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Winter foraging by a top predator, the grey seal, in relation to the distribution of prey

Alimentation hivernale du phoque gris en relation avec la distribution des proies

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ABSTRACT

Identifying areas of restricted search (ARS) of an individual and correlating them with resource abundance may allow a better understanding of predator-prey relationships. Using satellite telemetry data from a large marine predator, the grey seal, collected between 1993 and 2005 and trawl survey data on the winter distribution of ground-fish prey species in 1994-1997, we examined whether seal movements were associated with overwintering concentrations of several commercially important fish species in the Cabot Strait area of Atlantic Canada. The distribution of ARS sites differed between males and females. Male foraging zones were distinguished from female foraging zones by higher densities of herring and medium and large cod. The distribution of searching effort of males varied throughout the winter. In early winter, males were more likely to use habitats around St. Paul's Island where their ARSs were positively related to the abundances of medium and large cod. In late winter, they were found to the southeast of this area and their ARS were negatively associated with large turbot, medium cod and small witch flounder. Females ARSs were also more likely to occur in this southern region. They were negatively related to high abundance of small witch flounder while the probability of having an ARS along their path increased with the abundance of medium sized redfish and decreased with large redfish and white hake. Spatiotemporal differences in distribution and fish communities targeted by male and female ARS may reflect sexual differences in energetic requirements for reproduction. By concentrating their activity in areas of high abundance of large fishes targeted by the fishery in early winter, male grey seals may have an impact on fishes of commercial concern.

RÉSUMÉ

Identifier les aires de recherche restreinte d'un animal et les corrélérer à l'abondance de ressources peut aider à mieux comprendre les relations prédateurs-proies. Nous avons utilisé les données d'émetteur satellite posés sur les phoques gris entre 1993 et 2005 et les données d'abondance de poissons obtenues des relevés au chalut par navire scientifique réalisés à l'hiver entre 1994-1997 et démontrant la distribution des poissons de fond pour examiner si les déplacements des phoques étaient associés aux concentrations hivernales de plusieurs espèces de poissons dans le région du détroit de Cabot de l'Atlantique Canada. La distribution des ARS diffère entre les mâles et les femelles. Les zones de chasse des mâles se distinguent de celles des femelles par une plus grande densité de hareng, de morues de taille intermédiaire et de grande taille. La distribution de l'effort de recherche des mâles varie au cours de l'hiver. Au début de l'hiver, les mâles sont plus susceptibles d'utiliser les habitats autour de l'Île St-Paul où leurs aires de recherche restreinte sont associées à l'abondance de morue de taille intermédiaire et de grande taille. Plus tard en hiver, les mâles sont concentrés au sud-est de cette région où ils sont négativement associés au turbot de grande taille, à la morue de taille intermédiaire et à la petite plie grise. Les aires de recherche restreinte des femelles sont aussi concentrées dans cette région. Celles-ci sont négativement reliées à l'abondance de petites plies grises alors que la probabilité d'avoir un comportement de recherche restreinte le long du trajet des femelles augmente avec la densité de sébaste de taille intermédiaire et décroît avec l'abondance de grand sébastes et merluche blanche. Les différences spatiales et temporelles observées dans la distribution des ARS et des communautés de poissons recherchés par les mâles et les femelles peuvent refléter des différences dans les besoins énergétiques pour la reproduction. En concentrant leur activité dans des endroits où l'abondance des poissons de grande taille est importante au début de l'hiver, les phoques gris mâles peuvent avoir un impact sur les poissons d'intérêt commercial.

INTRODUCTION

Several studies have explored the direct or indirect impacts of marine mammals and other predators on prey using ecosystem models, and have suggested that upper level consumers contribute to maintaining structure in marine ecosystems (Yodzis 1998, Morissette et al. 2006; Savenkoff et al. 2007a). At a local scale, prey choice by marine mammals may be determined by preferences for particular prey within the context of availability of alternative prey species (Lawson et al. 1998, Wathne et al. 2000, Smout and Lindstrøm 2007). At a larger scale, prey selection can be viewed as the impact that the predation by marine mammals can have on marine resources of commercial or conservation concern (Mohn and Bowen 1996, Estes et al. 1998, FRCC 2004, Yodzis 1998). Relationships between predators and their prey can be quite complex, including both direct and indirect effects operating at different trophic levels (Yodzis 1998, Morissette et al. 2006). Often only direct impacts of predation are considered but, predators can influence prey populations and the broader community through prey needing to develop costly anti-predator strategies as well (Creel and Christianson 2008). The importance of these indirect effects in structuring terrestrial and fresh-water communities has been examined extensively (e.g. Werner and Peacor 2003, Preisser et al. 2005, Verdolin 2006), but these effects remain poorly documented in marine systems (Dill et al. 2003, Wirsing et al. 2008).

Northwest Atlantic ecosystems have undergone significant changes in recent decades (e.g., Savenkoff et al. 2007a,b). 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. Following this decline in large piscivorous fish, the abundance of small fish increased sharply (Benoît and Swain 2008). In addition to these changes in the fish community, there have been major increases in the abundance of two marine mammals, the harp seal (*Pagophilus groenlandicus*) and the much larger grey seal (*Halichoerus grypus*) (Hammill and Stenson 2008, Thomas et al. 2008), of which the grey seal is considered the more important consumer of commercial stocks (Hammill and Stenson 2000).

Demersal fish populations in the Gulf have failed to recover despite limited fishing over the last fifteen years due to elevated natural mortality of adult fish (e.g., 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). Diet information for grey seals indicates that they prey primarily on fish of intermediate sizes (e.g., cod 25-35 cm in length), not large adult fish for which the recent elevated natural mortality levels have been documented (Hammill et al. 2007b). 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 has not occurred where grey seals and large fish overlap.

The availability and distribution of resources is expected to affect the distribution of animals as well as their space-use strategy (Johnson 1980, Manly et al. 2002). In a heterogeneous and dynamic environment, foraging animals undertake increasingly complicated movement patterns and maximise their foraging success by concentrating effort in areas with the highest probability of capturing prey (Fauchald and Tveraa 2003). This modification of movement patterns occurs at different levels because predators respond to a range of environmental features at different spatial scales (Johnson 1980, Rettie and Messier 2000, Weimerskirch et al. 2007). Identifying areas of intensive use

and correlating them with the environmental and resource attributes is a first-step in understanding the relationship between large marine predators and their prey.

If seals are significant predators on large cod, both cod and grey seals would overlap extensively. We would then expect seals to occur in areas or periods of the year where cod are aggregated. This may occur in the Cabot Strait/northeast Cape Breton island area, an area where we have little information on seal diet. To examine if there is a potential for grey seal predation on large, aggregated, overwintering cod, we examine the winter movement patterns of grey seals in the Cabot Strait area at the entrance to the Gulf, based on satellite transmitters that have been deployed on grey seals on Sable Island and in the Gulf over the past 10 years (Breed et al. 2006, Harvey et al. 2008). This area is an important overwintering area for a number of commercially important fish species (Swain et al. 1998). Using data from synoptic bottom-trawl surveys, we compared the foraging patterns of grey seals to size-specific spatial distributions of fishes to gain insights into potential predator-prey interactions at this time of year.

MATERIALS AND METHODS

Study area

The study encompassed an area of 68 000 km² in Cabot Strait between the northeast coast of Cape Breton Island and the southwest coast of Newfoundland (Figure 1). This area is dominated by the deep Laurentian Channel (>300m), with a shallow shelf (<200 m) to the southwest and a number of shallow banks to the northeast. In autumn, when ice begins to form in the Gulf, there is a defined movement of grey seals which leave the southern Gulf, the St. Lawrence Estuary and northern Gulf (mean=25 November, Range=8 October-25 January). They move either into the Northumberland Strait between Prince Edward Island and Nova Scotia or exit the Gulf and move onto the Scotian Shelf (Lavigneur and Hammill 1993). Between December and February, breeding aggregations form on small islands and on the pack-ice in Northumberland Strait, along the Nova Scotia Eastern Shore and on Sable Island. After the reproductive season seals move into the Cabot Strait/Sydney Bight and Scotian Shelf areas where they usually remain until the spring. Animals that summer in the Gulf return in the spring (Lavigneur and Hammill 1993).

The shallow southern Gulf is largely ice covered in winter. Most commercial fish species leave the area in the fall (November), overwintering in the deep waters of the Laurentian Channel or south of the Channel in the Cabot Strait and Sydney Bight areas (Fig. 1)(e.g. Swain et al. 1998).

Fish data

Data are from bottom trawl surveys conducted in the Cabot Strait area in January of 1994-97 by the research vessels *Alfred Needler* (1994-95) or *Wilfred Templeman* (1996-97). The 1994 survey followed a stratified random design. Stations for the 1995-1997 surveys were allocated following a regular 12 × 12 nautical mile grid (with an additional station located midway between the regular grid points in areas along the 200-m contour where cod concentrations were expected). The 1994 survey was restricted to the south side of the Laurentian Channel (in NAFO divisions 4T and 4Vn) whereas the 1995-1997 surveys also covered the north side of the Channel (in divisions 4R and 3Pn). Surveys

conducted by the *Alfred Needler* used a Western IIA bottom trawl whereas those conducted by the *Wilfred Templeman* used a Campelen 1800 trawl. Target fishing procedures were a 30-min tow at 3.5 kn by the *Alfred Needler* or a 15-min tow at 3 kn by the *Wilfred Templeman*. All catches were adjusted to a standard tow of 1.75 nautical miles for the *Alfred Needler* surveys or 0.75 nautical miles for the *Wilfred Templeman*.

Seven common and commercially important fish species were selected for this analysis, including both species frequently reported in grey seal diets (e.g., herring, cod) as well as species rarely reported in the diet of this seal species (e. g., witch flounder, turbot). For each fish species, survey catches were divided into two or three size classes (Table 1), for a total of 16 fish groups. To adjust for the size-dependent differences in fishing efficiency between the Western IIA and Campelen trawls, catch rates for a particular species and size class were adjusted to produce the same average value in each year in a subset of the survey area sampled in all years. This was done as follows. First, a_y , the weighted average catch rate in this subset of the survey area, was calculated for each year y . The weight used for each site was based on the spatial sampling design (see Swain et al. 1998, p.2551 for details). Then the catch rate at each tow in year y was adjusted by the factor:

$$\left(0.25 \sum_{y=1994}^{1997} a_y \right) / a_y, \quad \text{where the 0.25 is to correct the ratio to 1 year.}$$

The correlation in abundance between the 16 fish groups was examined and only variables with a correlation <0.8 were included in the same analysis (Appendix A).

The Geostatistical Analyst extension of ArcGIS v9.2 (Environmental System Research Institute, Inc (ESRI), 380 New York Street Redlands, CA 92373-8100) was used to produce prediction maps of fish density for each of the 16 groups, combining the data from all four years. The “ordinary kriging” method was used to model spatial structure based on an omni-directional, spherical semivariogram model. Catch rates were averaged when more than one value was available at the same location. The boundary of the study area was defined as a polygon that extended 10 km beyond the survey stations.

Principal components analysis (PCA) was used to summarize similarities and differences in spatial distribution among fish groups. A PCA with a normalized varimax rotation was performed on the correlation matrix of the 16 fish groups. Prior to analysis, variables were log-transformed to improve the normality of their distribution.

Grey seals

Grey seals were captured between 1993 and 2005, during the breeding season (January), the moult (May-June) or during late summer (August-October) at Sable Island and at various sites in the Gulf and Estuary of the St. Lawrence (Fig. 1) (Breed et al. 2006, Harvey et al. 2008). Animals were classified as juveniles (<6 years old) or adults (≥ 6 years old) (Harvey et al. 2008). All animal handling procedures followed the guidelines of the Canadian Council on Animal Care (1993). A satellite time-depth recorder was glued to the upper neck or head of each seal using a quick-setting epoxy (Harvey et al. 2008). Three types of transmitters were deployed; half-watt satellite time-depth recorders (SDRL-Wildlife Computers, Redmond, WA), ST-18 (Telonics, Mesa AZ,

USA) and Series 7000 and 9000 Satellite Relay Data Loggers (SRDL) (Sea Mammal Research Unit (SMRU), Univ. of St. Andrews, Scotland)

Modelling path trajectories

A state-space model was used to handle error in the position data 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 locations along a track. A first-difference correlated random walk model with a 480 min time-step (3 locations per day) was used to describe seal movements (Breed et al. 2009). The resulting estimated locations included few points on land and were evenly spaced in time.

The path of each individual was analysed to identify seals that overwintered within the study area. Only locations obtained after the seals had left their summer range, without returning to this area, were considered in this analysis. Winter was identified as the period from 12 December, the mean date of departure for the autumn migration, until 30 April. The breeding season (the two first weeks of January) was excluded from the analyses and the parts of the path before and after the reproductive period were considered separately in the analyses.

Identification of foraging zones

To better understand how seals used the study area, we calculated the time spent by seals along different parts of their tracks using first-passage time (FPT) analyses (Fauchald and Tveraa 2003). FPT is defined as the time required for an animal to cross a circle of a given radius. This analysis allowed us to identify where individuals concentrated their time along the path and at which scale they adopted an Area Restricted Search (ARS) behavior (Fauchald and Tveraa 2003). For each track, we calculated the FPT for points interpolated at 2 km intervals along the path for radii ranging from 4 to 100 km. Radii increased at intervals of 1 km from 4 to 20 km and at intervals of 10 km from 20 to 100 km to minimise computation time (Freitas et al. 2008). For each individual, we calculated the variance of the log-transformed FPTs and plotted these according to radius to identify the radius at which the maximum variance occurred (Fauchald and Tveraa 2003). The log-transformed FPT was used to make the variance independent of the magnitude of the mean FPT. The radius at which the peak was detected corresponds to the scale that best differentiates between high and low passage times and so, to the spatial scale at which the animal concentrated its time. The FPT at each point along the track calculated at this scale was then used to compare the time spent by the animal along the different parts of its track. We performed the FPT analyses only on tracks with more than 15 locations, since detection of peak variance is sensitive to the accuracy and the number of locations observed within the ARS (Pinaud 2008). Analyses of FPT were performed using custom software developed by Arnaud Mosnier (Dept. of Biology, University of Quebec at Rimouski, Rimouski, QC, Canada).

The presence of multiple, spatially distinct ARS zones along the path was determined following Lemieux-Lefèvre (2009). Briefly, a circle was created around the point considered as the center of each ARS zone and the radius of each ARS zone was set to the scale with the maximum variance (Fauchald and Tveraa 2003). Piecewise-regressions were then used to detect the presence of a threshold or breakpoint across FPT values at a given scale, discriminating FPT values corresponding to restricted

search behavior from other values. To define this threshold, values of FPT (at Var-max) for each segment were sorted in ascending order. Two and three process (one and two breakpoints) piecewise-regression models were then applied to the data series using the MODEL procedure in SAS (SAS Institute Inc, 100 SAS Campus Drive Cary, NC 27513-2414 USA). Piecewise-regression models assume homogeneity of variances and independence and normality of residuals, assumptions that were not met in this study. To correct for autocorrelation of residuals, autoregressive moving average error processes (FIT statement of the MODEL procedure in SAS) were applied to the data. The autoregressive order was determined using a Durbin-Watson test. Violation of the heteroscedasticity assumption was addressed by using a heteroscedastic-consistent covariance matrix estimator (the “jackknife”, Davidson and MacKinnon 1993). Once corrected for heteroscedasticity and autocorrelation, differences between slopes were tested using two-sample paired t-tests. A significant difference between slopes indicated the potential occurrence of other ARS zones.

The value corresponding to the 95% lower confidence interval of the calculated breakpoint was selected as a threshold to determine the presence of multiple spatially distinct ARS zones. Interpolated points with FPT values falling above this threshold were mapped in ArcGIS with the associated circle of a radius equal to Var-max. Then, starting with the highest FPT value, subsequent points were considered as the centre of a new ARS zone when the circle around the point did not overlap with segment sections forming part of another ARS zone of the same segment. This step was repeated until no more points above the threshold could be considered as a new ARS zone centre (Appendix B).

The effects of sex, season, age class and region within the study area, on ARS size (dependent variable) were determined using a general linear mixed models fitted by maximum-likelihood parameter estimation. To account for repeated measures on some individuals, ‘individual’ was considered as a repeated factor in the model. All possible models with two-way interactions were tested and compared to the mean model: $y = \mu + \epsilon$. Variables included in each model were entered simultaneously. The ARS size was \log_e -transformed as necessary to meet the assumptions of parametric analyses. Model selection based on ΔAIC and AIC weights was used to select the most parsimonious model. Models with $\Delta AIC \leq 2$ were considered to be equivalent. When models were equivalent, the model with fewest parameters was retained as the best one.

Habitat selection analyses

Two approaches were examined, 1) logistic regression analyses relating the probability of occurrence of an ARS zone to fish density (Manly et al. 2002) and 2) a descriptive analysis comparing the fish community between foraging (ARS) and non-foraging zones. Both analyses compared fish density between observed ARS zones and randomly located circles. For each individual seal, 40 circles randomly located within the study area were generated at the ARS scale observed for that individual. Random circles were retained if 50% of their area overlapped the study area (Dussault et al. 2005). Forty circles were retained because the mean density for each fish group converged to the average in the study area with this number of samples. Three very large ARS zones (radius > 80 km) were omitted from the analyses because they occupied an extremely large area and the seal track occupied only a very small zone within the circle. Logistic regressions were conducted at both the landscape scale (at the level of the study area) and along the path that animals moved. For the analyses at the scale of the path, non-

overlapping circles were positioned along the path. The number of non-overlapping circles varied from 2 to more than 20, depending on path length and ARS scale. These analyses were completed separately for males and females because sex differences in space use strategies have been observed among grey seals (Beck et al. 2007, Breed et al. 2006, Harvey et al. 2008). We also conducted separate logistic regression analyses for males in early and late winter because of a striking difference between these periods in the location of their ARSs (see results). In each period, each ARS was compared to 20 random circles located in their vicinity, determined by creating a polygon around all ARSs considered in each period.

Mean density of each fish group was estimated for each ARS and random circle. Each fish group was split into 10 density classes based on its density distribution. The median value of each class was multiplied by the proportional area of that class within a circle, and these values were summed to give the average density for the circle.

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 (ARS) zone to fish density. 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 (Burnham and Anderson 2002), the Δ QICu and QICu weights were computed to select the most parsimonious model. Models with Δ QICu \leq 2 were considered to be equivalent. When models were equivalent, the model with fewest parameters was chosen as the best one. When a variable was included in several equivalent models, a weighted average of the estimate and standard error for this variable across all the models tested was computed (Burnham and Anderson 2002). To avoid model over-parameterization, only models in which the number of variables did not exceed $n/5$ were explored, where n is the sample size, i.e. the number of individuals.

Since many species and size classes of fish were considered ($n=16$), habitat selection was initially examined for each species separately. For each fish species, spatial scale (landscape or along the path) and sex, length classes that had a significant effect on the relative probability of use were identified, then compared with all possible models incorporating the fish groups that had significant effects in the single-species analyses.

To assess model performance, the percentage of correct predictions was calculated by comparing the observed outcome (e.g. true ARS) with the expected probability estimated by the model. A prediction was classified as correct if the outcome was 0 and the probability was below 50% or if the outcome was 1 and the probability was above 50%. The coefficient value of each parameter estimated by the model, β , is equivalent to selection ratios. 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 more than would be expected if the animal was making a selection simply in proportion to availability (positive selection) and less if $\beta < 0$ (negative selection). Odd-ratios ($\exp\beta$) (with 95% confidence intervals), are also presented as a measure of effect size used in logistic regression. Odd-ratios are the odds of an event occurring with an increase of one unit of the variable. Logistic regressions were performed using SAS (Littell et al. 2002). Results are presented as means \pm SE.

Community analyses

To compare fish communities between foraging and non-foraging zones, the 62 random circles that had less than 1% overlap with the observed ARS zones were selected as non-foraging zones. Densities of each fish group were compared between male foraging zones (N=26), female foraging zones (N=19) and these non-foraging zones (N=62). A Bray-Curtis similarity matrix was computed to compare the 107 zones based on their fish community composition. Based on this similarity matrix, an ordination of the zones was produced using non-metric, multi-dimensional scaling (MDS). Differences in the fish community between male foraging zones (MF), female foraging zones (FF) and non-foraging zones (NF) were tested by analysis of similarity (ANOSIM, Clarke and Green 1988). This uses randomisation tests based on permutations of the similarity matrix. The test statistic R was:

$$R = \frac{\overline{r_B} - \overline{r_W}}{\frac{1}{2}M}$$

where $\overline{r_W}$ is the average of all rank similarities among zones of the same type (FF, MF, or NF), $\overline{r_B}$ is the average rank similarity among zones of different types, $M = n(n-1)/2$ and n is the total number of zones. Zones were randomly re-assigned to types and R was calculated for each of 999 random permutations. The significance level for the difference between zone types was given by $(N+1)/1000$, where N is the number of random permutations yielding an R greater than or equal to that of the observed data. Fish groups making important contributions to the similarity within zone types and to the dissimilarity between zone types were identified based on their average contribution to Bray-Curtis similarity between pairs of zones of the same type and to Bray-Curtis dissimilarity between pairs of zones of different types. Computations were made using PRIMER (Clarke and Gorley 2001).

RESULTS

Grey seal telemetry

A total of 172 grey seals were tagged between 1993 and 2005; 53 of them were tagged before 1998; 119 after 1998 (Table 2). Animals were tracked for a mean duration of 164 ± 7 (range=19-359) days with a total of 28,428 days of tracking. Among all individuals, 35 seals (14 from Sable Island; 21 from Gulf of St. Lawrence; 15 males, 20 females) travelled within the study area during the winter period at least once, for a total of 2,908 locations (970 days). Seals stayed in the study area for an average of 10.9 ± 1.35 (range=0.3-61) days. Seven of the seals were within the study area both before and after breeding.

Fish distribution and abundance

Atlantic cod was the most abundant fish species caught in the January surveys, accounting for 19% of the total catch by number and 38% of the catch by weight. The greatest concentrations of cod occurred along the southern slope of the Laurentian

Channel near the 200-m depth contour (Fig. 2); these cod belong to the southern Gulf population (Swain et al. 2001). Additional aggregations, belonging to the northern Gulf population, occurred in deeper water on the north side of the Channel. On the south side of the Channel, a dense concentration of all size classes of cod, evident in all years (Appendix C1), occurred just north of Cape Breton in the vicinity of St. Paul Island (Fig. 2). Additional concentrations of large cod (mainly >35 cm) occurred further to the southeast near the 200-m contour. The location and importance of these additional aggregations varied from year to year (Appendix C1). The dense aggregation of large cod at the south-eastern edge of the study area is due to a single large catch in 1994. Smaller cod tended to occupy shallower depths than larger cod.

Redfish were the second most common species caught, accounting for 15% of the total catch by number and 18% of the catch by weight. Redfish were mostly distributed on the north side of the Laurentian Channel, with the larger fish in deeper water (Fig. 2). Some small redfish also occurred along the southern slope of the Laurentian Channel, mostly around St. Paul Island and at the south-eastern end of the study area. Herring, the third most common species in our analysis (9% by number, 6% by weight), occurred mostly on the shelf, south of the Laurentian Channel, again with smaller fish in shallower water (Fig. 2). The highest concentrations of herring occurred between Cape Breton and St. Paul Island, along the 200-m contour to the southeast of this area and near the south-eastern limit of the study area.

The remaining species were mostly restricted to the Laurentian Channel in waters deeper than 200 m (Fig. 2). White hake occurred mainly along the south slope of the Laurentian Channel, just beyond the 200-m contour. Plaice were also largely confined to the deep waters of the Laurentian Channel, mostly in the northern part of the study area. Witch flounder and turbot were distributed predominantly in deep waters (> 400 m) in the central region of the Laurentian Channel.

The PCA identified five components (eigenvalue>1), which explained 72% of the total variability in fish abundance (Table 3). Witch flounder, redfish >20cm as well as turbot>35cm and white hake >35 cm dominated the weighting of the first axis. These fish groups were widely distributed throughout the deep waters of the Laurentian Channel and the basins in the north-eastern part of the study area (Fig. 2). The second axis represented species that were most abundant in the northern part of the Laurentian Channel (American plaice and turbot<35cm; Fig. 2). The third axis was correlated with herring and white hake <35cm, groups that were concentrated along the southern slope of the Laurentian Channel from St. Paul's Island to the southern edge of the study area (Fig. 2). The fourth component was associated with the three length classes of cod, which were most abundant around St. Paul's Island, near the southern edge of the study area and off Newfoundland (Fig. 2). Within this area, cod densities were as high as 6 000 individuals/ tow, whereas their abundance was less than 20 fish/tow in the other parts of the study area. Redfish <20cm was the only group strongly correlated with the fifth component. Aggregations of these fish occurred along both the northern and southern slopes of the Laurentian Channel (Fig. 2).

Considering all sixteen fish groups, fish concentrations were greatest in three areas. One concentration, consisting of high densities of cod and herring (all size classes) occurred in the area from Cape Breton to St. Paul Island. A second concentration consisting of large cod and large herring, as well as American plaice, white hake, small redfish and large witch flounder, occurred along the southern slope of the Laurentian

Channel at the south-eastern limit of the study area. A third concentration consisting of cod (>35cm) and redfish (>20cm) occurred in the Burgeo Bank area.

FPT analyses

FPT analysis was applied to 56 segments or paths of 35 seals that entered the study area, where the segment of the path observed before the breeding season was distinct from the segment that occurred after the breeding season. A peak in variance was detected in 52 of those paths resulting in a total of 158 ARS zones (Fig. 3). Excluding three very large ARS>80 km, forty-five of the ARS (16 adult females, 3 juvenile females, 7 adult males, 19 juvenile males), created by 20 individuals, were within the study area (26 before 1998, 19 after 1998; 3 females, 2 males tagged at Sable Island; 6 females, 9 males tagged within the Gulf) (Fig. 4a). Five individuals concentrated their searching effort at two different spatial scales and were then considered as different individuals at each of the two scales in our analysis. The radii of the ARS varied from 8 to 60 km for a mean scale of 19.5 ± 1.5 km. Only males exhibited ARSs within the study area before the breeding period whereas both males and females demonstrated searching effort within the study area after the breeding period. There was no difference in the time animals spent before and after breeding within the study area ($F_{1,10}=-1.00$; $P=0.34$). Nor were there any sex ($F_{1,24}=-1.27$; $P=0.22$), age class ($F_{1,24}=0.20$; $P=0.84$) or capture site ($F_{1,24}=0.14$; $P=0.89$) effects on the size of ARSs. Overall, seals stayed for 15.3 ± 2.6 days within a given ARS. Age class ($F_{1,46}=-0.84$; $P=0.41$) and capture site ($F_{1,46}=-0.04$; $P=0.96$) did not influence time spent within the ARS, but males ($19.1 \text{ d} \pm 3.8$) spent more time within their ARSs than females ($10.1 \text{ d} \pm 2.97$) ($F_{1,46}=-1.79$; $P=0.08$).

The ARSs within the study area were concentrated near St. Paul Island and in the southern part of the study area on the Scotian Shelf. The ARSs observed around St. Paul Island occurred at the beginning of the winter (mean date: 14th Dec. to 6th Jan.) whereas the other ARS in the southern part of the study area, were observed later in winter (23 Jan. to 15th Feb). Males and females concentrated their searching efforts in different parts of the study area. The ARSs of males from the Gulf (n=7) and one male from Sable Island were concentrated around St. Paul Island (11 ARSs). Males (Gulf=5; Sable=2) also exhibited foraging effort offshore, north of Cape Breton (14 ARSs). Males that foraged around St. Paul Island also hauled out there between trips at sea. Nine ARS associated with male seals tagged at Sable Island were within the southern part of the study area. These animals made return trips to Sable Island. Females (n=19) concentrated their searching effort in the southern portion of the study area, from which they also made return trips to Sable Island. Twelve of 33 animals tagged before 2000 had an ARS around St. Paul Island, while only 4 out of 27 animals captured after 2000 had an ARS in the St. Paul Island area.

Habitat selection analyses

ARS at the landscape scale

Habitat selection varied by sex and with the spatial scale at which analysis was conducted. When compared to the abundance of fish within the whole study area, our analyses indicated that the ARS of seals were not randomly distributed and that the pattern of habitat selection varied between sexes (Tables 4, 5). Based on the best models in the single-species analyses (Table 4a), ARS locations of males were positively related to the abundance of all size classes of herring as well as medium and

large cod, with small herring and medium-sized cod having the strongest effects. ARS location was also positively related to the abundance of small plaice and hake, but negatively related to the abundances of large individuals of these species. In the multispecies analyses (Tables 5a and 6a), the best model for males included weak positive selection for areas highly used by medium-sized cod [$\beta=0.003 \pm 0.001$, odd-ratio (95% CI) = 1.003 (1.00;1.005)] and small herring [$\beta=0.003 \pm 0.002$, odd-ratio (95% CI) = 1.003 (1.0;1.006)], and negative selection for areas used by large turbot [$\beta= -0.09 \pm 0.03$, odd-ratio (95% CI) = 0.91 (0.85;0.97)].

Different fish species were related to the spatial distribution of male ARSs located around St. Paul Island compared to males located elsewhere in the study area. Single-species analyses indicated that ARSs located around St. Paul Island were positively related to where small American plaice, >30cm herring, small hake, redfish 20-30 cm and >25 cm cod were abundant. However, they were negatively related to areas used by >30cm American plaice, >35cm white hake, turbot, small witch flounder and large redfish (Table 4a). Multispecies analyses indicated that males, within this area, tended to positively use the areas of high abundance of 25-35 cm [$\beta=0.168 \pm 0.091$ odd-ratio (95% CI) = 1.182 (0.989;1.141)] and >35cm cod [$\beta=0.0003 \pm 0.003$ odd-ratio (95% CI) = 1.001 (0.993.;1.007)] (Table 4a and 5b). In later winter, in the area away from St. Paul's Island, single species models indicated that the ARS distribution of males was influenced by the abundance of all fish species (Table 4a). Nevertheless, in the multi-species analyses, small witch flounder [$\beta=-0.022 \pm 0.02$ odd-ratio (95% CI) = 0.978 (0.958.;0.997)], large turbot [$\beta=-0.008 \pm 0.009$ odd-ratio (95% CI) = 0.992 (0.982;1.001)] and 25-35 cm cod [$\beta=-0.033 \pm 0.029$ odd-ratio (95% CI) = 0.967 (0.939.;0.996)] all had negative effects on the likelihood that males would perform ARS (Table 5a and 6c).

For females, the best models in the single species analyses indicated that their ARSs were positively related to the presence of large cod and medium-sized redfish and negatively related to both small and large witch flounder, turbot and redfish and medium-sized cod. Effects were strongest for large witch flounder and turbot (Table 4a). However, in the multi-species analyses, the best model included only a negative effect of large witch flounder [$\beta=-0.08 \pm 0.04$, odd-ratio (95% CI) = 0.92 (0.86; 0.99)] (Tables 5a and 6d).

ARS along the path

Paths of males and females were not uniformly distributed over the study area. Both males and females transited in a north-south direction over shallow areas off Cape Breton Island (Fig. 4b, c). Along their paths, they encountered high variability in fish abundance with high densities of cod and other fish in the area surrounding St. Paul Island and a low abundance of fish including cod along the southern part of their paths. The single species analyses indicated that overall (Table 4b), the ARSs of males were positively related to areas with high abundance of American plaice, witch flounder, herring and cod. Males also selected for areas used by medium sized redfish and small white hake but they avoided large white hake. In the multi-species analyses, several models provided equally suitable descriptions of the probability that males increased their searching activities in an area along the path (Table 6e). ARS by males was positively correlated with areas with <35cm white hake [$\beta=0.031 \pm 0.03$, odd-ratio (95% CI) = 1.031 (1.00;1.063)], but negatively selected areas with high abundance of >35cm

white hake [$\beta = -0.404 \pm 0.01$, odd-ratio (95% CI) = 0.667 (0.428;1.039)] (Table 5b). The probability of using areas along their path also increased slightly with an increase of redfish <20cm [$\beta = 0.005 \pm 0.008$, odd-ratio (95% CI) = 1.005 (0.989;1.021)].

According to the best model in the single species analyses for female seals, the probability of an ARS along the path increased with the density of small white hake, small and medium redfish as well as large cod and herring, and decreased with an increase in American plaice, turbot, witch flounder, small herring, cod <35 cm, and large white hake and redfish. The latter two species had the strongest effect on habitat selection patterns for females along their paths. For females, the best predictive model in multispecies analyses (Table 6f) showed positive selection along the path for areas where redfish <20 cm [$\beta = 0.06 \pm 0.016$, odd-ratio (95% CI) = 1.06 (1.05;1.08)] was abundant, but female ARS were negatively correlated to area where large white hake [$\beta = -0.459 \pm 0.08$, odd-ratio (95% CI) = 0.637 (0.585;0.639)] and large redfish [$\beta = -0.042 \pm 0.0119$, odd-ratio (95% CI) = 0.959 (0.947;0.97)] were highly concentrated (Table 5b).

Fish community differences between foraging and non-foraging zones

Densities of large herring, small size groups of plaice, hake and redfish and all sizes of cod were relatively high in the male foraging zones compared to the non-foraging zones (Fig. 5). The large size classes of witch flounder, turbot and redfish were considerably more abundant in the non-foraging zones than in the foraging zones. Estimated densities of the fish species examined here were generally low in the female foraging zones, though abundance of small plaice and redfish did tend to be higher in these zones than in the non-foraging zones.

The MDS ordination indicated that the fish communities within non-foraging zones were similar to each other, but were distinct from those of foraging zones (Fig. 6). The foraging zones were more widely dispersed in the ordination, indicating a more variable fish community. Based on the permutation test, highly significant ($P = 0.001$) differences in fish community composition occurred among the three types of zones (male foraging, female foraging, non-foraging). Differences were also significant in all pairwise comparisons between zone types, though the differences between the two types of foraging zones (male or female) and non-foraging zones were much more significant ($P = 0.001$) than the difference between male and female foraging zones ($P = 0.048$).

The main fishes (in order of importance) contributing to the average similarity between sites within groups were medium and large sized redfish and large turbot and witch flounder for the non-foraging zones (the NF group), small plaice and redfish and large cod for the female foraging zones (the FF group), and large cod and herring, small plaice and medium sized cod for the male foraging zones (the MF group) (Table 7). The main fishes contributing to the average dissimilarity between the NF and FF groups were medium and large redfish and large turbot, with all three fish groups at higher density in the NF zones (Table 8). The NF and MF groups were distinguished by relatively high densities of medium and large cod in the MF zones and relatively high densities of medium and large redfish in the NF zones. Male foraging zones were distinguished from female foraging zones by higher densities of medium and large cod and both size classes of herring (Table 8).

DISCUSSION

In this study, we used movement information obtained from free-ranging grey seals equipped with satellite transmitters (1993-2005) and winter bottom-trawl survey data collected between 1994-1997 to examine the possibility that there was strong overlap between grey seals and overwintering cod and other fish species in the Cabot Strait/northeast Cape Breton area. Unfortunately, there is a temporal separation between the seal data and the fish data. The winter survey ended in 1997, due to budgetary concerns, and too few transmitters were deployed in the early years of the study to limit our analyses to only the 1994-1997 period. Our results indicate that there is a strong potential for overlap between grey seals and overwintering cod, and if we assume that there has been no change in the winter distribution of cod, then our results indicate that there is a strong potential for grey seal predation on overwintering large cod in the Cabot Strait area. Recent diet sampling indicates that some grey seals are in fact feeding heavily on large cod in this area (Stenson et al. 2011).

Grey seals are capable of diving to depths of over 400 m, but do so infrequently; they are strongly associated with shallow waters (Harvey et al. 2008). They are also central place foragers (McConnell et al. 1999, Austin et al. 2004), but in Canada, the distribution of haulout sites is often limited to areas where human disturbance is minimal or benign (Hammill personal observation). The necessity to alternate hauling-out with foraging trips at sea may limit the searching range of seals. Within the study area grey seal foraging zones were concentrated in shelf and slope areas on the south side of the Channel, particularly, around St. Paul Island and on the Scotian Shelf in the southern part of NAFO fishing zone 4Vn (Fig. 1). The presence of high prey densities in proximity to the isolated St. Paul Island allows grey seals to increase their foraging effort in spite of fish occurring at greater depths because of the proximity to a haul-out site.

The foraging zones around St. Paul Island were primarily associated with male seals of Gulf origin that foraged in the early winter prior to the January-February breeding season in the Gulf. Females foraged further to the south. Spatial segregation of males and females either horizontally or vertically is frequently observed in terrestrial and marine mammals (LeBoeuf et al. 2000, Ruckstuhl and Neuhaus 2000, Bajzak et al. 2009), and has been reported among grey seals (Breed et al. 2006). There also appears to be some separation at least among males between the 'Gulf' and 'Sable' herds. In previous work, males captured on Sable Island foraged in winter along the shelf edge, but in contrast to animals from the Gulf herd, Sable Island males foraged to the west of Sable Island, while females were concentrated on mid-shelf banks located north of Sable Island and in the Sydney Bight area (Breed et al. 2006).

The fish communities differed greatly between winter foraging and non-foraging zones in the Cabot Strait. The composition of the fish community among non-foraging zones was very similar. Few grey seals foraged on the banks in the northern part of the study area or in the deep waters of the Laurentian Channel, the areas where redfish (particularly those >20 cm in length), witch flounder and turbot were distributed. Composition of the fish community was more variable among foraging zones. Although as a species the grey seal is considered a generalist predator, individual grey seals are often specialists (Tucker et al. 2008) and this may have contributed to the variability observed in fish communities within different foraging zones. Male foraging zones were distinguished from non-foraging zones by the absence of deepwater fish groups, and by high densities of cod and herring. Female foraging zones were also distinguished from non-foraging

zones by the absence of deepwater fish groups, and a tendency to be associated with higher densities of large cod and small plaice.

The habitat selection analyses were generally consistent with the differences in fish communities between foraging and non-foraging zones, though strong positive selection was generally not detected. At the scale of the study area, males showed positive selection for areas where medium-sized (25-35 cm) cod and small herring were common and avoided areas where large turbot were common. However, there was a striking difference in the distribution of male foraging zones between early and late winter. Early in the winter, males (mostly of Gulf origin) foraged in the vicinity of St. Paul Island, showing positive selection for areas where large and medium-sized cod were aggregated. Later in the winter, male foraging zones were concentrated on the shelf further to the southeast, where they were not positively associated with any fish group. At this scale of the study area, females also did not show positive selection for any fish group but avoided large turbot and witch flounder. The lack of strong positive selection may partly reflect individual variation in targeted prey, seals are targeting some prey not well sampled by the groundfish survey or our assumption that there has been no change in fish distribution between the surveys (1993-1997) and the telemetry deployments is incorrect. In addition, it may be partly due to grey seals targeting some but not all aggregations of a particular prey group. For example, combining early and later winter periods, male grey seals showed significant selection for medium-sized cod, but not for large (>35 cm) cod. This was reflected in the concentration of male foraging zones in the vicinity of St. Paul Island, where extremely high densities of medium-sized cod also occurred. A dense aggregation of large cod was consistently observed in this area, but selection for areas with large cod may have been overwhelmed by the strength of the signal from the abundance of medium sized cod. Aggregations of large cod also occurred elsewhere in the study area (off Burgeo Bank and along the slope of the Laurentian Channel in the southern part of the study area), but the aggregations further to the southeast along the southern slope of the Laurentian Channel were less predictable, their location and size varying from year to year (Appendix C1). Thus, the concentration of foraging zones around St. Paul Island may reflect targeted predation on medium-sized cod or predation targeting the only predictable locations where large cod aggregate consistently in the southern Gulf.

Grey seals are primarily piscivorous, with invertebrates accounting for only a very small fraction of their diet (Bowen et al. 1993, Hammill et al. 2007). Almost 30 species of fish and invertebrates have been identified in the diet of Gulf grey seals, but usually less than 8 species account for about 80% of the diet with spatial and temporal variability and sex effects being demonstrated in the prey consumed (Bowen et al. 2006, Hammill et al. 2007). Herring <30cm, hake and cod 25-35cm are among the species most commonly observed in stomach samples from grey seals in the Gulf of St. Lawrence in summer (Benoît and Bowen 1990, Murie and Lavigne 1992, Hammill and Stenson 2000, Hammill et al. 2007), while sandlance, redfishes, flatfishes, cod and witch flounder are thought to be important prey on the Scotian Shelf (Bowen and Harrison 1994, Bowen et al. 2006, Beck et al. 2007). Redfish have been identified as important prey in the fall-winter diet of female grey seals (Beck et al. 2007), which is in agreement with selection by females for this species at the path level.

A failure to detect strong positive associations between female foraging zones and any fish group may reflect predation by females on prey not included in this analysis. For example in other areas capelin can be an important prey species (Hammill et al. 2007),

and diet data from animals captured on Sable Island indicate that the post-breeding diets of female grey seal are dominated by sandlance, redfish and other small pelagic fish (Beck et al. 2007). We observed positive selection by females for small redfish, but did not examine capelin or sandlance in our analyses. The fish species selected for in this analysis comprised the majority of the total catch in the January surveys (59% by number and 77% by weight). Much of the remainder (22% by number and 13% by weight) was comprised of three species: black dogfish (*Centroscyllium fabricii*), common grenadier (*Nezumia bairdi*), and longfin hake (*Phycis chesteri*). These three species are confined to the deep waters of the Laurentian Channel, an area rarely used by foraging grey seals in our study. Capelin (*Mallotus villosus*) also made an important contribution to the total catch in the surveys (11% by number, 0.4% by weight) and large catches of capelin did occur on the Scotian Shelf in the southern part of the study area where female foraging zones were frequently situated (Appendix C2). However, these large catches were restricted to 1995, and catches of capelin in the other three survey years were small (Appendix C2). Sandlance (*Ammodytes* spp) were very rare in the January survey catches (0.04% by number and 0.001% by weight). The trawls used in the January survey will catch sandlance when they are abundant, so this suggests that sandlance are not an abundant in our study area. This is confirmed by the annual July survey of the Scotian Shelf, which catches large numbers of sandlance on the banks south of our study area, but virtually none within our study area (Appendix D).

Our fish distributions are based on surveys conducted early in winter. Major features of fish distribution identified by these surveys, such as the depths occupied by the different species and size classes, likely apply throughout the winter season. However, there may be some movement within depth zones over the winter. For example, when ice coverage extends into the Cabot Strait later in winter, southern Gulf cod may extend their distribution further south along the slope of the Channel. This may partly explain the difference in the distribution of male foraging zones between early and late winter, and the stronger association between foraging zones and prey distributions early in winter when the surveys were conducted than later in winter when fish distribution may have shifted somewhat from that observed during the surveys.

The reasons for the late fall exodus of cod and other demersal fish from the Gulf into the Cabot Strait are unclear. Cod may be selecting for warmer temperatures to promote gonad maturation (Castonguay et al. 1999), but these warm temperatures are also available in the deep channels inside the Gulf. The fall migration of northern Gulf cod shifted to earlier dates and into deeper waters in the early 1990s (Castonguay et al. 1999). For the southern Gulf stock, there are indications that overwintering cod also now occur at greater depths than in the past (Jean 1964, Swain et al. 1998), and the timing of the fall migration has shifted progressively to earlier dates from the late 1970s to the late 1990s (Comeau et al. 2002). The reasons for these changes are uncertain, but they might be occurring to avoid predation by harp and grey seals. A shift into deeper waters in recent decades may likewise be a response to an increasing predation threat from increasing numbers of marine mammals, the 'seascape of fear' hypothesis (Wirsing et al. 2008), but further work is needed to examine this hypothesis.

Our analysis compared winter movements of seals during 1993-2005 with the distribution of fish surveyed in 1994-1997. Fish distributions were generally consistent from year to year, suggesting that it may be reasonable to extrapolate distributions from the mid 1990s to more recent years, but we cannot rule out the possibility that there have been changes in fish distributions since they were surveyed in the mid 1990s.

However, the limited commercial fishing in recent winters indicates that the aggregation of large cod observed near St. Paul Island in January 1994-1997 have likely persisted in recent years (e.g., see Fig. 3 in Swain et al. 2009).

The distributions of fish and grey seal foraging areas in our study are generally consistent with information on the mortality patterns in these fish. Foraging by grey seals was mostly restricted to the south side of the Laurentian Channel where southern Gulf cod overwinter, and was rare on the north side of the Channel where northern Gulf cod overwinter. Natural mortality is currently elevated in southern Gulf cod but is near normal levels in northern Gulf cod (Fréchet et al. 2009). Unlike most large-bodied demersal fish in the southern Gulf, turbot and witch flounder have not declined to low levels of abundance (Benoît and Swain 2008), suggesting that natural mortality levels are not unusually high for these species, which are distributed in deeper areas where foraging by grey seals is rare.

Natural mortality of adult southern Gulf cod has risen to very high levels in recent years (Chouinard et al. 2005, Swain and Chouinard 2008). The instantaneous rate of natural mortality is currently estimated to be about 0.6 for this stock; approximately three times the level considered normal for cod (Swain et al. 2009). One hypothesis proposed to explain this high natural mortality is that it results from increased grey seal predation (Chouinard et al. 2005). This hypothesis is not consistent with the size distribution of cod otoliths collected from grey seal stomachs, which indicate that grey seals consume mostly medium-sized cod (Hammill et al. 2007). However, these samples have been collected primarily during summer and early fall from nearshore areas where large cod are rare. Large cod are highly aggregated on the overwintering grounds along the southern slope of the Laurentian Channel in Cabot Strait, where they may still represent an attractive prey source, despite low overall abundance. Foraging by grey seals, particularly males of Gulf origin, is concentrated in the vicinity of the cod aggregation near St. Paul Island. This is consistent with the hypothesis that grey seals are preying on large adult cod overwintering in this area. Currently, it is not possible with our data to distinguish between potential predation on large cod versus smaller cod, because both size classes are aggregated in the same area. However, our results do suggest that if a management decision was taken to limit seal numbers, then removing seals from specific areas, in contrast to more a generalized removal may be more effective in favouring cod recovery.

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Table 1. Fish species and size classes used in this study. N is the total catch of each fish group in the January 1994-1997 surveys following adjustments for differences in fishing efficiency between years (see text for details).

Fish	Length	Adjusted catch				
	class (cm)	1994	1995	1996	1997	Total
American plaice	<30	3 236	6 037	3 707	2 746	15 725
<i>(Hippoglossoides</i>						
<i>platessoides)</i>	>30	2 023	2 860	1 889	1 175	7 945
White hake	<35	1 437	2 213	1 401	1 244	6 292
<i>(Urophycis tenuis)</i>	>35	587	842	675	446	2 548
Turbot (<i>Reihhardtius</i>	<35	93	270	267	94	723
<i>hippoglossides)</i>	>35	693	1 613	2 385	1 076	5 765
Witch flounder	<30	1 195	3 196	2 920	1 392	8 701
<i>(Glyptocephalus</i>						
<i>cynoglossus)</i>	>30	1 001	2 221	2 245	1 171	6 637
Herring	<30	881	1 571	1 911	7 986	12 347
<i>(Clupea harengus)</i>	>30	2 339	7 047	2 939	4 792	17 116
	<20	1 978	3 261	4 444	4 380	14 062
Redfish	20-30	730	3 306	10 325	2 551	16 910
<i>(Sebastes sp.)</i>	>30	1 200	4 167	11 595	3 426	20 387
	<25	807	1 271	2 150	599	4 826
Cod	25-35	3 303	4 758	4 599	6 314	18 973
<i>(Gadus morhua)</i>	>35	12 226	8 121	7 120	8 985	36 451

Table 2. Number of satellite transmitters deployed by herd, year and month.

Year	Month							Total
	1	5	6	7	8	9	10	
<i>a) Gulf</i>								
1993	5					5		10
1994					3	2		5
1995					1			1
1996						4		4
1997					4	2		6
1999				3			4	7
2003			9					9
2004			17					17
<i>b) Sable Island</i>								
1995							4	4
1996		3	2				4	9
1997		2	3				5	10
1998			5					5
1999						1	2	3
2000						11		11
2001						12		12
2003	15							15
2004	4	10	28					42
2007	1							1

Table 3. Eigenvectors derived from principal component analysis (PCA) of fish abundance measured at 477 stations survey within the Cabot Strait in January 1994-1998. High correlation loadings are in boldface.

Variables	Eigenvector				
	1	2	3	4	5
	31.11*	14.80	9.95	8.48	7.79
Redfish>30cm	0.86	-0.01	-0.19	0.00	0.17
Witch flounder>30cm	0.84	0.30	-0.18	0.01	-0.08
White hake>35 cm	0.82	0.04	0.20	-0.03	-0.16
Redfish 20-30 cm	0.78	-0.13	0.01	-0.06	0.46
Turbot>35 cm	0.75	0.41	-0.15	0.04	-0.08
Witch flounder<30cm	0.74	0.42	-0.10	0.01	0.00
American plaice<30cm	-0.09	0.79	0.34	-0.10	-0.07
American plaice>30cm	0.35	0.77	0.17	-0.12	-0.10
Turbot<35cm	0.25	0.53	-0.08	0.02	0.19
Herring>30cm	-0.29	0.14	0.73	-0.04	0.21
Herring<30cm	-0.46	0.07	0.66	0.05	0.09
White hake<35cm	0.43	0.14	0.65	-0.03	-0.05
Cod 25-35cm	-0.02	-0.09	-0.04	0.94	-0.01
Cod<25cm	0.16	-0.27	0.24	0.66	-0.33
Cod>35cm	-0.17	0.24	-0.32	0.59	0.33
Redfish<20cm	0.04	0.00	0.17	-0.03	0.81

*Percentages of variability in fish distribution explained by each PCA axis

Table 4. Effect of fish groups on the probability of occurrence of ARS by male and female grey seals a) within the study area and b) along the path. Separate analyses were conducted for each fish species. '+' indicates that the relative probability of use increases with an increase of fish abundance whereas '-' indicates the opposite effect. '=' indicated that the estimate and its related confidence interval included 0 while the sign given in () indicated the tendency of the estimate to increase (+) or decrease (-) with an increase of the abundance of the variable. Variables for which no signs are given were not included in best predictive models for each species. Number of individuals tested in each scale of analyses are given in brackets ().

Species	Length class (cm)	a) within the study area			b) along the path		
		All males (11)	males early winter (9)	males late winter (7)	All females (9)	All males (10)	All females (9)
American plaice	<30	+	+	=(+)		=(+)	=(+)
	>30	-	-	=(+)		=(+)	=(+)
Herring	<30	+	=(+)	=(+)		=(+)	=(+)
	>30	=(+)	+	=(+)		=(+)	=(+)
White hake	<35	+	+	=(+)		+	=(+)
	>35	=(+)	-	=(+)		-	-
Witch flounder	<30	=(+)	-	-	=(+)	=(+)	=(+)
	>30	-		=(+)	-	=(+)	=(+)
Turbot	<35	=(+)	=(+)	=(+)	=(+)	=(+)	=(+)
	>35	-	-	-	-	=(+)	=(+)
Redfish	<20	=(+)		=	=(+)	+	=(+)
	20-30	=(+)	+	=	=(+)	=(+)	+
Cod	>30	-	-	=(+)	=(+)		=(+)
	<25			=(+)		=(+)	=(+)
	25-35	+	+	-	=(+)	=(+)	=(+)
	>35	=(+)	+	=(+)	=(+)	=(+)	=(+)

Table 5. The effects of multi- species and length classes on the probability of increasing time spent in the ARS by male and female greys seals a) within a landscape scale and b) along the path by Northwest Atlantic grey seals in Cabot Strait in winter period (1995-2008). '+' indicates increased probability of use with increased fish abundance whereas '-' indicates decreased probability of use. '=' indicates that the estimate and its related confidence interval included 0. Only variables included in the selected models are presented.

Species	Length class (cm)	a) within the study area			b) along the path		
		All Males	Males early winter	Males late winter	All females	All males	All females
American plaice	<30						
	>30						
Herring	<30	=(+)					
	>30						
White hake	<35					+	
	>35					-	-
Witch flounder	<30			-			
	>30					-	
Turbot	<35						
	>35	-		-			
Redfish	<20					=(+)	+
	20-30						
	>30						-
Cod	<25						
	25-35	=(+)	=(+)	-			
	>35		=(+)				

Table 6. Logistic regression results: effect on fish species on the probability that seals increasing time spending within study area and along the path for models considering males and models included only females ARS. All possible models were tested, the 5 best are shown here. Best models are shown in bold and equivalent models ($\Delta QICu \leq 2$) in italics. I=Intercept of the model.

Parameters	NP	QICu	$\Delta QICu$	W
<u>a) ARS within study area – All males</u>				
<i>I + herring<30 + cod 25-35+ turbot>35</i>	4	190.09	0	0.17
<i>I + cod 25-35+ turbot>35 + redfish>30</i>	3	193.19	3.1	0.04
<i>I + American plaice<30 + cod 25-35+ turbot>35</i>	3	193.35	3.26	0.03
<i>I + herring<30 + cod 25-35+ redfish>30</i>	3	193.43	3.33	0.03
<i>I + herring<30 + cod 25-35+ flounder>30</i>	3	193.48	3.38	0.03
<u>b) ARS within the study area - males around St. Paul Island</u>				
<i>I + cod 25-35 + cod>35</i>	3	17.78	0	0.92
<u>c) ARS within the study area - males in other part of the study area</u>				
<i>I + flounder<30 + cod 25-35</i>	3	109.23	0	0.25
<i>I + turbot>35 + cod 25-35</i>	3	110.92	1.69	0.11
<i>I + founder<30 + turbot>35 + cod 25-35</i>	4	110.95	1.72	0.11
<i>I + flounder<30</i>	2	111.12	1.89	0.09
<i>I + turbot>35</i>	2	111.93	2.70	0.06
<u>d) Ars within study area - females</u>				
<i>I + flounder>30</i>	2	145.58	0	1
<u>e) ARS along the path – males</u>				
<i>I + white hake<35 + white hake>35</i>	3	60.82	0	0.67
<i>I + white hake<35 + white hake>35 + redfish<20</i>	4	62.79	1.97	0.248
<i>I + white hake>35</i>	2	65.54	4.73	0.063
<i>I + white hake>35 + redfish<20</i>	3	67.54	6.72	0.023
<i>I + redfish<20</i>	2	134.3	73.48	0
<u>f) ARS along the path - females</u>				
<i>I + white hake>35 + redfish<20 + redfish>30</i>	4	37.27	0	0.86
<i>I + white hake>35 + redfish>30</i>	3	42.54	5.27	0.06
<i>I + white hake>35</i>	2	44.05	6.78	0.03
<i>I + white hake>35 + redfish<20</i>	3	45.89	8.62	0.01
<i>I + redfish <20</i>	2	99.6	62.33	0

Table 7. Main fish groups contributing to the similarity between zones within a zone type (male foraging zones, female foraging zones, randomly placed non-foraging zones). \bar{C} is the average catch rate in a zone type, \bar{S} is the average Bray-Curtis similarity between pairs of zones within a zone type, \bar{S}_i is the contribution of fish group i to similarity within a zone type averaged over all pairs of zones in the type, %S is the percent contribution to \bar{S} and SD $_i$ is the standard deviation of S_i . A high value for \bar{S}_i/SD_i indicates that fish group is typical for a given zone type (i.e., is found at consistently high abundance throughout the zone type).

Fish group	\bar{C}	\bar{S}_i	\bar{S}_i/SD_i	%S	Cum %S
Non-foraging zones, $\bar{S}=59.77$					
redfish 20-30 cm	126.49	23.07	1.96	38.59	38.59
redfish >30 cm	93.92	17.04	2.01	28.50	67.10
turbot ≥ 35 cm	44.11	7.61	1.28	12.72	79.82
witch flounder ≥ 30 cm	27.23	5.43	1.75	9.08	88.90
Male foraging zones, $\bar{S}=26.10$					
cod >35 cm	163.94	4.15	0.63	15.89	15.89
Herring ≥ 30 cm	98.34	3.40	0.64	13.04	28.92
plaice <30 cm	39.74	3.26	0.82	12.51	41.43
cod 25-35 cm	130.50	3.08	0.59	11.79	53.22
redfish <20 cm	26.98	2.09	0.81	8.02	61.24
Herring <30 cm	60.34	1.84	0.52	7.04	68.28
Female foraging zones, $\bar{S}=26.25$					
plaice <30 cm	30.47	7.27	0.92	27.69	27.69
redfish <20cm	21.93	3.73	1.00	14.22	41.91
cod >35 cm	58.91	2.47	0.69	9.43	51.33
plaice ≥ 30 cm	13.25	2.04	0.69	7.79	59.12
cod 25-35 cm	15.64	1.58	0.99	6.02	65.14
cod <25 cm	4.98	1.34	0.48	5.11	70.25

Table 8. Main fish groups contributing to the dissimilarity between zones in different zone types (male foraging zones, female foraging zones, randomly placed non-foraging zones). \bar{C}_1 is the average catch rate in zone type 1, $\bar{\delta}$ is the average Bray-Curtis dissimilarity between pairs of zones in different zone types, $\bar{\delta}_i$ is the contribution of fish group i to dissimilarity between zone types, % δ is the percent contribution to $\bar{\delta}$ and SD_i is the standard deviation of $\bar{\delta}_i$. A high value for $\bar{\delta}_i/SD_i$ indicates that fish group is a good discriminating variable between groups and between zone types.

Fish group	\bar{C}_1	\bar{C}_2	$\bar{\delta}_i$	$\bar{\delta}_i/SD_i$	% δ	Cum % δ
Non-foraging zones (type 1) versus Male foraging zones (type 2), $\bar{\delta}=78.21$						
redfish 20-20 cm	126.49	60.34	14.82	1.07	18.95	18.95
cod >35 cm	25.09	163.94	10.60	0.95	13.55	32.50
redfish >30 cm	93.92	22.32	10.57	1.15	13.51	46.01
cod 25-35 cm	12.60	130.50	7.86	0.88	10.05	56.07
Herring ≥ 30 cm	1.18	98.34	6.86	0.93	8.77	64.84
turbot ≥ 35 cm	44.11	4.82	5.70	0.94	7.29	72.13
Herring <30 cm	0.16	78.14	5.41	0.58	6.92	79.05
Non-foraging zones (type 1) versus Female foraging zones (type 2), $\bar{\delta}=81.56$						
redfish 20-20 cm	126.49	56.55	22.97	1.75	28.16	28.16
redfish > 30 cm	93.92	23.16	16.09	1.63	19.73	47.89
turbot ≥ 35 cm	44.11	2.26	8.46	1.18	10.37	58.27
cod >35 cm	25.09	58.91	6.89	0.53	8.44	66.71
plaice <30 cm	10.99	30.47	4.79	0.87	5.87	72.58
witch flounder ≥ 30 cm	27.23	4.61	4.74	1.46	5.81	78.39
Female foraging zones (type 1) versus Male foraging zones (type 2), $\bar{\delta}=76.64$						
cod >35 cm	58.91	163.94	13.73	0.96	17.91	17.91
redfish 20-30 cm	56.55	60.34	9.91	0.62	12.93	30.84
Herring ≥ 30 cm	20.48	98.34	9.24	0.99	12.06	42.90
cod 25-35 cm	15.64	130.50	9.10	0.94	11.87	54.77
Herring <30 cm	24.11	78.14	7.72	0.67	10.07	64.84
plaice <30 cm	30.47	39.74	5.66	0.95	7.39	72.23
redfish >30 cm	23.16	22.32	4.72	0.69	6.16	78.39

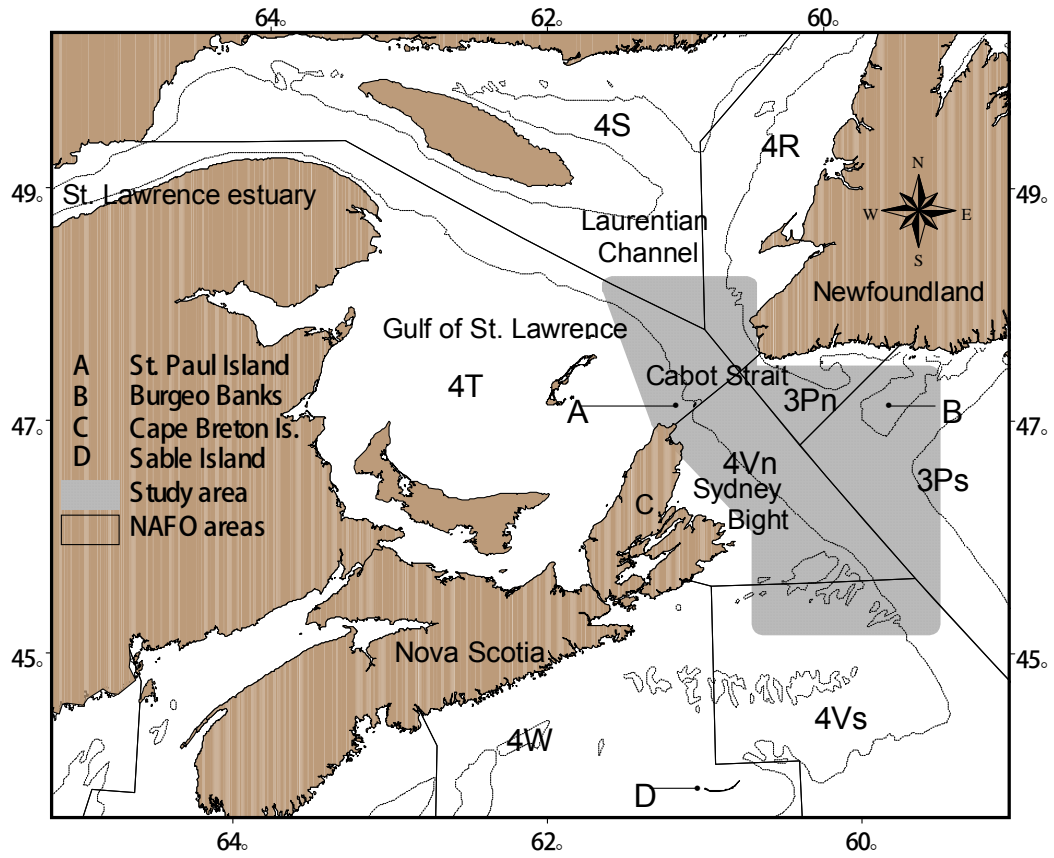


Figure 1. Fig. 1. Study area (grey shading) and the surrounding region. Solid lines denote Northwest Atlantic Fishery Organization (NAFO) divisions (e.g., 4T) and subdivisions (e.g., 4Vn).

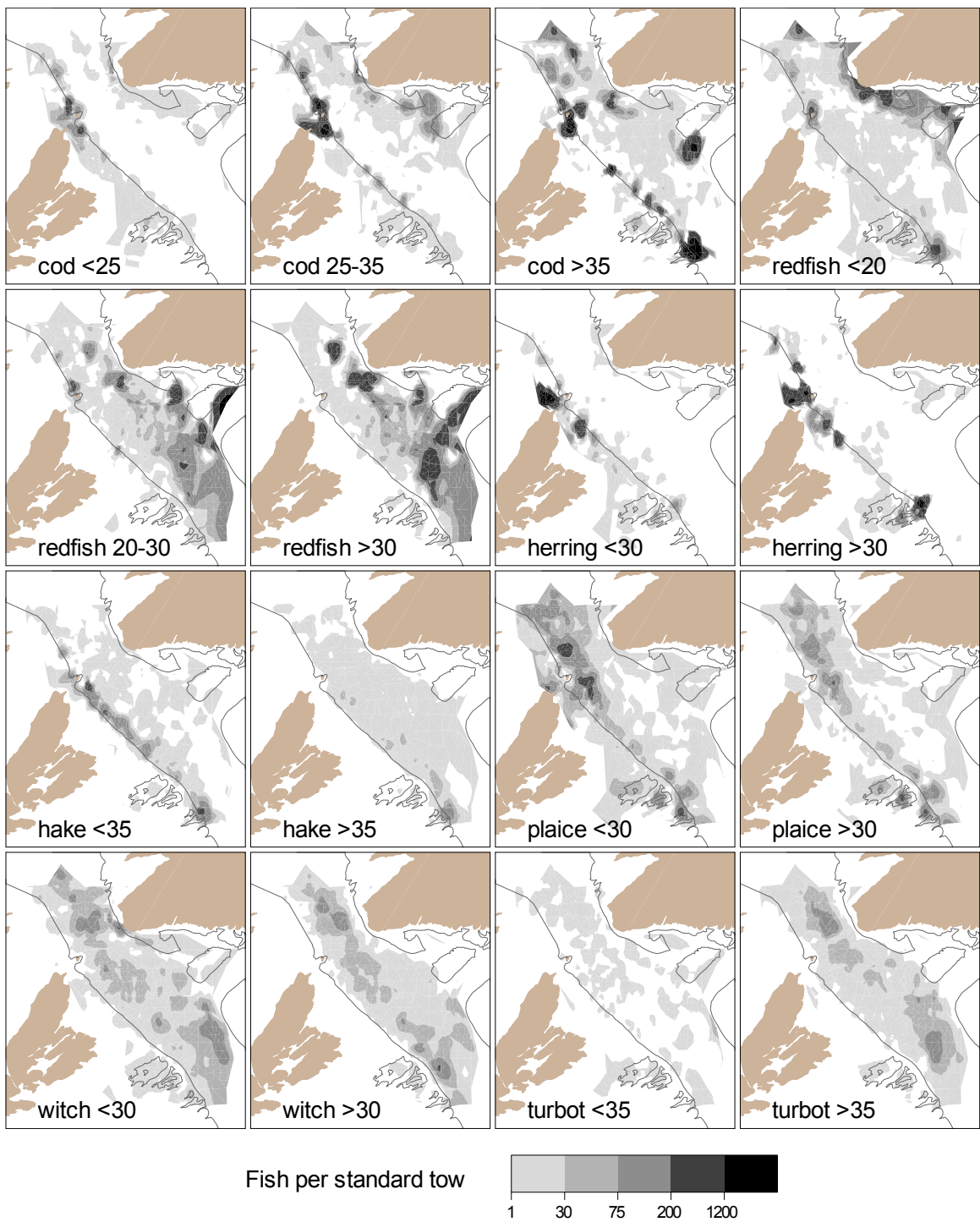


Figure 2. Fish distribution in the Cabot Strait area in January 1994-1997 derived from bottom-trawl surveys. Shaded contours were drawn using Delaunay triangles.

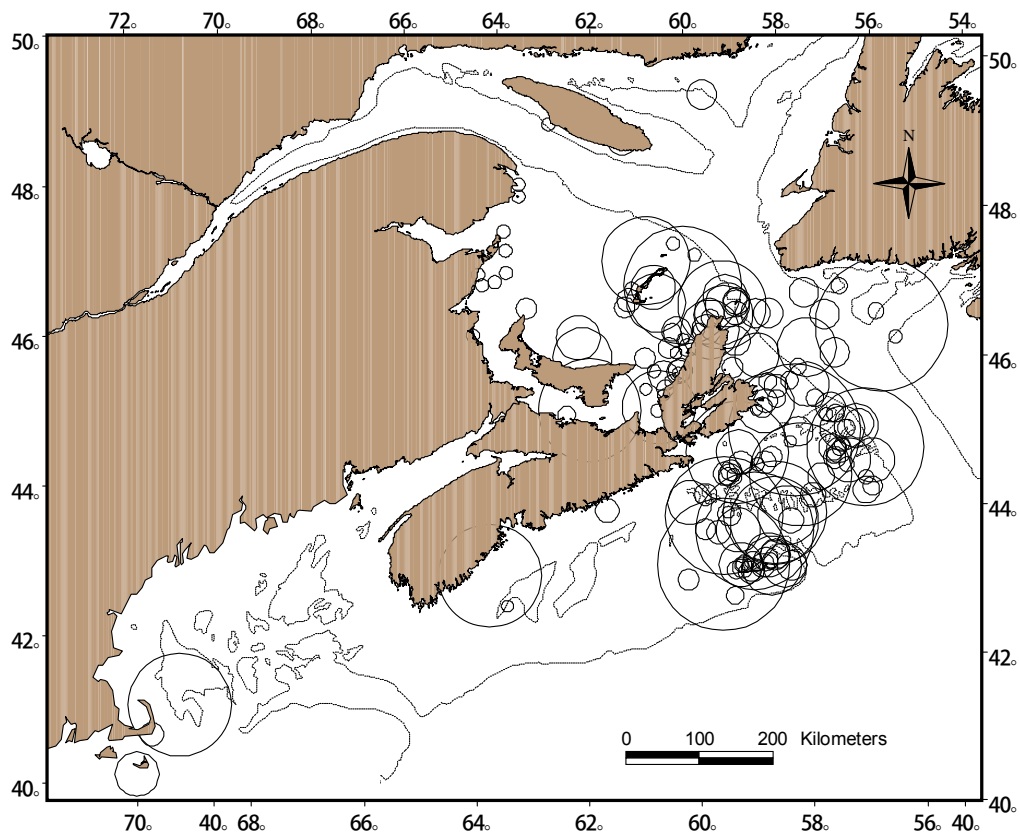


Figure. 3. Areas of restricted search of satellite equipped Northwest Atlantic grey seals during the winter period.

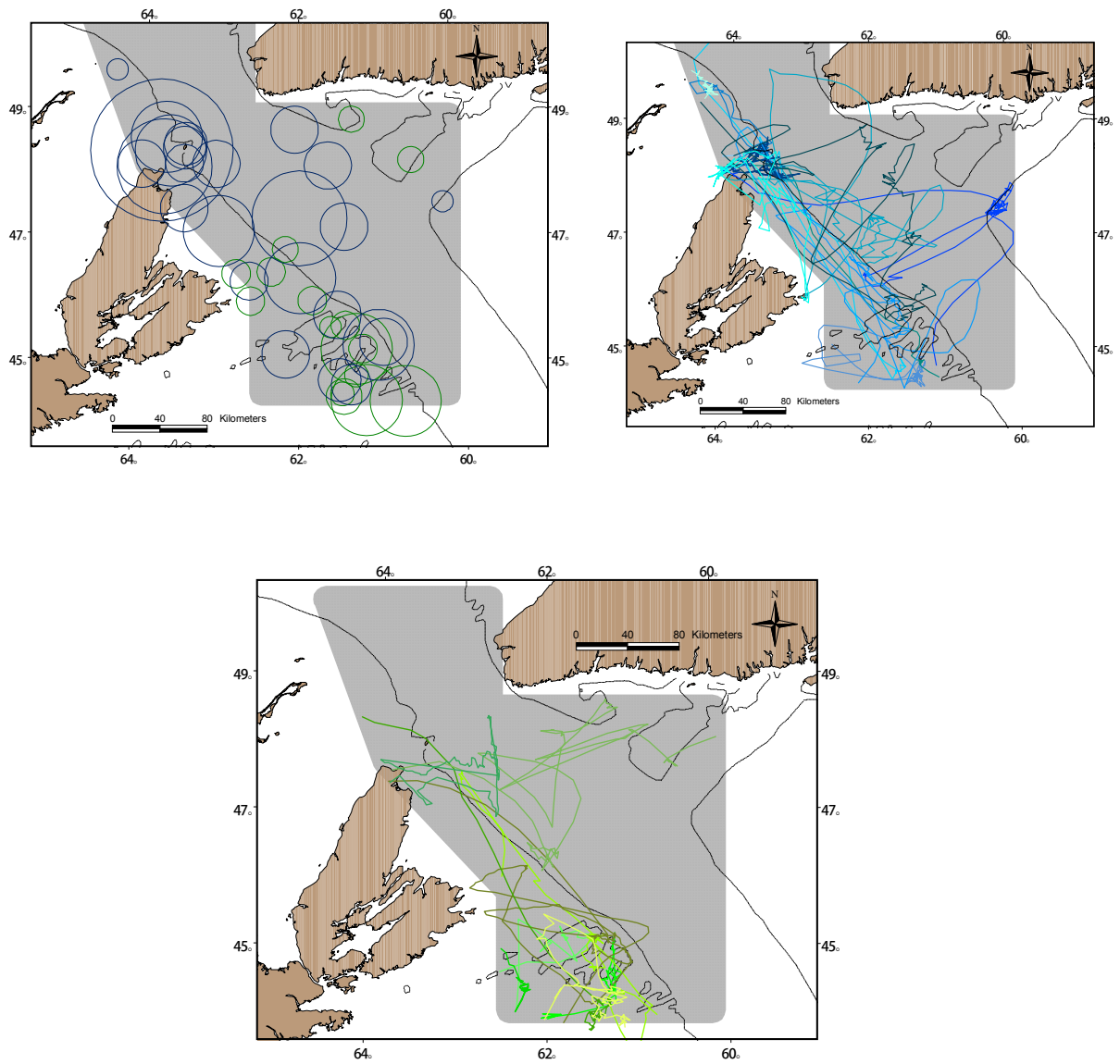


Figure 4. Areas of restricted search of satellite equipped grey seals (males=26; females=19) (top left) and path of b) males (top right) and c) females (bottom) in the Cabot Strait during the winter period according to their relative position within the study area

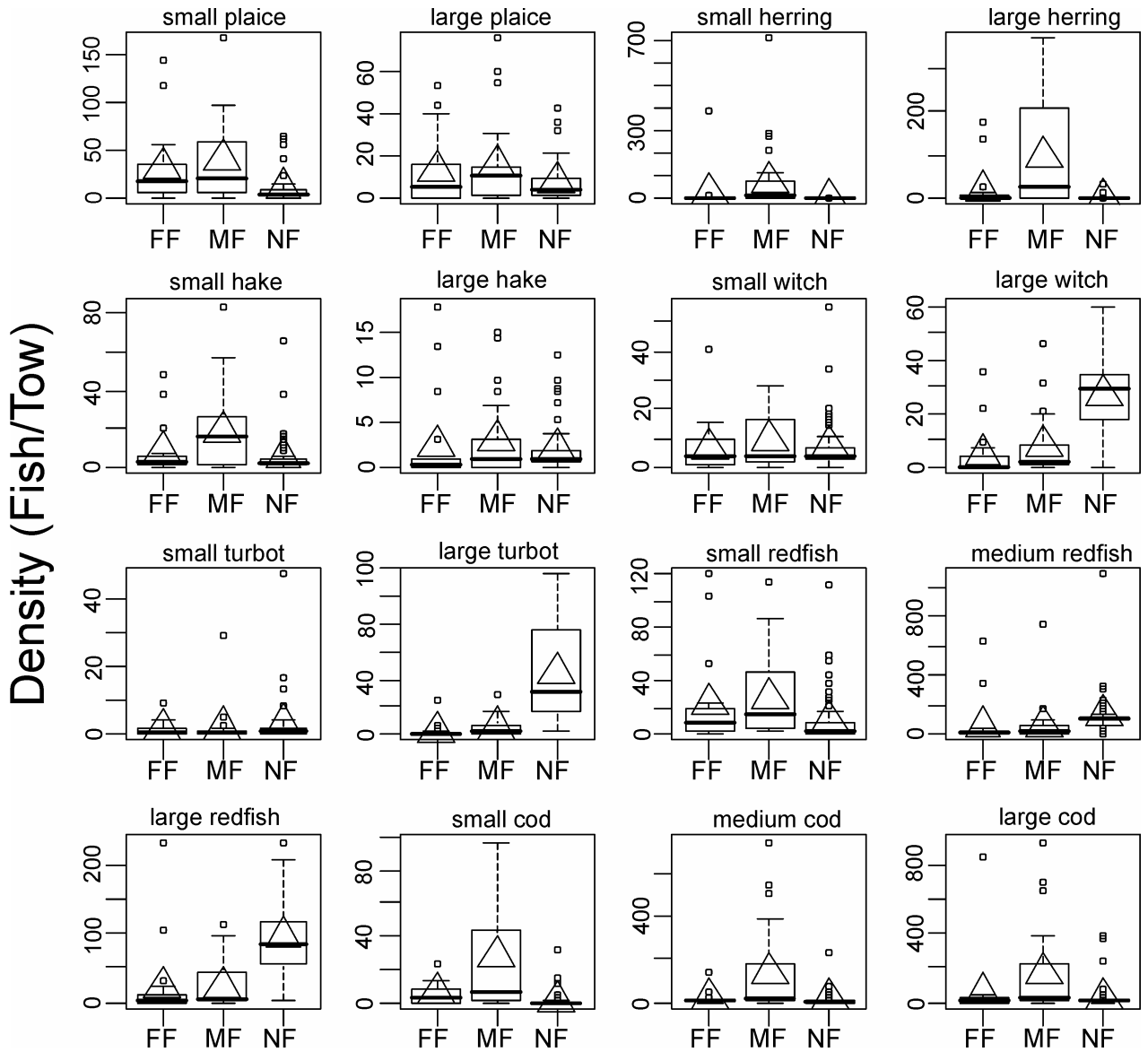


Figure 5. Mean density class distributions by species and size class in female foraging zones (FF), male foraging zones (MF), and randomly-place non-foraging zones (NF). Heavy lines show the median and triangles the mean. Boxes show the interquartile range, whiskers extend to the most extreme data point not more than 1.5 times this range from the box, and circles show more extreme data points.

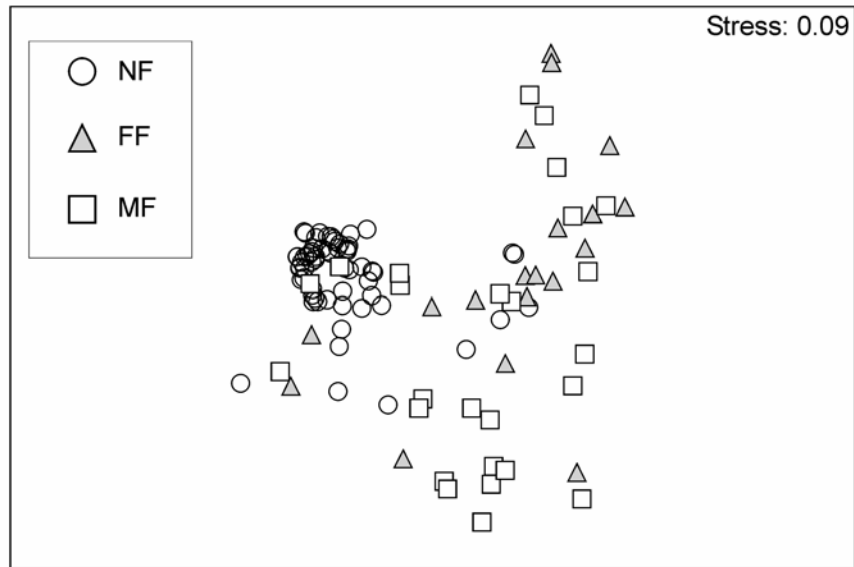


Figure 6. MDS ordination of male foraging zones (MF), female foraging zones (FF) and randomly-placed non-foraging zones (NF), based on the species and size composition of their fish communities. Stress is a measure of the distortion in rank similarity resulting from the two-dimensional ordination (values <0.1 are considered to indicate a good representation of the similarities between samples).

Appendix A. Pearson correlation coefficients among fish groups within the Cabot Strait during winter. Catch rates were log transformed.

Fish	length class (cm)	American plaice		White hake		Turbot		Witch flounder		Herring		Redfish			Cod		
		<30	>30	<35	>35	<35	>35	<30	>30	<30	>30	<20	>20	20-30	<25	25-35	<35
Mean		1.60	0.08	-1.20	-1.34	-2.73	-0.61	0.51	-0.75	-2.55	-2.66	0.96	0.38	0.07	-2.09	-0.32	0.54
Standard error		2.92	3.31	3.37	3.27	2.66	3.56	3.41	3.70	3.20	3.25	3.07	3.46	3.78	3.33	3.47	3.28
N		477	477	478	478	477	477	477	477	477	477	477	477	477	477	477	477
American plaice (<i>Hippoglossoides platessoides</i>)	<30	1.00	0.61	0.21	0.01	0.20	0.14	0.16	0.06	0.20	0.26	0.14	-0.09	-0.10	0.12	0.08	0.10
	>30	0.61	1.00	0.33	0.37	0.29	0.46	0.48	0.45	-0.08	0.04	0.08	0.22	0.31	-0.25	-0.01	0.34
Herring (<i>Clupea harengus</i>)	<35	0.21	0.33	1.00	0.57	0.12	0.28	0.31	0.30	0.06	0.18	0.09	0.29	0.22	-0.18	0.00	0.31
	>35	0.01	0.37	0.57	1.00	0.16	0.57	0.55	0.65	-0.31	-0.20	0.00	0.52	0.58	-0.54	-0.32	0.35
White hake (<i>Urophycis tenuis</i>)	<35	0.20	0.29	0.12	0.16	1.00	0.41	0.40	0.32	-0.07	-0.01	0.07	0.24	0.26	-0.14	0.02	0.18
	>35	0.14	0.46	0.28	0.57	0.41	1.00	0.72	0.76	-0.33	-0.17	-0.05	0.49	0.66	-0.46	-0.17	0.35
Witch flounder (<i>Glyptocephalus cynoglossus</i>)	<30	0.16	0.48	0.31	0.55	0.40	0.72	1.00	0.74	-0.30	-0.15	0.07	0.50	0.63	-0.45	-0.20	0.27
	>30	0.06	0.45	0.30	0.65	0.32	0.76	0.74	1.00	-0.44	-0.30	0.00	0.59	0.75	-0.53	-0.27	0.35
Turbot (<i>Reinhardtius hippoglossoides</i>)	<30	0.20	-0.08	0.06	-0.31	-0.07	-0.33	-0.30	-0.44	1.00	0.64	0.03	-0.27	-0.43	0.50	0.31	-0.13
	>30	0.26	0.04	0.18	-0.20	-0.01	-0.17	-0.15	-0.30	0.64	1.00	0.10	-0.09	-0.30	0.42	0.35	0.07
Redfish (<i>Sebastes</i> sp.)	<20	0.14	0.08	0.09	0.00	0.07	-0.05	0.07	0.00	0.03	0.10	1.00	0.33	0.09	0.25	0.39	0.33
	20-30	-0.09	0.22	0.29	0.52	0.24	0.49	0.50	0.59	-0.27	-0.09	0.33	1.00	0.75	-0.23	0.08	0.52
	>30	-0.10	0.31	0.22	0.58	0.26	0.66	0.63	0.75	-0.43	-0.30	0.09	0.75	1.00	-0.41	-0.13	0.39
	<25	0.12	-0.25	-0.18	-0.54	-0.14	-0.46	-0.45	-0.53	0.50	0.42	0.25	-0.23	-0.41	1.00	0.53	-0.11
Cod (<i>Gadus morhua</i>)	25-35	0.08	-0.01	0.00	-0.32	0.02	-0.17	-0.20	-0.27	0.31	0.35	0.39	0.08	-0.13	0.53	1.00	0.40
	>35	0.10	0.34	0.31	0.35	0.18	0.35	0.27	0.35	-0.13	0.07	0.33	0.52	0.39	-0.11	0.40	1.00

Appendix B

Piecewise-regressions were used to detect the presence of a threshold or breakpoint across FPT values at a given scale, discriminating between FPT values corresponding to restricted search behaviour from other values. To define this threshold, values of FPT (at Var-max) for each segment were classified in ascending order (figure B1). A two and three processes (one and two breakpoints) piecewise-regression model was then applied to the data series using the MODEL procedure in SAS (SAS Institute 2003). The continuous function for the one-breakpoint model took the following form:

$$\begin{aligned} y &= a_1 + b_1x && \text{for } c_1 \geq x \\ y &= \{a_1 + c_1(b_1 - b_2)\} + b_2x && \text{for } c_1 < x \end{aligned}$$

whereas the continuous function for the two-breakpoints model took the following form:

$$\begin{aligned} y &= a_1 + b_1x && \text{for } c_1 \geq x \\ y &= \{a_1 + c_1(b_1 - b_2)\} + b_2x && \text{for } c_1 < x \leq c_2 \\ y &= \{a_1 + c_1(b_1 - b_2)\} + c_2(b_2 - b_3)\} + b_3x && \text{for } x > c_2 \end{aligned}$$

Where y and x were the coordinate of the slopes described by the ordinate at origin a_i , the slope b_i and separated at the breakpoint c_i .

Piecewise-regression models assume homogeneity of variances, and independency and normality of residuals, assumptions that were not met in this study. To correct for autocorrelation of residuals, autoregressive moving average error processes (FIT statement of the MODEL procedure in SAS) was applied to the data. The autoregressive order was determined with a Durbin-Watson test. Violation of the heteroscedasticity assumption was minimized by applying the FIT statement `hccme3` of the same SAS procedure. Once corrected for heteroscedasticity and autocorrelation, the differences between slopes were tested using two-sample paired t-tests. A significant difference between slopes indicated the potential occurrence of other ARS zones.

To determine the presence of multiple spatially distinct ARS zones, the value corresponding to the 95% lower confidence interval of the calculated breakpoint was selected as a threshold. Interpolated points with FPT values falling above this threshold were extracted and mapped in ArcGIS with the associated circle of a radius equal to Var-max (Figure B2). Then, starting with the highest FPT value, points were screened one by one. A point was considered the centre of a new ARS zone when the circle around the point did not overlap with segment sections part of another ARS zone of the same segment. This step was repeated until no more point above the threshold could be considered as a new ARS zone centre, based on the aforementioned criteria.

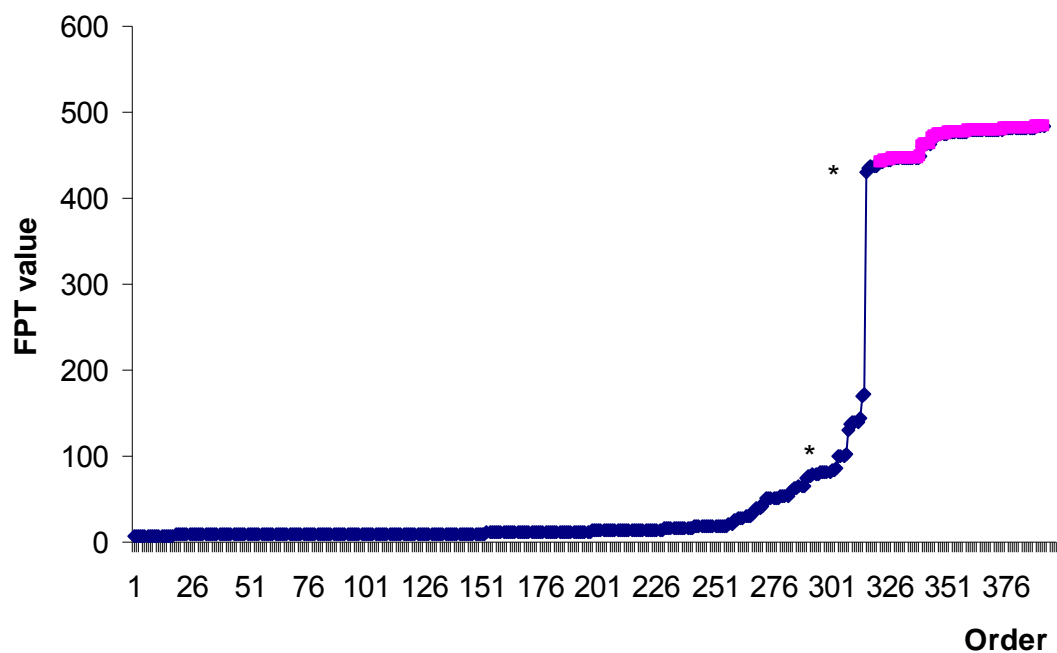
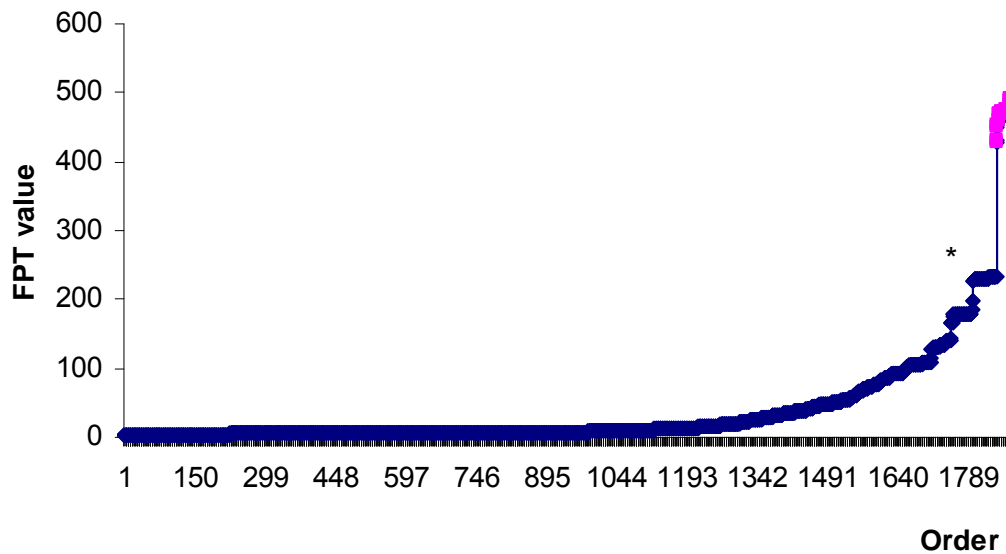
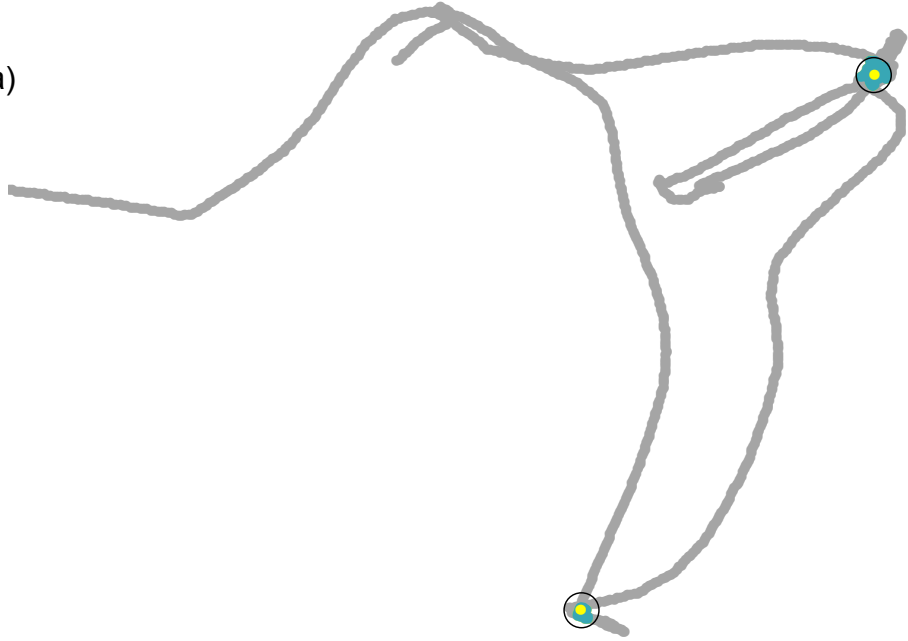


Figure B1. Example of FPT at Var-max classified in ascending order for a) one-breakpoint model and b) two-breakpoint model. (*) indicated the breakpoint (c_1 , c_2) defined by the SAS nlin procedure. Pink points are points with FPT values the failed above the breakpoint.

a)



b)



Figure B2. ARS obtained using the piecewise regressions for a) 1 breakpoint model and b) 2 breakpoints model. Green dots represented value over the 95% confidence interval of the calculated breakpoint. Yellow dots represented the center of the ARS. Black circle corresponded to the ARS

Appendix C.

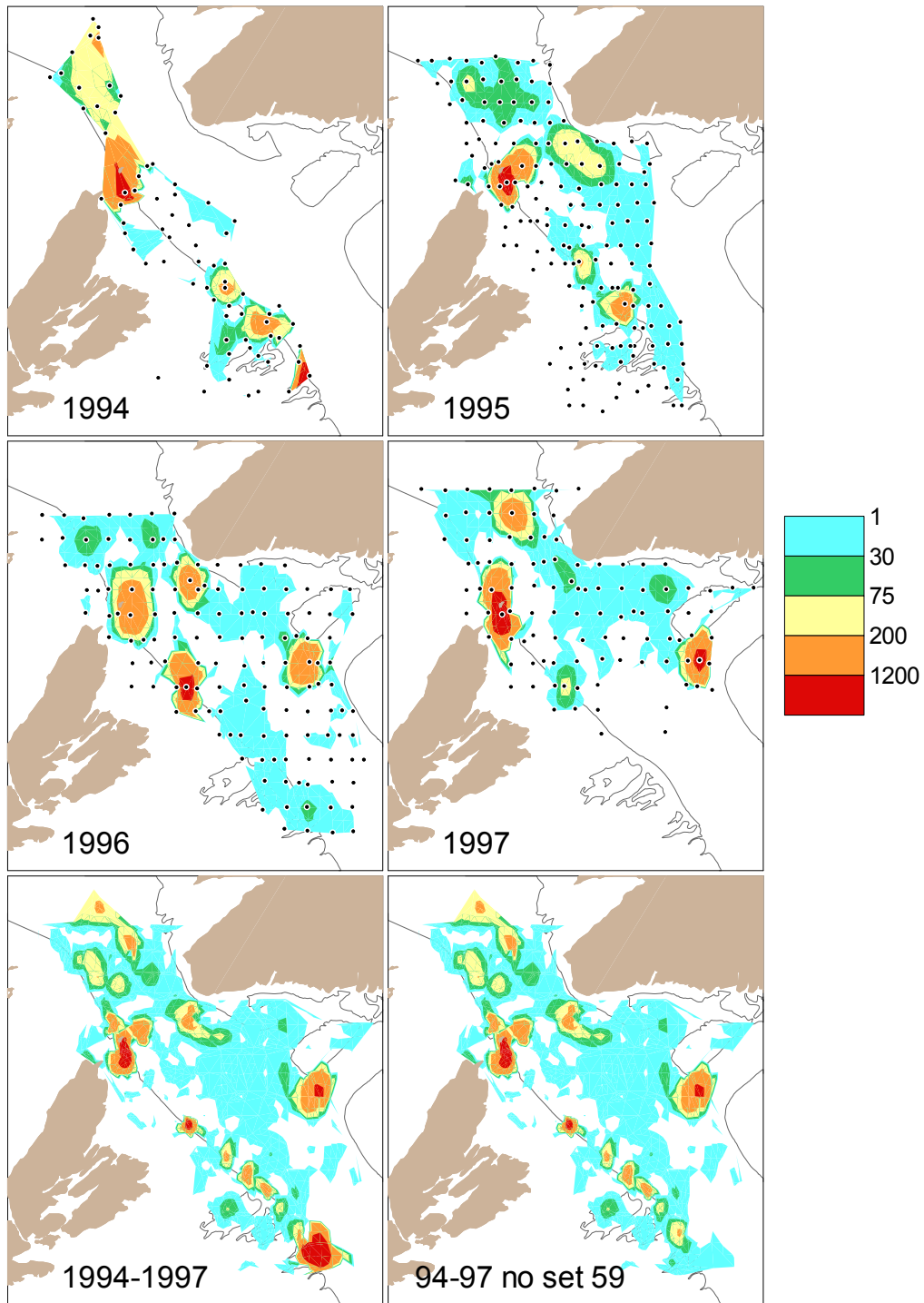


Figure C1. Distribution of cod >35 cm in length in January surveys. The very dense aggregation apparent at the southern extreme of the study area is due to a single tow in the 1994 survey (set 59). The bottom right panel shows the average 1994-1997 distribution omitting this tow.

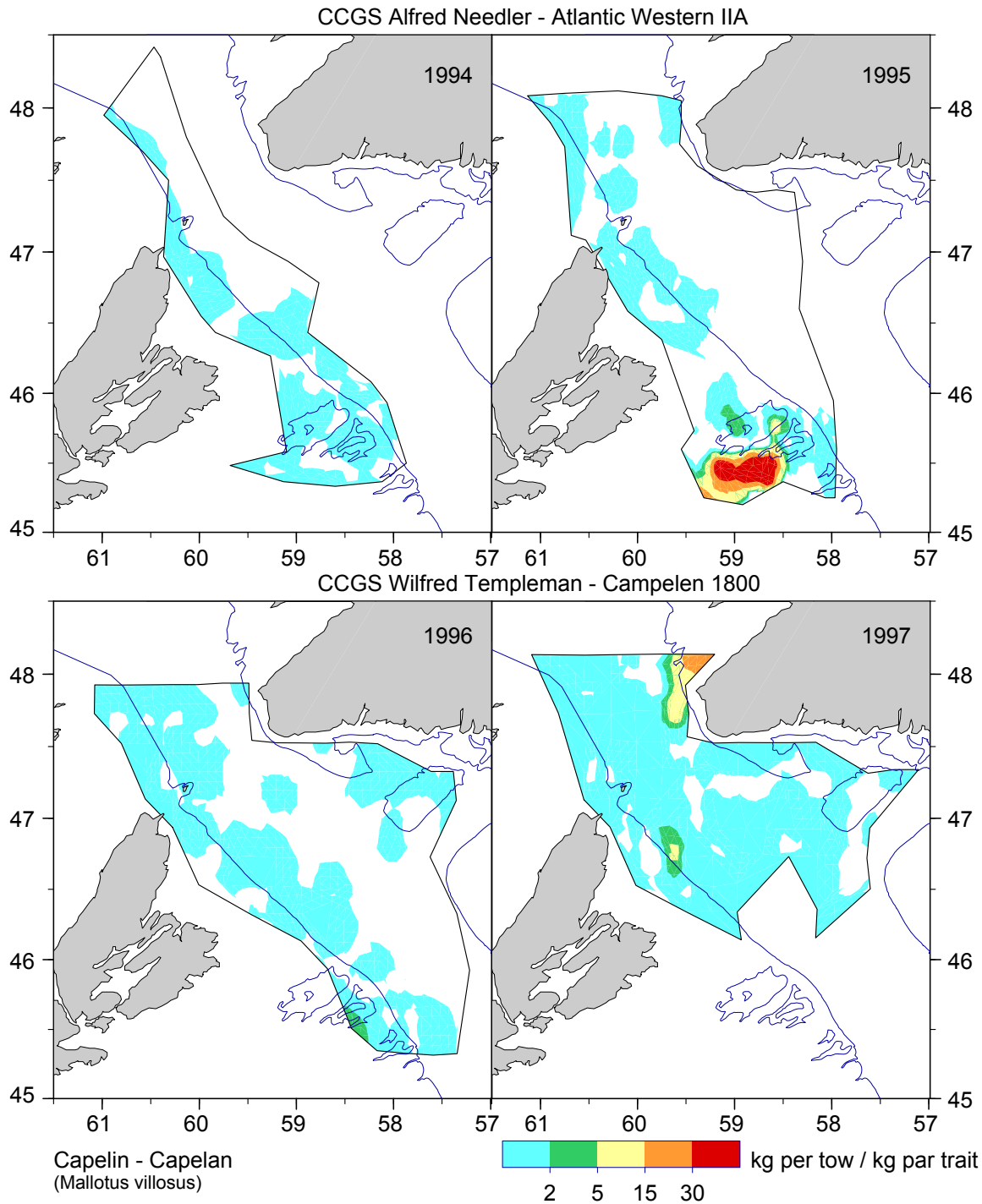


Figure C2. Distribution of capelin (*Mallotus villosus*) catches (weight per tow) during January surveys conducted in Cabot Strait, 1994–1997.

Appendix D

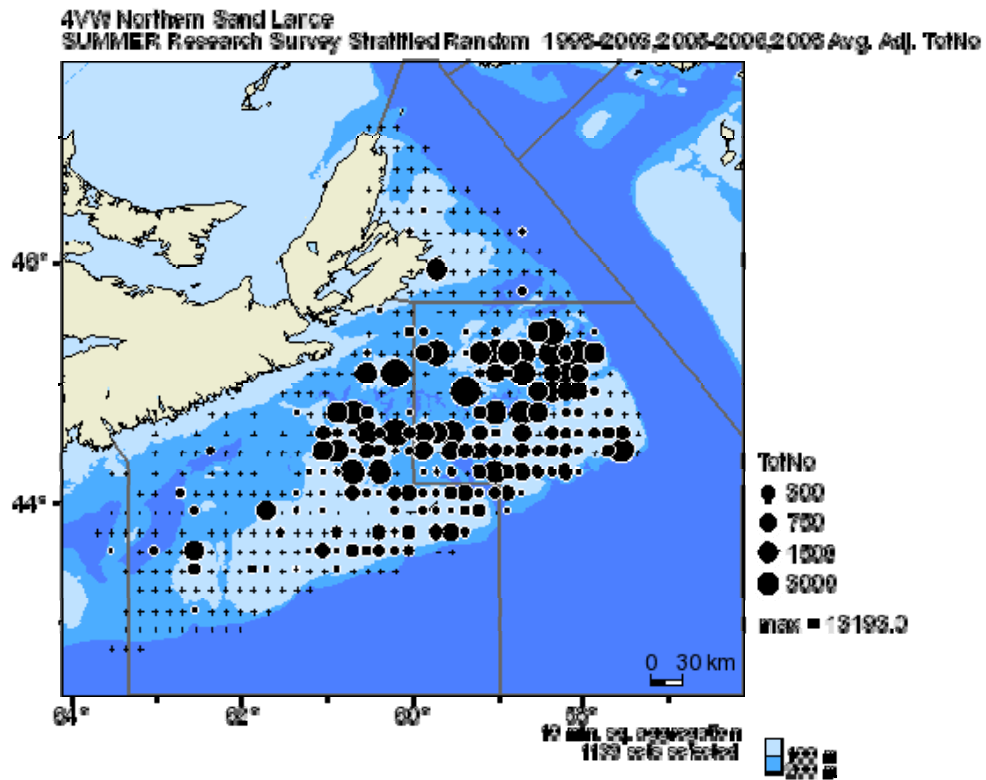


Figure D1. Distribution of northern sand lance in July surveys of the eastern Scotian Shelf, 1998-2008. Data extracted and figure produced using the Maritimes Region Virtual Data Centre (Fisheries and Oceans Canada).