evidence for size-related changes in the mortality of sGSL fishes. We first look at various indicators of size-dependent mortality at the population and community level. We then look at estimates of mortality from age-disaggregated indices and population models. Throughout we discuss the evidence for the contribution of various causes of fish mortality, including fishing and predation. All of the analyses rely on standardized data from the annual research vessel (RV) survey of the sGSL conducted each September since 1971 (Hurlbut and Clay 1990; Benoît and Swain 2003; Benoît 2006b). This work was undertaken as a contribution to the October 2010 Zonal Advisory Process on the Impacts of Grey Seals on Fish Populations in Eastern Canada (DFO 2010).

EVIDENCE FROM THE SIZE- AND SPECIES COMPOSITION OF THE FISH COMMUNITY

There are numerous interdependent lines of evidence that suggest that recently diminished mortality of small or young fish and elevated mortality of large adult fish may be a feature of a number fish species in the sGSL. In this section we explore three of these evidence lines: changes in size composition within species, changes in size composition within the community and size-related changes in species composition within the community. We also present and discuss the available evidence related to the causes of these changes: fishing, predation by fish, predation by seals and environmental changes.

Changes in size composition within species

Fish species with declining biomass trends in the sGSL share two features. On one hand, small individuals increased in abundance in the 1990s and 2000s in these species (Fig. 1). On the other hand, the abundance of the largest fish observed for each species has decreased considerably, while the abundance of mid-sized fish has varied less. The patterns are observed both for commercially exploited species, and species of no commercial importance.

Length frequency distributions for species whose biomass trends are stable or increasing also indicate recent increases in the abundance of small individuals (Fig. 2). However in contrast to species in decline, there are few indications that losses of the largest fish of each species have increased. Species with stable or increasing abundance include commercially exploited species, such as Greenland halibut (*Reinhardtius hippoglossoides*) and Atlantic halibut (*Hippoglossus hippoglossus*, not shown), as well as species of no commercial importance. These species do have one or more characteristics that distinguish them from the species in decline: smaller-bodied (e.g., seasnails, *Liparis* sp. and rockling, *Enchelyopus cimbrius*), spined (long- and

shorthorn sculpins, *Myoxocephalus octodecemspinosus* and *M. scorpius*) or powerful swimmers (e.g., Greenland and Atlantic halibut).

Given their increased abundance at small sizes, the continued decline of many species suggests that mortality has increased on intermediate or large-sized fish in these species, even for intermediate size classes that appear largely stable. There are no indications from other species that growth rates have declined during the last 25 years (Fig. 3), so the lack of increase at intermediate and large sizes, despite increased abundance at small sizes, does not appear to reflect reductions in growth.

Changes in size composition within the community

The changes in the size-structure within species appear to be part of a larger ecosystem-level phenomenon (Fig. 4). The abundance of the smallest fish in the community (<20 cm) was relatively high during the 1970s, relatively low during much of the 1980s, and has been increasing steadily since then. Fish 20-39 cm in length increased during the early to mid 1970s, largely fuelled by the recovery from an earlier collapse of the American plaice stock and then the cod stock. Abundance in this size category has varied without a directional trend since the mid 1980s. Fish sized 40-59 cm likewise increased during the late 1970s and remained high until the early 1990s, when the cod stock began collapsing. Abundance has been declining steadily since then. Finally, the abundance of fish >60 cm fluctuated largely without trend from 1971-1995, but has declined dramatically since then. Again, the recent changes in the abundance of mid and large-size fish are unlikely to be driven by decreases in the growth rate. Conditions for growth of these fish since at least the late 1990s are probably good given an abundance of prey, such as small fish (Fig. 4) and shrimp (Worm and Myers 2003), and environmental conditions that have been average to warm (Fig. 5). Overall, changes in the size composition of the community are consistent with decreased mortality on the smallest fish since the early 1990s, and increased mortality on larger fish (40+ cm) since the early to mid 1990s.

Size-related changes in species composition within the community

Changes in the species composition of the sGSL marine fish community have also largely been structured by size (Fig. 6). For the most part, the larger-bodied species in the community have experienced the strongest declines in abundance since 1971, while the smaller-bodied species have tended to increase dramatically, particularly since the mid 1990s. There are exceptions to the pattern however. For example, rainbow smelt, *Osmerus mordax mordax*, is a small bodied species that has declined in abundance. However, it is one of the few small bodied sGSL species that is commercially harvested (Benoît and Swain 2008) and, as a coastal species is probably not well sampled by the survey. Other exceptions include Atlantic halibut and Greenland halibut. These large-bodied demersal species are all commercially harvested, yet have increased in abundance since the early 1990s. They share one trait in common though, they do not appear to be consumed much by grey or harp seals (Hammill and Stenson 2000; Hammill et al. 2007; Benoît and Swain 2008).

Potential causes of the size-dependent changes

It is well known that fishing results in important size-dependent changes in fish communities (e.g., Bianchi et al. 2000; Daan et al. 2005; Pope et al. 2006). On one hand, fisheries, particularly those targeting groundfish, tend to select the larger species and individuals within species. The resulting declines in the largest fish (a direct effect) often lead to released predation mortality for their prey (an indirect effect). In this section, we discuss the evidence for

the direct and indirect effects of fishing in the sGSL. We then consider the evidence for predation by top predators, with a focus here on grey seals.

Most of the demersal fishing effort in the sGSL has been targeted at cod (Fig. 7). Though data are not available to estimate fishing effort prior to the late 1980s, the estimated fishing mortality (F) of cod is likely a good proxy for effort in that prior period. Total cod F varied around 0.4-0.5 during much of the 1970s and 1980s, increasing rapidly during the late 1980s and early 1990s to reach very high levels. Since the first moratorium on cod, which began in 1993, F and effort have remained at a relatively low level. These decreases in fishing effort since the early 1990s have generally led to decreases in bycatch levels for incidentally captured species (Benoît 2006a; Benoît and Hurlbut 2010).

Patterns in the relative fishing mortality (annual catch/ RV survey biomass; Sinclair 1998) of most other sGSL groundfish species show a similar pattern to cod (Fig. 8). Fishing related mortality has declined considerably for most demersal species and cannot explain the continued apparent high mortality of adult fish. Fishing related mortality has not declined for Greenland halibut and yellowtail flounder, the latter of which is subjected to a very small fishery localized to the Magdalen Islands.

Benoît and Swain (2008) calculated an index of piscivory by fishes for the sGSL, based on an allometric relationship between body mass and consumption, and size- and species-dependent relationships describing the proportion and size composition of fish prey in predator diets. They found a close inverse correspondence between trends in the index of piscivory and the biomass of small fish (Fig. 9). This pattern is consistent with predation-driven changes in small fish abundance (predator release) and with an indirect effect of fishing, given that periods of low piscivore abundance were largely fishery-induced.

Benoît and Swain (2008) also used a traits-based approach to relate similarity among 52 sGSL marine fish species in their abundance trends (Fig. 6) to similarities in their ecological traits. The analysis was based on the a priori assumption that if species with similar traits have similar population dynamics, the nature of the traits may indicate the drivers of the observed changes. The authors defined four traits which were chosen to reflect a species' susceptibility to four forcing factors: fishing-driven declines, reductions due to predation by grey seals, changes in bottom-water temperatures and bottom-up changes in prey abundance. A value for each trait was derived for each species based on semi-quantitative scoring schemes. For example, the traits representing vulnerability to fishing and vulnerability to seal predation were scored based on estimated removals by fisheries and seals, respectively, as a function of estimated standing stock biomass and corrected for the species' productivity, and then placed into ordinal categories based on the scores. In both cases adjustments for species' productivity were made because more productive species should be able to withstand higher rates of removal.

Benoît and Swain (2008) found that with few exceptions, species that increased in abundance over the study period were characterized by one or more of the following traits: little susceptibility to fishing, little susceptibility to grey seal predation, or a large portion of their biogeographic range occurring in arctic/subarctic waters (i.e., indicative of possible cold-water tolerance). Those species showing an overall decline in abundance since 1971 were almost all susceptible to both fishing and seal predation, and tended to have a more southerly biogeographic distribution. Species susceptible to fishing included those that were targeted by commercial fisheries as well as incidentally captured ones. These relationships can be seen in Figure 10, which is a plot of the first two eigenvectors of a correspondence analysis of the species-year matrix shown in Figure 6, along with the centroids for each category of the three

traits found to be associated with changes in the community species composition. The eigenvector plot reflects a community that has continually evolved away from the state observed in the 1970s. The relative location of the trait centroids in the plot indicates that the nature of the species dominating the community has also shifted over the years, from a community dominated by more temperate water species that were susceptible to both fishing and seal predation, to a community dominated by cold-water species that are directly affected little, if at all, by fisheries and seals.

The apparent trait-dependency of population dynamics reflects trends in the relevant external drivers (Benoît and Swain 2008). Mean bottom-water temperatures cooled throughout the 1980s, resulting in a period of record-low temperatures in the early to mid 1990s (Fig. 5; Gilbert and Pettigrew 1997; Drinkwater and Gilbert 2004). 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 warmed to more average recent levels (Benoît and Swain 2008). Because the cooler-water species also tended to be smaller-bodied, changes in bottom-temperatures also contributed to changes in the size-structure of the sGSL fish community, though this contribution was considerably smaller than the apparent effect of predation release. Much of the decline in abundance of the species most impacted by fisheries occurred during the period of very high fishing effort of the late-1980s and early 1990s (Fig. 7). The lack of recovery or continued decline of many of these species, despite large subsequent reductions in fishing effort, appears to correspond with dramatic increases in the abundance of grey seals in the ecosystem (Hammill 2005). Bioenergetic modelling confirms that grey seals may have indeed largely replaced fisheries in terms of fish removals (Fig. 11; see also Savenkoff et al. 2008).

ESTIMATES FROM INDICES AND POPULATION MODELS

Estimating mortality rates for fish species requires information on age-structure, either from regular age-determination using fish hard parts (mainly otoliths) or based on assumed values from the literature. Sufficient ageing for mortality estimation has only been undertaken for three sGSL groundfish species: cod, white hake (*Urophycis tenuis*) and American plaice (*Hippoglossoides platessoides*). In addition, there is sufficient information from the literature and recent preliminary ageing studies to make assumptions about the growth rate and age/size at maturity for the three sGSL skates. In this section we describe the results of studies of the size or stage dependent mortality of these sGSL species. We begin by looking at recruitment rates (number of recruits/ spawning stock biomass), an index of juvenile survival (note here, recruitment is defined as the numbers at ages varying from 2-5 years, depending on the species). We then consider patterns in the mortality rate of adult white hake, and thorny (*Amblyraja radiata*), smooth (*Malacoraja senta*) and winter skates (*Leucoraja ocellata*). Age-dependent mortality of cod is not reviewed here since it was described in detail by Swain (2010). However, the results reported for cod are consistent with the patterns reported here: natural mortality of young cod (aged 2-4 years) declined in the early 1990s whereas natural mortality of older cod (aged 5+ years) increased to high levels throughout the 1990s and 2000s.

Recruitment rates

The recruitment rates of all three skate species, white hake and to a lesser extent, American plaice, have been increasing for the past 20-30 years (Fig. 12). This has occurred as the biomass of their adult stages and of other demersal fish predators have been declining. This increased survival of juvenile fish is consistent with the pattern for other species, as inferred from length frequency distributions from the RV survey (Figs. 1 and 2). The recruitment rate of cod was high during the late 1970s and early 1980s, but has been average since that time. Swain and Sinclair (2000) found that cod recruitment rate was strongly related to the biomass of pelagic fishes in the ecosystem, presumably as a result of predation on cod eggs and larvae, as well as to cod spawning stock biomass (SSB), perhaps owing to cannibalism. The recruitment rate of herring was high during the early 1980s, a period of very low SSB, and has been average since then.

Trends in the mortality of adult white hake

The total mortality ($Z = M + F$) of adult white hake was estimated using a modified catch-curve analysis (Sinclair, 2001). This is an analysis of covariance with log-transformed survey catch rate as the dependent variable, cohort as a factor (accounting for variation in cohort strength) and age as a covariate. Assuming that all ages in the analysis are equally catchable in the survey, the slope provides an estimate of Z . The analysis was restricted to ages 5-7 years because younger fish were not fully catchable by the survey and older fish were too rare. Analyses were conducted within moving seven-year windows between 1971 and 2009. Instantaneous fishing mortality (F) for age 5-7 white hake in year t was estimated using Baranov's catch equation based on estimated absolute abundance (N_t) and fishery catches (C_t) (Ricker 1975):

$$F_t = \left(\frac{C_t}{N_t} \right) \cdot \left(\frac{Z_t}{1 - \exp(-Z_t)} \right) \quad (1)$$

Absolute abundance was estimated using the estimated catch-at-length from the RV survey and adjusted for catchability (i.e., survey efficiency) using a length-dependent relationship derived for demersal roundfishes (Harley and Myers, 2001).

Total mortality in age 5-7 white hake has generally increased steadily since the mid-1980s (Fig. 13). Whereas sGSL white hake as old as 12-15 years of age were caught in surveys in the mid-1980s, none older than 7 years have been captured since 2000. A moratorium on directed white hake fishing has been in place since 1995, with only small incidental fishery catches since then (Fig. 13). Based on the catchability corrections applied to estimate absolute abundance, values for natural mortality (M) during the 2000s are estimated at about 1.9. In contrast, estimated M varied between 0.1-0.2 prior to 1985. These early 1980s values are more typical of what would otherwise be expected for white hake, a (formerly) long-lived gadoid species (Gislason et al. 2010).

Trends in the mortality of juvenile and adult skates

We estimated trends in the mortality of juvenile and adult skates using stage-structured population models fit to the time series of survey data on relative abundance at length. Mortality trends were examined for the three skate species that commonly occur in the southern Gulf: winter, thorny and smooth skates. We used Bayesian state-space models, consisting of two

coupled components, a process model describing the unobserved stochastic processes governing the dynamics of the population, and an observation model describing the relationship between the unobserved population states and the data on relative abundance that are observed with error.

The population model is described by the following equations:

$$N_{1,t} = (N_{1,t-1}(1 - \theta) + \frac{1}{2}(rN_{2,t-a}))e^{-Z_{1,t}} e^{\eta_{1,t}} \quad (2)$$

$$N_{2,t} = (N_{2,t-1} + N_{1,t-1}\theta)e^{-Z_{2,t}} e^{\eta_{2,t}} \quad (3)$$

where $N_{1,t}$ and $N_{2,t}$ are the abundances of juveniles and adults, respectively, in year t , θ is the transition probability from the juvenile to the adult stage, a is the time between laying of egg cases and recruitment to juvenile stage, $Z_{i,t}$ is the stage-specific instantaneous rate of total mortality in year t , and r is the recruitment rate (i.e., annual fecundity per female discounted by egg case mortality and mortality between hatching and recruitment). In the models presented here, the Z parameters were allowed to vary on a decadal scale. A sex ratio of 1:1 was assumed to compute recruit production. The $\eta_{1,t}$ and $\eta_{2,t}$ are independent normal random variables with mean 0 and variance σ_i^2 , representing process stochasticity in each of the stages. We assumed that recruitment and transition between stages occurred prior to mortality events.

Survey catch rates $y_{i,t}$ were related to $N_{i,t}$ with the following observation model,

$$y_{i,t} = q_i N_{i,t} e^{\varepsilon_{i,t}} \quad (4)$$

where q_i is the catchability coefficient of stage i that scales relative abundance to $N_{i,t}$ and $\varepsilon_{i,t}$ are independent normal random variables with mean 0 and variance τ_i^2 , representing observation error in the abundance index for stage i . Survey catch rates were adjusted for size selectivity using the research-trawl selectivity curve estimated by Harley and Myers (2001) for flatfish. Small and large individuals were adjusted to the same relative catchability, but not to 100% catchability, by setting the maximum catchability (γ' in Harley and Myers 2001) to 1.

Uniform priors were placed on the mortality and error parameters. Priors were uninformative for mortality and process error. Lower limits for the priors for observation error were based on the CV of the survey data. Informative priors were placed on other parameters. For example, information on fecundity, growth and mortality prior to recruitment were used to set the priors for r and θ (θ depends on growth rate) (see Swain et al. (2009a) for further details).

Models which allowed for decadal variation in mortality fit the survey data significantly better than those which imposed time-invariant mortality (Swain et al. 2009a; D.P. Swain, unpublished analyses). For all three species, juvenile mortality declined to low values in the 1990s and 2000s whereas adult mortality increased to high values in these decades (Fig. 14, and Swain et al. 2009a).

In the southern Gulf, all three skate species are caught primarily as bycatch in fisheries for other groundfish. Because fishing effort declined to very low levels in the 1990s and 2000s, the increases in adult mortality likely reflect increases in natural mortality. This was investigated in winter skate using models that incorporated estimated bycatch (Benoit 2006a) and were fit to catchability-adjusted survey data (Swain et al. 2009a). These analyses confirmed that the changes in winter skate mortality reflected changes in natural mortality (Swain et al. 2009a, and Figs. 15 and 16).

It is possible that the changes in population dynamics interpreted as changes in mortality in these models instead reflect changes in juvenile growth, with growth declining to low values in the 1990s and 2000s. Changes in juvenile growth were simulated in models for winter skate (Swain et al. 2009a) and thorny skate (D.P. Swain unpublished analyses) by allowing or imposing decadal variation in θ . These models indicated that the patterns in the data attributed to changes in mortality cannot be attributed to changes in growth. Sensitivity of the results to the catchability adjustments (e.g., for size selectivity) were also examined. Levels of the mortality estimates depended slightly on the particular adjustments used but the decadal patterns (trends) in mortality were not sensitive to these adjustments (Swain et al. 2009a, and Fig. 17).

CONCLUSIONS

Natural mortality of young cod declined in the early 1990s whereas natural mortality of older cod increased to unusually high levels throughout the 1990s and 2000s (Swain 2010). The same pattern is widespread throughout the marine fish community in the southern Gulf of St. Lawrence. Small-bodied fish species increased to high levels of abundance in the 1990s and 2000s. In large-bodied species, mortality declined to low levels for small individuals and increased to high levels for large individuals in the 1990s and 2000s. A plausible hypothesis to explain this widespread pattern is that small fish were released from predation when large demersal fish declined to very low levels of abundance in the 1990s due to overfishing, whereas the predation mortality experienced by large individuals increased to high levels in the 1990s due to the combination of their low abundance and the high abundance of an important predator, the grey seal.

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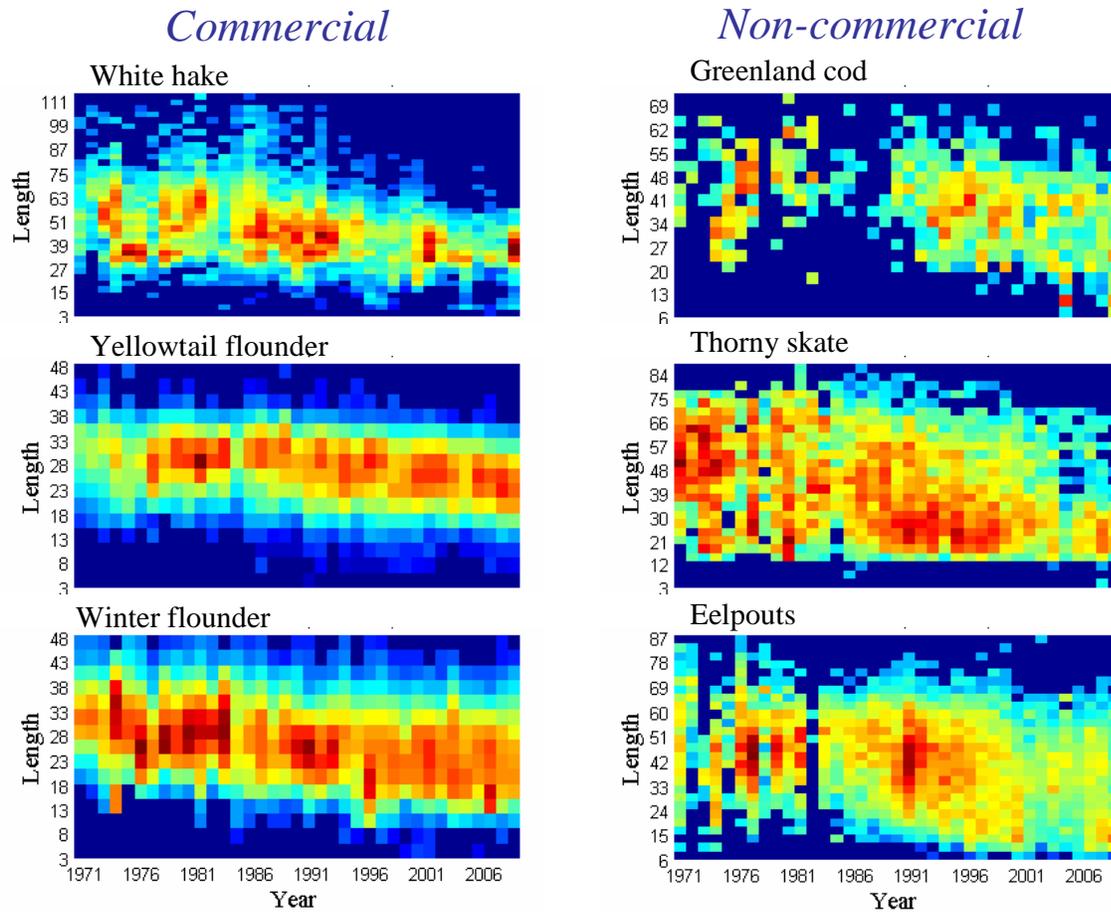


Figure 1. Annual length frequency distributions from the RV survey for six sGSL marine fish species with declining trends in abundance (three example commercially-fished species and three non-fished species). Abundance (\log_e -transformed) is color-coded such that dark red indicates sizes/years with relatively high abundance and dark blue indicates absence.

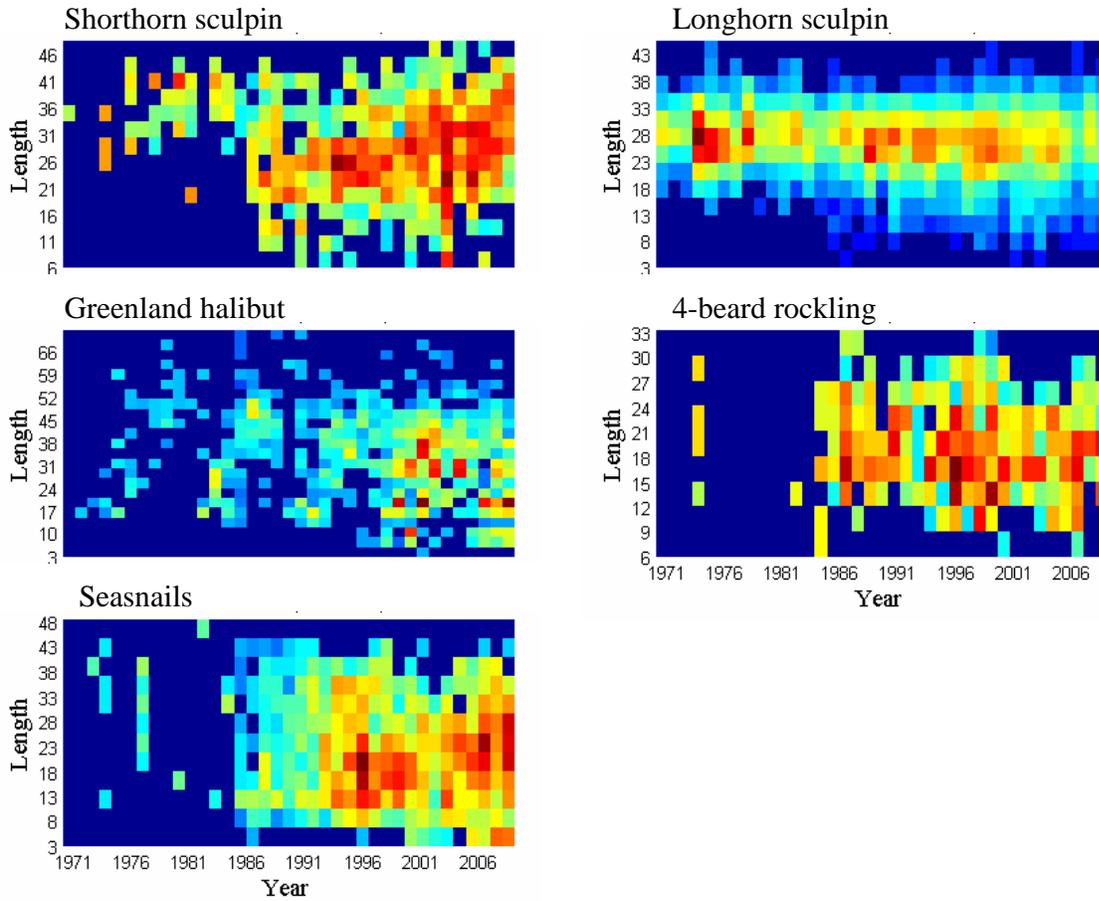


Figure 2. Annual length frequency distributions from the RV survey for five sGSL marine fish species with stable or increasing trends in abundance. Abundance (\log_e -transformed) is color-coded such that dark red indicates sizes/years with relatively high abundance and dark blue indicates absence. Of these species in the graph, Greenland halibut is the only commercially-fished species.

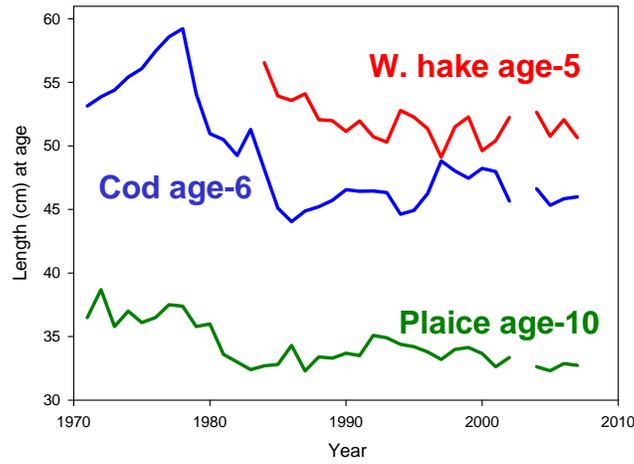


Figure 3. Trends in growth rate (length-at-age) for three sGSL marine fish for which there is annual age determination.

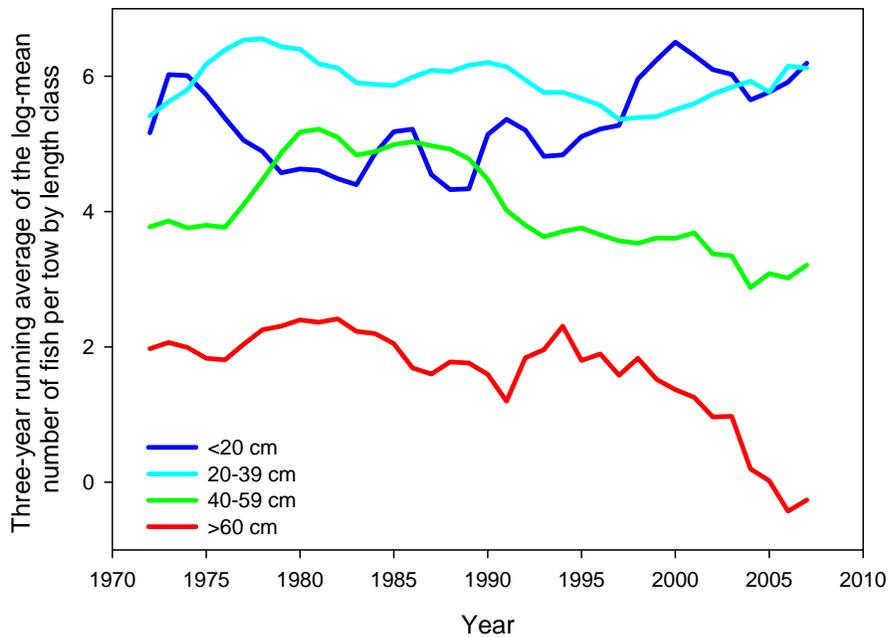


Figure 4. Three-year running average of abundance (log-transformed mean number per tow) of sGSL fish in four size categories (irrespective of species) in the RV survey.

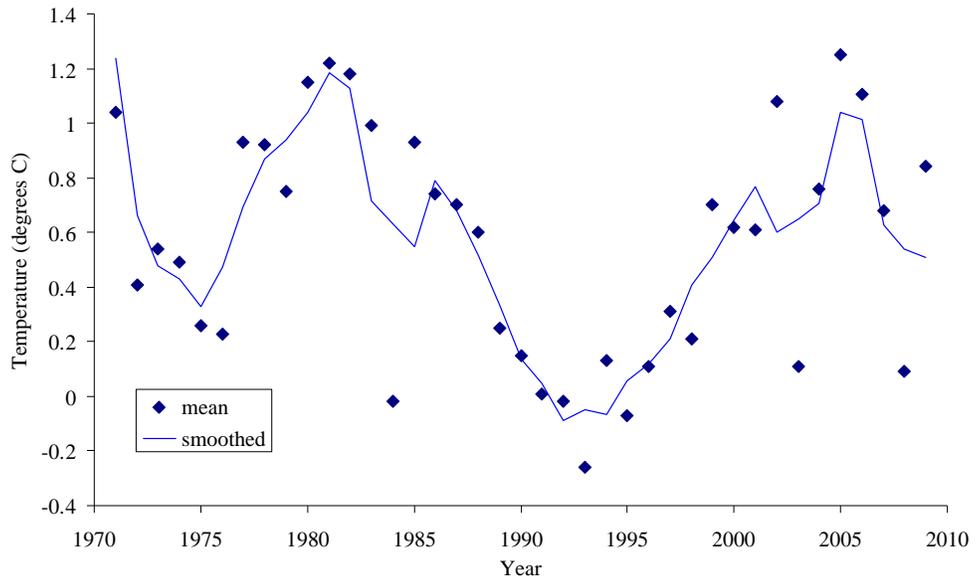


Figure 5. Mean summer bottom-water temperature (60-120m, roughly the cold-intermediate layer) in the sGSL, 1971-2009.

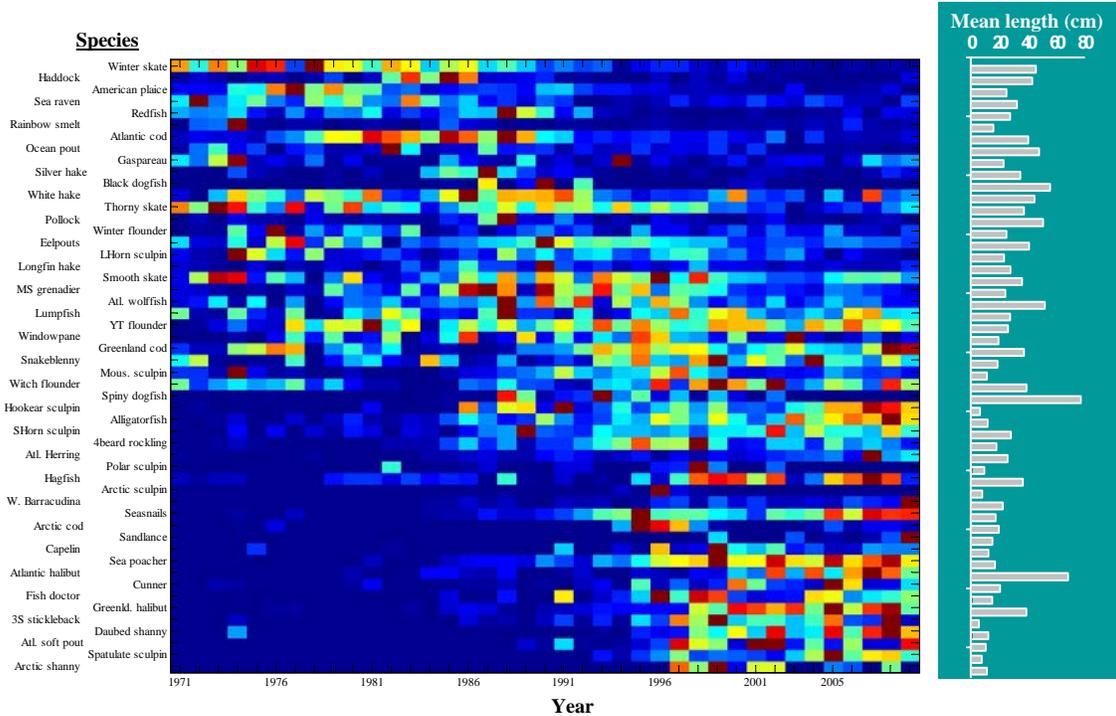


Figure 6. Main panel: Interannual changes in abundance for 52 sGSL marine fish species (rows) in the RV survey (redrawn from Benoît and Swain 2008). Abundance is color-coded for each species such that dark red indicates relatively high abundance and dark blue indicates relatively low abundance or absence in the survey. Species have been sorted according to the first eigenvector of a correspondence analysis of the species-year abundance matrix. Right panel: The mean body length (cm) corresponding to each species in the main panel.

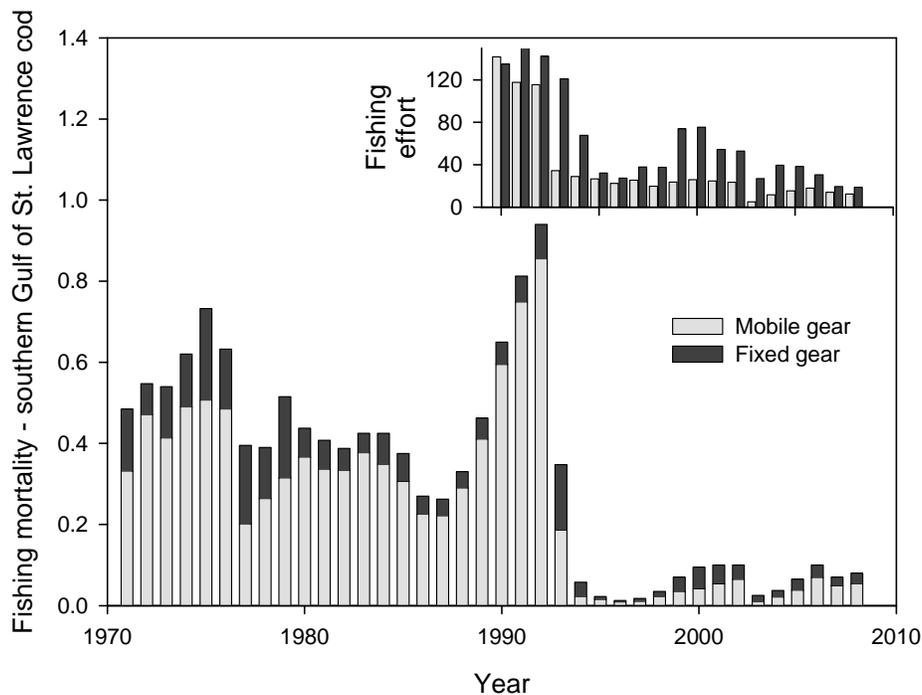


Figure 7. Main panel: Southern Gulf of St. Lawrence cod fishing mortality by gear type. Mobile gear includes otter trawls and seines (Danish and Scottish) and fixed gear includes principally groundfish gillnets, bottom-set longlines and handlines. Inset panel: total fishing effort for mobile gear (1000 hours) and fixed gear (100 trips) in the southern Gulf. Because cod is the principal groundfish species fished, trends in fishing mortality provide an index for fishing effort in the area.

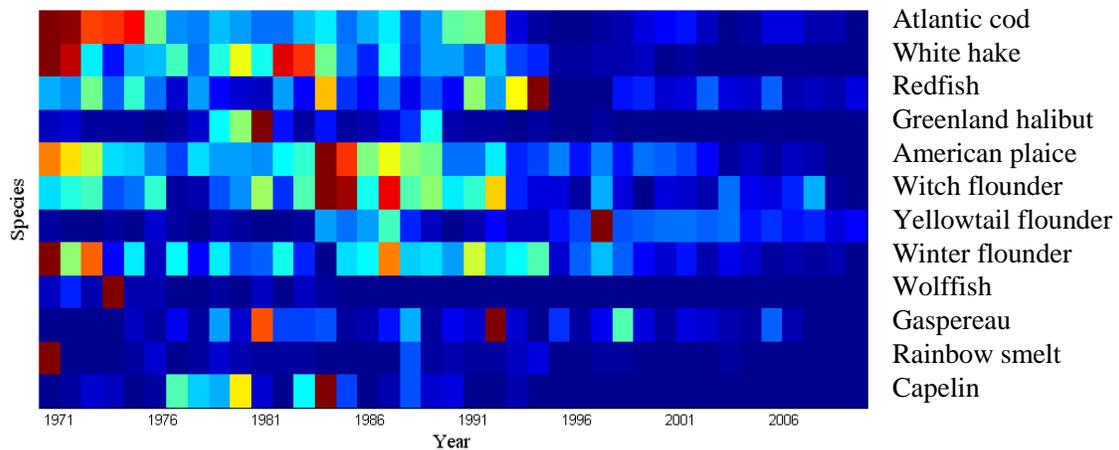


Figure 8. Relative fishing mortality (catch/RV abundance) for 12 sGSL marine fish species (row) captured in commercial fisheries from 1971-2008 (columns). Relative fishing mortality is color-coded such that dark red indicates relatively high levels and dark blue indicates relatively low levels.

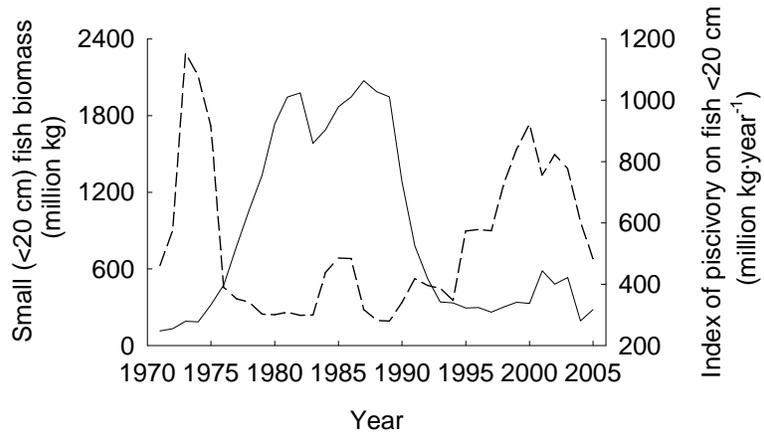


Figure 9. Total annual biomass of fish <20cm in length (----) and an index of potential predation by piscivorous fish on those small-bodied fish (—), 1971-2005 (redrawn from Benoît and Swain 2008). Both quantities are estimated using catchability-adjusted research survey catches and are presented as 3-year running averages.

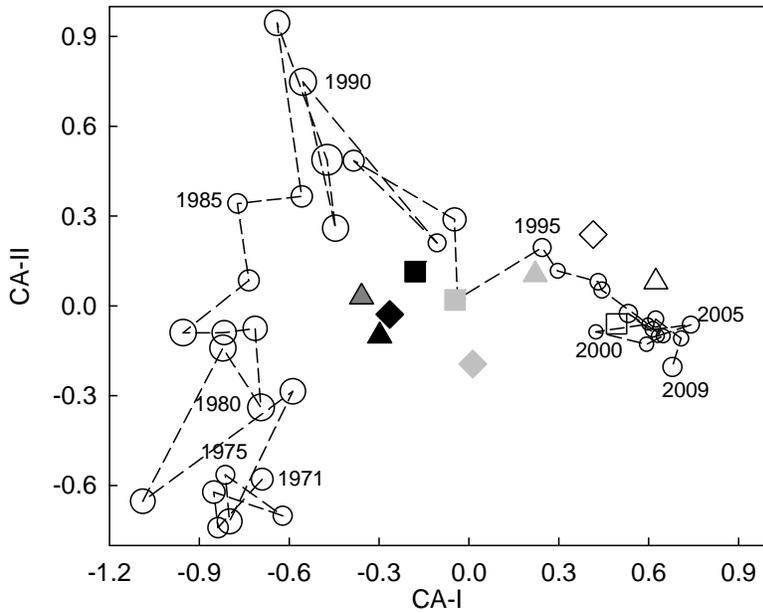


Figure 10. Temporal trends in the species and trait composition of the southern Gulf marine fish community (redrawn from Benoît and Swain, 2008). The plot presents the ordination of years (circles) with respect to axes I and II of the correspondence analysis of fish species abundance in the southern Gulf (1971-2009). The distance between years in the plot reflects their similarity in species composition. Trait centroids are plotted for three traits: susceptibility to exploitation (▲ score =1 (high), ▲ 0.67 (intermediate), ▲ 0.33 (low), △ 0 (no capture)); susceptibility to seal predation (◆ 1 (above median), ◆ 0.5 (below median), ◇ 0 (no predation)); and biogeographic distribution (■ temperate, ■ boreal, □ sub-arctic). The survey-derived mean annual body length in the community is indicated by the size of the circle for each year (○-10 cm, ○-25 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., sub-Arctic species were a more important component of the community in the 2000s than in the 1970s).

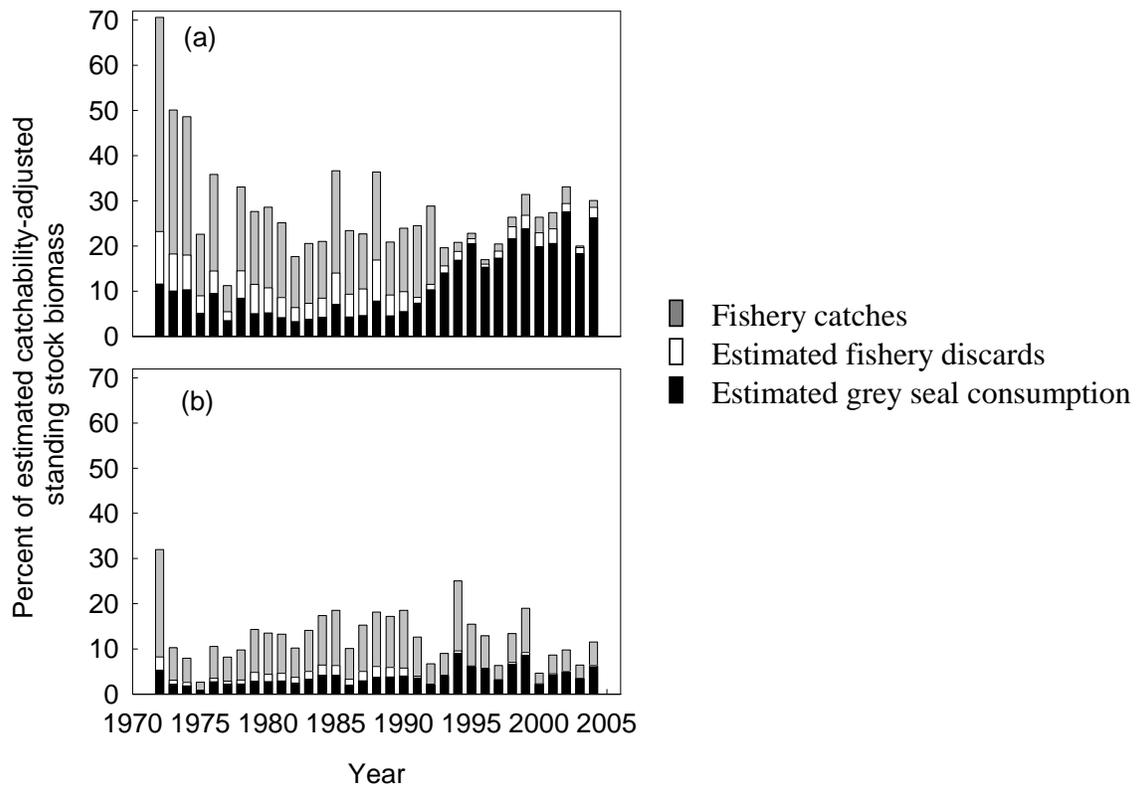


Figure 11. Total annual fishery landings (■), estimated fishery discards (□) and estimated grey seal consumption (■) as a percentage of fish standing stock biomass (redrawn from Benoît and Swain, 2008). The percentages in (a) are for the 50% of grey seal prey species with the highest susceptibility to a predation effect, 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 species.

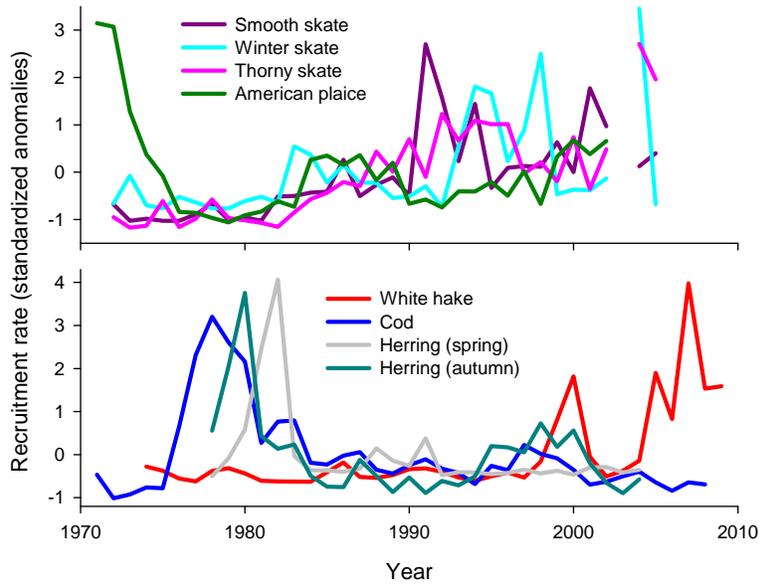


Figure 12. Recruitment rate (standardized anomalies of the number of recruits/ spawning stock biomass) for sGSL species for which there is ageing (plaice, cod, white hake and herring) or for which size at recruitment is assumed (skates).

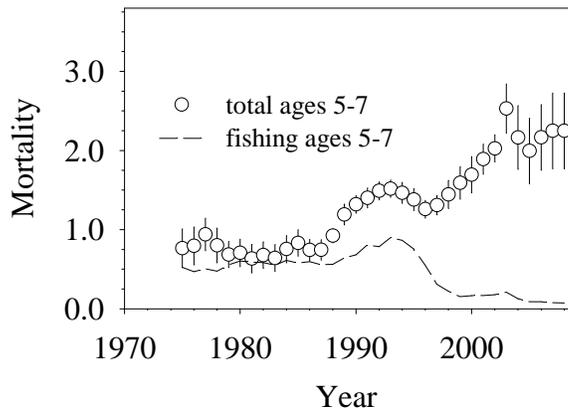


Figure 13. Total mortality (Z) of adult white hake ages 5-7 years estimated using the modified catch curve analysis, and estimated fishing mortality (F) using Baranov's equation based on commercial landings and catchability-adjusted abundance from the RV survey.

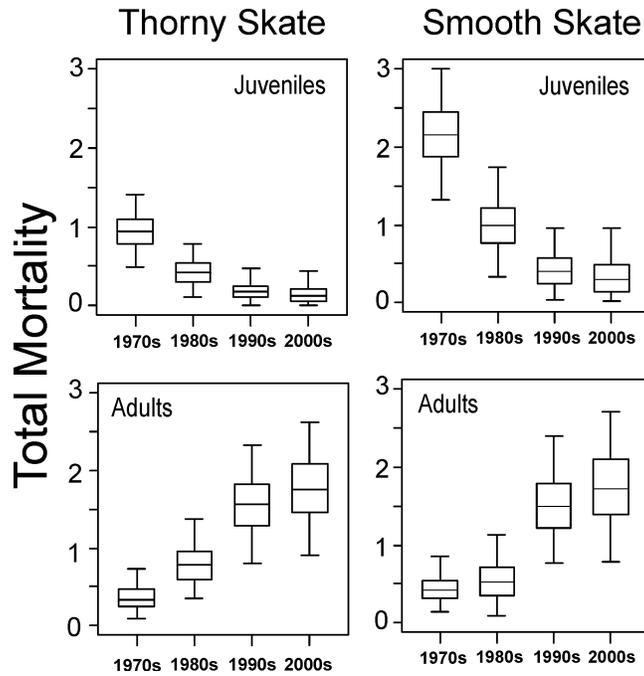


Figure 14. Decadal variation in estimated mortality (Z) of juvenile and adult thorny and smooth skate in the southern Gulf of St. Lawrence (1971-2006). Juveniles are defined as skates less than 54 (thorny skate) or 48 (smooth skate) cm in total length. Box plots show the 2.5th, 25th, 50th, 75th and 97.5th percentiles of the posterior distributions for mortality parameters.

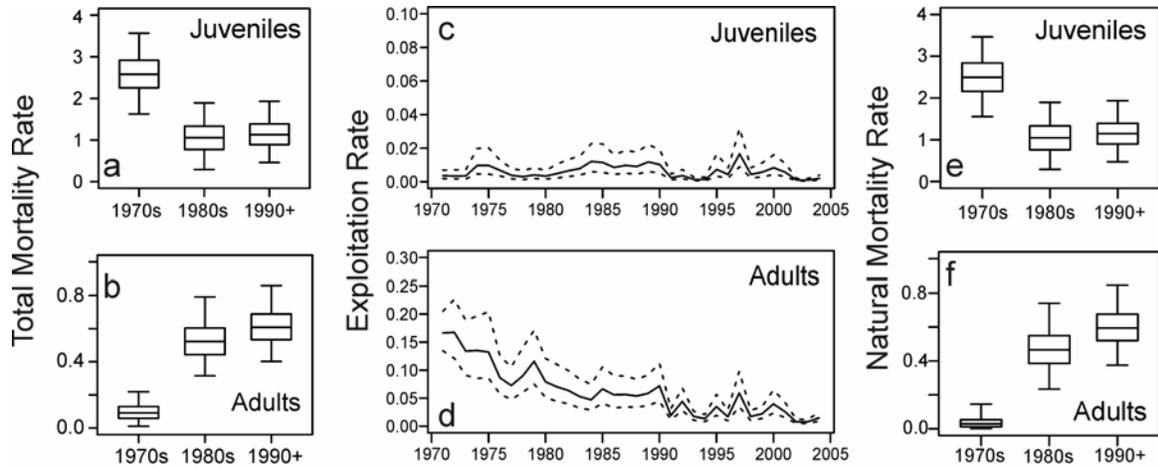


Figure 15. Changes in total mortality (Z), exploitation rate and natural mortality (M) of winter skate in the southern Gulf of St. Lawrence (from Swain et al. 2009a). Juveniles are defined as skates under 42 cm in total length. Box plots are interpreted as in Figure 14. In panels c and d, solid lines are posterior medians and dashed lines are the 2.5th and 97.5th percentiles of the posterior distributions. 1990+ refers to the 1990-2004 period.

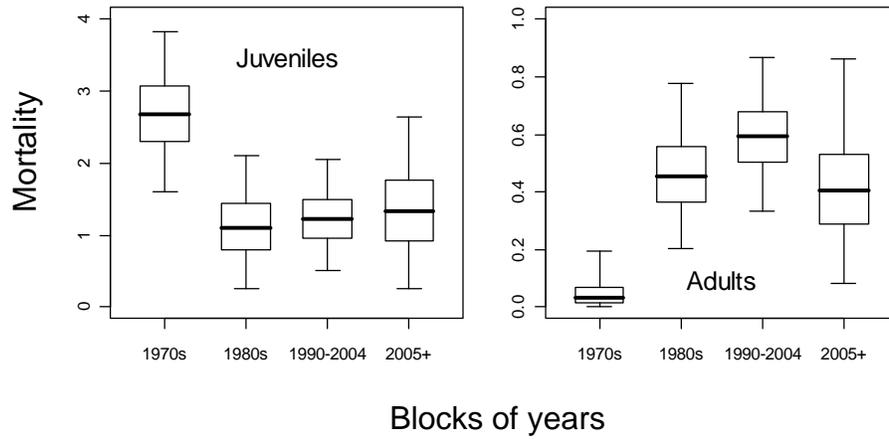


Figure 16. Estimated natural mortality (M) of juvenile and adult winter skate updated to 2009.

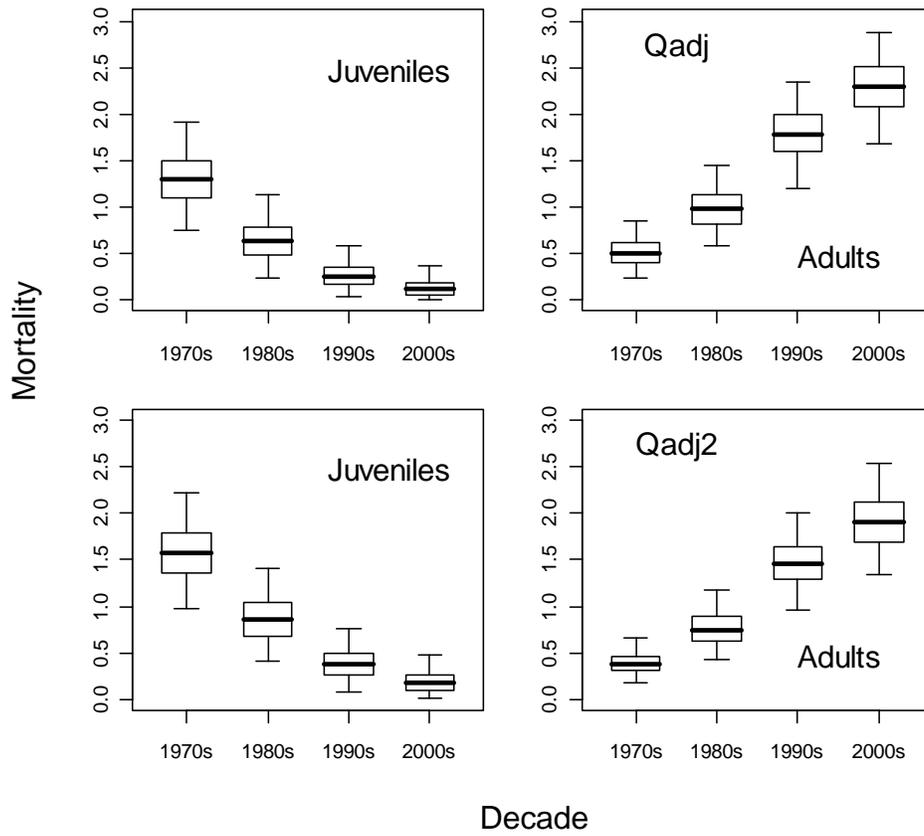


Figure 17. Decadal variation in total mortality (Z) of juvenile and adult thorny skate with different adjustments for size selectivity. The upper panels use the Harley and Myers (2001) adjustment as described in the text; the lower panels use an adjustment which is half as severe.