



CSAS

Canadian Science Advisory Secretariat

SCCS

Secrétariat canadien de consultation scientifique

Research Document 2010/133

Document de recherche 2010/133

Spatial overlap between a pinniped predator, the grey seal and several prey species on the Scotian Shelf (NAFO zone 4VsW)

Chevauchement spatial entre le phoque gris, un prédateur et plusieurs espèces de proies sur le plateau néo-écossais (zone OPANO 4VsW)

Valérie Harvey and Mike O. Hammill

Maurice Lamontagne Institute
Box 1000, Mont-Joli, QC. G5H 3Z4

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

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

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

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

This document is available on the Internet at:

<http://www.dfo-mpo.gc.ca/csas/>

Ce document est disponible sur l'Internet à:

ISSN 1499-3848 (Printed / Imprimé)

ISSN 1919-5044 (Online / En ligne)

© Her Majesty the Queen in Right of Canada, 2011

© Sa Majesté la Reine du Chef du Canada, 2011

Canada

Correct citation for this publication:

Harvey, V. and Hammill, M. O. 2011. Spatial overlap between a pinniped predator, the grey seal and several prey species on the Scotian Shelf (NAFO zone 4VsW). DFO Can. Sci. Advis. Sec. Res. Doc. 2010/133. iv + 23 p.

ABSTRACT

The spatial overlap between 56 grey seals equipped with satellite transmitters and 11 fish species including cod on the Scotian Shelf (4VsW) was examined. Foraging patches of males and females overlapped considerably. Seals remained within their foraging patches for an average of 6.1 ± 0.53 days. Patches were located on average at 97.3 ± 4.6 km from Sable Island. Foraging patch area was larger during the 1990s (493.5 ± 151.3 km²) than during the 2000s (225.4 ± 41.3 km²). The probability of a foraging patch occurring varied with a combination of fish abundance and distance from Sable Island. Overall, the probability of occurrence of a foraging patch decreased with distance from Sable Island. Species selected at close proximity to Sable Island differed than those that overlap with the foraging patches of seals further offshore. In July, female grey seals showed some selectivity for medium size cod, and small silver hake, while no selectivity for cod was observed among males. During March, males showed selectivity for medium (pre-2000) and for large (decade=2000's) cod. While the foraging patches of males overlapped with large haddock and large cod at close proximity to Sable Island, this association declined gradually with distance from the Island

RÉSUMÉ

Le chevauchement spatial entre 56 phoques gris équipés d'émetteurs satellites et 11 espèces de poissons dont la morue a été examiné sur le plateau néo-écossais (4VsW). Les aires de recherche de nourriture des mâles et des femelles se chevauchent considérablement. En moyenne, les phoques restent dans leurs aires d'alimentation $6,1 \pm 0,53$ jours. Ces aires d'alimentation étaient situées à $97,3 \pm 4,6$ km de l'Île de Sable. Les aires de recherche de nourriture étaient plus grandes pendant les années 1990 ($493,5 \pm 151,3$ km²) que durant les années 2000 ($225,4 \pm 41,3$ km²). La probabilité d'observer une aire de recherche variait en fonction de l'abondance du poisson et de la distance de l'île de Sable. Dans l'ensemble, la probabilité d'occurrence d'une aire de recherche de nourriture diminuait avec la distance de l'Île de Sable. Les espèces sélectionnées à proximité de l'Île de Sable différaient de celles qui chevauchaient les aires de recherche des phoques au large. En juillet, les phoques gris femelles montraient une certaine sélectivité pour la morue de taille moyenne, et le merlu argenté petits, tandis que pas de sélectivité pour le cod n'a été observée chez les mâles. En mars, les mâles ont montré une sélectivité pour les morues de taille moyenne (pré-2000) et de grande taille (2000's). Bien que les aires de recherches de nourriture des mâles chevauchent les concentrations d'aiglefin et de morue grande taille à proximité de l'île de Sable, cette association diminuait progressivement avec la distance de l'île

INTRODUCTION

Predation is a pervasive feature of marine ecosystems (Bax 1998). Losses to predation may exceed losses to fisheries, yet it is often assumed that fisheries alone are responsible for variation in fish survival (Morissette et al. 2006). Predation impacts on a population may be direct, in the form of consumption of prey species or indirect through forcing prey species to develop costly anti-predator strategies to minimize predation mortality (Creel and Christianson 2008, Wirsing et al. 2008).

Several Atlantic Canada groundfish stocks collapsed near the end of the 1980s, due largely to overfishing, but in spite of continued restrictions, many of these stocks have shown limited or no signs of recovery, among these is the cod stock in NAFO fishing zone 4VsW. Predation by grey seals has been suggested as an important reason for this lack of recovery. Attempts to examine this have indicated that grey seal might account for a significant component of natural mortality (Mohn and Bowen 1996, Fu et al. 2001, Trzcinski et al. 2006), but this has been questioned (Bowen et al. 2009, Bundy et al. 2009).

Evaluating the magnitude of the consumption of cod by grey seals and its contribution to mortality of cod, requires information on population size, energetic requirements, diet composition, size classes and energy density of the prey, as well as the distribution of marine mammal feeding effort (Harwood and Croxall 1988, Harwood 1992).

Over the last decade, our information on populations, distribution, energy requirements and understanding of diet have improved immensely. However, our understanding of diet in an operational sense remains uncertain. Several approaches have been developed including analyses of digestive tract contents, fatty acid and stable isotope analyses (Iverson et al. 2004, Hammill et al. 2005). Additional approaches have attempted to associate seal diet, with prey availability, to improve our understanding of the functional relationships involved in prey selection (Smout and Lundstrøm 2007, Lindstrøm et al. 1998). However, all of these approaches have different biases associated with them, complicating attempts to understand true diet composition. Hence, although important, diet information is difficult to obtain owing to challenges in obtaining samples (stomachs), difficulties in sampling in offshore areas (digestive tracts), inability to separate age and sex effects (faecal analyses) considerable laboratory expense (digestive tracts), uncertainty in correction factors (faecal analyses), uncertainty in the time-frame or spatial region being sampled and the need for extensive prey libraries (fatty acid, stable isotope ratios), and variability in calibration or enrichment factors (fatty acid, stable isotope ratios).

Developments in wildlife telemetry have substantially increased our ability to study movements and diving behaviour of marine mammals at sea. Furthermore, the increase in numbers of deployments has opened the way for more sophisticated analyses to try to understand habitat selection and foraging behaviour of marine predators (Breed et al. 2006, Weimerskirch et al. 2007, Freitas et al. 2008, Harvey et al. 2008). Harvey et al. (2011b) have demonstrated that the movement patterns of grey seals in the Cabot Strait area (NAFO zone 4Vn), indicated overlap between aggregations of overwintering cod from the southern Gulf of St. Lawrence (NAFO zone 4T) and male grey seals of Gulf origin in the vicinity of northern Cape Breton Island. In a second studies, Harvey et al. (2011a) examined the overlap between grey seals and several prey species in 4T during summer. They observed that male grey seals tended to forage further offshore than females. They also demonstrated that several species of fish including cod had higher densities in areas where grey seals did not appear to be foraging extensively, and also

showed an increasing abundance as distance from haulout sites increased suggesting a response by certain prey to minimize predation from seals.

Here we examine the movement patterns of grey seals on the Scotian Shelf (NAFO zone 4VsW) based on satellite transmitters that have been deployed on grey seals on Sable Island and in the Gulf of St. Lawrence over the past 15 years (Goulet et al. 2001, Austin et al. 2006, Breed et al. 2006, Harvey et al. 2008) to provide some comparison of behaviour across a large region using similar approaches. We compare the distribution and foraging activities of these animals to size-specific spatial distributions of fishes obtained from synoptic bottom-trawl survey data to gain insights into potential predator-prey interactions.

MATERIAL AND METHODS

STUDY AREA AND DATA COLLECTION

The Scotian Shelf comprises the continental shelf off Nova Scotia of about 200 km width bounded by the Laurentian Channel in the northeast and the Northeast channel and the Gulf of Maine in the southwest. With an average depth of 90 m, this shelf has an irregular bathymetry, consisting of a number of basins and channels that separate shallow offshore banks. Sable Island is located approximately 300 km southeast of the Nova Scotia coast on the eastern part of the shelf (Fig 1). Between 1993 and 2008, grey seals were captured at Sable Island as well as within the Gulf during either May-June (post-moult), or September-October from 1993 to 2008. In the Gulf, seals tagged were anaesthetised (Baker et al. 1990) and an incisor tooth was extracted to determine their age (Bernt et al. 1996). The brands or tags of seals from Sable Island allowed age determination. Animals were classified as juveniles (<6 years) and adults (≥6 years old) (Hammill and Gosselin 1995). Argos satellite transmitters (tag models deployed include: SDR -Wildlife Computers, Redman, WA, USA; ST-18, Telonics, Mesa AZ, USA or SRDL 7, Sea Mammal Research Unit, St. Andrews, UK) were glued to seals using 5-minute epoxy. All animal handling procedures followed the guidelines of the Canadian Council on Animal Care (1993).

Standard groundfish bottom trawl surveys have been conducted in the 4VsW and 4X NAFO areas by the Department of Fisheries and Oceans during July, 1970 to present and during March 1979-1984, 1986-2009. The northern portion of the area was not completely surveyed in March 1996 and 2009, mainly due to heavy ice coverage. There were also no March surveys for 1998 and 2004. The fish data presented here and used for our analysis were obtained from these surveys. The surveys used a stratified random survey design (Smith and Page 1996). The sample unit for the survey was defined as the area over the bottom covered by a trawl 12.5 m wide towed at 3.5 knots for a distance of 1.75 nautical miles. These sample units or sets were selected before the cruise and randomly located in each stratum. At each survey station, fish abundance was sampled. The area covered by those fish surveys was considered as the study area for our analyses (Fig. 1).

SPATIAL OVERLAP BETWEEN FISH AND SEALS

We fitted a two-state switching CRW model described in Breed et al. (2009), to the grey seal data using WinBUGS 5 (available online) and R (R Development Core Team 2008). This allowed us to correct for erroneous satellite locations and to normalize the number of locations obtained for each individual per day. We used a first difference correlated random walk model with a 480 min time-step (3 locations by day) to determine whether a seal was foraging or

travelling as described by (Breed et al. 2009). Locations for which the state-space model had inferred uncertain behaviour, which represented less than 10% of the dataset, were excluded from our analyses. Any area of at least three consecutive foraging locations was identified as a foraging patch. The time within each foraging patch was estimated and measured the area of foraging patches using a minimum convex polygon method (Breed et al. 2009) and kept only those that were located (>50%) within 4Vs and 4W NAFO areas in July and March.

Eleven fish species sampled by the survey were selected because they were known to be important prey (eg. herring) or are considered to be minor prey (eg. haddock) of grey seals. Fish were separated into 2 or 3 length classes when possible (Table 1). We used the *Geostatistical Analyst* extension of ArcGIS v9.3 (Environmental System Research Institute, Inc (ESRI), 380 New York Street Redlands, CA 92373-8100) to produce prediction maps of fish density for each group of fish, combining the data from decades 1990 (as an average for fish data obtained between 1990 and 1999) and 2000 (for fish obtained between 2000 and 2009) as well as for each year separately for which a foraging patch was identified. We repeated these analyses for each survey dataset. We used the “ordinary kriging” method to model spatial structure based on an omni-directional, spherical semivariogram model. When more than one value was available at the same location, catch rates were averaged. The area of less than 100 m deep along the Nova Scotia as well as around Sable Island was excluded from the analysis since surveys did not sample these areas.

STATISTICAL ANALYSES

We used *t-tests* as well as general linear models to assess the difference in residence time, area of foraging patch and distance from Sable Island between sex, decades and seasons (July and March)

Overlap between seals and fish was evaluated by fitting Resource Selection Functions (RSFs) based on a use/availability design (Manly et al. 2002, Johnson 1980). Fish densities within foraging patches were compared using logistic regression to the characteristics of foraging patches randomly located throughout the study region. We then randomly selected foraging patches (using rotation and translation) 50 times within the survey area (Wilson et al. 1998, Dussault et al. 2005). Random permutations of the foraging patch were retained if $\geq 50\%$ of range area overlapped the study area to avoid an underestimation of the study area boundary (Wilson et al. 1998, Dussault et al. 2005). ArcGIS 9.3 was then used to calculate the abundance of each fish group within a foraging patch and the random permutation patches. Each foraging patch was related to the density of the fish in the same year. When there was no survey in the year of the foraging patch, we used the average fish density calculated for that decade.

As grey seals are central place foragers, the area available to them is limited to the area surrounding their haulout site. We applied a distance-based model to incorporate potential spatial clustering of habitats surrounding the central place and to account for potential bias in the selection estimates (Rosenberg and McKelvey 1999, Carrete and Donázar 2005, Beest et al. 2010). We used the distance between the middle of a foraging patch and Sable Island as an explanatory variable in the models tested.

Logistic regressions using generalized estimating equations (GEE) to control for repeated observations on the same individual were used to relate the probability of occurrence of a foraging zone to fish abundance. We performed these analyses for each sex, season (July, March) and decade (1990s and 2000s) separately.

The most predictive model was selected based on the quasi-likelihood information criterion (QIC) developed by Pan (2001) and QIC weights (w) (Burnham and Anderson 2002). Models with $\Delta QIC \leq 2$ were considered to be equivalent. When models were equivalent, the model with the fewest parameters was selected (Burnham and Anderson 2002). We considered n , the sample size, as the number of seals. To avoid model over-parameterization, only models in which the number of variables did not exceed $n/5$ were explored. We tested all models of each fish group, distance and the interaction between fish group and distance.

RSF scores were then calculated :

$$1 \quad \text{RSF scores} = \exp[\beta_0 + \beta_1 x_1 + \beta_2 x_2 \dots],$$

where β_0 is the intercept of the RSF model and β_1 and β_2 are the coefficients of independent variables x_1 and x_2 , respectively. RSF scores should reflect the relative probability of occurrence of a foraging patch of seals within the study area (Johnson 1980). The confidence interval limit of the Wald's statistic was used to determine if β differed from 0. When $\beta > 0$, the probability of use by a seal is higher than in reference category and lower if $\beta < 0$. All analyses were performed using SAS (Littell et al. 2002). Results are presented as means \pm SE.

RESULTS

GREY SEAL DISTRIBUTION

A total of 207 grey seals were tagged at Sable Island and within the Gulf of St Lawrence between 1993 and 2008. Data were obtained from 56 (Sable Island=23; Gulf=53) individuals during both July and March. Forty individuals (6 females juvenile, 20 females adults, 6 males juveniles, 8 male adults) were tracked during both months and spent time within more than 50% of the area encompassed by the groundfish survey. A total of 368 foraging patches were identified in the Scotian Shelf area during both months. These could be broken down into 81 foraging patches (10 females juvenile, 18 females adults, 27 males juveniles, 26 male adults) in July and 74 foraging patches (11 females juvenile, 38 females adults, 9 males juveniles, 16 male adults) created by 35 seals (7 females juvenile, 5 females adults, 11 males juveniles, 12 male adults) during March.

Overall, foraging patches were mostly located over shallow banks that surrounded Sable Island (Fig. 2a). Foraging patches of males and females overlap considerably. Seals remained in their foraging patches for 6.1 ± 0.53 d, which were on average located 97.3 ± 4.6 km from Sable Island. The foraging patches encompassed an area of 288.4 ± 48.1 km². Distance from Sable Island ($F_{3,31}=17.9$, $P < 0.01$) as well as residency time within foraging patches ($F_{3,31}=17.9$, $P < 0.01$) did not vary with decades but foraging patch area was larger during the 1990s (493.5 ± 151.3 km²) than during the 2000s (225.4 ± 41.3 km²) ($t_{147}=2.40$, $P < 0.01$). In July, females had larger foraging patches ($243.6 \pm$ vs 131.3 ± 17.6 km²; $t_{77}=2.16$, $P=0.03$) and they foraged closer to Sable Island than males (65.2 ± 7.2 vs 91.1 ± 5.9 km; $t_{77}=-2.70$, $P < 0.01$). Both sexes however, stayed for a similar time period within their foraging patches (6.5 ± 1.1 (female) vs 5.5 ± 0.7 (male) d; $t_{77}=0.79$, $P=0.43$). In March, the residence time in a foraging patch (7.3 ± 1.3 vs 4.7 ± 0.7 d; $t_{68}=1.36$, $P=0.18$), area (476.7 ± 133.1 vs 316.4 ± 110.7 km²; $t_{68}=0.11$, $P=0.91$) as well as distance (114.0 ± 9.1 vs 112.1 ± 14.8 km) of foraging patches from Sable Island ($t_{68}=0.78$, $P=0.44$) did not vary between sexes. Overall, adults had larger foraging patches (151.4 ± 30.7 km² vs $394.4 \pm$

80.4 km²; $t_{147}=-2.5$, $P=0.01$) that were located farther from Sable Island than juveniles (86.9 ± 6.7 vs 105.5 ± 6.2 ; $t_{147}=-2.04$, $P=0.04$).

OVERLAP SEALS AND COD

Overall, the probability of having a foraging patch decreased with increasing distance from Sable Island. However, this varied differently among fish groups.

July

The number of foraging patches utilized by females in the study area prior to the year 2000 was too low ($n=1$) for any statistical analysis of the spatial overlap between seals and fish.

During the 2000s, the best ranking models indicated that females were more likely to have a foraging patch associated with small silver hake and medium cod was greater at 50 km than at more than 100 km from the Island. However, this probability decreased with the abundance of small and large white hake (Fig. 3a). Small redfish were included in the best model, but their selectivity did not vary with availability within the 4VsW NAFO area covered by the study area (Table 3).

Males, in the 1990s, showed a positive selection for small haddock as well as for small silver hake at 50 km. Selection for both fish groups became negative with increasing distance from Sable Island (Fig. 3b). The probability of having a foraging patch also did not vary with the abundance of small thorny skates (Table 3).

During the 2000s, males had a foraging patch in areas of high concentration of small haddock at distances of less than 100 km from the Island. Moreover, this probability decreased more rapidly at >100 km than at 50 km from Sable Island. Males also avoided large white hake at 50 km. This aversion became gradually less important with increasing distance from Sable Island while a neutral selection for this fish group was observed at 200 km.

March

During the 1990s, females selected for the small haddock group at distances of 50 km, but showed an aversion for small haddock at 100 km and greater distances from Sable Island (Fig. 4a). No pattern of selection was observed for large thorny skates (Table 3).

In 2000s, foraging patches of females were negatively associated with large haddock at 50 km but this association gradually became positive with increasing distance from Sable Island (Fig. 4b). Overall females also avoided areas associated with large concentrations of small silver hake but selection for this fish group was higher at 50 km than at greater distances. Small as well as large white hake, small witch flounder and small redfish, were also included in the best predictive models, were avoided by seals. Selection for those species did not vary with distance from Sable Island (Table 3).

Before 2000, the probability of having a foraging patch of males decreased with an increase in large american plaice abundance. This aversion however became less important with increasing distance from Sable Island. Foraging patches of males were also positively associated with medium cod at 50 km. This association was negative at other distances (Fig. 4c). Small american plaice, sand lance, small witch flounders, large white hake and large

thorny skates were also included in the best predictive models but these fish groups did not have a significant effect on the probability of having a foraging patch of males in the study area.

In the 2000s, foraging patches of males were associated with large haddock and large cod at 50 km. This association however became gradually negative with increasing distance from Sable Island.

DISCUSSION

Grey seals prefer shallow areas of less than 50 m depth (Harvey et al. 2008). Their limited offshore movement may be linked to physiological limitations on their diving capacity (Halsey et al. 2006) and need to haulout. In winter, seals foraged further offshore than in July. As also demonstrated by previous studies (Breed et al. 2006, Harvey et al. 2008, Harvey et al. 2011b), we observed a spatial segregation between sexes around Sable Island while offshore foraging areas were more frequently used by males than by females. The average distance of foraging patches areas from Sable Island did not vary between sexes in March. This result was surprising since the most striking spatial segregation between sexes has been observed in this period while males dispersed widely along the shelf between Sable Island and Cape Cod and females concentrated more around Sable Island (Breed et al. 2006). However, the distance at which males foraged from Sable Island in winter was more variable than those of females (180 ± 209 vs 82 ± 65 km, from Breed et al. 2009). According to Breed et al. (2006), most males appeared to concentrate in 4X in this time of the year. Although we observed foraging patches of males in this area during March, we limited our study to the 4VsW NAFO area only. This may explain the absence of statistical differences in distance between foraging patches. Males and females have different foraging strategy patterns. Females gain body mass during spring suggesting they have a higher foraging effort than males at this time of the year. Later during summer both males and females apparently increase their foraging effort (Beck et al. 2003a, b). The competition for food resources in summer may force sexes to segregate and males to use habitats further offshore (see Breed et al. 2006).

As seen in the southern Gulf in summer (Harvey et al. 2011a), we observed that the probability of a foraging patch occurring varied with a combination of fish abundance and distance from Sable Island. Overall, the probability of occurrence of a foraging patch decreased with distance from Sable Island. Interestingly, species selected at close proximity to Sable Island differed from those that overlap with the foraging patches of seals further offshore. While the foraging patches of males overlapped with large haddock and large cod at 50 km from Sable Island, this association declined gradually with distance from Sable Island. Central place foraging strategy states that searching and foraging efforts should decrease as distance from the central place increases, but animals that forage at a greater distance from the central place should increase their energy gain in the patch encountered in the furthest habitats (Orians and Pearson 1979). Gadoid and demersal species fish have lower energy density than small pelagic fish species. Aggregations of those fish species at close distances to colonies or haulout sites allows marine predators to reach prey patches at low energetic costs (Guinet et al. 2001, Weimerskirch et al. 2005, Baylis et al. 2008, Winter et al. 2009). However, when foraging at great distance from Sable Island seals may compensate for the increase in travelling costs by foraging on more energetic fish species. Here, we limited our analyses to the best predictive models in the habitat selection analyses. In these models no pelagic fishes were selected.

One surprising result from this study was the insignificance of sandlance, herring and redfish in our analyses. Both species are important prey in grey seal diets from Sable Island and other

areas (Bowen et al. 2011, Hammill 2011, Stenson and Hammill 2011). Visual inspection showed considerable overlap between grey seals, particularly some females and some concentrations of sandlance and herring. However, these species were absent from other areas where foraging was identified. Differences in foraging strategy between individuals may then have led to the neutral selection for these species in our statistical analysis.

Overall, the pattern of selection observed according to species was coherent with our understanding of diet composition. The spatial distributions of foraging patches of grey seals were negatively related to haddock, american plaice, redfish and white hake. All of these species have been demonstrated to be under-represented in grey seal diets according to their availability (Bowen and Harrison 2006). Contrary to what was seen in the diet analysis, seals appeared to overlap with concentrations of medium and large cod at 50 km from Sable Island. This association is demonstrated by males in March in 1990s and 2000s respectively as well as by females (medium cod) during summer in the 2000s. Males have also been observed to overlap with large cod in winter period in 4Vn area (Harvey et al. 2011b). The analysis of stomach contents in an area where cod are aggregated and seals overlap with these aggregations demonstrated that large cod can make an important contribution to the diet of males grey seals in winter (Stenson and Hammill 2011). Analyses from the southern Gulf also demonstrated that males selected for offshore areas where large cod occurred suggesting that large cod may be an important prey species there during in summer as well (Harvey et al. 2011a). However, some of these may have been digested by the time that seals would be sampled leading to a bias in diet composition estimated using stomach contents. The positive relationship between the probability of occurrence of foraging patches of seals and medium as well as large cod over the Scotian shelf suggests that the interaction between these two species is more important than formerly considered. However, sampling should be undertaken to determine if seals are feeding on cod in these areas, or on some other prey found in association with cod.

ACKNOWLEDGEMENTS

We would like to thank Jerry Black (DFO, Dartmouth, NS) for help in extracting fish data. As well as Christian Dussault for statistical advice.

REFERENCES

- Austin, D., Bowen, W.D., McMillan, J.I. and Iverson, S.J. 2006. Linking movement, diving and habitat to feeding in a large marine predator. *Ecology* 87:3095-3108.
- Baker, J. R., Fedak, M. A., Anderson, S. S., Arnborn, T. and Baker, R. 1990. Use of Tiletamine–Zolazepam mixture to immobilize wild gray seals and southern elephant seals. *Veterinary Record* 126: 75-77.
- Baylis, A.M.M., Page, B. and Goldsworthy, S.D. 2008. Effect of seasonal changes in upwelling activity on the foraging locations of a wide-ranging central-place forager, the New Zealand fur seal. *Canadian Journal of Zoology* 86:774-789.
- Bax, N.J. 1998. The significance and prediction in marine fisheries. *ICES Journal of Marine Sciences* 55:997–1030.

-
- Beck, C. A., Bowen, W. D. and Iverson, S. J. 2003a. Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *Journal of Animal Ecology* 72: 280-291.
- Beck, C. A., Bowen, W. D. McMillan, J. I. and Iverson, S. J. 2003b. Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Animal Behaviour* 66: 777-789.
- Beest, F. M.V., Loe, L.E., Mysteryd, A. and Milner, J.M. 2010. Comparative space use and habitat selection of moose around feeding stations. *Journal of Wildlife Management* 74:219–227.
- Bernt, K. E., Hammill, M. O. and Kovacs, K. M. 1996. Age estimation of grey seals (*Halichoerus grypus*) using incisors. *Marine Mammal Science* 12: 476-482.
- Bowen, W.D., and Harrison, G. 2006. Seasonal and interannual variability in grey seal diets on Sable Island, eastern Scotian Shelf. *In* The grey seal. NAMMCO Scientific Publications Volume Six, Tromso, Norway.
- Bowen, W.D., Carter, P. and Hammill, M.O. 2011. Estimated grey seal diets near Sable Island from fecal samples: 1991 to 2010. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/024.
- Bowen, W.D., Hammill, M.O., Koen-Alonso, M., Stenson, G., Swain, D.P. and Trzcinski, K. 2009. Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada (Part 2). DFO Can. Sci. Advis. Sec. Proceed. Ser. 2009/020.
- Breed, G. A., Bowen, D., McMillan, J. I. and Leonard, M. L. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proceedings of the Royal Society of London B* 273:2319-2326.
- Breed, G. A., Jonsen, I. D., Myers, R. A., Bowen, W. D. and Leonard, M. L. 2009. Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. *Ecology* 90:3209-3221.
- Bundy, A., Heymans, J. J., Morissette, L. and Savenkoff, C. 2009. Seals, cod and forage fish: A comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. *Progress in Oceanography* 51:188–206.
- Burnham, K.P. and Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edition. Springer, New York.
- Canadian Council on Animal Care 1993. *Guide to the care and use of experimental animals* (Vol. 1, 2nd ed.). Bradda Printing Services, Ottawa.
- Carrete, M. and Donázar, J.A. 2005. Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture, *Aegypius monachus*. *Biological Conservation* 126:582-590.
- Creel, S. and Christianson, D. 2008. Relationships between direct predation and risk effects. *TRENDS in Ecology and Evolution* 23:194-201.

-
- Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L. and Jolicoeur, H. 2005. Linking moose habitat selection to limiting factors. *Ecography* 28: 619-628.
- Freitas C, Kovacs, K.M., Lydersen, C. and Ims, R.A. 2008. A novel method for quantifying habitat selection and predicting habitat use. *Journal of Applied Ecology* 45:1213-1220.
- Fu, C., Mohn, R. and Fanning, L.P. 2001. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1613–1623.
- Goulet, A.M., Hammill, M.O. and Barrette, C. 2001. Movements and diving of grey seal females (*Halichoerus grypus*) in the Gulf of St. Lawrence. *Polar Biology* 24:432-439.
- Guinet, C., Dubroca, L., Lea, M.A., Goldsworthy, S., Cherel, Y., Duhamel, G., Bonadonna, F. and Donnay, J.-P. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series* 219:251-264.
- Halsey, L.G., Blackburn, T.M. and Butler, P.J. 2006. A comparative analysis of the diving behaviour of birds and mammals. *Functional Ecology* 20:889-899.
- Hammill, M.O. 2011. Feeding by grey seals in the southern Gulf of St Lawrence. Canadian Sciences Advisory Secretariat Research Document 2010/130.
- Hammill, M.O. and Gosselin, J.F. 1995. Grey seal (*Halichoerus grypus*) from the northwest Atlantic: female reproductive rates, age at first birth, and age of maturity in males. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2757-2761.
- Hammill, M.O., Lesage, V. and Carter P. 2005. Problems associated with determining diet composition in harp seals by reconstruction of stomach contents or faecal samples. *Canadian Journal of Zoology* 83:1365-1372.
- Harvey, V., Côté, S.D. and Hammill, M.O. 2008. The ecology of 3-D space use in a sexually dimorphic mammal. *Ecography* 31:371-380.
- Harvey, V., Hammill, M. O. and Swain, D. P. 2011a. Summer overlap between a central-place forager and its prey in the southern Gulf of St. Lawrence. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/131.
- Harvey, V., Hammill, M.O., Swain, D.P., Breed, G.A., Lydersen, C. and Kovacs, K.M. 2011b. Winter foraging by a top predator, the grey seal, in relation to the distribution of prey. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/124.
- Harwood, J. 1992. Assessing the competitive effects of marine mammal predation on commercial fisheries. *South African Journal of Marine Science* 12: 689–693.
- Harwood, J. and Croxall, J.P. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. *Marine Mammal Sciences* 4:13–33.

-
- Iverson, S. J., Field, C., Bowen, W.D. and Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs* 74: 211-235.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71.
- Lindstrøm, U., Harbitz, A., Haug, T. and Nilssen, K.T. 1998. Do harp seals *Phoca groenlandica* exhibit particular prey preferences? *ICES Journal of Marine Science* 55: 941–953.
- Littell, R. C., Stroup, W. W. and Freund, R. J. 2002. SAS for Linear Models. SAS Institut Inc., Cary, North Carolina.
- Manly, B. F. J., McDonald, L.L., Thomas, D.L., McDonald, T.L. and Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer.
- Mohn, R., and Bowen, W.D. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2722-2738.
- Morissette, L., Hammill, M.O. and Savenkoff, C. 2006. The trophic role of marine mammals in the northern Gulf of St. Lawrence. *Marine Mammal Science* 22:74-103.
- Orians, G.H. and Pearson, N.E. 1979. On the theory of central place foraging. *In* Analysis of ecological systems. Ohio State university Press.
- Pan, W. 2001. Akaike's Information Criterion in Generalized Estimating Equations. *Biometrics* 57:120-125.
- Rosenberg, D.K. and McKelvey, K.S. 1999. Estimation of habitat selection for central-place foraging animals. *Journal of Wildlife Management* 63:1028-1038.
- Smith, S. J. and Page, F.H. 1996. Associations between Atlantic cod (*Gadus morhua*) and hydrographic variables: implications for the management of the 4VsW cod stock. *ICES Journal of Marine Science* 53:597-614.
- Smout, S. and Lindstrøm, U. 2007. Multispecies functional response of the minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. *Marine Ecology Progress Series* 341:277-291.
- Stenson, G.B. and Hammill, M.O. 2011. Winter Diet of Grey Seals in Cabot Strait. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/128.
- Tzcinski, M.K., Mohn, R. and Bowen, W.D. 2006. Continued decline of an Atlantic cod population: how important is gray seal predation? *Ecological Applications* 16: 2276-2292.
- Weimerskirch, H., Corre, M.L., Jaquemet, S. and Marsac, F. 2005. Foraging strategy of a tropical seabird, the redfooted booby, in a dynamic marine environment. *Marine Ecology Progress Series* 288:251-261.

-
- Weimerskirch, H., Pinaud, D., Pawlowski, F. and Bost, C.-A. 2007. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *American Naturalist* 170:734-743.
- Wilson, F.W., Shackelton, D.M. and Campbell, K.L. 1998. Making habitat-availability estimates spatially explicit. *Wildlife Society Bulletin* 26:626-631.
- Winter, A., Foy, R.J. and Wynne, K. 2009. Seasonal differences in prey availability around a Steller sea lion haulout and rookery in the Gulf of Alaska. *Aquatic Mammals* 35:145-162.
- Wirsing, A.J., Heithaus, M.R., Frid, A. and Dill, L.M. 2008 Seascapes of fear: evaluating sublethal predators effects experienced and generated by marine mammals. *Marine Mammal Science* 24:1-15.

Table 1. Fish species and size classes used in this study.

Group fish	Size class (cm)	size
American plaice (<i>Hippoglossoides platessoides</i>)	<30	small
	>30	large
Cod (<i>Gadus morhua</i>)	<25	small
	25-35	medium
	>35	large
Haddock (<i>Melanogrammus aeglefinus</i>)	<20	small
	20-30	medium
	>30	large
Herring (<i>Clupea harengus</i>)	<30	small
	>30	large
Pollock (<i>Pollachius genus</i>)	<30	small
	>30	large
Sandlance (<i>Ammodytes sp.</i>)	all	
Redfish (<i>Sebastes sp.</i>)	<20	small
	20-30	medium
	>30	large
Smooth skate (<i>Anacanthobatis sp.</i>)	≤45	small
	>45	large
Thorny skate (<i>Amblyraja radiata</i>)	≤45	small
	>45	large
White hake (<i>Urophycis tenuis</i>)	≤35	small
	>35	large
Winter flounder (<i>Pseudopleuronectes americanus</i>)	≤30	small
	>30	large
Witch flounder (<i>Glyptocephalus cynoglossus</i>)	≤30	small
	>30	large

Table 2. Logistic regression results: effect on fish species on the probability of the occurrence of foraging path of grey seals according to fish data obtained from RV trawl survey conducted on a) July and b) March in 4VsW NAFO areas in 1990s and 2000s for both females and males. All models including second order interaction terms between fish group and distance were tested. Only the 5 best will be shown here. Best models are shown in bold and equivalent models ($\Delta QIC_u \leq 2$) in italics. I =Intercept of the model. K (number of estimated parameters including the intercept) is 4 for all models presents here.

1990-1999				2000-2009			
model	QIC	ΔQIC	ω	model	QIC	ΔQIC	ω
a) July							
<i>female</i>							
				<i>$I + dist + whak > 35 + dist * whak > 35$</i>	220,9	0,0	0,1
				<i>$I + dist + had > 35 + dist * had > 35$</i>	221,1	0,2	0,1
				<i>$I + dist + shak < 35 + dist * shak < 35$</i>	221,6	0,7	0,1
				<i>$I + dist + wtfl < 30 + dist * wtfl < 30$</i>	221,8	0,9	0,1
				<i>$I + dist + red < 20 + dist * red < 20$</i>	221,9	0,9	0,1
				<i>$I + dist + cod\ 25-35 + dist * cod\ 25-35$</i>	222,6	1,7	0,1
				<i>$I + dist + whak < 35 + dist * whak < 35$</i>	222,9	2,0	0,1
<i>male</i>							
				<i>$I + dist + tsk < 45 + dist * tsk < 45$</i>	100,0	0,0	0,3
				<i>$I + dist + had < 25 + dist * had < 25$</i>	100,8	0,8	0,2
				<i>$I + dist + shak < 35 + dist * shak < 35$</i>	103,0	3,0	0,1
				<i>$I + dist + had > 35 + dist * had > 35$</i>	103,2	3,2	0,1
				<i>$I + dist + wtfl < 30 + dist * wtfl < 30$</i>	104,7	4,7	0,0
				<i>$I + dist + had < 25 + dist * had < 25$</i>	396,2	0,0	0,3
				<i>$I + dist + whak > 35 + dist * whak > 35$</i>	396,3	0,0	0,3
				<i>$I + dist + shak > 35 + dist * shak > 35$</i>	398,6	2,3	0,1
				<i>$I + dist + ampl < 30 + dist * ampl < 30$</i>	399,4	3,2	0,1
				<i>$I + dist + her < 30 + dist * her < 30$</i>	400,1	3,9	0,0

Table 2 (end).

1990-1999				2000-2009			
Model	QIC	Δ QIC	ω	Model	QIC	Δ QIC	ω
b) March							
<i>Female</i>							
<i>I + dist + tsk<45 + dist*tsk<45</i>	100,0	0,0	0,3	<i>I + dist + whak>35 + dist*whak>35</i>	218,2	0,0	0,2
<i>I + dist + had<25 + dist*had<25</i>	100,8	0,8	0,2	<i>I + dist + had>35 + dist*had>35</i>	218,7	0,5	0,1
<i>I + dist + shak>35 + dist*shak>35</i>	103,0	3,0	0,1	<i>I + dist + wtfl<30 + dist*wtfl<30</i>	219,4	1,2	0,1
<i>I + dist + had>35 + dist*had>35</i>	103,2	3,2	0,1	<i>I + dist + red<20 + dist*red<20</i>	219,5	1,2	0,1
<i>I + dist + wtfl<30 + dist*wtfl<30</i>	104,7	4,7	0,0	<i>I + dist + shak<35 + dist*shak<35</i>	219,5	1,3	0,1
				<i>I + dist + whak<35 + dist*whak<35</i>	219,8	1,6	0,1
<i>Male</i>							
<i>I + dist + ampl>30 + dist*ampl>30</i>	90,9	0,0	0,2	<i>I + dist + had>35 + dist*had>35</i>	128,3	0,0	0,5
<i>I + dist + ampl<30 + dist*ampl<30</i>	91,0	0,2	0,1	<i>I + dist + cod>35 + dist*cod>35</i>	130,3	2,0	0,2
<i>I + dist + whak>35 + dist*whak>35</i>	91,6	0,7	0,1	<i>I + dist + shak>35 + dist*shak>35</i>	132,7	4,4	0,1
<i>I + dist + cod 25-35 + dist*cod 25-35</i>	91,7	0,9	0,1	<i>I + dist + her1 + dist*her1</i>	133,6	5,3	0,0
<i>I + dist + tsk>45 + dist*tsk>45</i>	91,9	1,1	0,1	<i>I + dist + whak<35 + dist*whak<35</i>	134,4	6,1	0,0
<i>I + dist + wtfl>30 + dist*wtfl>30</i>	92,5	1,6	0,1				
<i>I + dist + wtfl<30 + dist*wtfl<30</i>	92,7	1,9	0,1				
<i>I + dist + slance + dist*slance</i>	92,8	2,0	0,1				

Table 3. Most parsimonious models (see Table 2) of fish selection by females and males grey seals in 4VsW NFO areas in a) July and b) in March for both in 1990s and 2000s.

Covariate	β	SE	IC		Z	P
			lower	upper		
a) July						
<i>female after 2000</i>						
<i>I + dist + whak>35 + dist*whak>35</i>						
I	0,34	0,82	-1,27	1,95	0,42	0,68
dist	-0,04	0,01	-0,05	-0,02	-4,97	<0,01
whak<35	-2,56	1,12	-4,76	-0,37	-2,29	0,02
dist*whak<35	0,01	0,01	0,00	0,02	2,48	0,01
<i>I + dist + had>35 + dist*had>35</i>						
I	-1,56	0,51	-2,55	-0,57	-3,09	<0,01
dist	-0,03	0,01	-0,04	-0,02	-4,47	<0,01
had>35	0,02	0,01	0,00	0,04	2,04	0,04
dist*had>35	0,00	0,00	0,00	0,00	-1,67	0,09
<i>I + dist + shak<35 + dist*shak<35</i>						
I	-2,01	0,56	-3,10	-0,92	-3,61	<0,01
dist	-0,02	0,01	-0,03	-0,01	-3,50	<0,01
shak<35	0,01	0,00	0,01	0,02	3,39	<0,01
dist*shak<35	0,00	0,00	0,00	0,00	-3,26	<0,01
<i>I + dist + red<20 + dist*red<20</i>						
I	-1,37	0,58	-2,50	-0,24	-2,38	0,02
dist	-0,03	0,01	-0,04	-0,02	-4,59	<0,01
red<20	0,00	0,01	-0,02	0,02	0,24	0,81
dist*red<20	0,00	0,00	0,00	0,00	0,60	0,55
<i>I + dist + cod 25-35 + dist*cod 25-35</i>						
I	-1,77	0,52	-2,79	-0,75	-3,39	<0,01
dist	-0,02	0,01	-0,04	-0,01	-4,00	<0,01
cod 25-35	0,67	0,23	0,22	1,13	2,88	<0,01
dist*cod 25-35	-0,01	0,00	-0,02	0,00	-2,50	0,01

Table 3 (cont'd).

*I + dist + whak<35 + dist*whak<35*

I	0,60	0,83	-1,03	2,24	0,72	0,47
dist	-0,04	0,01	-0,06	-0,02	-4,73	<0,01
whak>35	-3,46	1,27	-5,93	-0,98	-2,73	0,01
dist*whak>35	0,02	0,01	0,01	0,03	2,88	<0,01

male before 2000

*I + dist + tsk<45 + dist*tsk<45*

I	-1,76	0,76	-3,24	-0,27	-2,32	0,02
dist	-0,02	0,01	-0,04	-0,01	-4,12	<0,01
Tsk<45	-0,07	0,15	-0,37	0,23	-0,47	0,64
dist*tsk<45	0,00	0,00	0,00	0,00	1,70	0,09

*I + dist + had<25 + dist*had<25*

I	-3,51	0,57	-4,62	-2,40	-6,18	<0,01
dist	0,00	0,00	-0,01	0,01	-0,33	0,74
had<25	0,10	0,02	0,05	0,14	4,09	<0,01
dist*had<25	0,00	0,00	0,00	0,00	-3,59	<0,01

*I + dist + shak<35 + dist*shak<35*

I	-3,08	0,40	-3,86	-2,30	-7,77	<0,01
dist	0,00	0,00	-0,01	0,00	-1,09	0,28
shak<35	0,01	0,01	0,00	0,03	2,20	0,03
dist*shak<35	0,00	0,00	0,00	0,00	-2,03	0,04

Male after 2000

*I + dist + had<25 + dist*had<25*

I	-2,66	0,26	-3,17	-2,15	####	<0,01
Dist	-0,01	0,00	-0,02	0,00	-3,78	<0,01
had<25	0,19	0,09	0,02	0,36	2,14	0,03
dist*had<25	0,00	0,00	-0,01	0,00	-2,82	0,00

*I + dist + whak>35 + dist*whak>35*

I	-1,25	0,44	-2,11	-0,40	-2,87	<0,01
Dist	-0,02	0,00	-0,03	-0,01	-6,07	<0,01
whak>35	-3,27	1,24	-5,69	-0,85	-2,65	0,01
dist*whak>35	0,02	0,01	0,00	0,03	2,49	0,01

Table 3 (cont'd).

b) March

Female before 2000

*I + dist + tsk<45 + dist*tsk<45*

I	-1,76	0,76	-3,24	-0,27	-2,32	0,02
dist	-0,02	0,01	-0,04	-0,01	-4,12	<0,01
tsk1	-0,07	0,15	-0,37	0,23	-0,47	0,64
dist*tsk1	0,001	0,001	-0,01	0,01	1,7	0,08

*I + dist+ had<25 + dist*had<25*

I	-3,51	0,57	-4,62	-2,4	-6,18	<0,01
dist	-0	0,04	-0,01	0,01	-0,33	0,74
had1	0,1	0,02	0,05	0,14	4,09	<0,01
dist*had1	0	0,00	-0	-0	-3,59	<0,01

Female after 2000

*I + dist + whak>35 + dist*whak>35*

I	-3,55	0,42	-4,37	-2,73	-8,46	<0,01
dist	0,00	0,00	-0,01	0,00	-0,70	0,48
whak>35	-0,13	0,17	-0,47	0,20	-0,78	0,44
dist*whak>35	0,00	0,00	0,00	0,00	-1,00	0,32

*I + dist + had>35 + dist*had>35*

rcept	-3,04	0,40	-3,83	-2,25	-7,57	<0,01
dist	-0,01	0,00	-0,01	0,00	-1,79	0,07
had>35	-0,07	0,03	-0,13	-0,01	-2,26	0,02
dist*had>35	0,00	0,00	0,00	0,00	2,42	0,02

*I + dist + wtfl<30 + dist*wtfl<30*

I	-3,86	0,65	-5,13	-2,60	-5,99	<0,01
dist	0,00	0,00	-0,01	0,01	-0,17	0,87
wtfl<30	0,02	0,02	-0,03	0,06	0,67	0,51
dist*wtfl<30	0,00	0,00	0,00	0,00	-0,67	0,50

*I + dist + red<20 + dist*red<20*

I	-3,75	0,44	-4,61	-2,90	-8,62	<0,01
dist	0,00	0,00	-0,01	0,00	-0,42	0,67
red1	0,00	0,00	0,00	0,00	0,39	0,70
dist*red1	0,00	0,00	0,00	0,00	-0,20	0,84

Table 3 (cont'd).

*I + dist + shak<35 + dist*shak<35*

I	-3,47	0,39	-4,23	-2,70	-8,91	<0,01
Dist	0,00	0,00	-0,01	0,00	-1,06	0,29
shak1	-0,01	0,00	-0,01	0,00	-2,30	0,02
dist*shak1	0,00	0,00	0,00	0,00	2,09	0,03

*I + dist + whak<35 + dist*whak<35*

I	-3,32	0,50	-4,29	-2,35	-6,69	<0,01
dist	0,00	0,00	-0,01	0,00	-0,98	0,33
whak<35	-0,22	0,13	-0,47	0,03	-1,69	0,09
dist*whak<35	0,00	0,00	0,00	0,00	0,84	0,40

male before 2000

*I + dist + ampl>30 + dist*ampl>30*

I	-1,34	0,65	-2,62	-0,06	-2,05	0,04
dist	-0,02	0,01	-0,03	0,00	-2,43	0,02
ampl>30	-0,36	0,14	-0,62	-0,09	-2,60	0,01
dist*ampl>30	0,00	0,00	0,00	0,00	2,25	0,02

*I + dist + ampl<30 + dist*ampl<30*

I	-1,63	0,82	-3,24	-0,03	-1,99	0,05
dist	-0,01	0,01	-0,02	0,01	-1,22	0,22
ampl<30	-0,03	0,13	-0,28	0,22	-0,21	0,83
dist*ampl<30	0,00	0,00	0,00	0,00	-0,87	0,38

I	-2,06	0,77	-3,58	-0,55	-2,68	0,01
dist	-0,01	0,01	-0,03	0,01	-1,31	0,19
wtfi>30	0,13	1,63	-3,06	3,32	0,08	0,94
dist*wtfi>30	-0,02	0,02	-0,06	0,02	-0,78	0,43

*I + dist + whak>35 + dist*whak>35*

I	-2,39	0,86	-4,08	-0,70	-2,77	0,01
dist	-0,01	0,01	-0,03	0,01	-1,16	0,25
whak>35	1,65	1,77	-1,81	5,12	0,93	0,35
dist*whak>35	-0,04	0,03	-0,11	0,02	-1,31	0,19

Table 3 (cont'd).

*I + dist + cod 25-35 + dist*cod 25-35*

I	-1,77	0,5216	-2,79	-0,75	-3,39	<0,01
Dist	-0,02	0,0062	-0,04	-0,01	-4	<0,01
cod 25-35	0,673	0,2337	0,215	1,131	2,88	0,004
dist*cod 25-35	-0,01	0,0037	-0,02	-0	-2,5	0,012

*I + dist + tsk>45 + dist*tsk>45*

I	-1,43	0,67	-2,75	-0,12	-2,13	0,03
dist	-0,02	0,01	-0,03	0,00	-2,45	0,01
tsk2	-3,51	5,78	-14,83	7,82	-0,61	0,54
dist*tsk2	0,00	0,05	-0,09	0,10	0,09	0,93

*I + dist + wfl>30 + dist*wfl>30*

I	-2,58	0,57	-3,71	-1,45	-4,49	<0,01
dist	-0,01	0,01	-0,02	0,00	-2,52	0,01
wfl2	-0,05	0,09	-0,22	0,12	-0,61	0,54
dist*wfl2	0,00	0,00	0,00	0,00	1,16	0,24

*I + dist + wfl<30 + dist*wfl<30*

I	-2,35	0,90	-4,12	-0,58	-2,60	0,01
dist	-0,01	0,01	-0,03	0,01	-1,33	0,18
wfl<30	0,08	0,09	-0,09	0,25	0,92	0,36
dist*wfl<30	0,00	0,00	0,00	0,00	-1,29	0,19

*I + dist + slance + dist*slance*

I	-2,43	0,93	-4,25	-0,62	-2,63	0,01
dist	-0,01	0,01	-0,03	0,00	-1,47	0,14
slance	0,72	0,55	-0,36	1,79	1,30	0,19
dist*slance	-0,01	0,01	-0,03	0,01	-1,32	0,18

male after 2000

*I + dist + had>35 + dist*had>35*

I	-6,49	1,23	-8,91	-4,07	-5,26	<0,01
Dist	0,02	0,01	0,00	0,04	2,07	0,04
had>35	0,17	0,06	0,06	0,28	2,95	<0,01
dist*had>35	0,00	0,00	0,00	0,00	-2,51	0,01

*I + dist + cod>35 + dist*cod>35*

I	-5,27	0,73	-6,71	-3,84	-7,20	<0,01
Distance	0,01	0,01	0,00	0,02	1,84	0,07
cod3	0,62	0,21	0,22	1,03	3,03	<0,01
cod3*dist	0,00	0,00	-0,01	0,00	-2,17	0,03

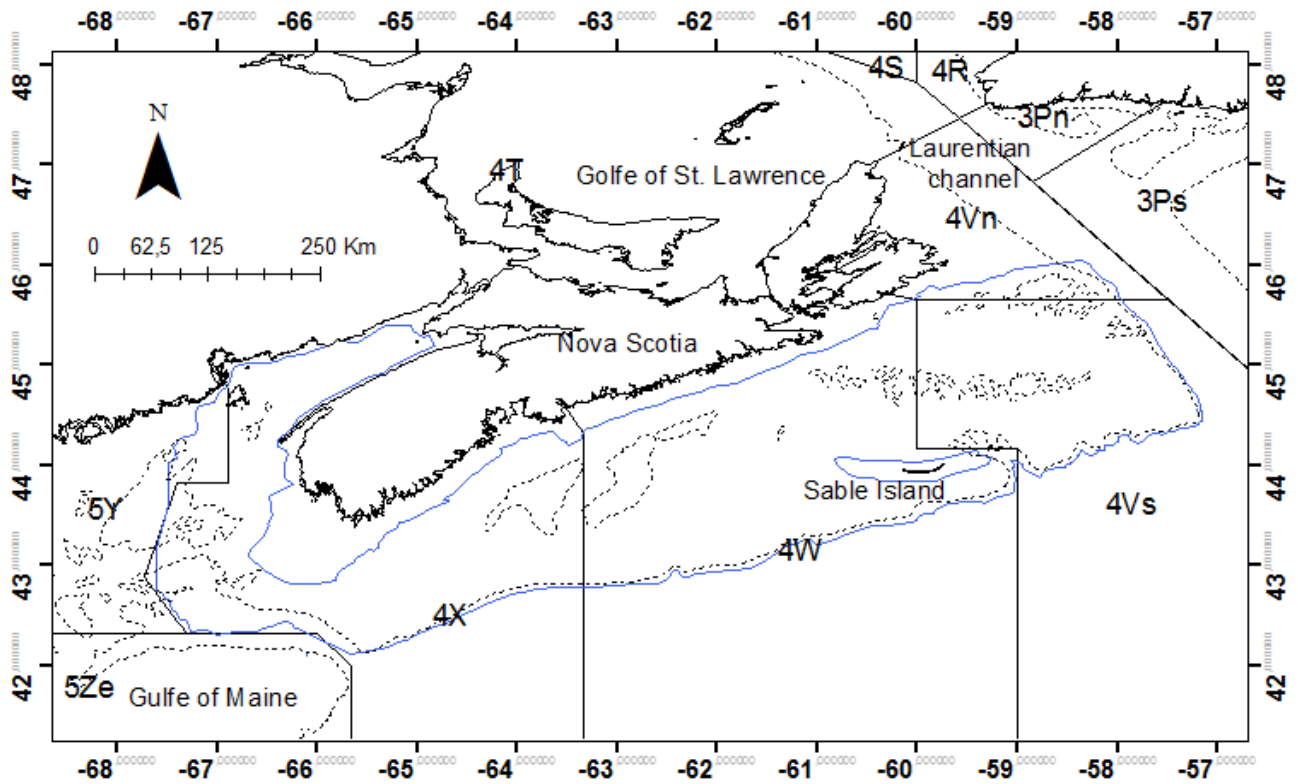


Figure 1. Scotian shelf and the surrounding area. The blue line represents the area encompassed by the RV groundfish survey conducted in NAFO fishing areas 4X and 4VsW during March and July in the 1990s and 2000s. The dashed line represents the 200 m isobath.

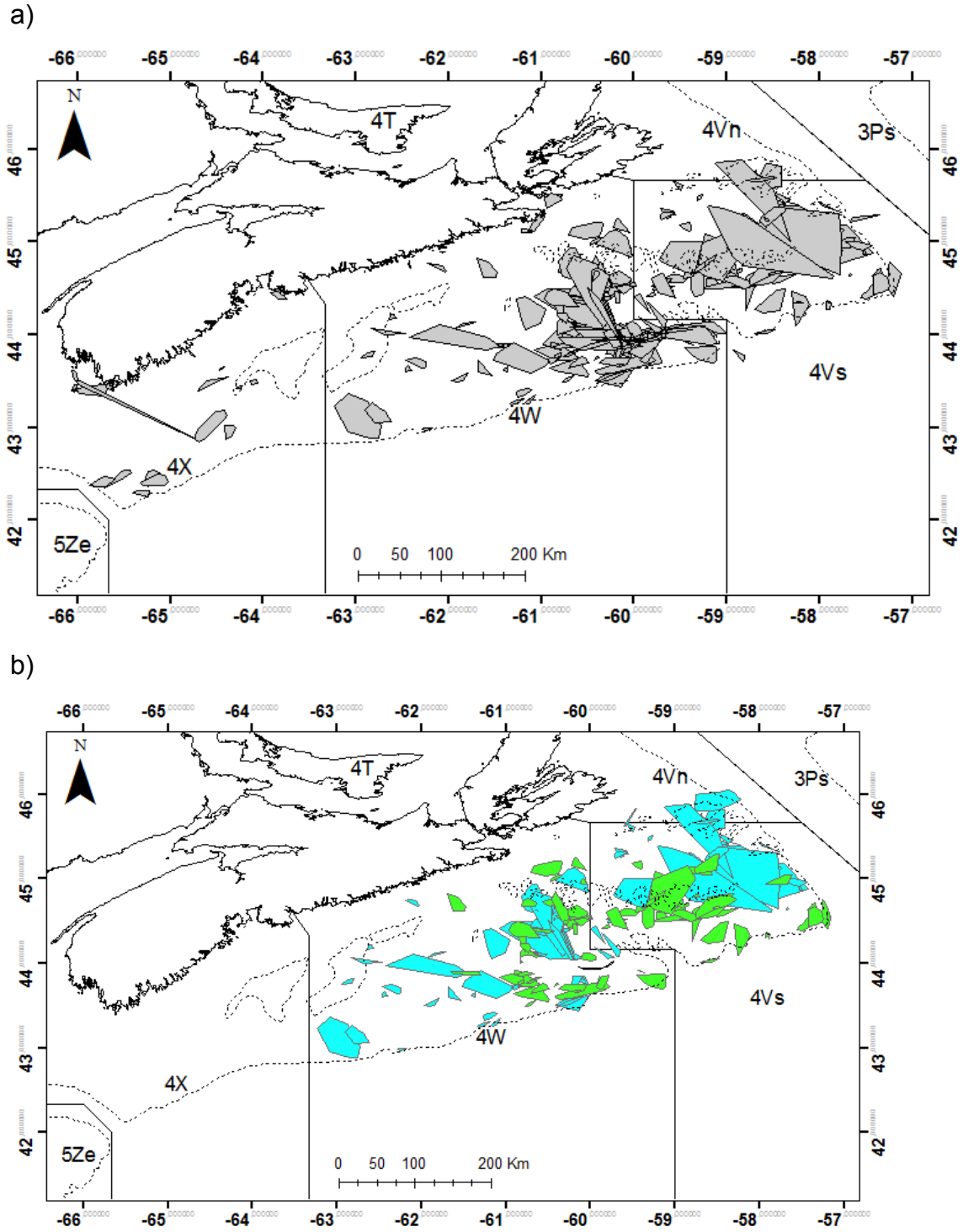


Figure 2. All foraging patches of grey seals (a) and foraging patches of seals within the area covered by the RV fish surveys in 4VsW NAFO area in both March (blue) and July (green) between 1993 and 2009.

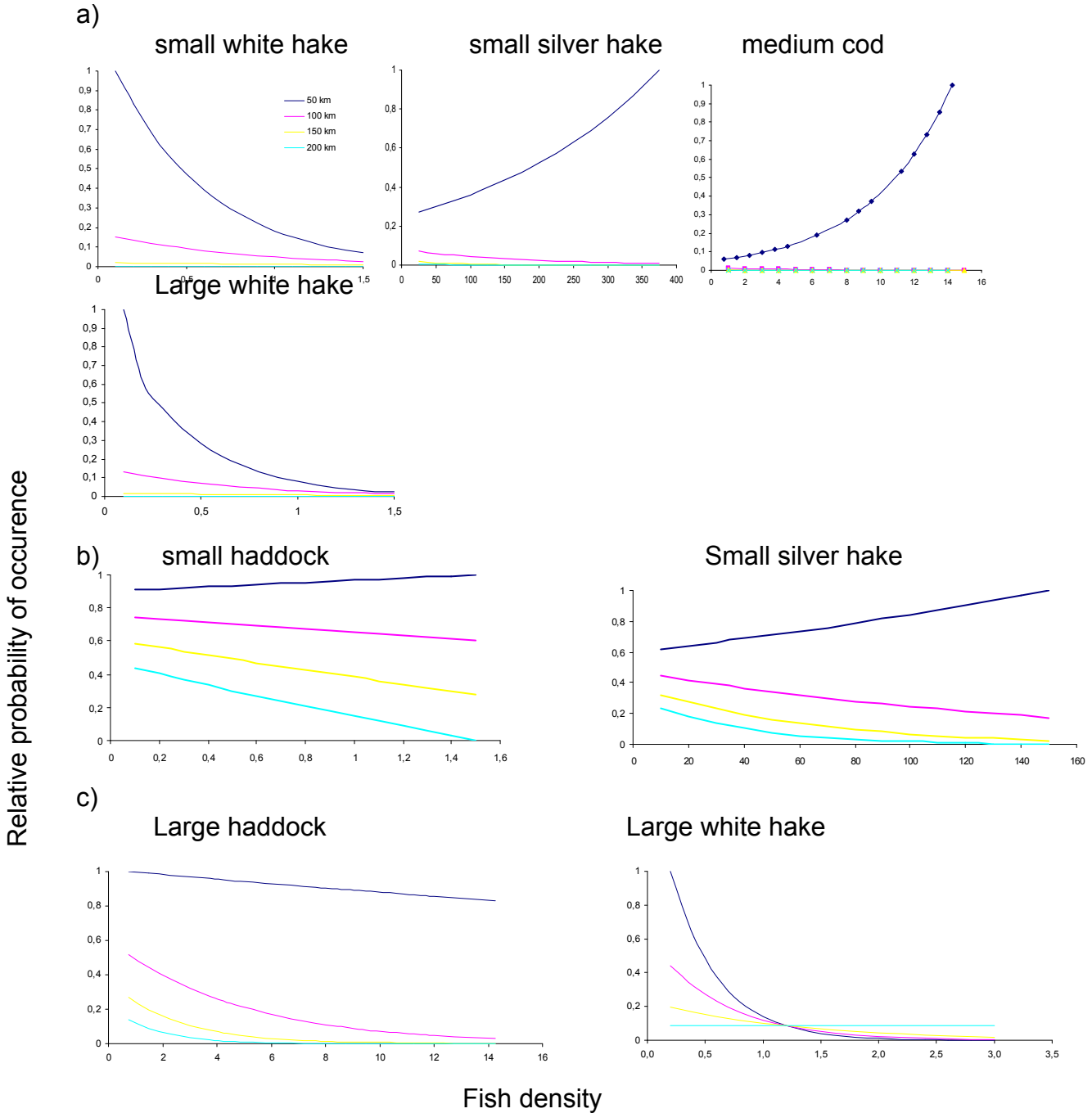


Figure 3. The relative probability of occurrence of grey seal foraging patch in July as a function of fish density in the area covered by the RV groundfish survey over the 4VsW NAFO area according to decades and sex (a) females in 2000s, b) males in 1990s, c) males in 2000s). Relative probabilities were estimated using the best predictive models (Table 3). The relative probabilities are provided for distances from Sable Island (50(blue line), 100 (pink line), 150 (yellow line) and 200 (green line) km from Sable Island).

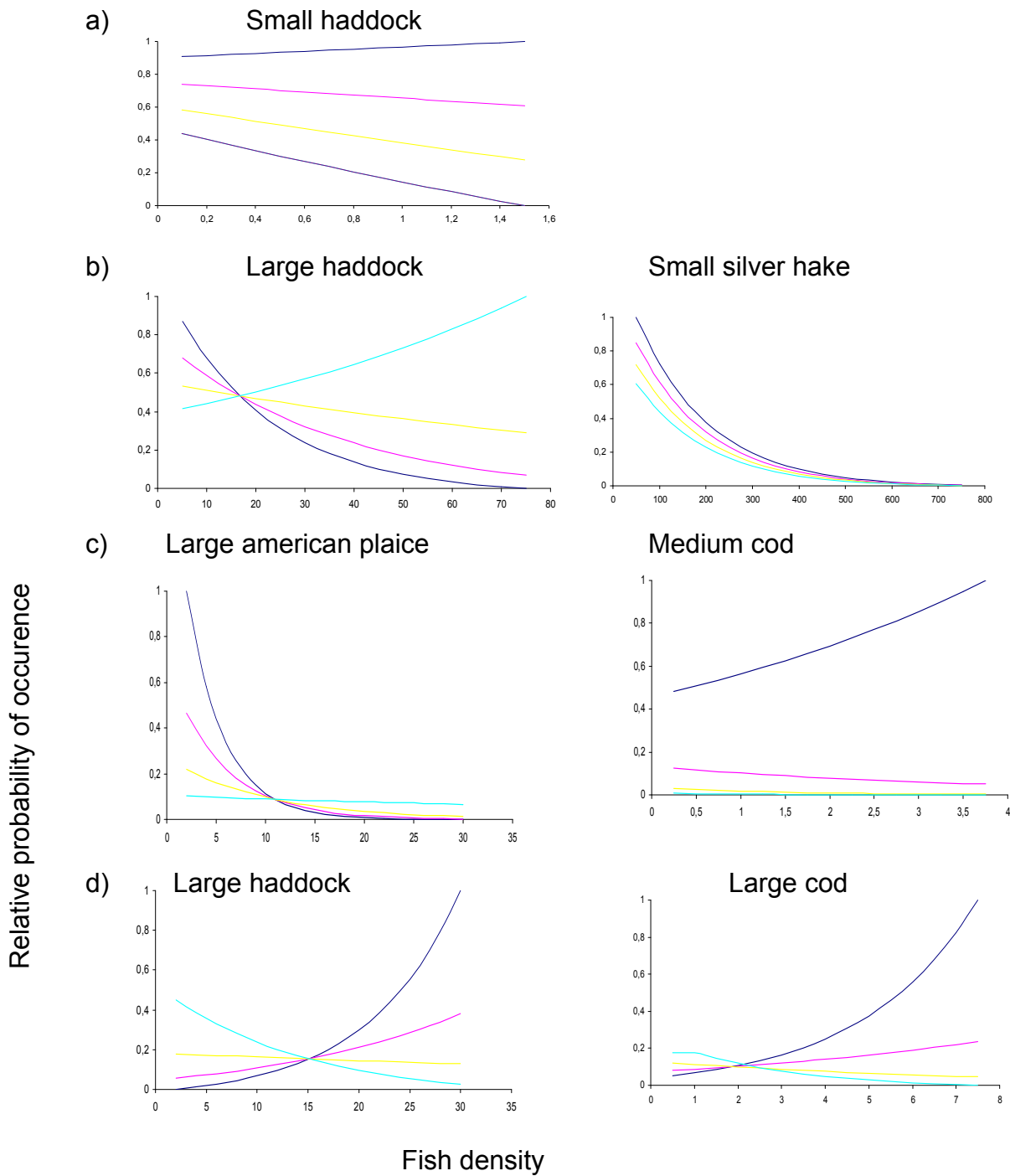


Figure 4. The relative probability of occurrence of grey seal foraging patch in March as a function of fish density in the area covered by the RV groundfish survey over the 4VsW NAFO area according to decades and sex (a) females in 1990s, b) females in 2000s, c) males in 1990s, d) males in 2000s). Relative probabilities were estimated based on best predictive models (Table 3). The relative probabilities are provided for distances from Sable Island (50 (blue line), 100 (pink line), 150 (yellow line) and 200 (green line) km) to illustrate the gradual changed in fish selection by grey seals with distance from Sable Island.