

# CSAS

Canadian Science Advisory Secretariat

Research Document 2011/036

**Gulf Region** 

Alternative hypotheses for causes of the elevated natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence: the weight of evidence

## SCCS

Secrétariat canadien de consultation scientifique

Document de recherche 2011/036

Région du Golfe

La balance des probabilités des hypothèses alternatives sur les causes du taux élevé de mortalité naturelle de la morue (*Gadus morhua*) dans le sud du Golfe du Saint-Laurent

D. P. Swain, H. P. Benoît, M. O. Hammill<sup>1</sup>, G. McClelland and É. Aubry

Department of Fisheries and Oceans Gulf Fisheries Centre P.O. Box 5030 Moncton, NB E1C 9B6 CANADA

<sup>1</sup> Fisheries and Oceans Canada Maurice Lamontagne Institute P.O. Box 1000 Mont Joli, QC G5H 3Z4 CANADA

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

La présente série documente les fondements scientifiques des évaluations des ressources et des écosystèmes aquatiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

This document is available on the Internet at: Ce document est disponible sur l'Internet à: http://www.dfo-mpo.gc.ca/csas/

> ISSN 1499-3848 (Printed / Imprimé) ISSN 1919-5044 (Online / En ligne) © Her Majesty the Queen in Right of Canada, 2011 © Sa Majesté la Reine du Chef du Canada, 2011

#### Correct citation for this publication:

Swain, D. P., Benoît, H. P., Hammill, M. O., McClelland, G., and Aubry, É. 2011. 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. iv + 33 p.

#### ABSTRACT

Natural mortality (M) of older (ages 5+ yr) cod in the southern Gulf of St. Lawrence has been unusually high throughout the 1990s and 2000s. We compared the weight of evidence for a suite of alternate hypotheses for the causes of this elevated M. A significant portion of the losses attributed to M in the late 1980s and early 1990s may instead be due to unreported catch, but the contribution of unreported catch to estimated M from the mid 1990s to the present can only be negligible. The hypothesis that the losses represent emigration rather than mortality can be rejected. While data are limited, there is no evidence to support the hypothesis that disease is a major contributor to the elevated M. Likewise, the hypothesis that contaminantinduced mortality is a significant component of the elevated M is not supported by the evidence. Life-history change (early maturation) in combination with poor fish condition may have contributed to moderate increases in M (by 0.1-0.2) in the early to mid 1980s, but M due to these causes would have declined when fish condition subsequently improved. Neither life history change (early maturation, early scenescence) nor poor fish condition are supported as important factors in the current high level of M in the 2000s. Parasite-induced mortality related to direct damage to organs and tissues or depletion of energy reserves is small in this population. However, it is possible that parasite infection may contribute the elevated M by increasing the susceptibility of heavily infected fish to predators. The sharp increase in M of 5+ cod as their abundance collapsed in the late 1980s and early 1990s is consistent with the predator-pit hypothesis for the cause of this high M. Given the diets, distributions and abundances of potential predators of large cod, grey seals are most likely to be the predominant predator producing this pit. The available diet information indicates that grey seals consume large cod (>40 cm in length), that they appear to show positive selection for large cod over small cod, and that when foraging in the vicinity of cod aggregations large cod can be a major component of the diet. Due to data gaps, the quantity of large cod consumed by grey seals is uncertain. However, some assumptions for filling data gaps lead to consumption estimates that account for a high proportion of the M of 5+ cod. There is also indirect (correlative) evidence that grey seal predation plays a role in the elevated M of adult cod and other large demersal fish. The hypothesis most strongly supported by the weight of evidence is that a major component of the current high M of 5+ southern Gulf cod is due to predation by grey seals.

## RÉSUMÉ

La mortalité naturelle (M) des morues plus âgées (de 5 ans et plus) dans le sud du Golfe du Saint-Laurent était anormalement élevée durant les années 1990 et 2000. Nous avons comparé l'évidence disponible pour une série d'hypothèses possibles concernant les causes de cette M élevée. Les pertes attribuées à la M à la fin des années 1980 et au début des années 1990 pourraient être dues en partie à une forte proportion à des prises non déclarées, mais la contribution de telles prises à la M estimée entre le milieu des années 1990 et maintenant ne peut être que négligeable. L'hypothèse selon laquelle les pertes seraient dues à la migration plutôt qu'à la mortalité peut être rejetée. De plus, parmi le peu de données dont on dispose, aucun élément de preuve n'appuie l'hypothèse selon laquelle la maladie serait un important facteur du taux élevé de M. L'hypothèse selon laquelle la mortalité due à un agent de contamination soit un important facteur en cause, quant à elle, n'est pas appuyée par des données probantes. Les changements du cycle biologique (maturation précoce), de concert avec une faible condition physiologique, ont pu contribuer à des augmentations modérées de la M (de 0,1-0,2) dans la première moitié des années 1980, mais la M liée à ces causes aurait décliné lorsque la condition des poissons se serait ensuite améliorée. Ni les changements du cycle biologique (maturation précoce, sénescence précoce), ni la faible condition des poissons ne semblent être d'importants facteurs du taux actuellement élevé de M des années 2000. La mortalité d'origine parasitaire liée aux lésions directes aux organes et aux tissus ou à la déplétion des réserves d'énergie est faible chez cette population. Cependant, il se peut qu'une infection parasitaire contribue au taux élevé de M en rendant les poissons fortement infectés davantage vulnérables aux prédateurs. L'augmentation prononcée du taux de M chez les morues de 5 ans et plus, dont le nombre a chuté à la fin des années 1980 et au début des années 1990, peut confirmer l'hypothèse de la « fosse aux prédateurs » comme élément causal. Cette fosse serait principalement créée par le phoque gris, si l'on se fie aux données sur les préférences alimentaires, la distribution et l'abondance des prédateurs potentiels de la grande morue. Les données disponibles sur le régime alimentaire du phoque gris indiquent que cette espèce consomme la grande morue (> 40 cm de longueur), que ce prédateur semble la préférer à la petite morue et que, lorsqu'il se trouve à proximité de grandes concentrations d'individus, la grande morue puisse occuper une place importante de son alimentation. En raison du manque de données, on ignore la quantité de grandes morues que consomment les phoques gris. Cependant, certaines hypothèses visant à combler cette lacune ont recours à des estimés de consommation représentant une partie importante de la *M* des morues de 5 ans et plus. Des données probantes indirectes (corrélatives) indiquent également que la prédation des phoques gris joue un rôle dans le taux élevé de M des morues adultes et des autres grands poissons de fond. Selon l'hypothèse la mieux soutenue par le poids des données probantes, la prédation par les phoques gris serait un important facteur du taux actuellement élevé de M des morues de 5 ans et plus du sud du Golfe du Saint-Laurent.

#### INTRODUCTION

Many populations of large demersal fishes in the Northwest Atlantic, in particular Atlantic cod (*Gadus morhua*), declined to low levels of abundance in the early 1990s. Some of these populations have failed to recover despite very low fishing mortality. One of these populations is the cod population in the southern Gulf of St. Lawrence. A principle reason for the lack of recovery of this population is high *M*, the instantaneous rate of natural mortality (Swain et al. 2009). Coincident with the decline in demersal fish biomass, the abundance of grey seals in Atlantic Canada has increased dramatically. In October 2010, the Department of Fisheries and Oceans held a workshop to examine possible interactions between grey seals and cod and other large demersal fishes (DFO 2010).

Natural mortality of cod in the southern Gulf of St. Lawrence has been at an unusually high level throughout the 1990s and 2000s (e.g. Swain 2011b). This increase in natural mortality appears to be restricted to older cod (ages 5+ years). For younger cod, natural mortality appeared to decline to a relatively low level in the early 1990s. A similar pattern is seen throughout the marine fish community in the southern Gulf, with improved survival of small fish and decreased survival of large fish in the 1990s and 2000s (Benoît and Swain 2011). In this paper, we examine the evidence for and against alternate hypotheses for the causes of the elevated natural mortality of older (5+) southern Gulf cod. We attempt to examine a comprehensive suite of hypotheses to determine which factors are most likely to be important causes of this elevated mortality based on the weight of evidence.

We examined the following potential causes of the elevated estimates of natural mortality: unreported catch, emigration, disease, contaminants, poor fish condition, life-history change, parasites, and predation.

#### 1. UNREPORTED CATCH

This hypothesis postulates that much of the elevated mortality attributed to natural causes actually reflects unreported catch. Figure 1.1 compares the reported catch of 5+ cod to the removals attributed to *M*. Reported catch greatly exceeded the estimated removals attributed to *M* in the early to mid 1970s, the two sources of removal were roughly equal in the late 1970s, and the estimated removals due to *M* has exceeded the reported catch since then<sup>1</sup>. As the fishery intensified in the late 1980s and early 1990s, removals attributed to *M* increased to about 1.5-2.5 times the reported catch (Fig. 1.2). With the sharp reduction in fishing effort for cod in 1993, the ratio between losses to *M* and catch increased sharply, with losses to *M* varying between 30 and 155 times the reported catch during the moratoria on directed cod fishing in 1994-1997, 2003 and 2009-2010, and averaging over ten times the catch in the other years since 1993 when there were small directed fisheries for cod.

It is likely that some of the mortality attributed to M in the late 1980s and early 1990s was actually due to unreported catch. It is thought that the level of misreporting increased as the fishery intensified during this period. Using a modelling approach that incorporated censoring of the catch data, Bousquet et al. (2010) estimated that unreported catch was substantial for this stock in the 1988-1992 period. Thus, the true M during this period was likely lower than the estimated value. For example, if 35% of the catch in 1991 was unreported, 5+ F would be

<sup>&</sup>lt;sup>1</sup> The spike in estimated removals due to M in 1990 is likely partly an artifact of estimating M in blocks of years.

estimated to be 0.45 (compared to the current estimate of 0.29) and 5+ M would be estimated to be 0.59, 77% of the current estimate of 0.77.<sup>2</sup>

Fishing effort for groundfish in the southern Gulf dropped dramatically in the early 1990s (Fig. 1.3). This is reflected in sharply reduced fishing mortality, both for cod (Fig. 1.3) and for other commercially-important species of groundfish (Fig. 1.4, e.g., American plaice, white hake and witch flounder). In addition, catch surveillance increased substantially with the introduction of programs such as dock-side monitoring, and management measures were taken to reduce cod bycatch (reported or not) in other fisheries. For example, the spring opening of the witch flounder fishery is now delayed to allow migration of cod through the fishing grounds prior to the opening. Given the very low fishing effort and added management measures, unreported catch of cod in groundfish fisheries must now be very low.

Catch of cod in other fisheries in the southern Gulf is also very low. Fishery observers report that the catch of cod in the snow crab fishery is negligible. Cod are occasionally caught in the lobster fishery early in the spring, but these are for the most part Greenland cod, not Atlantic cod. Furthermore, given the gear, any cod caught in this fishery would be small cod less than 5 years old. The scallop fishery in the southern Gulf operates in near-shore areas in the Northumberland Strait, and does not encounter any quantity of adult cod. The shrimp fishery in the Gulf does not operate on southern Gulf cod grounds and, at any rate, uses the Nordmore grate to exclude groundfish.

Thus, unreported catch of cod must be very low since the mid 1990s. Even if the true catch was twice the reported catch, which is very unlikely, the effect on estimates of M would be negligible. For example, if the catch in 2008 is doubled, the estimate for 5+ M drops by only 5%, from 0.63 to 0.60. In recent years, only a negligible portion of estimated M can be attributed to unreported catch.

#### 1.1 CONCLUSION

Unreported catch may have accounted for a significant portion of the mortality attributed to *M* in the late 1980s and early 1990s, but only a negligible portion of that mortality since then. This hypothesis can be rejected for the recent period (mid 1990s to present).

#### 2. EMIGRATION

This hypothesis supposes that, instead of dying, the missing fish have emigrated to another area. The stocks neighbouring the southern Gulf stock are the northern Gulf stock (3Pn4RS), the 4Vn stock in the Sydney Bight area, and the eastern Scotian Shelf stock (4VsW). The 4Vn stock has been estimated to be about 2% of the abundance of the southern Gulf stock (Swain et al. 2001), so an influx of non-negligible quantities of southern Gulf cod into this stock would have been noticed in the July survey of this area. The estimated number of 5+ fish lost to *M* each year in the southern Gulf stock also exceeds the estimated abundances at these ages in the northern Gulf and 4VsW stocks (Fig. 2.1). Again, the influx of substantial quantities of southern Gulf cod into these stocks would have been noticed in these stocks (e.g., Swain et al. 2003). Emigration to the northern Gulf is also unlikely because a long history of tagging cod indicates that movement of cod across the Laurentian Channel is very rare

<sup>&</sup>lt;sup>2</sup> This calculation assumes that underreporting occurred at the same rate for all ages (5-12+ years).

(McCracken 1959; Martin and Jean 1964; Gascon et al. 1990). Similarly, a stock mixing study conducted in the mid 1990s indicated that southern Gulf cod were virtually absent from cod aggregations on the north side of the Channel: based on vertebral number, the estimated contribution of southern Gulf cod to the aggregations north of the channel was <0.1% (Swain et al. 2001). Finally, the 4VsW stock has also suffered from elevated natural mortality throughout the 1990s and 2000s, with the estimated level even greater than that of southern Gulf cod (e.g., Fanning et al. 2003). This high estimate for M would not be expected if abundance at older ages in the 4VsW stock was being supplemented by substantial numbers of immigrants from the southern Gulf stock. This hypothesis is not credible as an explanation for a non-negligible portion of M.

It could also be argued that *M* is estimated to be high because older fish are migrating to the overwintering grounds in the 4Vn area before the annual September survey which does not normally cover these grounds. This variant of the hypothesis can also be ruled out. The September survey was extended to cover the 4Vn area in 1994, 1995 and 2006. Only a negligible portion of the southern Gulf stock (<3%) was estimated to be in the 4Vn area in these years (Swain et al. 2001; Swain et al. 2007). Likewise, estimates of mortality based on data from the August sentinel survey are also very high, similar in magnitude to those from the September survey data (e.g., Swain et al. 2009). The idea that older fish are migrating to the overwintering area before August is not credible (and was ruled out in 1994, 1995 and 2006).

#### 2.1 CONCLUSION

This hypothesis can be rejected.

## 3. DISEASE

Between 2000 and 2008, the Fish Health (FHU) and Microbiology units at the Gulf Fisheries Centre, Moncton, surveyed "wild" marine fish for bacterial and viral pathogens which are frequently encountered in the grow-out industry. Infections were detected using PCR (polymerase chain reaction) based procedures and by cultivation of the pathogen from tissue pools. Kidney was used for general PCR viral screening, and eye and brain specifically for NNV (nodavirus). The majority of fish screened in the study were sampled from DFO research vessels. During dedicated disease and parasite cruises conducted between Cape North and Digby NS, tissues were dissected from fish and frozen at sea for subsequent processing at the FHU. Fish sampled from Passamaquoddy Bay, however, were transferred live to the Huntsman Marine Lab where the tissues were collected and subsequently forwarded on ice to the FHU. Fish from the southern Gulf of St. Lawrence were sampled from research vessels during the annual groundfish survey or from commercial vessels involved in sentinel surveys, and reached the FHU, in the round, on ice, within 24h of catch.

Of a total of greater than 3,460 fish screened, 68% were from Scotia-Fundy, and 22%, from the southern Gulf of St. Lawrence (Table 3.1). Cod comprised most (94%) of the specimens from Newfoundland, and were the most frequently screened species overall (29%) followed by American plaice (15%) and winter flounder (12%). Positive tests for viral and bacterial pathogens were relatively rare (Table 3.2). Among 254 cod from the southern Gulf, NNV was detected by PCR in 7 of 10 specimens taken from St. George's Bay in 2000. Tissue pools from the St Georges Bay cod were negative, however, and positive PCR results, from these cod and numerous other samples screened during the early years of the survey, were considered to be unreliable. No pathogens were detected in the 120 southern Gulf cod screened in 2008. In

Scotia-Fundy, bacterial pathogens were detected by cultivation from tissue pools from three cod and two haddock from Passamaquoddy Bay, while viral pathogens were detected, by PCR and tissue pool approaches, in single specimens of winter flounder from Passamaquoddy Bay (NNV) and Digby NS (IPNV). Notably, the grow-out industry is active in both of these areas. All 45 of the Newfoundland cod infected with NNV were from grow-out operations.

In summary, there are no confirmed detections of bacterial or viral pathogens in cod screened from the southern Gulf, including the 120 fish screened in 2008. Numbers of wild fish screened were sufficiently numerous that positive PCRs and/or tissue pools might be expected for pathogens if they contributed significantly to the elevated M (45% annually) of southern Gulf cod. Furthermore, we are aware of no reports of sick or diseased cod from fish harvesters or processors, or from samplers on the annual September survey who have conducted detailed biological examinations of over 31,000 individual cod since 1995. However, the probability of capture of infected fish might be low if they are relatively rare in the population and die quickly from their infection.

#### 3.1 CONCLUSION

Data are limited, but there is no evidence to support the hypothesis that disease is a major contributor to the elevated natural mortality of southern Gulf cod.

## 4. CONTAMINANTS

Contaminants in 4T cod were periodically monitored by DFO from the mid-1970s to the late 1990s. The data after 1985 are not available, but the earlier data do not indicate any increasing trend in contaminants (Misra et al. 1993). In addition, a fish health survey was conducted on the Scotian Shelf between May 1998 and November 2000. This survey of diseases and parasites of marine life was developed as a tool for monitoring environmental changes, including pollution (Bucke et al. 1996). Some disease signs found during the survey have been considered possible direct indicators of pollution, but these were encountered at a very low rate (see Appendix I for further details).

Concentrations of 'traditional' contaminants (heavy metals, PAHs, PCBs and organochlorine pesticides such as DDT) have declined or remained constant in the environment over the past 20 years or so, though concentrations of some 'new' contaminants (e.g. antifoulants, flame retardants, surfactants) may be increasing (Couillard et al. 2003). Levels of contaminants in the Gulf outside of the St. Lawrence estuary are very low, though it is possible that effects may occur even at low concentrations (Couillard et al. 2003). In an evaluation of the marine environment of the Estuary and Gulf of St. Lawrence, White and Johns (1997) concluded that the Gulf was less contaminated than other semi-enclosed seas such as the Baltic and North Seas because of the relatively low population density along its shores and because chemical and oceanographic processes in the Estuary removed contaminants from the water before it reached the Gulf. They further concluded that there had been no significant deterioration in the marine resources of the Gulf due to chemical contaminants.

The Baltic is one of the most polluted seas in the world (Fitzmaurice 1993). Reproductive disorders have occurred in top consumers in the Baltic such as seals, due to biomagnification of toxic substances such as DDT and PCBs (Breitholtz et al. 2001). Concentrations of these contaminants are lower in seals from the St. Lawrence estuary (Bernt et al. 1999). Concentrations of PCBs and organochlorine pesticides are also much higher in cod from the

Baltic Sea than in those from the Gulf of St. Lawrence (Schnell et al. 2003; Lebeuf et al. 1999). Despite their higher concentrations of contaminants, we are aware of no reports of elevated *M* in Baltic Sea cod. Assessments of the Baltic Sea cod stocks use an *M* of 0.2 for ages 2 years and older (<u>http://www.ices.dk/reports/ACOM/2010/WGBFAS/Annex%2004%20-%20%20Stock%20Annex%20-%20Cod%20in%20Subdivisions%2022-24.pdf</u>).

Contaminant concentrations are also considered to be higher in the North Sea than in the Gulf of St. Lawrence (White and Johns 1997). North Sea cod stock assessments do use an increasing trend in M for older ages (3-6 years), but the rationale for this increase in M is estimated increases in mortality due to seal predation, not contaminant-induced mortality (http://www.ices.dk/reports/ACOM/2010/WGNSSK/Sec%2014%20Cod.pdf).

#### 4.1 CONCLUSION

The evidence does not support the hypothesis that contaminant-induced mortality is a significant component of the elevated 5+M of southern Gulf cod.

## 5. POOR FISH CONDITION

It has been proposed that poor fish condition resulting from harsh (cold) environmental conditions contributed to increased *M* in the northern Gulf cod stock in the early 1990s (Lambert and Dutil 1997; Dutil and Lambert 2000). This hypothesis was examined for cod and other marine fish in the southern Gulf by Swain et al. (2011b). Their main conclusions are summarized here.

- Bottom water temperature in the southern Gulf was below normal in the early to mid 1990s but has since warmed and has been above average throughout the 2000s.
- The ambient temperature of southern Gulf cod (i.e., the bottom temperature in areas occupied by cod) in September (i.e., during the feeding season) was lowest in the early to mid 1980s and has been near average levels throughout the 1990s and 2000s.
- Condition of cod in September was high in the early to mid 1970s, declined to the lowest levels observed in the 40-yr record in the late 1970s to mid 1980s, and then increased to levels near the long-term average throughout the 1990s and 2000s.
- Cod in the southern Gulf exhibit a marked seasonal cycle in condition, with lowest condition in the spring, following the overwintering period when little feeding occurs. Seasonal changes in the condition of southern Gulf cod have been monitored since 1991. Based on this monitoring, southern Gulf cod are in better condition in spring than was reported for the northern Gulf stock in the early to mid 1990s.
- Cod are suggested to be at an increased risk of mortality when their condition factor K is less than 0.7. In spring in the early 1990s, the proportion of cod with K < 0.7 was much lower in the southern Gulf stock than observed in the northern Gulf stock. This proportion has since dropped to even lower levels. Overwinter mortality of fish in poor condition might be expected to result in truncation in the distribution of K at low values in spring. There is no indication of this in southern Gulf cod.
- Condition of southern Gulf cod in spring increased substantially in the early 2000s and has been at a relatively high level since then.
- There is no association between patterns in condition and trends in abundance or mortality among species within the marine fish community of the southern Gulf. Some species with elevated natural mortality show little seasonal variation in condition (e.g., winter skate);

others with strong seasonal cycles in condition do not appear to have elevated natural mortality (e.g., Greenland halibut, herring). Similar interannual patterns in condition are shared between species that have declined in abundance and have elevated mortality and those with stable abundance. For species with estimated trends in *M*, periods of low condition are generally not coincident with periods of increasing or high *M*.

#### 5.1 CONCLUSIONS

The hypothesis that poor fish condition (i.e., depleted energy reserves) is an important cause of the high M of 5+ southern Gulf cod can be rejected, at least for the 2000s. Although there is no direct evidence, it is possible that poor fish condition was a more important cause of cod M in the early to mid 1980s, when condition was relatively low in September, or in the early 1990s, when condition in spring was lower than the levels observed in the 2000s. Elevated M of other large demersal fish in the southern Gulf does not appear to be associated with poor fish condition (Benoît et al. 2011c).

## 6. LIFE HISTORY CHANGE

#### 6.1 EARLY MATURITY

A decline in age and size at maturation is the expected evolutionary response to the increase in mortality that is imposed by fishing (Law and Grey 1989; Law 2000). (An exception occurs when fisheries are confined to the spawning grounds, targetting spawners and thus generating an advantage to delayed maturation). Survival costs to reproduction are expected to increase as age and size at maturity decline (Roff 2002; Hutchings 1994). This led Hutchings (2005) to suggest that the recent increases in natural mortality in Northwest Atlantic cod stocks may be partly due to fisheries-induced declines in age and size at maturation. Swain (2011a) examined this hypothesis in detail for the southern Gulf of St. Lawrence cod stock. His findings and conclusions are summarized here.

Age and length at 50% maturity of southern Gulf cod declined dramatically in cohorts produced in the 1950s and 1960s but have changed little since then (Fig. 6.1). These changes reflect changes in maturation reaction norms (Fig. 6.2), and likely represent an evolutionary response to intensified fishing.

Contrary to the predictions of this hypothesis, M of adult cod remained low following the dramatic decline in length at maturity in the 1960s (Fig. 6.3). Furthermore, subsequent increases in adult M, particularly the large increase between the late 1980s and the early 1990s, occurred over a period when size at maturity changed little compared to the changes observed in the 1960s.

Costs to reproduction may be more evident under stressful physiological or ecological conditions (Reznick 1985; Roff 2002). Condition of southern Gulf cod was at a low level in the early to mid 1980s (Swain et al. 2011b). Perhaps the increase in M from about 0.1 to a level near 0.25-0.3 in the early to mid 1980s resulted from the interacting effects of early maturation and harsh conditions (e.g., low per capita food resources). The magnitude of such an effect would be comparable to that reported by Beverton et al. (1994), who concluded that M of Northeast Arctic cod appeared to increase from about 0.15 to 0.25 as age at maturation declined from 8 years or older to 6 years. If this is the case, a decline in M due to this cause

would be expected when physiological and ecological conditions improved. Condition of southern Gulf cod has been at a high level throughout the 2000s (Swain et al. 2011b). Thus, early maturation does not appear to be an important factor in the current high level of M experienced by 5+ southern Gulf cod.

Finally, high M is the main factor contributing to the low productivity and apparent inviability of this population (Swain and Chouinard 2008). For the most part, this high M must be due to some factor external to the population. Early maturation is expected to evolve if adult mortality is high due to some external factor like fishing or predation (Reznick and Ghalambor 2005). It would not evolve if early maturation was itself the main cause of this high mortality. For the most part, the current high natural mortality of adult southern Gulf cod appears to be a cause, rather than a consequence, of the continued early maturation in this population.

#### 6.2 EARLY SENESCENCE

Another hypothetical effect of high mortality is the evolution of earlier or more rapid senescence, either as a byproduct of intense selection for increased investment in reproduction early in life or because of reduced selection against deleterious mutations acting late in life (Medawar 1952; Williams 1957). Thus, it might be argued that high mortality due to fishing will favour the evolution of early senescence, resulting in increased natural mortality in old individuals. However, more derived theories for the evolution of earlier senescence, later senescence, or no change in the pattern of senescence, depending on additional factors (e.g., Abrams 1993). Finally, empirical support for the original prediction is limited, and recent research has produced results inconsistent with these predictions (e.g., Reznick et al. 2004).

There is an indication that M may be particularly high (>1.0) in very old southern Gulf cod (ages 11-15 yr; Swain et al. 2009). Possibly this reflects the evolution of early senescence in response to high mortality at younger mature ages (5-10 yr), initially a response to high fishing mortality but now maintained by high natural mortality. However, based on the gonadosomatic index (GSI, gonad weight as a percent of carcass weight), there is no indication of a decrease in reproductive investment in old individuals, as would be expected in senescent individuals (Fig. 6.4). Furthermore, it is unclear that there has been sufficient time for the evolution of early senescence in the relatively short period of intensive exploitation of this stock. Evolution can be rapid when it is driven by strong selection acting on pre-existing additive genetic variation (e.g., Reznick et al. 1997). However, it would be less rapid when driven by the accumulation of a particular type of deleterious mutation (though this caveat may not apply to the pleiotropic mechanism for the evolution of senescence). Finally, it is clear that the evolution of early senescence cannot provide an explanation for the current high M of younger adult cod (i.e., ages 5-10 yr). First, early senescence would be expected to evolve in older individuals who have experienced a number of reproductive events, not in young maturing or recently mature individuals (only about 70% of five-year old southern Gulf cod are mature). Second, like early maturation, early senescence would be expected to evolve if mortality is high due to some external factor and would not evolve if it was itself the main cause of high mortality.

#### 6.3 CONCLUSIONS

Early maturation is not an important factor in the current high level of M experienced by 5+ southern Gulf cod. Early maturation in combination with harsh ecological conditions (resulting in poor fish condition) may have contributed to moderate increases in M (by 0.1-0.2) in earlier periods (e.g., in the early to mid 1980s). It is unlikely that early senescence contributes to the high M of very old cod (e.g., ages 11-15 years), and it cannot provide an explanation for the current high level of M experienced by younger adult cod (e.g., ages 5-10 yr).

#### 7. PARASITES

This hypothesis was examined for southern Gulf cod by McClelland et al. (2011). Only their main conclusions are summarized here.

- Abundance of larval anisakine parasites in southern Gulf cod increased to unprecedented levels in 2008 and 2009, possibly in response to a warming trend in sea temperatures.
- A weak positive relationship occurred between cod condition and intensity of infection by these parasites. This relationship likely results from variation in feeding intensity or foraging success among cod. Cod which consume more food are in better condition but acquire more parasites. There was no tendency for this relationship to become less positive over the winter period when little feeding occurs. These results indicate that any direct negative effect of parasite infection on cod condition is weak relative to other factors affecting condition.
- Because sub-lethal effects should become apparent before lethal effects, these results also suggest that parasite-induced mortality related to direct damage to organs and tissues or depletion of energy reserves is small in this population. This is consistent with the expectation that a parasite should not kill its intermediate host except by facilitating its consumption by a subsequent host.
- Analyses of changes in frequency distribution of parasite abundance with cod size or age do not appear to indicate mortality of heavily infected southern Gulf cod, but losses resulting from parasitism may be offset by increases in incidence of infection as the cod grow and exploit more heavily infected prey.
- Analyses of worm count frequency distributions in other areas or species provide evidence of parasite-induced mortality.
- Parasite infection may contribute to the elevated natural mortality of southern Gulf cod by increasing the susceptibility of heavily infected fish to predators. This could result from effects of ketones secreted by parasites on cod behaviour.

#### 7.1 CONCLUSIONS

It is unlikely that parasite-induced mortality related to direct damage to organs and tissues or depletion of energy reserves is a major component of the elevated M of 5+ southern Gulf cod. However, parasite infection may contribute to M by increasing the susceptibility of heavily infected fish to predators.

#### 8. PREDATION

Mortality due to predation is often expected to increase as prey abundance declines to a low level. If predators have a type II functional response, this can lead to a predation-driven Allee effect, with mortality experienced by prey steadily increasing as their abundance declines (e.g., Gascoigne and Lipcius 2004). If predators have a type III functional response, then prey mortality will decline at some very low level of abundance (e.g., due to prey switching by predators), and a predator pit will occur (Fig. 8.1). The "depth" of the predator pit (i.e., the level of mortality experienced by prey) will depend on predator abundance. Estimated natural mortality of 5+ southern Gulf cod increased sharply in the late 1980s and early 1990s, coincident with the sharp drop in their abundance (Fig. 8.2). This is consistent with the hypothesis that the current high M of these cod reflects a predation-driven Allee effect or a fall into a predator pit. If this hypothesis is correct, the depth of the pit (i.e., the high level of M) suggests that predator abundance is high.

All predators of large cod will contribute to their natural mortality. We will focus here on grey seals, which are abundant year-round residents of the areas occupied by southern Gulf cod, and which are known to eat large cod (e.g., Stenson et al. 2011; Benoît et al. 2011b). Harp seals are even more abundant in the area in winter, but Hammill and Stenson (2000) estimated that their consumption of 4T fish would be slight. Because of their smaller size, harp seals are generally considered to eat smaller prey than do grey seals. However, harp seal predation on large cod by belly-biting has been documented in waters off Newfoundland. If this is an important foraging strategy of harp seals (see below), predation by harp seals may also contribute to cod M. However, their contribution would likely be minor because they are distributed mostly in the northern Gulf, except during pupping and breeding when they feed little. After breeding the majority of the population moves to the northern Gulf to moult, then leaves the Gulf. Hooded seals are also present in the area in winter, but their numbers are small and their seasonal residency is short. Harbour seals also occur in the ecosystem. They are much less abundant than grey seals and their feeding habits in the ecosystem are poorly known. Predation by harbour seals may be contributing to the elevated adult M, but this contribution is expected to be small given their low abundance. Their smaller size and more coastal nature likely also restricts them to feeding on smaller fish in inshore areas.

Other potential predators include large groundfish, sharks and cetaceans. Given their size, individuals with elevated M would be vulnerable only to the largest (>100 cm) groundfish predators in the ecosystem (Scharf et al. 2000). Fish predators of this size have been all but absent for over 15 years, and would never have been very abundant. Adult cod would also be invulnerable to predation by dogfish sharks (Scharf et al. 2000). Larger sharks likely contribute to predation on large cod, but their abundance has declined to a low level (e.g., Baum et al. 2003). The diet of harbour porpoise is dominated by small pelagic fish (Fontaine et al. 1994), and it is unlikely that they would consume any quantity of large (>40 cm) cod. Minke whales also typically eat smaller fish, such as herring and capelin, as well as decapods (e.g., Smout and Lindstrøm 2007). Consumption by other toothed whales is unquantified, though there is little evidence that abundance has increased in tandem with increases in fish M (Lawson and Gosselin 2009).

#### 8.1 GREY SEAL PREDATION

It is certain that grey seals consume large cod (>40 cm in length, i.e. the cod with high M). However, there is great uncertainty in the level of this consumption due to a number of data gaps related to seal diets and the extent of spatial overlap between seals and cod. Information on the diet of grey seals comes either from the hard parts (e.g. otoliths) recovered from digestive tracts or scats, or from Quantitative Fatty Acid Signature Analysis (QFASA) (Iverson et al. 2004) of their blubber. In both cases, size composition of the prey is inferred largely from the recovered hard parts.

The QFASA method has not been used to estimate the diet of grey seals in the Gulf. It has the advantage that it can integrate foraging activity over a longer period than the other methods. However, it must adjust for modification of ingested lipids during seal metabolism and account for variation in the fatty acid signature of prey related to ontogeny, physiological condition and seasonal cycles. The most extensive experimental validation of the QFASA technique that we are aware of is the study by Nordstrom et al. (2008). A review of this study by the North Pacific Universities Marine Mammal Research Consortium concluded "the QFASA model could directly distinguish which seals were on single-species diet…but further research is needed to effectively quantify mixed diets, especially those containing an unknown array of prey species." (http://www.marinemammal.org/2008/nordstrom.php).

Diet information for the Gulf comes from digestive-tract samples. These are collected from seals near shore, mostly in spring and summer (Benoît et al. 2011b). These samples represent recent feeding activity, and the foraging zones covered by these samples are restricted to nearshore areas (Fig. 8.3, Benoît et al. 2011b). Based on satellite tagging data, grey seals occur over a much broader area than that represented by diet samples, and there are areas of apparent grey seal aggregation that are poorly or not represented in the diet data (Benoît et al. 2011b). The cod distributed in the nearshore areas covered by the diet samples are mostly small cod (<35 cm in length). Larger cod tend to be distributed further offshore in areas poorly covered by these samples. Thus, consumption of large cod is underestimated by these samples. Gender biases in the stomach samples also underestimate the consumption of large cod. Large cod are more frequently consumed by males than by females (Stenson et al. 2011), but males are underrepresented in the diet samples.

If predation by grey seals is an important component of the high M of 5+ cod, much of this predation likely occurs at times and places where these cod are aggregated and where predation success would remain high despite low cod abundance. Cod are highly aggregated on the spawning grounds, during their spring and fall migrations and on the overwintering grounds. Until recently, no diet samples were available from these places and times. However, data on satellite tracked seals indicate that some seals, in particular males, do forage in the vicinity of these cod aggregations, where cod would represent the bulk of the fish biomass available to them (Fig. 8.4, Harvey et al. 2011b). Recently, diet samples were obtained from an area of cod aggregation (Stenson et al. 2011). The composition of this sample was very different from that of the nearshore samples. Based on stomach contents of 50 seals, about 50% of the prev energy consisted of cod. Based on the hard parts in intestines (91 seals), the percent cod in the diet was 24% for males and 10% for females, after down-weighting cod consumption to correct for the slower digestion of the relatively robust otoliths of cod. The majority of the cod consumed by these seals were large cod (>40 cm in length). This recent work indicates that the consumption of large cod by grey seals is greater, possibly much greater, than previously estimated. Given some assumptions for filling data gaps, estimates of the consumption of 5+ southern Gulf cod can account for a high percentage of M in recent years (Benoît et al. 2011b, Swain et al. 2011a). The actual percentage of M that can be accounted for by predation by grey seals depends on the interpretation of the seal diet data, which has changed a number of times over the past year. Based on the interpretation agreed to at the seal impacts workshop, predation by grey seals could account for up to 50% of *M*, depending on the assumptions used to fill data gaps.

Spatial aliasing of grey seal diets also has important implications for the perceived sizeselectivity of seals feeding on cod. The traditional view has been that grey seals prey preferentially on small cod (<35 cm in length). However, the size composition of cod in the spring/summer diet samples suggests that grey seals selectively prey on the larger, less available cod (Benoît et al. 2011b). Likewise, the sample collected in winter from an area of cod aggregation, where small and large cod were roughly equally available, clearly suggests positive selection of large cod by seals.

Partial consumption of prey is another factor which may bias estimates of cod consumption by grey seals. Predation on large cod will be underestimated if heads of large cod are often not consumed (since their otoliths would not appear in stomachs or scats). Selective rejection of fish heads has been suggested to occur in a number of seal species (e.g., Roffe and Mate 1984; Moore 2003; Hauser et al. 2008; Phillips and Harvey 2009). "Belly-biting" of large cod by seals is also frequently reported by fish harvesters and has been documented for harp seals in Newfoundland (Lilly and Murphy 2004). The frequency of partial consumption of cod by grey seals is unknown, but optimal foraging theory suggests that it may not be a rare behaviour. Optimal foraging theory predicts that when prey density is high predators should consume only the most energy-dense portions of individual prey (Sih 1980). This prediction has been supported by a number of predator-prey studies (e.g., Gende et al. 2001). The most energydense portion of a cod is its liver, where most of its lipids (energy reserves) are stored. As noted above, cod are densely aggregated at certain times of year, and the density of cod in these aggregations remains very high even at the current low level of abundance. Thus, belly-biting would be expected to be an optimal foraging strategy for grey seals feeding on these dense cod aggregations. The concentration of sealworm parasites in the belly flaps of large cod is also consistent with the hypothesis that belly-biting of large cod may be a common foraging strategy of grey seals (McClelland et al. 2011). If so, the proportion of 5+ M accounted for by grey seal predation will be underestimated unless effects of belly-biting can be taken into account.

Benoît et al. (*In press*) estimated the plausibility that different seal diet compositions could explain observed *M* levels based on Monte Carlo simulations using data on the spatial overlap between grey seals and cod and a seal food-consumption model. They found that there was a 50% probability that seal predation could explain 70% of adult *M* with no belly-biting. With 30% belly-biting, there was a 50% probability that predation by grey seals could explain all of M and a 95% probability that it could explain 60% of M.

Information on the spatial overlap between seals and cod is another data gap influencing estimates of consumption of cod by seals (Benoît et al. 2011a). Movement patterns of seals are inferred from a very small number of tagged seals, particularly given the need to account for gender and stage-specific differences in grey seal movements. Because of this low sample size, areas that are visited by only a small proportion of the herd have a high probability of being underrepresented in the inferred distributional areas, particularly when a fairly fine spatial resolution is used. To the extent that these are areas where cod occur, seal-cod overlap will be underestimated. For periods when cod are aggregated (winter, spawning, migration) in particular, potential consumption of cod by seals may therefore also be underestimated. Unfortunately, the sample size of tagged seals is especially low during some of these periods. For example, in April and May when southern Gulf cod are highly aggregated as they move from the overwintering to the spawning grounds, the number of tagged Gulf seals is 0 or 1 in 3 of 6 cases (month/gender-stage cells), and less than 5 in 5 of 6 cases (Benoît et al. 2011a). Bias in seal tagging (e.g., with respect to haul-out site) may also produce biases in consumption estimates.

In addition to the direct evidence that predation by grey seals contributes to the high M of 5+ cod, there are a number of indirect lines of evidence that grey seal predation contributes to the increased M of cod and other large demersal fish (also see Benoît et al. 2011c for further details). As noted above, the sharp increase in 5+ M southern Gulf cod was coincident with a sharp decline in cod abundance and with increasing abundance of grey seals to a high level, consistent with the predator-pit hypothesis. It might be argued that a close positive correlation should be observed between cod M and grey seal abundance if grey seal predation is an important cause of high M. M was at a high level throughout the 1990s and 2000s, and did not increase with increasing seal abundance during this period (Swain 2011b). A number of factors may contribute to this apparent inconsistency. First, grey seal predation likely accounted for a lower proportion of *M* in the 1990s than in the 2000s. For example, it is likely that unreported catch accounted for a substantial portion of estimated M in the early to mid 1990s, but was a negligible component of M in more recent years (see above). Secondly, a simple linear relationship between prey mortality and predator abundance may not occur for a number of reasons, such as prey switching when abundance of the focal prey declines to very low levels or abundance of alternate prev increases.

High levels of cod M and grey seal abundance are also correlated spatially. The region where cod M rose to the highest levels is the eastern Scotian Shelf (e.g., Fanning et al. 2003), the region where grey seal densities are highest. This region is followed by the southern Gulf, both in terms of high cod M and high grey seal density. More recently, high M of large adult cod has been reported for the western Scotian Shelf (4X; Clark and Emberley 2010), a region where grey seal densities are increasing. In contrast, in areas north of the Laurentian Channels, where grey seals are absent or considerably less abundant, cod M is thought or estimated to be lower.

Increased grey seal abundance is also correlated with increased mortality of large demersal fish throughout the marine fish community of the southern Gulf (Benoît and Swain 2011). Other explanations for the increased mortality of these species are not evident (e.g., Benoît et al. 2011c). Finally, in an analysis of changes in the species composition of the southern Gulf marine fish community, Benoît and Swain (2008) reported a significant association between species abundance trends and a measure of the susceptibility of those species to grey seal predation. As grey seal abundance increased over the 1971-2005 study period, the community shifted from one dominated by species common in grey seal diets to one dominated by species rare in grey seal diets.

Finally, work on fish distribution in relation to the foraging distribution of grey seals in the southern Gulf in summer indicates that large cod are occupying areas where the risk of predation by grey seals is reduced (Harvey et al. 2011a). Over the long term, there has been a shift in the distribution of large cod away from areas where the risk of predation is now highest (Fig. 8.5), again suggesting that grey seals are an important predator of large cod. Other demersal fish in the southern Gulf have also shown shifts in distribution which may reflect increased risk of predation by grey seals (and for which no other explanations are evident). A striking example is thorny skate (Fig. 8.6, Swain and Benoît 2006), which have also suffered from an elevated level of adult mortality since the 1990s (Benoît and Swain 2011).

#### 8.2 CONCLUSIONS

The sharp increase in M of 5+ cod as their abundance collapsed in the late 1980s and early 1990s is consistent with the predator-pit hypothesis for the cause of this high M. Given their high abundance and what is known of the diets of grey seals and other potential predators, grey

seals are most likely to be the predominant predator producing this pit. The available diet information indicates that grey seals consume large cod (>40 cm in length), that they appear to show positive selection for large cod over small cod, and that when foraging in the vicinity of cod aggregations large cod can be a major component of the diet. Due to data gaps, the quantity of large cod consumed by grey seals is uncertain. However, some assumptions for filling data gaps lead to consumption estimates that account for a high proportion of the *M* of 5+ cod. There is also indirect (correlative) evidence that grey seal predation plays a role in the elevated *M* of adult cod and other large demersal fish. This is the hypothesis most strongly supported by the weight of evidence.

#### REFERENCES

- Abrams, P. 1993. Does increased mortality favor the evolution of more rapid senescence? Evolution 47: 877–887.
- Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. Prog. Ocean. 68: 271-288.
- Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., and Doherty, P. A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299: 389-392.
- Benoît, H. P., and Swain, D. P. 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, H. P., and Swain, D. P. 2011. Changes in size-dependent mortality in the southern Gulf of St. Lawrence marine fish community. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/039.
- Benoît, H. P., Swain, D. P., and Hammill, M. O. 2011a. Seasonal patterns in the spatial overlap of southern Gulf cod and grey seals, with a discussion of sources of error and possible bias. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/018.
- Benoît, H. P., Hammill, M. O., and Swain, D. P. 2011b. Estimated consumption of southern Gulf cod by grey seals: bias, uncertainty and two proposed approaches. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/041.
- Benoît, H. P., Swain, D. P., and Hammill, M. O. 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.
- Benoît, H. P., Swain, D. P., Bowen, W. D., Breed, G. A., Hammill, M. O., and Harvey, V. (*In Press*). 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. Progr. Ser.
- Bernt, K. E., Hammill, M. O., Lebeuf, M., and Kovacs, K. M. 1999. Levels and patterns of PCBs and OC pesticides in harbour and grey seals from the St Lawrence Estuary, Canada. Sci. Total Environ. 243-244: 243-262.

- Beverton, R. J. H., Hylen, A., and Ostvedt, O. J. 1994. Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod. ICES J. Mar. Sci. Symp. 198: 482-501.
- Bousquet, N., Cadigan, N., Duchesne, T., and Rivest, L.-P. 2010. Detecting and correcting underreported catches in fish stock assessment: trial of a new method. Can. J. Fish. Aquat. Sci. 67: 1247-1261.
- Breitholtz, M., Hill, C., and Bengtsson, B.-E. 2001. Toxic substances and reproductive disorders in Baltic fish and crustaceans. Ambio 30: 210-216.
- Bucke, D., Vethaak, D., Lang, T., and Mellergaard, S. 1996. Common diseases and parasites of fish in the North Atlantic: Training guide for identification. ICES Techniques in Marine Environmental Sciences No. 19: 27pp.
- Clark, D. S., and Emberley, J. 2010. Assessment of Cod in Division 4X in 2008. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/018.
- Couillard, C., Lebeuf, M., Hellou, J., Payne, J., Yeats, P. 2003. Potential role of contaminants in current cod recovery problem. Unpublished report prepared for the zonal assessment of cod in February 2003.
- DFO. 2010. Impacts of Grey Seals on Fish Populations in Eastern Canada. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2010/071.
- Dutil, J.-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 57: 826-836.
- Fanning, L. P., Mohn, R. K., and MacEachern, W. J. 2003. Assessment of 4VsW cod to 2002. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/027.
- Fitzmaurice, M. 1993. The new Helsinki convention on the protection of the marine environment of the Baltic Sea area. Mar. Pollut. Bull. 26: 64-67.
- Fontaine, P.-M., Hammill, M. O., Barette, C., and Kingsley, M.C. 1994. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 51: 172-178.
- Fréchet, A., Gauthier, J., Schwab, P., Lambert, Y., Le Bris, A., Tournois, C., Way, M., and Collier, F. 2009. The status of cod in the Northern Gulf of St. Lawrence (3Pn, 4RS) in 2008. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/090.
- Gascoigne, J. C., and Lipcius, R. N. 2004. Allee effects driven by predation. J. Appl. Ecol. 41: 801-810.
- Gascon, D., Aparicio, M., and Mercille, B. 1990. Estimations du mélange entre les stocks de morue du Nord du Golfe du Saint Laurent (Divisions 3Pn4RS) et les stocks adjacents (2J3KL, 3Ps, et 4TVn [Janvier-Avril]) à partir de résultats de marquage. CAFSAC Res. Doc. 90/61.
- Gende, S. M., Quinn T. P, and Willson M. F. 2001. Consumption choice by bears feeding on salmon. Oecologia 127: 372-382.

- Hammill, M. O., and Stenson, G. B. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), grey seals (*Halichoerus grypus*), harbour seals (*Phoca vitulina*) and hooded seals (*Cystophora cristata*). J. Northw. Atl. Fish. Sci. 26: 1-23.
- Harvey, V., Hammill, M. O., Swain, D. P. 2011a. Summer overlap between a central-place forager and its prey in the southern Gulf of St. Lawrence. DFO Can. Sci. Advis. Secr. Res. Doc. 2011/131.
- Harvey, V., Hammill, M. O., Swain, D. P., Breed, G. A., Lydersen, C., and Kovacs, K. M. 2011b. Winter foraging by a top predator, the grey seal, in relation to the distribution of prey. DFO Can. Sci. Advis. Secr. Res. Doc. 2011/124.
- Hauser, D. D. W., Allen, C. S., Rich, H. B. J., and Quinn, T.P. 2008. Resident harbor seals (*Phoca vitulina*) in Iliamna Lake, Alaska: summer diet and partial consumption of adult sockeye salmon (*Oncorhynchus nerka*). Aquat. Mamm. 34: 303-309.
- Hutchings, J. A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. Oikos 70: 12-20.
- Hutchings, J. A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod. Can. J. Fish. Aquat. Sci. 62: 824-832.
- Iverson, S. J., Field, C., Bowen, W. D., Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecol. Monogr. 74: 211-235.
- Lambert, Y., and Dutil, J.-D. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Can. J. Fish. Aquat. Sci. 54: 2388-2400.
- Law, R. 2000. Fishing, selection and phenotypic evolution. ICES J. Mar. Sci. 57: 659-668.
- Law, R., and Grey, D. R. 1989. Evolution of yields from populations with age-specific cropping. Evol. Ecol. 3: 343-359.
- Lawson, J. W., and Gosselin, J. F. 2009. Distribution and preliminary abundance estimates for cetaceans seen during Canada's marine megafauna survey a component of the 2007 TNASS. DFO Can. Sci. Advis. Secr. Res. Doc. 2009/031.
- Lebeuf, M., St-Pierre, I., Clermont, Y., and Corbeil, C. 1999. Concentration de biphényles polychlorés (BPC) et de pesticide organochlorés chez trois espèces de poissons de fond de l'estuaire et du golfe du Saint-Laurent et du fjord du Saguenay. Rapp. Stat. Can. Sci. Hali. Aquat. 1059.
- Lilly, G. R., Murphy, E. F. 2004. Biology, fishery and status of the 2GH and 2J3KL (northern) cod stocks: information supporting an assessment of allowable harm under the Species at Risk Act for the COSEWIC-defined Newfoundland and Labrador population of Atlantic cod (*Gadus morhua*). DFO Can. Sci. Advis. Secr. Res. Doc. 2004/102.
- Martin, W. R., and Jean, Y. 1964. Winter cod taggings off Cape Breton and on offshore Nova Scotia banks, 1959-62. J. Fish. Res. Board Can. 21: 215-237.

- McClelland, G., Swain, D. P., and Aubrey, É. 2011. Abundance of larval anisakine parasites in southern Gulf of St. Lawrence cod (*Gadus morhua*), and their possible effects on cod condition and mortality. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/038.
- McCracken, F. D. 1959. Cod tagging off northern New Brunswick in 1955 and 1956. Fish. Res. Board Can. Atl. Prog. Rep. 72: 8-19.

Medawar, P. B. 1952. An Unsolved Problem of Biology. H. K. Lewis and Co., London.

- Misra, R. K., Uthe, J. F., Chou, C. L., Scott, D. P., and Musial, C. J. 1993. Trend analysis using a multivariate procedure for data with unequal residual covariance and regression coefficient matrices: Application to Canadian Atlantic cod contaminant data. Marine Pollution Bulletin 26: 73-77.
- Moore, P. G. 2003. Seals and fisheries in the Clyde sea area (Scotland): traditional knowledge informs science. Fish. Res. 63: 51-61.
- Nordstrom, C. A., Wilson, L. J., Iverson, S. A., and Tollit, D. J. 2008. Evaluating quantitative fatty acid signature analysis (QFASA) using harbour seals *Phoca vitulina richardsi* in captive feeding studies. Mar. Ecol. Prog. Ser. 360: 245-263.
- Phillips, E. M., Harvey, J. T. 2009. A captive feeding study with the Pacific harbor seal (*Phoca vitulina richardii*): implications for scat analysis. Mar. Mamm. Sci. 25: 373-391.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44: 257-267.
- Reznick, D. N., and Ghalambor, C. K. 2005. Can commercial fisheries cause evolution? Answers from guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 62: 791-801.
- Reznick D. N., Bryant, M. J., Roff, D., Ghalambor, C. K., and Ghalambor, D. E. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. Nature 431: 1095–1099.
- Reznick, D. N., Shaw, F. H., Rodd, F. H., and Shaw, R. G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275: 1934-1937.
- Roff, D. A. 2002. Life history evolution. Sinauer, Sutherland, Mass.
- Roffe, T. J., Mate, B. R. 1984. Abundance and feeding habits of pinnipeds in the Rogue River, Oregon. J. Wildl. Manage. 48: 1262-1274.
- Scharf, F. S., Juanes, F., and Rountree, R. A. 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol. Prog. Ser. 208: 229-248.
- Schnell, S., Schiedek, D., Schneider, R., Balk, L., Vuorinen, P. J., Vuontisjärvi, H., and Lang, T. 2003. Some indications of contaminant effects on Baltic cod (*Gadus morhua* L.). ICES CM 2003/M:09.

Sih, A. 1980. Optimal foraging: partial consumption of prey. Am. Nat. 116: 281-290.

Smout, S., and Lindstrøm, U. 2007. Multispecies functional response of the minke whale

*Balaenoptera acutorostrata* based on small-scale foraging studies. Mar. Ecol. Prog. Ser. 341: 277-291.

- Stenson, G. B., Hammill, M. O., and Flight, J. 2011. Winter diet of grey seals in Cabot Strait. DFO Can. Sci. Advis. Secr. Res. Doc. 2011/128.
- Swain, D. P. 2011a. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). Evol. Appl. 4:18-29.
- Swain, D. P. 2011b. Natural mortality and projected biomass of southern Gulf of St. Lawrence cod (*Gadus morhua*). DFO Can. Sci. Advis. Secr. Res. Doc. 2011/040.
- Swain, D. P., and Benoît, H. P. 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, D. P., and Chouinard, G. A. 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, D. P., Benoît, H. P., and Hammill, M. 2011a. Grey seal reduction scenarios to restore the southern Gulf of St. Lawrence cod population. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/035.
- Swain, D. P., Benoît, H. P., Savoie, L., and 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.
- Swain, D. P., Currie, L. G., Chouinard, G. A., Poirier, G. A., Savoie, L., Hurlbut, T., and Daigle, D. .2007. Assessment of the southern Gulf of St. Lawrence cod stock, March 2007. DFO Can. Sci. Advis. Sec. Res. Doc. 2007/033.
- Swain, D. P., Frank, K. T., and Maillet, G. 2001. Delineating stocks of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence and Cabot Strait areas using vertebral number. ICES J. Mar. Sci. 58: 253-269.
- Swain, D. P., Savoie, L., Hurlbut, T., Surette, T., and Daigle, D. 2009. Assessment of the southern Gulf of St. Lawrence cod stock, February 2009. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/037.
- Swain, D. P., Sinclair, A. F., Castonguay, M., Chouinard, G. A., Drinkwater, K. F., Fanning, L. P., and Clark, D. S. 2003. Density- versus temperature-dependent growth of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence and on the Scotian Shelf. Fish. Res. 59: 327-341.
- White, L. et Johns, F. 1997. Évaluation du milieu marin de l'éstuaire et du golfe du Saint-Laurent. Pêches et Océans Canada, Darmouth, Nouvelle-Écosse, Mont-Joli, Québec
- Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. Evolution 11: 398–411.

Table 3.1. Numbers of marine fish screened for bacterial and viral<sup>1</sup> pathogens from Newfoundland, the southern Gulf of St. Lawrence (4T) and the Scotia-Fundy region (4VWX) in 2000-08 by the DFO Fish Health Laboratory, Gulf Fisheries Centre, Moncton, NB.

Species	Number screened				
	Nfld	4T	4VWX	Total	
Herring		60	181	241	
Smelt		60		60	
Sandlance		25		25	
Atlantic cod	310	254	448	1012	
Greenland cod		12		12	
Tomcod	2	5	12	19	
Haddock			243	243	
Pollock	17		92	109	
Red hake			74	74	
Silver hake			202	202	
White hake		9	164	173	
Hake, unspecified			64	64	
Halibut			1	1	
Amer. plaice		271	236	507	
Yellowtail fl.		60	65	125	
Winter flounder		8	399	407	
Turbot			59	59	
Witch flounder			122	122	
Windowpane			7	7	
Total	329	764	2369	3462	

1. Viruses screened include infectious pancreatic necrosis (IPNV), infectious hematopoietic necrosis (IPNV), viral hemorrhagic septicemia (VHSV), infectious salmon anaemia (ISAV) and nervous necrosis virus (nodovirus) (NNV).

Table 3.2. Bacterial and viral pathogens detected in marine fish from Newfoundland, the southern Gulf of St. Lawrence(4T) and the Scotia-Fundy region from 2000 to 2008 by the DFO Fish Health and Microbiology units at the Gulf Fisheries Centre, Moncton, NB; pathogens cultured from tissue pools and/or identified by PCR.

Species	Results		Details		
	Tissue	PCR	-		
	pools				
Atlantic cod	-ve	+ve	PCR positive for nervous necrosis virus (NNV) in 7 of 10 cod collected from St. George's Bay (4T) in September, 2000		
	+ve	-ve	<i>Vibrio</i> sp(p) cultured from three of 20 tissue pools collected from Passamaquoddy Bay (4X) in April, 2004.		
	+ve	-ve	<i>Vibrio</i> sp(p) cultured from one of 27 Passamaquoddy Bay (4X) cod in May, 2004.		
	+ve	-ve	<i>Photobacterium</i> sp cultured from one of 21 pools from Passamaquoddy Bay in September, 2004		
	+ve	+ve	NNV cultured from 6 of 20 cod tissue pools from Newfoundland in November, 2004 and confirmed by PCR in 5 of 6 cases.		
	+ve	+ve	NNV cultured and confirmed in from one of 20 Newfoundland cod screened in December, 2004; cod were from a grow-out operation.		
		+ve	PCR for NNV positive for three of five Newfoundland cod screened in April 2005; grow-out cod.		
	+ve	+ve	Four of six tissue pools from Newfoundland positive for NNV in May, 2005. NNV confirmed by PCR of one sub- cultured pool; grow-out cod		
Haddock	+ve	-ve	<i>Flavobacter</i> -like sp cultured from a single Passamaquoddy Bay haddock pool in May, 2004.		
	+ve	-ve	<i>Pseudomonas</i> -like sp cultured from 9 of 16 pools from Passamaquoddy Bay haddock in August, 2004.		
Winter flounder	+ve	+ve	NNV cultured from one of 40 tissue pools from Passamaquoddy Bay flounder in October, 2000; confirmed by PCR conducted by the Research and Productiviy Council, Fredericton, NB.		
	+ve		Infectious pancreatic necrosis virus (IPNV) cultured from one of 12, five-fish pools collected from Digby, NS (4X) in November, 2000.		



Figure 1.1. Biomass of age-5+ cod removed as reported catch or by natural mortality (M). Estimated biomass lost to M is based on mid-year weights at age.



Figure 1.2. Ratio of 5+ biomass loss to natural mortality (M) versus the loss to reported catch. 7+ F is the estimated fishing mortality of cod 7 years and older.



Figure 1.3. 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 (1000 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. (from Benoît and Swain 2011, Fig 7).



Figure 1.4. Relative fishing mortality (catch/RV abundance) for twelve 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 (from Benoît and Swain 2011, Fig 8).



Figure 2.1. Estimated numbers of southern Gulf (4T) cod 5 years and older (5+) lost to M each year and the total 5+ abundances of the northern Gulf (3Pn4RS) and eastern Scotian Shelf (4VsW) cod stocks. Numbers are in millions. Abundance estimates for 4VsW cod are from fitting a model equivalent to model 8 in Swain (2011b) to data for this stock (D.P. Swain and B. Mohn, unpublished analyses). Estimates for the northern Gulf stock are from Fréchet et al. (2009).



Figure 6.1. Age and length at 50% maturity for female and male cod in the southern Gulf of St. Lawrence (from Swain 2011a). Vertical lines are 95% confidence intervals. Horizontal lines indicate the range of cohorts grouped together for an estimate. Time trends are summarized by a smoothing spline (heavy line)  $\pm 2$  SE (dotted lines). Lengths have been adjusted to September values.



Figure 6.2. Temporal trends in maturation reaction norm midpoints for southern Gulf of St. Lawrence cod at ages 4 and 5 years (from Swain 2011a). Vertical lines are 95% confidence intervals. Horizontal lines indicate the range of cohorts grouped together for an estimate.



Figure 6.3. Trends in length at 50% maturity of female (red solid line) and male (dashed line) southern Gulf cod (from Swain 2011a) and M of 5+ cod. The heavy black horizontal line indicates an approximate value for M, based on independent studies which estimated M in the 1970s and earlier to be 0.07 - 0.15 (see Swain 2011b for details). Circles show estimates of M for later years based on a population model (model 8 in Swain 2011b); vertical lines are  $\pm 2SE$ , horizontal lines denote the block of years used for the estimate.



Figure 6.4. Gonadosomatic index (GSI, gonad weight as a percentage of carcass weight) of southern Gulf of St. Lawrence cod aged 1-11+ years caught in April and May, 2001-2009. N = 2076.



Figure 8.1. Schematic diagram of a predator pit. Redrawn from Bakun (2006).



Figure 8.2. Estimated trends in abundance and M of 5+ southern Gulf cod. Abundance is in millions.



Figure 8.3. Probable foraging areas represented by seal gut content sampling conducted during a) the spring and summer, and b) the late fall and early winter. The concentric circles represent percentiles of net potential distance travelled by seals during the period represented by the diet samples, based on an analysis of movements from satellite tagged seals. The percentiles were calculated assuming that stomach samples represent a maximum of 8 hours of feeding prior to sampling and intestine/scat samples represent feeding during the period from 8-64 hrs before sampling. Probable foraging areas represented by diet sampling on Sable Island are presented for illustration purposes only in panel a (from Benoît et al. 2011b)



Figure 8.4, a) Distribution of cod (>35 cm) in the Cabot Strait in January. Cod along the southern slope of the Laurentian Channel are southern Gulf cod. b) Areas of restricted search of satellite-tagged grey seals in winter (blue- males, green – females). (from Harvey et al. 2011b).



Figure 8.5. Distribution of cod >35 cm in length in September during periods of low abundance. The rectangle in the upper panel denotes an area of heavy use by grey seals (Harvey et al. 2011a).



Figure 8.6. Distribution of thorny skate in the southern Gulf of St. Lawrence in September during four periods (from Swain and Benoît 2006). Shading shows the local density of skates based on survey catch rates (fish/tow). Catch rates have been adjusted to the same average level in each period in order to emphasize changes in distribution rather than changes in abundance. Contour levels are the 10<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup>, 75<sup>th</sup> and 90<sup>th</sup> percentiles of the adjusted catch rates over all four periods, with darker shading indicating higher catch rates.

#### Appendix I. Fish Health Survey

Between May 1998 and November 2000, The Fish Health Unit (FHU) at the Gulf Fisheries Centre, Moncton (NB) conducted a survey of diseases and parasites of marine fish as a tool for monitoring environmental changes, including pollution (Bucke et al. 1996). During the survey more than 3,500 cod and flatfish were examined at sea on dedicated research cruises, and in one instance, a sample of 250 cod, at a fish plant in Sambro (NS). The latter were taken off Sambro by long-liner with the cooperation of the 'Fishermen and Scientists Research Society'. Samples were collected throughout Scotia-Fundy from the mouth of the Smokey Channel to Digby Gap, and included samples from the coastal shelf of Shelburne and the approaches to Halifax Harbour. The survey was ultimately discontinued for a number of reasons:

1. The survey was developed for European waters and the two species of flatfish used do not occur in the Northwest Atlantic. It was necessary to substitute yellowtail flounder, American plaice or winter flounder depending on availability.

2. Given the state of the ground-fishery in Atlantic Canada, it was often difficult to fill the various cod and flatfish length categories with the numbers called for in the sampling protocol.

3. Many of the disease signs and parasites monitored in the ICES survey were uncommon or lacking in eastern Canadian cod and flatfish.

4. Unlike Europe, pollution in the marine environment in eastern Canada is largely confined to effluents of mills and power plants (thermal), and agricultural run-off in estuaries and along the coastal shelf. Use of parasites as indicators of pollution has proven useful e.g. in Newfoundland estuaries (Khan 2010).

Some disease signs found during the survey have been considered possible direct indicators of pollution. Lymphocystis, hypertrophic connective cell forming nodules under the skin and along the fin rays of flatfish is caused by an iridovirus, but the disease seems to be promoted by thermal pollution. Heavy metals, among other possible physiological or environmental factors are thought to cause skeletal deformities such as curvature of the spine or shortening of the upper or lower jaw ("pug-head") in cod and flatfishes. Lipid metabolic disorder (a.k.a. steatitis or yellow fat disease), marked by deposition of fatty yellow or orange clumps among the fin rays of flatfishes has also been attributed to pollution by some investigators who feel that the metabolic scenario is unlikely in a marine environment where food is plentiful and varied. Finally, contaminants are believed to be implicated in the occurrence of nodules on the liver, when the latter are the foci of cellular alteration or carcinoma.

Nodules were found on the liver of 4% of yellowtail flounder (n = 227) from Sable Island Bank during the ICES survey, but microscopy revealed they were nodules of the fungal pathogen *lchthyophonus hoferi*. Lymphocystis was detected in <1% of American plaice surveyed here (n = 1,735) and has been observed with similar frequency in other parasitological surveys. Infected plaice have almost invariably been taken from the Cape Breton Shelf, and have also been turned in for diagnosis by port samplers from Cape Breton. While only detected in a single fish, a winter flounder from south-western Nova Scotia (n = 261), steatitis has often been observed, although unfortunately not recorded, in plaice as well as yellowtail and winter flounder from other parasitological surveys, and in samples submitted to FHU for diagnoses. Similarly, curvature of the spine was recorded in only a single fish, one of 1,735 American plaice surveyed here, but both the spinal and "pug-head" forms of skeletal deformity have been noted frequently, though not documented in cod and plaice during other surveys.

#### References

- Bucke, D., Vethaak, D., Lang, T., and Mellergaard, S. 1996. Common diseases and parasites of fish in the North Atlantic: Training guide for identification. ICES Techniques in Marine Environmental Sciences No. 19: 27pp.
- Khan, R A. 2010. Two species of commercial flatfish, *winter flounder*, *Pleuronectes americanus*, and American plaice, *Hippoglossoides platessoides*, as sentinels of environmental pollution. Bulletin of environmental contamination and toxicology. 85(2): 205-208