Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem

Douglas P. Swain*, Hugues P. Benoît

Fisheries and Oceans Canada, Gulf Fisheries Centre, 343 Avenue de l'Université, Moncton, NB, E1C 9B6, Canada

ABSTRACT: Improved understanding of the dynamics of populations at low abundance is needed in the face of global biodiversity loss. We examined the dynamics of depleted demersal fish populations in the southern Gulf of St. Lawrence, Canada. Twenty years ago, a number of these populations collapsed due to overexploitation. Since then, others have declined to low abundance. Despite negligible levels of fishing mortality and strong rates of production of small juvenile fish, these populations have shown no sign of recovery and some continue to decline. Lack of recovery is due to dramatic increases in the natural mortality of larger individuals in these populations. In some of these fishes, natural mortality has risen to levels typical of high-turnover forage fishes rather than long-lived demersal fishes. We hypothesize that these high levels of mortality reflect a 'predator pit' or predation-driven Allee effect, resulting from the severely depleted abundance of these fishes and the high and rising abundance of their marine mammal predators, in particular grey seals. Recovery of collapsed demersal fish populations does not appear to be possible under current conditions in this ecosystem, even in the absence of fishing. Our results indicate a need for more precautionary management regimes in order to avoid population collapses that are not reversible by reducing exploitation.

KEY WORDS: Allee effect · Natural mortality · Population recovery · Predation · Marine fishes

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Because of widespread biodiversity loss, including unprecedented rates of population extirpation and species extinction (Butchart et al. 2010), there is an urgent need for improved understanding of the ecology and dynamics of populations at low abundance (Bourbeau-Lemieux et al. 2011, Hutchings et al. 2012). Classical population-dynamics theory postulates that the per-capita rate of population increase is negatively density dependent (Nicholson 1933). Given this, rates of increase are highest at low population sizes due to a relaxation of density-dependent constraints on production. This concept underpins much of the theory of sustainable exploitation of wild populations, such as by fisheries. However, there is

increasing concern that in some cases density dependence may instead be positive at very low population sizes, with population growth rate declining as abundance decreases below some threshold (Courchamp et al. 1999, Stephens & Sutherland 1999). This effect, termed an Allee effect, increases the likelihood of extinction or extirpation for species or populations at low abundance.

Studies of exploited marine fishes are an important source of information on the dynamics of populations at low abundance (Hutchings 2000, Hutchings & Reynolds 2004, Neubauer et al. 2013). Overfishing is a global environmental and economic concern, with many exploited fish stocks severely depleted, in some cases to the point of stock collapse (Hutchings & Baum 2005, Worm et al. 2009). Some depleted

stocks are now rebuilding due to reduced exploitation rates while others remain at low abundance due to continued overfishing (Worm et al. 2009). However, there is concern that reductions in fishing effort may not always be sufficient to effect recovery (Hutchings & Reynolds 2004, Hutchings & Rangeley 2011). A well-known example is provided by the collapse of Atlantic cod *Gadus morhua* populations in the Northwest Atlantic in the early 1990s due to overfishing. Twenty years later, these populations have shown little sign of recovery. While overfishing persists in some populations, lack of recovery also reflects a decline in productivity (Shelton et al. 2006, Hilborn & Litzinger 2009). It has been suggested that this decline in productivity may reflect a reproductive Allee effect (Keith & Hutchings 2012), or changes in food webs, whereby depleted cod stocks no longer limit the abundance of their pelagic-fish prey, resulting in increased predation or competition by these fishes on early life stages of cod (Walters & Kitchell 2001, Minto & Worm 2012).

In the present study, we examined the dynamics of cod and other large-bodied demersal fishes in the southern Gulf of St. Lawrence (sGSL) in eastern Canada (Fig. 1). These fishes have declined to very low levels of abundance, with no recovery despite low fishing mortality over the past 15 to 20 yr. For some stocks, declines have been so severe that they are considered to be at a heightened risk of extirpation, with extirpation predicted to occur within decades at current levels of productivity (COSEWIC 2005, Swain & Chouinard 2008, Benoît et al. 2011c). We demonstrate that, contrary to the suggestions above, these populations have failed to recover despite strong rates of recruitment (i.e. the number of 'recruits' or young juveniles produced per unit of spawner biomass). Instead, recovery is being prevented by widespread increases in natural (non-fishing) mortality among large demersal fish in this ecosystem. The abundance of grey seals *Halichoerus grypus*, an important piscivore in this ecosystem, has increased about 15-fold since 1960, and we suggest that these high levels of natural mortality may reflect a 'predator pit' or predation-driven Allee effect (Gascoigne & Lipcius 2004), resulting from the low abundance of large demersal fish and the high abundance of their marine mammal predators.
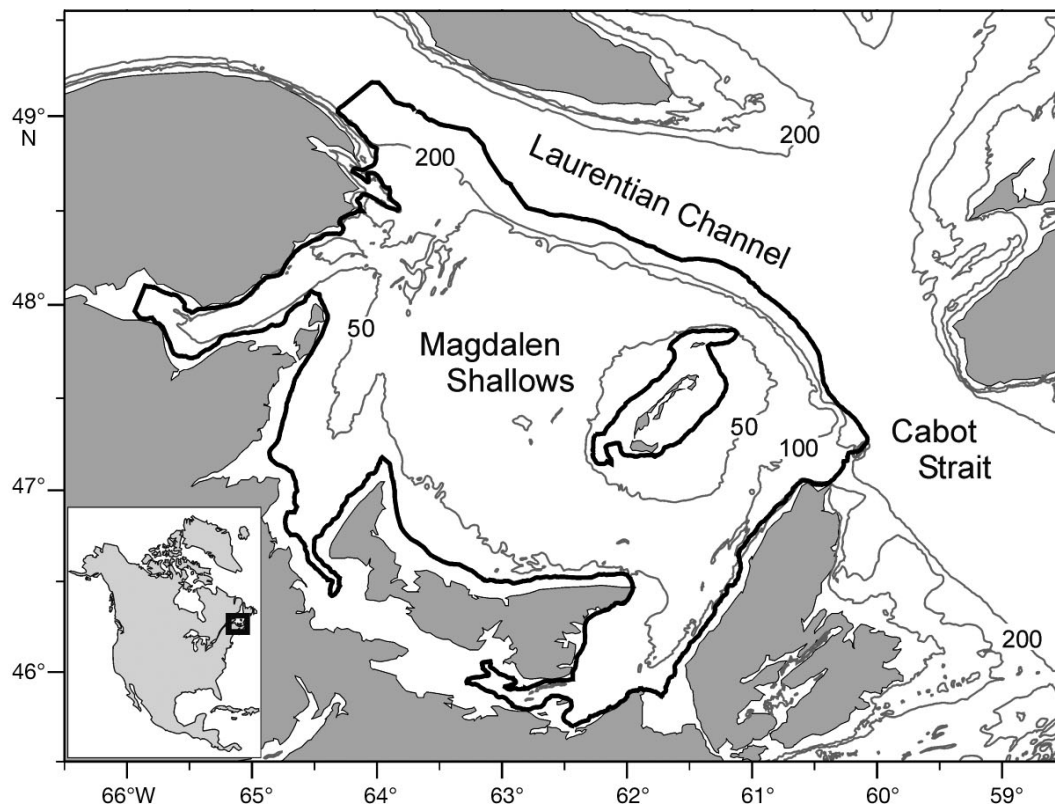

Fig. 1. The southern Gulf of St. Lawrence, Canada, showing the bottom-trawl survey area (heavy black line) and the 50, 100 and 200 m isobaths (grey lines). Survey covers depths from 15 to 350 m. Inset shows the study area within North America

MATERIALS AND METHODS

Study area

The sGSL covers an area of roughly 75 000 km^2. It consists of a shallow shelf, the Magdalen Shallows, with depths mostly less than 100 m, bordered by land and a 500-m trench, the Laurentian Channel (Fig. 1). Most large-bodied demersal fishes in this ecosystem (e.g. Atlantic cod, American plaice *Hipplglossoides platessoides*, white hake *Urophycis tenuis* and thorny skate *Amblyraja radiate*) feed on the Magdalen Shallows in spring, summer and early autumn and over-winter in deeper waters of the Laurentian Channel in the gulf or the adjoining Cabot Strait area. Other fishes (e.g. winter skate *Leucoraja ocellata* and winter flounder *Pseudopleuronectes americanus*) remain on the Magdalen Shallows and in adjoining coastal waters year round (Clay 1991, Benoît 2013a).

Study species

The population dynamics of the following species are examined here for the sGSL: Atlantic cod, American plaice, white hake, thorny skate, winter skate, smooth skate *Malacoraja senta*, winter flounder, yellowtail flounder *Limanda ferruginea*, Greenland cod *Gadus ogac*, sea raven *Hemitripterus americanus*, longhorn sculpin *Myoxocephalus octodecemspinosus* and eelpouts *Lycodes* spp. Historically, Atlantic cod, American plaice and white hake supported the largest groundfisheries in the sGSL and played key roles in the ecosystem. Atlantic cod (hereafter, cod) was the dominant predatory fish in this ecosystem, plaice the most abundant and widely distributed flatfish, and white hake the dominant piscivorous fish in inshore waters. Trends in the mortality of these species were examined using age-based analyses (see below).

Thorny skate is the most abundant skate in the sGSL, and was historically widely distributed over the Magdalen Shallows, though its distribution has since contracted (Swain & Benoît 2006). The other common skates in the sGSL are winter skate, occurring primarily at depths under 40 m in summer and early fall, and smooth skate, occurring mostly at depths over 100 m (Swain et al. 2005). Age data are not available for these skates but trends in their mortality were inferred from changes in abundance and length composition and estimated using length-based population models (see 'Length-based analyses', below). For the remaining species, acceptable population models have not been developed and trends in mortality over time were inferred directly from changes in size composition and abundance.

Data

A stratified-random bottom-trawl survey has been conducted by the Canadian Department of Fisheries and Oceans (DFO) in the sGSL each September since 1971 (Fig. 1, Fig. S1 in Supplement 1 at www.int-res. com/articles/suppl/m519p165_supp.pdf). The target fishing procedure in all years was a 30-min tow at 3.5 knots. Total number and weight caught and representative length–frequency distributions were obtained for each fish species in each trawl tow. Length-stratified subsamples of ageing material (otoliths) were obtained from all catches of selected species. The stratified mean catch per standard 3.24-km tow was used to construct time series of relative abundance and biomass by length or age group.

Comparative fishing experiments were conducted to test for changes in fishing efficiency whenever there was a change in research vessel (1985, 1992 and 2004/2005), trawl gear (1985) or survey protocol (i.e. a change from day only to 24-h fishing in 1985). These paired fishing experiments were conducted during or shortly before the survey in each of these years. When a difference in fishing efficiency was detected, survey catches were adjusted to maintain a consistent time series, as summarized in Supplement 1 and described by Benoît & Swain (2003) and Benoît (2006).

We also used additional standardized time series of relative abundance at age available from 'sentinel' programs conducted by the DFO in collaboration with the fishing industry. Indices from a stratified-random bottom-trawl survey conducted since 2003 were used for cod and plaice. Indices for cod were also available from a sentinel longline program conducted since 1995. See Supplement 1 for further details on these sentinel programs and the DFO survey.

Fishery landings by species were obtained from DFO records. Age composition of the fishery catches of cod, American plaice and white hake was estimated based on samples collected in port by sampling technicians and at sea by on-board observers. For American plaice, the estimated fishery catch at age also incorporates discarded catch, which was substantial for young ages prior to the early 1990s (Morin 2012). Catch at age is available for cod since 1950, for plaice since 1976 and for hake since 1978.

For the skates, which are mostly discarded at sea, annual fishery catches were estimated based on the reported landings and on discarding data collected by at-sea observers (Benoît 2013b; Supplement 1).

The grey seal is an important piscivore in this eco-system. Grey seals in Atlantic Canada are divided into 3 groups: the Sable Island, Gulf of St. Lawrence and coast of Nova Scotia (or Eastern Shore) herds. Currently, 81% of pups are born on Sable Island, 15% in the gulf and 4% along the eastern Nova Sco-tia coast (DFO 2014). Estimates of the abundance of each herd were obtained from DFO (2014) and are based on age-structured population models that incorporate information on removals and reproduc-tive rates. Models are fitted to time series of esti-mated pup production by adjusting initial population size, carrying capacity and adult mortality rate. The years in which estimated pup production is available for fitting these models are shown in Fig. 8. We esti-mated the number of seals foraging in areas occupied by sGSL groundfish using the population abundance estimates of each herd (DFO 2014) and the propor-tion of each herd foraging in the sGSL or the adjoin-ing overwintering grounds of sGSL fish stocks. These proportions were based on the seasonal distributions of satellite-tagged seals and are given in Benoît et al. (2011d).

Age-structured population models

Age-structured population models were used to estimate time series of abundance, biomass and instantaneous rates of fishing mortality (F) at age and natural mortality (M) by age group for cod, American plaice and white hake. Stock assessment models typ-ically use a constant assumed value for M. However, using simulation-estimation studies, Lee et al. (2011) demonstrated that in many cases M is estimable given informative length or age composition data. Furthermore, Fu & Quinn (2000) and Jiao et al. (2012) have demonstrated that it is possible to estimate time-varying M.

The sGSL cod stock is assessed using virtual popu-lation analysis (VPA). Since Sinclair (2001) demon-strated that M of sGSL cod had increased between the 1970s and the 1990s, VPA models with time-varying M have been used in the assessment of this stock. Initially, M was estimated in blocks of years, starting from a fixed value of 0.2 in the early 1970s and using the same values for all cod aged 2 yr and older (Chouinard et al. 2005). Subsequently it be-came apparent that temporal variation in M differed

between age groups of cod (Swain et al. 2009), and the most recent assessment of this stock has mod-elled M using independent random walks for the 2–4 and 5+ yr age groups (Swain et al. 2012b). This ap-proach has also been used for the most recent assess-ments of sGSL plaice (Morin et al. 2012) and hake (Swain et al. 2012a). The models used here are the same as those used in these peer-reviewed assess-ments, except that separate M trends were estimated for 3 rather than 2 age groups for each stock and a number of technical refinements were incorporated in the models (e.g. a prior distribution for initial M was used instead of fixing initial M at an assumed value; see Supplement 2 for details at www.int-res.com/articles/suppl/m519p165_supp.pdf). Models were implemented using AD Model Builder (Four-nier et al. 2011).

Chouinard et al. (2005) found that VPA could reli-ably identify the general trend in age-aggregated M over time in simulated populations, though the esti-mated level of M was sometimes biased. In a simula-tion study using a VPA model with separate random walks in M of cod aged 2–4 and 5+ yr, Swain (2011a) obtained similar results for cod aged 5+ yr but failed to identify changes in the M of 2- to 4-yr-old cod when vulnerability of these cod to the fishery was very low and changes in M were modest. In these earlier simulation tests, observation error was added to the simulated abundance indices but the fishery catch at age was known without error (as is assumed in VPA). We conducted simulation tests of the models used here incorporating observation error in both the abundance indices at age and the fishery catch at age. These tests indicated that, given data with the characteristics of the sGSL survey data for these 3 species, these models can reliably estimate both the time trends and level of M for age groups that are well recruited to the fishery and well represented in the population. For older ages that have been very rare in the surveys since the early 1990s (ages 15+ yr for plaice and 6+ yr for hake), details of the trends in M were not well estimated, but general conclusions about changes in M were correct (see Supplement 2 for details).

In the models used here we provide prior distribu-tions for M of each age group in the initial year of the analysis and specify the standard deviation of pro-cess error in M. Sensitivity analyses indicated that conclusions about changes in M were not affected by the prior distribution for initial M, though this prior affected the estimated level of M for hake and the 2–4 yr age group of cod (Supplement 2). These analy-ses also indicated that the value used for the standard

deviation of process error represented a reasonable compromise between an undue influence of noise in the survey data when the standard deviation in process error is set too high and a poor fit to the data when process error is too severely constrained. The possibility that the non-stationarity modelled here as changes in M instead reflects changes in survey selectivity or catchability is examined in Supplement 3 (www.int-res.com/articles/suppl/m519p165_supp.pdf) and discussed below, and is deemed to be implausible.

Model-independent estimates of mortality

Model-independent estimates of mortality were produced to corroborate the model-based estimates. The instantaneous rate of total mortality (Z) was estimated from survey indices at age for cod, American plaice and white hake 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. If all ages in the analysis are equally catchable in the survey, the slope provides an estimate of Z. Young ages that did not appear to be fully catchable in the survey and old ages that were rare in survey catches were excluded from analysis. Ages included in analyses were 7–11 yr for cod, 12–16 yr for plaice and 5–7 yr for hake. Analyses were conducted in moving 5-yr windows for cod and American plaice and 7-yr windows for white hake. The wider window was used for white hake because of the more restricted usable age range for this species. For cod and plaice, estimates of Z were also obtained from the catch rates in the sentinel bottom-trawl survey (Supplement 1). These estimates and those obtained from the models are not independent because both types of estimates are based on the abundance indices at age, but unlike the model-based estimates these estimates are not influenced by the fishery catch at age or model structure.

Trends in Z were compared to trends in a survey-based index of fishing mortality, relative fishing mortality (RF) (Sinclair 1998), to infer trends in natural mortality. RF is fishery catch in numbers divided by 'trawlable abundance', where trawlable abundance is the stratified mean catch rate (fish per standard tow) in the survey expanded from the area swept by a standard tow to the area encompassed by the survey. RF is proportional to F when the survey is conducted near the middle of the fishing year, as is the case here. We calculated RF over the same age ranges as Z, and averaged over the same moving blocks of years. Note that RF is an annual rate while Z is an instantaneous rate and that the level of RF will depend on catchability to the survey. RF was also calculated for species without age data by dividing fishery catch in weight by trawlable biomass aggregating over all lengths. See Supplement 1 for further details.

Length-based analyses

For species without age data, trends in mortality by size group were inferred based on catch rates at length in the annual DFO survey. Abundance trends were described separately for small and large individuals. When information on size at maturity in the sGSL was available (skates, yellowtail and winter flounder), these size groups corresponded to juveniles and adults. For thorny and smooth skates, juveniles were divided further into small and large size groups based on previously identified differences in abundance trends (Swain et al. 2005). Abundance trends for each size group were summarized using generalized additive models (GAMs) assuming a log link with variance proportional to the mean. GAMs were implemented using the R package mgcv. For the 3 skate species, inferences based on changes in size composition were supplemented by estimates of decadal trends in mortality by length group, obtained by Swain et al. (2013) using stage-structured state–space models. Model details are given in Swain et al. (2013) and summarized in Supplement 4 (www.int-res.com/articles/suppl/m519p165_supp.pdf). In addition to changes in size composition within species, catches in the RV survey were grouped across fish species into length groups to examine community-wide changes in size composition. The 52 species used for this community-wide analysis are listed in Benoît & Swain (2008).

RESULTS

Age-based analyses

Population modelling

Estimated biomass of commercial-sized cod (5 yr and older) declined from the mid-1950s to the mid-1970s due to high fishing mortality (Fig. 2A). Biomass recovered rapidly in the late 1970s despite continued
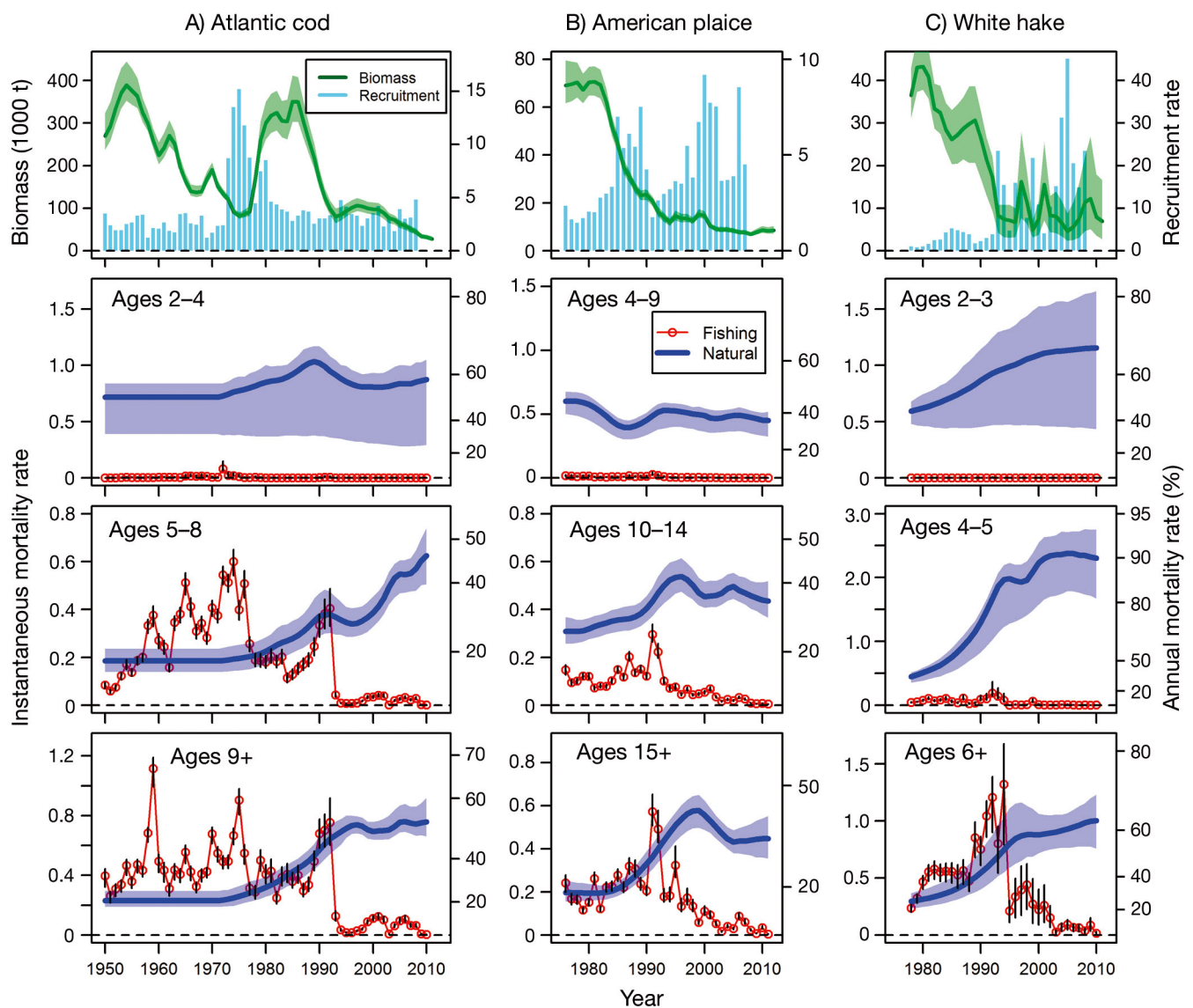
Fig. 2. Estimated biomass (×1000 tons), recruitment rate (recruits per kilogram of spawner biomass) and rates of fishing and natural mortality for (A) Atlantic cod, (B) American plaice and (C) white hake in the southern Gulf of St. Lawrence. Biomass is for cod 5 yr and older, plaice 10 yr and older, and hake 4 yr and older, corresponding to the ages caught in the fishery. Recruitment rates are for fish aged 2 yr for cod and hake and 4 yr for plaice. Natural mortality rates are estimated for 3 age groups for each species. Fishing mortality rates, shown for the same age groups, are weighted averages of the estimates for each age in the groups, with weighting based on estimated abundance at age. Shaded bands (biomass, natural mortality) and vertical lines (fishing mortality) show 95% confidence intervals

fishing. However, biomass collapsed equally rapidly in the late 1980s and early 1990s, and a moratorium on directed fishing for cod was imposed in 1993. Although small directed fisheries were periodically re-opened, fishing mortality of cod has remained very low since the mid-1990s. Despite these negligible levels of fishing mortality, cod biomass has continued to decline since the early 2000s.

The rapid recovery of cod biomass in the late 1970s was fueled by unusually strong recruitment (Fig. 2A).

The continued decline of cod despite low fishing mortality cannot be attributed to poor reproductive success; estimated cod recruitment rates in the 1990s and 2000s averaged 34% higher than the rates that prevailed from 1950 to the early 1970s.

The estimated natural mortality of cod 5 yr and older was about 20% annually in the early 1970s (Fig. 2A), a level considered normal for cod and consistent with independent estimates for sGSL cod in the 1950s and 1960s (Dickie 1963, Beverton 1965,

Paloheimo & Kohler 1968). Since then, natural mortality has progressively increased, reaching levels in recent years >40% annually for cod aged 5–8 yr and >50% for older cod, close to the estimates for juvenile cod (ages 2–4 yr). These unusually high rates of natural mortality are the principal cause of the continued decline in this cod stock despite negligible levels of fishing mortality (Fig. 2A). In contrast to cod aged 5 yr and older, there is no indication that natural mortality has changed substantially for younger cod (ages 2–4 yr).

Similar patterns are evident for American plaice and white hake (Fig. 2B,C). For both species, the biomass of commercial-sized fish had declined to very low levels by the late 1990s. Fishing mortality of plaice dropped sharply following the closure of the cod fishery in 1993 and declined to extremely low levels in the 2000s as fishing effort declined further. Similarly, fishing mortality of hake declined sharply with the imposition of a moratorium on directed fishing for hake in 1995 and was reduced to negligible levels in the 2000s. However, these stocks falied to recover despite negligible fishing mortality and recruitment rates that were strong (plaice) or unusually high (hake) in the recent period.

The principal cause of failed recovery for plaice and hake was increased natural mortality of recruited fish. For plaice, no increase in natural mortality was evident for young fish (ages 4–9 yr), but significant increases occurred for older fish, from an average of 27% annually in the 1970s to an average of 38% since 1993 for 10- to 14-yr-olds and from 18% to an average of 39% for plaice 15 yr and older. Although estimated natural mortality declined with age in the 1970s, natural mortality of older plaice (10+ yr) was near or above that of young plaice (4–9 yr) in the 1990s and 2000s. For hake, estimated natural mortality increased sharply over time for all 3 age groups. There was great uncertainty in the extent of the increase for the 2–3 yr age group (Fig. 2C), and simulations indicated that the estimated change in M could be strongly biased for this age group (Supplement 2). However, the model results clearly indicated a large increase in M of the older age groups and simulations indicated that model results were reliable in this regard. Estimated natural mortality increased from 36% annually in 1978 to an average of 89% annually in 1995–2010 for 4- to 5-yr-old hake, and from 26% annually to 60% for hake 6 yr and older. These estimates for older hake were near (ages 6+) or substantially above (ages 4–5 yr) the estimated natural mortality of juvenile hake (ages 2–3 yr) in the 1990s and 2000s.

Recent rates of natural morality of hake aged 4–5 yr are so high that few hake now live beyond these ages (Fig. S6 in Supplement 2), and the population persists only because recent recruitment rates have been unusually high.

Model-independent results

The time trends in Z and RF of cod aged 7–11 yr indicate a substantial increase in natural mortality of these cod over the 1971–2010 time series (Fig. 3A). Estimated Z was below RF in the 1970s but greater than RF in the 1980s, indicating an increase in natural mortality between these periods. The difference between Z and RF increased between the 1980s and the 1990s and again in the 2000s, indicating further increases in natural mortality. This pattern of increasing natural mortality is consistent with the model estimates of M for the 5–8 and 9+ yr age groups of cod.

Estimates of Z for American plaice are less precise and fluctuate more than the estimates for cod. However, the time trends in Z and RF of plaice again indicate an increase in natural mortality of these fish (Fig. 3B). In the 1970s and early to mid-1980s, estimated Z and RF averaged 0.41 (34%) and 21%, respectively. Estimated Z increased in the late 1980s and early 1990s, a period of stable or declining RF. Estimates of Z and RF averaged 0.77 (54%) and 14%, respectively, in the 1990s, and 0.57 (43%) and 4% in the 2000s. Thus, the difference between Z and RF increased between the 1970s and the 1990s, consistent with the model estimate of an increase in M between these periods.

Estimates of Z and RF of white hake (ages 5–7 yr) indicate a large increase in natural mortality of these fish between the mid-1980s and the 2000s (Fig. 3C). Estimated Z and RF both averaged about 0.6 in the 1978–1986 period. Between the mid-1980s and the 2000s, RF declined to a very low level (~5%) while Z increased to a level above 2 (86%). This indicates a large increase in natural mortality of hake between the mid-1980s and the 2000s, consistent with the large increase estimated by the population model.

Indices of fishing mortality

Population models indicate that rates of fishing mortality have declined to negligible levels for cod, American plaice and white hake (Fig. 2). The index of fishing mortality RF extends this result to other
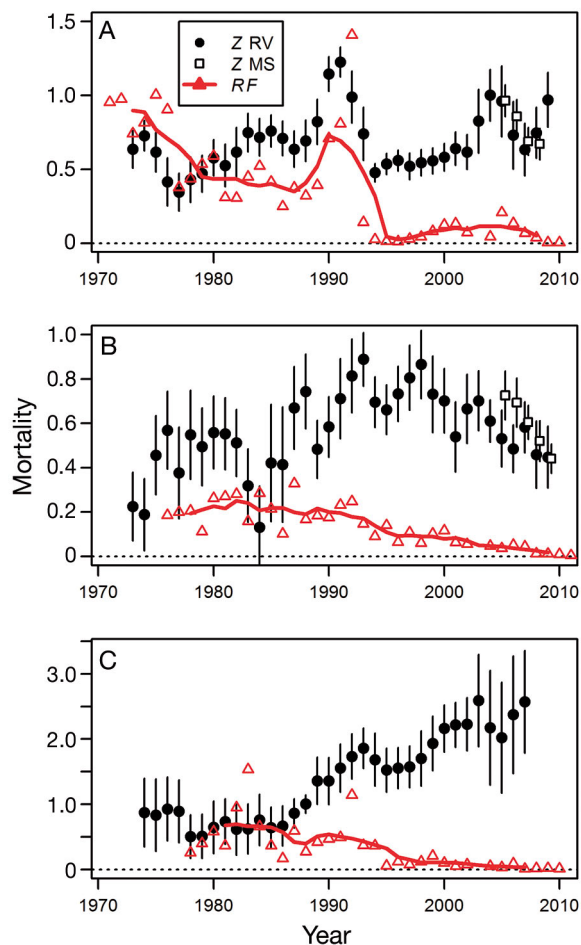
Fig. 3. Relative fishing mortality (*RF*) and estimates of the instantaneous rate of total mortality (*Z*) for (A) Atlantic cod (ages 7–11 yr), (B) American plaice (ages 12–16 yr) and (C) white hake (ages 5–7 yr) in the southern Gulf of St. Lawrence. Estimates of *Z* are derived from catch rates at age in the research vessel survey (RV) or the mobile-gear sentinel survey (MS). Estimates are for moving 5-yr (A,B) or 7-yr (C) blocks, plotted at the center of each block. Vertical lines are ±2 SE. *RF* is shown for individual years (red triangles) or averaged over the same blocks of years as *Z* (red line)
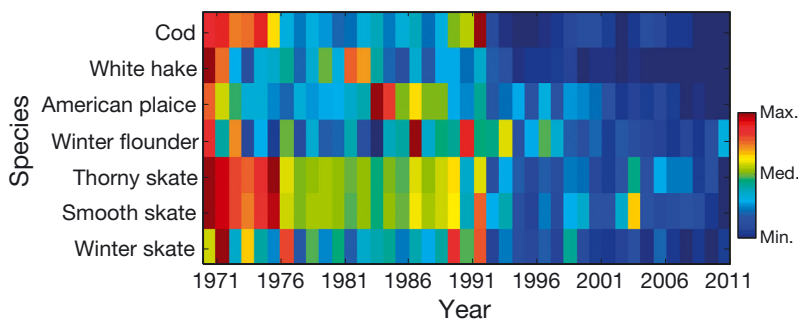

Fig. 4. Interannual trends in relative fishing mortality for 7 southern Gulf of St. Lawrence marine fish species. For each species, cells are shaded based on the annual relative fishing mortality values, ranging from the highest observed value (dark red) to the lowest (dark blue)

large-bodied demersal fishes in this ecosystem (Fig. 4), including both commercial species (winter flounder) and non-commercial species for which estimates of bycatch are available (thorny skate, winter skate and smooth skate). In all of these cases, fishing mortality declined to very low levels by the 2000s.

Length-based analyses

Catch rates at length in the annual DFO survey indicate that the patterns reported here for cod, American plaice and white hake are also evident in other large-bodied demersal fishes in this ecosystem. Mature thorny and winter skate have undergone severe declines in abundance since the 1970s, and may be continuing to decline (Fig. 5A,C). In contrast, small juveniles increased to relatively high abundance in the 1980s for winter skate and in the 1990s for thorny skate. Strong abundance at small sizes despite declining spawner abundance suggests declining mortality at small sizes. Declining abundance at large sizes despite relatively strong abundance at small sizes suggests increasing mortality at large sizes. Mortality estimates from stage-structured models (Swain et al. 2013) support these inferences. Estimated total mortality rates declined sharply for small juveniles and increased substantially for larger individuals between the 1970s and 2000s for both species (Fig. 5A,C). Although declines in mature abundance are less marked for smooth skate, length-dependent abundance trends suggest, and stage-structured models estimate, that total mortality has also declined for small juveniles and increased for larger individuals in this species (Fig. 5B). Because exploitation rate declined during this period for all 3 skate species (Fig. 4), these results indicate increasing natural mortality of large individuals in these skates, a conclusion confirmed for winter skate by stage-structured models that disentangle rates of fishing and natural mortality (Swain et al. 2009).

Similar length-dependent abundance trends are evident for other large-bodied demersal fishes in the sGSL (Fig. 6). Abundance of adult yellowtail flounder was relatively high throughout the 1980s and early 1990s despite low juvenile abundance in the 1970s and 1980s (Fig. 6A). In contrast, adult abundance declined sharply beginning about 2000 despite high and increasing juvenile abundance. For winter flounder, eelpouts and Greenland cod (Fig. 6B,E,F),
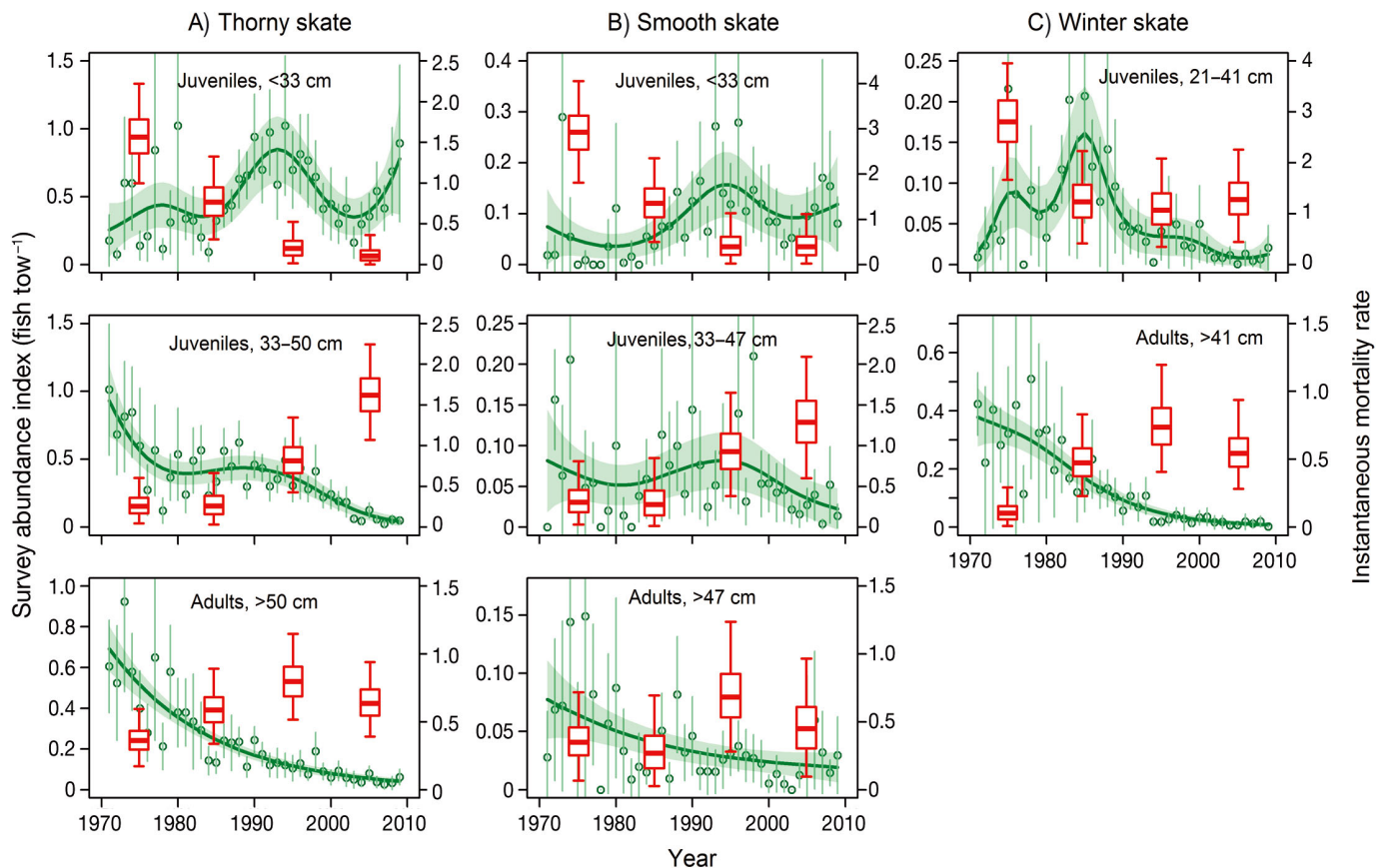
Fig. 5. Abundance trends by length group (green circles and line) and decadal estimates of total mortality by length group (red box plots) for (A) thorny, (B) smooth and (C) winter skate in the southern Gulf of St. Lawrence. Circles show annual stratified mean catch rates in the research vessel survey (±2 SD, indicated by light vertical lines). Heavy lines show the generalized additive model fit to the survey indices (±2 SE, indicated by the green shading). Box plots show the median, inter-quartile range and 95% confidence interval for mortality estimates from Swain et al. (2013)

the abundance of small fish had increased to relatively high levels in the 1990s and 2000s whereas the abundance of large individuals declined during this period, reaching very low levels in recent years. For sea raven (Fig. 6D), the abundance of large individuals declined sharply in the late 1980s and has remained low since then despite a relatively high abundance of small individuals since the mid-1990s. These results suggest increased survival of small individuals and increased mortality of larger individuals beginning in the late 1980s or in the 1990s. For longhorn sculpins (Fig. 6C), abundance trends were roughly parallel between small and large individuals, with both groups declining to low abundance in the 2000s.

Because fishing mortality of winter flounder declined after the early 1990s (Fig. 4), high mortality since then of large individuals of this species would reflect high natural mortality. Because fishing mortality of the principle target species in the sGSL (cod,

American plaice and white hake) also decreased to very low levels after the early 1990s (Fig. 2), high mortality of large individuals of the bycatch species shown in Fig. 6C–F would also reflect high natural mortality. Because a localized fishery for yellowtail flounder is ongoing, high mortality of large individuals of this species in the 2000s could reflect high fishing mortality, high natural mortality or a combination of the two.

At the community level, fish less than 20 cm in length increased in abundance throughout the 1990s and 2000s (Fig. 7). Abundance of fish 20 to 39 cm in length decreased slightly in the late 1980s and early 1990s but has increased sharply since about 2005. Abundance of fish in the 40 to 59 cm length group increased sharply in the late 1970s and declined sharply in the late 1980s. Abundance of this length group decreased slightly throughout the 1990s and early 2000s and sharply in recent years. Abundance of the largest length group fluctuated without trend
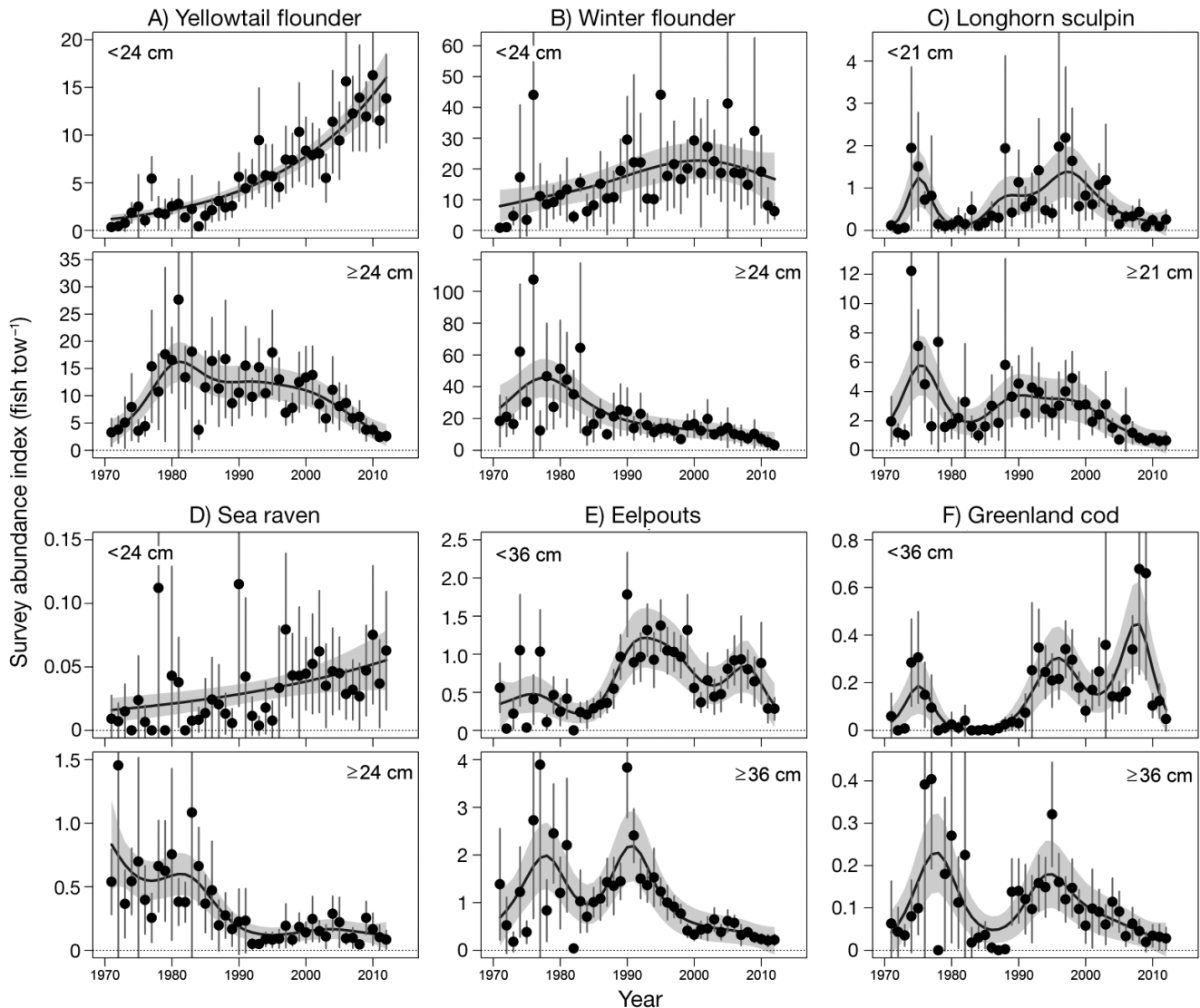
Fig. 6. Abundance trends by length group for (A) yellowtail flounder, (B) winter flounder, (C) longhorn sculpin, (D) sea raven, (E) eelpouts and (F) Greenland cod in the southern Gulf of St. Lawrence. The length groups roughly correspond to juveniles and adults. Circles show annual stratified mean catch rates in the research vessel survey (±2 SD, indicated by light vertical lines). Heavy lines show the generalized additive model fit to the survey indices (±2 SE, indicated by the grey shading)
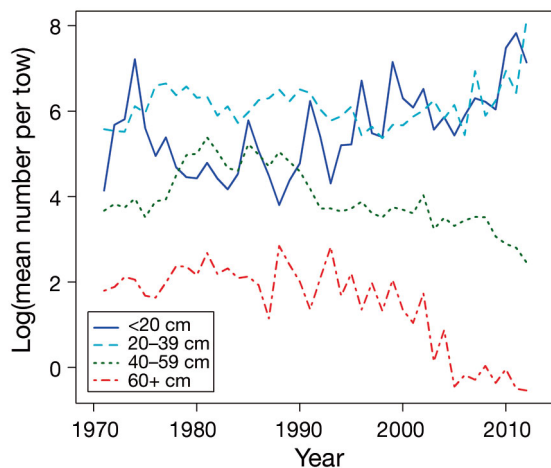
over much of the time series, but decreased sharply in the early 2000s and has remained at a very low level since then. These patterns, evident for an aggregate of over 50 fish species, are consistent with the size-dependent mortality trends observed for the species examined in detail and suggest that these mortality trends are a community-wide phenomenon.

Fig. 7. Changes in the size composition of the fish community in the southern Gulf of St. Lawrence. Lines show the log-transformed mean number per tow in the annual research vessel survey for 4 length categories, grouping over fish species

Grey seal abundance

The estimated abundance of grey seals spending part or all of the year foraging in areas used by sGSL fish has increased roughly exponentially over the past 50 yr, from <10 000 animals in 1960 to >110 000 in 2010 (Fig. 8).

DISCUSSION

The biomass of most large-bodied demersal fishes in the sGSL ecosystem collapsed in the 1980s and early 1990s due to overexploitation. Fishing effort for demersal fish was reduced to very low levels following these population collapses (e.g. Benoît & Swain 2008, Morin & LeBlanc 2012). However, despite negligible levels of fishing mortality, these populations have shown no sign of recovery and in some cases have declined further. Explanations for the lack of recovery of collapsed fish stocks have often focussed on the early life-history stages, when the scope for variability in productivity is high (Minto et al. 2014). For example, Keith & Hutchings (2012) reported unexpectedly weak recruitment rates at low abundance in a number of fish stocks, and suggested that this might account for slow recovery of depleted stocks. Similarly, Walters & Kitchell (2001) suggested that recovery of large piscivorous fishes such as cod

Fig. 8. Estimated abundance of grey seals foraging in the southern Gulf of St. Lawrence (sGSL) and the adjoining overwintering grounds of sGSL fishes, based on the abundance estimates given in DFO (2014). Grey symbols indicate years with pup counts available for fitting the population models for the Sable Island, Gulf of St. Lawrence and coastal Nova Scotia (CNS) grey seal herds

may be delayed by increased abundance of forage fishes that are prey of adult piscivores but predators or competitors of their young.

Minto & Worm (2012) reported a negative relationship between herring abundance and recruitment success of many cod stocks including the sGSL stock. The remarkably high recruitment rates of sGSL cod in the late 1970s coincided with a collapse in the biomass of pelagic fishes (herring and mackerel) in this ecosystem and are thought to result from reduced predation by these fishes on cod eggs and larvae (Swain & Sinclair 2000). Following fishery restrictions, pelagic fish biomass recovered in the 1980s and cod recruitment rates returned to more normal levels. While not as high as the unusually high rates in the late 1970s, recent recruitment rates of sGSL cod exceed those in the 1950s, 1960s and early 1970s (also see Minto et al. 2014). At current recruitment rates, sGSL cod would recover rapidly if fishing mortality was low and natural mortality of adult cod was at more normal levels, such as those estimated for the early 1970s (Swain & Chouinard 2008).

Recent recruitment rates have been strong for plaice and exceptionally high for hake. Survival rates are currently relatively high for small juveniles of all 3 skate species in the sGSL. Abundance at small sizes has increased to relatively high levels for most other large-bodied demersal fishes in the sGSL despite depleted abundance at larger sizes, again suggesting high productivity at early life stages. The delayed recovery or continued decline of large demersal fishes in the sGSL cannot be attributed to reduced productivity at early life-history stages.

The lack or recovery of collapsed demersal fish populations in the sGSL instead appears to reflect increases in natural mortality among large individuals throughout the demersal fish community of this ecosystem. For many of the species in this community, the estimated increases in natural mortality have been extreme. The natural mortality rates of large individuals of these formerly long-lived groundfish now resemble those of high turnover species such as pilchard *Sardinops* sp., anchovy *Engraulis* sp. and sand lance *Ammodytes* sp. (Pauly 1980, Hoenig 1983, Gislason et al. 2010). These extreme increases in natural mortality have not been accompanied by commensurate and compensatory changes in other life-history traits (e.g. correspondingly extreme declines in age at maturity to the young ages that characterize high turnover species), and are thus not sustainable.

The changes in size structure reported here within species are also evident at the level of the marine fish community, suggesting that the size-dependent mor-
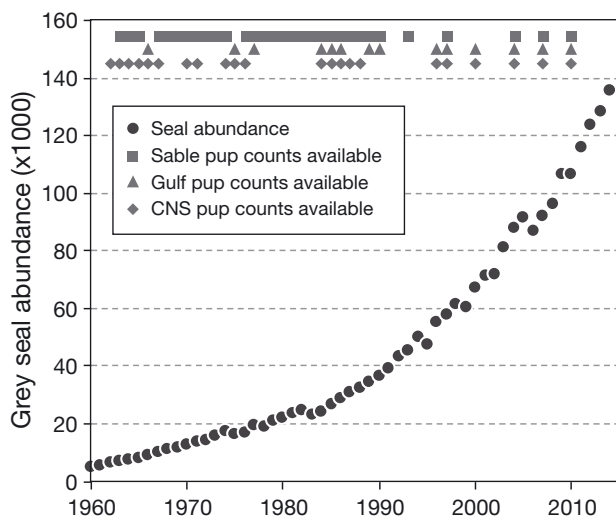
tality trends estimated for a subset of large-bodied demersal fishes in the sGSL ecosystem are a community-wide phenomenon. These changes are also reflected in the species composition of the community. Large-bodied species generally declined to low abundance by the 1990s or 2000s whereas small-bodied species have tended to increase dramatically since the early 1990s (Benoît & Swain 2008). Similar dynamics also appear to be occurring in the neighbouring eastern Scotian Shelf ecosystem, where recent productivity has been high at early life stages for cod (Swain & Mohn 2012, Minto et al. 2014) and the skates (Swain et al. 2013), whereas natural mortality has risen to high levels for adult cod (Swain & Mohn 2012) and large skates (Swain et al. 2013).

In the present study, a rapid loss of older fish from survey catches despite reductions in fishing effort has been attributed to increased natural mortality. An alternative possibility is that this instead reflects changes in the selectivity or catchability of the survey. We have endeavoured to maintain a consistent survey time series by adjusting survey catch rates as necessary to account for any changes in fishing efficiency related to changes in the survey in 1985, 1992 and 2004. Nonetheless, it is possible that some changes in fishing efficiency were poorly estimated or were undetected due to low statistical power of the comparative fishing experiments for some species. However, the changes in catchability or selectivity that would be required to account for our data are not plausible (see Supplement 3 for details). Assuming that natural mortality was constant over time, catchability would need to increase in 1992 and/or 2004 to levels that are too high to be possible (e.g. an increase in fully recruited catchability of hake from 0.57 prior to 1985 to 6.3 in 1992). Furthermore, these large changes would need to occur in years when only the vessel changed and would involve changes in catchability that are greater than estimated vessel effects by an order of magnitude or more. Such large effects would have been apparent in the comparative fishing experiments even when statistical power was low. In addition, such high levels of catchability result in estimates of recent fishing mortality that are too high to be plausible given the sharp decline in fishing effort that occurred in the early 1990s (Benoît et al. 2012). The changes in selectivity that would be required to account for our data assuming constant natural mortality are likewise implausible. If both catchability and natural mortality are allowed to change, either estimated changes in catchability are minor and changes in natural mortality remain similar to those reported here (cod), or estimated changes

in natural mortality are reduced but changes in catchability remain implausibly high (plaice and hake). In contrast to catchability and selectivity, the extreme changes in natural mortality required to account for our data are not implausible if the physical or biological environment becomes sufficiently harsh (Benoît et al. 2011b). Indeed, given the current low level of fishing effort, the high productivity of these fishes at early life stages and the characteristics of the monitoring surveys in the sGSL (see Supplement 1), no other plausible explanation for the continued low abundance of these fishes is evident.

An additional alternative explanation for the changes in size composition in the length-based analyses is that these changes reflect reductions in growth rates rather than increases in the mortality rates of large individuals. However, this does not appear likely because (1) the required reductions in growth would be extreme; (2) conditions for growth of these fish appear to have been good since at least the late 1990s; and (3) there are no indications from other species for which growth information is available that growth rates have declined during the past 20 to 25 yr in this ecosystem (see Supplement 5 at www.int-res.com/articles/suppl/m519p165_supp.pdf). Finally, based on sensitivity analyses, the increases in mortality estimated for thorny and winter skates could not be attributed instead to changes in growth rates within plausible limits (Swain et al. 2009, 2013).

Increased survival and abundance of small fish in this ecosystem have been attributed to a release from predation following the collapse in biomass of large demersal fish, possibly combined with reduced incidental mortality in fisheries due to sharp declines in fishing effort (Benoît & Swain 2008, Swain et al. 2013). Causes of increased natural mortality of older/larger fish have been examined in most detail for Atlantic cod. Swain et al. (2011a) examined a suite of hypotheses for causes of apparent increases in natural mortality of cod in this ecosystem, namely unreported catch (i.e. some of the increased mortality is unknown fishing mortality, not natural mortality), emigration (i.e. older fish are leaving the ecosystem, not dying) and increased natural mortality due to disease, contaminants, poor fish condition as a result of harsh environmental conditions, life-history change (early maturation, early senescence), heavy parasite loads or increased predation mortality. Conclusions about the relative likelihoods of these hypotheses are summarized below.

Any unreported catch will contribute to the estimates of natural mortality from our population models. It is thought that the level of misreporting in-

creased as the cod fishery intensified in the late 1980s and early 1990s (Bousquet et al. 2010), and it is likely that some of the mortality attributed to natural causes during this period was actually due to unreported catch. For example, if 30% of the catch was unreported in 1990, unreported catch would account for 39 and 51% of the estimated M for ages 5–8 and 9+ yr, respectively (assuming that the catch was unreported in the same proportion for all ages). However, since the early 1990s, fishing effort for groundfish has dropped sharply, catch surveillance has increased substantially and management measures have been taken to reduce cod bycatch in the small fisheries remaining open for other groundfish. Furthermore, the catch of 5+ yr cod in fisheries for invertebrates and pelagic fishes appears to be negligible. Thus, the contribution of unreported catch to estimated M must be minor since the mid-1990s. For example, even if 30% of the catch were unreported, unreported catch would account for only 4 and 0.2% of the estimated M in 2000 and 2010 for ages 5–8 yr, and 7 and 0.3% of the estimated M in these years for ages 9+ yr.

Poor fish condition as a result of harsh (cold) environmental conditions has been proposed as a cause of increased natural mortality of cod in the northern Gulf of St. Lawrence (nGSL) in the early 1990s (Lambert & Dutil 1997, Dutil & Lambert 2000). Bottom water temperatures were also unusually cold in the sGSL between the late 1980s and late 1990s, but then warmed to above average levels since 1999 (Swain et al. 2011b). An index of cod condition near the middle of the feeding season is available since 1971 based on cod collected during the September survey. This index of condition should be more closely linked to the ambient temperature of cod than to the general temperature index. Interannual variation in the ambient temperature of cod in September differed from the trends in the general index due to changes in cod distribution (Swain 1999). Ambient temperature was warmest in the mid-1970s, coldest in the early to mid-1980s and near the long-term average throughout the 1990s and 2000s. Variation in cod condition in September showed a congruent pattern, with condition highest in the early to mid-1970s, lowest in the late 1970s to the mid-1980s, and near the long-term average throughout the 1990s and 2000s (Swain et al. 2012b). Based on these results, increases in M due to poor cod condition would be expected to be greatest in the late 1970s to the mid-1980s. However, M in that period remained low relative to recent levels. Cod show a strong seasonal cycle in condition in the sGSL, with condition lowest in the spring following

the winter period when little feeding occurs. Thus, the link between poor condition and mortality would be expected to be most evident in the spring. Condition of sGSL cod has been monitored in the spring since 1992. Compared to levels in the fall, indices of spring condition were low in the 1990s, though higher than those reported for nGSL cod (Swain et al. 2011b). However, the spring condition indices rose to substantially higher levels in the 2000s, and mortality due to poor condition would be expected to be low during this period. In contrast to this expectation, estimated M of cod remained high or increased in the 2000s (Fig. 2).

There is increasing evidence for evolutionary changes in response to fishing (Kuparinen & Merilä 2007, Hutchings & Fraser 2008), and these changes have been predicted to result in increases in natural mortality (Hutchings 2005, Jørgensen & Fiksen 2010). One expected consequence of the increased mortality imposed by fishing is the evolution of earlier ages and sizes at maturation (Ernande et al. 2004, Olsen et al. 2004). Reproduction is costly, leading to trade-offs between reproductive investment and subsequent survival (Roff 2002). This survival cost to reproduction is expected to be higher in individuals maturing at an earlier age and smaller size (Roff 2002, e.g. Hutchings 1994), leading Hutchings (2005) to suggest that elevated natural mortality of cod in the Northwest Atlantic may be partly due to fishing-induced declines in age and size at maturation and the consequent increases in survival costs to reproduction. Age and size at maturation of sGSL cod decreased sharply in cohorts produced in the 1950s and 1960s, coincident with large increases in fishing mortality in this period (Swain 2011b). However, age and size at maturation have changed little since the early 1970s. Estimated M of adult cod remained low in the early 1970s, indicating that the large declines in age and size at maturation in the 1950s and 1960s did not appear to result in substantial increases in natural mortality. Costs to reproduction may be more evident under stressful physiological or ecological conditions (Reznick 1985, Roff 2002). Possibly, early maturation contributed to the increases in natural mortality between the late 1970s and the early 1990s, a period when ecological conditions appeared to be relatively harsh for cod. If so, M would be expected to decline in the late 1990s and the 2000s when conditions improved. Instead, M remained high or increased further during this period, indicating that other factors must be implicated in the current high level of M.

Jørgensen & Fiksen (2010) used a life-history model to examine effects of evolutionary responses

to harvesting on natural mortality. They predicted that natural mortality rates should increase with increased harvesting due to the evolution of smaller fish size, more risky foraging and elevated reproduction. However, contrary to these predictions, increased reproductive investment related to early maturation did not appear to result in increased M in sGSL cod, at least when conditions were favourable. Furthermore, most of the increase in M of sGSL cod occurred between 1985 and 2010 (Fig. 2A), when cod size-at-age was stable (see Fig. S18 in Supplement 5 at www.int-res.com/articles/suppl/m519p165_supp. pdf). It is possible that increases in reproductive investment beyond that associated with early maturation (e.g. increased size-specific fecundity) contribute to the increase in M since the mid-1980s. However, the limited evidence available indicates that if reproductive allotment has changed, it has declined, not increased, between the mid-1950s and the late 1990s (McIntyre & Hutchings 2003). The greatest difficulty in reconciling the estimated increase in M of sGSL cod and the predicted change due to fishing-induced evolution is the scale of the change. For example, Beverton et al. (1994) concluded that M of Northeast Arctic cod increased from 0.15 in individuals maturing at 8 yr of age to 0.25 in those maturing at 6 yr of age. Based on their life-history model, Jørgensen & Fiksen (2010) predicted that the increase in M resulting from adaptations to harvesting should equal about half the harvesting rate. In the case of sGSL cod, this would correspond to an increase in M of about 0.14 or 0.23 depending on age group. The estimated increases in M of sGSL cod are considerably greater than these values, equalling an increase of 0.44 to the current level of 0.63 for cod aged 5–8 yr and of 0.53 to the current level of 0.76 for cod aged 9 yr and older. The sGSL cod population does not appear to be viable at these high levels of M (Swain & Chouinard 2008). An adaptation would not be expected to occur in a population if it resulted in mortality that was so high that the population was inviable. Instead, much of the increase in M of sGSL cod must be due to factors external to the population, such as harsh environmental conditions or increased predator abundance.

The abundance of grey seals foraging in this ecosystem has increased dramatically over the past 50 yr (Fig. 8), coincident with the increases in natural mortality of cod and other large demersal fishes in the sGSL (Chouinard et al. 2005, Swain et al. 2009). With the exception of skates, these fishes are all known to be important prey of grey seals foraging in the sGSL (Hammill et al. 2007, 2014). Skates lack the bony parts normally used to identify prey in seal diet studies in the sGSL but have also been identified as prey of grey seals in this region (Benoît & Bowen 1990, Beck et al. 2007). Until recently, diet samples from the sGSL represented feeding in nearshore areas, primarily between May and October. Based on otoliths recovered from seal digestive tracts, cod was usually among the top 5 prey species, averaging 15% of the diet by weight (Hammill et al. 2007). White hake (15%) and flatfish (19%) were also important prey in these inshore areas. Densities of cod, particularly large cod, are generally relatively low in shallow inshore areas in summer (Swain 1993), and no samples are available that would represent feeding in areas further offshore, where cod densities are highest at this time of year. In late fall and winter, foraging by grey seals, in particular males, appears to be associated with overwintering aggregations of cod in the Cabot Strait (Harvey et al. 2012). The contribution of cod to the diet of seals foraging in the vicinity of these aggregations is much greater than has been reported elsewhere: 52 to 79% of prey weight based on prey recovered from stomachs and 25 to 63% based on prey recovered from intestines (Hammill et al. 2014). Flatfish, likely mainly American plaice, comprised 20 to 60% of the diet of these seals based on intestines. White hake was also an important component of the diet of these seals (4 to 15% in stomachs, 3 to 6% in intestines) and in seals feeding along the migratory route of hake in fall and winter (33% in stomachs, 17% in intestines).

The mean length of cod in the nearshore diet samples was 26 to 28 cm (Hammill et al. 2007). The cod consumed in winter offshore samples were considerably larger, ranging between 10 and 76 cm and averaging 34 to 45 cm (Hammill et al. 2014). The majority of cod in the offshore samples were estimated to be greater than 35 cm in length (51, 67 and 75%, depending on year). Comparisons between the sizes of cod in seal digestive tracts and the size composition in the cod population suggest that seals may select larger cod (Benoît et al. 2011a,b, DFO 2011). The hake consumed in the offshore samples were also relatively large, averaging 29, 36 or 40 cm in length (Hammill et al. 2014).

The wide spatial, seasonal and individual variation in seal diets, combined with spatial and seasonal gaps in the diet sampling, make it difficult to obtain reliable estimates of the average annual diet of grey seals (Benoît et al. 2011a,b,d). Furthermore, consumption of large fish will be underestimated if heads of large individuals are often not consumed (because their otoliths would not appear in digestive

tracts). Belly biting, in which only the viscera are consumed, has been reported by fish harvesters and documented for harp seals in Newfoundland, Canada. Consumption of all but the heads of fish has also been documented for seals in other areas (references in Benoît et al. 2011b). The frequency of partial consumption of prey by grey seals is unknown, but optimal foraging theory suggests that it may not be a rare behaviour. The most energy-dense portion of a cod is its liver, where most of its energy reserves are stored. Optimal foraging theory predicts that when prey density is high, predators should consume only the most energy-dense or easiest-to-process portions of individual prey (Sih 1980). Because of these difficulties it is not yet possible to obtain reliable estimates of the contribution of predation by grey seals to the natural mortality of cod and other fishes in the sGSL. Nonetheless, based on the energy requirements of seals and estimates of spatiotemporal overlap between seals and selected fishes (Atlantic cod, white hake and winter skate), Benoît et al. (2011b) concluded that it was plausible that predation by grey seals could account for a high proportion of the natural mortality of these fishes, even if their contribution to the average seal diet was modest (15% for cod, 4% for hake and 0.2% for winter skate). At the community level, abundance trends over the 1971 to 2005 period are correlated with susceptibility to predation by grey seals, with abundance declining to low levels for fishes with high susceptibility and increasing for those with low susceptibility (Benoît & Swain 2008). Among ecosystems, large increases in natural mortality of cod are also evident on the neighboring eastern Scotian Shelf, where grey seal abundance is also very high (O'Boyle & Sinclair 2012, Swain & Mohn 2012), but not on the southern Grand Bank, where grey seals are rare (Power et al. 2010).

Other hypotheses for the apparent increase in M of sGSL cod were emigration and increased natural mortality due to contaminants, disease or parasites. There was no support for any of these hypotheses (see Swain et al. 2011a for details). Fisheries-induced life-history change, poor fish condition due to harsh environmental conditions and unreported catch may have contributed to the estimated increases in M between the late 1970s and mid-1990s, but do not appear to be important components of the high M since then. The hypothesis most strongly supported for the current high level of M of sGSL cod is increased mortality due to predation by grey seals. Similarly, Benoît et al. (2011c) concluded that predation by grey seals was the most likely cause of elevated natural mortality of white hake and winter skate.

Both theory and empirical evidence indicate that predation can be a source of Allee effects on survival (Gascoigne & Lipcius 2004, Courchamp et al. 2008). Given common forms of functional and aggregative responses of predators to prey, prey mortality is expected to increase with decreasing prey abundance, generating an Allee effect on prey survival (Gascoigne & Lipcius 2004). Alternatively, if predators avoid areas with very low densities of a particular prey (type III aggregative response), or switch to alternative prey when a particular prey is at low density (type III functional response), then a 'predator pit' occurs. In this case, prey survival decreases as abundance declines below a threshold and then increases as abundance declines further below a second threshold, trapping prey at a very low level of abundance. Because grey seals are generalist predators, they are not expected to show a type III aggregative response. Instead, foraging by grey seals continues to be seasonally concentrated in the vicinity of aggregations of cod and other demersal fishes (Harvey et al. 2012). In the North Sea, there is evidence of weak prey switching by grey seals (Smout et al. 2014), indicating the possibility of a predator pit for some prey species.

Allee effects result from a causal relationship between a component of fitness and population abundance. A decline in fitness at low abundance, caused by some density-independent factor (e.g. temperature change) that happens to be correlated with changes in population abundance, is not an Allee effect (Courchamp et al. 2008). However, Allee effects need not result only from an inherent dynamical component of a population, i.e. a demographic Allee effect such as reduced fertilization efficiency or mate-finding success at low population size (Courchamp et al. 2008, e.g. Rowe et al. 2004). Instead, they may reflect emergent effects such as ecosystem changes to which an increasingly depleted population becomes increasingly vulnerable (Hutchings & Rangeley 2011). One example of an emergent Allee effect would be reductions in the growth rate of a depleted prey population due to increases in predator abundance (Hutchings 2014).

Hunting had reduced grey seal abundance in the northwest Atlantic to a low level by the mid- to late 1800s, but grey seals were very abundant in earlier centuries (Lavigueur & Hammill 1993). It is often assumed that in these earlier centuries cod and seals co-existed in a predator–prey balance, with cod natural mortality sustained at a moderate level (O'Boyle & Sinclair 2012). However, estimated cod abundance during this earlier period was also very high, about

4 times the estimated levels within recent periods of high cod abundance (Rosenberg et al. 2005). It appears that predation by a high abundance of grey seals could be sustained by cod and other large demersal fishes in earlier periods when they were also very abundant, but not in the current period when they have been reduced to very low levels of abundance. The susceptibility of these fishes to predation may also have been further increased by fisheries-induced life-history and behavioural changes (Jørgensen & Holt 2013).

Natural mortality of large demersal fish has increased to unprecedented levels throughout the demersal fish community in the sGSL. Because of this high mortality, recovery of depleted demersal fishes does not appear to be possible in this ecosystem even with no fishing. Many piscivorous marine mammal populations are recovering worldwide from past over-harvesting (Costa et al. 2006) and increasing natural mortality may be occurring in the fish communities of other ecosystems, where it may be obscured by continued heavy fishing. Our results indicate an urgent need for more precautionary fisheries management regimes in the face of increasing abundances of top predators in order to avoid population collapses that cannot be reversed by stopping fishing.

LITERATURE CITED

Beck CA, Iverson SJ, Bowen WD, Blanchard W (2007) Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. J Anim Ecol 76:490–502

Benoît HP (2006) Standardizing the southern Gulf of St. Lawrence bottom-trawl survey time series: results of the 2004–2005 comparative fishing experiments and other recommendations for the analysis of the survey data. DFO Can Sci Adv Sec Res Doc 2006/008. Fisheries and Oceans Canada, Ottawa

Benoît HP (2013a) An empirical model of seasonal depth-dependent fish assemblage structure to predict the species composition of mixed catches. Can J Fish Aquat Sci 70:220–232

Benoît HP (2013b) Two decades of annual landed and discarded catches of three southern Gulf of St. Lawrence skate species estimated under multiple sources of uncertainty. ICES J Mar Sci 70:554–563

Benoît D, Bowen WD (1990) Seasonal and geographic variation in the diet of grey seals (*Halichoerus grypus*) in eastern Canada. Can Bull Fish Aquat Sci 222:215–226

Benoît HP, Swain DP (2003) Standardizing the southern Gulf of St. Lawrence bottom-trawl survey time series: adjusting for changes in research vessel, gear and survey protocol. Can Tech Rep Fish Aquat Sci No. 2505. Fisheries and Oceans Canada, Ottawa

Benoît HP, Swain DP (2008) Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. Can J Fish Aquat Sci 65:2088–2104

Benoît HP, Hammill MO, Swain, DP (2011a) Estimated consumption of southern Gulf of St. Lawrence cod by grey seals: bias, uncertainty and two proposed approaches. DFO Can Sci Advis Sec Res Doc 2011/041. Fisheries and Oceans Canada, Ottawa

Benoît HP, Swain DP, Bowen WD, Breed GA, Hammill MO, Harvey V (2011b) Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. Mar Ecol Prog Ser 442:149–167

Benoît HP, Swain DP, Hammill MO (2011c) A risk analysis of the potential effects of selective and non-selective reductions in grey seal abundance on the population status of two species at risk of extirpation, white hake and winter skate in the southern Gulf of St. Lawrence. DFO Can Sci Advis Sec Res Doc 2011/033. Fisheries and Oceans Canada, Ottawa

Benoît HP, Swain DP, Hammill MO (2011d) Seasonal patterns in the spatial overlap of southern Gulf of St. Lawrence cod and grey seals, with a discussion of sources of error and possible bias. DFO Can Sci Advis Sec Res Doc 2011/018. Fisheries and Oceans Canada, Ottawa

Benoît HP, Gagné JA, Savenkoff C, Ouellet P, Bourassa MN (eds) (2012) State-of-the-Ocean Report for the Gulf of St. Lawrence Integrated Management (GOSLIM) Area. Can Manuscr Rep Fish Aquat Sci 2986. Fisheries and Oceans Canada, Ottawa

Beverton RJH (1965) Catch effort of some ICNAF fisheries. Res Bull Int Comm Northwest Atl Fish 2:59–72

Beverton RJH, Hylen A, Ostvedt OJ (1994) Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod. ICES J Mar Sci Symp 198:482–501

Bourbeau-Lemieux A, Festa-Bianchet M, Gaillard JM, Pelletier F (2011) Predation-driven component Allee effects in a wild ungulate. Ecol Lett 14:358–363

Bousquet N, Cadigan N, Duchesne T, Rivest LP (2010) Detecting and correcting underreported catches in fish stock assessment: trial of a new method. Can J Fish Aquat Sci 67:1247–1261

Butchart SHM, Walpole M, Collen B, van Strien A and others (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Chouinard GA, Swain DP, Hammill MO, Poirier GA (2005) Covariation between grey seal (*Halichoerus grypus*) abundance and natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can J Fish Aquat Sci 62:1991–2000

Clay D (1991) Seasonal distribution of demersal fish (*Osteichthyes*) and skates (*Chondrichthyes*) in the southeastern Gulf of St. Lawrence. In: Therriault JC (ed) The Gulf of St Lawrence: small ocean or big estuary? Can Spec Publ Fish Aquat Sci 113:241–259

COSEWIC (2005) COSEWIC assessment and status report on the winter skate *Leucoraja ocellata* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. Available at www.sararegistry.gc.ca/status/status_e.cfm

Costa DP, Weise MJ, Arnould JPY (2006) Potential influences of whaling on the status and trends of pinniped populations. In: Estes JA, DeMaster DP, Doak DF, Williams TM, Brownell RLJ (eds) Whales, whaling and ocean ecosystems. University of California Press, Berkeley, CA, p 344–359

Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends Ecol Evol 14:405–410

Courchamp F, Berek L, Gascoigne J (2008) Allee effects in ecology and conservation. Oxford University Press, Oxford

DFO (Fisheries and Oceans Canada) (2011) Impacts of grey seals on fish populations in eastern Canada. DFO Can Sci Advis Sec Sci Advis Rep 2010/071. Fisheries and Oceans Canada, Ottawa

DFO (Fisheries and Oceans Canada) (2014) Stock Assessment of Canadian Grey Seals (*Halichoerus grypus*). DFO Can Sci Advis Sec Sci Advis Rep 2014/010. Fisheries and Oceans Canada, Ottawa

Dickie LM (1963) Estimation of mortality rates of Gulf of St. Lawrence cod from results of a tagging experiment. Spec Publ Int Comm Northwest Atl Fish 4:71–80

Dutil JD, Lambert Y (2000) Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 57:826–836

Ernande B, Dieckmann U, Heino M (2004) Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proc R Soc B 271: 415–423

Fournier DA, Skaug HJ, Ancheta J, Ianelli J and others (2011) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim Methods Softw 27:233–249

Fu C, Quinn TJ II (2000) Estimability of natural mortality and other population parameters in a length based model: *Pandalus borealis* in Kachemak Bay, Alaska. Can J Fish Aquat Sci 57:2420–2432

Gascoigne JC, Lipcius RN (2004) Allee effects driven by predation. J Appl Ecol 41:801–810

Gislason H, Daan N, Rice JC, Pope JG (2010) Size, growth, temperature and the natural mortality of marine fish. Fish Fish 11:149–158

Hammill MO, Stenson GB, Proust F, Carter P, McKinnon D (2007) Feeding by grey seals in the Gulf of St. Lawrence and around Newfoundland. In: Haug T, Hammill M, Olafsdottir D (eds) Grey seals in the North Atlantic and the Baltic. NAMMCO Sci Publ 6, Tromsø, p 135–152

Hammill MO, Stenson GB, Swain DP, Benoît HP (2014) Feeding by grey seals on endangered stocks of Atlantic cod and white hake. ICES J Mar Sci 71:1332–1341

Harvey V, Hammill MO, Swain DP, Breed GA, Lydersen C, Kovacs KM (2012) Winter foraging by a top predator, the grey seal *Halichoerus grypus*, in relation to the distribution of prey. Mar Ecol Prog Ser 462:273–286

Hilborn R, Litzinger E (2009) Causes of decline and potential for recovery of Atlantic cod populations. Open Fish Sci J 2:32–38

Hoenig JM (1983) Empirical use of longevity data to estimate mortality rates. Fish Bull 81:898–903

Hutchings JA (1994) Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. Oikos 70:12–20

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406:882–885

Hutchings JA (2005) Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 62:824–832

Hutchings JA (2014) Renaissance of a caveat: Allee effects in marine fish. ICES J Mar Sci 71:2152–2157

Hutchings JA, Baum JK (2005) Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. Philos Trans R Soc B Biol Sci 360: 315–338

Hutchings JA, Fraser DF (2008) The nature of fisheries- and farming-induced evolution. Mol Ecol 17:294–313

Hutchings JA, Rangeley RW (2011) Correlates of recovery for Canadian Atlantic cod. Can J Zool 89:386–400

Hutchings JA, Reynolds JD (2004) Marine fish population collapses: consequences for recovery and extinction risk. Bioscience 54:297–309

Hutchings JA, Butchart SHM, Collen B, Schwartz MK, Waples RS (2012) Red flags: correlates of impaired species recovery. Trends Ecol Evol 27:542–546

Jiao Y, Smith EP, O'Reilly R, Orth DJ (2012) Modelling non-stationary natural mortality in catch-at-age models. ICES J Mar Sci 69:105–118

Jørgensen C, Fiksen Ø (2010) Modelling fishing-induced adaptations and consequences for natural mortality. Can J Fish Aquat Sci 67:1086–1097

Jørgensen C, Holt R (2013) Natural mortality: Its ecology, how it shapes fish life histories, and why it may be increased by fishing. J Sea Res 75:8–18

Keith DM, Hutchings JA (2012) Population dynamics of marine fishes at low abundance. Can J Fish Aquat Sci 69: 1150–1163

Kuparinen A, Merilä J (2007) Detecting and managing fisheries-induced evolution. Trends Ecol Evol 22:652–659

Lambert Y, Dutil JD (1997) Condition and energy reserves of Atlantic cod (*Gadusmorhua*) during the collapse of the northern Gulf of St. Lawrence stock. Can J Fish Aquat Sci 54:2388–2400

Lavigueur L, Hammill MO (1993) Distribution and seasonal movements of grey seals, *Halichoerus grypus*, born in the Gulf of St. Lawrence and eastern Nova Scotia shore. Can Field Nat 107:329–340

Lee HH, Maunder MN, Piner KR, Methot RD (2011) Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. Fish Res 109:89–94

McIntyre TM, Hutchings JA (2003) Small-scale temporal and spatial variation in Atlantic cod (*Gadus morhua*) life history. Can J Fish Aquat Sci 60:1111–1121

Minto C, Worm B (2012) Interactions between small pelagic fish and young cod across the North Atlantic. Ecology 93: 2139–2154

Minto C, Mills Flemming J, Britten GL, Worm B (2014) Productivity dynamics of Atlantic cod. Can J Fish Aquat Sci 71:203–216

Morin R (2012) Estimating the age composition of discards in the NAFO 4T American plaice fishery. DFO Can Sci Advis Sec Res Doc 2012/081. Fisheries and Oceans Canada, Ottawa

Morin R, LeBlanc SG (2012) Assessment of the southern Gulf of St. Lawrence (NAFO Division 4T) American plaice (*Hippoglossoides platessoides*). DFO Can Sci Advis Sec Res Doc 2012/099. Fisheries and Oceans Canada, Ottawa

Morin R, Swain DP, LeBlanc SG (2012) A biomass Limit Reference Point for the NAFO 4T American plaice (*Hippoglossoides platessoides*) fishery. DFO Can Sci

Advis Sec Res Doc 2012/108. Fisheries and Oceans Canada, Ottawa

Neubauer P, Jensen OP, Hutchings JA, Baum JK (2013) Resilience and recovery of overexploited marine populations. Science 340:347–349

Nicholson AJ (1933) The balance of animal populations. J Anim Ecol 2:131–178

O'Boyle R, Sinclair M (2012) Seal–cod interactions on the Eastern Scotian Shelf: reconsideration of modelling assumptions. Fish Res 115-116:1–13

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428:932–935

Paloheimo JE, Kohler AC (1968) Analysis of the southern Gulf of St. Lawrence cod population. J Fish Res Board Can 25:555–578

Pauly D (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J Cons Int Explor Mer 39:175–192

Power D, Morgan J, Murphy EF, Brattey J, Healey B (2010) An assessment of the cod stock in NAFO Divisions 3NO. NAFO SCR Doc No 10/42. Fisheries and Oceans Canada, Ottawa

Reznick D (1985) Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267

Roff DA (2002) Life history evolution. Sinauer, Sunderland, MA

Rosenberg AA, Bolster WJ, Alexander KE, Leavenworth WB, Cooper AB, McKenzie MG (2005) The history of ocean resources: modeling cod biomass using historical records. Front Ecol Environ 3:84–90

Rowe S, Hutchings JA, Bekkevold D, Rakitin A (2004) Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). ICES J Mar Sci 61:1144–1150

Shelton PA, Sinclair AF, Chouinard GA, Mohn R, Duplisea DE (2006) Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 63:235–238

Sih A (1980) Optimal foraging: partial consumption of prey. Am Nat 116:281–290

Sinclair AF (1998) Estimating trends in fishing mortality at age and length directly from research surveys and commercial catch data. Can J Fish Aquat Sci 55:1248–1263

Sinclair AF (2001) Natural mortality of cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. ICES J Mar Sci 58:1–10

Smout S, Rindorf A, Hammond PS, Harwood J, Matthiopoulos J (2014) Modelling prey consumption and switching by UK grey seals. ICES J Mar Sci 71:81–89

Stephens PA, Sutherland WJ (1999) Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol Evol 14:401–405

Swain DP (1993) Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can J Fish Aquat Sci 50:1255–1264

Swain DP (1999) Changes in the distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence — effects of environmental change or change in environmental preferences? Fish Oceanogr 8:1–17

Swain DP (2011a) Natural mortality and projected biomass of southern Gulf of St. Lawrence cod. DFO Can Sci Advis Sec Res Doc 2011/040. Fisheries and Oceans Canada, Ottawa

Swain DP (2011b) Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). Evol Appl 4:18–29

Swain DP, Benoît HP (2006) Change in habitat associations and geographic distribution of thorny skate (*Amblyraja radiata*) in the southern Gulf of St. Lawrence: density-dependent habitat selection or response to environmental change? Fish Oceanogr 15:166–182

Swain DP, Chouinard GA (2008) Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can J Fish Aquat Sci 65:2315–2319

Swain DP, Mohn RK (2012) Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. Can J Fish Aquat Sci 69:997–1001

Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can J Fish Aquat Sci 57:1321–1325

Swain DP, Hurlbut T, Benoît HP (2005) Changes in the abundance and size of skates in the southern Gulf of St. Lawrence, 1971–2002. J Northwest Atl Fish Sci 36:19–30

Swain DP, Jonsen ID, Simon JE, Myers RA (2009) Assessing threats to species-at-risk using stage-structured state-space models: mortality trends in skate populations. Ecol Appl 19:1347–1364

Swain DP, Benoît HP, Hammill MO, McClelland G, Aubry É (2011a) Alternative hypotheses for causes of the elevated natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence: the weight of evidence. DFO Can Sci Advis Sec Res Doc 2011/036. Fisheries and Oceans Canada, Ottawa

Swain DP, Benoît HP, Savoie L, Surette T (2011b) Can poor fish condition explain the elevated natural mortality of cod and other marine fish in the southern Gulf of St. Lawrence? DFO Can Sci Advis Sec Res Doc 2011/037. Fisheries and Oceans Canada, Ottawa

Swain DP, Hurlbut TR, Benoît HP (2012a) Pre-COSEWIC review of variation in the abundance, distribution and productivity of white hake (*Urophycis tenuis*) in the southern Gulf of St. Lawrence, 1971–2010. DFO Can Sci Advis Sec Res Doc 2012/066. Fisheries and Oceans Canada, Ottawa

Swain DP, Savoie L, Aubry É (2012b) Recovery Potential Assessment for the Laurentian South designatable unit of Atlantic Cod (*Gadus morhua*): the southern Gulf of St. Lawrence cod stock (NAFO Div. 4T-4Vn(Nov–Apr)). DFO Can Sci Advis Sec Res Doc 2012/052. Fisheries and Oceans Canada, Ottawa

Swain DP, Jonsen ID, Simon JE, Davies TD (2013) Contrasting decadal trends in mortality between large and small individuals in skate populations in Atlantic Canada. Can J Fish Aquat Sci 70:74–89

Walters C, Kitchell JF (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can J Fish Aquat Sci 58:39–50

Worm B, Hilborn R, Baum JK, Branch TA and others (2009) Rebuilding global fisheries. Science 325:578–585