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**Summer Overlap Between a Central-
place Forager And Its Prey in the
Southern Gulf of St. Lawrence**

**Chevauchement estival entre un
prédateur s'alimentant depuis un point
central et ses proies dans le sud du
golfe du Saint-Laurent**

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TABLE OF CONTENTS

ABSTRACT	V
RÉSUMÉ	VI
INTRODUCTION.....	1
METHODS	3
STUDY AREA AND DATA COLLECTION	3
GREY SEALS	4
DATA COLLECTED	4
MODELLING PATH TRAJECTORIES	4
CENTRAL PLACE FORAGING BEHAVIOUR	5
STATISTICAL ANALYSIS	5
AREA AND RESOURCES AVAILABLE	5
SPATIAL OVERLAP BETWEEN FISH AND SEALS	6
RESULTS	7
FISH DISTRIBUTION AND ABUNDANCE	7
GREY SEAL DISTRIBUTION	8
CENTRAL PLACE FORAGING BEHAVIOUR	8
RESOURCE AVAILABILITY ACCORDING TO DISTANCE TO HAUL-OUT SITE	10
HABITAT SELECTION PATTERNS	10
ONSHORE SURVEY	11
WG SURVEY	11
DISCUSSION	11
ACKNOWLEDGMENTS	14
REFERENCES.....	15
TABLE.	22
FIGURE.....	38

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ABSTRACT

Predators affect prey populations by consuming individuals and inducing spatial changes in their behaviour. For the prey population, indirect effects of predation may be more important than predation itself by inducing reduced survival, growth or reproduction. The biomass of large demersal fishes of northwest Atlantic collapsed in early 1990s and failed to recover whereas the abundance of grey seals (*Halichoerus grypus*) is currently at historically high levels which could amplify their predation pressure on the fish stock. We followed 14 grey seals equipped with satellite transmitters in the southern Gulf of St. Lawrence during the summer period. Overall, seals were concentrated at <50 km from haulout place with a decreasing probability of foraging in areas away from haulout sites. Small white hake, small herring, and winter flounder were more abundant at distances of less than 50km from the haulout sites, whereas cunner, capelin, herring were more abundant further offshore. In August, seals overlap more with small cod near the haulout-sites compared to the overlap observed at 50-100km offshore, whereas the reverse was observed for sandlance. During September, the probability of having a foraging patch in areas of high density of cod was highest in between 50-100 km from the haulout site than in closer areas. The distribution of fish near haulout sites suggests that they try to minimize exposure to predation from grey seals, which could on a longer term affect recovery.

RÉSUMÉ

Les prédateurs peuvent affecter les populations de proies en consommant les individus et en induisant des changements spatiaux dans leur comportement. Pour les proies, les effets indirects de la prédation peuvent être plus importants que la prédation en elle-même en affectant négativement la survie, la croissance ou la reproduction. La biomasse des poissons démersaux de grande taille de l'Atlantique Nord-Ouest s'est effondrée au début des années 1990 et n'a pas récupérée depuis alors que l'abondance de phoques gris (*Halichoerus grypus*) est actuellement à des niveaux historiquement élevés ce qui peut amplifier la pression de prédation qu'ils exercent sur les stocks de poissons. Nous avons utilisé des émetteurs satellite pour suivre les déplacements de 14 phoques gris autour de leur site de repos au cours de l'été dans le sud du golfe du Saint-Laurent afin d'évaluer leur chevauchement avec les poissons d'intérêt commercial dont nous avons quantifié l'abondance et la distribution spatiale à partir de données de recensement. Généralement, les phoques sont concentrés à moins de 50 km de leur site de repos et la probabilité qu'ils démontrent un comportement d'alimentation décroît avec la distance au site d'échouerie. À l'opposé de ce qui est observé où aucun site d'échouerie n'est connu, le lançon, les petites merluches blanches, les petits harengs et les petites plies rouges sont concentrés à moins de 50 km des sites de repos alors que la tanche, le capelan et le hareng de grande taille étaient plus abondants au large des côtes. En août, le chevauchement entre les phoques et les petites morues est plus important à proximité des sites de repos qu'entre 50-100 km alors que l'inverse est observé pour le lançon. En septembre, la probabilité d'avoir une aire d'alimentation dans les régions de fortes abondances de morue est plus élevée entre 50 et 100 km qu'à proximité des sites de repos. La distribution des poissons autour des échoueries de phoques gris suggère que les poissons tentent de minimiser les menaces de prédation que les phoques gris et les autres prédateurs exercent ce qui, à long terme, peut nuire au rétablissement des stocks.

INTRODUCTION

Predators affect prey populations most obviously by killing and consuming individuals (Wirsing et al. 2008). Their success in doing this will depend on the degree of spatial and temporal overlap in distribution between a predator and its prey, which in turn determines the rate of spatial encounters between them (Fauchald 2009). From the perspective of the predator, it is assumed that they maximize foraging efficiency, by moving between foraging patches as effort expended to obtain energy shows a decline in some measure of cost to benefit. In response to predation threats, prey species may undergo seasonal or spatial changes in their own behaviour to avoid or minimize predation risk. Such responses may involve changes in habitat use, foraging, aggregation, and movement patterns (Creel and Christianson 2008, Wirsing et al. 2008). For example in Shark Bay Australia, dolphins alter their foraging behaviour, moving to deeper less prey rich waters when tiger sharks are present during the warm season, then return to feed in the more prey-dense shallow water areas when tiger sharks are less abundant during the cooler parts of the year (Wirsing et al. 2008). Foraging by large baleen whales at depth in Antarctic waters may reduce the depths that krill descend during their vertical migration (Willis 2007). The costs of these responses can be manifested by reduced survival, growth or reproduction (Creel & Christianson 2008). Recent empirical research has shown that risk effects on prey dynamics may be greater than direct effects (Creel and Christianson 2008, Wirsing et al. 2008). Therefore, it is important when examining the effects of predators on prey, that risk effects be considered as well.

Spatial and foraging constraints may also be placed on predators due to threats from other predators, inter and intraspecific competition and ties to some physical feature of the landscape. For example harbour seals in Prince William sound, Alaska, must balance expected energy gains obtained from feeding on herring near the surface against potential predation risk from killer whales versus expected energy gains feeding on less energy dense but larger Pollock at depth where exposure to predation risk from sleeper sharks will be greatest (Frid et al. 2007, Wirsing et al. 2008). The predicted level of risk taking will vary among individuals according to fat reserves, age and experience (Wirsing et al. 2008). In this case human resource use, such as overfishing of near-surface herring would result in an increasing proportion of seals foraging in deeper and apparently more dangerous strata (Frid et al. 2007, Wirsing et al. 2008). Seabirds that are adapted for efficient flying may have low costs of transport but are only able to utilize the upper meter of the sea and prey may escape by hiding at depth, where exposure to predation from predatory fish, diving seabirds and sea mammals would have the opposite effect of forcing schools of prey fish and krill to the surface, making them available to surface-feeding seabirds (Hoffman et al. 1981, Safina and Burger 1985, Mills 1998, Fauchald 2009).

Many species are limited to a specific location at certain times of the year. Seabirds are constrained to the nesting site during breeding, but may forage at large distances away from the site (Weimerskirch et al. 2005). Similarly, the seal life history strategy is characterized by marine foraging interspersed with a requirement for a solid platform (land or ice) for giving birth and caring for offspring, moult and resting. The spatial constraint associated with returning to a central place between successive foraging bouts will influence the distribution of foraging effort of central-place foragers. Central place foraging theory predicts that space use and foraging decisions are a function of the distance from the haul-out site (Orians and Pearson 1979) where central-place foragers show both lower selection for preferred resources and a lower overall variation in selection of resources close to the central point (Schoener 1979). As the risk of predation decreases with increasing distance from the colony, prey availability would increase (Lewis et al. 2001, Ainley et al. 2003). Similarly, different patterns have evolved to decrease intraspecific competition around the central place. Differences in diet and foraging areas

between sexes have been observed among many species (Beck et al. 2005, Breed et al. 2006). Among seals, food limitations close to haul-out sites, aggression from larger conspecifics, or lack of experience in how and where to exploit resources might force juveniles to move further from the haul-out sites or to dive deeper than adults to acquire food (Sjöberg and Ball 2000, Lowry et al. 2001; Harvey et al. 2008). Ultimately, those differences in habitat use might affect the foraging success, growth and possibly survival of individuals (Tupper and Boutilier 1997, Cresswell et al. 2010).

The grey seal is a medium sized phocid (approx 300 kg) occurring throughout the North Atlantic. Abundant throughout the North Atlantic up to the 17th or 18th centuries, population declined in the 19th and 20th centuries but have shown marked increases since the 1970s (Lavigne and Hammill 1993, Bowen et al. 2003, Thomas et al. 2008). Grey seals are strongly associated with coastal habitats, alternating hauling out on isolated islands, or reefs with foraging trips to sea. The reason why they frequently return to land to haulout is unknown but may be associated with costs incurred for processing food (Sparling et al. 2007). The central place foraging behaviour is predominant in summer, when grey seals are concentrated in coastal areas and widely dispersed throughout their range. The distribution of haul-out sites within the southern gulf is not uniform. Grey seals are sensitive to disturbance, and although several areas would appear to be suitable for hauling out, the majority of sites are limited to more isolated areas or protected areas (National Parks) (Hammill personal observation). In winter, grey seals use more offshore areas since they may utilize drifting ice as a platform to haulout on in some areas (Harvey et al. 2008). Grey seals are also relatively shallow divers. Although capable of diving to 400 m, most dives are less than 200 m deep; much less than is observed with the similar sized hooded seal, which regularly dives to 400 m or more and with maximum dives of over 1 km in depth (Bajzak et al. 2009).

In the southern Gulf of St. Lawrence (Gulf) the biomass of large demersal fishes, notably Atlantic cod (*Gadus morhua*), collapsed in the late 1980s and early 1990s, mostly due to overfishing. Despite limited fishing over the last 15 years, demersal fish populations in the Gulf, most notably cod, have failed to recover due to elevated natural mortality among adult fish (Swain and Chouinard 2008, Swain et al. 2009) and it has been suggested that predation by grey seals may be an important factor (Chouinard et al. 2005, Benoît and Swain 2008, Swain et al. 2009). Available diet information indicates that they prey primarily on fish of intermediate sizes (e.g., mean length of cod 28 cm in length), not large adult fish for which the recent elevated natural mortality levels have been documented. However, the consumption of large fish by grey seals may be underestimated if their heads are not consumed (e.g., Hauser et al. 2008, Phillips and Harvey 2009) or if sampling to determine diet composition has not occurred when and where grey seals and large fish overlap. Many groundfish spawn and are widely distributed throughout the southern Gulf during the summer. However, in late autumn, they exit the Gulf to overwinter in Cabot Strait and off the northeast coast of Cape Breton Island. Harvey et al. (2011) examined the winter distribution of some groundfish species and grey seals equipped with satellite transmitters and concluded that male grey seals, in particular, may feed on highly aggregated large cod in early winter in Cabot Strait, off northern Cape Breton Island. Subsequent diet sampling based on analyses of stomach contents in the area confirmed that grey seals were consuming considerable numbers of large cod (average length 42 cm; Stenson and Hammill unpublished data).

In this study, we used telemetry data to analyse movement and to quantify the spatial distribution of the foraging behaviour of grey seals in late summer. As grey seals are central place foragers, we predict that their foraging effort decreases with increasing distance from haul-out site. Using fish data survey, we also estimated the overlap of grey seals with fish of

commercial concern. Since much of the available information on diet composition is based on near-shore sampling we examined the spatial overlap between grey seals and fish to determine if the information on diet may be biased, particularly with respect to size composition of fish consumed in the diet versus what is available where grey seals are foraging. If grey seals are important predators within the region, then we would predict that prey densities would increase as distance from the haul-out site (central place foraging) increased, but we expected that abundance of non-preferred prey would show little change with distance to haul-out site. We also expect that seals will overlap more with high energetic fish in areas further offshore than at close distances to the haulout site.

METHODS

STUDY AREA AND DATA COLLECTION

This study occurred in the Gulf of St. Lawrence (Gulf), a wide and shallow shelf of <100 m deep, included in the Northwest Atlantic Fishing Organization (NAFO) fishing zone of 4T (Fig. 1). Seals were captured in the western part of the Gulf, consequently we limited our study area to the western Gulf (WG), a region that was bounded by the eastern coast of New Brunswick and Gaspé, the Laurentian channel and the western coast of Magdalen Islands (Fig. 1). Bottom-trawl surveys to evaluate fish abundance of the southern Gulf have been conducted by the Department of Fisheries and Oceans in August since 2003 and in September since 1971 (only data since 2000 are used here). Surveys followed a stratified random design, with stratification based on depth and geographic area. The survey area was divided into 16 regions or “strata”, and fishing locations were randomly selected within each stratum. The number of sites sampled each year has varied from about 65–75 in the 1970s to 140–200 in years since 1989. The target fishing procedure in all years was a 30-min tow at 3.5 knots. All catches were adjusted to a standard tow of 1.75 nautical miles. Fishing was conducted only during daylight hours (07:00–19:00) prior to 1985, and 24 h per day since then. Catchability of some fish (e.g., thorny skate) to the survey is higher at night than in day, and night catches were adjusted to be equivalent to day catches as described in Benoît and Swain (2003a,b). When necessary, based on the results of comparative fishing experiments, catches of fish were adjusted for a change in survey vessel in 1992 and for a change in vessel and gear in 1985 (Benoît and Swain, 2003b). Depths covered during the survey varied between 20 to 400 m (Fig. 1) (Swain and Benoit 2006).

A fish survey has also been conducted in Northumberland Strait (NS survey), which separates Prince Edward Island from the mainland, in July since 2000 (Fig. 1). This trawl survey used a random-block experimental design developed from a 2 x 2 nautical mile grid placed over all of Northumberland Strait and adjacent waters. A total of 1,100 permanent stations were identified over this area. The potential survey area was divided into 10 experimental blocks (based on substrate characteristics); five zones/strata were included in this study. For each block, 30 to 50 primary stations and up to 15 alternate stations were chosen at random (without replacement) from within each block. As our study was limited to the WG, we only considered fish abundance sampled at the western end of the area covered by this survey (Hanson 2009) (Fig. 2c).

Most of the demersal and pelagic fish species as well as crustaceans that occurred within the area covered by the surveys were sampled. We selected ten common and commercially important fish species including both species frequently (e.g., herring, cod) and rarely (e.g., winter flounder, skates) reported in grey seal diets (Table 1). When possible, we divided the survey catch of fish species into two or three size classes (Table 2). This resulted in a total of 10, 12 and 18 fish groups considered respectively for the NS, August and September WG

surveys. We used principal components analysis (PCA) to summarize similarities and differences in spatial distribution among fish groups on each fish survey. A PCA was performed using a normalized varimax rotation on the correlation matrix of the fish groups. Variables were log-transformed to improve the normality of their distribution prior to analysis. We used the *Geostatistical Analyst* extension of ArcGIS v9.2 (Environmental System Research Institute, Inc (ESRI), 380 New York Street Redlands, CA 92373-8100) to produce prediction maps of fish density for each groups of fish, combining the data from all years. These analyses were repeated 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.

GREY SEALS

We captured grey seals during either May-June (post-moult), or September-October from 2000 to 2008 at Sable Island, and within the Gulf. Seals were anesthetised (Baker et al. 1990) and an incisor tooth was extracted for age determination (Bernt et al. 1996). 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-8, 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).

DATA COLLECTED

Satellite transmitter signals were received by satellite, and processed under the ARGOS system, which provided information on animal position (Argos 1989). A pressure sensor sampled depth and a wet/dry sensor also included in tags used, allowed inferring about the diving and haul-out activity of seals. Wildlife Computers tags sampled depths at every 10 s and at a resolution of 2 m. Dive data were assigned to user-programmed bins that recorded the number of dives as well as time spent in each depth category and the number of dive in each duration category. The binned data were collected and transmitted over 6 h periods. The SMRU transmitters recorded dive parameter information at 4 seconds intervals at a resolution of 2 m. These tags transmitted summary statistics of the diving and haul-out activity of seals throughout a 3-h time period. A haul-out begins when the SRDL has been continuously dry for at least 10 minutes and ends when continuously wet for 40 seconds. The duration and the approximate positions for the start and the end of each haul-out event, interpolated along the track joining the locations obtained for each individual, were also obtained. Similar information was also obtained for individual dives performed by seals.

MODELLING PATH TRAJECTORIES

Differences in satellite uplink rates, duty cycles, and batteries life as well as location error rates can cause large differences in both track duration and in the number of locations collected from each animal per unit time. We fit 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, <http://cran.r-project.org>) to handle erroneous satellite locations and normalized the number of locations obtained for each individual per day. State-space models handle erroneous points by estimating the true location using the error structure of the entire set of satellite locations. 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 (less

than 10% of the dataset) were excluded from some of our behavioural analyses. Most fishes begin to migrate out of the Gulf by mid-October. Thus, we only considered locations of seals between July and mid-October.

CENTRAL PLACE FORAGING BEHAVIOUR

We used haul-out information obtained by the SMRU tags to investigate movement of seals at-sea. We calculated the proximate distance to land for each haul-out event. Haul-out conditions occasionally occurred at sea. This was probably due to the seal remaining motionless at the surface at sea or to the inaccuracy of the Argos system. As the Argos precision was about 1 km (Argos 1989, Vincent et al. 2002), only haul-out events that occurred within a distance of 1 km of the coastline were considered as terrestrial haul-out events. We calculated duration of each haul-out event and the distance between successive terrestrial haul-outs. Trip-to-sea was defined as an excursion between two successive terrestrial haul-out events. Haul-out events that occurred at more than 1 km from the shore were designated as extended at-sea surface intervals. Each of these events was assigned to their relevant trip to sea. Altogether, we assigned 3 053 locations to their relevant trips to sea (N=489), providing us with the distance of each location from the haul-out site from which the seal began its trip to sea. The location with the greatest distance from the haulout within each single trip to sea was used as a proxy for the maximum distance travelled during that trip. Trip duration was estimated by extracting the time elapsed between when the animal left the start haulout site, travelled to sea then hauled out again.

STATISTICAL ANALYSIS

We used linear mixed models to test the influence of different parameters (see table 4) on the haul-out and trip duration, distance between successive haul-outs, maximum distance reach during a trip to sea, extended at-sea surface duration, and return trip duration to haul-out. To account for repeated measures on the same individuals and for differences between individuals, an “individual” was considered as a repeat factor in the models. We applied a log transformation to variables tested prior to the analysis to improve the normality of residuals. We calculated the Akaike information criterion (AIC), delta AIC and Akaike weights to determine the factors that best explained the variation in the data. Model selection was performed following the parsimony principle (Burnham and Anderson 2002a). However, when models with similar AIC values were observed ($\Delta AIC \leq 2$), we estimated parameter values and standard errors using a model averaging procedure based on model AIC weight (Burnham and Anderson 2002a). Only the best models for each analysis are reported below. All models tested and their associated AIC values are presented in appendix A. All statistical analyses were carried out using SAS (SAS® version 9.1; SAS Institute Inc, 100 SAS Campus Drive Cary, NC 27513-2414 USA) with a probability level set at 0.05. All results are presented as means \pm se.

AREA AND RESOURCES AVAILABLE

To assess foraging behaviour of seals, we defined any area of at least three consecutive foraging locations as a foraging patch. We then measured the area of foraging patches using a minimum convex polygon method (Breed et al. 2009). This was done considering all locations obtained for seals that concentrated their activities within the southern Gulf between July and mid-October. Logistic regression analyses, relating the probability of occurrence of a foraging patch to fish abundance (Manly et al. 2002), were then used to estimate the overlap between seals and fish. This analysis compared fish density between observed and randomly located foraging patches created in the area available for seals.

As grey seals are central place foragers, the area available to them is limited to the area surrounding the haul-out site. The maximum distance reach by a seal during a trip to sea was 170 km. We then considered the area located at less than 170 km from a haul-out as habitat available to seals. Trips in which the foraging patch of grey seals occurred were concentrated around four haul-out site areas: Gaspé, Miscou Island, Neguac and Kouchibouguac (Fig. 1). We calculated the average coordinates for the haul-out sites that occurred in each of these areas and created a circle of 170 km of radius around each of these 'average haul out sites' (Fig. 1). We determined if fish abundance within the area available for seals differed from fish abundance within the area covered by the survey. We also performed *t*-tests to estimate how abundance of each fish group varied within the area used by seals according to different distances classes (0-10; 10-30; 30-50; 50-100; 100-170; >170 km) from the haul-out site. No large persistent haulout sites occur along the northern coast of the PEI Island. Using the same distance classes as in the previous analyses, we also performed *t*-tests to determine if fish abundance in this area was different from areas where seals were observed to occur.

SPATIAL OVERLAP BETWEEN FISH AND SEALS

Habitat selection was determined by comparing the abundance of a fish group within a seals' foraging patch to fish group abundance within the study area. The availability of fish was determined by randomly positioning each foraging patch (using rotation and translation) 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). We repeated this exercise over the areas covered by the NS survey and by the WG survey by creating 10 to 30 random permutations over each of these areas, respectively. We used ArcGIS 9.2 to calculate the abundance of each fish group within a foraging patch and random permutations.

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 the haul-out site as an explanatory variable in the models tested. For the foraging patch for which the coordinates of the departure haul-out site were unknown, we visually examined the path of the individual and calculated trip distance using the average coordinates of haul-out site area that occurred in the vicinity of the haul-out site from which trip began for that seal. We considered 5 distance classes, in our analysis (0-10; 10-30; 30-50; 50-100; 100-170 km). Models estimated did not converge if we included distance classes within which no foraging patch occurred. We then excluded distance class for which no foraging patch occurred from our analysis. We excluded the following distance class from our analyses: NS survey: 100-170km; WG August: 0-10;100-170km; WG September: 0-10;10-30;100-170.

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. The quasi-likelihood information criterion (QICu) developed by Pan (2001) was used instead of the Akaike information criterion (AIC) because GEEs are not based on maximum likelihood estimation. Similar to AIC, the Δ QICu and QICu weights were computed to select the most parsimonious model (Burnham and Anderson 2002b). Models with Δ QICu ≤ 2 were considered to be equivalent. When models were equivalent, the model with the fewest parameters was selected (Burnham and Anderson 2002b). We considered 'n', the

sample size, as the number of foraging patches. To avoid model over-parameterization, only models in which the number of variables did not exceed $n/5$ were explored. We tested all models including each fish group and distance separately as well as the interaction between fish group and distance. Only foraging patches observed over the NS's area in July and August were used for the analysis of NS survey. Foraging patches that occurred in August and September in the WG area were respectively used for the analysis involving data obtained from the WG survey conducted in August and September.

The coefficient value for each parameter estimated by the model, known as the log odds ratio (β), are equivalent to what are known as selection ratios (Manly et al. 2002). Log odd-ratios are the odds of an event occurring with an increase of one unit of the variable. As we considered categorical variables in our models, we could not derive absolute probabilities of selection. However, the calculation of odds ratios relative to a reference category consisting of a chosen combination of levels of the categorical independent variables is informative and reliable (Godvik et al. 2009). We set the reference category in our logistic model to the farthest distance class. 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 $\beta < 0$. Logistic regressions were performed using SAS (Littell et al. 2002). Results are presented as means \pm SE.

RESULTS

FISH DISTRIBUTION AND ABUNDANCE

The estimated abundance of fish of all species in the area covered by the NS survey was 227.4 ± 343.8 . The estimated abundance of fish of all species in the area covered by the WG survey was 111.5 ± 147.3 in August and 390.9 ± 289.6 during September. Winter flounder, herring and sand lance were the three most abundant fish species caught in the area covered by the NS fish survey accounting for 31%, 30% and 28% of the total number of fish caught (Table 2a). Thorny and smooth skates as well as capelin were not sampled in the NS survey. In the WG survey seasonal changes in the abundance of fish occurred. In August, herring, cod and winter flounder were the most common fish species accounting for 52%, 39% and 3% of the total number of fish caught (Table 2b). However, between August and September there was a 4-fold increase in fish abundance due primarily to increases in capelin abundance over the 100-200 m deep area located in the middle of the southern Gulf. During September capelin accounted for 60% of the fish caught (vs only 5% in August), followed by herring (21%), cod (12%) and winter flounder (8%) (Table 2c).

Fish were not uniformly distributed throughout the study area. Within the NS survey region, the PCA identified 2 fish assemblages which explained 42% of the variability of fish distribution (Table 3a). Winter flounder, cod and herring were associated with the first axis of the PCA. These fish were widely distributed over the NS survey area with the highest concentrations observed off Néguaç and Kouchibouguac and along the western coast of PEI (Fig. 3a). The second axis of the PCA was composed of winter skate and cunner. The highest concentration of these fish was observed along the northern coast of PEI. Cunner was also abundant in the Kouchibouguac area and high concentrations of winter skate occurred in Northumberland Strait. Sandlance, were very abundant in the northern part of the NS survey area but were absent in Kouchibouguac area as well as along the northern coast of PEI. This fish was negatively associated with the second axis. White hake were abundant off western coast of PEI and were associated with both axes of the PCA (Fig. 3a).

In the WG surveys, during both August and September, the highest concentrations of fish were observed off the Gaspé and New Brunswick coasts over areas 100-200m deep but a change in the distribution of fish in the WG area occurred between the August and September surveys, with a shift in most fishes migrating towards the south-western part of the study area in September (Fig. 3b,c). A PCA analysis explained 62% of the total variability in spatial distribution of fish in both months, along five components (Table 3b,c). White hake, thorny and smooth skates aggregated along the slope of the Laurentian channel dominated one axis in both months. Herring, cunner and winter flounder as well as small cod in September were associated with the second axis. These fish groups occurred along the coast of New Brunswick, between Chaleur Bay and Néguaac in areas where water depths were less than 100 m with the highest concentration of fish observed around Miscou Island. They were also concentrated along the northern shore of PEI. No winter flounder and cunner were caught at depths greater than 50 m. In September, the abundance of herring over water depths of 100-200m increased, while this fish was concentrated in the south western part of the study area. However, some spatial segregation was observed with small herring forming dense aggregations along the coast of New-Brunswick while large herring were concentrated on the northern shore of PEI. Medium and large cod, as well as small cod in August dominated the third axis of the PCA. Cod was most abundant off the coast of New Brunswick during August, but their distribution shifted to the south of the study area in September when aggregations formed along the northern coast of PEI. Shifts in depth preferences were also observed with cod being concentrated in areas 100-200m deep in August, then shifting to shallower water in September. Spatial segregation according to length class was observed in their distribution with small cod located closer to shore while large cod occurred further offshore and along the slope of the Laurentian channel. Cod were also stratified with respect to depth. The largest concentrations of small, medium and large cod were respectively observed at less than 60 m, at greater than 150 m and at 200 m deep. A fourth axis of the PCA was dominated by sandlance (+ve) and capelin (-ve) in both August and September. During August, capelin was also negatively associated with the axis composed of medium and large cod. Sandlance were aggregated off Kouchibouguac (New Brunswick) coast as well as along the edge of the Laurentian channel, while capelin, were highly concentrated between Gaspé and the Magdalen Islands. The fifth PCA axis was dominated by winter skates, which were abundant in the southwestern Gulf off Shippagan during both August and September.

GREY SEAL DISTRIBUTION

From July to mid-October seals were located around Sable Island, in the northern Gulf of St. Lawrence, along Anticosti Island and in the southern shore of St. Lawrence estuary (Fig. 1). Fourteen individuals, all tagged within the Gulf (6 male adults; 6 male juveniles; 2 female adults), concentrated their activities within the southern Gulf at Kouchibouguac, Néguaac, Miscou Island and offshore Gaspé (Fig. 1). Locations of adults and juveniles as well as males and females overlapped broadly. Each tagged seal used one major site most of the time, but the preferred area varied among individuals. Most seals remained in the same area from July to mid-October with the exception of two individuals that travelled to the St. Lawrence estuary and back, during this period. In the month of October, no seal was located in the Gaspé area.

CENTRAL PLACE FORAGING BEHAVIOUR

Seals tracked in the southern Gulf alternated haul-out periods on land ($n=782$) of 4.69 ± 0.01 h with foraging trips-at-sea that lasted, on average, 2.05 ± 0.14 d. The duration of both the haulout and trip-at-sea increased during the fall, averaging two and three times longer respectively in

October compared to July and August ($F_{3,32}=2.97$ $p=0.04$) (Table 4a,c ,5a). Age class ($F_{1,12}=0.44$ $p=0.52$) and sex ($F_{1,12}=1.40$ $p=0.26$) had no effect on duration of haulout ($F_{1,12}=1.88$, $p=0.37$) and trip duration (Table 5a) when included in the competitive models. The average distance at which seals were located from shore increased gradually throughout the summer period and was almost twice as far in October (52.6 ± 3.5 km) compared to August (27.8 ± 1.1 km) (Table 4b, 5b; month effect: $F_{3,31}=17.9$, $P<0.01$). Overall, 90% of the time, seals were located at less than 50 km and 90% of their trips were less than 50 km from their haulout site (Fig. 4b,c). On average, seals spent 0.49 ± 0.05 d travelling outwards to the furthest location and 1.6 ± 0.12 d to return to the haulout site. The maximum distance from shore ($F_{1,474}=23.67$, $p<0.01$), time to travel to the furthest point ($F_{1,468}=59.29$, $p<0.01$) and time to return to the haulout site increased with an increase in trip duration (Table 4g,h,i). However, the maximum distance was not affected by sex ($F_{1,12}=0.08$, $p=0.78$) or age class ($F_{1,12}=0.73$, $p=0.41$). Most trip-at-sea (90%) ended less than 10 km from where they began (Fig. 4a).

Seals performed 635 extended at-sea surfaces during 204 trips-at-sea. The occurrence of the extended surface periods did not vary with sex ($F_{1,12}=0.01$, $p=0.93$) or age class ($F_{1,12}=2.87$, $p=0.12$). Extended time at the surface was observed to occur closer to the haulout sites in August than in October (Table 4e, 5c) (month effect: $F_{3,29}=2.79$, $p=0.06$), but overall, 70% of the extended at-sea surface time occurred within 30 km of the haul-out (Fig. 4d). Seals surfaced less frequently at-sea in October (22%) than during July (28%) (Table 5c). Both the duration of the extended at-sea surfaces ($3.59\text{h}\pm 0.617\text{h}$ vs $0.59\text{h}\pm 0.06\text{h}$; t -test: $t_{774}=-8.95$, $P < 0.01$) and distance travelled (15.58 ± 1.01 vs 4.41 ± 0.38 ; t -test: $t_{64}=-13.65$, $P < 0.01$) were greater in October than at the beginning of summer. On trips for which we had locations ($n=624$), 72% of the extended at-sea surface time occurred during the return to the haul-out site. Extended at-sea surfacing occurred farther from haul-out site while maximum distance of trip increased ($F_{1,585}=259.99$, $p<0.01$; Table 4e). The duration of extended at-sea surfacings did not vary with trip duration ($F_{1,596}=0.16$, $p=0.69$), but juveniles had longer extended at sea-surfacing bouts than adults ($F_{1,12}=5.77$, $p=0.03$) (Table 4d, 5c).

Seals were in foraging states as inferred by the state-space model for 78% of locations obtained within the southern Gulf. We identified 242 foraging patches between July and mid-October (Fig. 5a), of which, 44 zones were used by 11 individuals (1 female juvenile; 2 female adults, 3 males juvenile, 5 males adults) in the NS survey area in July, and 38 foraging zones were used by 13 individuals between August mid-October (23 August ; 15 September-mid-October) in the WG survey area (Fig. 5b). On average, seals stayed 2.7 ± 0.2 days within these foraging areas that covered an average area of 87.1 ± 11.2 km². Most foraging areas were located off Kouchibouguac (66%) and Néguauc (31%) and only 3 foraging areas occurred off Miscou Island (August).

All foraging patches were located within 100 km of the haul-out site, at an average distance of 30.5 ± 3.2 km from the haul-out (Fig. 4g, 7). Foraging zones were located closer to the haul-out site in July and August than in September and October (Anova: $F_{3,75} = 11.26$, $P<0.01$) (Table 5d). Females foraged two times closer (t -test: $t_{1,77} = 2.06$, $P=0.04$) and stayed longer (t -test: $t_{1,81} = 1.63$, $P=0.11$) in their foraging patch than did males. Age class did not affect the location of foraging zones (t -test: $t_{1,77} = 1.83$, $P=0.3$) as well as time spent within these zones (t -test: $t_{1,81} = 0.46$, $P=0.64$). Time within the foraging patch and distance from the foraging patch to the haulout site increased significantly as the maximum distance reached during the trip-at-sea increased (GLMM: $\log(\text{temps})=\log(\text{temps})*0.046+2.1$; $F_{1,52}=8,37$; $P=0.01$; $\log(\text{distance})=\log(\text{distance})*0.19+0.32$; $F_{1,52}=38,4$; $P<0.01$).

RESOURCE AVAILABILITY ACCORDING TO DISTANCE TO HAUL-OUT SITE

The NS survey overlapped with the area used by seals at the Kouchibougauc and Néguauc, haulout sites. In this area, winter skates were more abundant at >10 km from the haulout site than at closer distance to the haulout site. The abundance of all others fish species did not vary with distance from shore (Table 6a).

In the southern Gulf, no difference in abundance of fish was observed between the area available for seals and the whole area covered by the fish survey in both August and September, with the exception of smooth and thorny skates that were more abundant in the whole survey area than in the area used by seals in September (Table 2). Some species of fish were not uniformly distributed within the area used by seals. During August, medium cod, large cod and cunner were more abundant between 50-100 km and/or 100-170 km from shore than in closer areas. The opposite was observed for small winter flounder (Table 6b). The abundance of herring, sand lance, skates, white hake, large winter flounder and small cod did not vary with distance (Table 6b).

In September, the abundance of capelin and large herring was lower nearer to the haulout site (Table 6c). At the opposite, the abundance of sand lance, small white hake, small herring and small winter flounder decreased with increasing distance from the haulout site (Table 6c). A gradient in cod abundance was also observed with distance from the haulout site. Small cod were more abundant at less than 50 km from a haulout site than at greater distances, while the highest density of medium cod was observed between 50 and 170 km from the haulout site. The abundance of large cod was greater at 50-100 km from the haulout site than in all other distance classes (Table 6c). No difference in abundance according to distance from haulout site was observed for large white hake, large winter flounder, cunner and skates.

Fish abundance near haulout sites differed from abundances at similar distances off the PEI coast, an area where grey seals are not thought to haulout in any significant numbers. In August, large, small and medium cod were less abundant at, respectively, 10-30 km, 30-50 km and 50-100 km from the haulout site than at similar distances from the PEI coast. Small cod, medium cod and capelin were also more abundant at a distance of 100-170 km from haulout than at similar distance off the PEI coast (Fig. 6a, 7a). At the opposite of what was seen at 50-100km, herring was more abundant around the haulout site than offshore PEI island between 10-30 km and at >100 km. The abundance of cunner, winter flounder, white hake, sand lance and skates was the same in the vicinity of haulout areas and off the coast of PEI island.

In September, large herring, large white hake and all size classes of cod, were less abundant at less than 50 km from the haulout site than at similar distances from the PEI coast. Small herring, between 10-30 km and at >50 km, sandlance, at less than 50 km, and winter flounder, between 30-50 km and 50-100 km, were more abundant in areas surrounding haulout sites, compared to off the PEI coast (Fig. 6b, 7b). The abundance of cunner, small white hake and skates in the areas surrounding haulout sites was similar to that at similar distances off the PEI coast.

HABITAT SELECTION PATTERNS

In both the NS and WG survey areas, the probability of having a foraging zone was strongly influenced by the combination of overall fish abundance, and distance from the haulout site (Table 7).

ONSHORE SURVEY

In the NS survey area, the probability that a foraging zone overlapped with winter flounder was greatest at 30-50 km than between 50-100 km. The probability that a foraging patch overlapped with concentrations of winter flounder at 0-10 km and 10-30 km from haulout site did not differ than the probability observed between 50-100 km. The probability of having a foraging patch in areas of high density of cod was highest in areas located 50-100 km from the haulout site than at closer areas. Selection for sandlance areas did not vary with distance to the haulout site (Tables 8a;9a).

WG SURVEY

In the area covered by the August WG survey, the best model indicated that sandlance preferred areas 50-100 km offshore instead of nearshore areas (Tables 8b, 9b). Selection for high density of small cod was higher within 10-30 km than between 50-100 km of the haulout site whereas selection for this fish group did not vary between 30-50 km and 50-100 km. The probability of having a foraging patch according to abundance of large winter flounder, medium cod and large cod did not vary with distance from the haulout site (Table 8b, 9b).

In September, in the WG survey area, the likelihood of having a foraging patch in an area used by medium cod was higher between 50-100 km than between 100-170 km from the haulout site (Tables 8c, 9c). The best models also pointed out that habitats with high densities of large cod were less used within 30-50 km of the haulout, but had a similar probability of being used between 50-100 km and 100-170 km. The probability of having a foraging patch according to distance did not vary with the abundance of small winter skate and winter flounder.

DISCUSSION

During the summer grey seals in the Gulf spend most of their time within 50 km of their preferred haulout sites from which they complete relatively short return trips-at-sea (McConnell et al. 1999, Sjöberg and Ball 2000, Austin et al. 2004). In the northwest Atlantic these preferred areas appear to be located in areas where human disturbance is minimal or benign such as in parks or areas with limited human access (Hammill personal observation). Their preference for relatively shallow areas (Harvey et al. 2008), and limited offshore movement may be linked to physiological limitations on their diving capacity (Halsey et al. 2006) and need to haulout. In late summer, when seals performed longer trips-at-sea and foraged further offshore, they also stayed longer at haulout sites when they returned. The reasons for the need to haulout are not clear but it has been suggested that this behaviour is in response to avoid predators, processing food, thermoregulate, or to rest (Thompson et al. 1989, Watts 1992, McConnell et al. 1999, Sparling et al. 2007). However, there are few predators (sharks) in the southern Gulf.

Grey seals spent 90% of their time within 50 km of their haulout sites. The proximity of prey aggregations 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). In September, when the distribution of many fish groups shifted to the south-western part of the Gulf and abundance increased in offshore areas, a shift in foraging activity occurred as animals made longer trips to areas located further offshore. Seasonal changes in distances travelled and location of diving activity have been observed in other marine predators (Guinet et al. 2001, Baylis et al. 2008, Winter et al. 2009) and may be associated with seasonal changes in

energy buildup prior to the January breeding season (Beck et al. 2003b). Often, shifts in foraging location have been associated with ecosystem productivity with marine predators concentrating their foraging effort in areas where the highest aggregation of prey occurs (Lowry et al. 2000). Birds, otariids and Steller sea lions changed colony or haulout sites and to alternate nearshore and offshore foraging areas to track changes in the distribution of highly aggregated preys (Lowry et al. 2000, Weimerskirch et al. 2005, Baylis et al. 2008, Winter et al. 2009). However, we did not observe major shifts in haulout use between areas suggesting that sufficient resources were available within range of currently used sites, or that alternative secure sites may not be available.

We observed that the probability of a foraging patch occurring varied according to a combination of fish abundance and distance from the haulout site. Differences were also observed between male and female grey seals in the amount of time spent near haulout sites versus offshore areas. Central place foraging strategy states that searching and foraging efforts should decrease as distance from the central place, 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). Marine predators and breeding bird species that forage in distant areas generally consume more food items with high-energy content and deliver either larger single prey items or larger loads of smaller items to their offspring (Staniland et al. 2007). Grey seals are capital breeders and the seasonal motivation to buildup fat reserves differs between the sexes (Beck et al. 2003b) resulting in spatial partitioning of foraging areas, for limited resources around central place, as is commonly observed in colonial insects, land birds and seabirds foraging in adjacent colonies (Dukas and Edelman-Keshet 1998, Adler and Gordon 2003, Ainley et al. 2003). Male grey seals generally prey on a wide range of prey with more emphasis on demersal species whereas females appear to consume more high energy small pelagic fish (Beck et al. 2003a, Beck et al. 2007, Tucker et al. 2007, Hammill, this meeting). Offshore foraging areas (≥ 50 km from the haulout) are more frequently used by males than by females (Breed et al. 2006, Harvey et al. 2008, Harvey et al. 2011). These offshore areas are characterized by high densities of larger cod in the Northumberland Strait area, high densities of the energy rich sandlance in August, and high densities of medium and large cod in September in the Western Gulf region.

Generally, fish abundance was higher in areas where large grey seal haulouts are not known or increased with distance from the haulout site among most species, with abundance peaking about 50-100 km offshore suggesting that seal predation had reduced fish abundance as one moved closer to a haulout site, or prey responded by shifting their distribution to minimize predation or a combination of the two mechanisms. Changes in the size distribution of fish also occurred suggesting that other habitat factors might have been involved. Generally, larger, older demersal fish occur in deeper waters whereas small fish are found in shallower water depths (Werner and Gilliam 1984, MacPherson and Duarte 1991). We observed such a pattern among cod, with smaller cod found closer to shore, medium sized cod at intermediate distances and large cod found farthest offshore. Although small cod would be exposed to predation from seals, this inshore movement may also provide greater protection from large cod, which would represent a much more significant predation threat than would grey seals. Small herring, an important prey for cod (Hanson and Chouinard 2002) were also more abundant in nearshore waters, whereas large herring occurred off the north coast of PEI where grey seals are not as abundant. Similar responses to predation threats have been observed among migrant pied flycatchers (*Ficedula hypoleuca*), which selected to nest in areas where predation from sparrowhawks (*Accipiter nisus*) represented a threat, but also one that was likely to be lower than predation threats from other avian or mammal predators (Thomson et al. 2006). The abundance of large cod increased with increasing distance from shore, particularly beyond

distances normally visited by grey seals, suggesting attempts to minimize predation threats. Although this offshore distribution might represent a selection for cooler water to lower metabolic costs in the face of low prey levels. Such shifts, possibly in response to limited food resources would be expected when cod biomass was quite high. However, current cod biomass levels are quite low and higher densities of large cod would be expected to be observed in warmer waters closer to shore, as has been observed in the past when the Northwest Atlantic grey seal population was only a tenth of its current size (Chouinard and Swain 2002, Thomas et al. 2008).

However, in our study, other species, such as sandlance did not show similar displacement, but their numbers may be so abundant that predation from grey seals would have little impact, threats of predation from other fish such as cod may represent a more significant threat (Morissette et al. 2006, Savenkoff et al. 2007), aspects of their biology to avoid predators (hiding in the substrate) may be an effective strategy to minimize predation mortality or aspects of their biology do not favour an offshore distribution.

Direct and indirect predation effects might be quite significant in the case of rarer species such as skates and hake. Significant shifts in the distribution of winter, smooth and thorny skate within the southern Gulf have been observed over the last 3 decades. During the 1970s, smooth, winter and thorny skate were widely distributed throughout the southern Gulf (COSEWIC 2005, Swain and Benoit 2006). However currently thorny skate and smooth skate are limited to the deeper waters of the southern slope of the Laurentian Channel, while the now Endangered population of winter skate are limited to a small area in the southwestern Gulf (Swain et al. 2005, Swain and Benoit 2006).

This 'halo' effect where prey densities have declined around areas where predators are abundant has also been observed among colonies and haulout sites of seabirds (Lewis et al. 2001, Ainley et al. 2003) and is likely a prey response to reduce predation risk. This indirect effect of predators on their prey can be subtle but energetically expensive where prey are forced to select less suitable habitat or foraging areas to reduce threats from predators (Werner and Peacor 2003, Cresswell et al. 2010). Dolphins allocated significantly more time to deep habitats than expected based on food resources when sharks were common compared to period where abundance of sharks is low (Heithaus and Dill 2002). Among elk, predation risk affected calf recruitment in subsequent years (Creel et al. 2007) whereas had lowest clutch size when they breed in the vicinity of sparrowhawk nests (Thomson et al. 2006).

An understanding of diet composition is an important in trying to understand the role of grey seals within the southern gulf ecosystem. Among marine mammals diet has been estimated using stable isotopes, fatty acids and analyses of digestive tract contents. All of these techniques are associated with various strengths and weaknesses (see Phillips and Harvey 2009). In the southern Gulf, analyses of digestive tracts have been the preferred approach, assuming that digestive content recovery reflects the spatial and temporal variation in diet composition. In this study, grey seals spent much of their time within 50 km for the haulout site, with the average trip at sea lasting for approximately 3 days. In studies using recovery of faecal material to determine diet, the majority of otoliths and beaks ingested by seals were passed within 3 days (Grellier and Hammond 2006). This indicates that much of the diet would be captured using analyses of digestive tracts among seals in the southern Gulf, but for longer trips extending further offshore e.g., those often undertaken by males some diet material may already have been passed before animals returned to the haulout site. There was also some evidence that animals may have remained at sea, spending extended periods of time at the surface. Similar, extended at-sea surfaces have been related to the digestion process among

elephant seals and in captive grey seals (Crocker et al. 1997, Bonermann et al. 2000, Sparling et al. 2007). In the absence of at-sea sampling of animals, diets based on shore collections of faecal material might under-estimate foraging in these offshore regions. Seals spent 4.45 ± 1.15 hours (range 0.67-14.7) in their foraging patch located in areas of high concentration of large cod. Representation by large cod as well as other species that show higher densities further offshore may then be under-represented in shore-based collections. This may be particularly true for the fall when seals go further offshore and spend more time in areas of high concentration of large cod.

The current collapse has been accompanied by a significant change in ecosystem structure, where the ecosystem formerly dominated by large piscivores demersal fish is now dominated by small pelagic forage species and marine mammals (Morissette et al. 2006, Savenkoff et al. 2007, Bundy et al. 2009). The current recovery has been limited by a combination of continued fishing and high levels of natural mortality even when no fishing has occurred. During that time the NW Atlantic grey seal population has increased from approximately 25,000 animals during the 1970s to over 300,000 animals in 2008. At current levels, the grey seal may be playing an important role in structuring the southern Gulf ecosystem through direct predation (Savenkoff et al. 2007) and in influencing the distribution of prey species in the southern Gulf. This could have longer term implications on the recovery of groundfish in this area.

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Table 1. Diet composition of grey seals collected from the Miramichi (southern Gulf of St. Lawrence) area (from Hammill 2011).

Miramichi	Fall intestine				Spring intestine			
	females (N=46)		males (23)		females (27)		males (5)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Sandlance	88.9	3.2	77.7	11.4	92.9	3.6	64.5	27.7
Hooker sculpin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Atlantic herring	1.3	0.8	10.5	6.1	0.5	0.5	0.0	0.0
Sculpin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wrymouth	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lumpfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fourbeard rockling	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fourline snakeblenny	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Atlantic cod	0.9	0.6	6.0	6.2	2.5	2.1	22.3	18.1
Gadid	1.2	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Arctic staghorn sculpin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sea raven	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
American plaice	0.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Yellowtail flounder	1.5	0.9	0.1	0.1	1.6	0.8	10.3	8.4
Snakeblenny	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Daubed shanny	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Blenny	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Checker eelpout	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eelpout	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ocean pout	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Capelin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Longhorn sculpin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Shorthorn sculpin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sculpin	0.0	0.0	0.8	0.9	0.0	0.0	0.0	0.0
White barracudina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Smelt	0.1	0.1	0.0	0.0	0.3	0.3	0.0	0.0
Butterfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Flounders	1.7	0.7	1.2	0.7	0.4	0.2	0.0	0.0
Winter flounder	2.7	0.9	1.7	1.1	1.2	0.8	1.5	1.3
Mackerel	0.9	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Windowpane	0.1	0.1	0.0	0.0	0.1	0.1	0.0	0.0
Redfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arctic shanny	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prickleback/Blenny	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cunner	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unspecified	0.2	0.1	1.1	1.3	0.1	0.1	0.4	0.4
White hake	0.0	0.0	1.0	0.6	0.2	0.3	0.9	0.8
Eelpout	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphipod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 1. (End)

Miramichi	Fall intestine				Spring intestine			
	females (N=46)		males (23)		females (27)		males (5)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Bivalvia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Shrimps	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crab	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Squid	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cumacean	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphausid	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isopod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ave mass per stomach (g)	4398.4	4429.3	4468.3	8342.3	5095.4	5986.2	4092.2	2637.0

Table 2. Fish species and size classes used in this study. N is the a) total and b) average number of fish caught in the area covered by the fish survey conducted in Northumberland Strait (NS) and in the Western Gulf (WG) of St. Lawrence in both August and September. The average number of fish within the area available for seal is also given in c.

Group fish	Class length (cm)	NS survey		WG survey					
		a	b*	August			September		
				a	b	c	a	b	c
Cod (<i>Gadus morhua</i>)	<25			4,535	4.0 ± 7.6	6.5 ± 1	6,350	5.7 ± 14.8	8.5 ± 1.6
	25-35			12,368	12.6 ± 15.8	14 ± 0.7	8,719	9.1 ± 14.9	10.1 ± 1.5
	>35			27,760	30.5 ± 33.6	36.1 ± 1.2	35,475	39.9 ± 117.9	38.7 ± 5.2
White hake (<i>Urophycis tenuis</i>)	all	5,600	9.4 ± 3.5	44,656	47.6 ± 46.7	56.6 ± 2.8	59,544	55.3 ± 137.1	57.8 ± 8.4
	≤35			543.0	0.5 ± 4.2	0.2 ± 0.2	468	0.4 ± 1.2	0.1 ± 0.1
	>35			851.0	0.7 ± 2.2	0.2 ± 0.2	920.4	0.9 ± 2.4	0.3 ± 0.2
Winter flounder (<i>Pseudopleuronectes americanus</i>)	all	155	0.1 ± 0.4	1,394	1.2 ± 3.6	0.4 ± 0.3	1,388.36	1.4 ± 3.6	0.4 ± 0.2
	≤30			3,432	2.9 ± 7.0	4.5 ± 0.7	37,538	31.1	50.3 ± 7.8
	>30			489.0	0.4 ± 1.1	0.7 ± 0.1	2,236	1.9	3 ± 0.5
Herring (<i>Clupea harengus</i>)	all	38,043	46.9 ± 37.5	3,921	3.3 ± 7.9	5.2 ± 0.8	39,774	32.9 ± 109.8	53.2 ± 8.3
	<30						83,727	72.8 ± 163.3	115.7 ± 20.8
	>30						18,743	17.1 ± 40.7	26.8 ± 5.1
Capelin (<i>Mallotus villosus</i>)	all	36,804	37.8 ± 90.8	57,568	51.4 ± 135.7	79.7 ± 14.4	102,470	80.3 ± 176.6	126.5 ± 23.5
	all	1	0 ± 0.01	6,015	10.6 ± 80.9	8.9 ± 3.9	290,783	240 ± 447.2	230.2 ± 39.4
Cunner (<i>Tautogolabrus adspersus</i>)	all	8,672	7.1 ± 14.9	120	0.1 ± 0.4	0.2 ± 0	839	0.6 ± 2.4	1 ± 0.2
sandlance (<i>Ammodytes dubius</i>)	all	33,731	131.7 ± 376.8	15	0 ± 0.1	0	848	0.8 ± 2.5	0.5 ± 0

Table 2. (End)

Group fish	Class length (cm)	NS survey		WG survey					
				August			September		
		a	b*	a	b	c	a	b	c
Thorny skate (<i>Amblyraja radiata</i>)	≤45						357	0.4 ± 0.8	0.1 ± 0.1
	>45						62.7	0.1 ± 0.2	0
	all	0	0	551	0.5 ± 1.2	0.2 ± 0.1	419	0.5 ± 0.9	0.1 ± 0.1
Smooth skate (<i>Anacanthobatis</i> sp.)	≤45						118	0.1 ± 0.4	0
	>45						19	0 ± 0.6	0
	all	0	0	77.1	0.1 ± 0.2	0	137	0.2 ± 0.5	0
Winter skate (latin name??)	≤45						20	0 ± 0.1	0
	>45						11	0 ± 0.1	0
	all	931	0.8 ± 1.0	4.4	0 ± 0.02	0	31	0 ± 0.1	0
All fish group		123,938		114,323	111.5 ± 147.3	148.2 ± 15.7	487,234	390.9 ± 289.6	448.2 ± 12.5

* The area available for seals is larger than the area covered by the NS survey

Table 3. Eigenvectors derived from principal component analysis (PCA) of fish abundance measured at stations survey within the southern Gulf of St. Lawrence in a) Northumberland Strait in July (2001-2006) b) August (2003-2009) and c) September (2000-2008). High correlation loadings are in boldface. Percentage of variability in fish distribution explained by each PCA axis for each survey is given in italics characters.

Factor	1	2	3	4	5
Fish group					
<i>a) Northumberland Strait*</i>	<i>21.1</i>	<i>20.6</i>			
winter flounder	0.76	0.23			
cod	0.70	-0.40			
Herring	0.39	-0.03			
white hake	0.35	0.38			
winter skate	-0.19	0.71			
Cunner	0.27	0.63			
sandlance	0.07	-0.45			
<i>b) August</i>	<i>19.3</i>	<i>15.3</i>	<i>12.9</i>	<i>7.5</i>	<i>7.3</i>
white hake ≤35	0.83	-0.03	-0.06	0.04	-0.03
white hake >35	0.82	-0.01	-0.17	0.02	-0.04
thorny skate	0.70	-0.11	0.11	-0.03	0.08
smooth skate	0.68	-0.02	-0.06	0.00	-0.03
winter flounder ≤30	-0.14	0.88	-0.17	0.11	0.00
winter flounder >30	-0.08	0.87	0.00	0.05	-0.04
Cunner	-0.01	0.46	-0.02	-0.18	0.44
Herring	0.05	0.42	0.10	0.39	0.04
cod 25-35	-0.03	0.05	0.91	0.04	0.00
cod >35	-0.10	-0.21	0.82	-0.04	-0.02
cod <25cm	-0.05	0.51	0.56	0.10	-0.03
sandlance	-0.06	-0.10	-0.08	0.85	-0.07
Capelin	-0.04	-0.20	-0.06	-0.35	-0.10
winter skate	-0.02	-0.07	-0.03	0.13	0.92
<i>c) September</i>	<i>22.0</i>	<i>17.1</i>	<i>10.4</i>	<i>6.7</i>	<i>5.7</i>
thorny skate >45	0.77	-0.05	-0.08	-0.06	0.00
white hake >35	0.77	0.16	-0.16	0.06	-0.10
thorny skate ≤45	0.74	-0.20	0.10	-0.02	0.01
white hake ≤35	0.70	0.11	-0.18	0.11	-0.04
smooth skate >45	0.69	-0.14	0.06	0.03	0.04
smooth skate ≤45	0.59	0.02	-0.09	-0.06	-0.06
herring ≤30	0.02	0.84	0.16	-0.03	-0.12
herring >30	0.10	0.74	0.23	-0.15	-0.19
winter flounder ≤30	-0.11	0.74	-0.02	0.45	0.20
winter flounder >30	-0.08	0.71	-0.01	0.42	0.14
cod <25cm	-0.12	0.50	0.45	0.15	0.12
cunner	-0.05	0.40	-0.12	0.33	0.11
cod 25-35	-0.06	0.10	0.87	0.00	-0.02
cod >35	-0.17	0.03	0.77	-0.04	-0.15
capelin	0.04	-0.39	-0.49	-0.10	-0.42
winter skate >45	0.07	0.05	0.05	0.82	-0.05
winter skate ≤45	0.00	0.15	0.03	0.80	0.01
Sandlance	-0.07	-0.03	-0.11	-0.01	0.88

* Capelin as well as smooth and thorny skates were not included in this analysis since they were absent from the area covered by the survey

Table 4. Linear mixed models testing the effects of individuals and trip characteristics as well as month on haul-out and trip-at-sea behaviour of grey seals ($n=XX$) followed with satellite telemetry within the southern Gulf of the St. Lawrence between July and mid-October (2003-2008). Best models are shown in bold, competitive models ($\Delta AIC < 2$) in italics. (NP = number of parameters; I = intercept; age class = juvenile (<6)/adult (≥ 6); trip dur.=trip duration; dur. prev. trip= duration previous trip; h-out dur.=haul-out duration; dist. max=maximum distance during trip-at-sea).

Models	Np	a) haul-out duration			c) time at-sea			d) duration of extended at-sea surface		
		AIC	ΔAIC	ω	AIC	ΔAIC	ω	AIC	ΔAIC	ω
1 I	1	2 428.1	28.1	0	3 393.9	6.2	0	1 814.8	66.0	0
2 I + sex	2	2 429.0	29.0	0	3 392.2	4.5	0	1 814.6	65.8	0
3 I + age class	2	2 429.2	29.2	0	3 394.2	6.5	0	1 811.3	62.5	0
4 I + month	2	2 400.0	0.0	0.6	3 389.1	1.4	0.2	1 819.2	70.4	0
5 I + sex + age class	3	2 430.9	30.9	0	3 392.6	4.9	0	1 811.6	62.8	0
6 I + sex + month	3	<i>2 401.4</i>	<i>1.4</i>	<i>0.3</i>	3 387.7	0.0	0.4	1 818.9	70.1	0
7 I + age class + month	3	<i>2 402.3</i>	<i>2.3</i>	<i>0.2</i>	3 389.4	1.7	0.2	1 815.7	66.9	0
8 I + trip dur.	2	1 752.8	4.0	0.1
9 I + trip dur. + sex	3	1 752.6	3.8	0.1
10 I + trip dur. + age class	3	1 748.8	0.0	0.8
11 I + trip dur. + month	3	1 756.3	7.5	0
12 I + dur. prev. trip	2	2 457.3	57.3	0	3 421.8	34.1	0	.	.	.
13 I + dur. prev. trip + sex	3	2 458.2	58.2	0	3 420.1	32.4	0	.	.	.
14 I + dur. prev. trip + age class	3	2 458.4	58.4	0	3 422.2	34.5	0	.	.	.
15 I + dur. prev. trip + month	3	2 428.5	28.5	0	3 416.7	29.0	0	.	.	.
16 I + h-out dur.	2	.	.	.	3 392.5	4.8	0	1 838.8	90.0	0
17 I + h-out dur. + sex	3	.	.	.	3 390.5	2.8	0.1	1 838.6	89.8	0
18 I + h-out dur. + age class	3	.	.	.	3 392.7	5.0	0	1 835.2	86.4	0
19 I + h-out dur. + month	3	.	.	.	3 393.1	5.4	0	1 843.7	94.9	0
20 I + dist. max	2
21 I + dist. max + sex	3
22 I + dist. max + statut	3
23 I + dist. max + month	3

Table 4. (End)

Models	Np	e) extended at-sea surface dist.			f) dist. between location and h.-out			g) maximum trip dist.			h) trip to furthest dist. duration			i) Return trip duration		
		AIC	ΔAIC	ω	AIC	ΔAIC	ω	AIC	ΔAIC	ω	AIC	ΔAIC	ω	AIC	ΔAIC	ω
1	1	2 239.5	311.9	0	10 899.2	62.8	0	1 765.3	15.2	0	1 761.5	71.8	0	1 971.0	222.9	0
2 + sex	2	2 236.8	309.2	0	10 896.0	59.6	0	1 765.7	15.6	0	1 761.7	72.0	0	1 969.4	221.3	0
3 + age class	2	2 238.2	310.6	0	10 899.0	62.6	0	1 766.9	16.8	0	1 762.5	72.8	0	1 969.8	221.7	0
4 + month	2	2 178.5	250.9	0	10 856.0	19.6	0	1 769.8	19.7	0	1 765.1	75.4	0	1 973.7	225.6	0
5 + sex + age class	3	2 235.2	307.6	0	10 896.5	60.1	0	1 767.1	17.0	0	1 762.4	72.7	0	1 969.1	221.0	0
6 + sex + month	3	2 175.9	248.3	0	10 853.2	16.8	0	1 770.2	20.1	0	1 765.4	75.7	0	1 972.0	223.9	0
7 + age class + month	3	2 177.3	249.7	0	10 856.2	19.8	0	1 771.4	21.3	0	1 766.1	76.4	0	1 972.4	224.3	0
8 + trip dur.	2	2 084.8	157.2	0	10 890.7	54.3	0	1 750.1	0.0	0.4	1 689.7	0.0	1	1 748.1	0.0	1
9 + trip dur. + sex	3	2 082.3	154.7	0	10 887.9	51.5	0	1 750.8	0.7	0.3	1 771.1	81.4	0	1 956.0	207.9	0
10 + trip dur. + age class	3	2 083.7	156.1	0	10 890.7	54.3	0	1 751.4	1.3	0.2	1 771.9	82.2	0	1 955.5	207.4	0
11 + trip dur. + month	3	2 086.9	159.3	0	10 836.4	0	1	1 753.0	2.9	0.1	1 774.5	84.8	0	1 961.3	213.2	0
12 + dur. prev. trip	2
13 + dur. prev. trip + sex	3
14 + dur. prev. trip + age class	3
15 + dur. prev. trip + month	3
16 + h-out dur.	2	1 789.2	39.1	0
17 + h-out dur. + sex	3	1 789.7	39.6	0
18 + h-out dur. + age class	3	1 791.0	40.9	0
19 + h-out dur. + month	3	1 791.1	41.0	0
20 + dist. max	2	1 930.1	2.5	0.1	1 748.4	58.7	0	.	.	.
21 + dist. max + sex	3	1 929.6	2.0	0.1	1 749.5	59.8	0	.	.	.
22 + dist. max + statut	3	1 927.6	0.0	0.4
23 + dist. max + month	3	1927.9	0.3	0.3

Table 5. Average parameters estimated (means \pm se) for a) haul-out, b) trip-at-sea with location, c) extended at-sea surface interval and d) foraging patch characteristics according to sex, age class and month.

Variable	a) haul-out				b) trip-at-sea with location						
	nb	duration (hr)	distance between successive (km)	Time between successive haul-out (d)	nb	duration (d)	nb location	distance location to haul-out (km)	Max. distance (km)	trip to max. dist. (d)	trip from max. dist. (d)
all	782	4.69 \pm 0.01	7.47 \pm 1.01	1.47 \pm 0.17	489	2.05 \pm 0.14	3 053	34.74 \pm 097	21.6 \pm 1.7	0.48 \pm 0.05	1.58 \pm 0.1
Sex											
fille	94	4.73 \pm 0.83	7.39 \pm 2.44	1.94 \pm 0.45	64	2.66 \pm 0.63	546	22.86 \pm 2.03	11.9 \pm 1.8	0.38 \pm 0.12	2.27 \pm 0.5
gars	688	5.63 \pm 0.41	7.10 \pm 1.03	1.41 \pm 0.19	425	1.96 \pm 0.13	2 507	37.3 \pm 1.09	23.1 \pm 1.9	0.49 \pm 0.05	1.48 \pm 0.1
age class											
jeunes	390	5.02 \pm 0.29	7.01 \pm 1.29	1.26 \pm 0.12	245	1.96 \pm 0.17	1 444	38.98 \pm 1.51	23.5 \pm 2.5	0.5 \pm 0.07	1.45 \pm 0.2
adultes	392	4.36 \pm 0.24	7.27 \pm 1.41	1.68 \pm 0.33	244	2.15 \pm 0.22	1 631	30.98 \pm 1.24	19.8 \pm 2.4	0.46 \pm 0.07	1.72 \pm 0.2
month											
July	258	4.27 \pm 0.36	4.66 \pm 0.63	1.23 \pm 0.15	158	1.98 \pm 0.22	968	27.84 \pm 1.07	18.9 \pm 2.3	0.54 \pm 0.09	1.48 \pm 0.2
August	283	3.77 \pm 0.31	3.35 \pm 0.46	1.12 \pm 0.16	169	1.81 \pm 0.25	976	30.83 \pm 1.77	18.5 \pm 2.8	0.39 \pm 0.07	1.41 \pm 0.2
September	167	5.95 \pm 0.6	3.43 \pm 0.52	1.66 \pm 0.22	108	2.53 \pm 0.31	831	40.90 \pm 2.26	21.5 \pm 3.9	0.58 \pm 0.14	1.95 \pm 0.3
October	74	7.82 \pm 1.08	4.66 \pm 0.89	3.31 \pm 1.66	54	2.06 \pm 0.45	300	52.64 \pm 3.51	30.2 \pm 5.8	0.34 \pm 0.11	1.69 \pm 0.5

Table 5. (end)

Variable	c) extended at-sea surface				d) foraging patch		
	nb	nb with extended at-sea surface	distance from haul-out (km)	duration (hr)	nb	distance (km)	duration (d)
All	635	204	16.52 ± 5.65	2.64 ± 0.12	83	30.54 ± 3.2	3.31 ± 0.47
Sex							
Fille	102	27	17.27 ± 8.18	2.16 ± 0.21	12	14.45 ± 3.84	5.13 ± 2.12
Gars	533	177	16.46 ± 3.29	2.73 ± 0.14	71	33.15 ± 3.58	2.99 ± 0.41
age class							
jeunes	229	95	11.91 ± 3.07	3.32 ± 0.21	43	31.9 ± 4.25	2.84 ± 0.63
adultes	406	109	21.11 ± 4.60	2.25 ± 0.15	40	28.92 ± 4.91	3.81 ± 0.69
Month							
July	242	73	17.27 ± 3.11	2.39 ± 0.16	25	17.54 ± 3.01	3.0 ± 0.94
August	193	71	13.52 ± 2.51	2.46 ± 0.19	41	26.82 ± 3.22	3.58 ± 0.74
September	131	44	16.71 ± 3.28	2.60 ± 0.30	8	59.26 ± 17.23	4.25 ± 0.24
October	69	16	22.73 ± 5.65	4.08 ± 0.62	9	64.22 ± 13.51	2.11 ± 0.58

Table 6. Difference of fish abundance estimated using data obtained throughout the a) Northumberland Strait survey (2001-2006) and the Western Gulf survey conducted a) in August (2003-2009) and c) in September (2000-2008) according to distance to haulout site used by grey seals in the southern Gulf. Letters indicate significant differences across distance with abundance (A>B>C). 'AB' means that the abundance at a specific distance class is similar to the 'A' and 'B' abundance.

Fish group	distance (m)	Fish survey											
		a) NS				b) WG August				c) September			
		0-10	10-30	30-50	50-100	10-30	30-50	50-100	100-170	10-30	30-50	50-100	100-170
Cod (<i>Gadus morhua</i>)	<25					A	A	A	A	AB	A	B	B
	25-35					B	B	A	A	B	B	A	AB
	>35					B	B	A	A	C	BC	A	B
White hake (<i>Urophycis tenuis</i>)	all	A	A	A	A								
	≤35					A	AB	AB	B
	>35					A	A	A	A	A	A	A	A
Winter flounder (<i>Pseudopleuronectes americanus</i>)	all												
	≤30					A	A	A	B	AB	A	AB	AB
	>30					A	A	A	A	A	A	A	A
Herring (<i>Clupea harengus</i>)	all	A	A	A	A								
	<30									A	A	AB	B
	>30									B	AB	A	AB
Capelin (<i>Mallotus villosus</i>)	all	A	A	A	A	A	A	A	A	B	B	B	A
Cunner (<i>Tautoglabrus adspersus</i>)	all	A	A	A	A	B	B	A	AB	A	A	A	A
sandlance (<i>Ammodytes dubius</i>)	all	A	A	A	A	A	A	A	A	A	A	AB	AB
Thorny skate (<i>Amblyraja radiata</i>)	≤45								
	>45								
	all					A	A	A	A				
Smooth skate (<i>Anacanthobatis</i> sp.)	≤45								
	>45								
	all								
Winter skate (which is the best latin name??)	≤45									A	A	A	A
	>45									A	A	A	A
All fish group	all	B	AB	AB	AB	A	A	A	A				
	all					A	A	A	A	A	A	A	A

Table 7. 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 a) onshore survey, b) august survey and c) September survey. All possible models including second order interaction terms were tested, and, eventually, only the 5 best will be shown here. Best models are shown in bold and equivalent models ($\Delta QICu \leq 2$) in italics. I=Intercept of the model.

Model	QICU		
	a) NS	b) WG - August	c) WG - September
I	295.9	154.4	125.6
I + dist. class	199.4	117.0	96.8
I + cod	297.7		
I + cod1		152.9	120.9
I + cod2		144.8	127.0
I + cod3		133.6	127.1
I + herring	297.9	147.1	
I + herring1			109.8
I + herring2			127.5
I + capelin		151.2	120.0
I + white hake	297.3		
I + white hake1		155.1	113.2
I + white hake2			127.5
I + w. flounder	297.7		
I + w. flounder1		151.7	106.2
I + w. flounder2		159.5	127.6
I + cunner	297.3	156.7	128.0
I + sandlance	297.9	134.2	108.3
I + w. skate	297.5	155.7	
I + w. skate1			101.0
I + w. skate2			126.7
I + t. skate			
I + t. skate1			127.6
I + dist. class + cod + dist. class*cod	195.9		
I + dist. class + cod1 + dist. class*cod1		114.1	97.7
I + dist. class + cod2 + dist. class*cod2		115.4	85.5
I + dist. class + cod3 + dist. class*cod3		113.3	89.2
I + dist. class + herring + dist. class*herring	205.6	119.7	
I + dist. class + herring1 + dist. class*herring1			99.0
I + dist. class + herring2 + dist. class*herring2			99.8
I + dist. class + cunner + dist. class*cunner	198.7	121.8	95.9
I + dist. class + capelin + dist. class*capelin			100.9
I + dist. class + sandlance + dist. class*sandlance	196.5	104.9	98.2
I + dist. class + w. flounder + dist. class*w. flounder	194.1		
I + dist. class + w. flounder1 + dist. class*w. flounder1		119.1	90.5
I + dist. class + w. flounder2 + dist. class*w. flounder2		117.6	94.6
I + dist. class + w. skate + dist. class*w. skate		191.3	
I + dist. class + w. skate1 + dist. class*w. skate1			93.2
I + dist. class + w. skate2 + dist. class*w. skate2			97.9

Table 8. Selection estimates (log odds ratio \pm 95% confidence intervals limits (ci)) of fish groups included in the 5 best logistic-regression models predicting the probability of having a foraging patch of juveniles and adults grey seals in the southern Gulf of St. Lawrence in a) Northumberland Strait survey's area and in Western Gulf survey's area in b) August and c) September between 2003-2008. (distance classes (km) : 1: 0-10; 2: 10-30; 3: 30-50; 4: 50-100; 5: 100-170).

Parameters	log odds-ratio	std. err.	ci	
			lower	upper
a) Northumberland Strait survey				
<u>1. I + distance class + winter flounder + distance class*winter flounder</u>				
Intercept	-3.16	0.69	-4.50	-1.81
<i>distance class</i>				
1	4.41	1.01	2.44	6.39
2	2.94	0.93	1.13	4.76
3	-1.15	1.30	-3.68	1.39
4	0.00	0.00	0.00	0.00
winter flounder	-0.03	0.01	-0.05	0.00
<i>Fish group*distance class</i>				
winter flounder*dist1	0.02	0.02	-0.01	0.06
winter flounder*dist 2	0.00	0.02	-0.03	0.03
winter flounder*dist 3	0.04	0.02	0.01	0.07
winter flounder*dist 4	0.00	0.00	0.00	0.00
<u>2. I + distance class + cod + distance class*cod</u>				
Intercept	-7.78	1.23	-10.20	-5.36
<i>distance class</i>				
1	9.53	1.43	6.72	12.34
2	5.38	1.27	2.88	7.88
3	4.19	1.31	1.62	6.77
4	0.00	0.00	0.00	0.00
cod	0.28	0.08	0.13	0.44
<i>Fish group*distance class</i>				
cod*dist1	-0.34	0.09	-0.52	-0.17
cod*dist 2	-0.24	0.08	-0.41	-0.08
cod*dist 3	-0.27	0.08	-0.43	-0.11
cod*dist 4	0.00	0.00	0.00	0.00
<u>3. I + distance class + sandlance +distance class*sandlance</u>				
Intercept	-5.09	0.66	-6.38	-3.79
<i>distance class</i>				
1	6.57	0.86	4.88	8.26
2	3.01	0.67	1.70	4.31
3	1.59	0.83	-0.04	3.22
4	0.00	0.00	0.00	0.00
sandlance	0.00	0.00	0.00	0.00
<i>Fish group*distance class</i>				
sandlance*dist1	-0.01	0.00	-0.01	0.00
sandlance*dist 2	0.00	0.00	0.00	0.00
sandlance*dist 3	0.00	0.00	-0.01	0.00

sandlance*dist 4	0.00	0.00	0.00	0.00
<u>4. I + distance class</u>				
Intercept	-4.01	0.53	-5.04	-2.98
<i>distance class</i>				
1	5.07	0.71	3.68	6.46
2	2.04	0.57	0.93	3.15
3	0.67	0.63	-0.56	1.90
4	0.00	0.00	0.00	0.00

5. I + distance class + cunner +distance class*cunner

Intercept	-2.40	0.62	-3.61	-1.19
<i>distance class</i>				
1	2.95	0.86	1.27	4.63
2	0.22	0.72	-1.18	1.63
3	-0.82	0.79	-2.37	0.73
4	0.00	0.00	0.00	0.00
sandlance	-1.35	0.36	-2.06	-0.64
<i>Fish group*distance class</i>				
cunner*dist1	1.38	0.36	0.67	2.09
cunner*dist 2	1.37	0.36	0.65	2.08
cunner*dist 3	1.31	0.37	0.57	2.04
cunner*dist 4	0.00	0.00	0.00	0.00

b) August

1. I + distance class + sandlance +distance class*sandlance

Intercept	-3.99	0.50	-4.96	-3.01
<i>distance class</i>				
2	3.37	0.91	1.59	5.15
3	2.82	0.64	1.56	4.07
4	0.00	0.00	0.00	0.00
sandlance	18.78	3.72	11.49	26.07
<i>Fish group*distance class</i>				
sandlance*dist 2	-10.11	3.68	-17.32	-2.89
sandlance*dist 3	-19.13	3.97	-26.92	-11.35
sandlance*dist 4	0.00	0.00	0.00	0.00

2. I + distance class + cod3 + distance class*cod3

Intercept	-2.41	0.59	-3.55	-1.26
<i>distance class</i>				
2	2.69	1.01	0.71	4.67
3	1.68	0.74	0.22	3.14
4	0.00	0.00	0.00	0.00
cod3	-0.04	0.02	-0.08	0.00
<i>Fish group*distance class</i>				
cod3*dist 2	0.03	0.06	-0.09	0.15
cod3*dist 3	0.02	0.03	-0.04	0.08
cod3*dist 4	0.00	0.00	0.00	0.00

3. I + distance class + cod2 + distance class*cod2

Intercept	-2.57	0.57	-3.69	-1.45
<i>distance class</i>				
2	2.25	1.20	-0.11	4.61
3	1.56	0.68	0.23	2.90
4	0.00	0.00	0.00	0.00
cod2	-0.08	0.05	-0.18	0.01
<i>Fish group*distance class</i>				
cod2*dist 2	0.31	0.41	-0.50	1.12
cod2*dist 3	0.03	0.08	-0.12	0.18
cod2*dist 4	0.00	0.00	0.00	0.00

4. I + distance class + cod1 + distance class*cod1

Intercept	-4.87	0.98	-6.79	-2.96
<i>distance class</i>				
2	2.70	1.18	0.39	5.01
3	3.93	1.26	1.45	6.41
4	0.00	0.00	0.00	0.00
cod1	0.09	0.05	0.00	0.18
<i>Fish group*distance class</i>				
cod1*dist 2	0.09	0.05	0.00	0.18
cod1*dist 3	-0.12	0.07	-0.26	0.02
cod1*dist 4	0.00	0.00	0.00	0.00

5. I + distance class + winter flounder2 + distance class*winter flounder2

Intercept	-3.30	0.54	-4.36	-2.25
<i>distance class</i>				
2	2.28	1.14	0.04	4.52
3	2.79	0.80	1.23	4.35
4	0.00	0.00	0.00	0.00
winter flounder2	-0.30	0.19	-0.68	0.08
<i>Fish group*distance class</i>				
winter flounder2*dist 2	1.19	0.93	-0.63	3.00
winter flounder2*dist 3	-0.17	0.35	-0.87	0.52
winter flounder2*dist 4	0.00	0.00	0.00	0.00

c) September

1. I + distance class + cod2 + distance class*cod2

Intercept	-3.85	0.81	-5.44	-2.27
<i>distance class</i>				
3	5.27	1.47	2.39	8.16
4	2.35	1.05	0.29	4.41
5	0.00	0.00	0.00	0.00
cod2	-0.39	0.10	-0.58	-0.20
<i>Fish group*distance class</i>				
cod2*dist 3	0.07	0.19	-0.31	0.45
cod2*dist 4	0.31	0.10	0.11	0.51
cod2*dist 5	0.00	0.00	0.00	0.00

2. I + distance class + cod3 + distance class*cod3

Intercept	-4.49	0.98	-6.41	-2.57
<i>distance class</i>				
3	5.91	1.45	3.08	8.74
4	2.79	1.13	0.58	5.00
5	0.00	0.00	0.00	0.00
cod3	-0.02	0.02	-0.07	0.03
<i>Fish group*distance class</i>				
cod3*dist 3	-0.46	0.22	-0.89	-0.03
cod3*dist 4	0.00	0.03	-0.05	0.05
cod3*dist 5	0.00	0.00	0.00	0.00

3. I + distance class + winter flounder1 + distance class*winter flounder1

Intercept	-5.10	0.68	-6.43	-3.76
<i>distance class</i>				
3	4.81	1.17	2.51	7.11
4	0.78	1.15	-1.47	3.04
5	0.00	0.00	0.00	0.00
winter flounder1	0.00	0.00	0.00	0.01
<i>Fish group*distance class</i>				
winter flounder1*dist 3	-0.01	0.00	-0.01	0.00
winter flounder1*dist 4	0.01	0.00	0.00	0.02
winter flounder1*dist 5	0.00	0.00	0.00	0.00

4. I + distance class + winter skate1 + distance class*winter skate1

Intercept	-5.37	0.77	-6.87	-3.87
<i>distance class</i>				
3	1.48	2.49	-3.40	6.35
4	2.53	0.92	0.71	4.34
5	0.00	0.00	0.00	0.00
winter skate1	13.99	8.36	-2.40	30.38
<i>Fish group*distance class</i>				
winter skate1*dist 3	0.14	12.12	-23.61	23.89
winter skate1*dist 4	-16.92	9.00	-34.57	0.72
winter skate1*dist 5	0.00	0.00	0.00	0.00

5. I + distance class + winter flounder2 + distance class*winter flounder2

Intercept	-5.03	0.68	-6.37	-3.70
<i>distance class</i>				
3	-4.55	5.37	-15.08	5.98
4	2.18	0.83	0.54	3.81
5	0.00	0.00	0.00	0.00
winter flounder1	0.00	0.01	-0.02	0.02
<i>Fish group*distance class</i>				
winter flounder2*dist 3	2.18	1.26	-0.29	4.65
winter flounder2*dist 4	-0.03	0.04	-0.11	0.05
winter flounder2*dist 5	0.00	0.00	0.00	0.00

Table 9. Selection for fish group according to distance class by grey seals in southern Gulf of St. Lawrence in August and September 2003-2008. All selection signs are in comparison with the reference category: distance class 4 (50-100km) for NS and WG survey conducted in August survey and distance class 5 (100-170km) WG survey in September. '+/-' indicated that fish group have been used more/less than in reference category. Habitat categories with CI interval overlapping with the reference category are used at a similar rate ('=').

Fish group	Distance class (km)				
	0-10	10-30	30-50	50-100	100-170
<i>a) NS survey</i>					
winter flounder	=	=	+		
cod	-	-	-		
sandlance	=	=	=		
distance	+	+	=		
cunner	+	+	+		
<i>b) WG survey – August</i>					
sandlance		-	-		
small cod		+	=		
medium cod		=	=		
large cod		=	=		
large winter flounder		=	=		
<i>c) WG survey - September</i>					
medium cod			=	+	
large cod			-	=	
small winter flounder			=	=	
small winter skate			=	=	
large winter flounder			=	=	

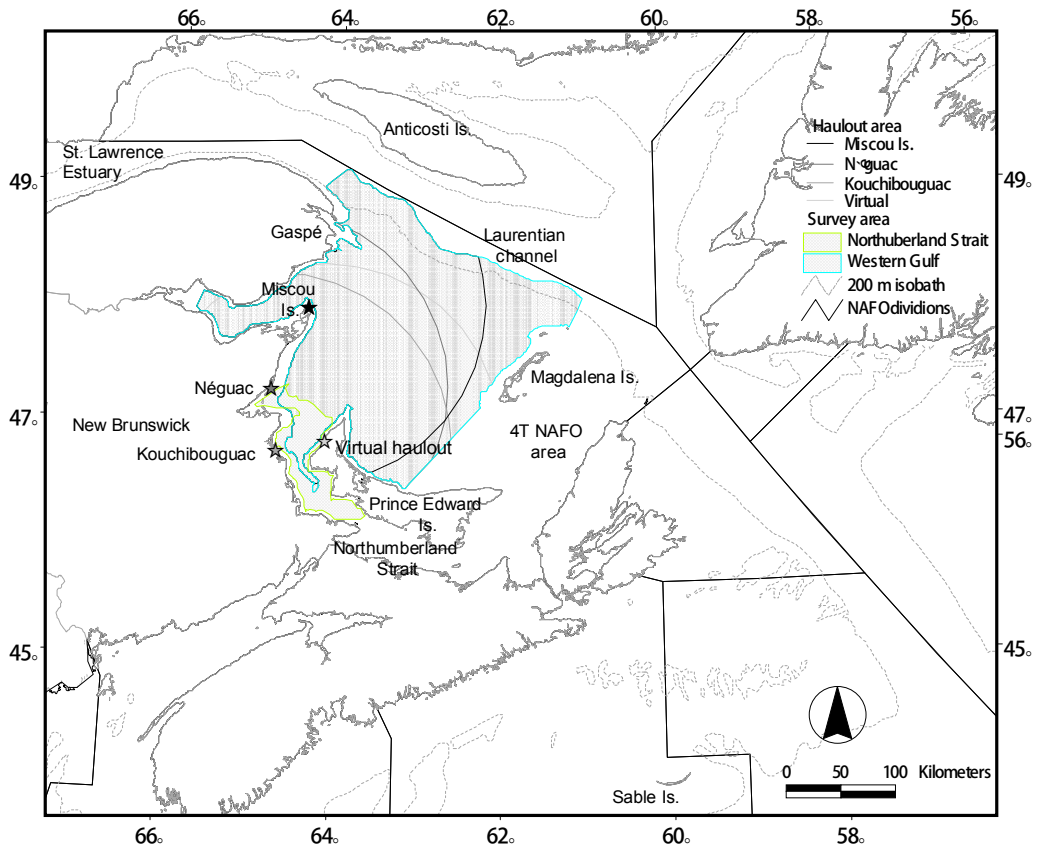
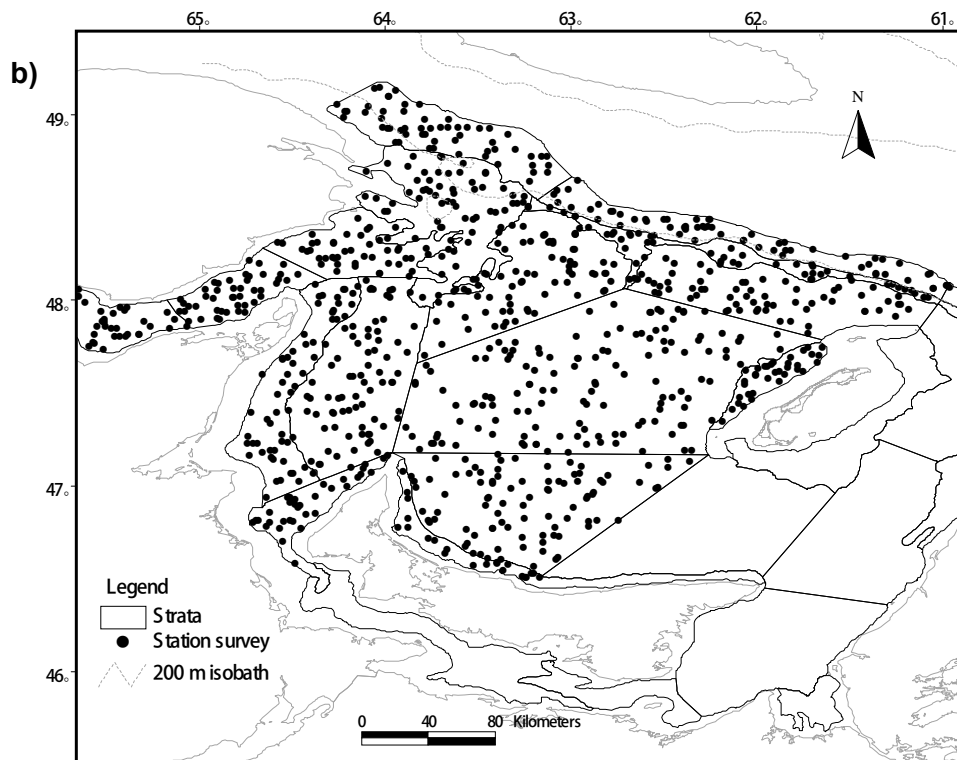
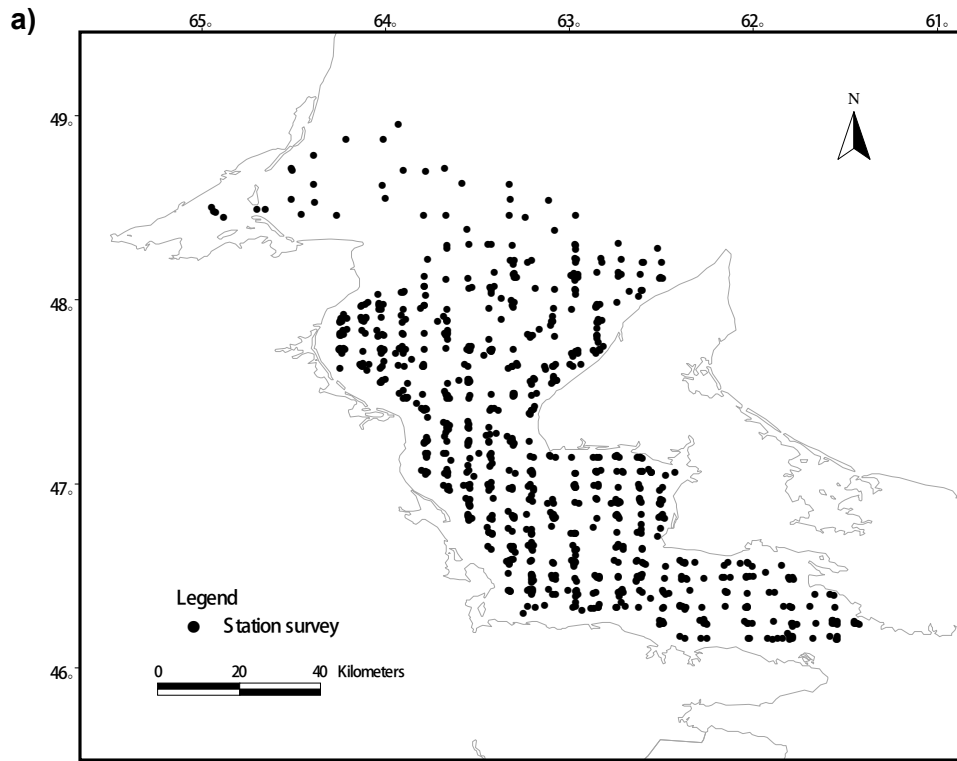


Figure 1. Part of the Gulf of St. Lawrence covered by the Northumberland Strait and Western Gulf fish survey, haul-out sites from area available for seals around those areas and the surrounding region. Dashed lines denote Northwest Atlantic Fishery Organization (NAFO) divisions (e.g., 4T) and subdivisions (e.g., 4Vn). Grey seals were captured at Kouchibouguac, Néguaac, Anticosti Island and Sable Island.



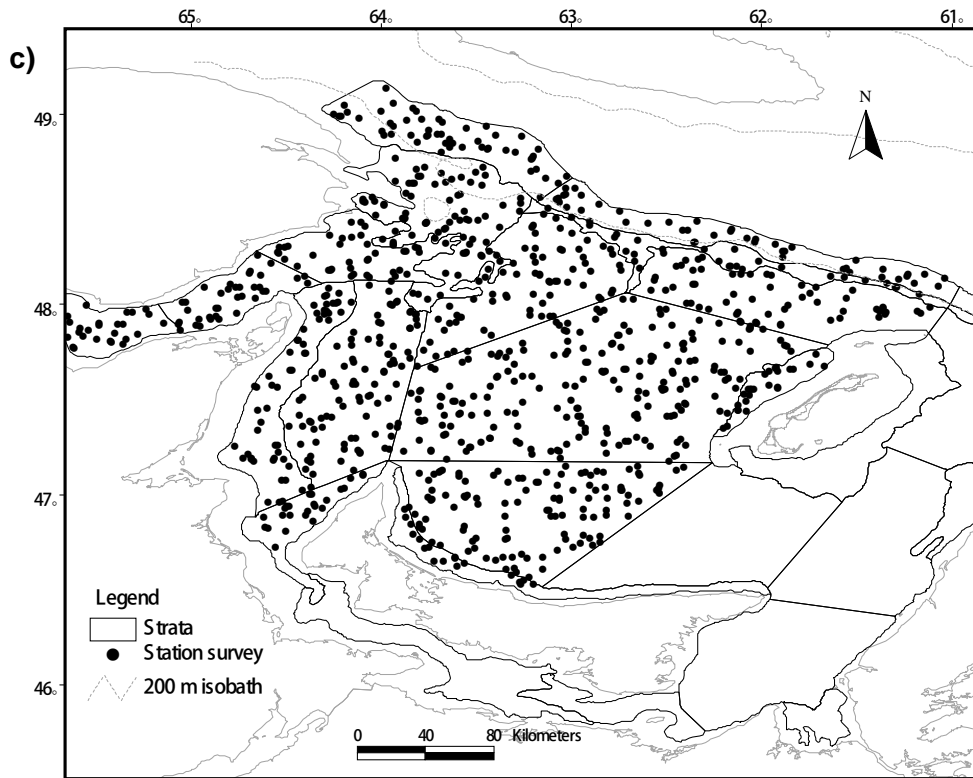
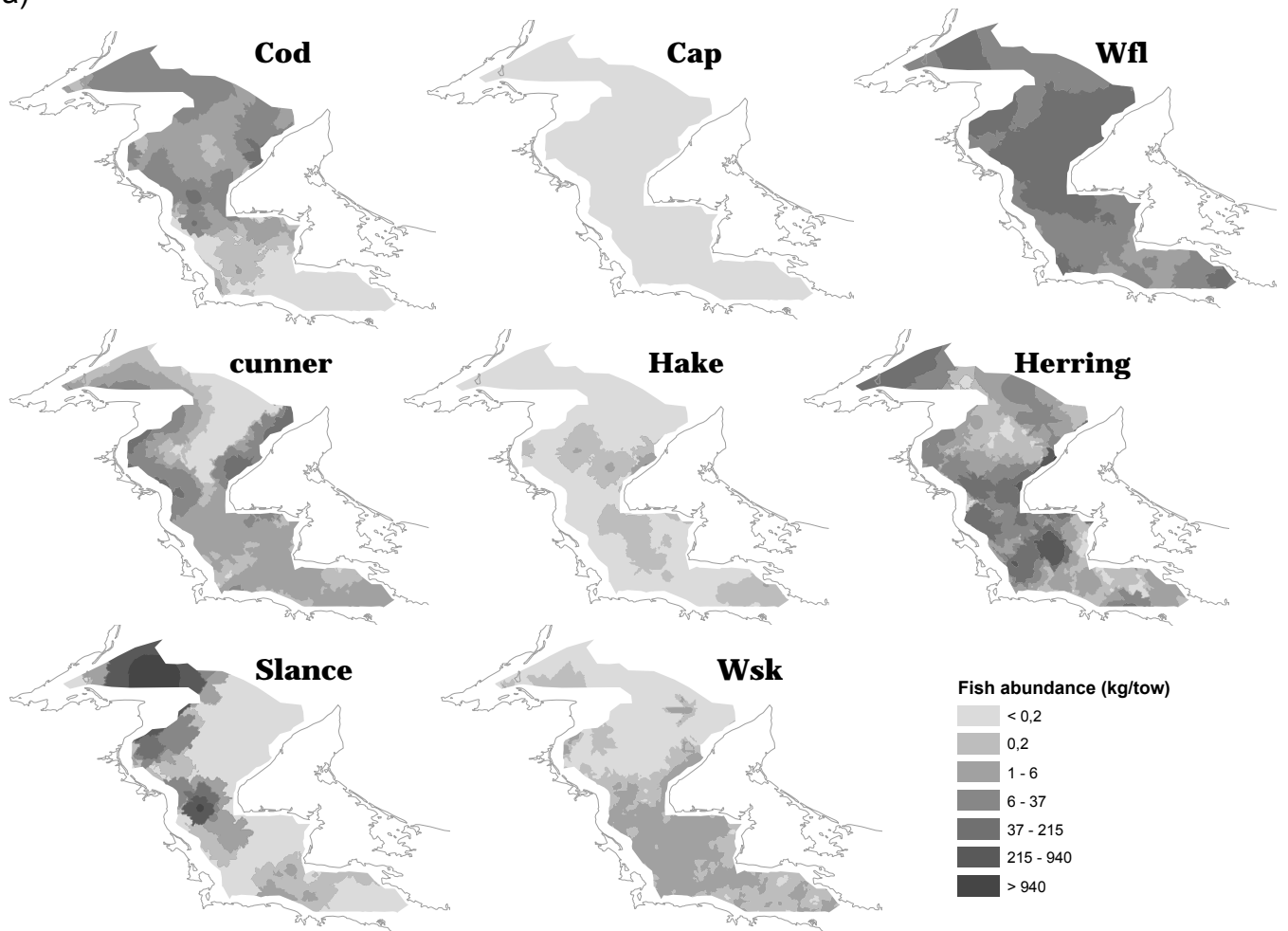
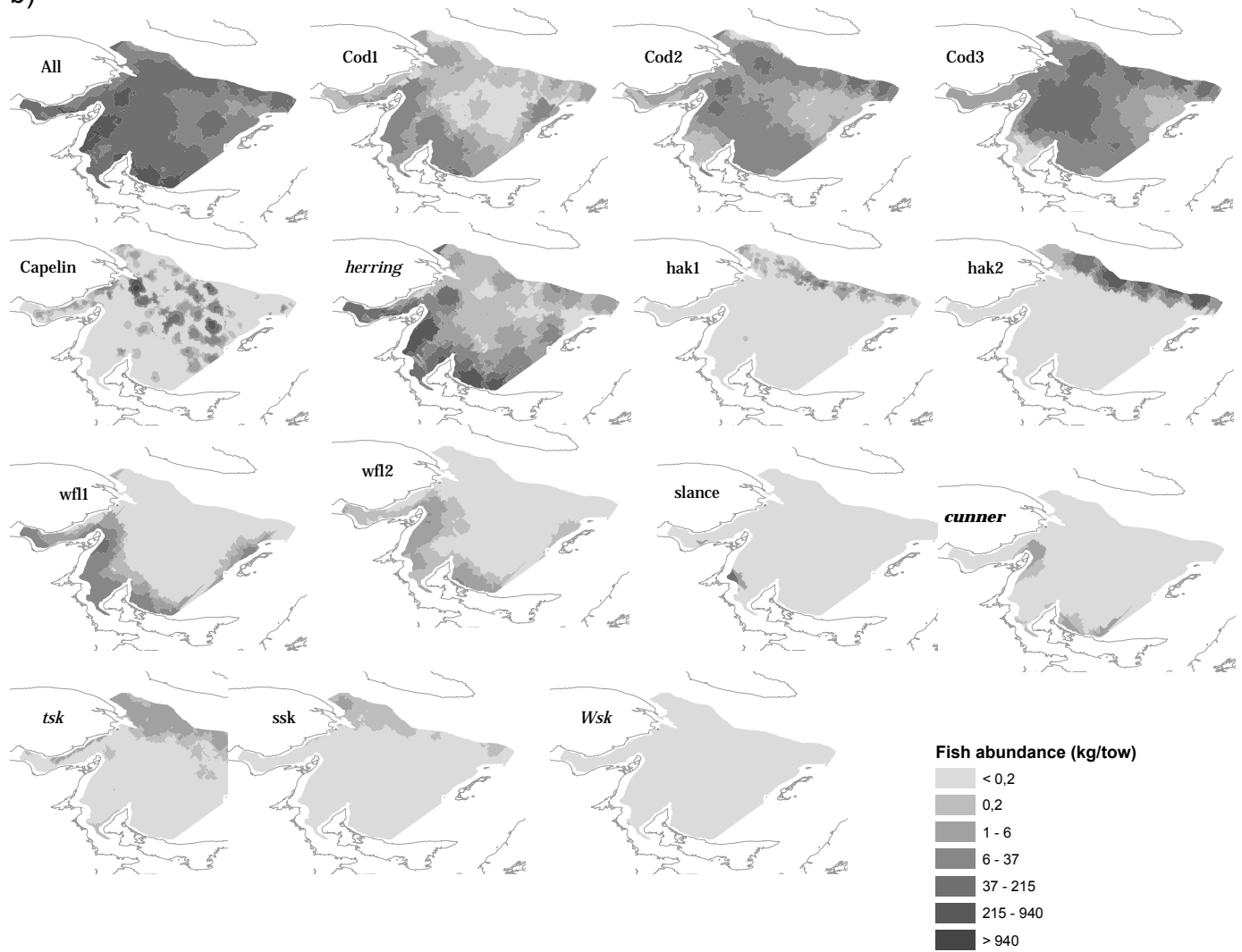


Figure 2. Stations sampled during the fish survey conducted in a) the Northumberland Strait in July as well as in the Western Gulf of St. Lawrence in b) August and c) in September.

a)



b)



* 1=small; 2=medium; 3=large

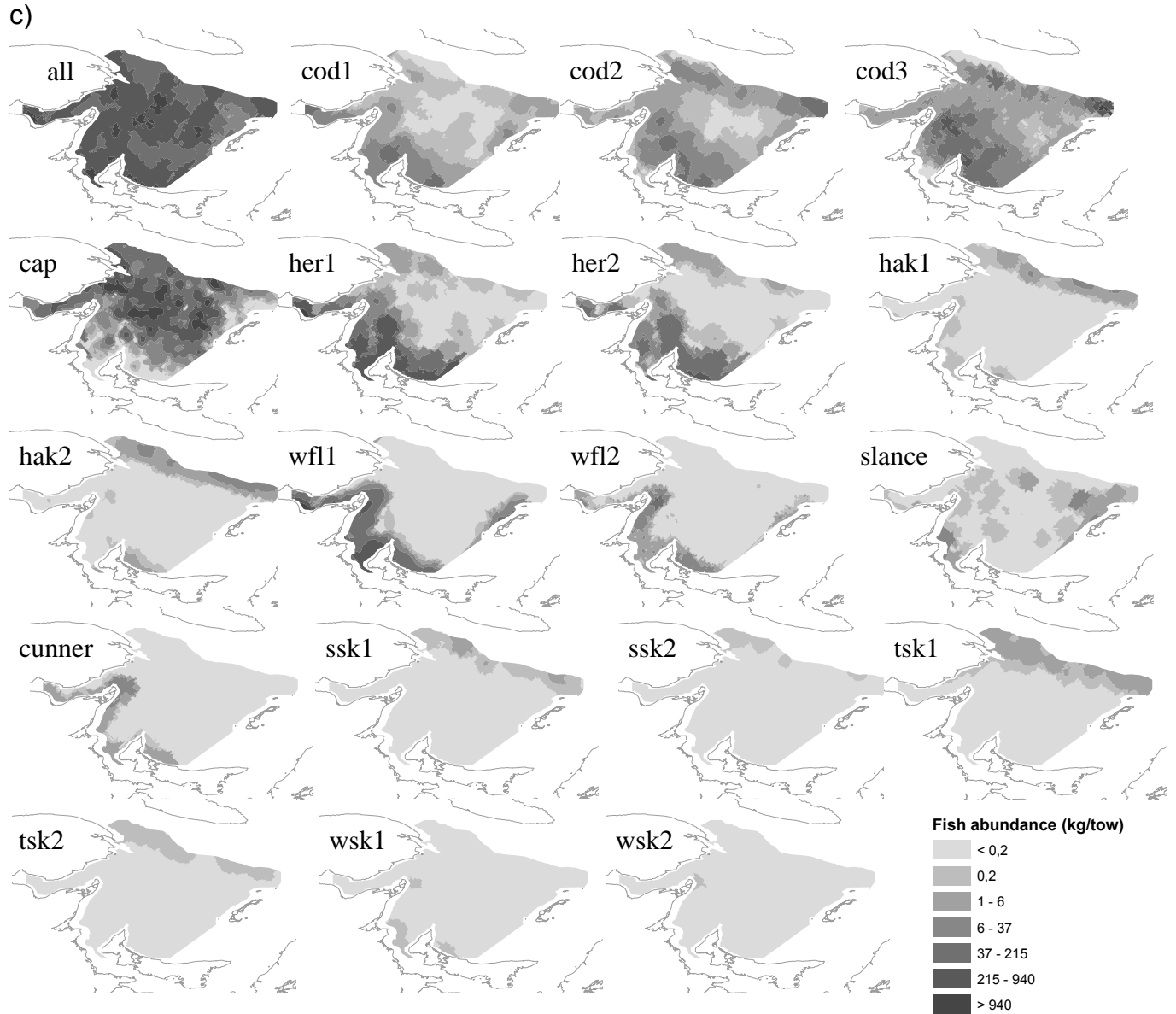


Figure 3. Fish distribution in a) the western Northumberland strait in July 20xx-2006 and the western southern Gulf of St. Lawrence b) August as well as c) September 20xx- 20xx derived from bottom-trawl surveys.

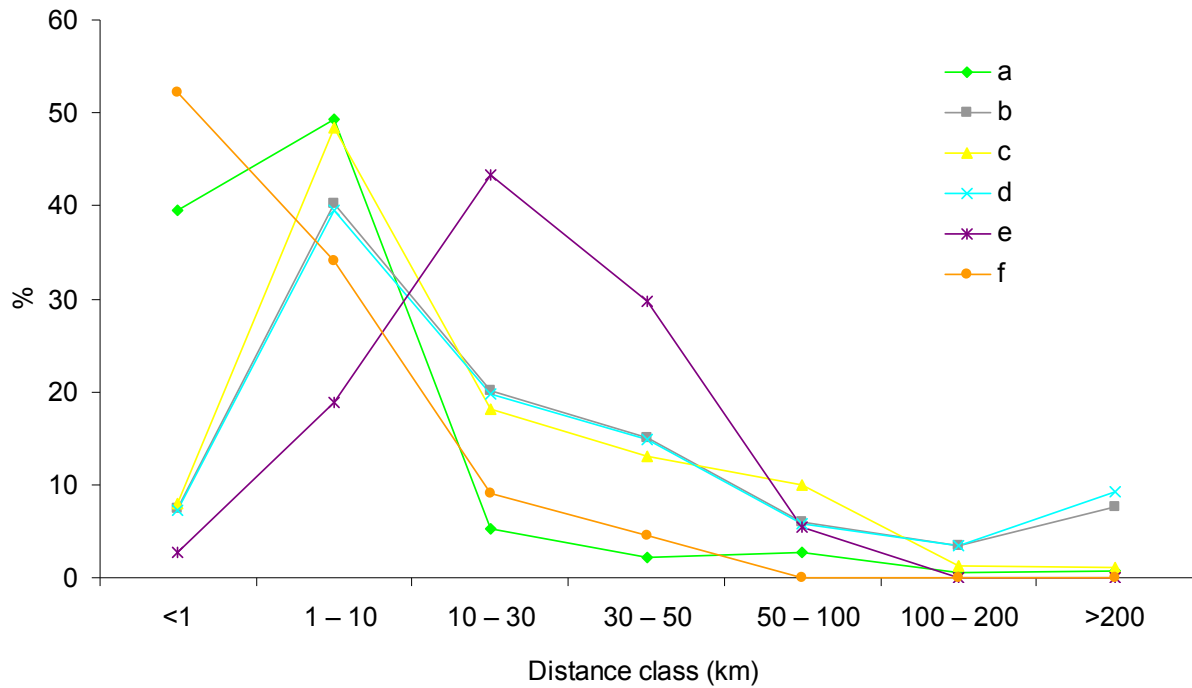


Figure 4. Frequency distribution of distance between haulout and a) the previous haul-out event, b) maximum distance reach during a trip-at-sea, c) locations, d) extended at-sea surface, distance between foraging path used by seals in e) NS fish survey area and f) Western Gulf fish survey area haul out site used by northwest Atlantic grey seals in the southern Gulf between between July and October 15th, 2004 and 2008.

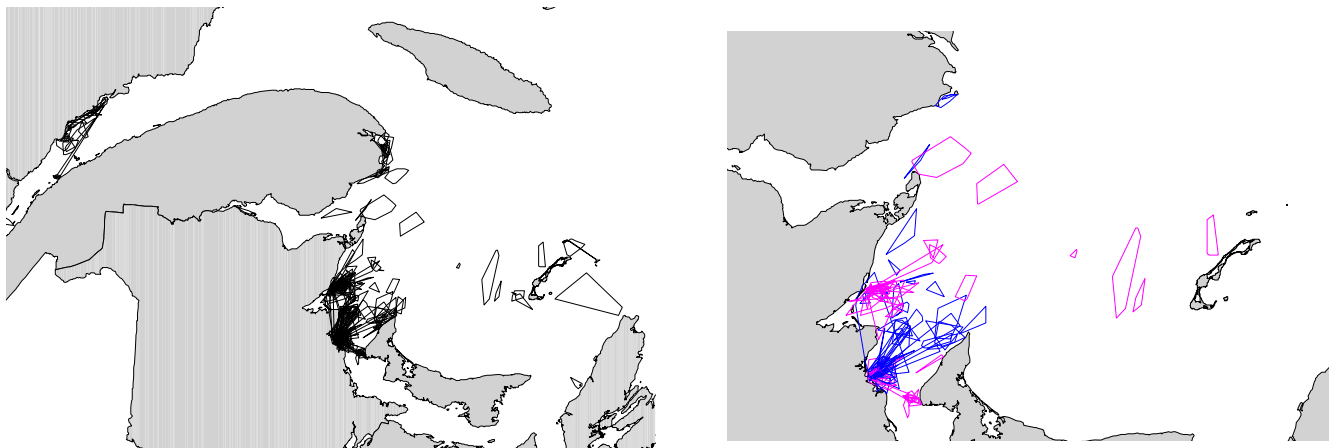


Figure 5. A) All foraging patch and b) foraging patch that occurred over the areas covered by the Northumberland Strait survey and Western Gulf survey conducted in August and September fish of satellite equipped grey seals in the southern Gulf of St. Lawrence between July and mid-October period.

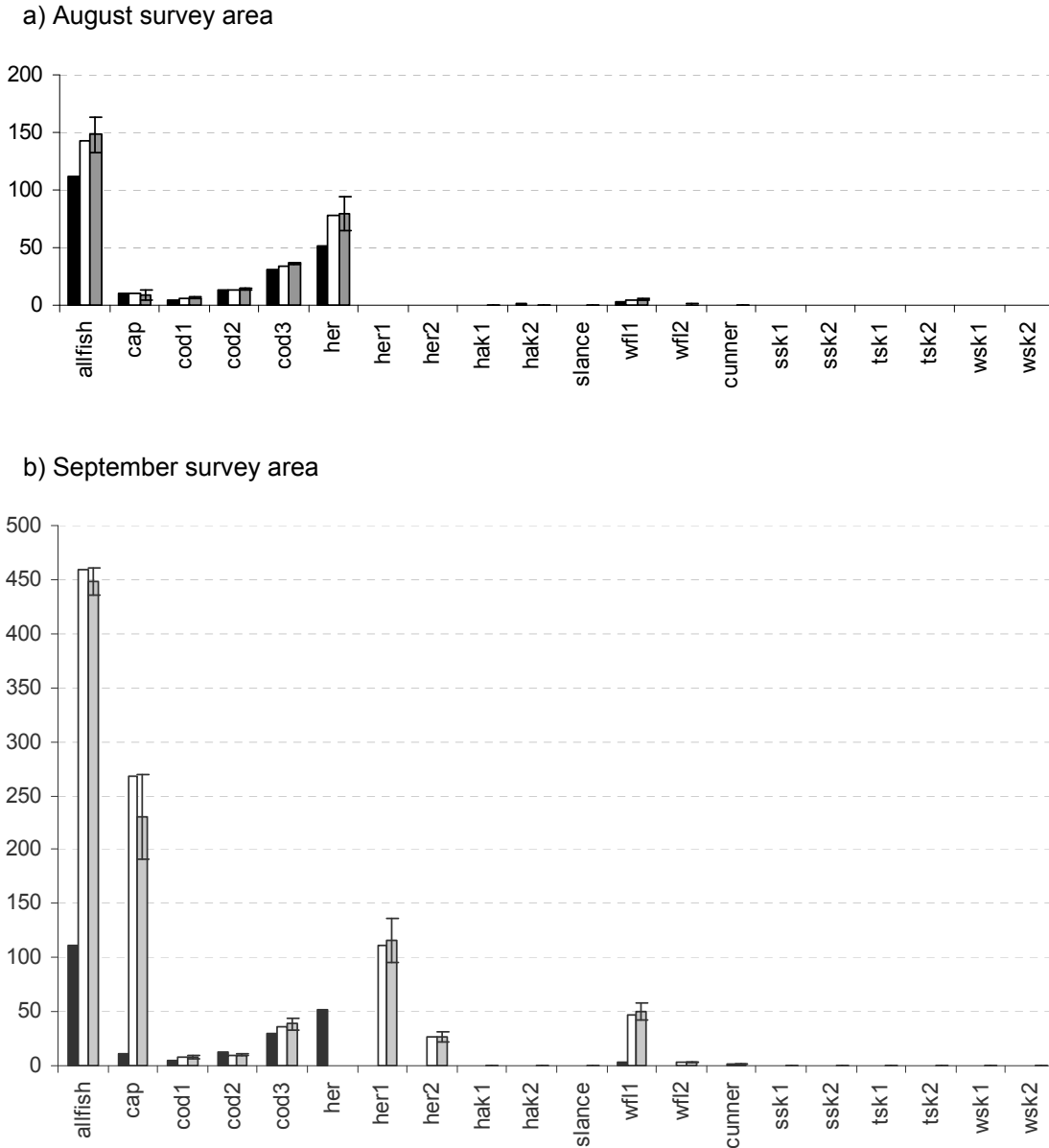
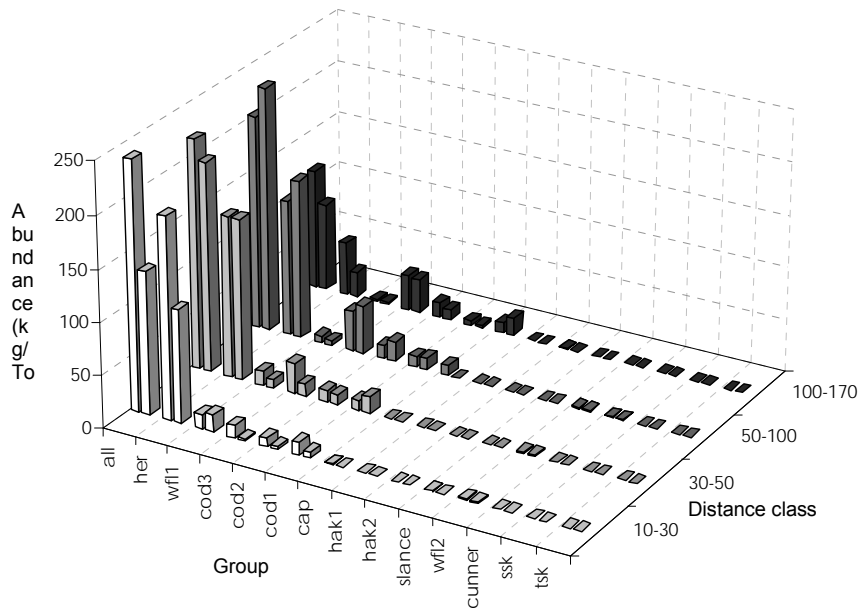


Figure 6. Abundance of each group fish over Western Gulf survey area (black bars), in areas where no haulout site was observed (white bars) and in areas around haulout site (means \pm se) (grey bars) in a) August and b) September (1=small; 2=medium/large; 3=large).

a)



b)

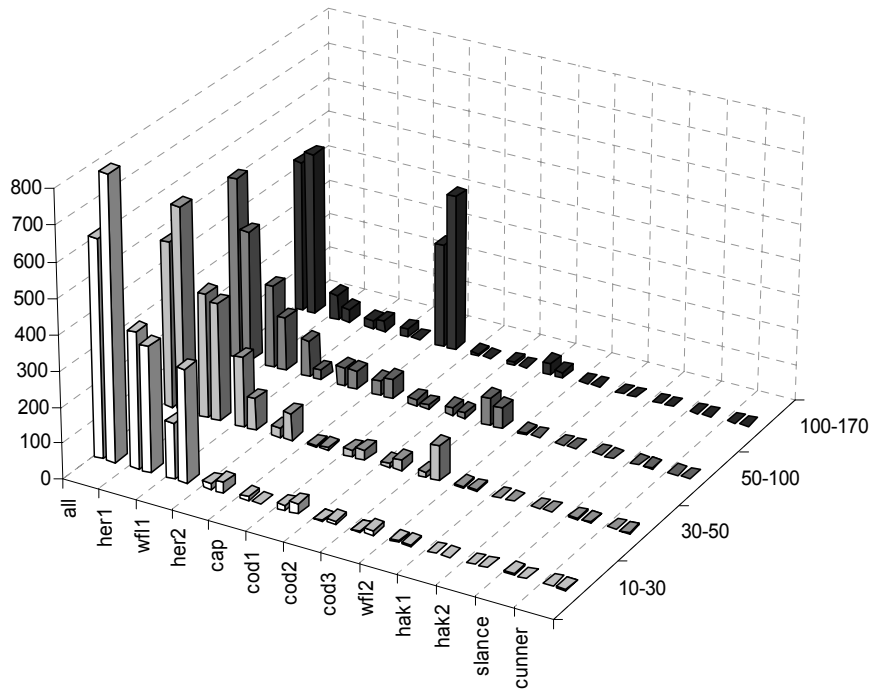


Figure 7. Fish abundance according to distance from distance to haulout site (the first bar of each group fish) and from distance from the coast of Prince Edward Island where no grey seals haulout site (second bar) are known to occurred in a) August and b) September.