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Estimated consumption of southern Gulf of St. Lawrence cod by grey seals: bias, uncertainty and two proposed approaches

Estimation de la consommation de morue du sud du golfe du Saint-Laurent par les phoques gris : biais, incertitude et proposition de deux approches

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ABSTRACT

A Zonal Assessment Process on the potential impacts of grey seals (*Halichoerus grypus*) on fish populations in eastern Canada was held October 4-8, 2010. The terms of reference for that meeting included providing stock/area-specific estimates of grey seal diet and prey consumption, and assessing the possible sources of bias and uncertainty in estimates of grey seal diets. This research document was prepared to address these questions as it relates to grey seals feeding in the southern Gulf of St. Lawrence (sGSL) and neighboring areas, with an emphasis on the consumption of sGSL cod (*Gadus morhua*) by grey seals. The diet of grey seals in the sGSL has been inferred using prey hard parts recovered from seal stomachs and intestines. Based on an analysis of grey seal movements using satellite telemetry data, the median stomach and intestine sample generally reflects prey that were consumed within 5 and 12 km of the diet sampling location, respectively. Taking into consideration the geographic locations of grey seal diet samples and the spatial distribution of different sizes of cod, the size composition of cod in the diet suggests that grey seals selectively prey on larger cod. Furthermore, based on the geographic distribution of diet sampling sites, we conclude that the diet of grey seals remains unknown in many areas where they occur. In particular, during the spring and summer, there are no diet estimates from areas where there would be a high probability of sampling seals that foraged offshore. This precludes directly estimating a representative and reliable grey seal diet for the sGSL based on the existing data. We therefore used two different approaches to estimate possible consumption of two size classes of cod (<35 cm and 35+ cm) by seals in the chosen focal year of 2005. The first approach was based on fine scale spatio-temporal overlap between cod and seals, with assumptions concerning the diets of seals where they overlap with cod. Using this approach seals were estimated to consume on average approximately 1800-2300 t of cod <35 cm and 1600-2000 t of 35+ cm cod, depending on assumptions. The second approach was based on spatio-temporal overlap at the scale of Northwest Atlantic Fisheries Organization areas, with assumptions concerning the average diet of grey seals in the areas. Using this second approach, seals were estimated to consume on average approximately 8200-9800 t of cod <35 cm and 7600-8900 t of 35+ cm. Both approaches for estimating diet are sensitive to unverified assumptions, and their reliability cannot be assessed. The estimates presented should therefore be interpreted as scenarios that indicate possible consumption given particular assumptions for filling data gaps, rather than reliable estimates.

RÉSUMÉ

Un processus d'évaluation zonale sur l'incidence potentielle des phoques gris (*Halichoerus grypus*) sur la population de poissons de l'est du Canada s'est déroulé du 4 au 8 octobre 2010. Une composante du mandat convenu pour cette réunion était de fournir des estimations de la prédation et du régime alimentaire du phoque gris propres au stock ou à la région, et d'évaluer les sources possibles de biais et d'incertitude dans l'estimation du régime alimentaire du phoque gris. Le présent document de recherche, préparé pour aborder ces questions, se rapporte à l'alimentation des phoques gris dans le sud du golfe du Saint-Laurent (SGSL) et des régions avoisinantes, notamment en ce qui concerne la consommation de morues (*Gadus morhua*) du SGSL par les phoques gris. Le régime alimentaire du phoque gris dans le SGSL a été estimé à partir des parties dures des proies retrouvées dans l'estomac et l'intestin des phoques. En se fondant sur une analyse des déplacements du phoque gris basée sur des données de télémesure satellitaire, les échantillons prélevés dans l'estomac et l'intestin médians proviennent généralement de proies qui ont été consommées pas loin de 5 et 12 km de la zone d'échantillonnage, respectivement. En prenant en considération l'emplacement géographique des sites d'échantillonnage alimentaire et la répartition spatiale par taille des morues, il semblerait que le phoque gris cible les morues de plus grande taille parmi les morues consommées. En outre, la répartition géographique des sites d'échantillonnage nous amène à conclure que le régime alimentaire des phoques gris reste inconnu dans de nombreuses zones. En effet, l'absence d'estimations durant le printemps et l'été pour les zones dans lesquelles il y aurait de fortes chances de prélever des échantillons sur des phoques partis chercher leur nourriture au large empêche d'estimer de manière fiable et représentative le régime alimentaire des phoques gris dans le SGSL à partir des données disponibles. C'est la raison pour laquelle nous avons utilisé deux approches différentes pour estimer la consommation par les phoques de deux catégories de morues (morues de moins de 35 cm d'une part, et de plus à 35 cm d'autre part) pour une année ciblée, notamment 2005. La première approche reposait sur un chevauchement temporel à échelle fine entre les morues et les phoques, ainsi que sur des hypothèses concernant le régime alimentaire du phoque durant cette période. Cette approche a permis d'estimer que les phoques consommaient en moyenne entre 1 800 à 2 300 tonnes de morues de moins de 35 cm, et entre 1 600 à 2 000 tonnes de morues de plus de 35 cm, les chiffres variant en fonction des hypothèses. La seconde approche était fondée sur un chevauchement spatio-temporel à l'échelle des zones de l'Organisation des pêches de l'Atlantique Nord-Ouest, ainsi que sur des hypothèses concernant le régime alimentaire moyen des phoques gris dans ces régions. Cette seconde approche a permis d'estimer que les phoques consommaient en moyenne entre 8 200 à 9 800 tonnes de morues de moins de 35 cm, et entre 7 600 à 8 900 tonnes de morues de plus de 35 cm. Étant donné que les deux approches d'estimation du régime alimentaire reposent sur des hypothèses non vérifiées, il est impossible d'en évaluer la fiabilité. Les estimations présentées doivent donc être interprétées comme des scénarios indiquant la consommation potentielle compte tenu d'hypothèses particulières destinées à combler les lacunes statistiques, plutôt que comme des estimations fiables.

OBJECTIVE

A Zonal Assessment Process (ZAP) on the potential impacts of grey seals (*Halichoerus grypus*) on fish populations in eastern Canada was held October 4-8, 2010. The terms of reference for that meeting included providing stock/area-specific estimates of grey seal diet and prey consumption, and assessing the possible sources of bias and uncertainty in estimates of grey seal diets. This research document was prepared to address these questions as it relates to grey seals feeding in the southern Gulf of St. Lawrence (sGSL) and neighboring areas, with an emphasis on the consumption of sGSL cod (*Gadus morhua*) by grey seals.

Information on the diet of grey seals foraging in and around the sGSL comes largely from the analysis of hard parts recovered from the digestive tracts of shot animals. In this working paper, we first examine the extent to which these samples are representative of seals foraging in the sGSL. Finding that they indeed are not directly representative, we then present two approaches based on the digestive tract data to estimate the possible consumption of sGSL cod by grey seals. Limitations of the diet data and their use in estimating consumption are discussed.

ARE THE DIET DATA REPRESENTATIVE?

BACKGROUND

To understand whether the existing diet data properly reflect grey seal feeding in the sGSL and neighboring areas, we first estimated the probable foraging zones represented by the existing seal diet samples. These estimates are derived from approximate gut passage times of fish consumed by grey seals and an analysis of seal displacement (movements), based on satellite tagging data.

The majority of grey seal diet samples from the sGSL processed to date are from stomachs and intestines, whereas samples from the northern Gulf and coastal Newfoundland are for stomachs only (Hammill et al. 2007; Stenson et al. 2011). Digestion times associated with these samples vary with meal size, prey type and prey size (Grellier and Hammond 2006). Seal stomach samples generally represent feeding that occurred in a period of at least 6 hrs preceding sampling (Murie and Lavigne 1985). The apparent retention of otoliths in the stomachs of a seal having consumed large meals composed of larger-bodied fish (Stenson et al. 2011) suggests that passage times through the stomach can be longer, on occasion. The median passage time of most fish prey species, from consumption to excretion, is approximately two days, and the vast majority of fish are excreted within 64 hrs (Grellier and Hammond 2006). Prey recovered from grey seal intestines were therefore generally consumed 6-64 hrs prior to sampling.

METHODS

We used data from satellite tagged NW Atlantic grey seals (Goulet et al., 2001; Breed et al. 2006; Harvey et al. 2008) to construct the frequency distribution of the net spatial displacements of juveniles (Gulf), males and females over the time periods pertinent to the gut samples. These displacements were then used to determine the spatial areas most likely represented by the existing gut samples. The movement tracking data used were state-space model posterior estimates (i.e., accounting for process and observation error), spaced evenly every 8-hr (Jonsen et al. 2005). All of the position data were used, without regard for the type of movement (e.g., small-scale movements vs. directed migratory movements; Austin et al. 2004) surrounding a given datum. This was because we had no a priori basis for determining the type(s) of movement that would have occurred during the period of up to 3 days prior to diet sampling.

Displacements (km) over individual 8-hr periods were assumed to be indicative of the extent of the foraging zone represented by seal stomach samples. The foraging zone reflected in intestine or scat samples was assumed to be characterized by displacements occurring during a period beginning 8-hrs prior to a given point in time (the purported sampling event) and ending either 16, 48 or 64 hrs prior to the time (i.e., covering the range of prey passage times through the entire gut, based on Grellier and Hammond 2006). Net spatial displacements were calculated as the straight-line distance (km) from the purported sampling location.

RESULTS

The median displacement of grey seals over an 8-hr period was approximately 5 km (inter-quartile range: 2-10 km) (Fig.1). In other words, half the seal stomachs in a given sample likely represent feeding within 5 km of the sampling location. At the other extreme, the median of displacements occurring during an interval 8-64 hrs prior to a purported sampling event was 12 km (inter-quartile range: 5-35 km). Thus, half of intestine or scat samples likely represent feeding within 12 km of the sampling location.

Over all time intervals considered, females undertook a higher frequency of short-distance trips, compared to males and then juveniles, consistent with the sex-related differences in movement patterns reported by Austin et al. (2004). The frequency distribution of displacements was remarkably consistent for same-sexed seals tagged in different areas (e.g., females shown in Fig. 2).

Likely foraging areas represented by existing stomach and intestine samples were mapped, based on the cumulative frequency distributions of displacements (Fig. 3). The most likely foraging areas (taken here as the 75^{th} percentile of displacements) represented by intestine samples obtained in the sGSL during the spring and summer cover small areas in and around New Brunswick's Miramichi estuary, the eastern-most portion of the Northumberland strait, part of the Cape Breton shoreline and the southern tip of the Magdalen islands (Fig. 3a). In addition, existing stomach samples cover very localized foraging areas on the north and south coast of Anticosti Island and around south-western Newfoundland. Gut samples during the late fall and winter cover even more restricted foraging areas: the eastern-most portion of the Northumberland Strait and parts of the Cape Breton coast (Fig. 3b).

Grey seals occur over a much broader area than that represented by diet samples (Fig. 4). There are areas of apparent grey seal aggregation that are poorly or not represented in the diet data such as the Gaspé and Acadian peninsulas (western Gulf) in spring/summer (though, see Benoît et al. 2011 for a discussion of the limitations of inferring grey seal distribution based on satellite tagging).

Diet samples collected during the spring/summer cover foraging areas where cod <35 cm occur (e.g., Northumberland Strait, off of the Miramichi estuary), but largely miss feeding that occurs in areas of cod aggregation off the north-western portion of Prince Edward Islantd (P.E.I.) and north of the Magdalen Islands (Fig. 5a). These same samples often do not cover feeding in areas where cod 35+ cm occur, let alone aggregate. In contrast gut samples collected on the northern tip of Cape Breton Island (near St. Paul's Island) during the winter (Fig. 3b) should reflect feeding that occurred in an area of aggregation for both size classes of cod (Fig. 5b).

However, diet samples collected from seal intestines in this area will also represent to an extent feeding that occurred outside the areas of cod aggregation (Fig. 3b).

Spatial aliasing of grey seal diets has important implications for the perceived size-selectivity of seals feeding on cod. Based on spring/summer sampling (Hammill et al. 2007), the size distribution of cod in seal diets closely matches the size distribution in the population over the 15-65 cm length range (Fig. 6). This might be interpreted as indicating that grey seals consume cod in proportion to their availability for cod 15-65 cm, but select against cod <15 cm and the now very rare cod >65 cm in length. However, as we have shown in this section, these diet samples were obtained from foraging areas where seals were much more likely to have encountered small (<35 cm) rather than larger cod. Hence, the proportion of large cod is much lower in the foraging area represented by these diet samples than in the cod population as a whole. Thus, the size composition of cod in these spring/summer diet samples suggests that grey seals may in fact be selectively preying on the larger (e.g., 40+ cm), less available cod. Likewise, the samples collected in winter off northern Cape Breton (Stenson et al. 2011), where small and large cod were available roughly in proportion to their abundance in the population, clearly suggest positive selection of large cod by seals (Fig. 6). This apparent selection for larger fish may be partly due to a greater recovery rate for larger otoliths, though this effect appears to be relatively slight for cod (Grellier and Hammond 2006), and might be offset by a higher likelihood of missing large cod in seal diets due to stochastic effects related to their lower abundance and the modest number of seals sampled (n=100).

LIMITATIONS OF THE AVAILABLE SEAL DIET DATA - SUMMARY

Diets inferred from the analysis of recovered prey hard parts reflect foraging within a restricted area (generally <35 km) from the point of sampling. Based on the geographic distribution of diet sampling sites, we conclude that the diet of grey seals remains uncharacterized in many areas where grey seals occur in and around the sGSL. In particular, during the spring and summer, there are no diet estimates from areas where there would be a high probability of sampling seals that foraged offshore. Because the composition of the 'offshore' fish community is considerably different from the composition inshore (e.g., Darbyson and Benoît 2003), it would be inappropriate to assume that the gut contents of seals that foraged inshore would be representative of offshore feeding by seals. It is therefore not possible to directly estimate a representative and reliable grey seal diet for the sGSL based on the existing data. Different approaches are therefore required. In the next section we estimate cod consumption based on a combination of seal diets where cod and the foraging zones of sampled seal overlap, and the relative spatial overlap of cod and seals. In a subsequent section we estimate cod consumption using a simpler approach, based on arguments for how the percentage of cod in seal diets might change seasonally.

ESTIMATING CONSUMPTION OF COD:
I - SEAL DIETS WHERE COD AND SEALS OVERLAP

APPROACH I - BACKGROUND AND METHODS

Because of large spatial and seasonal gaps in grey seal diet sampling, consumption of cod by seals was estimated by first deriving two seal diet states: one for seals foraging in areas where cod are aggregated and a second for seals foraging in areas where cod are dispersed. These were then combined with estimates of the number of seals that overlap spatially with cod during seasons when cod are dispersed and seasons when cod are aggregated, as well as a bioenergetics model for grey seals, to estimate total annual consumption of cod in two length classes, <35 cm and 35+ cm.

The diet samples collected in November-December 2008 off northern Cape Breton represent the food habits of grey seals feeding in the area where both small and large cod are aggregated during the winter. These samples are the only diet samples from the Northwest Atlantic that were taken from seals whose probable foraging area substantially overlapped with areas of cod aggregation. Given that cod and other important grey seal prey species that overwinter in the Cabot Strait area (e.g., Atlantic herring, white hake) remain there until spring, these diet samples are likely to represent the diets of seals foraging in the area throughout the winter. For the purposes of consumption estimation we have further assumed that these samples generally represent the diet of seals feeding on cod aggregations in other seasons (henceforth called the aggregated diet). The extent to which this assumption is correct is not known, given that cod aggregations at other times of the year occur in areas that are shallower and that comprise a different composition of alternate prey, and occur at a time when cod are in a behavioural state (e.g., reproductive, migratory) that is different from their overwintering state.

Based on prey retention times during digestion and typical seal movement, stomach contents are more likely to reflect prey consumed near the point of seal diet sampling, compared to intestinal contents. Seal stomach samples collected at a location where cod aggregate, such as the samples collected in November-December 2008, would therefore normally be expected to better reflect seal feeding in the immediate area. However, there are two considerations that precluded using the prey composition observed in stomachs to infer local diet. First, unlike seal diet samples collected from intestines or from faeces, correction factors have not been developed to account for differential loss within the stomach of otoliths from different species and sizes of fish (e.g., Bowen 2000). Second, stomach contents of one seal in the 2008 sample implied a very large meal, providing some evidence that the otoliths of large cod might be differentially retained for some time in the stomachs (Stenson et al. 2011). It was therefore agreed at the ZAP that the species composition inferred from numerically corrected seal intestine samples should be used in the subsequent analyses, even if these samples would reflect feeding that occurred over a broader geographic area that might include places where there are no cod (DFO 2010). Because Atlantic cod are the only member of their genus present in the St. Paul's Island area during winter, individual fish identified as *Gadus* sp. in the diet samples were assumed to be *G. morhua*. It also became apparent after the ZAP that 10 of the 100 seals purported to have been taken near St. Paul's Island in 2008 had in fact been taken off south-west Cape Breton, an area where Atlantic cod do not occur in winter. The gut contents of these seals were not included in the estimate of diet composition presented here.

Based on these considerations, the average proportion of cod in the diet of grey seals foraging around St. Paul's island during the late fall and early winter of 2008 was 0.25 for male seals and 0.10 for females. The size composition of consumed cod was inferred from measurements of non-eroded otoliths recovered from both the stomach (24 cod from 8 stomachs) and intestine samples (9 cod from 5 intestines). Based on those samples, 58% (8% S.E.) of consumed cod were 35 cm or longer (Fig. 6; Stenson et al. 2011). These estimates were taken to represent the “aggregated” diet.

During the spring/summer, the available diet samples might represent some feeding of grey seals in areas where cod <35 cm occur, but are not aggregated. To a lesser degree, this is true also of cod 35+ cm. In both cases, the inferred summer diets likely underestimate the proportion of cod given that the most probable foraging areas represented by the available samples include mostly areas where cod are absent or at low densities (Fig. 5). Nonetheless, we take these diets to represent the feeding of seals in areas where cod occur but are not highly aggregated (henceforth, the dispersed diet). Atlantic cod represented 11.9% (1.7 s.d.) of the energy in the dispersed diet, of which 62.2% was cod <35 cm and 37.8% was cod 35+ cm (Hammill et al. 2007).

The second component of estimating cod consumption by grey seals was to define the spatial and temporal overlap between the two species. Benoît et al. (2011) defined the monthly geographic areas of overlap between seals and cod and calculated the degree of overlap, based on the seal satellite transmissions data and cod distribution as inferred from fishery independent surveys and spatial patterns in the commercial fishery (Figs. 7 and 8). Furthermore, the authors placed the inferred monthly distribution of two size classes of cod, <35 cm and 35+ cm, in one of three categories: aggregated, migratory (i.e., aggregated yet transitioning through the area) and dispersed. Here we assume that seals overlapping with cod during months of aggregation (November-April, as well as June for cod 35+ cm) feed on them at the rate indicated by the aggregated diet. The diet of overlapping seals during months in which cod are dispersed was assumed to follow the dispersed diet, and diet during months of cod migration was assumed to be an even mix of aggregated and dispersed diets.

The third component of estimating consumption was to define the food requirements of grey seals, using a commonly employed bioenergetics model (e.g., Mohn and Bowen 1996; Hammill and Stenson 2000). The average gross energy intake (*GEI*, in kilojoules) for grey seals of a given sex *s* and age *a*, during month *n* is defined as:

$$1)\qquad GEI_{nsa} = \alpha W_{nsa}^{\beta} \cdot AF \cdot GP_a \cdot ME^{-1} \cdot D_{nsa}$$

where αW_{nsa}^{β} is the Kleiber equation (Kleiber 1975) describing the allometric relationship between seal body mass (*W*) and metabolism, *AF* is the ‘activity factor’ that accounts for increased metabolism due to activity in the field, *GP* is an age-specific growth premium that accounts for the additional energy required by rapidly growing young seals, *ME* is the metabolizable energy (i.e., assimilation efficiency or the proportion of GEI available to the seal for maintenance and growth) and *D* is the age and sex-specific average number of days spent feeding during month *n*. The parameter *D* accounts for known periods of fasting: 21 days during lactating/breeding for females ages 5+ (occurring between late December and February), 24 days for adult males (ages 9+) during breeding, and two weeks during moulting (May for females, June for males).

Sex-specific seal mass-at-age W_{sa} (in kg) was estimated using a Gompertz growth model (e.g., Mohn and Bowen 1996) fit to individual seal masses collected in the Gulf of St. Lawrence during the summer:

2) $W_{sa} = \gamma_{1s} \cdot \exp(-\gamma_{2s} \cdot \exp(-\gamma_{3s} \cdot a))$

where γ_1, γ_2, and γ_3 are model parameters. The W_{sa}, which were taken to represent mass in August, were adjusted for seasonal changes in mass due to growth, lactation and reduced feeding during moulting and breeding following Beck et al. (2003), to produce monthly mass-at-age for males and females, W_{nsa} (Fig. 9). The values for the parameters of eqns. 1 and 2 are given in Appendix I.

The total annual consumption of cod in size class *x* (either <35 or 35+ cm), C_x, was then estimated as:

3) $$C_x = \sum_{n=1}^{12}\sum_{h=1}^{3}\sum_{s=1}^{2}\sum_{a=1}^{40} o_{xnhsa} \cdot p_{ns} \cdot q_x \cdot N_{hsa} \cdot \exp(-M_{ha} \cdot n/12) \cdot GEI_{nsa} \cdot ED^{-1}$$

where o_{xnhsa} is the proportion of grey seals in herd *h* (either Sable, Gulf or Eastern Shore), of sex *s* and age *a*, that overlapped with the distribution of cod in size class *x* in month *n* (from Benoît et al. 2011), p_{ns} is the proportion of cod in the diet of grey seals of sex *s* during month *n*, q_x is the proportion of consumed cod that are in size class *x*, *M* is the natural mortality rate of seals and *ED* is the energy density of cod (see Appendix I for the values of the parameters).

The value of p_{ns} is determined by whether grey seals are overlapping with cod during periods of aggregation or dispersal. Because there has been no satellite tracking of seals in the Eastern Shore herd, the seasonal distribution of these animals is not well characterized. We assumed their distribution, and therefore their overlap with cod, could be described as a mixture of the respective overlap of the Sable and Gulf herd seals with cod:

4) $$o_{EasternShore,xmsa} = r \cdot o_{Sable,xnsa} + (1-r) \cdot o_{Gulf,xnsa}$$

where *r* is the proportion of the Eastern Shore herd that adopts a seasonal spatial distribution like that of seals from Sable Island. The choice of value for *r* was largely arbitrary, though we assumed that there was a greater propensity for Eastern Shore grey seals to behave like those from Sable Island (Appendix I).

The uncertainty in cod consumption by seals was estimated using a Monte Carlo simulation. For each iteration of the simulation, values for most of the parameters of eqns. 1-4 were drawn from the respective probability distribution assumed to characterize the uncertainty of each parameter (Appendix I; see Benoît et al. 2010 for details). Uncertainty in o_{xnhsa} for the Gulf and Sable herds was included using a non-parametric bootstrap of the grey seal satellite-tracking data, treating individual tagged seals as sampling units, and sampling these seals with replacement from within each month and seal category cell (details in Benoît et al. 2011). Because of low numbers of tagged Gulf seals in certain cells, data from adjoining months were combined, as described in Benoît et al. (2011). For the reasons described in that paper, uncertainty in cod distribution was not included. Uncertainty in the proportion of cod in the diet of grey seals (p_{ns}) was incorporated using a non-parametric bootstrap of the original diet samples.

Two quantities related to consumption were calculated. The first is the per-capita-consumption of cod by individual grey seals for each of the Gulf and Sable herds. These numbers, along with some appropriate functional response, would allow speculation on the consumption of cod by grey seals in the past and future. The second quantity is the total biomass of cod consumed in

2005. That year was chosen as roughly the mid-point of the available diet samples, and is included in the period covered by the satellite telemetry data. The 2005 estimate can then be compared to estimated available cod biomass and losses due to natural mortality.

APPROACH I -RESULTS

The mean annual per capita consumption of sGSL cod <35 cm by Gulf grey seals was 0.028 t/seal (95% confidence interval, 0.017-0.046), and consumption by Sable grey seals was 0.002 (0.001-0.004) t/seal. Based on the estimated numbers of grey seals in each herd in 2005, and adding the seals from the Eastern Shore, this resulted in an average consumption of 1800 (1060-3000) t of cod <35 cm that year (Fig. 10a). Similarly, the mean annual per capita consumption of sGSL cod 35+ cm by Gulf grey seals was 0.027 (0.016-0.044) t/seal, and consumption by Sable grey seals was 0.002 (0.001-0.003) t/seal. It yielded an average estimated consumption of 35+ cm cod of 1550 (890-2500) t for 2005 (Fig. 10a).

There is some evidence that the winter distribution of cod can extend into the northern portion of Northwest Atlantic Fisheries Organization (NAFO) area 4Vs (pink area in Figs. 7 and 8; see Benoît et al. 2011 for details). Including this area in the estimation increases the number of seals overlapping with cod, particularly the number of females from Sable Island (Breed et al. 2006). As a result, the mean per capita consumption of cod <35 cm was 0.030 (95% C.I., 0.018-0.048) and 0.002 (0.001-0.004) t for Gulf and Sable Island grey seals respectively. Likewise, the per capita consumption of cod 35+ cm was 0.030 (0.017-0.048) and 0.002 (0.001-0.004) t for Gulf and Sable Island grey seals respectively. It yielded an average consumption of 1950 (1100-3200) t of <35 cm cod and 1700 (950-2800) t of 35+ cm cod for 2005 (Fig. 10b).

The preceding estimates are based on Gulf grey seal numbers estimated by the traditional population model (51 311 ± 2696 individuals in 2005; Hammill 2005). A more recent population model which accounts for ice-related mortality in pups (e.g., Hammill and Stenson 2010) predicts a higher abundance for the herd (62 820 ± 2696 individuals in 2005). Using these numbers increases the consumption of both size classes of cod by around 14-16% (Fig. 11).

Though there is uncertainty in the seal diet proportions to apply to consumption in each month, the proper proportions to use for the months of cod migration are probably most uncertain. We therefore re-ran the simulations assuming that the diet of seals during cod migration was 90% of the dispersed diet and 10% of the aggregated diet, for the scenario that includes northern 4Vs in winter and is based on the Gulf grey seal numbers from the traditional model. This resulted in a mean 2005 consumption of 1930 t of <35 cm cod (a 1% decrease) and 1550 t of 35+ cm cod (a 10% decrease). In contrast, if the diet of seals during cod migration was composed of 10% of the dispersed diet and 90% of the aggregated diet, mean 2005 consumption was 1970 t of <35 cm cod (a 1% increase) and 1860 t of 35+ cm (a 10% increase).

APPROACH I - DISCUSSION

There are two principal sources of possible bias that were not accounted for in the estimates from Approach I. The first is the assumed proportions of cod in the monthly seal diets. We have presented arguments to support our assumptions on diet proportions, but have not looked at sensitivity to assumed proportions other than during migration. The basis for changing the numbers isn't clear and any changes would have been arbitrary, leading to somewhat predictable results (i.e., increasing the proportion increases consumption). So, while we feel for example that the assumed diet during the summer almost certainly under-represents the proportion of cod consumed by overlapping seals, we do not know by how much or whether this might be counterbalanced by an overestimation in other months. Given the spatially and seasonally clustered origin of the seal diet samples, the relatively small number that have been collected, and the few fish that have been measured to estimate prey size composition (particularly in winter), the reliability of existing diet information may be low even when used to characterize two diet states.

The second major source of bias is an inaccurate summary of the number of seals overlapping with cod, and may be considerably more important than bias in diet proportions. Benoît et al. (2011) argue that the movement patterns of tagged seals may not be representative of movements in the population, particularly for seals tagged in the Gulf. Furthermore, because the number of tagged seals is small, some important areas frequented by seals may be underrepresented in the recorded positions of seals. If these areas happen to also be areas of cod aggregation, consumption would also be underestimated (the converse being true if they are areas of low cod density). Bias in the estimated distribution of seals based on satellite tagging is likely to be greatest for inferences drawn at fine spatial scales, but will decrease as spatial scale increases. Consequently for the second approach to estimating cod consumption (next section) overlap between cod and grey seals was assessed at the coarser spatial scale of Northwest Atlantic Fisheries Organization (NAFO) areas.

ESTIMATING CONSUMPTION OF COD:
II - ASSUMED SEASONAL CHANGES IN SEAL DIETS

APPROACH II - BACKGROUND AND METHODS

For the second approach, we summarized the monthly proportion of grey seals residing in each of the two NAFO areas, 4T and 4Vn, in which sGSL cod reside for at least part of the year. Summaries by herd and for adult males, adult females and juveniles were produced using the satellite tagging data and following the methods of Benoît et al. (2011) (Table 1). Consistent with that study, data from a 3-month window were used to calculate the proportions for a given month because there were too few tagged seals in particular months (especially April-June).

As in the first approach, we assumed that the existing grey seal diet data can be used to estimate a diet for seals feeding when cod are aggregated and one for when cod are dispersed. Rather than focus only on the consumption of seals that closely spatially overlap with cod (Approach I), we present a scenario based on arguments for the assumed proportions of each diet to apply to seals residing in a NAFO area occupied by sGSL cod in a given month.

From December to March, we assumed that only half of the seals in NAFO 4T would be feeding on cod aggregated in the Cape Breton trough and along the slope of the Laurentian channel (Table 2). This proportion is based on observations of seals residing around the Magdalen

Islands (Clay and Nielsen 1985). The other half of seals in 4T would be feeding in the Northumberland Strait or other areas where cod are absent. Meanwhile for grey seals residing in NAFO 4Vn, 80% of individuals would be feeding on cod aggregations in the Cabot Strait and Sydney Bight areas, whereas the remaining seals would be feeding closer to shore where cod do not occur or are less aggregated (based on Harvey et al. 2010).

During the migration of cod into the sGSL in April and May, half of the seals in 4T were assumed to feed on the cod aggregations, while the other half were assumed to feed in areas where cod are dispersed or absent (Table 2). Because some cod remain in 4Vn in April, diet composition there was assumed to be half of the winter value. Similar assumptions for seal diets in 4T and 4Vn were made for the migration out of the Gulf in November.

During the summer, the diet of grey seals was assumed to be largely represented by the existing summer diet samples (i.e., the dispersed diet). However, as noted earlier, these samples do not include seals feeding offshore or in many of the areas of cod aggregation. Consequently we assumed that 90% of seals adopted the dispersed diet and the remaining 10% of seals fed on cod aggregations (Table 2). In June, when adult cod are aggregated to spawn, the proportion of seals adopting the aggregated diet was set at 20%.

The total annual consumption of cod in both size classes was estimated using eqns. 1-4. As for Approach I, we used a Monte Carlo simulation to assess the variability in cod consumption, based on variability in the inputs to the calculation. Variability in seal distribution, the bioenergetic model and the proportion of cod in both the aggregated and dispersed seal diets was simulated. However, the assumed proportion of seals adopting different diets (Table 2) was taken as a fixed input. Clearly the results of the calculation will be very sensitive to the assumed diets in Table 2 and we did not deem it practical to undertake a detailed sensitivity analysis of these values. Again, we take the resulting estimates as the results of one plausible scenario for filling data gaps rather than a reliable estimate.

APPROACH II - RESULTS

Under this approach, the mean annual per capita consumption of southern Gulf cod <35 cm by Gulf grey seals was 0.128 (95% C.I., 0.073-0.208) t/seal, and consumption by Sable grey seals was 0.009 (0.005-0.016) t/seal. Based on the estimated numbers of grey seals in each herd in 2005, and adding the seals from the Eastern Shore, this resulted in an average consumption of 8300 (4700-13600) t of cod <35 cm that year (Fig. 12a). Similarly, the mean annual per capita consumption of cod 35+ cm by Gulf grey seals was 0.120 (0.066-0.202) t/seal, and consumption by Sable grey seals was 0.008 (0.004-0.014) t/seal. For 2005, this yielded an average consumption of 35+ cm cod of around 7600 (4150-12900) t (Fig. 12a). Consumption estimates for simulations based on 2005 Gulf grey seal abundance from the model incorporating ice-related pup mortality are 9800 (5400-16400) t of cod <35 cm and 8900 (4800-15150) t of cod 35+ cm (Fig. 12b).

GENERAL DISCUSSION

In 2005, the estimated biomass of cod ages 4+ (roughly cod >35 cm) was 62 000 t (Swain et al. 2009). The instantaneous rate of natural mortality (*M*) on those fish was estimated at around 0.6, implying a 45% annual loss in biomass to causes other than fishing (i.e., 28 000 t of 35+ cod lost in 2005). If the satellite telemetry data does indeed provide an unbiased representation of grey seal movements in the sGSL and neighboring areas, and if the assumed diet proportions are reasonable, then the results from Approach I suggest that consumption by grey seals (~1600-2000 t) can explain only about 6% of natural mortality of cod >35 cm, on average. If the assumptions of Approach II are met, then consumption by grey seals (7600-8900 t) can explain on average about 30% of current natural mortality.

Much of the discussion at the 2010 ZAP focused on the natural mortality of cod 5+ years of age (roughly corresponding to 38+ cm). The biomass of 5+ cod in 2005 was estimated at 47 000 t in the most recent assessment (Swain et al. 2009). The estimated *M* on those fish was also 0.6, implying a loss of around 21 000 t of 5+ cod in 2005. Cod 38+ cm comprise around 54.5% and 25% of the cod consumed in the 'aggregated' and 'dispersed' diets respectively (Hammill et al. 2007; data from Stenson et al. 2011). Using these percentages and the methods described above, we estimate that the average consumption of cod by grey seals ranges from 1300-1700 t, or about 7% of *M*, under the assumptions of Approach I. Likewise, estimated average consumption under the assumptions of Approach II ranged from 6200-7200 t, or approximately 33% of *M*.

Though consumption of the two size classes of cod was approximately 4-5 fold higher under Approach II compared to Approach I, we have little basis to judge their relative or absolute reliability. While the first approach may appear more rigorous because it is more reliant on existing data to quantify the finer scale overlap of cod and seals, it is also most subject to bias due to improper characterization of the seal distribution. Both approaches are subject to possible biases in estimated seal diets and are sensitive to a number of assumptions in the estimation methods, and should therefore be taken as no more than 'what-if' scenarios to evaluate the potential consumption of sGSL cod by grey seals.

Partial consumption of prey by seals is another source of potential bias in estimated diets that has not yet been discussed in this document. The consumption estimates presented are based on seal diets inferred from the analysis of prey hard parts recovered from seal guts. Otoliths are the main hard part used to identify fish prey. Prey with few or no hard parts (e.g., cartilaginous fish) typically do not show up in the diet. Likewise, fish prey that are incompletely consumed will not show up in the diet if their heads are not consumed. Selective rejection of fish heads has been documented 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 frequently reported by fish harvesters in and outside the Gulf of St. Lawrence (personal communications to the authors) and has been documented for harp seals in Newfoundland (Lilly and Murphy 2004). The extent to which partial consumption of sGSL cod by grey seals occurs is unknown, but would likely be most pronounced for larger cod, if it occurs. To the extent that it occurs, the proportion of cod in seal diets, especially large cod, will be underestimated.

ACKNOWLEDGEMENTS

Thanks to V. Harvey and N. den Heyer for providing the seal geolocation data and G. Stenson for providing the winter seal diet data from St. Paul's Island. Detailed thoughtful comments were provided by M. Comeau, P. Hammond, G. Lily, and M. Hanson.

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Table 1. Monthly total number of reporting tagged seals and proportion of tagged-seal satellite transmissions originating from NAFO divisions 4T and 4Vn for juvenile, adult male and adult female grey seals tagged in the Gulf of St. Lawrence and pups, adult males adult females tagged on Sable Island. Note that the numbers and proportions are based on a 3-month window centered on the month in question.

Seal tagging location:		Gulf			Sable Island		
Area	Month	Juveniles	Males	Females	Pups	Males	Females
Total number reporting tagged seals							
All	1	18	14	10	13	35	38
	2	16	14	10	13	22	26
	3	13	14	8	11	16	20
	4	11	12	8	8	14	19
	5	7	17	5	24	19	17
	6	9	15	5	24	17	15
	7	12	13	6	24	15	15
	8	19	13	12	23	23	26
	9	21	13	11	22	34	36
	10	21	12	11	19	33	36
	11	20	12	11	18	32	34
	12	18	11	10	16	27	33
Proportion in the area							
4T	1	0.325	0.547	0.794	0	0.022	0.094
	2	0.177	0.405	0.671	0.019	0.047	0
	3	0.080	0.343	0.562	0	0	0
	4	0.116	0.261	0.451	0	0	0
	5	0.823	0.494	0.455	0	0	0
	6	0.984	0.790	0.620	0.010	0	0.130
	7	0.962	0.868	0.714	0.044	0.033	0.174
	8	0.882	0.855	0.617	0.045	0.067	0.183
	9	0.849	0.860	0.603	0.054	0.051	0.155
	10	0.822	0.877	0.646	0.029	0.041	0.093
	11	0.717	0.802	0.764	0	0.001	0.070
	12	0.543	0.655	0.825	0	0	0.078
4Vn	1	0.228	0.171	0.072	0	0.003	0.044
	2	0.258	0.154	0.048	0	0.013	0.081
	3	0.256	0.151	0.038	0	0.006	0.029
	4	0.196	0.149	0.020	0	0	0
	5	0	0.108	0	0	0	0
	6	0.009	0.035	0	0.008	0.003	0.048
	7	0.008	0	0	0.014	0.074	0.047
	8	0.005	0	0	0.033	0.065	0.047
	9	0.002	0.005	0	0.014	0.045	0.004
	10	0.030	0.031	0.006	0	0.037	0
	11	0.083	0.096	0.038	0	0.020	0
	12	0.163	0.151	0.058	0	0.005	0.003

Table 2. Assumed proportion of grey seals residing in each of NAFO 4T and 4Vn that adopted either an 'aggregated' or 'dispersed' diet. This table is used in Approach II to estimating consumption of cod.

	Seals in:	NAFO 4T		NAFO 4Vn	
Month	*Diet type:*	Aggregated	Dispersed	Aggregated	Dispersed
1		0.5	0	0.8	0.2
2		0.5	0	0.8	0.2
3		0.5	0	0.8	0.2
4		0.5	0.5	0.4	0.1
5		0.5	0.5	0	0
6		0.2	0.8	0	0
7		0.1	0.9	0	0
8		0.1	0.9	0	0
9		0.1	0.9	0	0
10		0.2	0.8	0	0
11		0.5	0.5	0.4	0.1
12		0.5	0	0.8	0.2

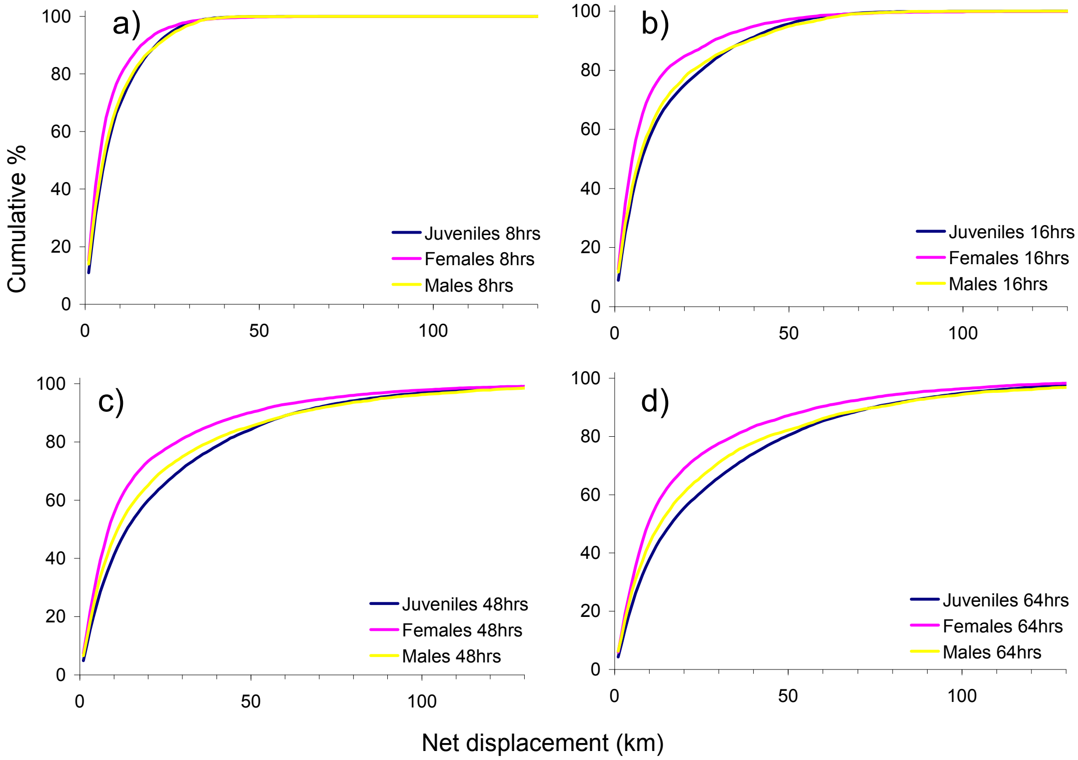


Figure 1. Cumulative frequency distributions of the net horizontal displacement (km) of juvenile, male and female grey seals a) over an 8-hr period, and the maximum displacement occurring during a period beginning 8 hours and ending b) 16 hr, c) 48 hr or d) 64 hr prior to a given point in time. The 8-hr period roughly represents the passage time of food through the stomach, and the displacement therefore reflects the plausible extent of the foraging area represented by seal stomach samples. The periods of time in panels b-d represent the range of expected residence times of food in seal intestines and the displacements therefore reflect the plausible extent of the foraging area represented by seal intestine and scat samples.

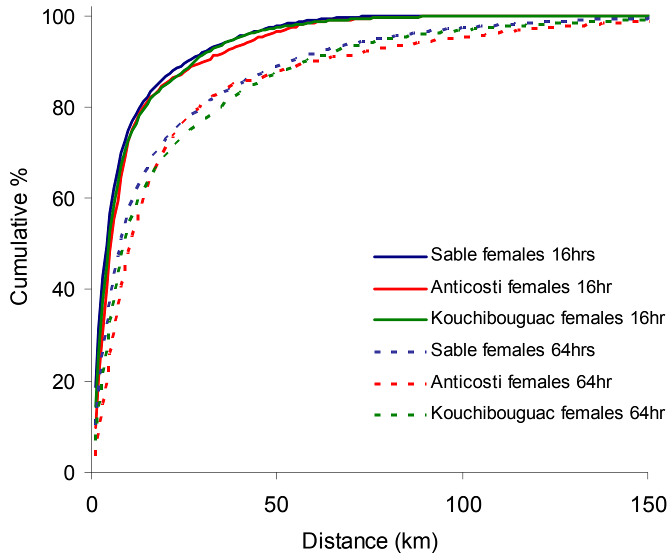


Figure 2. Cumulative frequency distributions of the maximum horizontal displacement (km) over periods beginning 8 hours and ending either 16 hr or 64 hr prior to a given point in time for female grey seals tagged at Sable Island, Anticosti Island and Kouchibouguac.

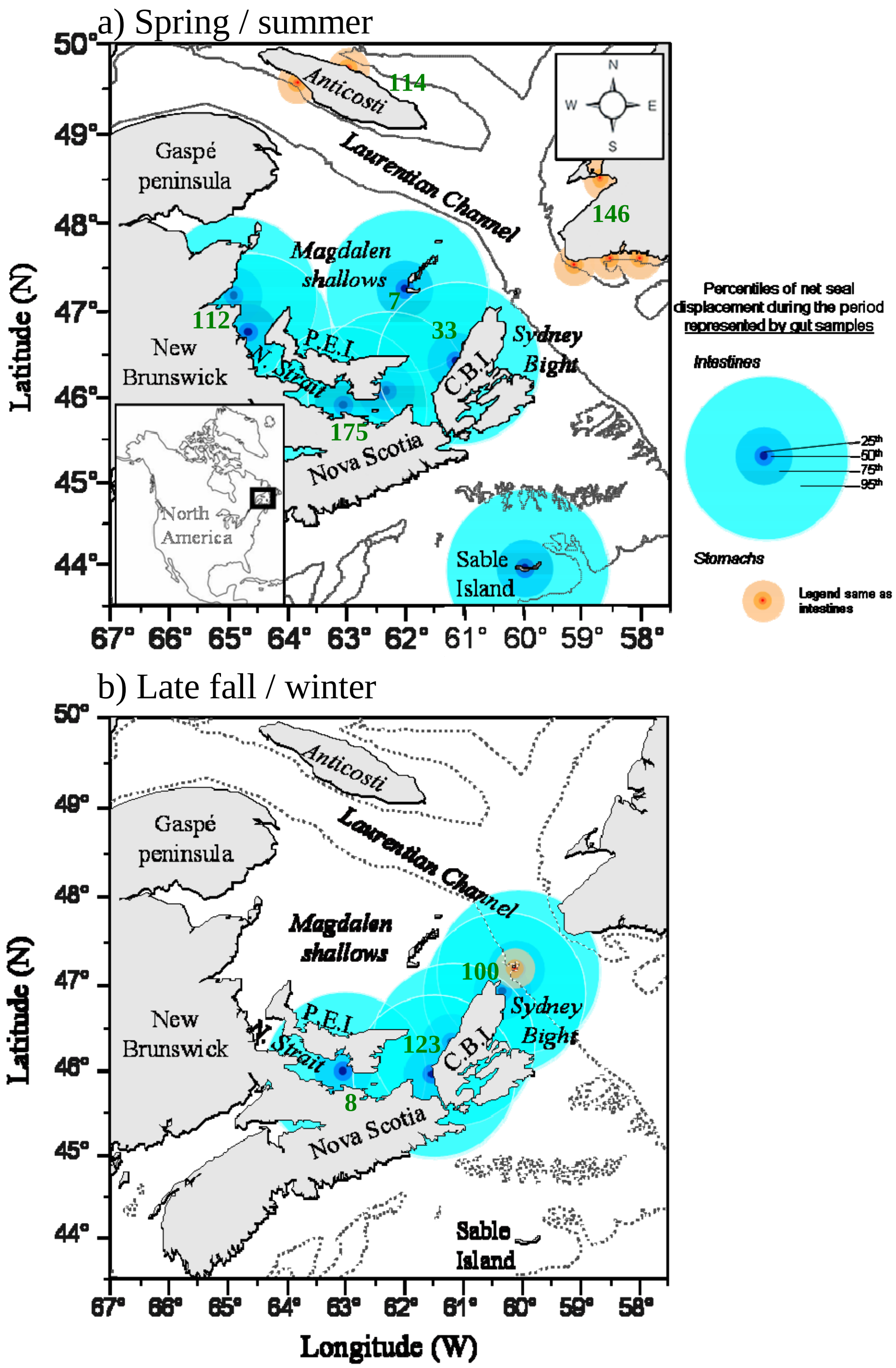


Figure 3. Probable foraging areas represented by seal gut content sampling conducted during a) the spring and summer, and b) the late fall and early winter. The number of seals sampled in each area and season are indicated in green on the maps. The concentric circles represent percentiles of net potential distance traveled by seals during the period represented by the diet samples, based on an analysis of movements from satellite tagged seals (see Fig. 1). 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 (a).

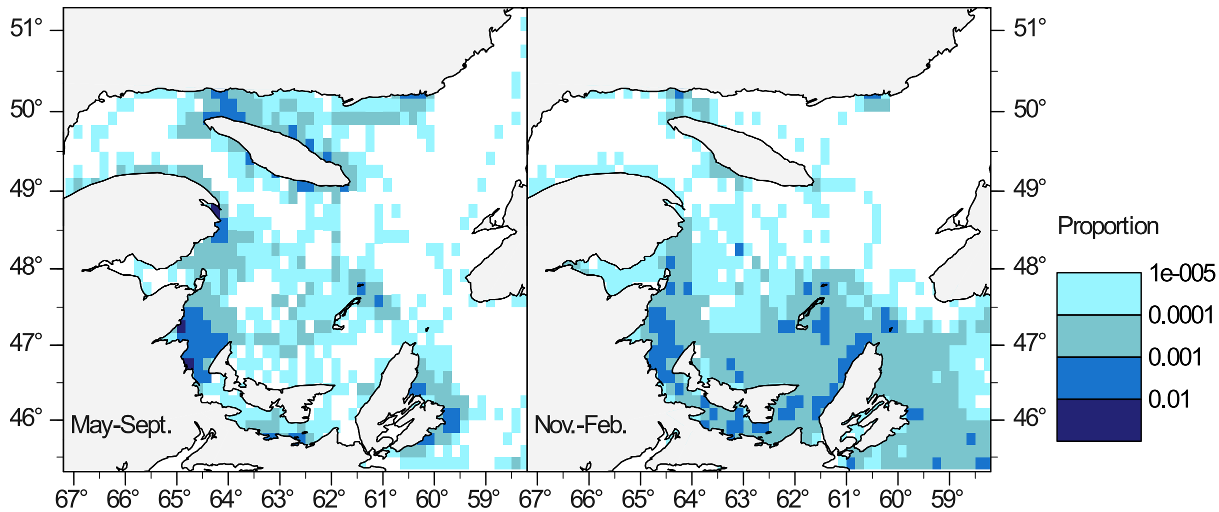


Figure 4. Summary of the geographic distribution of transmitting satellite-tagged seals in the Gulf of St. Lawrence during May-September and November-February, expressed as a proportion of transmissions originating from individual 10x10 minute squares in the area during each period.

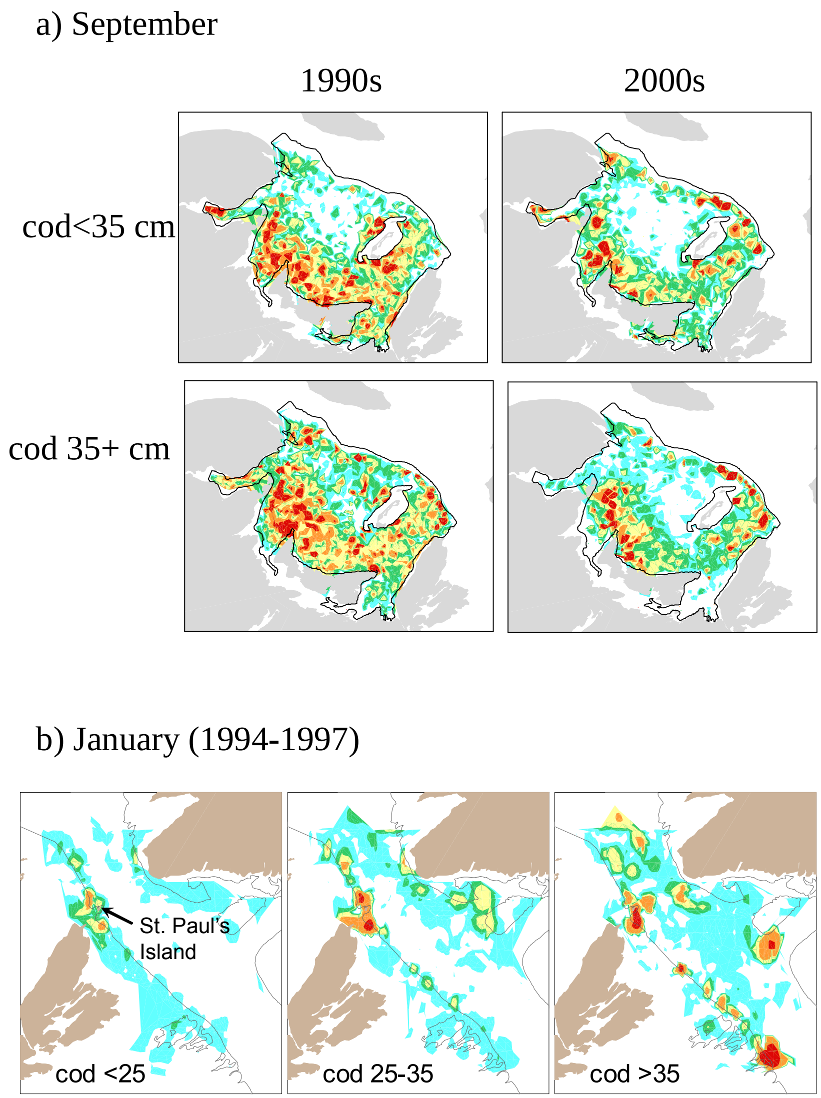


Figure 5. Geographic distribution (kg/tow) of cod <35 cm and 35+ cm a) on their summer feeding grounds in the southern Gulf of St. Lawrence in September and b) on their overwintering grounds in the Cabot Strait in January. Colour contouring is based on the percentiles of non-zero catches during the respective surveys: 10th percentile (blue), 25th (green), 50th (yellow), 75th (orange) and 90th (red).

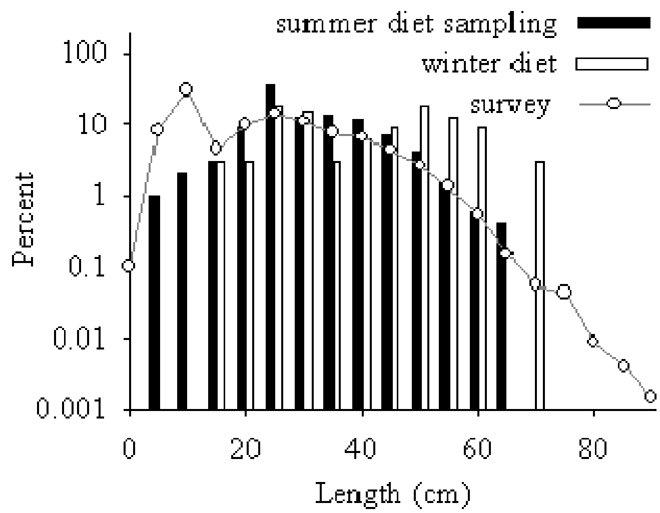


Figure 6. Frequency distribution of southern Gulf of St. Lawrence cod lengths in the 2005 population, and in spring/summer and winter grey seal diet samples (Hammill et al. 2007; Stenson et al. 2011). The population frequency distribution is based on catchability-adjusted estimates from the annual September survey. Note that the percentage axis is on the log-scale.

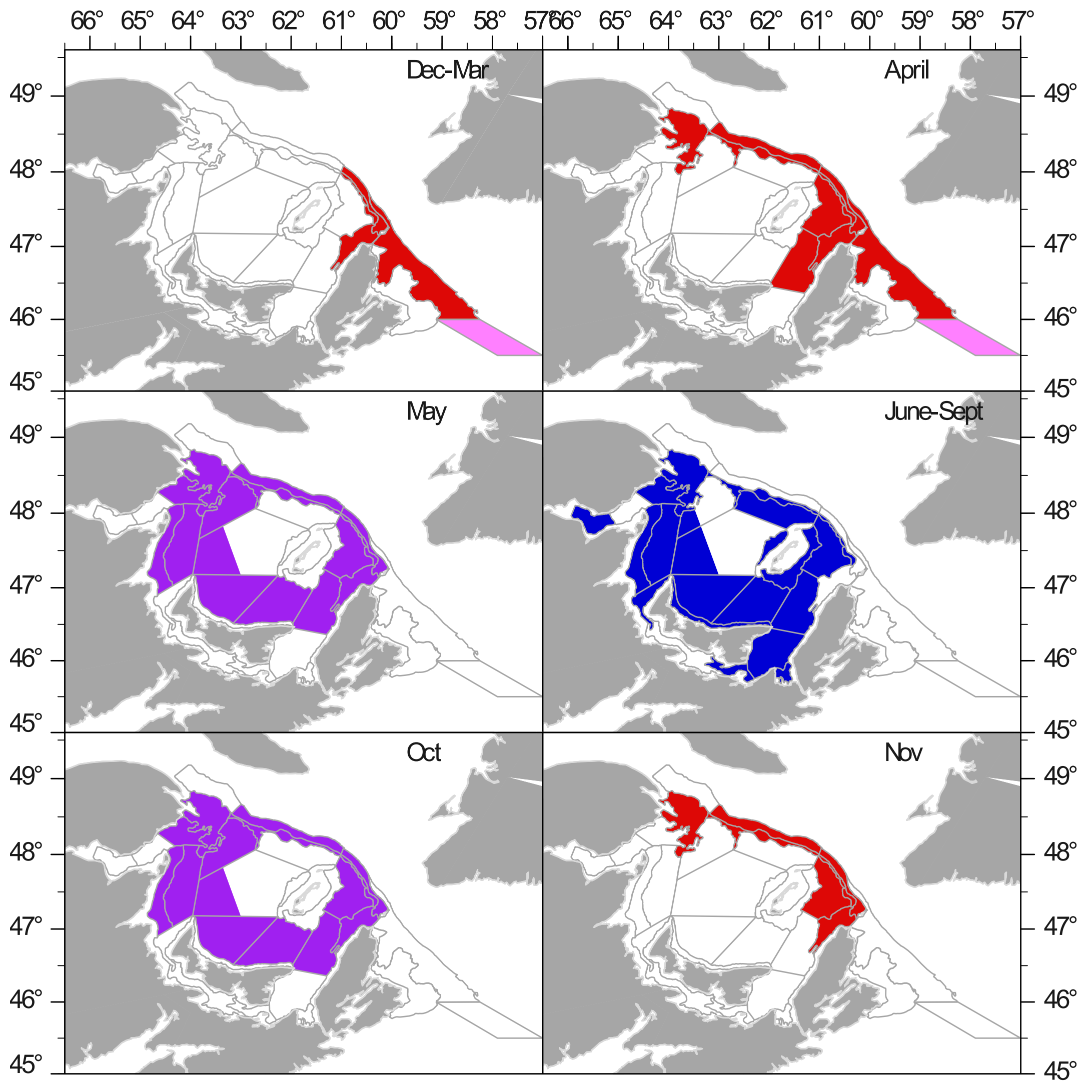


Figure 7. Inferred spatial distribution (i.e., stratum occupancy, coloured areas) of southern Gulf cod <35 cm. Areas coloured in red indicate strata occupied by aggregated cod, strata in blue are occupied by dispersed cod and areas in purple are those through which aggregated cod move during their annual spring or fall migrations (details in Benoît et al. 2011). The area coloured in pink is an area believed to be occupied by southern Gulf cod during winter in at least some years, based on fishery logbook information.

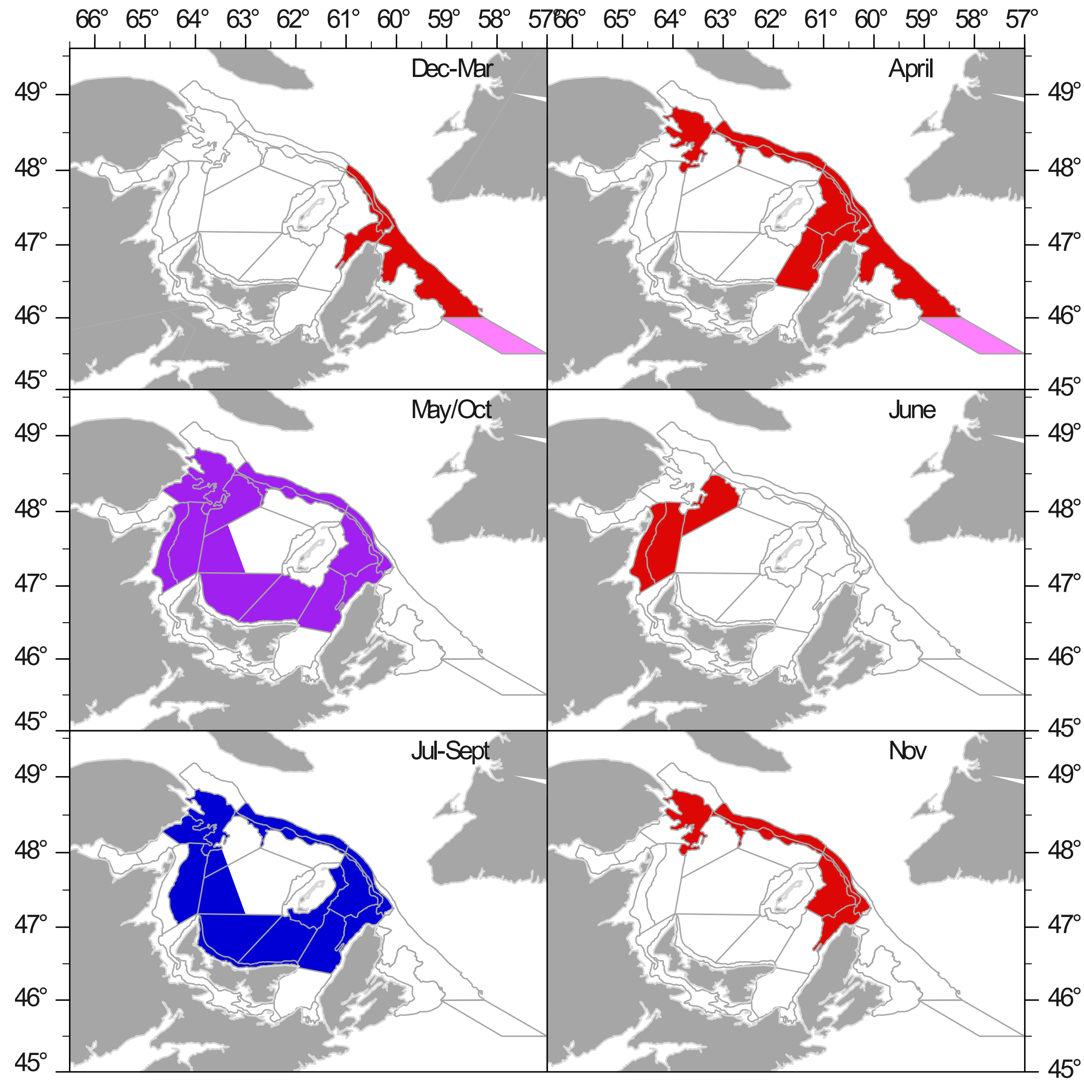


Figure 8. Inferred spatial distribution (i.e., stratum occupancy, coloured areas) of southern Gulf cod 35+ cm (details in Benoît et al. 2011). See the caption for Fig. 6 for an explanation of the colours used.

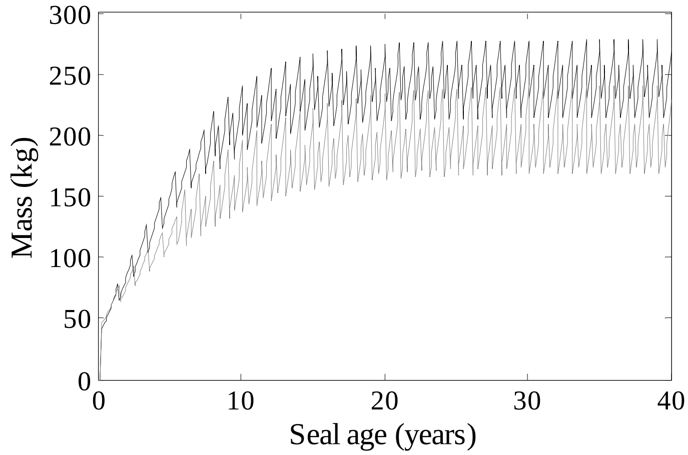
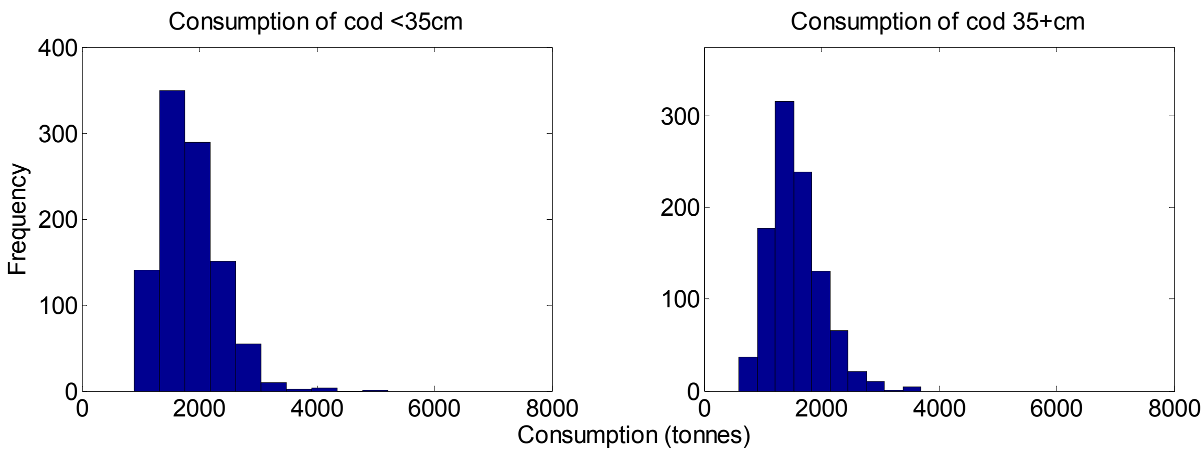


Figure 9. Seasonal and interannual patterns in the mass of male (black) and female (grey line) grey seals.

a) Excluding northern NAFO 4Vs during winter



b) Including northern NAFO 4Vs during winter

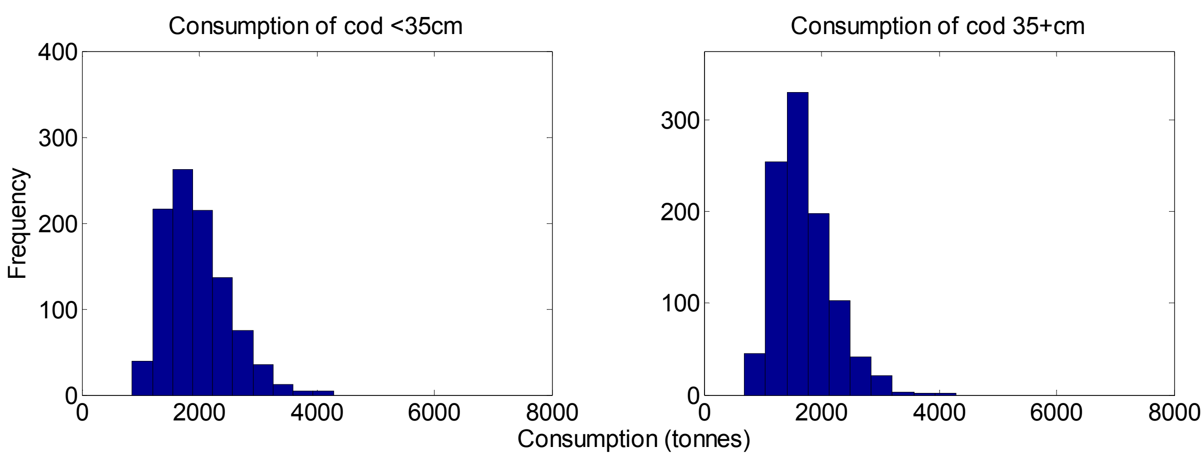
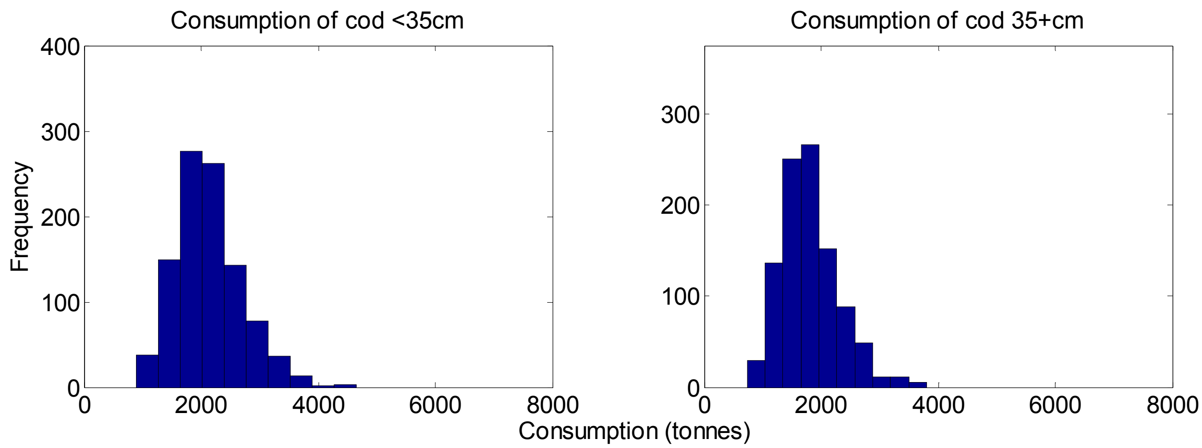


Figure 10. Frequency distribution of bootstrap estimates of the total consumption (t) of cod <35 cm (left panels) and 35+ cm (right) in 2005, based on a winter distribution of cod that a) exclude and b) include the northern portion of NAFO 4Vs (Approach I to estimating consumption).

a) Excluding northern NAFO 4Vs during winter



b) Including northern NAFO 4Vs during winter

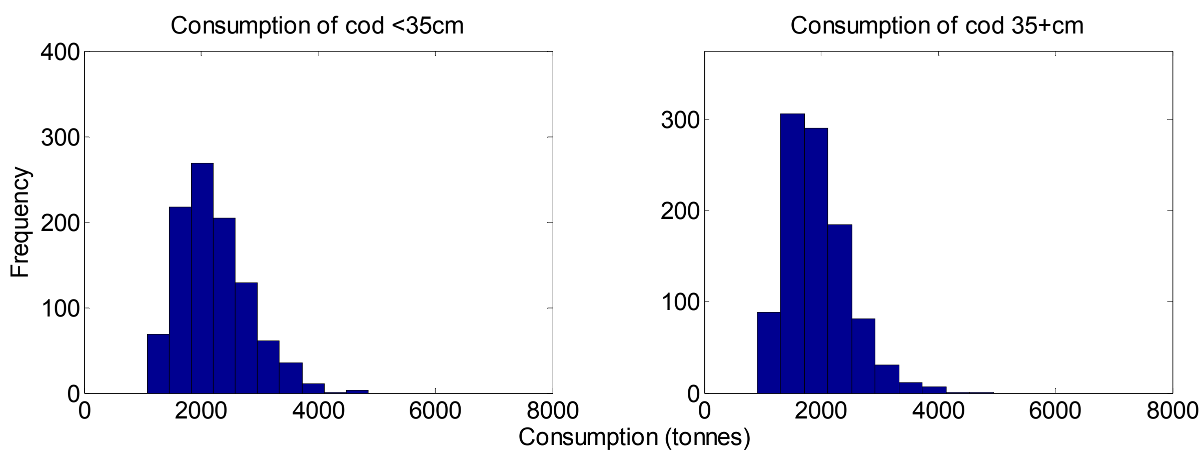
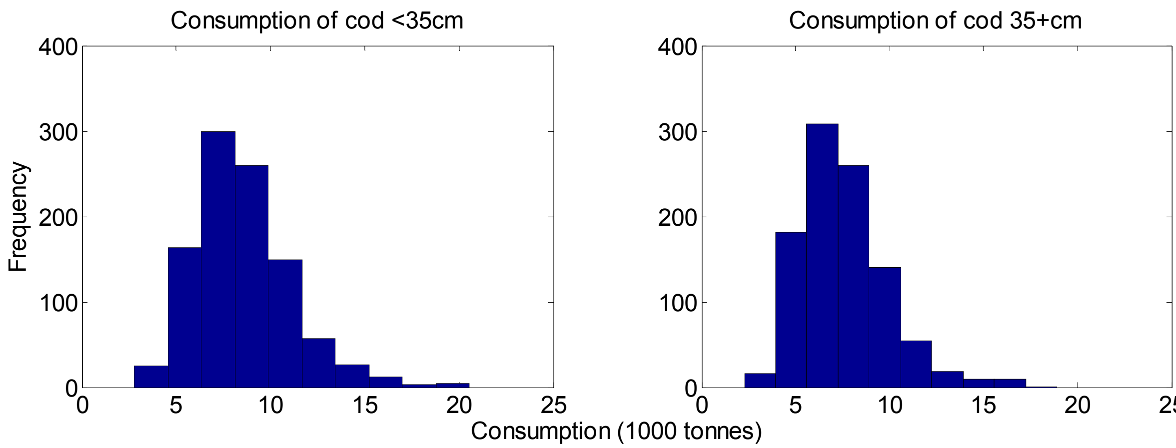


Figure 11. Frequency distribution of bootstrap estimates of the total consumption (t) of cod <35 cm (left panels) and 35+ cm (right) in 2005, based on a winter distribution of cod that a) exclude and b) include the northern portion of NAFO 4Vs (Approach I to estimating consumption) and abundance of Gulf grey seals estimated using the model that accounts for ice-related pup mortality

a)



b)

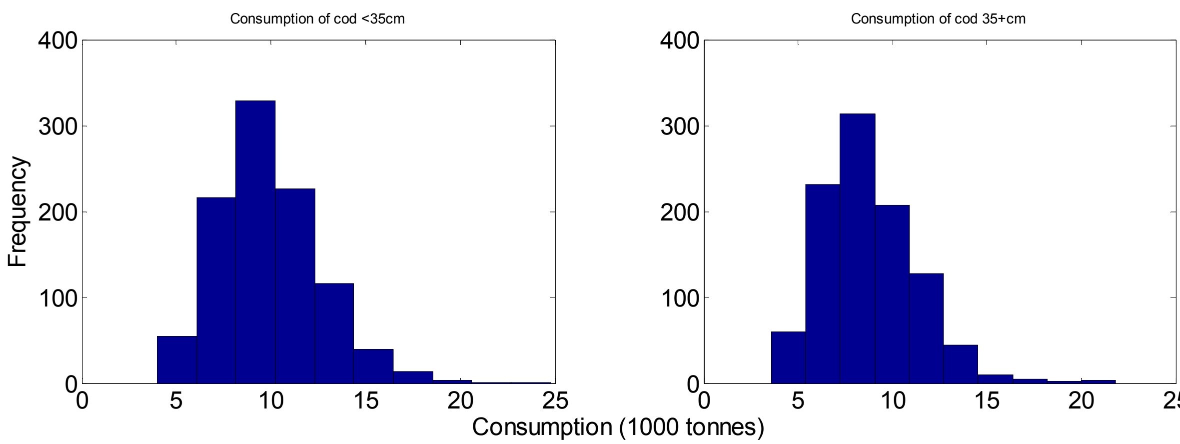


Figure 12. Frequency distribution of bootstrap estimates of the total consumption (1000 t) of cod <35 cm (left panels) and 35+ cm (right) in 2005 for Approach II to estimating consumption based on different models to estimate Gulf grey seal abundance: a) the traditional model and b) the model that accounts for ice-related pup mortality.

Appendix I. Summary of the probability distribution functions for the parameters of eqns 1-4. The notation ~ indicates 'distributed according to'. Five theoretical distributions were used: normal [~*N*(mean, standard deviation)], lognormal [~*logN*(mean, standard deviation)], multivariate normal [~$N(\mu,\Sigma)$, where μ is a vector of means and Σ is the covariance matrix], uniform [~unif(minimum, maximum)] and pert.

Parameter name	Symbol	Probability distribution function	References
Kleiber equation parameters	α β	$\sim N(\mu,\Sigma)$ $\mu=\begin{bmatrix}\alpha = 293.75 \\ \beta = 0.75\end{bmatrix}$ $\Sigma=\begin{bmatrix}1941.5 & -4.461 \\ -4.461 & 0.013\end{bmatrix}$	Kleiber 1975; Hammill and Stenson 2000
Gompertz parameters, eqn. 2 (seal mass-at-age, by sex)	γ_{1s} γ_{2s} γ_{3s}	$\gamma_{1m} \sim N(230.60, 6.93)$, $\gamma_{1f} \sim N(183.70, 3.57)$ $\gamma_{2m} \sim N(1.521, 0.074)$, $\gamma_{2f} \sim N(1.242, 0.048)$ $\gamma_{3m} \sim N(0.250, 0.022)$, $\gamma_{3f} \sim N(0.190, 0.014)$	M.O. Hammill unpublished analysis
Activity Factor	*AF*	~pert with median=2.0 and range=[1.7, 3.0]	Innes et al. 1987; Worthy 1987a,b, 1990; Castellini et al. 1992; Sparling and Fedak 2004
Growth premium (at age)	GP_a	GP_0~unif (1.80, 2.00), GP_1~unif (1.50, 1.70) GP_2~unif (1.25, 1.45), GP_3~unif (1.10, 1.30) GP_4~unif (1.05, 1.20), GP_5~unif (1.03, 1.13), GP_{6+}=1.00	Ronald et al. 1984; Worthy 1987a,b; Olesiuk 1993; Mohn and Bowen 1996
Metabolizable energy	*ME*	$\sim N(0.830, 0.048)$	Ronald et al. 1984
Grey seal abundance	N_{herd}	$N_{Gulf} \sim N(51\,311, 2\,696)$, $N_{Sable} \sim N(244\,787, 6\,462)$, $N_{EasternShore} \sim N(12\,172, 568)$. Total abundance in each herd, N_h, was then multiplied by the stable age distribution (proportion at age) and 0.5 (assuming a 50:50 sex ratio) to obtain the numbers at age and sex by herd, N_{hsa}	Hammill 2005 (updated)

Parameter name	Symbol	Probability distribution function	References
Grey seal natural mortality (assumed to be fixed)	M_{ha}	$$= \begin{cases} 0.103, & \text{if } h = \text{Sable or Eastern Shore}, a = 0 \\ 0.146, & \text{if } h = \text{Gulf}, a = 0 \\ 0.051, & \text{if } h = \text{all}, a = 1+ \end{cases}$$	Trzcinski et al. 2006
Cod energy density (in kilojoules/kg)	*ED*	*ED* ~*N*(4.20E3, 0.60 E3)	Steimle and Terranova 1985; Lawson et al. 1998
Proportion of seals in the Eastern shore herd that adopt a seasonal spatial distribution like Sable Island seals	*r*	~unif (0.3, 1.00)	Benoît et al. 2010
Proportion of cod in the grey seal diet	p_{ms}	Calculated as a function of the aggregated and dispersed diets (see text). Listed below are the mean proportions by diet and sex. Uncertainty in the diets was incorporated in the simulation using a non-parametric bootstrap of the original samples. Diet type / Males / Females Aggregated 0.25 0.10 Dispersed 0.12 0.12	Hammill et al. 2007; Stenson et al. 2011
Proportion of cod consumed by grey seal that are in each cod size class	q_x	Listed below are the mean proportions by diet and size class. Uncertainty was incorporated in the simulation using a non-parametric bootstrap of the original diet samples. Diet type / <35 cm / 35+ cm Aggregated 0.42 0.58 Dispersed 0.62 0.38	Hammill et al. 2007; Stenson et al. 2011