



# The ecology of 3-D space use in a sexually dimorphic mammal

Valérie Harvey, Steeve D. Côté and Mike O. Hammill

V. Harvey, S. D. Côté (steeve.cote@bio.ulaval.ca), Dépt de biologie and Centre d'études nordiques, Univ. Laval, Québec, QC, Canada, G1K 7P4. – M. O. Hammill, Dept of Fisheries and Oceans, Maurice Lamontagne Inst., 850 Route de la Mer, P. O. Box 1000, Mont Joli, QC, Canada, Q5H 3R4.

The distribution of animals is the result of habitat selection according to sex, reproductive status and resource availability. Little is known about how marine predators investigate their 3-dimensional space along both the horizontal and vertical axes and how temporal variation affects space use. In this study, we assessed the spatio-temporal movement of a sexually dimorphic marine mammal, the grey seal *Halichoerus grypus* by 1) determining seasonal home range size, 2) testing whether space use of seals was affected by water depth, and 3) investigating the vertical movement of seals according to the maximum depth of each dive. Between 1993 and 2005, we fitted 49 grey seals in the Gulf of St. Lawrence with satellite transmitters. We estimated seasonal 95% fixed-kernel home ranges for each individual. For each seal, we tested for selectivity and preference for 4 water depth classes at the home range scale and within the home range. We also evaluated the proportional number of dives made in each water depth classes according to the maximum depth of each dive. Home ranges were 10 times larger in winter than in summer. Seals generally selected habitats <50 m deep. They also mainly dove to depths of 40 m or less. At both scales of selection, preference for shallow areas decreased in winter. We also observed that adults used shallow habitats more than juveniles to establish their home range. A spatial segregation based on sex also occurred at the finer scale of selection where females were more concentrated in the shallowest parts of their home range than males. Segregation in space use according to age and sex classes occurred at both the horizontal and vertical scales. Our results emphasise the importance of studying habitat selection of marine predators in 3-dimensional space, in addition to the temporal scale.

Animals are normally not distributed uniformly throughout their range. Instead, they actively use habitats in response to a combination of factors including resource availability, life-history strategies and individual variability (Orians and Wittenberger 1991, Rettie and Messier 2000, McLoughlin et al. 2002). Habitat use often results from a hierarchical process of behavioural responses involving the disproportionate use or selection of certain habitats, a process called habitat selection (Manly et al. 2002). The distribution of animals or habitat use patterns are then the end result of habitat-selection processes occurring at a range of scales (Johnson 1980). The availability of resources and factors that influence habitat selection often vary both temporally and spatially and animals have been shown to select different resources at different scales (McLoughlin et al. 2002, Dussault et al. 2005). Consequently, habitat selection patterns may vary with the scale at which the system is viewed.

Home range is generally defined as the space used by an animal over a specific period of time to carry out its activities (Burt 1943). It is the spatial representation of the behaviours performed by animals to survive and reproduce (Börger et al. 2006). The size and the position of individual home ranges as well as the distribution of individuals within

different parts of their home range are commonly analysed in ecological studies to describe the relationship between an individual's spatio-temporal movements and resource availability (McLoughlin et al. 2002, Dussault et al. 2005). Seasonal variability in the patterns of distribution are also commonly observed, for example in ungulates living in temperate regions with individuals increasing their use of areas providing shelter from extreme snow depths in winter (Boyce et al. 2003). Moreover, differences in morphology and size may cause males and females, or juveniles and adults, to use different foraging strategies and habitat (Conradt et al. 1999).

Few studies have attempted to examine these concepts within the marine environment. Marine mammals spend most of their time underwater, in offshore areas, which are highly dynamic and difficult to characterise. However, developments in satellite telemetry over the last 10 yr have provided opportunities to obtain information on how marine animals exploit their 3-dimensional space (Lowry et al. 2000, Mauritzen et al. 2001, Laidre et al. 2004). As top predators, the distribution of marine mammals at sea is thought to be linked to areas of high prey availability. Various oceanographic metrics such as water depth, salinity, chlorophyll concentration, and currents, have been used to

develop associations between food availability and marine mammal distribution (Guinet et al. 2001, Bradshaw et al. 2004, MacLeod et al. 2007). However, few studies have explored the spatio-temporal dynamics of habitat use patterns of marine mammals along both the horizontal and vertical axes, which are linked by water depth, nor have they tested how habitat selection patterns vary according to intra-specific and environmental variability. Since marine mammals exploit a highly dynamic 3-dimensional world, simultaneous information on the diving behaviour and foraging range according to the availability of different water depths is essential to understand their habitat use, because segregation by age or sex at the horizontal scales may not represent segregation in the vertical axes of the water column.

The grey seal *Halichoerus grypus* is a large seal found throughout the temperate coastal areas of the North Atlantic. Adult males are ca 1.5 times heavier than adult females in the Northwest Atlantic population (Beck et al. 2003b). Grey seals are capital breeders that rely on energy reserves to satisfy their energy requirements during the breeding season (Tinker et al. 1995). Sexual differences have been reported in the annual pattern of energy expenditure and accumulation of reserves of grey seals (Beck et al. 2003b, Sparling et al. 2006). Females are more selective while foraging and consume a lower quantity of higher-quality preys than males (Beck et al. 2007). Although grey seals are generally associated with shallow depths (Sjöberg and Ball 2000, MacLeod et al. 2007), females are known to be shallower divers and exhibit a higher diving effort in smaller and distinctive foraging areas than males (Beck et al. 2003a, Austin et al. 2004, Breed et al. 2006). Sex differences in energy storage, diet composition, and diving behaviour likely reflect differences in the costs and benefits of energy storage for reproduction. As a result, sexes may differ in their spatio-temporal patterns of habitat use.

Little is known about space use by juvenile phocids. In grey seals, the diet of juveniles is more diverse and less energy dense than that of adults (Beck et al. 2007, Tucker et al. 2007). However, juveniles likely have lower foraging efficiency than adults due to inexperience and physiological limitations in their diving abilities (Noren et al. 2005). Juveniles may then use habitat differently than adults.

We used satellite telemetry to examine the seasonal distribution of seals and investigated habitat selection at the home range scale, which is the process through which an individual selects its home range within the landscape, and within the home range scale, which refers to the use of various habitat components within the home range, according to an abiotic habitat descriptor, water depth. We hypothesized that males would have larger home ranges than females and use deep areas more frequently than females, particularly in winter. Given that they are non-reproductive and less experienced, patterns of habitat use by juveniles should not differ with sex, but juveniles should have larger home ranges than adults. Because the diving abilities of juveniles are more limited than those of adults, we also predicted that juveniles should be more concentrated in shallow habitats than adults.

## Methods

### Study area and habitat description

The Gulf of St. Lawrence (Gulf) is a semi-closed sea naturally divided into two distinct ecosystems by the deep (>300 m) Laurentian channel (Fig. 1). The lower estuary and the northern Gulf are characterized by deep trenches and channels that exceed 300 m in depth. In contrast, the southern Gulf is characterized by a wide and shallow shelf of <100 m deep. To the east and outside the Gulf, the Scotian Shelf extends ca 400 km off the coast of Nova Scotia. This area is characterized by a series of shallow banks, often  $\leq 100$  m deep, and basins of 200–400 m. With an estimated Northwest Atlantic population of 197 000 individuals in 1997, the grey seal is one of the most abundant coastal pinnipeds inhabiting this ecosystem throughout the year (Lesage and Hammill 2001). In summer, they are concentrated in coastal areas of the Gulf of St. Lawrence and on the continental Shelf off Nova Scotia (Fig. 1) (Stobo et al. 1990, Lavigne and Hammill 1993). In autumn, there is a defined movement as seals leave the St. Lawrence estuary and northern Gulf, moving into the southern Gulf or exiting the Gulf altogether (Lavigne and Hammill 1993, Goulet et al. 2001). During winter (December–February), breeding aggregations form on the pack-ice in the southern Gulf of St. Lawrence and on Sable Island (Lesage and Hammill 2001). After pupping (January–February), seals move offshore where they likely remain until the spring moult (May–June) (Lavigne and Hammill 1993).

### Animal handling and data recording

We captured 59 grey seals (16 adult males, 16 juvenile males, 16 adult females, 11 juvenile females) between May and September 1993–2004 using gill nets set perpendicular to the shore (Goulet et al. 2001). Ten animals were captured in the northern Gulf of St. Lawrence at Anticosti Island, three animals in the St. Lawrence River Estuary, 41 in the southern Gulf of St. Lawrence and five in the breeding site during the reproductive period (Fig. 1). Animals were weighed to the nearest 0.5 kg and then immobilized with an intramuscular injection (0.7–1.1 mg kg<sup>-1</sup> body mass) of Telazol (Wyeth Animal Health, Guelph, ON) (Baker et al. 1990). An incisor tooth was extracted for age determination (Bernt et al. 1996). Animals were classified as juveniles (1–5.5 yr) and adults ( $\geq 6$  yr old) (Hammill and Gosselin 1995). 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 (Goulet et al. 2001). Two types of transmitters were deployed; half-watt satellite time-depth recorders (Wildlife Computers, Redmond, WA,  $n = 42$ ), and Series 9000 Satellite Relay Data Loggers (SRDL) (Sea Mammal Research Unit (SMRU), Univ. of St. Andrews, Scotland,  $n = 17$ ). A pressure sensor sampled dive depth at 10 s intervals. Dive data collected by the Wildlife Computers tags were assigned to user-programmed bins that recorded

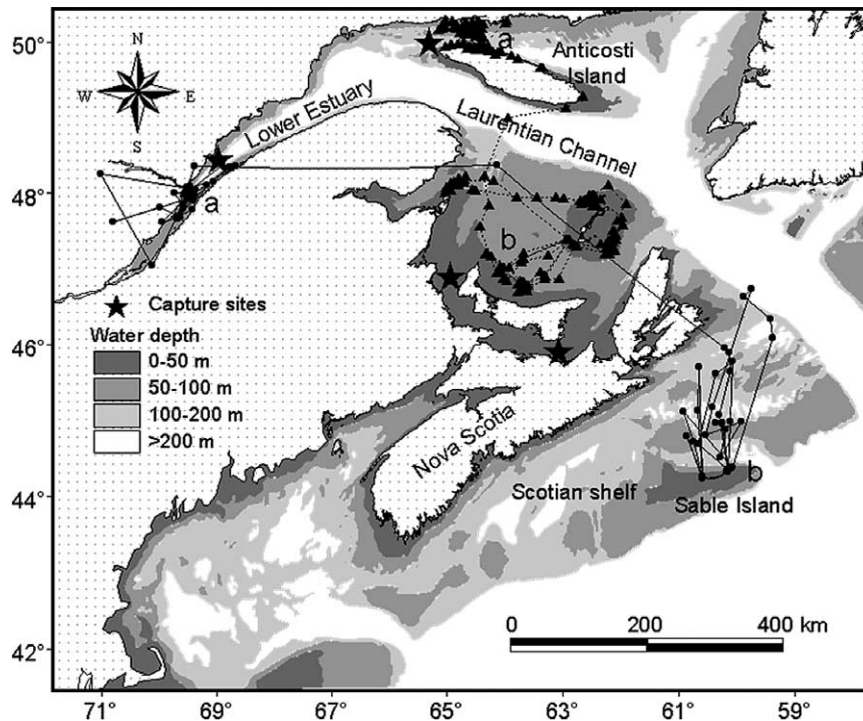


Figure 1. Study area and bathymetry of the Gulf of St. Lawrence and Nova Scotia shelf as well as the paths of two grey seals fitted with satellite transmitters in summer (a) and followed until the end of the winter (b). The seal from the lower estuary was followed in 1994 and the one from Anticosti in 2004.

the number of dives in each depth category. The binned data were collected and transmitted over 6 h periods. The SMRU transmitters recorded dive parameter information at 4 s intervals and transmitted summary statistics of the diving activity of seals throughout a 3-h time period. The threshold depth value to record dives varied with the year of deployment and transmitter (Supplementary material, Table S1). Dives started when the depth sensor was deeper than a predefined threshold depth (Supplementary material, Table S1) for >10 s, and ended when seals returned to depths shallower than the threshold for >40 s. Thirty-eight transmitters were active every day, while 21 were duty-cycled (e.g. programmed to transmit at every two or three days), to increase their longevity. Transmissions were received by satellite, and processed under the ARGOS system, which provided location information (Argos 1989).

Argos locations are coded with a quality index indicating accuracy (Argos 1989). We applied a three-stage algorithm filter (Austin et al. 2003) to remove unrealistic positions based on an average swimming speed of  $2 \text{ m s}^{-1}$  (Thompson and Fedak 1993). Filtered data were used for all subsequent analyses. Because we had many locations per seal, we conserved only one location per day separated by at least 12 h from the previous location to minimise the risk of temporal autocorrelation (Swihart and Slade 1985). The daily location with the highest quality index that met these conditions was used.

### Seasonal home range size

To examine seasonal effects, the year was divided into three periods: summer, migration and winter. The summer

started when transmitters were deployed in June and ended with the beginning of the autumn migration which usually occurred in early November. Migration started when seals left the vicinity of their summer range without returning to this area. We used ANOVAs to evaluate if the beginning and the duration of the autumn migration varied according to the region occupied during summer (north vs south), sex or age class. The winter season began after the end of the migration when the locations were clumped, (i.e. about December) and ended when transmitters ceased to function, normally in March. The individual summer and winter home ranges were estimated using 95% fixed-kernels with the Animal Movement Extension (Hooge and Eichenlaub 2000) in ARCVIEW 3.2. We used the least squares cross validation method to select the smoothing parameter of the kernel estimators (Seaman and Powell 1996). We verified the sensitivity of the kernel method to the number of locations used (Seaman et al. 1999) and calculated seasonal home ranges for all individuals with at least 35 locations for each period (Girard et al. 2006). To determine the effects of season, sex and age class on home range sizes, the 95% fixed kernel home range size was used as the dependent factor in a general linear mixed model with these independent variables. To account for repeated measures on some individuals over different seasons, “individual” was considered as a repeated factor in the model. Year was included as a random factor. We applied a log transformation on home range size prior to analysis to improve normality of residuals.

Prior to conducting these analyses, the effect of the period of capture on individual home range sizes was examined. To evaluate this, we used data from 10 individuals caught in June for which uplinks were received

every day. We split the dataset for each individual into two sub-samples: one from June to October, and one from October until the end of the migration (about December). Home range sizes estimated using the dataset from June to December or only locations from June–October or October–December did not differ (ANOVA:  $F_{2,27} = 0.17$ ;  $p = 0.85$ ).

The time-interval between successive locations might also influence home range size (Austin et al. 2004). To determine if transmitter duty cycle affected home range size estimates, we also simulated 48 and 72 h duty cycles by randomly choosing one location per day separated by at least 48 and 72 h from the previously chosen location. ANOVA were performed to compare the mean home range sizes of true and simulated duty cycles. Home range sizes estimated from the complete dataset or the 48 or 72 h simulated duty cycles did not differ ( $F_{2,27} = 0.01$ ;  $p = 0.99$ ).

### Habitat selection

We defined the study area as the region available for individuals that we tracked and delineated it by creating a minimum convex polygon around all individual seasonal home ranges (Mohr 1947). Seasonal habitat selection within the study area was determined for each seal by relating use to availability of 4 water depth classes (0–50, 50–100, 100–200, >200 m). Availability of these water depth classes was determined using bathymetric maps (GEBCO Digital Atlas, British Oceanographic Data Centre, Liverpool). We analysed habitat selection at two hierarchical scales, using the individual as the sampling unit. Habitat selection was first investigated at the home range scale, which corresponds to where individuals establish their home range within the study area. For this scale of analysis, the proportional area of each seasonal home range occupied by each water depth class was compared to the proportional area occupied by each water depth class within the study area. Habitat selection was also investigated within the home range by studying selection for each water depth class available within the home range (Johnson 1980). At this scale, habitat use was estimated by the proportion of locations of each home range within each water depth class and availability was estimated by the proportional area occupied by each water depth class within the home range.

Individual variation in the availability of water depth classes could influence the use of each depth class. To account for this, at each scale of analysis, we divided the ratio obtained for each water depth class for each individual by the sum of all ratios found for that individual. This led to Manly's standardized selection ratios, which always totalled 1.0 and which could be interpreted as the probability that a habitat would be selected if all habitats were equally available (Manly et al. 2002). Those ratios were used as the basic unit in all subsequent statistical analyses of habitat use and preference. To account for the inter-dependence in Manly's standardized selection ratios for each water depth classes for one individual, we created 3 synthetic variables based upon differences in adjacent pairs of values (Arthur et al. 1996, McLoughlin et al. 2002, Dussault et al. 2005). We included the synthetic variables in

a multivariate analysis (MANOVA), using the Hotelling's statistic to test for the effects of sex, age class, season and their two-way interactions on habitat selection patterns at the home range scale. Our dataset extends over more than 10 yr. Because it is not possible to include random factors in a MANOVA, we forced the variable "year" in the model to account for between-year variation prior to assessing the influence of the other variables.

The availability of all water depth classes must be greater than zero to include an individual seasonal home range in the analyses (McLoughlin et al. 2002). The analyses at the finer scale of selection were thus conducted on a reduced sample size. To avoid over-parameterisation of the model, we did not test for the interactions between fixed effects at this finer scale of selection. If a significant effect was detected in the overall MANOVA, we performed pair-wise t-tests for each combination of habitat types (depths) to establish a rank order of habitat preference (Rettie and Messier 2000, McLoughlin et al. 2002, Dussault et al. 2005). Pair-wise t-tests were also conducted to determine the effects of season, sex and age class on the value of Manly's selection index for each habitat type. Since multiple testing increases the likelihood of obtaining a significant result when the null hypothesis is true, we selected a significance level of 0.01 to decrease the probability of identifying selectivity differences between habitats when there was none. In this paper, "preferred" and "avoided" are used as relative terms and only when comparing pairs of habitat types for which significant differences were detected.

### Dive analyses

We used the maximum depth of individual dives to evaluate if water depths selected by seals on a horizontal scale reflected their vertical distribution throughout the water column. For each individual in each season, we calculated the proportion of maximum depth dives between 0–40, 40–100, 100–200 and >200 m. The first 2 classes were slightly different than the water depth classes used for the analysis at the horizontal scale (water depth classes: 0–50, 50–100, 100–200, >200 m) due to the settings of the Wildlife Computers transmitters that differed from the bathymetric maps used to establish the water depth classes in the analysis of habitat selection at the horizontal scale. A MANOVA was performed to determine if season, age class, sex and their interactions influenced the number of dives performed in each water depth class. We also included year as a fixed effect in the model to account for annual variability. If a significant effect was detected in the overall MANOVA, we performed a posteriori LSMEANS comparisons and presented p values.

Variability in habitat features between the southern and the northern part, including the estuary, of our study area might have influenced the diving behaviour and space use of grey seals. We therefore compared home range sizes, patterns of habitat selection within the home range and dive frequencies of grey seals between these areas. The analysis at the home range scale of selection considered the whole study area as the area available. Hence, we could not compare the two areas of the Gulf at this scale of selection. All statistical analyses were carried out with SAS

(SAS ver. 9.1; SAS Inst. 2002) with a probability level set at 0.05, unless otherwise stated. All results are presented as means  $\pm$  SE.

## Results

Five out of 59 transmitters functioned for  $<24$  h. The 54 remaining animals were tracked for 20–294 d, with a mean duration of  $186 \pm 11$  d and a total of 10 238 daily samples and 53 346 locations. The three-stage algorithm filter retained 71% of the locations.

Twenty-two percent of individuals ( $n=54$ ) left the capture area within 9 d (mean =  $4 \pm 1$  d). Animals that left the capture area did so for 2 to  $>100$  d ( $26 \pm 11$  d). Two individuals did not return at all. No animals overwintered in the St. Lawrence Estuary or northern Gulf. In late autumn (mean = 25 November, range = 8 October–25 January), seals left their summering area and undertook a migration towards the southern Gulf or the Scotian Shelf that lasted an average of  $10 \pm 1$  d (range = 1–23 d) (Fig. 1). The location of the summer area did not affect when the migration began ( $F_{1,31}=0.01$ ;  $p=0.93$ ), but it lasted longer for seals starting from the northern Gulf or Estuary ( $n=12$ ; mean:  $13.3 \pm 4.8$  d) than for animals from the southern Gulf ( $n=12$ ;  $7.9 \pm 5.4$  d) ( $F_{1,31}=8.05$ ;  $p<0.01$ ). Although females tended to leave the summer area earlier than males, no differences in the timing or duration of migration were observed between males and females (timing:  $F_{1,31}=0.00$ ;  $p=0.99$ ; duration:  $F_{1,31}=2.02$ ;  $p=0.16$ ) or between adults and juveniles (timing:  $F_{1,31}=2.18$ ;  $p=0.15$ ; duration:  $F_{1,31}=0.66$ ;  $p=0.42$ ).

Within a season, two different scales of movement were observed. First, some animals concentrated their seasonal activities within one area and remained within 50 km of one or several haul-out sites separated by an average of  $73 \pm 10$  km. A second pattern involved travelling and spending time in distinct areas separated by several hundred kilometres ( $377 \pm 66$  km). Seals remained within a foraging area for an average of  $72 \pm 5$  d ( $n=110$ , all seals). Use of alternative foraging areas was more frequent in winter when 27% of seals ( $n=44$ ) concentrated in  $>2$  areas compared to 7% ( $n=47$ ) in summer.

### Seasonal home range size

We calculated home ranges of 49 different individuals: 36 home ranges in summer and 34 in winter. The track duration of 21 seals was long enough to determine home range during both seasons, while the home ranges of 28 other animals were determined for one season only (15 in summer and 13 in winter). In both seasons, home ranges were concentrated in the southern part of the Gulf and around Sable Island (Fig. 2a, b). Summer home range sizes did not differ between the northern and the southern parts of the Gulf ( $F_{1,34}=0.03$ ;  $p=0.9$ ). Winter home ranges (mean =  $91\,000 \pm 24\,000$  km<sup>2</sup>; range = 1016–322 771 km<sup>2</sup>) were significantly larger than summer home ranges (mean =  $8900 \pm 2000$  km<sup>2</sup>; range = 246–52 846 km<sup>2</sup>) (Table 1a). Juveniles ( $n=27$ ;  $41\,000 \pm 12\,000$  km<sup>2</sup>) had home ranges that were twice as large as those of adults

( $n=43$ ;  $20\,000 \pm 4000$  km<sup>2</sup>), but the difference was not quite statistically significant (Table 1a). Home range size did not differ between males ( $n=30$ ;  $22\,000 \pm 6000$  km<sup>2</sup>) and females ( $n=40$ ;  $39\,000 \pm 11\,000$  km<sup>2</sup>) (Table 1a).

### Habitat selection

The patterns of habitat selection did not vary between years. At the home range scale of selection, the pattern of habitat preference varied seasonally (Table 1b), but in both seasons seals preferred water depths of 0–50 m. In summer, the mean selection ratio for the depth class 0–50 m was about four times higher than the selection ratio for the 50–100 m class, the next preferred habitat type (Table 2a). In winter, a similar pattern was observed, but the preference for the 0–50 m class over the 50–100 m class was only about two times higher. When Manly's standardised ratios were compared between seasons, we found that seals used the shallowest areas significantly less and areas of 100–200 m significantly more in winter than in summer (Table 2a).

Overall, no difference in habitat selection was observed between males and females at the home range scale (Table 1b). Both sexes preferred areas with water depths of 0–50 m and their preference generally declined with increasing water depth. However, differences in habitat preference between the sexes approached significance when season was taken into account (Table 1b). Females preferentially established their home range in habitats of  $<50$  m during all seasons (Table 2a). Males preferentially established their summer home ranges in water depths of  $<50$  m, but were less selective in winter and Manly's standardized selection ratios did not reveal any preference for habitats of 0–50, 50–100 and 100–200 m. However, in winter, males used habitats of 0–50 m less and habitats of 100–200 m more than in summer. Our analyses indicated a non-significant trend for juveniles to exhibit a different pattern of habitat preference than adults. Adults established their home range in habitats with water depths of  $<50$  m. Juveniles preferred areas with water depths  $<100$  m, but no differences were detected among the depth classes shallower than 100 m (Table 2a).

Eleven summer home ranges and 25 winter home ranges were available to estimate habitat selection within the home range. No difference in habitat selection was detected between the northern and southern Gulf during summer ( $F_{3,32}=1.53$ ;  $p=0.3$ ). All data were therefore combined for subsequent analyses. Patterns of preference within the home range differed between seasons, age classes, and sexes (Table 1c). In summer, a preference was observed for areas  $<100$  m (Table 2b). In winter, seals preferred areas 0–50 m over those of 50–200 m. When Manly's standardised ratios were compared between seasons, there was a greater preference for areas 100–200 m deep in winter compared to summer (Table 2b), indicating that seals increased the use of the deeper parts of their home range in winter. Although the MANOVA indicated that there was a significant effect of age class on habitat preference patterns (Table 1c), the differences were subtle and the multiple comparisons of the selection ratios did not detect any difference between adults and juveniles (Table 2b). However, females demonstrated a strong preference for the parts

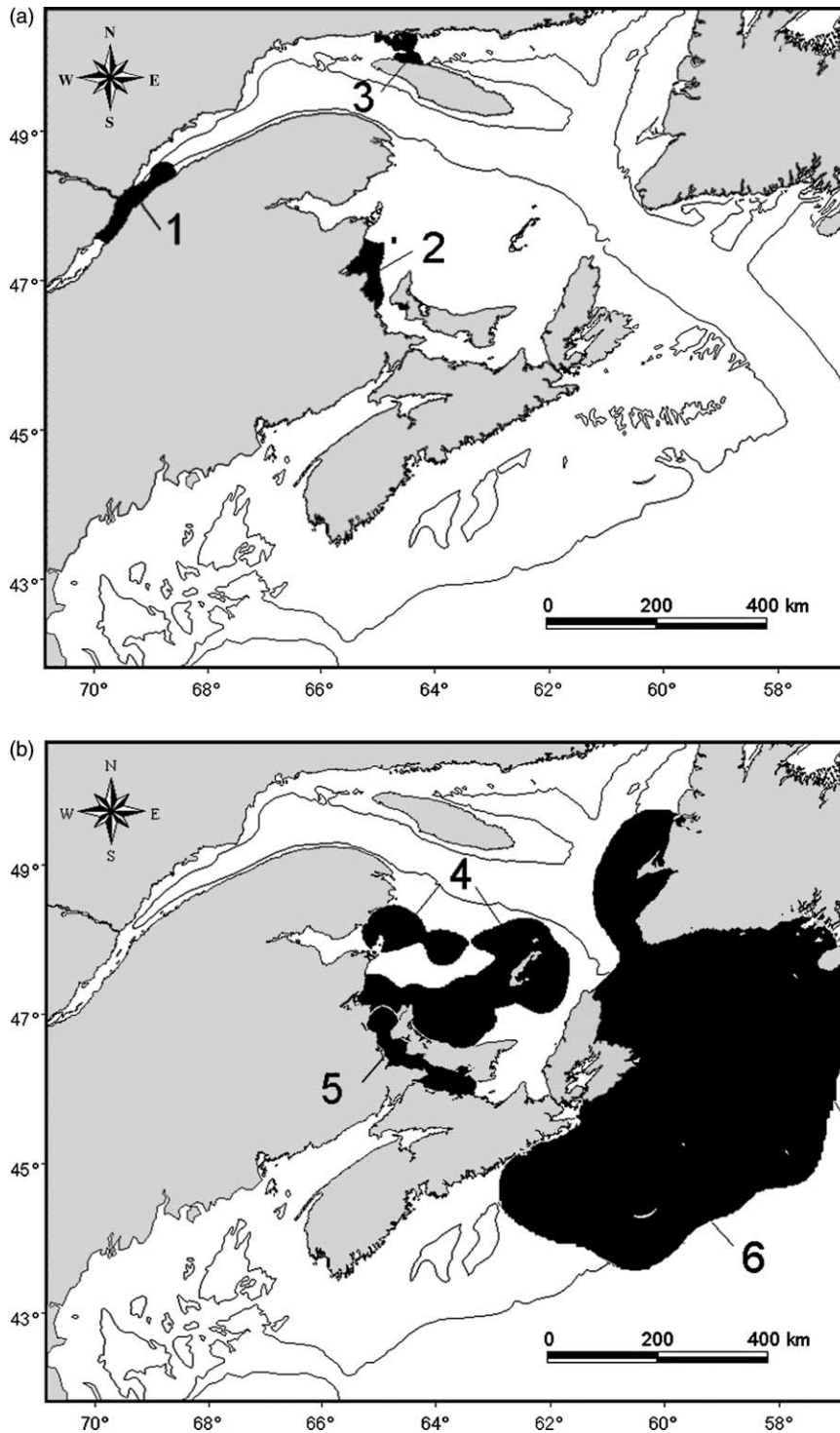


Figure 2. Summer (a) and winter (b) home ranges (95% fixed kernels), indicated by black shading, of six grey seals fitted with satellite transmitters in the Northwest Atlantic in 1996–2004. Solid line is the 200 m isobath.

of their home range of <100 m, while males strongly preferred the parts of their home range 0–50 m over those >50 m (Table 2b).

### Diving behaviour

The proportion of dives within each depth class did not vary between animals in the northern and southern Gulf in

summer (MANOVA:  $F_{4,19} = 0.8$ ;  $p = 0.54$ ). Overall, the proportion of dives was higher in shallow depth classes and decreased with increasing depth (0–40 m:  $0.79 \pm 0.03$ ; 40–100 m:  $0.17 \pm 0.02$ ; 100–200 m:  $0.04 \pm 0.01$ ; >200 m:  $0.01 \pm 0.00$ ). There was a significant sex  $\times$  season interaction in the number of dives according to their maximum depth (Table 1d; Fig. 3a). During winter, males dove less frequently at <40 m deep ( $p < 0.01$ ) and more frequently

Table 1. Linear mixed effect models on seasonal home range size of grey seals of the Atlantic Northwest (a) and Hotelling's tests (MANOVA), controlling for year, on habitat selection at the home range level (b), within the home range (c) and on the percentage of dives made in each water depth class (d).

Dependent variables	Coefficients	SE	F-values	DF	p-values
a) Home range size					
Constant	10.86	0.62			
Season	-2.21	0.69	40.75	1,18	<0.01
Sex	-0.19	0.71	2.08	1,45	0.13
Age class	-0.49	0.68	3.70	1,45	0.06
Season × sex	-0.22	0.72	0.09	1,18	0.75
Season × age class	-0.44	0.73	0.00	1,18	0.99
Sex × age class	-0.05	0.73	0.36	1,45	0.59
b) Habitat selection at the home range scale					
Season			7.98	3,53	<0.01
Sex			0.42	3,53	0.74
Age class			2.38	3,53	0.08
Season × sex			2.31	3,53	0.09
Season × age class			0.54	3,53	0.66
Sex × age class			0.83	3,53	0.48
c) Habitat selection within the home range					
Season			7.18	3,27	<0.01
Sex			3.13	3,27	0.04
Age class			3.34	3,27	0.03
d) Diving behaviour (maximum dive depth)					
Season			20.18	4,36	<0.01
Sex			5.61	4,36	<0.01
Age class			4.11	4,36	<0.01
Season × sex			3.69	4,36	0.01
Season × age class			2.50	4,36	0.06
Sex × age class			1.78	4,36	0.15

at depths >100 m than females (100–200 m:  $p < 0.01$ ; >200 m:  $p < 0.01$ ) (Fig. 3a). The number of dives of 40–100 m deep was similar for both sexes ( $p = 0.13$ ). During summer, however, no difference between males and females in the number of dives performed in each water depth class occurred (all  $p$ 's > 0.2).

The proportion of dives in each water depth class also varied significantly with age class (Table 1d). Juveniles dove less frequently between 0 and 40 m ( $p < 0.01$ ) and more often at depths >40 m than adults (40–100 m:  $p = 0.03$ ;

100–200 m:  $p < 0.01$ ; >200 m:  $p = 0.01$ ). The pattern was similar between seasons, but the effect of age class was stronger in winter (Fig. 3b).

## Discussion

We have demonstrated that the space use strategy of a sexually dimorphic marine mammal, the Northwest Atlantic grey seal, is dynamic along both the horizontal and

Table 2. Mean ( $\pm$ SE) Manly's standardized ratios for Northwest Atlantic grey seals. A ratio is presented for each water depth class for all significant effects detected by Manovas at the home range scale (a) and within the home range (b). Different letters indicate significant differences ( $p \leq 0.05$ ) between habitat selection ratios. Preference or order between adjacent habitats types is indicated by (>) and (=) symbols, which respectively indicate significant preference or the absence of preference. (\*) indicate significant multiple comparisons ( $p \leq 0.01$ ) between summer and winter for a particular water depth class.

Parameters	Water depth classes (m)			
	0–50	50–100	100–200	>200
a) At the home range scale				
Summer – all seals (n = 36)	0.71 ( $\pm 0.06$ ) <sup>a*</sup>	> 0.18 ( $\pm 0.04$ ) <sup>b</sup>	> 0.06 ( $\pm 0.02$ ) <sup>c*</sup>	= 0.05 ( $\pm 0.02$ ) <sup>c</sup>
Winter – all seals (n = 34)	0.45 ( $\pm 0.05$ ) <sup>a</sup>	> 0.24 ( $\pm 0.02$ ) <sup>b</sup>	= 0.20 ( $\pm 0.02$ ) <sup>b</sup>	> 0.11 ( $\pm 0.02$ ) <sup>c</sup>
All seasons – adults (n = 43)	0.66 ( $\pm 0.05$ ) <sup>a</sup>	> 0.17 ( $\pm 0.02$ ) <sup>b</sup>	> 0.11 ( $\pm 0.02$ ) <sup>c</sup>	> 0.06 ( $\pm 0.01$ ) <sup>d</sup>
All seasons – juveniles (n = 27)	0.47 ( $\pm 0.06$ ) <sup>a</sup>	= 0.27 ( $\pm 0.04$ ) <sup>a</sup>	> 0.16 ( $\pm 0.03$ ) <sup>b</sup>	> 0.10 ( $\pm 0.02$ ) <sup>c</sup>
Summer – females (n = 13)	0.60 ( $\pm 0.10$ ) <sup>a</sup>	= 0.24 ( $\pm 0.08$ ) <sup>ab</sup>	= 0.10 ( $\pm 0.03$ ) <sup>b</sup>	= 0.06 ( $\pm 0.03$ ) <sup>b</sup>
Winter – females (n = 17)	0.54 ( $\pm 0.07$ ) <sup>a</sup>	> 0.22 ( $\pm 0.03$ ) <sup>b</sup>	= 0.17 ( $\pm 0.04$ ) <sup>b</sup>	> 0.08 ( $\pm 0.02$ ) <sup>c</sup>
Summer – males (n = 23)	0.77 ( $\pm 0.06$ ) <sup>a*</sup>	> 0.15 ( $\pm 0.04$ ) <sup>b</sup>	> 0.04 ( $\pm 0.01$ ) <sup>c*</sup>	= 0.04 ( $\pm 0.02$ ) <sup>c</sup>
Winter – males (n = 17)	0.36 ( $\pm 0.05$ ) <sup>a</sup>	= 0.27 ( $\pm 0.03$ ) <sup>a</sup>	= 0.23 ( $\pm 0.03$ ) <sup>a</sup>	> 0.14 ( $\pm 0.03$ ) <sup>b</sup>
b) Within the home range scale				
Summer – all seals (n = 11)	0.53 ( $\pm 0.07$ ) <sup>a</sup>	= 0.31 ( $\pm 0.07$ ) <sup>ab</sup>	= 0.12 ( $\pm 0.03$ ) <sup>b*</sup>	> 0.04 ( $\pm 0.01$ ) <sup>c</sup>
Winter – all seals (n = 25)	0.39 ( $\pm 0.03$ ) <sup>a</sup>	> 0.25 ( $\pm 0.02$ ) <sup>b</sup>	= 0.22 ( $\pm 0.02$ ) <sup>b</sup>	> 0.13 ( $\pm 0.02$ ) <sup>c</sup>
All seasons – adults (n = 19)	0.44 ( $\pm 0.04$ ) <sup>a</sup>	> 0.28 ( $\pm 0.04$ ) <sup>b</sup>	= 0.17 ( $\pm 0.02$ ) <sup>b</sup>	> 0.11 ( $\pm 0.02$ ) <sup>c</sup>
All seasons – juveniles (n = 17)	0.43 ( $\pm 0.05$ ) <sup>a</sup>	> 0.26 ( $\pm 0.04$ ) <sup>b</sup>	= 0.22 ( $\pm 0.02$ ) <sup>b</sup>	> 0.09 ( $\pm 0.03$ ) <sup>c</sup>
All seasons – females (n = 16)	0.42 ( $\pm 0.04$ ) <sup>a</sup>	= 0.33 ( $\pm 0.05$ ) <sup>a</sup>	> 0.17 ( $\pm 0.03$ ) <sup>b</sup>	> 0.08 ( $\pm 0.02$ ) <sup>c</sup>
All seasons – males (n = 20)	0.46 ( $\pm 0.04$ ) <sup>a</sup>	> 0.21 ( $\pm 0.03$ ) <sup>b</sup>	= 0.21 ( $\pm 0.02$ ) <sup>b</sup>	> 0.12 ( $\pm 0.03$ ) <sup>c</sup>

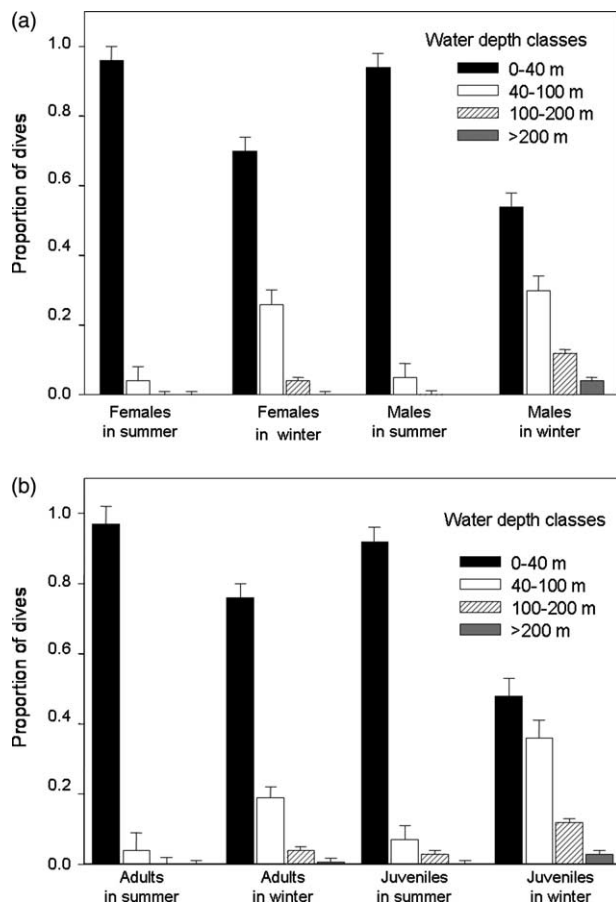


Figure 3. Seasonal variation in the mean ( $\pm$ SE) proportion of dives according to their maximum depth for Northwest Atlantic grey seals. Variations according to (a) sex and (b) age class of individuals are shown.

vertical axes of their 3-dimensional living space. We observed variability in seasonal home range sizes which could reflect different strategies in patterns of habitat use according to sex and age classes (Austin et al. 2004). Grey seals showed strong preferences for shallow depths at both the home range and within the home range scales and most of their dives were shallower than 40 m. Thus, grey seal's habitat use appeared similar whether they exploited the deepest or the shallowest parts of their home range. Considerable overlap in the space use patterns between males, females and juveniles was observed throughout the year. Nevertheless, home ranges were much larger and seals were more concentrated in deeper waters in winter than during summer. This shift towards deep areas in winter was particularly evident among males compared to females. Preference for shallow depths was also higher for adults than for juveniles.

Grey seals are central-place foragers (McConnell et al. 1999, Sjöberg and Ball 2000). They concentrate their activities within ca 50 km of one or several haul-out sites from which they perform a series of return trips to sea. During winter, much of the Gulf of St. Lawrence is ice-covered, and ice drifts out of the Gulf onto the Scotian Shelf. The formation and distribution of ice is expected to affect the distribution of grey seals (Stobo et al. 1990, Lavigne and Hammill 1993) by limiting access to

summer haul-out sites, but at the same time drifting pack-ice provides new platforms for hauling out. The presence of sea-ice might favour the expansion of the home range and, consequently, the use of deeper areas since seals can haul-out wherever they want and forage close to productive areas without travelling long horizontal distances to return to a terrestrial haul-out site between foraging bouts. Seasonal variability in distribution is commonly observed in ice-associated marine mammals living in highly variable ecosystems (Lowry et al. 2000, Mauritzen et al. 2001).

Bathymetric features affect the distribution of marine predators and thus they may be related to the distribution of prey resources (Lowry et al. 2000, Guinet et al. 2001). Data on the seasonal variation in fish biomass in the study area are limited. However, there is evidence that some prey eaten by grey seals migrate offshore or towards warmer deeper water in late autumn to avoid the winter cooling in the upper layers of the water column (Chadwick and Sinclair 1991). Winter might be a period of low prey availability compared to summer. If true, this might increase intraspecific competition in shallow depths and might force seals, especially less experienced juveniles, to move toward deep areas and forage over a wider area in winter.

We did not analyse in detail the horizontal overlap in home range between males and females. The visual inspection of their locations suggested that they generally use the same areas, but males preferred deeper areas than females. The shift towards deeper depths in winter was also more pronounced among males than females. Male home ranges in winter were uniformly distributed over water depths of <200 m deep and so were less concentrated in shallow habitats than in summer whereas the preference demonstrated by the smaller females for shallow depths persisted in winter. Segregation in horizontal distribution and variability in home range size between sexes are commonly observed among many sexually dimorphic marine and terrestrial species (Ruckstuhl and Neuhaus 2000, Shannon et al. 2006). Individuals of the smaller sex in both systems are usually more selective while foraging and have smaller foraging areas located in higher quality habitats than larger individuals due to several factors including their higher relative energetic requirements, reduced digestive efficiency, and reproductive constraints (Ruckstuhl and Neuhaus 2000, Beck et al. 2003a, Austin et al. 2004, Breed et al. 2006).

Overlap in habitat use by both sexes persisted at the finer scale of selection. However, although not statistically significant, there is evidence that males and females were distributed differently within their home ranges. Moreover, the two sexes segregated within the water column as males dove more frequently to deep depths than females. Life-history factors place temporal constraints on females, who must rapidly build-up energy reserves after the breeding period and maintain a minimum body condition throughout the year to support foetal growth and lactation (Beck et al. 2003b). The reproductive strategy of males allows them to concentrate their energy accumulation just before the breeding season (Beck et al. 2003b, Sparling et al. 2006). To minimize costs associated with searching for prey, females may concentrate their foraging effort in prey patches located around their haul-out sites and thus in the



shallowest parts of their home range (Boyd 1998). Their intensive foraging behaviour might increase competition for food resources between males and females near the haul-out sites. The response by males might be to forage in deeper portions of their home range or simply to dive deeper to increase their foraging efficiency. The concentration of males in suboptimal foraging areas compared to females has been observed in many terrestrial and sexually dimorphic mammal species (Ruckstuhl and Neuhaus 2000, Shannon et al. 2006).

The challenges facing juveniles are different from those of adults. Juveniles do not accumulate energy to support reproduction, but need to acquire energy for growth. Juvenile home ranges are larger and more variable than those of adults (Sjöberg and Ball 2000, this study). Although the home ranges of juveniles overlapped broadly with those of adults, they were less concentrated in habitats of <50 m. Within the home range, patterns of habitat selection were similar among age classes, but juveniles dove more frequently to deeper depths than adults, particularly during winter. Hence, without investigating space use at both scales simultaneously, we would not have detected that age classes were segregated in their patterns of habitat use. Due to their limited diving ability (Noren et al. 2005), juveniles might not be able to compete efficiently with adults in profitable foraging areas located at proximity to haul-out sites. 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 to acquire food than adults (Sjöberg and Ball 2000, Lowry et al. 2001). Ultimately, this might affect their foraging success, growth and possibly survival.

In our study area, grey seals overlap in distribution with the much smaller harbour *Phoca vitulina* and harp *Phoca groenlandica* seals (<100 kg), and the similar size hooded seal *Cystophora cristata*, 230 kg (Bowen et al. 1987, Kovacs et al. 1996). Harbour seals are concentrated in coastal areas (Lesage et al. 2004), while harp and hooded seals are associated with offshore areas diving frequently to depths of >400 m (Folkow and Blix 1999, Folkow et al. 2004). There are some indications that inter-specific competition at shallow depths between harbour and grey seals might affect the population dynamics of harbour seals (Bowen et al. 2003). Inter-specific competition for resources in offshore areas with harp and hooded seals perhaps limits the use of deep habitats by grey seals.

Generally, grey seals are shallow divers (Sjöberg and Ball 2000, Goulet et al. 2001, Beck et al. 2003a, this study). Among marine mammals, species that dive the deepest and for the longest durations have the greatest oxygen carrying capacity (Halsey et al. 2006). Despite their relatively large size, grey seals might be physiologically limited in their capacity to dive regularly to deep depths. Nevertheless, we demonstrated that the association of grey seals with shallow depths is temporally dynamic and varies at both the horizontal and the vertical scales. These differences in space use strategies might influence foraging success, particularly for juveniles, and may ultimately affect the dynamics of the population through changes in growth rates, age at maturity, and possibly survival.

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