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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

Une analyse de risque des effets possibles d'une réduction sélective ou non-sélective de l'abondance du phoque gris sur le statut de conservation de deux espèces à risque de disparaître, la merluche blanche et la raie tachetée du sud du golfe du Saint-Laurent

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ABSTRACT

Winter skate (*Leucoraja ocellata*) and white hake (*Urophycis tenuis*) both have populations that are endemic to the southern Gulf of St. Lawrence (sGSL). The population of winter skate may actually constitute a distinct, yet to be described, species. Elevated adult natural mortality (*M*) in both species is resulting in population declines, to the point that extirpation is possible within a few decades. Based on weight of evidence, predation by grey seals appears to be contributing significantly to the elevated *M*. However, existing grey seal diet estimates cannot be used reliably to directly determine if this is the case. Evidence for a predation effect is therefore largely indirect. Stochastic projections using models for the sGSL winter skate and white hake populations were used to determine the probable population trajectories under a number of scenarios including the status quo, increased predation from projected increases in grey seal abundance and grey seal population reductions. Three scenarios for grey seal removals were evaluated: 1) untargeted removals when seals are aggregated in the breeding colonies, 2) targeted removals of seals foraging in the winter skate or white hake ecosystem and 3) targeted removals of seals feeding in aggregation areas for the fish species. Based on simulations of hypothetical scenarios in which we assumed, among other things, that grey seals contribute considerably to adult fish *M*, we predicted that to have a 50% chance of stabilizing the abundance of winter skate at current low levels requires removing 174,300, 44,300 or 1,700 seals under removal scenarios 1, 2 and 3 respectively. Likewise, to increase age 3+ white hake abundance by 2020 to levels observed in the past decade would require removing 319,000, 79,000 or 13,000 under removal scenarios 1, 2 and 3 respectively. A risk analysis framework is then presented to evaluate the possible consequences of undertaking, or not, a grey seal population reduction, relative to whether or not grey seals actually are the main contributors to elevated fish *M*. Overall, ecological risks concerning white hake, winter skate and grey seals appear to be reduced by undertaking a reasonable reduction of grey seals in the NW Atlantic. Such reductions would pose minimal conservation risks to the grey seal population. For the fish, at best, reduced adult *M* will halt population decline and possibly promote recovery. At worst, the sGSL white hake and winter skate populations would be extirpated more rapidly than they would otherwise be.

RÉSUMÉ

La raie tachetée (*Leucoraja ocellata*) comme la merluche blanche (*Urophycis tenuis*) présentent des populations endémiques dans le sud du golfe du Saint-Laurent. La population de raie tachetée pourrait vraisemblablement constituer une espèce distincte, encore non décrite. Le taux élevé de mortalité naturelle (*M*) chez les adultes de ces deux espèces se traduit par une diminution de la population, à un point tel que la disparition pourrait survenir d'ici quelques décennies. Les résultats d'une évaluation de divers hypothèse pouvant expliquer les taux élevés de *M* permettent de conclure que la prédation exercée par les phoques gris semble contribuer considérablement au taux élevé de mortalité. Cependant, les estimations actuelles sur le régime alimentaire du phoque gris ne peuvent être utilisées pour affirmer que la prédation en est la cause directe. La preuve d'un effet de la prédation est par conséquent largement indirecte. On a réalisé des prévisions à l'aide d'un modèle stochastique pour les populations de raie tachetée et de merluche blanche dans le sud du golfe du Saint-Laurent afin de déterminer les trajectoires probables de la population en vertu d'un certain nombre de scénarios, y compris le statu quo et l'augmentation de la prédation exercée par les phoques gris dérivée de l'augmentation ou de la diminution de l'abondance projetée de cette espèce. On a évalué trois scénarios concernant une réduction potentielle du nombre de phoques gris : 1) enlèvements non ciblés lorsque les phoques sont regroupés dans les colonies; 2) enlèvements ciblés des phoques en quête de nourriture dans l'écosystème fréquenté par la raie tachetée ou la merluche blanche; et 3) enlèvements ciblés des phoques qui s'alimentent dans les aires de répartition de ces espèces. Selon les simulations réalisées à la lumière des nos scénarios hypothétiques voulant, entre autres, que les phoques gris contribuent considérablement à la mortalité chez l'adulte, nous avons prévu que pour obtenir une probabilité de 50 % de stabilisation de l'abondance de la raie tachetée aux bas niveaux actuels, il faudrait prélever 174 300, 44 300 ou 1 700 phoques suivant les scénarios d'enlèvement 1, 2 et 3, respectivement. Dans le même ordre d'idées, pour augmenter d'ici 2020 l'abondance de la raie tachetée âgée de plus de 3 ans pour l'amener aux niveaux observés au cours de la dernière décennie, il faudrait prélever 319 000, 79 000 ou 13 000 phoques suivant les scénarios d'enlèvement 1, 2 et 3, respectivement. On a donc présenté un cadre d'analyse du risque afin d'évaluer les conséquences possibles associées au fait d'entreprendre, ou non, une réduction de la population de phoques gris, qu'ils soient ou non les principaux responsables du taux élevé de mortalité des poissons. Dans l'ensemble, les risques écologiques concernant la merluche blanche, la raie tachetée et le phoque gris semblent être minimisés en entreprenant une réduction raisonnable de la population du phoque gris dans l'Atlantique Nord-Ouest. Cette réduction ne poserait qu'un risque minime sur le plan de la conservation de la population de phoques gris. Dans le meilleur des cas, pour les poissons, la réduction du taux de mortalité chez l'adulte mettrait un frein au déclin de la population et assurerait éventuellement le rétablissement de l'espèce. Dans le pire des cas, la disparition des populations de merluche blanche et de raie tachetée du sud du golfe du Saint-Laurent surviendrait plus rapidement.

1. INTRODUCTION

Winter skate (*Leucoraja ocellata*) and white hake (*Urophycis tenuis*) both have populations that are endemic to the southern Gulf of St. Lawrence (sGSL) and that have been in decline for a number of years (Benoît and Swain 2008; Swain et al. 2009). A review of the population status of sGSL winter skate in 2005 led to a designation of endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2005). A subsequent recovery potential assessment (RPA) identified elevated adult natural mortality (*M*) as the main demographic rate contributing to the decline (Fig. 1; Swain et al. 2006). The factors contributing to the elevated *M* are not well understood, though unaccounted bycatch mortality in the sGSL scallop fishery and, in particular, predation by grey seals (*Halichoerus grypus*) were identified as likely contributors in the RPA. Indeed, the perceived slight contribution of direct anthropogenic threats and the potential importance of grey seal predation were cited as principal reasons not to list winter skate under the Species at Risk Act (Canada Gazette 2010). White hake have yet to be fully reviewed by COSEWIC, however recent analyses clearly show that extremely elevated adult natural mortality is largely responsible for the decline (Fig. 2; Benoît et al. 2011b, submitted). The possible factors contributing to the elevated *M*, which include predation by grey seals, are examined in this document.

The objectives for this research document are to briefly examine the evidence for an effect of grey seal predation on adult *M* in winter skate and white hake, and to explore the consequences of a possible grey seal population reduction. First, we begin by briefly summarizing the available evidence for the uniqueness of these two fish species in the sGSL. Second, we look at the evidence concerning possible factors contributing to the elevated *M*. From that exercise we conclude that predation by grey seals likely contributes strongly to the elevated adult *M*. Third, we present projections of the sGSL winter skate and white hake populations, based on hypothetical scenarios aimed at determining the possible consequences of maintaining the status quo, allowing grey seal populations to continue to grow or undertaking seal abundance reductions. For the latter, scenarios concerning both untargeted and targeted reductions are considered. Fourth, we present a simple risk analysis framework in which we evaluate the general consequences for sGSL winter skate and white hake of undertaking, or not, a reduction of the Northwest (NW) Atlantic grey seal populations.

2. ARE THESE POPULATIONS UNIQUE?

There are two white hake stock components in the sGSL, one that occurs in deep water year round and is likely part of a larger NW Atlantic population, and another that occurs in shallow, near shore, waters during the summer (Fig. 3). The inshore stock component appears to constitute a unique population based on tagging (Kohler 1971), morphometric (Hurlbut and Clay 1998), parasite (Melendy et al. 2005) and genetic (Roy et al. 2009; T. Hurlbut, DFO Gulf Region personal communication) studies.

Winter skate in the sGSL mature at a considerably smaller size than they do elsewhere (McEachran and Martin 1977). This, combined with other morphological differences (McEachran and Martin 1977), clear geographic separation and differences in ecophysiology (Kelly and Hanson, MS in prep), suggests that winter skate in the sGSL may actually constitute a distinct species that has yet to be properly described.

3. POSSIBLE CAUSES OF ELEVATED ADULT M – THE WEIGHT OF EVIDENCE

We consider the evidence for different factors possibly contributing to adult sGSL winter skate and white hake *M*, following the framework of Swain et al. (2010b). There is however no data available to evaluate the evidence for some factors such as disease, contaminants or parasites, though prevalence of some of these factors should also be evident in the condition of the fish, which is considered here. Furthermore, based on the information available for cod (*Gadus morhua*), these factors appear to contribute little to adult cod *M* (Swain et al. 2011b) and there is no reason to believe that wouldn't be the case of white hake and winter skate.

3.1 CAPTURE IN FISHERIES

Population modeling for sGSL winter skate accounted for mortality due to incidental catch in groundfish and shrimp fisheries (Fig. 1), based on an analysis of data collected by at sea observers (Benoît 2006; Swain et al. 2006). Though the contribution of incidental mortality to total mortality was moderate in the 1980s, it dropped to a very low level in the late 1990s and into the 2000s. Estimates based on recent sampling of winter skate bycatch in the sGSL scallop fishery suggest that mortality in this fishery is also negligible; likely <0.2%, though perhaps as high as 0.4% of total adult *M* (Benoît et al. 2010d; see update in Benoît 2011). The lobster fishery is the only other fishery of which we are aware that may have contributed to mortality of adult winter skate. While winter skate were once occasionally captured incidentally in lobster traps of a wooden lath design, a shift to wire mesh traps in the mid-1980s eliminated capture of adult skates (Marc Lanteigne, DFO Moncton, pers. comm.). The number of winter skate captured annually in the past, and whether they were generally released alive, is unknown, though the trend in adult winter skate *M* is inconsistent with a predominant effect of bycatch mortality in this fishery. Mortality from causes other than fishing is therefore very likely responsible for the current elevated adult *M* in this species.

There was a directed fishery for white hake until 1995, when a moratorium was imposed. An average of 7,000-8,000 tonnes was landed annually in the fishery during the 1980s. White hake are also captured in fisheries targeting other species, such as cod and Atlantic halibut (*Hippoglossus hippoglossus*). Discard bans introduced in 1993 made it illegal to discard incidentally captured white hake (i.e., in principle, all caught hake were landed). Furthermore, bycatch quotas also introduced in 1993 (set as a % of target species catch) have limited the amount of white hake caught in other fisheries. Consequently, the estimated fishing mortality (*F*) of white hake based on reported (pre-1990) and dock-side measured (post 1990) catches declined from between 0.6-1.0 prior to 1995, to values <0.1 in recent years (Fig. 2; Benoît et al. 2011b). While some catches of white hake have likely gone unreported/unrecorded, unaccounted fishing mortality in groundfish fisheries has likely declined to very low levels as fishing effort has declined (Fig. 7 in Benoît and Swain 2011). This trend is opposite the trend in estimated adult white hake *M* and it is therefore unlikely that unaccounted *F* in groundfish fisheries contributes much to recent estimates of *M*.

Adult white hake are also incidentally captured in sGSL scallop and lobster fisheries. Preliminary analyses suggest that catches in the scallop fishery are very small (H. Benoît, unpublished analyses). White hake catch amounts in the lobster fishery are unknown, though adult white hake are very rarely encountered in the traps (M. Lanteigne, pers. comm.). Furthermore there have been no changes in that fishery that would have led to a continuous increase in incidental fishing mortality for adult white hake (M. Lanteigne, pers. comm.).

Mortality from causes other than fishing is therefore very likely responsible for the trend and current elevated adult *M* in white hake.

3.2 POOR CONDITION

Natural mortality appeared to be at an elevated level in the mid to late 1990s in many Northwest Atlantic cod stocks (e.g., Shelton et al. 2006). One hypothesis proposed to account for this observation is that natural mortality increased in the early 1990s due to poor fish condition (Lambert and Dutil 1997; Dutil and Lambert 2000). We consider the evidence for a possible contribution of poor condition to elevated *M* in adult winter skate and white hake (see also Swain et al. 2011a).

The condition of winter skate was near the long-term average from 1973-1990, then it began decreasing to a low value in the mid to late-1990s (Fig. 4). Condition has improved steadily since then, recently reaching the highest values observed. Adult winter skate *M* was considerably higher in the 1980s compared to the 1970s (Fig. 5), despite condition remaining the same or slightly improving over that period. *M* was even higher during the 1990s, when condition declined, and has perhaps decreased since then, as condition has improved again (Figs. 4 and 5). However estimated *M* remains high despite relatively very good condition. The results, taken over the whole series from 1971-present, are not consistent with a strong contribution of poor condition to elevated *M* in adult winter skate. Furthermore, winter skate do not have as pronounced a seasonal cycle in condition as do cod, and therefore susceptibility to mortality resulting from reduced winter feeding is not expected to be as strong (Swain et al. 2011a). At most, poor condition may have contributed an average of 0.1 to *M* during the 1990s, based on the patterns in total mortality associated with the period of poor condition (Fig. 5).

Because white hake have a pronounced seasonal cycle in *M* like cod (Swain et al 2010a), indicative of reduced winter feeding, they might also be vulnerable to some condition-related mortality. The condition of white hake was maximal in the early 1970s and declined almost continuously to a low in the early 1990s (Fig. 4). Condition then increased to reach levels that have been at or above the long-term average since the late 1990s. Meanwhile, *M* of adult white hake increased almost continuously from the low levels typical of long lived demersal fish (M<0.2) observed in the mid-1980s to the present very high levels (Fig. 6). While the principal trend in *M* is inconsistent with a strong effect of poor condition, a small temporary bump in the trend occurring in the late 1980s and early 1990s, might reflect condition-related mortality (see explanation later in this document for the attribution of the causes of *M* in Fig. 6). However that temporary bump in *M* could also be due to unaccounted *F* or incorrect catchability-adjustment in the estimate of *F*, since there was much fishing at that time (Fig. 2). The current elevated *M* levels are not consistent with possible condition-related mortality.

3.3 LIFE HISTORY CHANGE

An increase in *M* is a predicted consequence of fisheries-induced reductions in age and size at maturity of fish (Hutchings 2005), though the causality may also largely be opposite, such that high *M* is the cause of earlier maturation (Swain 2010). There is insufficient information to determine if there have been changes in the maturation schedule for sGSL winter skate. McEachran and Martin (1977) reported that mature winter skate in the Gulf ranged from 50 to 70 cm, but the authors did not estimate size at maturity. Recent analyses based on individuals collected in the mid-2000s indicate that size of 50% maturity is 40 cm for males and 42 cm for females (Kelly and Hanson, MS in prep.).

Mean age at 50% maturity for white hake has varied without trend since the late 1970s (Fig. 7). While there may have been reductions in maturity that occurred prior to this period, as was the case for cod (Swain 2010), changes in age at maturity cannot explain the rising trend in adult *M* since the mid 1980s.

3.4 PREDATION BY GREY SEALS

The grey seal is the most abundant year-round resident pinniped in the sGSL. During the summer, white hake and winter skate are aggregated in parts of the Northumberland Strait, near important grey seal haul out sites such as Miramichi, Kouchibouguac and Amet Island (Fig. 3). These aggregation areas include areas frequently used by satellite-tagged Gulf grey seals (Fig. 8). During the winter, winter skate are broadly distributed on the Magdalen shallows (Fig. 3), an area used by grey seals (Fig. 8). White hake overwinter along the Laurentian channel and in the Sydney Bight area, again a common area for grey seals. The degree of spatial overlap between seals and each of the two fish species is such that there is a very high potential for predation at a level at which much or all of the elevated adult *M* could be explained by predation (Benoît et al. 2011b). Furthermore, trends in estimated *M* in both species generally follow trends in the abundance of the NW Atlantic grey seal populations (Figs. 5, 6 and 9). Note that the decrease in the median posterior estimate of adult winter skate *M*, from the 1990s period to the 2000s (Fig. 5) is not inconsistent with an effect of grey seal predation. Theory on predator-pits indicates that when a prey becomes relatively rare, the predator may switch to alternate prey, thereby temporarily reducing the predation pressure on the rarer species (e.g., Bakun 2006). As the abundance of alternate prey declines, or that of the rarer species increases, *M* is predicted to increase again.

Evidence for predation on winter skate by grey seals is largely lacking (but see Benoît and Bowen 1990), likely because consumed winter skate leave few hard parts (spines) in seal guts or scat. Winter skate have been detected in NW Atlantic grey seal diets inferred using quantitative fatty acid signature analysis (QFASA; Beck et al. 2007). If the levels established to date are accurate (mean 0.5% of diet, range 0-2%, depending on sex and season), grey seal predation could explain all of sGSL adult winter skate *M* (Benoît et al. 2011b).

White hake commonly occur in the diet of grey seals in the sGSL (17% of the diet; Hammill et al. 2007), though only smaller white hake (<40 cm, ≤3 years old) are recovered in gut samples. However these diet samples may not be representative of grey seal feeding for the same reasons discussed by Benoît et al (2010a) for cod. First, a large proportion (36%) of the seals sampled for diets collected from spring to autumn were taken around southeastern Prince Edward Island (e.g., Amet Island) (Fig. 10). This is an area in which smaller white hake are common, but larger white hake do not occur (Fig. 11). Recent diet sampling in winter near St. Paul's Island (Fig. 10; Stenson et al. 2011), where both large and small hake aggregate, revealed a median consumed length of 32 cm (compared to a median ~23 cm in past samples, Hammill et al. 2007), and one of the 14 fish otoliths measured belonged to a 48 cm individual (Hammill et al. unpublished results). Second, the available seal diet estimates do not take into account possible partial consumption of larger hake (e.g., belly-biting). Partial consumption would be expected under optimal foraging by grey seals and would leave no direct evidence of predation in the seal guts (Benoît et al. 2011b). Adult white hake may be particularly vulnerable to predation by partial consumption given their high degree of spatial aggregation. Third, the relative rareness of large white hake relative to other grey seal prey means that even if their heads are consumed sometimes by grey seals, such a rare event may be difficult to detect in the absence of a very large seal diet sample size (Arim and Naya 2003). To explain 90% of adult white hake *M* in 2005, they would need to have constituted <4% of the mean diet of Gulf grey seals (Benoît et al. 2011b). Taken together, we believe that the existing diet data does not rule out predation by grey seals as an important contribution to adult white hake *M*.

3.5 OTHER PREDATORS

3.5.1 Fish

Given their size, individuals with elevated *M* would have been 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 in the sGSL for over 15 years, and would not have been very abundant for at least several decades. Adult white hake and winter skate would not be vulnerable to predation by dogfish sharks (Scharf et al. 2000). Rates of predation by larger sharks is unknown, but their abundance has declined to a low level over the period in question (Baum et al. 2003).

3.5.2 Cetaceans

Existing harbour porpoise diets from the neighboring northern Gulf of St. Lawrence do not include white hake or winter skate, and were dominated by small pelagic fish (Fontaine et al. 1994). Furthermore the fish consumed were all <40 cm in that study. Abundance of harbour porpoise also appears to have declined since the mid 1990s (Lawson and Gosselin 2009). Minke whales 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 their abundance has increased in tandem with increases in fish *M* (Lawson and Gosselin 2009).

3.5.3 Other seals

In seasons other than winter, the harbour seal is the only other pinniped in the ecosystem. They are much less abundant than grey seals and their feeding habits in the ecosystem are poorly known, but they tend to forage close to shore. 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 likely also restricts them to feeding on smaller fish than do grey seals.

During the winter, harp seals would be very abundant in the ecosystem, though Hammill and Stenson (2000) estimated that their consumption of 4T fish would be slight because most of the animals are in the northern Gulf except during the breeding season when they haul out on the ice near the Magdalen Islands. During the breeding season adult harp seals feed very little. After breeding most harp seals move into the estuary or northern Gulf, to feed, then into the northern Gulf to moult and then leave to return to the north. Harp seal beaters may be present in April in part of the southern Gulf, but since they are only learning to forage, and invertebrates would initially be consumed, hake and skate would not be important prey items. Hooded seals are also present in the area in winter, but their numbers are small and their seasonal residency is very short.

3.5.5 Seabirds

The seabird species of the sGSL prey on considerably smaller-sized fish than the sizes considered here for white hake and winter skate (Savenkoff et al. 2004).

3.6 CONCLUSIONS BASED ON WEIGHT OF EVIDENCE

Based on the available evidence, we conclude that while *M* may have increased temporarily during periods of low condition, poor condition cannot explain currently high levels for adult winter skate and white hake. The strongest available evidence suggested that predation by grey seals may be the largest contributor to high *M*. With the exception of predation on winter skate by grey seals, as inferred from QFASA (Beck et al. 2007), the available evidence is all indirect.

4. PROJECTIONS OF FISH POPULATION STATUS UNDER DIFFERENT SCENARIOS

Short-term projections of the sSGL winter skate and white hake populations were undertaken given assumptions on the causes of adult *M* described in section 3. In hypothetical simulations based on the weight of evidence, we assume that grey seal predation is presently the greatest contributor to adult winter skate and white hake *M*. This assumption also minimizes the risks associated with a decision related to a possible reduction of the NW Atlantic grey seal population (section 5). Using these projections, we consider the possible consequences of different grey seal population management scenarios.

4.1 PROJECTION METHODS

For both species we undertook stochastic projections, based on the current productivity conditions, to establish the consequences to the populations if current demographic rates persist. We then explored projections with different levels of adult *M*, aimed at determining the level of mortality reduction required to halt population decline and to promote recovery. Finally we estimate the number of grey seals that would need to be killed to achieve these *M* reductions, under the hypothetical scenarios. Different methodologies were used for the projections for the two fish species because of differences in the models used to estimate *M*.

4.1.1 Winter skate

The population model of Swain et al. (2009; also described in Benoît and Swain 2011) was used to project the possible trajectories of sGSL winter skate, based on recent population productivity conditions. Briefly, the process model used is composed of difference equations describing the abundance dynamics of juvenile and adult winter skate:

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

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

where $N_{1,t}$ and $N_{2,t}$ are the abundances of juveniles and adults, respectively, in year t, θ is the transition probability from the juvenile to the adult stage, a is the time between laying of egg cases and recruitment to juvenile stage, $Z_{i,t}$ is the stage-specific instantaneous rate of total mortality in year t, and r is the recruitment rate (i.e., annual fecundity per female discounted by egg case mortality and mortality between hatching and recruitment). In the models, the Z (= M + F) parameters were allowed to vary on a decadal scale, and the estimate for the most recent period (the 2000s) was used for the projections. A sex ratio of 1:1 was assumed to compute recruit production.

One thousand bootstrap iterations were used in each projection. Each iteration began by sampling from the joint posterior probability distribution of model parameters, and the estimated 2008 and 2009 population states (i.e. abundance), from the Bayesian state-space model (updated from Swain et al. 2009). Population abundance was then projected forward deterministically (i.e., no process error) using eqns.1 and 2. Total mortality (*Z*) for juveniles and for adults was set equal to the sum of their respective estimated *M* for the 2000s (Fig. 5) and mean *F* for the 2000-2009 period (0.002 for juveniles and 0.018 for adults). The population was considered extirpated when abundance fell below one thousand individuals.

Based on the weight of evidence, and for simplicity, we assumed that grey seals contribute all of adult winter skate *M* above the levels estimated for the 1970s (i.e. ~90% of 2000s *M*). Trends in juvenile winter skate *M* are inconsistent with a predominant effect of grey seal predation. Rather these trends are consistent with release from predation by formerly abundant large demersal fish, including adult winter skate. For simplicity, we therefore assumed that seals do not consume juvenile winter skate. Furthermore, given that we do not project dramatic increases in adult winter skate, we did not relate juvenile *M* to adult abundance.

4.1.2 White hake

Following Benoît et al. (2010b), we used a published size-dependent catchability relationship derived for groundfish (Harley and Myers, 2001) to scale survey-derived relative abundance-at-length to absolute abundance. Because sGSL white hake are aged annually, these numbers were then converted to abundance at age.

White hake are reliably caught in the annual bottom-trawl survey at ages 3+ and consequently age 3 white hake were considered the recruits. Because of strong trends in the recruitment rate (Fig. 12) that appeared related to spawning stock biomass (SSB), we fit two common stock recruitment relationships to the data, 1971-2009:

Ricker function: $$R = \alpha \cdot SSB \cdot e^{-\beta \cdot SSB} \qquad (3)$$

Beverton-Holt function: $$R = {SSB}\Big/{\delta + \phi \cdot SSB} \qquad (4)$$

where R is the number of recruits and α, β, δ and ϕ are parameters. Over the entire time series, the two relationships provided comparable fits to the data (ΔAIC=1.05; Fig. 13), consequently projections involving both were undertaken.

The stochastic population projections of the status quo situation, taking into account variability in the stock-recruitment relationship, growth and uncertainty in current levels of *M* and abundance-at-age proceeded as follows:

i) An abundance ($N_{i,2009}$) value for each age group (i, ages 3+) in 2009 was drawn from the catchability-adjusted estimates and their standard error, assuming a normal distribution. Abundances for 2007 and 2008, used to calculate a SSB and thereby predict recruitment in 2010 and 2011 (step iv below), were estimated in the same manner.

ii) In each year of the projection, *M* was randomly selected from a normal distribution with a mean and standard deviation (SD) equal to the value estimated for *M* in the terminal block of years (2002-2009) and the SD of this estimate (Fig. 2; see Benoît et al. 2011b for details). Though the original *M* estimates are for white hake ages 5-7, we assumed they applied to ages

3+. The fishing mortality, entirely due to capture in fisheries directed at other species, was set at the average estimated for 2007-2009 (F=0.08) and was considered fixed.

iii) For ages i =4+, abundance at the beginning of year t was given by:

$$N_{i,t} = N_{i-1,t-1}e^{-F_{t-1}-M_{t-1}} \tag{5}$$

iv) SSB at the beginning of year t, was given by:

$$SSB_t = \sum_{i=3}^{15} m_i b_{i,t} N_{i,t} \tag{6}$$

where m_{i} is the proportion mature at age i and

$b_{\mathrm{i,t}}$ is the mass (kg) for age i in year t. The value of b_{i} used for year t was randomly selected from a normal distribution for each age based on the mean mass and SD observed in the RV survey from 2000-2009.

v) Recruitment in year t (R=$N_{3,t}$) was given by either the Ricker or Beverton-Holt stock-recruitment relationship described above (eqns 3 and 4). The values for the parameters of the recruitment relationship were drawn from a multivariate normal distribution that included the mean parameter estimates and their joint covariance matrix.

A year class was considered extirpated in a given iteration of the simulation when abundance fell below 1000 individuals.

We also undertook stochastic projections that explicitly included predation by grey seals. To do so required defining a functional response that described how the rate of predation on adult white hake varied with their abundance and possibly with that of their predator, grey seals. Though grey seals are known to prey on juvenile white hake (Hammill et al. 2007), we did not consider the effect of that predation in the projections. This is because the trends in juvenile white hake survival, inferred from the recruitment rate, are not consistent with a strong effect of grey seal predation. Rather they are most consistent with release from predation from formerly abundant groundfish, including their adults, who are known to be cannibalistic (Davis et al. 2004; Benoît and Swain 2008).

To define a functional response, we first needed to determine the possible past consumption by grey seals. This in turn meant attributing trends in estimated adult white hake M to different causes (Fig. 6). Based on section 3, we hypothesized that there were three contributors to M: undefined causes (disease, other predators, etc), low condition and grey seals. M due to undefined causes (*Mresid*) was set at a fixed value of 0.05. Condition-related mortality was defined based on the period of below average condition observed for white hake beginning in the mid 1980s. The proportional contribution of low condition to M was set inversely to observed condition, and the maximum contribution (=0.1) was set such that changes in condition would explain the bump in the M trend mentioned in section 3. Predation by grey seals was assumed to explain the remainder of M (*Mseal*). The biomass, C_t, of age 3+ white hake eaten by grey seals in year t was equal to:

$$C_t = \frac{Mseal_t \cdot B_t \cdot (1-\exp(-F - Mresid - Mcondition_t - Mseal_t)}{(F + Mresid + Mcondition_t + Mseal_t)} \tag{7}$$

where $B_t = \sum_{i=3}^{15} b_{i,t} N_{i,t}$

The number of grey seals that contributed to this consumption was calculated using the estimated abundances of each herd from the seal population models (Fig. 9; Hammill and Stenson 2011) and estimates of the annual proportion of each herd that spend some time in the white hake ecosystem, defined as the entire southern Gulf of St. Lawrence (NAFO 4T) plus the Sydney Bight/Cabot Strait area (NAFO 4Vn) during the winter. The seal proportions were estimated following a similar methodology as used by Benoît et al. (2010c): an annual average of 86.9% of Gulf and 11.7% of Sable Island grey seals spend some time in the hake ecosystem. Separate analyses of grey seal satellite tracking data from the 1990s and the 2000s do not suggest that the proportion of Sable Island grey seals spending time in the ecosystem has increased, as might be predicted by a density-dependent expansion in area occupied (Table 1). Consequently the proportion was considered fixed over time. Seventy-five percent of Eastern shore grey seals were assumed to adopt the distribution patterns of Sable Island seals, the remainder was assumed to be distributed like Gulf seals.

We fit three different, yet related, functional response models to the calculated annual feeding rates: Type II, Type III and Type II including predator dependency. The first two are defined using a single equation:

$$P_t = {a \cdot B_t^{\,n}} \Big/ {1 + a \cdot h \cdot B_t^{\,n}} \qquad (8)$$

where the inputs are the predation rate in year *t* ($P_t = C_t$ / number of seals 4TVn in year *t*), the biomass of 3+ white hake ($B_t = \sum_{i=3}^{15} b_{i,t} N_{i,t}$), and the parameter *n*, which determines if the functional response is Type II (*n*=1) or Type III (*n*=2). The estimated parameters are the attack rate, *a*, and the handling time, *h*. The predator-dependent relationship suggested independently by Beddington (1975) and DeAngelis et al. (1975) is defined as

$$P_t = {a \cdot B_t} \Big/ {1 + a \cdot h \cdot B_t + \gamma S_t} \qquad (9)$$

where S_t is the effective number of seals in year *t* and γ (≥0) determines the degree of predator interference during foraging. When $\gamma = 0$, the functional response reverts to Type II. The three functional response models were fit using the least-square method and including bounds (≥0) on the parameters *h* and γ. We found that the Type II and Type III functional responses fit the data equally well (∆AIC=1.1; Fig. 14). The predator interference parameter γ was always stuck on its boundary (γ=0), suggesting that for the predation rates inferred here, there is no evidence for interference among seal predators. Though simulations of both Type II and III functional responses were undertaken, in reality a Type III response may be the most appropriate given that grey seals are generalist predators and that the two fish species are likely to be relatively minor prey items in the seal diet (Koen-Alonso and Yodzis 2005; Matthiopolous et al. 2008).

Separate stochastic projections explicitly including predation by grey seals, based either on a Type II or III functional response, proceeded as described above except that *M* was set to be a function of seal abundance, as we now describe:

i) The predation rate in year t, P_t, was estimated using eqn 8 with values for the parameters of the functional response drawn from a multivariate normal distribution that included the mean parameter estimates and their joint covariance matrix;

ii) The estimated biomass of white hake consumed in year t, C_t, was calculated as $C_t = S_t{}^*P_t$, where S_t was taken as the point estimate from the projected total number of grey seals in 4TVn, i.e., a deterministic input;

iii) The natural mortality due to seals implied by the resulting consumption in year t, $Mseal_t$, was estimated by iteratively solving Baranov's equation (eqn 7), with the maximum possible value of $Mseal_t$ set to 4;

iv) The projections then proceeded as described above, but with M=$Mseal$+$Mresid$, where $Mresid$=0.05 (i.e., assuming $Mcondition$=0).

4.2 PROJECTION RESULTS

4.2.1 Winter skate

Based on the estimates for *M* from the 2000s and other assumptions of the population model, sGSL winter skate have a 50% chance of extirpation by 2040, unless productivity improves (Fig. 15). An immediate and maintained 57% reduction in adult *M* results in a 50% chance of achieving population stability at around 0.5 million individuals (Fig. 16). Smaller reductions in *M* slow down but do not halt the population decline. The level of abundance achieved with a 57% reduction in adult *M* is considerably lower than the 1980s mean abundance of approximately 8 million (Fig. 15). To have a 50% chance of reaching abundance values comparable to the 1980s in 50 years would require a 75% reduction in adult *M* (results not shown).

To achieve a 57% percent reduction in adult winter skate *M* relative to values estimated for the 2000s, and assuming that grey seal predation contributes to 90% of that *M*, the number of grey seals that occur in NAFO 4TVn would need to be reduced by 42.6%, from the 104,028 grey seals projected to occur there for at least part of the year in 2011 (Table 2). Furthermore, additional growth of the herds would need to be halted. Such reductions are required because under this scenario winter skate comprise approximately 0.02% of the diet of the average grey seal in 4T.

If grey seals feeding in NAFO 4TVn are randomly removed, an average of around 16,600 seals from Sable Island, 2,700 from the Eastern Shore herd and 25,000 from the Gulf population (total 44,300 individuals) would need to be removed to achieve stability in the winter skate population, based on the relative presence of the herds in the area. To achieve this same goal using untargeted removals (i.e., reductions undertaken when grey seals are aggregated in their breeding colonies), an average of 135,600 seals from Sable Island, 8,500 from the Eastern Shore herd and 30,200 from the Gulf population (total 174,300 grey seals) would need to be removed.

Because winter skate are highly aggregated in the western portion of the Northumberland Strait during summer and early autumn (Fig. 3), it may be possible to target grey seals even further to achieve reductions in adult winter skate *M*, while removing fewer seals. It is difficult to speculate on the number of seals that would need to be removed, given possible biases in the existing information on the small-scale distribution of grey seals (see discussion in Benoît et al 2010c). However, as an example, if winter skate comprise 1% of the diet of grey seals in the area and approximately half of annual feeding by seals takes place during summer and early autumn, approximately 1,700 grey seals foraging in the western portion of the Strait would need to be removed to achieve the 57% reduction in adult winter skate *M*.

4.2.2 White hake

The Ricker stock-recruitment relationship predicts lower levels of sGSL white hake recruitment given the currently low SSB, compared to the Beverton-Holt relationship (Fig. 13). Consequently, projections based on the Ricker relationship are much more pessimistic on the future status of sGSL white hake; based on recent levels of productivity, the population is projected to be extirpated by 2040 (50% chance of extirpation by 2018; Fig. 17a). Even if adult *M* were cut in half, extirpation still occurs by 2050. In that simulation, unless *M* is cut by 68%, the population will continue to decline. With a 68% reduction, the population will stabilize at around 6 million individuals, a level comparable to the 2000s, but considerably lower than the abundances observed during the 1970s and 1980s. To reach those latter values, adult *M* would have to be permanently reduced by 75% (Fig. 17a).

Based on recent productivity conditions and a Beverton-Holt stock recruitment relationship, sGSL white hake have a 50% chance of extirpation by 2035 and 100% chance by 2070 (Fig. 17b). The population decline is largely halted by decreases in adult *M* of 40%, though a cut of 55% is required to stabilize age 3+ abundance at around 6 million individuals. Abundance levels comparable to the 1970-1990 period require a permanent 75% reduction in *M* (Fig. 17b).

Short-term projection results for sGSL white hake that assume grey seal predation is largely responsible for the increased adult *M* (i.e., based on Fig. 6) differ somewhat from projection results based on the estimated *M*. Under a Type III functional response, which predicts lower consumption rates at low hake biomass (Fig. 14), the risk of extirpation of sGSL white hake by 2020 is eliminated in the simulations, though population decline continues (Fig. 18, red lines). In contrast, under a Type II functional response, the risk of extirpation is increased compared to the status quo (Fig. 18, cyan lines). If recruitment follows a Ricker stock-recruitment relationship, extirpation is certain by 2015, if model assumptions are correct. Under a Beverton-Holt stock-recruitment relationship, there is a 50% extirpation risk by 2018.

Under the model assumptions and a Type II functional response for seal predation, at least 58-69% of seals feeding in the white hake ecosystem will need to be removed to halt the decline in white hake abundance and for the population to reach 2 million individuals ages 3+ by 2020 (Table 3). Considerably smaller reductions are required to reach the abundance target if a Type III functional response is assumed: 10% and capping seal population growth after 2018 respectively for Ricker and Beverton-Holt stock-recruitment functions. However, a slight declining population trend remains, and longer projections would be required to determine the level of removals to achieve longer-term stability. To have a 50% chance of achieving a sGSL age 3+ white hake population of 6 million individuals by 2020, reductions of seals feeding in the white hake ecosystem of between 51-76% (depending on the assumed functional response and stock-recruitment function) would be required (Table 3).

As described for winter skate, the actual number of seals required to achieve a given reduction of the number of seals feeding on white hake depends on how reductions are undertaken. If, for example, the goal is to have a 50% chance of obtaining 6 million age 3+ white hake by 2020, while minimizing all risks associated with the choice of functional response and stock-recruitment relationship, then 76% of seals feeding in the ecosystem need to be reduced. Such a reduction could be obtained by removing approximately 79,000 grey seals feeding in the system in 2011, and removing any surplus production in the seal herd in the following years. Alternatively, if reductions are undertaken when the seal herds are aggregated on their breeding grounds, then required removals in 2011 would be 251,000 on Sable Island, 17,000 on the Eastern shore and 51,000 in the Gulf (total 319,000 grey seals).

White hake are spatially aggregated during most of the year (Fig. 3). It may therefore be possible to particularly target seals that feed on them in the Laurentian Channel and Cheticamp trough year round, and in St. George's Bay in the summer. If, for example, white hake comprise 12% of the diet of grey seals foraging in white hake aggregation areas (e.g., Benoît et al. 2011b), then approximately 13,000 seals would need to be killed to have a 50% chance of obtaining 6 million sGSL white hake ages 3+ by 2020. Targeted removals in the Cheticamp trough/St. Paul's island area in the winter might also benefit large cod and removals in the eastern portion of the Northumberland Strait in summer might also benefit winter skate.

5.0 RISK ANALYSIS

We present a simple risk management framework that evaluates the ecological risks, as best we can evaluate them, of undertaking or not a grey seal population reduction, under the weight-of-evidence hypothesis that predation by grey seals is the greatest contributor to elevated and unsustainable adult *M* in sGSL white hake and winter skate. This discussion is structured according to the four matrix cells that are defined by two vertices, (i) whether the hypothesis is actually correct or not, and (ii) whether an appropriate reduction in the grey seal population is undertaken or not. Risks associated with the broader ecological, social, political or economic consequences of undertaking a seal population reduction, or those resulting from the perception of allowing extirpation of two marine fish populations, were explicitly not considered. We also do not comment on the possible consequences to biodiversity of losing distinct populations or species, deferring such a discussion to other fora.

5.1 THE HYPOTHESIS IS CORRECT, NO SEAL MANAGEMENT ACTION IS TAKEN

Trends in NW Atlantic grey seal populations are such that the populations are projected to continue to increase, though perhaps at a reduced rate at Sable Island (Bowen et al. 2007). Based on current productivity levels, sGSL white hake and winter skate are at heightened risk of extirpation. Because elevated adult natural mortality is the main contributor to the ongoing declines in these species, failure to reduce predation mortality by grey seals may likely result in the loss of these populations within a few decades. Because winter skate in the southern Gulf may actually be a distinct species that has yet to be fully described, this loss may constitute extinction. Alternatively, theory on the predator pit phenomenon suggests that the populations may simply be reduced to considerably smaller levels than observed today, given present trends. Such abundance levels would nonetheless heighten the vulnerability of the populations to extirpation by other causes.

5.2 THE HYPOTHESIS IS CORRECT, APPROPRIATE SEAL MANAGEMENT ACTIONS ARE TAKEN

Reduction of the seal herd will affect winter skate and white hake directly, via reduced predation, and indirectly via changes occurring in other parts of the food web. The direct effects are reasonably clear; reducing the number of grey seals that consume the two fish species will reduce their *M* and thereby reduce or delay the risk of extirpation. Substantial decreases in *M* could even lead to population recovery in as little as 15-30 years for white hake (Fig. 17).

It is impossible to anticipate all the indirect ways that a grey seal population reduction could affect the two fish species (e.g., Yodzis 2000, 2001), and consequently only the key pathways were explored. The focus in this report is on negative effects, not because they are necessarily more likely but because they would contribute to heightened risk to the status of the fishes.

A strong indirect effect on adult white hake or winter skate is not anticipated because grey seals are not suppressing any potential predators of these fish. Furthermore, even if the abundance of competitors were to increase, data from the high abundance period for large groundfish in the 1980s does not suggest that there would be large density-dependent consequences for survival resulting from poor condition (e.g., Swain et al. 2011a; this document).

Indirect effects of a seal population reduction, if they occur, may be most likely for juvenile fish. Population increase in species that are both prey of grey seals and predators or competitors with juvenile stages of winter skate or white hake may lead to reduced juvenile survival/performance:

> i) Indirect effects on the early life stages of white hake are not anticipated, given current information. Unlike cod (Swain and Sinclair 2000), recruitment of white hake is not related to the abundance of pelagic fish, such as herring and capelin, which are also prey for grey seals. This may be due in part to the neustonic (near surface) distribution of white hake larvae, compared to a broader distribution in the water column of cod eggs and larvae. Winter skate egg cases are most susceptible to predation by gastropods. A number of grey seal prey are gastropod predators (e.g., cunner, winter flounder), and increases in their numbers following release from grey seal predation may indirectly increase egg-case survival.
>
> ii) The main predators of these hake and skate juveniles are large fish (e.g., Savenkoff et al. 2007, 2008). In time, recovery of large adults is expected to reduce the survival of juveniles, thereby slowing population growth. With the collapse of large fish, juvenile mortality has been reduced to very low levels and there is considerable scope for increase to levels that are common in most marine fish populations worldwide and that nonetheless sustained large southern Gulf populations prior to the 1990s.
>
> iii) Important competitors of juvenile fish are other similar-sized fish (e.g., Savenkoff et al. 2007, 2008). These competitors are also prey for large demersal fish such as adult cod, white hake and skate, and may therefore not increase in abundance over the long term as fish become their main predators. It is unclear whether and how competitive interactions would affect juvenile performance, though decreased growth and perhaps increased risk of overwinter mortality are possible consequences. However, increases in mortality resulting from poor condition are expected to be small (e.g., Swain et al. 2011a), relative to the decrease in M that has occurred over the past three decades.

While this list is far from exhaustive, concrete strong indirect effects that would result in worsened population status for either sGSL white hake or winter skate were not identified. However, our understanding of the trophic dynamics in this and other coastal marine ecosystems is limited and therefore other unforeseen indirect effects cannot be ruled out.

Risks to the viability of the NW Atlantic grey seal population resulting from a moderate population reduction were deemed small. Recent trends in the three herds suggest that they are highly productive, and could rapidly increase to current levels even with an overall reduction of 50% (10 years for Sable Island, 18 years in the Gulf), if their productivity remains unchanged.

5.3 THE HYPOTHESIS IS NOT CORRECT, SEAL MANAGEMENT ACTIONS ARE (MISTAKENLY) TAKEN

Trends in adult fish *M* are predicted to persist. Because there are no other suspected causes of adult *M* that are directly amenable to management actions, nature will be left to take its course. Indirect effects on juveniles noted in section 5.2 may be produced by a grey seal population reduction. Because there is little evidence that adult *M* would decline substantially in the near future, decreased juvenile survival, if it occurs, would merely speed up the otherwise inevitable extirpation of the populations.

As described in 5.2, the seal populations are likely to rebound when seal population control ceases.

5.4 THE HYPOTHESIS IS NOT CORRECT, NO SEAL MANAGEMENT ACTION IS TAKEN

Trends in adult fish *M* are predicted to persist. Because there are no other suspected causes of adult *M* that are directly amenable to management actions, nature will be left to take its course.

5.5 CONCLUSIONS OF THE RISK ANALYSIS

On balance, the estimated ecological risks related to the population status of NW Atlantic grey seals, and sGSL white hake and winter skate, appear to be reduced by undertaking a reduction of grey seals in the NW Atlantic. Such reductions would pose minimal conservation risks to the grey seal population. Under the best case scenario for the fish, reduced adult *M* will halt population decline and possibly promote recovery. At worst, the sGSL white hake and winter skate populations are likely to be extirpated more rapidly than they would otherwise be. Furthermore the seal reduction may lead to unforeseen and unintended consequences for the ecosystem.

The risks can be further minimized by closely monitoring demographic rates in the fish populations. Evidence of increasing and unsustainable juvenile *M* and failure of adult *M* to decline should become apparent in approximately 5-10 years of monitoring. Cessation of seal population control would allow the seal populations to rapidly return to the status quo situation if their productivity remains high, slowing down an accelerated progression to extirpation on the part of the two fish species. Furthermore, if grey seal herd management is undertaken using highly targeted removals of those seals most likely to prey on sGSL white hake and winter skate, then by halting these removals, other grey seals in the population may rapidly begin using the removal areas.

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REFERENCES

Arim, M., and Naya, D.E. 2003. Pinniped diets inferred from scats: analysis of biases in prey occurrence. Can. J. Zool. 81: 67-73.

Bakun, A. 2006. Wasp-waist populations and marine ecosystemdynamics: Navigating the “predator pit” topographies. Prog. Oceanogr. 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.

Beddington, J.R. 1975. Mutual interference between parasites and its effect on searching efficiency. J. Anim. Ecol. 44: 331-340.

Beck, C.A., Iverson, S.J., Bowen, W.D., and Blanchard, W. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behavious and reproductive expenditure: evidence from quantitative fatty acid signature analysis. J. Anim. Ecol. 76: 490-502.

Benoit, D., and Bowen, W.D. 1990. Seasonal and geographic variation in the diet of grey seals (*Halichoerus grypus*) in eastern Canada. pp. 215-226 *In* Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. W.D. Bowen (editor). Can. Bull. Fish. Aquat. Sci., 222. 306 pp.

Benoît, H.P. 2006. Estimated discards of winter skate (*Leucoraja ocellata*) in the southern Gulf of St. Lawrence, 1971-2004. DFO Can. Sci. Adv. Sec. Res. Doc. 2006/002.

Benoît, H.P. 2011. Estimated amounts, species composition and pre-discard condition of marine taxa captured incidentally in the southern Gulf of St. Lawrence scallop fishery. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/031. iv + 20 p.

Benoît, H. P., Hammill, M.O, and Swain, D. P. 2011a. Estimated consumption of southern Gulf cod by grey seals: bias, uncertainty and two proposed approaches. DFO Can. Sci. Adv. Sec. Res. Doc. 2011/041. iv + 29 p.

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. Adv. Sec. Res. Doc. 2011/039. iv + 22 p.

Benoît, H.P., Swain, D.P., Bowen, W.D., Breed, G.A., Hammill, M.O., and Harvey, V. 2011b. Can predation by grey seals explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence? Submitted January 2011 to Mar. Ecol. Prog. Ser.

Benoît, H. P., Swain, D. P., and Hammill, M.O. 2011c. 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. Adv. Sec. Res. Doc. 2011/018.

Benoît, H.P., Swain, D.P., Niles, M., LeBlanc, S., and Davidson, L.-A. 2010. Incidental catch amounts and potential post-release survival of winter skate (*Leucoraja ocellata*) captured in the scallop dredge fishery in the southern Gulf of St. Lawrence (2006-2008). DFO Can. Sci. Adv. Sec. Res. Doc. 2010/043 iv + 20 p.

Bowen, W.D., McMillan, J.I., and Blanchard, W. 2007. Reduced population growth of gray seals at Sable Island: evidence from pup production and age of primiparity. Mar. Mamm. Sci. 23: 48-64.

Canada Gazette. 2010. Order amending Schedule 1 to the Species at Risk Act. Canada Gazette Part II 144: 240–407.

COSEWIC. 2005. COSEWIC assessment and status report on the winter skate *Leucoraja ocellata* in Canada. COSEWIC, Ottawa. (http://dsp-psd.pwgsc.gc.ca/Collection/CW69-14-439-2005E.pdf)

Davis, A., Hanson, J.M., Watts, H., and MacPherson, H. 2004. Local ecological knowledge and marine fisheries research: the case of white hake (*Urophycistenuis*) predation on juvenile American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 61: 1191-1201.

DeAngelis, D.L., Goldstein, R.A., and O'Neill, R.V. 1975. A model for trophic interaction. Ecology 56: 881-892.

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.

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.

Hammill, M.O., and Stenson, G.B. 2011. Modeling grey seal abundance in Canadian waters. DFO Can. Sci. Adv. Sec. Res. Doc. 2011/014. iv + 27 p.

Hammill, M.O., Stenson, G. B., Proust, F., Carter, P., and McKinnon, D. 2007. Feeding by grey seals in the Gulf of St. Lawrence and around Newfoundland. NAMMCO Sci.Publ. 6: 135-152.

Harley, S.J., and Myers, R. A. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Can. J. Fish. Aquat. Sci. 58: 1569-1584.

Hurlbut, T., and Clay, D. 1998. Morphometric and meristic differences between shallow- and deep-water populations of white hake (*Urophycis tenuis*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 55: 2274-2282.

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

Koen-Alonso, M. and Yodzis, P. 2005. Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. Can. J. Fish. Aquat. Sci. 62:1490-1512.

Kohler, A.C. 1971. Tagging of white hake, *Urophycis tenuis* Mitchill, in the southern Gulf of St. Lawrence. ICNAF Res. Bull. 8: 21-25.

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.

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. Adv. Sec. Res. Doc. 2009/031.

Matthiopoulos, J., Smout, S., Winship, A.J., Thompson, D., Boyd, I.L., and Harwood, J. 2008. Getting beneath the surface of marine mammal-fisheries competition. Mammal Rev. 38:167-188.

McEachran, J. D., and Martin, C.O. 1977. Possible occurrence of character displacement in the sympatric skates *Raja erinacea* and *R. ocellata* (Pisces: Rajidae). Envir. Biol. Fish. 2:121–130.

Melendy, J., McClelland, G., and Hurlbut, T. 2005. Use of parasite tags in delineating stocks of white hake (*Urophycis tenuis*) from the southern Gulf of St. Lawrence and Cape Breton Shelf. Fish. Res. 76: 392-400.

Roy, D., Paterson, I.G., Hurlbut, T.R., and Ruzzante, D.E. 2009. Development and design of five multi-locus microsatellite PCR panels for population genetic surveys of white hake (*Urophycis tenuis*) in the Northwest Atlantic. Conservation Genet. Resour. DOI 10.1007/s12686-009-9140-6.

Savenkoff, C., Bourdages, H., Swain, D.P., Despatie, S.-P., Hanson, J.M., Méthot, R., Morissette, L., and Hammil, M.O. 2004. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2529.

Savenkoff, C., Swain, D. P., Hanson, J. M., Castonguay, M., Hammill, M. O., Bourdages, H., Morissette, L., and Chabot, D. 2007. Effects of fishing and predation in a heavily exploited ecosystem: comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). Ecol. Model. 204: 115-128.

Savenkoff, C., Morissette, L., Castonguay, M., Swain, D. P., Hammill, M. O., Chabot, D., and Hanson, J. M. 2008. Interactions between marine mammals and fisheries: Implications for cod recovery. pp. 107-151 *In* Ecosystem Ecology Research Trends. J. Chen and C. Guo (editors). Nova Science Publishers Inc.

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.

Shelton, P.A., Sinclair, A.F., Chouinard, G.A., Mohn, R., and Duplisea, D.E. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 63: 235-238.

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., Flight, J., and Hammill, M.O. 2011. Winter diet of grey seals in Cabot Strait. DFO Can. Sci. Adv. Sec. Res. Doc. 2010/128.

Swain, D.P. 2010. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). Evol. Applic. 4:18-29.

Swain, D.P., and Benoît, H.P. 2001. Geographic distribution of selected marine fish in September in the southern Gulf of St. Lawrence based on annual bottom-trawl surveys. DFO Can. Sci. Adv. Sec. Res. Doc. 2001/118.

Swain, D.P., Benoît, H.P., Savoie, L., and Surette, T. 2011a. 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. Adv. Sec. Res. Doc. 2011/037.

Swain, D.P., Jonsen, I.D., and Myers, R.A. 2006. Recovery potential assessment of 4T and 4VW winter skate (*Leucoraja ocellata*): population models. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/004.

Swain, D. P., Jonsen, I.D., Simon, J.E., and Myers, R.A. 2009. Assessing threats to species-at-risk using stage-structured state-space models: mortality trends in skate populations. Ecol. App. 19: 1347-1364.

Swain, D. P., and Sinclair, A. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 57: 1321-1325.

Swain, D.P., Benoît, H.P., Hammill, M.O., McClelland, G., and Aubry, É. 2011b. Alternative hypotheses for causes of the elevated natural mortality of southern Gulf cod: the weight of evidence. DFO Can. Sci. Adv. Sec. Res. Doc. 2011/036

Yodzis, P. 2000. Diffuse effects in food webs. Ecology 81: 261-266.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? Trends Ecol. Evol. 16: 78-84.

Table 1. Percentage of time spent in NAFO 4T (year round) and 4Vn (Dec.-April) by satellite-tagged Sable Island grey seals and the total number of seals with active tags, by quarter (Q1: January-March; Q2: April-June; Q3: July-September; Q4: October-December), period (1990s and 2000s) and gender.

		Percent time in 4TVn					Number tagged			
	Period	Q1	Q2	Q3	Q4	Annual	Q1	Q2	Q3	Q4
Males	1995-2000	16.1	3.7	7.5	7.9	8.8	11	9	15	21
	2001-2009	4.0	6.7	10.1	7.9	7.2	19	13	13	29
Females	1995-2000	14.2	25.0	27.3	14.5	20.3	13	9	11	21
	2001-2009	27.9	17.7	10.9	4.8	15.3	28	15	15	40

Table 2. Estimated effects of grey seal population reductions on adult sGSL winter skate natural mortality (M).

% reduction in seal abundance	Effective number of seals affecting winter skate in 4TVn in 2011	Net reduction in effective seal abundance	Resulting winter skate biomass consumed (tonnes)	M due to seals	total M
0	104028		34.64	0.75	0.77
10	93625	10403	31.18	0.65	0.67
20	83222	20806	27.71	0.55	0.57
40	62417	41611	20.78	0.38	0.40
42.6[1]	59701	44327	14.76	0.26	0.28

[1] *This is the adult M level at which the population is expected to stabilize.*

Table 3. Consequences of different grey seal population reduction scenarios on sGSL white hake median population trajectories, as a function of the assumed stock-recruitment relationship and functional response. i) Mean values of adult white hake M (2011-2013) resulting from seal reductions. ii) Grey seal population reductions (%) and resulting mean adult white hake M, required for sGSL white hake to have a 50% chance of reaching a 3+ abundance of 2 or 6 million individuals. Note that in the projections, M resulting from seal predation was capped at a value of 4. The number of grey seals occurring in the sGSL white hake ecosystem in 2011, the year of the simulated cull, was estimated to be 104,027 individuals.

	Stock-Recuit function: Functional response:	Ricker Type II	Ricker Type III	BH Type II	BH Type III
i) Mean M resulting from different degrees of seal population reduction					
Seal reduction:	0%	>4	1.00	>4	1.44
	10%	>4	0.85	>4	1.15
	20%	>4	0.77	>4	0.97
	40%	>4	0.59	>4	0.71
ii) Reductions and resulting mean M to achieve white hake abundance targets					
Reduction for N_{2020}=2 million		69%	10%	58%	0%*
Resulting mean M		0.70	0.85	1.11	1.44
Reduction for N_{2020}=6 million		76%	63%	65%	51%
Resulting mean M		0.48	0.36	0.78	0.57

* *Target N_{2020} is achieved in the absence of a cull*

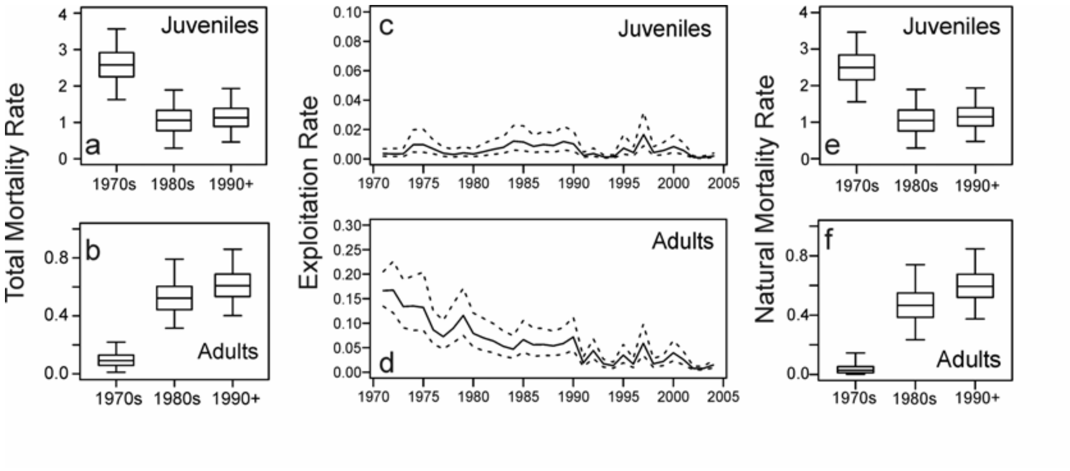


Figure. 1. Changes in total mortality, exploitation rate and natural mortality of winter skate in the southern Gulf of St. Lawrence (from Swain et al. 2009). Juveniles are defined as skates under 42 cm in total length. Box plots show the 2.5th, 25th, 50th, 75th and 97.5th percentiles of the posterior distributions for mortality parameters. In panels c and d, solid lines are posterior medians and dashed lines are the 2.5th and 97.5th percentiles of the posterior distributions. 1990+ refers to the 1990-2004 period (see Swain et al. 2009 for details).

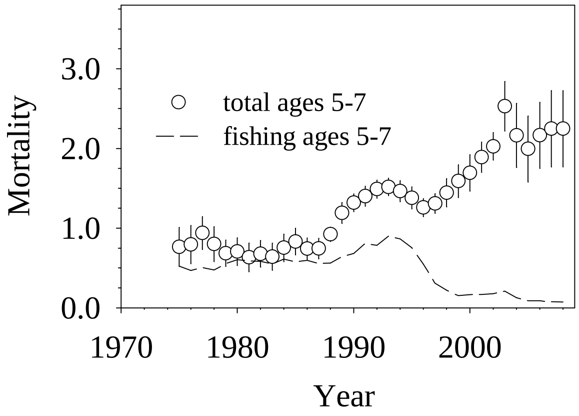


Figure 2. Total mortality (Z) of adult white hake ages 5-7 years estimated using the modified catch curve analysis, and estimated fishing mortality (F) using Baranov's equation based on commercial landings and catchability-adjusted abundance from the RV survey. Natural mortality (M) is equal to the difference between Z and F (see Benoît and Swain 2011b for details).

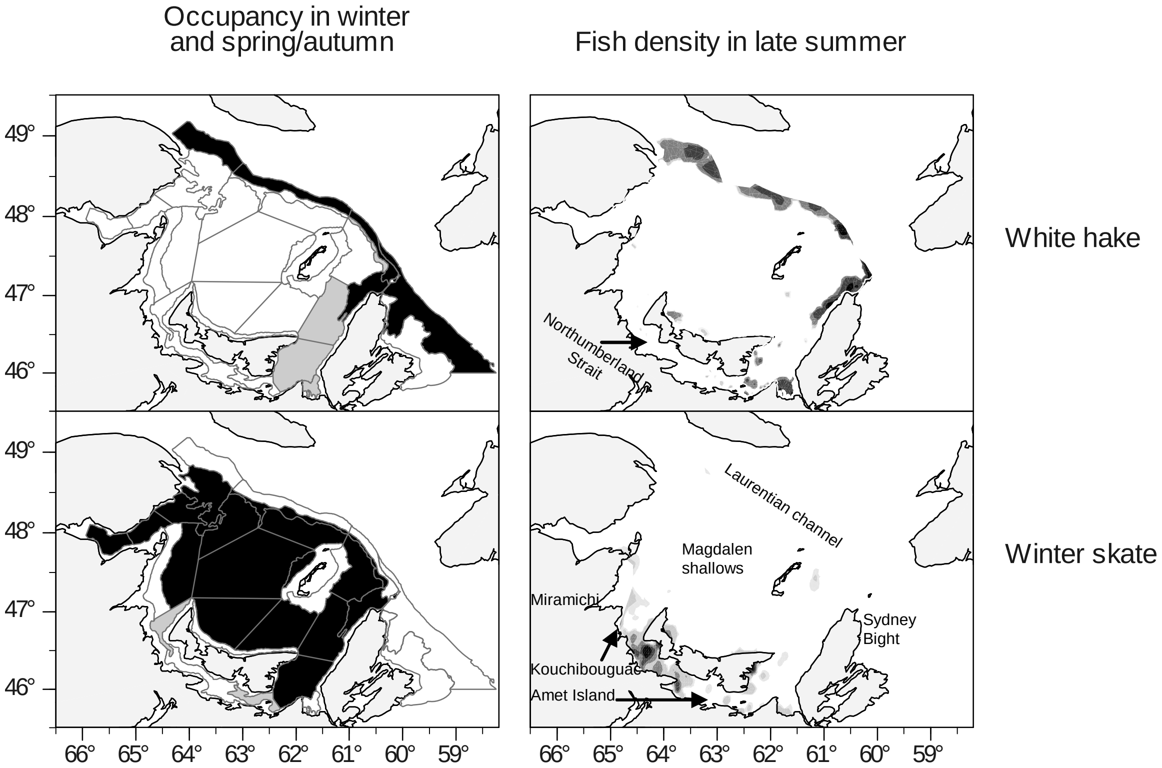


Figure 3. Summary of the geographic distribution of sGSL white hake and winter skate (redrawn from Benoît et al. 2011b). The panels in the left-hand column present the occupancy of each fish species at the stratum scale during the spring/autumn (light grey shading) and in both winter and spring/autumn (black), as inferred from seasonal bottom-trawl surveys. Strata occupied during winter and spring/autumn are shaded black. The panels in the right-hand column show the distribution of density for each fish species based on summer bottom-trawl surveys conducted 2004-2006. The incrementing grey shading represents increasing density based on the 10th (lightest grey), 25th, 50th, 75th and 90th (black) percentiles for density for each species.

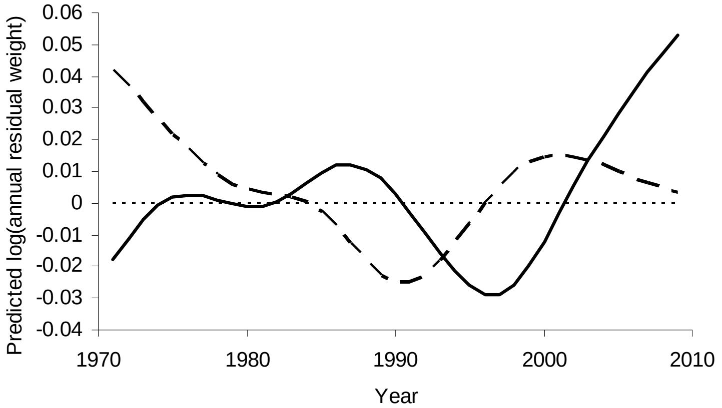


Figure 4. Inter-annual trends in the condition index for winter skate (solid line) and white hake (dashed line) (from Swain et al. 2011a).

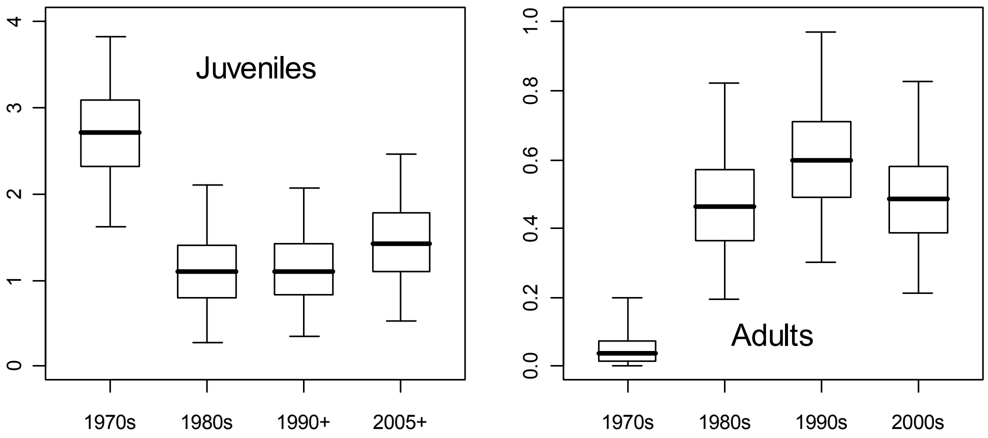


Figure 5. Estimated natural mortality of juvenile and adult winter skate updated to 2009, based on the model of Swain et al. (2009). Box plots show the 2.5th, 25th, 50th, 75th and 97.5th percentiles of the posterior distributions for mortality parameters.

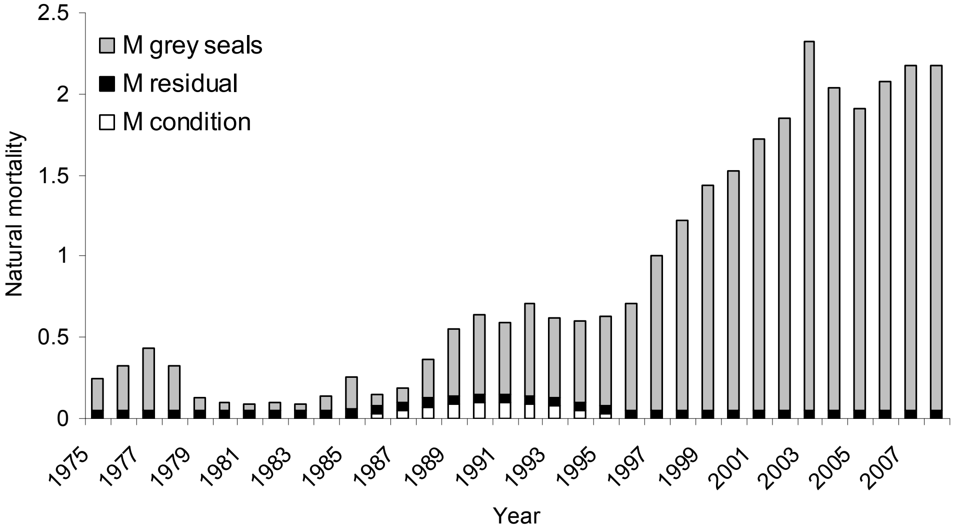


Figure 6. Assumed break-down of the contributions to adult white hake M of grey seal predation, poor condition and other (residual) causes.

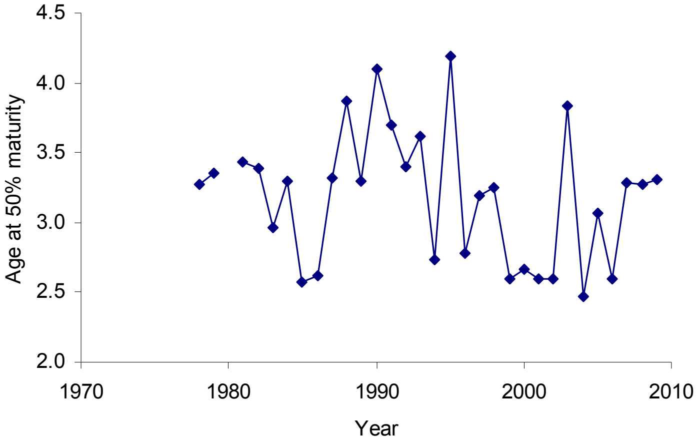


Figure 7. Mean age at 50% maturity for sGSL white hake, 1978-2009, based on a logistic regression analysis of maturity data collected during the annual RV survey of the sGSL and assuming a 50:50 sex ratio (T. Surette, DFO Moncton, unpublished analysis).

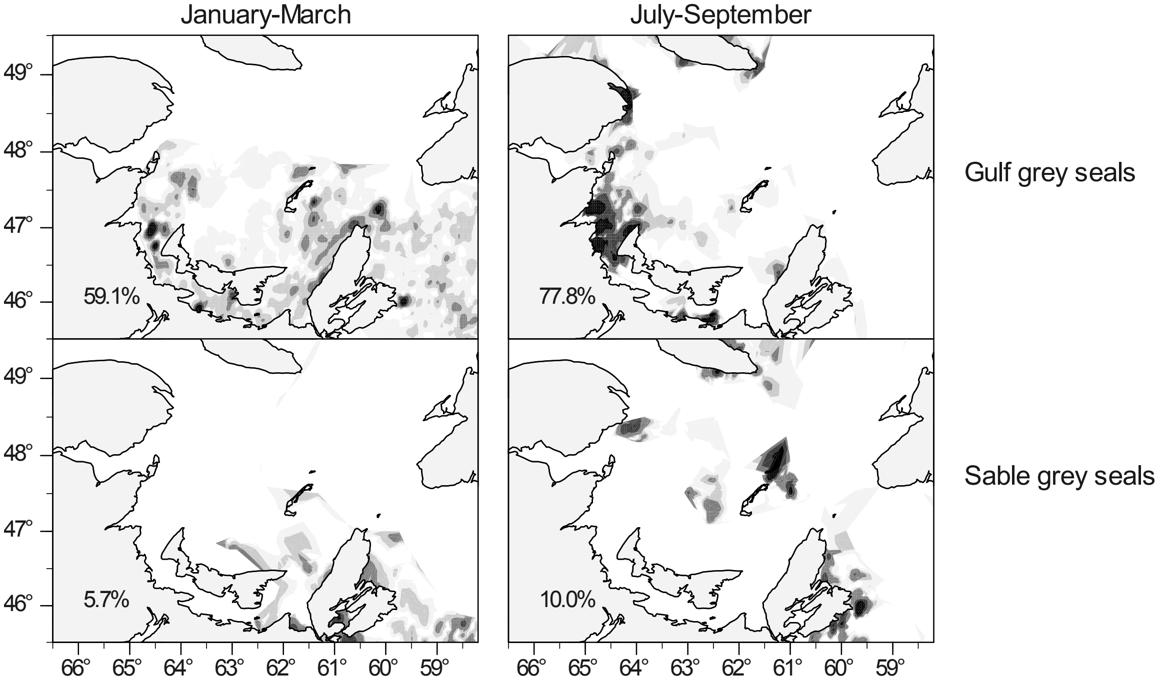


Figure 8. Summary of the geographic distribution of grey seals in the southern Gulf of St. Lawrence and neighboring areas, by population (rows) and for two example seasons, winter and summer (columns) (from Benoît et al. 2011b). The incrementing grey shading represents increasing grey seal density based on the 10th (lightest grey), 25th, 50th, 75th and 90th (black) percentiles for density in each panel. The percentage of transmitting tagged seals that occurred in the represented geographic area in the season in question is written in the left corner of each panel.

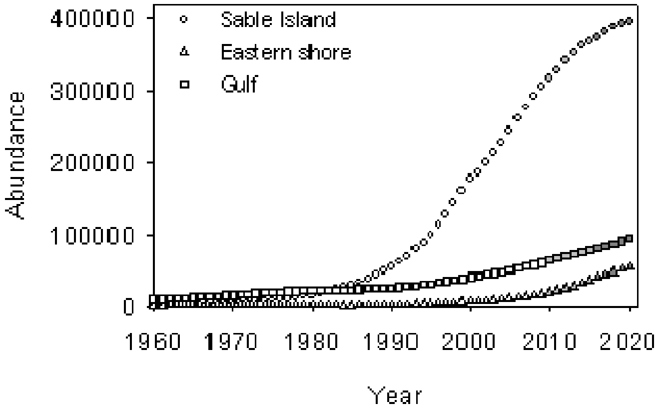


Figure 9. Estimated abundance of grey seals in the Gulf, Eastern Shore and Sable Island herds (Hammill unpublished results). Abundance values projected using the population model for 2010-2015 are in light grey (Hammill unpublished results), and those projected based on recent population trajectories are in dark grey (Benoît, unpublished results).

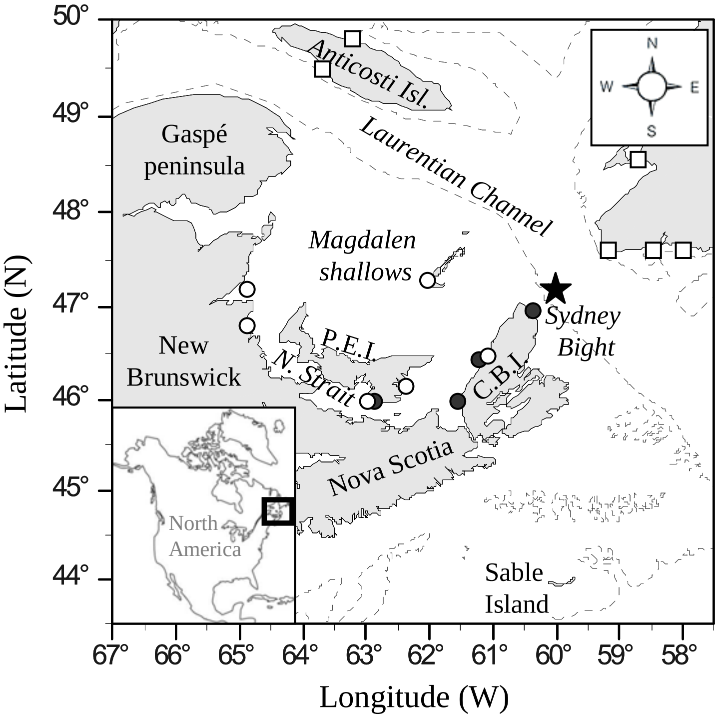
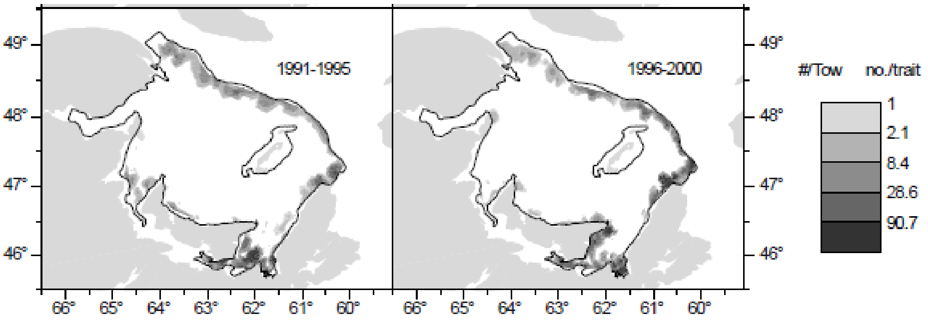


Figure 10. Map of the southern Gulf of St. Lawrence indicating the locations in the Gulf where grey seal stomach (squares) and intestine (circles) content samples have been taken either during spring and summer (white symbols) or during late autumn and winter (black) since 1994 (Hammill et al. 2007; Stenson et al. 2011). Winter samples collected near St. Paul's Island are indicated by a black star. Figure taken from Benoît et al. (2010b).

White hake <45 cm (approx. ages 0-4)



White hake 45+ cm (approx. ages 4+)

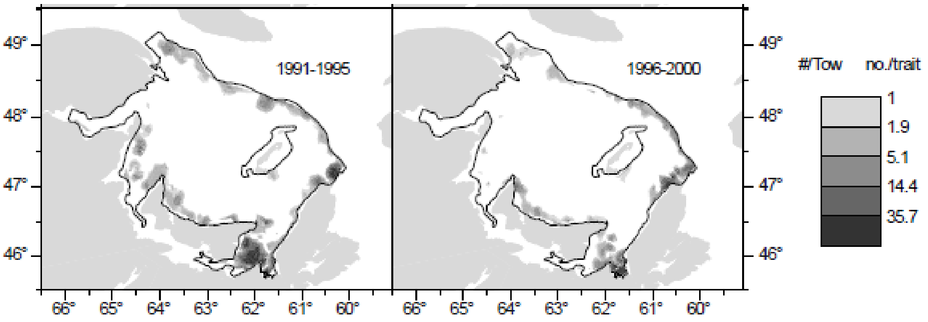


Figure 11. Distribution of two size classes of white hake during the 1990s (from Swain and Benoît 2001).

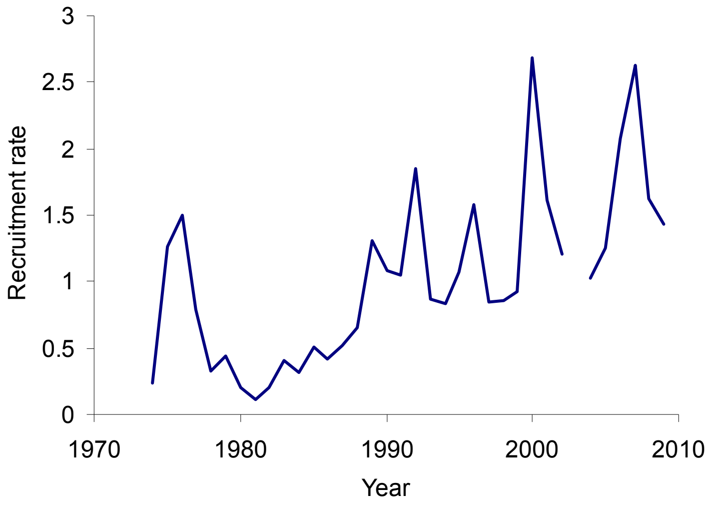


Figure 12. Interannual trends in the recruitment rate (age 3 numbers at time t/spawning stock biomass at time t-3) of sGSL white hake.

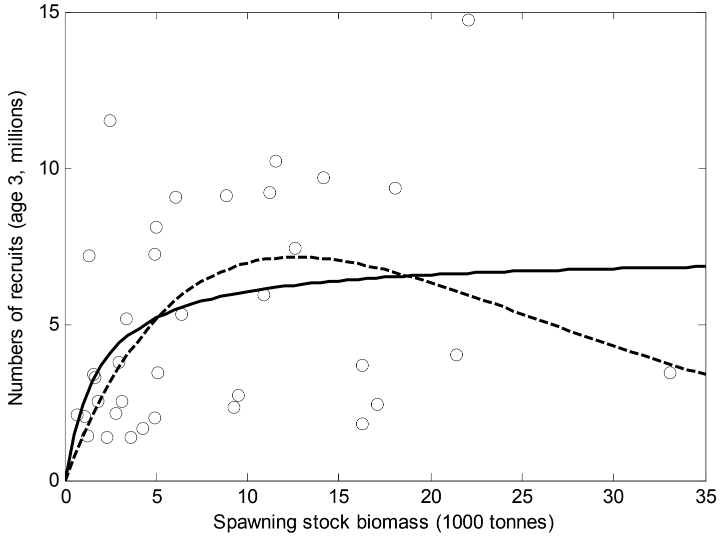


Figure 13. Number of sGSL white hake recruits (millions at age 3, time t) as a function of spawning stock biomass (tonnes, time t-3) with fitted Ricker (dashed line) and Beverton-Holt (solid line) stock-recruitment relationships.

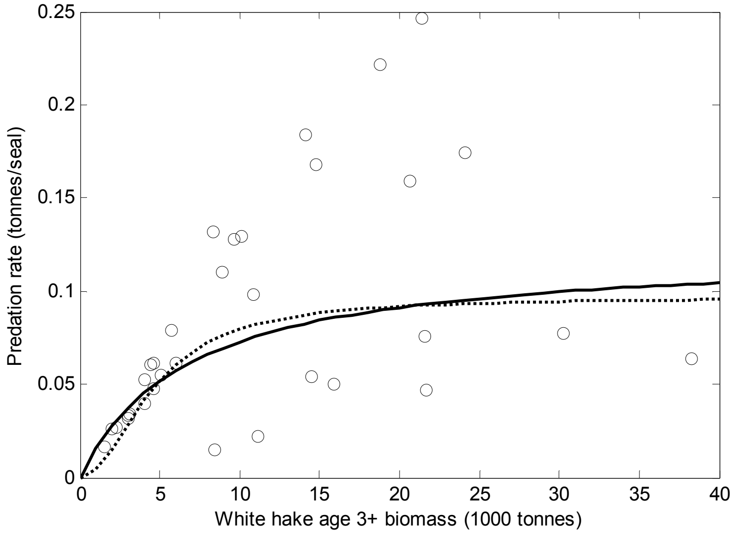


Figure 14. Inferred predation rate of 3+ sGSL white hake by grey seals as a function of white hake biomass, with fitted Type II (solid line) and Type III (dotted line) functional responses.

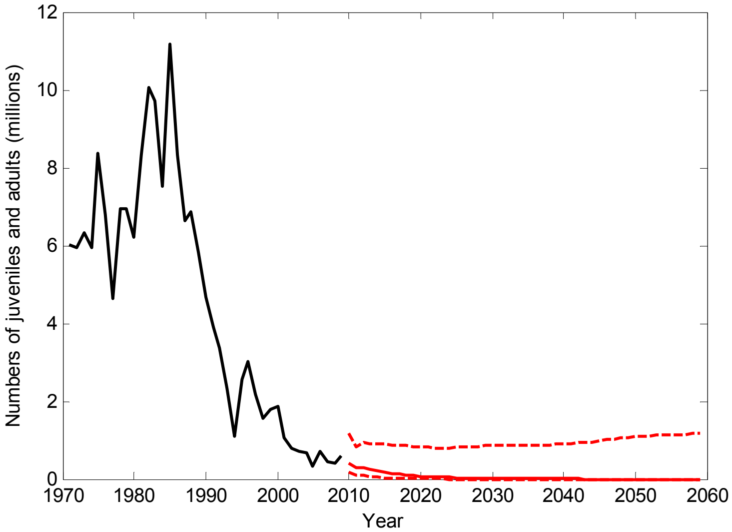


Figure 15. Estimated abundance of sGSL juvenile and adult winter skate from the state space model of Swain et al. (2009) (black line 1971-2009, median values from the posterior distribution of states) and projected abundance values based on mortality conditions from the 2000s (solid line is the median value, dashed lines are the 2.5th and 97.5th percentiles).

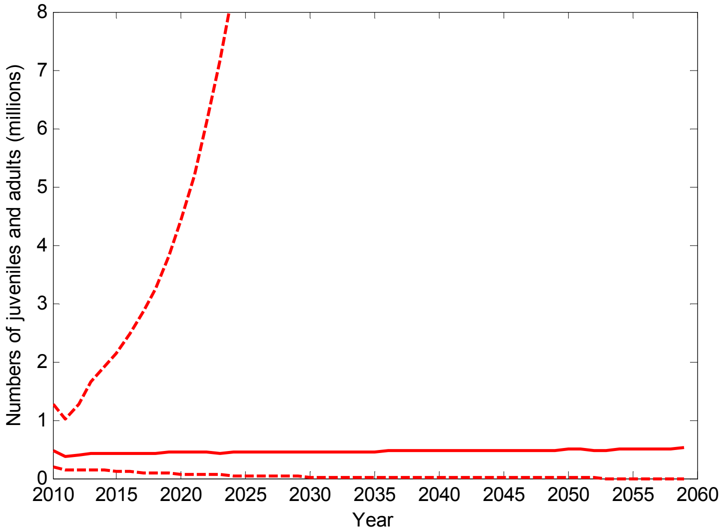
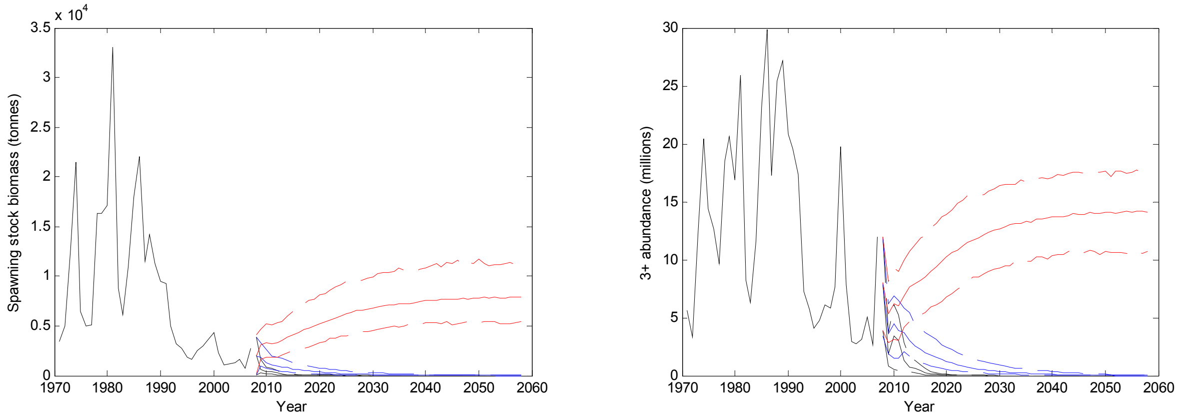


Figure 16. Projected abundance in the sGSL winter skate population assuming that M_{adult} is reduced by 57% (solid line is the median value, dashed lines are the 2.5th and 97.5th percentiles).

a) Ricker stock-recruitment relationship



b) Beverton-Holt stock-recruitment relationship

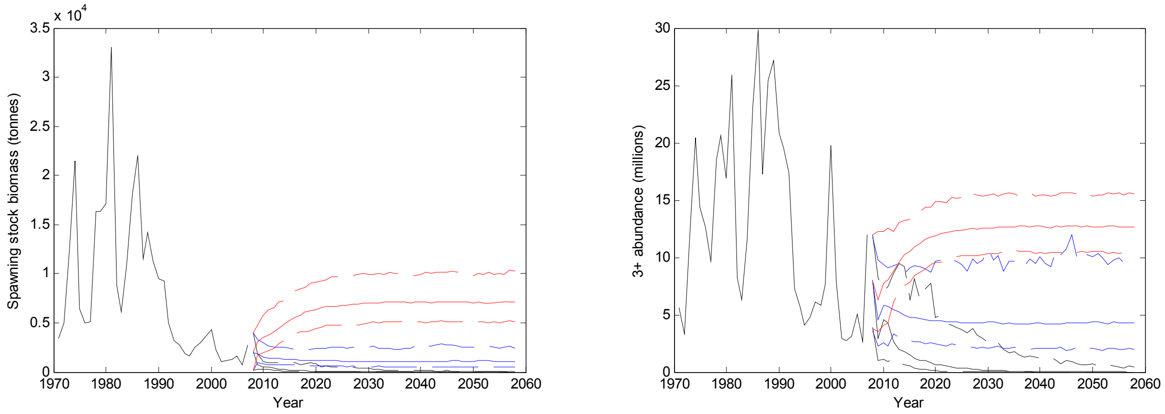


Figure 17. Observed (1971-2008) and projected (2009-2058) spawning stock biomass (left panels) and age 3+ abundance (right panels) of sGSL white hake. Values from 1971-2008 were estimated based on the annual RV survey. Projections were made using either a) Ricker or b) Beverton-Holt stock-recruitment relationships (solid line – median projection; dashed lines – 2.5 and 97.5th percentile) and assuming the current values of M (black), a 50% reduction in current M (blue) and a 75% reduction in M (red).

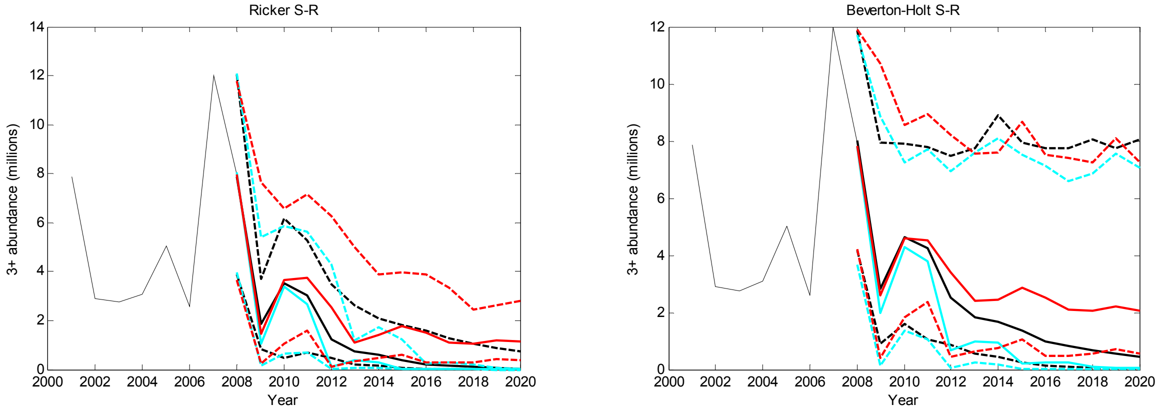


Figure 18. Observed age 3+ abundance (2001-2008) and projected values (2009-2020) based on a Ricker (left) or Beverton-Holt (right) stock-recruitment relationship (solid lines are the median projections, dashed lines indicate the 2.5th and 97.5th percentiles of stochastic projection). Projections were made using either the estimated M (±SE) for 2009 (black lines), or M resulting from grey seal predation following a Type II (cyan lines) or Type III (red lines) functional response.