

# Intersexual differences in the postbreeding foraging behaviour of the Northwest Atlantic hooded seal

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**ABSTRACT:** Sexual dimorphism and different reproductive strategies lead males and females to forage differently among a wide range of species. We used dive and location data collected from 23 hooded seals *Cystophora cristata* captured in the Gulf of St Lawrence (Canada) during the period from March to June, 1992 to 2005, as proxies for foraging behaviour. Females spent 12 d longer than males in the Gulf before undertaking their migration to Greenland. Females and males greatly overlapped on a horizontal scale but were segregated on a vertical scale, females diving on average 70 m shallower than males during the few weeks preceding the migration and 40 m deeper than males following the migration. Both sexes spent similar amounts of time diving and showed significant diel variation in dive depth but remained at significant depths at night (>200 m), suggesting that both sexes foraged mostly on benthopelagic prey. The relatively minor differences in foraging behaviour observed between sexes may be explained by similar mass loss during the reproduction and the constraints related to the extensive annual migration.

**KEY WORDS:** *Cystophora cristata* · Sex differences · Foraging ecology · Diving behaviour · Seasonal home range

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## INTRODUCTION

Differences in foraging behaviour between sexes have been observed among a wide range of vertebrates (Bowyer 2004, Baird et al. 2005, Bearhop et al. 2006, Loseto et al. 2006, Rode et al. 2006). Males and females often differ in their activity budget, spatial distribution, or diet quality (Bowyer 2004), and, in many cases, body size dimorphism and different reproductive strategies (for example whether they are capital or income breeders) appear to be the main factors leading sexes to forage differently (Main et al. 1996, Jönsson 1997, Mysterud 2000, Bowyer 2004).

Many large phocid species are sexually dimorphic (Weckerly 1998, Hammill & Stenson 2000, Lindenfors et al. 2002). Furthermore, while phocids are characterized by foraging at sea, they need to return to a solid substrate for reproduction and moulting, where they rely on energy reserves to

sustain either lactation (females) or competition for access to females (males) (Boness & Bowen 1996, Kovacs et al. 1996). Energy stored at the beginning of the breeding period is crucial, since initial body condition is correlated with reproductive success in both females (Pomeroy et al. 1999, Hall et al. 2001, Pistorius et al. 2004) and males (Haley et al. 1994, Lidgard et al. 2005).

Sexual differences in foraging behaviour have been documented among the sexually dimorphic grey seals *Halichoerus grypus*, as well as northern *Mirounga angustirostris* and southern *M. leonina* elephant seals. Among Northwest Atlantic grey seals, where males are approximately 40% heavier than females (males = 291 kg, females = 207 kg; Beck et al. 2003a), there is spatial segregation between males and females, and both sexes differ in their seasonal distribution of foraging effort (Beck et al. 2003a, Breed et al. 2006) and diet composition (Beck et al. 2007, Tucker et al. 2007).

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Females perform longer dives and spend more time diving in smaller and distinctive areas of higher prey abundance than males (Beck et al. 2003b,c, Austin et al. 2004, Breed et al. 2006). Energy requirements to support pregnancy may constrain females to forage on higher quality resources and to start accumulating body reserves earlier in the season, while males accumulate reserves more slowly. Males would benefit from rebuilding reserves as late as possible to reduce the potential costs associated with energy storage and transport (Beck et al. 2003a). Among the much larger elephant seal, where males can be between 1.5 and 10 times heavier than females, depending on whether it is the southern or northern species (southern: males = 3510 kg, females = 503 kg; northern: males = 2275 kg, females = 700 kg; Bininda-Emonds & Gittleman 2000), the sexes show much greater spatial segregation and also differ in their foraging strategies: females show a strong diurnal pattern in dive depths consistent with feeding on pelagic prey, whereas males dive at constant depth feeding on benthic prey (Campagna et al. 1998, 1999, Le Boeuf et al. 2000, Lewis et al. 2006). However, among northern elephant seals, males and females have similar postbreeding energy accumulation patterns (Le Boeuf et al. 2000).

The hooded seal *Cystophora cristata* is the largest phocid in the North Atlantic, with males and females weighing up to 434 and 300 kg, respectively (Kovacs & Lavigne 1992, Kovacs et al. 1996). Northwest Atlantic hooded seals moult on the drifting pack-ice off the southeast coast of Greenland in July, then summer in the Arctic near Greenland, but migrate in late fall to the waters off the east coast of Canada, near Newfoundland (Front), or into the Gulf of St Lawrence (Gulf), where pupping occurs on the pack-ice in March (Sergeant 1976, Hammill 1993). Lactation is extremely short, with pups doubling their weight (from about 22 to 44 kg) and being weaned in only 4 d (Bowen et al. 1985, Kovacs & Lavigne 1992). After breeding, males and females disperse (Hammill 1993).

Little is known about foraging behaviour among mature hooded seals. Normally associated with remote, offshore and heavy ice areas, hooded seals are difficult to study without extensive logistical support in the form of large ships. However, developments in satellite telemetry over the last 10 yr have provided new opportunities to obtain information on how marine predators exploit their 3-dimensional space (Harvey et al. 2008). Here we examine the diving behaviour and distribution of postbreeding hooded seals after the whelping period in the Gulf of St Lawrence, Canada, using satellite telemetry. Based upon their similar size, degree of sexual dimorphism and capital breeding strategy (Kovacs & Lavigne 1992, Kovacs et al. 1996, Jönsson 1997), we hypothesize that

hooded seals would show sex-related differences in foraging behaviour more similar to those observed in grey seals than to those seen in the more sexually dimorphic elephant seals. That is, we would predict that, following the breeding season, females would have smaller individual home ranges in different areas than males and females would perform longer dives, spend more time diving and show a stronger diurnal pattern in dive depth than males.

## MATERIALS AND METHODS

Adult hooded seals *Cystophora cristata* were captured on the sea-ice during the breeding season (March 1992 to 2005) in the Gulf of St Lawrence (approximately 47° 14' N, 61° 51' W). Seals were located by helicopter, then caught and handled using methods described by Kovacs et al. (1996). A satellite-linked, time–depth recording transmitter was glued to their head with a quick-drying epoxy (Cure 5, Industrial Formulators of Canada). Individuals were selected based on the presence of suitable ice to land the helicopter and work safely, as well as the age of the pup. Only females with a fat pup, indicating that it was near weaning, were selected (Bowen et al. 1987).

We used 2 types of transmitters: satellite-linked dive recorders (SDR), SDR-T16 (Wildlife Computers) and satellite relay data loggers (SRDL) series 9000 (Sea Mammal Research Unit [SMRU], University of St. Andrews, Scotland). Both types transmitted data via the ARGOS collection and location system (CLS/Service Argos), but differed in the way that they stored dive information before transmission.

Two similar versions of SDR were used: 0.5W4C (9 × 12 × 2.5 cm; 700 g) and 1W3C (10 × 11.25 × 5 cm; 1100 g) (Table 1). Both transmitters had a capacity of 100 000 transmissions and were programmed to transmit a maximum of 500 times d<sup>-1</sup>. They recorded depths to 500 or 1000 m, with a resolution of 2 and 4 m, respectively. Only dives deeper than 4 m and longer than 10 s were recorded as dives. SDRs were programmed to summarize data every 6 h between 00:00 to 06:00 h (night), 06:00 to 12:00 h (morning), 12:00 to 18:00 h (day) and 18:00 to 24:00 h (evening) UTC (universal time coordinated). We thus used these categories as time periods. For each time interval, the SDR units registered the number of dives performed into 6 dive depth bins (i.e. 4–50, 51–100, 101–200, 201–300, 301–450, >451 m) and 6 dive duration bins (i.e. <2, 2–5, 5–10, 10–15, 15–25, >25 min).

SRDL units (10.5 × 7 × 4 cm; 370 g) provided up to 80 000 transmissions, and recorded depth with a resolution of 0.5 m at 1500 m. Only dives >6 m and >8 s were recorded as dives. Tags were programmed to

Table 1. *Cystophora cristata*. Summary information on the 27 postbreeding hooded seals captured between 1992 and 2005 in the Gulf of St Lawrence, Canada

ID no.	Sex	Deployment date (dd/mm/yyyy)	Type of transmitter	Longevity of the transmitter (d)	Tracking length (d)
8198_92	M	15/03/1992	1W3C SDR SDR	101	85
8199_92 <sup>a</sup>	M	16/03/1992	1W3C SDR SDR	105	85
2016_92	M	17/03/1992	0.5W4C SDR	105	94
3020_92 <sup>a</sup>	M	17/03/1992	0.5W4C SDR	98	78
5059_92	M	18/03/1992	1W3C SDR SDR	87	70
2014_93	F	17/03/1993	0.5W4C SDR	99	94
2015_93	F	17/03/1993	0.5W4C SDR	95	87
2016_93	F	21/03/1993	0.5W4C SDR	99	95
3021_93	F	16/03/1993	0.5W4C SDR	92	87
5053_93 <sup>b</sup>	F	17/03/1993	0.5W4C SDR	98	–
5056_93	F	16/03/1993	0.5W4C SDR	108	103
9315_04	F	14/03/2004	SMRU SLDR	78	70
9338_04	F	14/03/2004	SMRU SLDR	90	80
9255_04	F	16/03/2004	SMRU SLDR	92	82
9256_04	F	14/03/2004	SMRU SLDR	117	94
9317_04	M	18/03/2004	SMRU SLDR	88	81
9324_04	M	16/03/2004	SMRU SLDR	91	82
9335_04	M	16/03/2004	SMRU SLDR	84	68
9336_04	M	16/03/2004	SMRU SLDR	126	91
9351_05	F	12/03/2005	SMRU SLDR	102	91
9353_05 <sup>b</sup>	F	11/03/2005	SMRU SLDR	0	–
9363_05	F	12/03/2005	SMRU SLDR	87	81
9398_05 <sup>b</sup>	F	11/03/2005	SMRU SLDR	0	–
9341_05	M	12/03/2005	SMRU SLDR	111	80
9354_05	M	12/03/2005	SMRU SLDR	103	94
9397_05	M	11/03/2005	SMRU SLDR	97	74
9399_05 <sup>b</sup>	M	11/03/2005	SMRU SLDR	5	–

<sup>a</sup>These individuals were not used for the kernel estimates of individual home ranges as they had <30 locations after filtering

<sup>b</sup>These individuals had defective transmitters and were not used in the analyses

record dive depth and duration of each individual dive and to summarize diving data every 3 h (in UTC starting at midnight). For each 3 h interval, the SRDL units provided mean dive depth, mean dive duration and the number of dives performed.

Dive depth and duration values were computed from SDR bin data assuming that the average dive depth within each bin was equal to the bin midpoint. For each 6 h period, mean dive depth and dive duration values were calculated using the median values of each depth/duration bin (Burns & Castellini 1998). For the upper bins, the upper limit was defined by the maximum dive depth/duration recorded with all SRDL tags.

For SRDL units, we combined the 3 h summary files according to the corresponding SDR 6 h time intervals, i.e. we averaged 2 successive SRDL 3 h periods for dive depth and duration and summed the number of dives. We ended up with 3 diving parameters for each 6 h period for both transmitter types: mean dive depth (m), mean dive duration (min) and number of dives performed. Finally, for each period for which we had both mean dive duration and number of dives, we calcu-

lated the proportion of time spent diving as: time spent diving (%) = (mean dive duration (min) × number of dives per 6 h) / (6 × 60).

The hooded seal breeding patch is normally located over the shallow waters of the Magdalen Shelf, in the southern Gulf of St Lawrence (Hammill 1993). After the pups are weaned, females mate and then leave the shelf area to move into the largely ice-free, deeper waters of the Laurentian Channel. Males, in their search for females, normally spend more time following the patch as it drifts with prevailing currents and winds. Males typically haul-out beside an eligible female and defend access to her from other males (Kovacs 1990). When the pup is weaned, the male follows the female off to the water, mates and then hauls out again to search for additional females (Kovacs 1990). For both sexes there is some shallow diving as females mate and then leave the area and as males continue breeding activities (Kovacs et al. 1996). We excluded this short period associated with breeding from our analyses. This resulted in excluding from the analyses an average of 2 d (SD = 1 d) for females and 11 d (SD = 6) for males.

We filtered location data with the 3-stage algorithm developed by Austin et al. (2003) to remove unrealistic positions based on a travel rate of  $3 \text{ m s}^{-1}$  (Folkow et al. 1996). The tracking period was divided into 3 phases: premigration, migration and postmigration, and we assumed that seals started their migration when they moved in a definite 1-way general direction, without backtracking. Northwest Atlantic hooded seals moult on the pack-ice off the southeast coast of Greenland (Sergeant 1976, Hammill 1993). Therefore, postmigration was defined as the period when seals had reached the moulting area along the Greenland shelf above  $59^\circ \text{N}$ , which is near the southern tip of Greenland.

The area used by seals before migration (i.e. seasonal home range) was estimated by calculating 95% fixed kernels with the Animal Movement Extension (Hooge & Eichenlaub 2000) in Arcview 3.2a (Environmental System Research Institute). We used the least squares cross validation method to select the smoothing parameter (Seaman & Powell 1996). Individual and sex-specific seasonal home ranges were computed. To avoid potential bias associated with location clustering and reduce temporal autocorrelation, we used only locations separated by at least 12 h (Hansteen et al. 1997, De Solla et al. 1999). The minimum sample size required to produce accurate kernel estimates was estimated by comparing kernel area based on different numbers of locations (Seaman et al. 1999, Harvey et al. 2008), and we found that individuals that had at least 30 locations had stable home range estimates.

The overlap between male and female seasonal home ranges was quantified as:  $\text{Overlap}_{\text{FM}} (\text{m}^2) / [\text{HR}_{\text{F}} (\text{m}^2) + \text{HR}_{\text{M}} (\text{m}^2)] - \text{Overlap}_{\text{FM}} (\text{m}^2)$ , where  $\text{HR}_{\text{F}}$  is the size of the seasonal home range of females,  $\text{HR}_{\text{M}}$  is the size of the seasonal home range of males and  $\text{Overlap}_{\text{FM}}$  is the size of the intersection area between the male and female seasonal home ranges. To take into account individual variability in the estimation of the overlap area between male and female seasonal home ranges, we quantified the proportion of individual seasonal home ranges within the sex overlap region (individual contribution).

All statistical analyses were completed using Version 9.1 of SAS (SAS Institute). We compared the duration of the 3 tracking phases between males and females using repeated-measure mixed models with the MIXED procedure and the REPEATED statement in SAS. Tracking phases and sexes were defined as fixed effects, and year was defined as a random effect to take into account potential interannual variability. The REPEATED statement included phase as a within-subject factor and sex  $\times$  year nested in individual as between-subject factors to consider the interdependence of tracking phases within each individual.

The effect of sex was tested on individual home range size and individual contribution to the sex overlap region using linear mixed models with the MIXED procedure. We defined sex as a fixed effect and year as a random effect to consider interannual variability. The effects of sex, tracking phase and time period on mean dive depth, mean dive duration and time spent diving were examined using linear mixed models with the MIXED procedure in SAS. All 2- and 3-way interactions were included, and we selected the most parsimonious model using a backward stepwise procedure. Year was included as a random effect to consider interannual variability in diving behaviour, while individual was included as a random effect to account for repeated measures within individuals. We assumed a compound symmetric variance-covariance matrix for the within-individual error term. The interaction sex  $\times$  year was nested within individual. We interpreted statistical significance with simple effect tests and post hoc multiple comparisons corrected with the Bonferroni method (Zar 1996).

Model fitting was estimated by calculating the squared correlation coefficient between observed and model-predicted values with the CORR procedure in SAS (Kvålseth 1985). For all statistical analyses, we verified assumptions for normality and homogeneity of variances and applied a log transformation on individual home range size to improve normality. Unless otherwise stated, all data are presented as means ( $\pm$  standard errors, SE), and the significance level was 0.05.

## RESULTS

Transmitters were deployed on 27 adult hooded seals *Cystophora cristata* (14 females, F; 13 males, M) (Table 1). Three transmitters (2 F, 1 M) failed and another (1 F) had a gap of 38 d in the data and was not considered in the analyses. Functional transmitters (11 F, 12 M) supplied location and dive data an average of  $98 \pm 5$  d each (Table 1). We received a total of 26 105 locations, and the 3-stage algorithm removed on average  $43 \pm 12\%$  of the locations with no difference between sexes ( $t_{1,21} = 0.49$ ,  $p = 0.5$ ). Once locations were re-sampled with at least 12 h between successive positions, 2 males were present at  $<30$  locations and were subsequently removed from the kernel analyses (Table 1). We obtained an average of  $61 \pm 3$  locations individual $^{-1}$  to estimate individual seasonal home ranges.

Females completed their breeding season earlier than males (F: 19 March [ $\pm 3$  d], M: 27 March [ $\pm 6$  d];  $F_{1,61} = 6.78$ ,  $p = 0.01$ ). Following breeding, both females and males moved from the whelping area to the deep waters of the Laurentian Channel ( $>200$  m deep; Fig. 1).

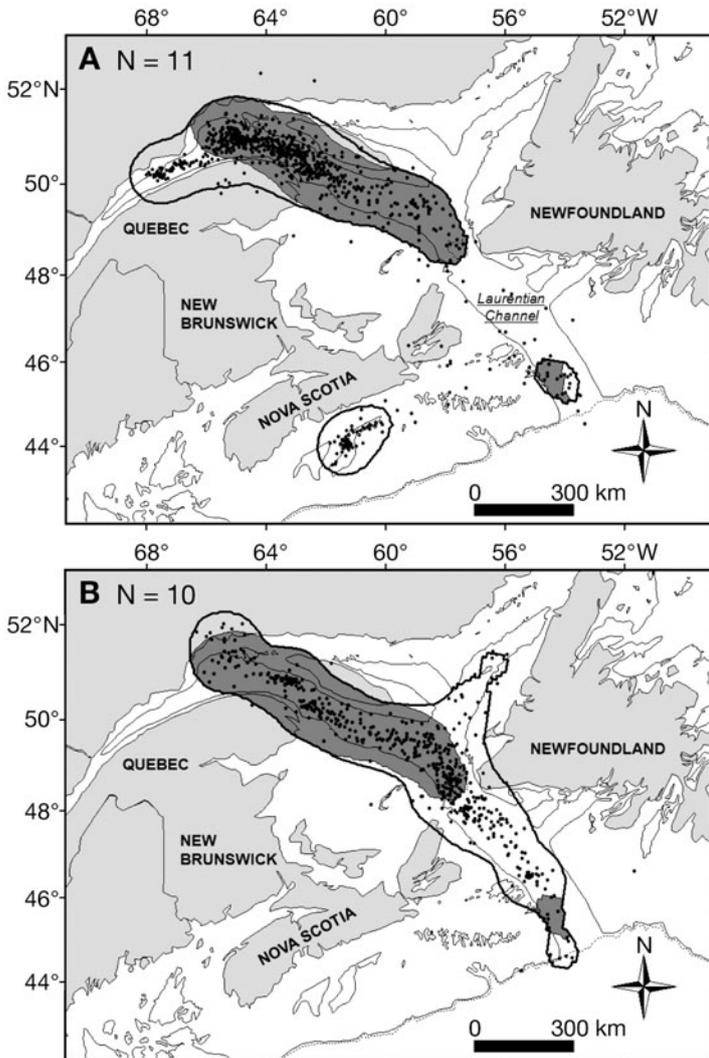


Fig. 1. *Cystophora cristata*. (A) Female and (B) male distribution in the period preceding migration for postbreeding hooded seals captured between 1992 and 2005 in the Gulf of St. Lawrence, Canada. Black dots: observed locations; outer thick black contour line: 95% kernel seasonal home range; dark-grey area: overlap area between female and male seasonal home ranges. Solid and dotted lines in the water: 200 and 500 m isobaths, respectively

Males ranged over an extensive portion of the channel ( $142\,549\text{ km}^2$ ), while females were concentrated in the northern part of the channel, close to the upper limit of the St. Lawrence Estuary ( $119\,625\text{ km}^2$ ). One female left the Gulf and moved onto the Scotian Shelf, off the east coast of Nova Scotia, and spent her time diving over the deeper canyons of this area (Fig. 1). The seasonal home range of both sexes overlapped by 40%. The intersexual overlap area represented 47% of the area used by males and 77% of the area used by females. On an individual level, females and males had similar proportions of their seasonal home ranges

within the intersexual overlap area (F:  $69 \pm 34\%$ , M:  $54 \pm 35\%$ ;  $F_{1,16} = 1.07$ ,  $p = 0.3$ ). Individual home range sizes varied considerably among individuals, but did not differ between females ( $58\,757 \pm 74\,831\text{ km}^2$ ; range =  $9\,333$  to  $273\,084\text{ km}^2$ ) and males ( $47\,118 \pm 56\,223\text{ km}^2$ ; range =  $3\,129$  to  $188\,917\text{ km}^2$ ;  $F_{1,15} = 0.03$ ,  $p = 0.9$ ).

Both sexes started their migration by early May (F: 6 May [ $\pm 10$  d], M: 1 May [ $\pm 11$  d];  $F_{1,61} = 0.50$ ,  $p = 0.48$ ). Overall, females spent 12 d more in the premigration area than males ( $48 \pm 13$  and  $36 \pm 13$  d for females and males, respectively;  $F_{2,38} = 9.10$ ,  $p = 0.004$ ). Of the 23 seals (11 F, 12 M) tracked, most (8 F, 9 M) left the Gulf of St. Lawrence through the Cabot Strait (Fig. 2), the others (3 F, 3 M) moved northward through the Strait of Belle Isle (Fig. 2). From the Cabot Strait, seals moved along the south coast of Newfoundland. Some seals (5 F, 2 M) left the continental shelf, moving directly to the east coast of Greenland (Fig. 2; circles), while others (3 F, 7 M) moved northward along the southern Labrador Shelf (until  $\sim 53^\circ\text{N}$ ) before crossing the Atlantic Ocean to Greenland (Fig. 2; triangles). From the Strait of Belle Isles, most seals (3 F, 1 M) moved in a relatively straight direction to Greenland (Fig. 2; squares). The 2 remaining males moved northward, 1 male going to Davis Strait and the other moving to  $\sim 58^\circ\text{N}$  before crossing the Labrador Sea to Greenland. Migration lasted on average  $27 \pm 6$  d for both sexes ( $F_{2,38} < 0.001$ ,  $p = 0.98$ ).

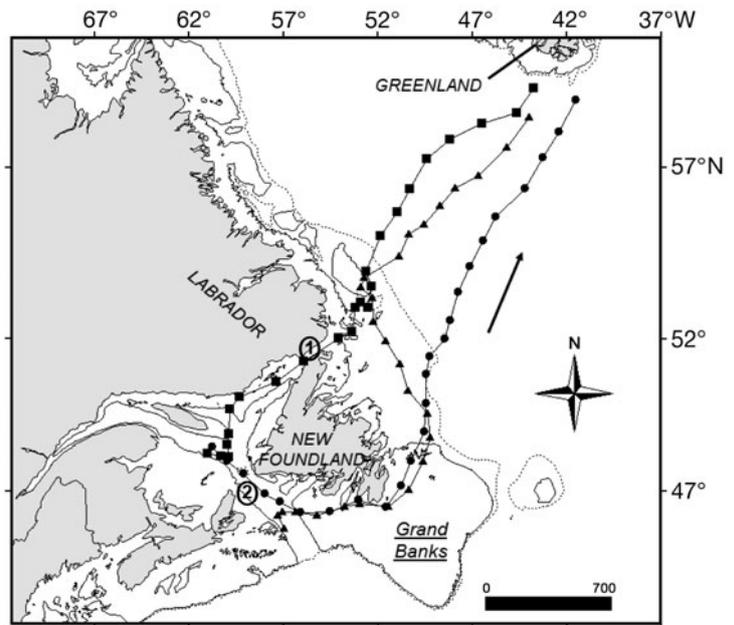


Fig. 2. *Cystophora cristata*. Details of 3 distinctive (typical) migratory tracks from the Gulf of St. Lawrence to Greenland for postbreeding hooded seals. (1): the Strait of Belle Isle; (2): the Cabot Strait. Solid and dotted lines in the water: 200 and 500 m isobaths, respectively

Females and males arrived along the east coast of Greenland by late May (F: 2 June  $\pm 11$  d, M: 30 May  $\pm 12$  d];  $F_{1,61} = 0.31$ ,  $p = 0.6$ ). Both sexes lost their transmitter, probably due to the moult, approximately  $16 \pm 6$  d later in mid-June (F: 15 June  $\pm 11$  d, M: 17 June  $\pm 7$  d];  $F_{1,61} = 1.08$ ,  $p = 0.3$ ) between  $\sim 60$  and  $\sim 66^\circ$  N on the continental shelf around the south-east coast of Greenland (Fig. 3).

There was a significant interaction between sex and tracking phase on dive depth (Table 2). During premigration, male dives were significantly deeper than female dives, while during postmigration, female dives were significantly deeper than male dives (Fig. 4). During migration, females and males dove to similar depths (Fig. 4). Overall, the dive depths of both sexes decreased significantly from premigration to postmigration (Fig. 4). Both sexes also performed deeper dives during daytime than during nighttime, but these diel variations were slightly less pronounced among females than among males (Table 2, Fig. 5). We found a significant interaction between time period and tracking phase on dive depth (Table 2); diel variations were significant during premigration and migration, but not during postmigration (Fig. 6).

There was a significant interaction between sex and tracking phase on dive duration (Table 2). During the premigration and migration phases, females and males did not differ in dive duration, while during postmigration females performed significantly longer dives than males (Fig. 4). In both sexes, dives were longer during migration than during premigration and postmigration, and shorter during postmigration than during premigration (Fig. 4). Both males and females performed longer dives during daytime than during nighttime, but these diel variations were less pronounced among females than among males (Table 2, Fig. 5). There was a significant interaction between time period and tracking phase on dive duration (Table 2); diel variations were significant during premigration and migration, but not during postmigration (Fig. 6).

Sex did not influence time spent diving (Table 2). However, there was a significant interaction between time period and tracking phase on time spent diving (Table 2). Males and females spent less time diving during postmigration than during the 2 other tracking phases (Fig. 6). Both sexes showed diel variations in the proportion of time spent diving during premigra-

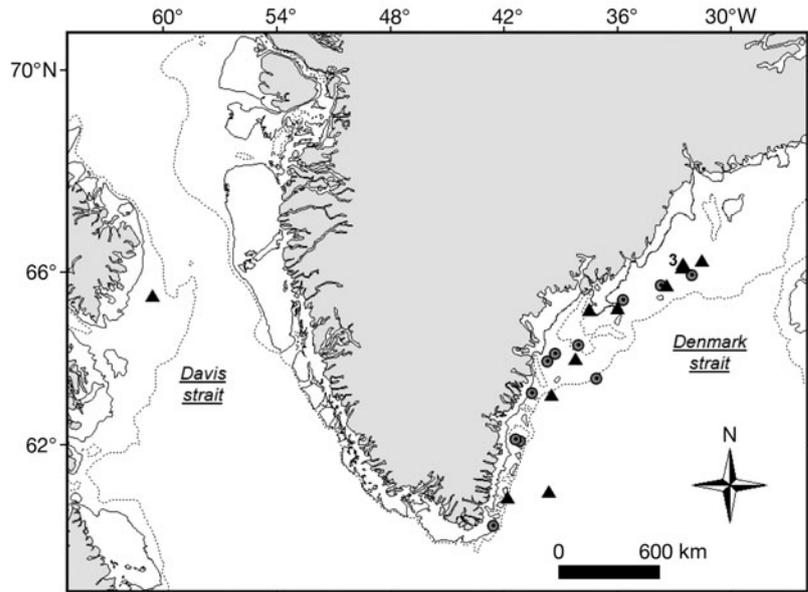


Fig. 3. *Cystophora cristata*. Distribution of the last transmissions of moulting hooded seals near Greenland from mid-May to late June. Females (●) 11 ind.; males (▲) 12 ind. (3 near ▲ indicates 3 superimposed symbols). Solid and dotted lines in the water: 200 and 500 m isobaths, respectively

Table 2. *Cystophora cristata*. Linear mixed models examining the effects of sex, time period (morning: 06:00 to 12:00 h; day: 12:00 to 18:00 h; evening: 18:00 to 00:00 h; night: 00:00 to 06:00 h) and tracking phases (premigration, migration, postmigration) on the mean dive depth, mean dive duration and the proportion of time spent diving in postbreeding hooded seals captured between 1992 and 2005 in the Gulf of St Lawrence, Canada

Model fixed effects	df	F	p-values	R <sup>2</sup>
<b>Mean dive depth</b>				
Sex	21	0.46	0.50	0.26
Period	6567	25.40	<0.0001	
Phase	6567	544.04	<0.0001	
Sex × Period	6567	3.45	0.02	
Sex × Phase	6567	126.75	<0.0001	
Period × Phase	6567	3.64	0.00	
<b>Mean dive duration</b>				
Sex	21	0.15	0.70	0.52
Period	6559	19.50	<0.0001	
Phase	6559	516.20	<0.0001	
Sex × Period	6559	3.56	0.01	
Sex × Phase	6559	112.69	<0.0001	
Period × Phase	6559	3.61	0.001	
<b>Proportion of time spent diving</b>				
Sex	21	0.20	0.70	0.28
Period	6621	3.08	0.03	
Phase	6621	419.51	<0.0001	
Sex × Period	6621	1.02	0.40	
Sex × Phase	6621	0.79	0.40	
Period × Phase	6621	13.95	<0.0001	

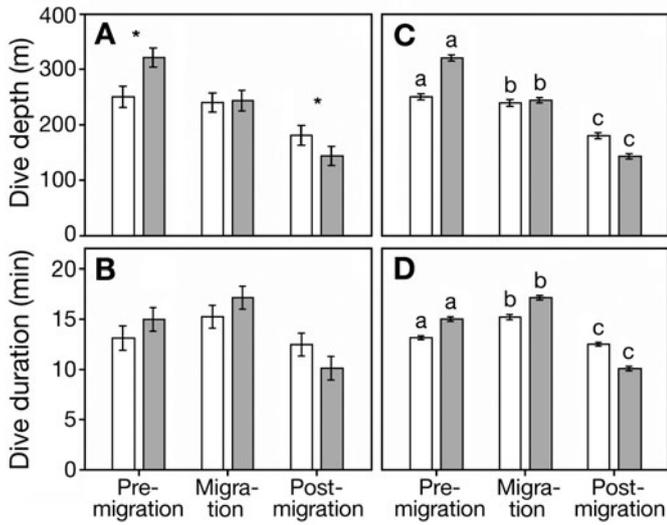


Fig. 4. *Cystophora cristata*. Least square means of (A,C) dive depth and (B,D) dive duration according to sex (white bars: females; grey bars: males) and tracking phase (premigration, migration, postmigration) for postbreeding hooded seals from the Gulf of St Lawrence, Canada. (A,B) Least square means ( $\pm$ SE) used to compare sexes within each tracking phase (asterisks indicate significant differences between sexes). (C,D) Same least square means but with SE used to compare tracking phases within each sex. Different lowercase letters indicate mean dive depths or durations that differed significantly between phases for each sex

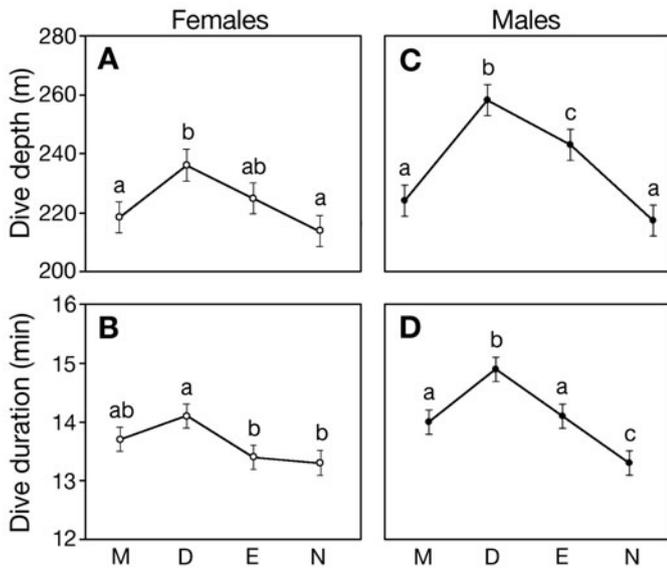


Fig. 5. *Cystophora cristata*. (A,C) Dive depth and (B,D) duration least square means ( $\pm$ SE) for female and male postbreeding hooded seals in the Gulf of St Lawrence according to time of the day: morning (06:00 to 12:00 h, M); day (12:00 to 18:00 h, D); evening (18:00 to 00:00 h, E); night (00:00 to 06:00 h, N). Identical lowercase letters identify mean dive depths or durations that did not differ significantly between diel periods within each sex

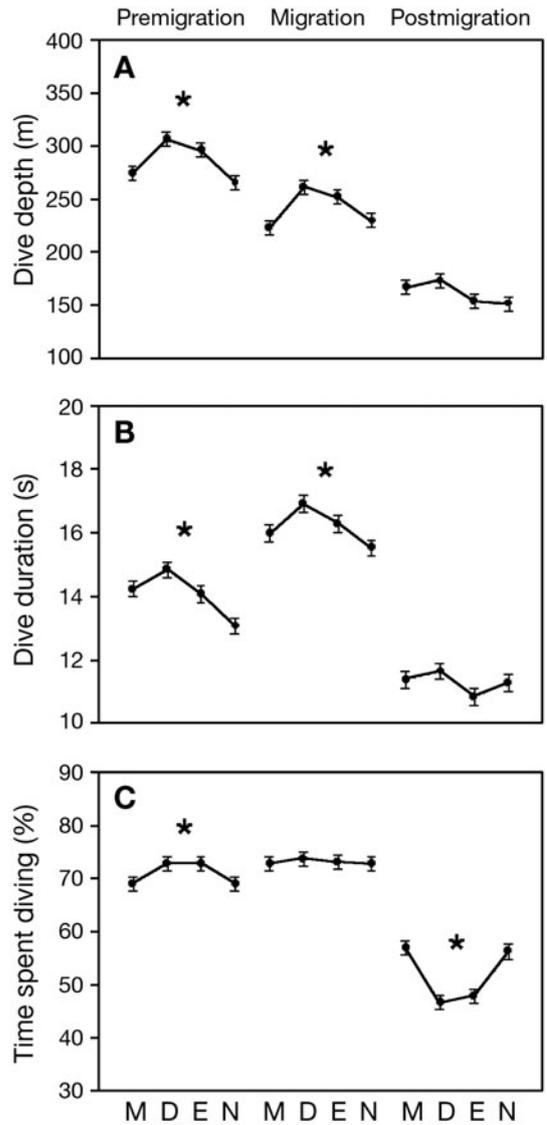


Fig. 6. *Cystophora cristata*. Least square means ( $\pm$ SE) for (A) dive depth, (B) dive duration and (C) time spent diving for postbreeding hooded seals in the Gulf of St Lawrence during 3 tracking phases (premigration, migration, postmigration). Diel periods are morning (06:00 to 12:00 h, M), day (12:00 to 18:00 h, D), evening (18:00 to 00:00 h, E) and night (00:00 to 06:00 h, N). Asterisks indicate significant effects of the period of the day within each tracking phase

tion and postmigration. During premigration, they spent more time diving during daytime than during the nighttime periods, whereas during postmigration both sexes spent significantly more time diving during the night than during the day (Fig. 6). During migration, males and females spent slightly more time diving during the morning and the night than during premigration, but no significant difference was noted (Fig. 6).

## DISCUSSION

We used dive and location data obtained from satellite transmitters to determine whether male and female hooded seals *Cystophora cristata* differed in their postbreeding foraging behaviour. We determined that males and females used similar geographical areas and both performed deep and long dives with a strong diurnal pattern, suggesting that they adopted similar foraging strategies. However, females spent more time in the Gulf of St Lawrence than males before migrating to Greenland. Furthermore, we observed distinct differences between males and females in dive depth and, during the postmigration phase, in dive duration. The overlap in distribution between male and female hooded seals, strong diurnal pattern in diving, timing of arrival in the moulting area and decrease in the proportion of time spent diving as animals move into the ice-covered waters off east Greenland in June are similar to satellite telemetry observations from Northeast Atlantic hooded seals (Folkow et al. 1996, Folkow & Blix 1999), although some interesting differences were also observed. Northeast Atlantic hooded seals dispersed more rapidly and much further from the breeding area, and sex-related differences in dive depths were not observed. However, it is difficult to make more detailed comparisons because the Northeast Atlantic hooded seal study monitored a combination of juveniles and adults, contained few males ( $N = 4$ ) and followed only a few animals during the March to June, postbreeding/premoult period ( $N = 7/15$ ) (Folkow et al. 1996, Folkow & Blix 1999). Grey seals are also found in our study area, but, although hooded seals from the Gulf of St Lawrence regularly dive to depths  $>200$  m and, outside of the breeding season, are largely restricted to the deep water areas of the Laurentian Channel, primarily within the Gulf, postbreeding grey seals perform few dives  $>200$  m, remain over the continental shelf areas and largely exit the Gulf after breeding to spend time on the Scotian Shelf off Nova Scotia (Breed et al. 2006, Harvey et al. 2008).

In many sexually dimorphic phocids, sexes differ in their spatial foraging strategies and use different bathymetric habitats related to differences in prey abundance and quality, or, presumably, differences in predation risk (Le Boeuf et al. 2000, Breed et al. 2006, Harvey et al. 2008). Elephant seals show strong sexual segregation, with males foraging along the northern continental shelf break after breeding, while females forage offshore in the deep open ocean. The areas used by female elephant seals are presumably poorer in terms of prey abundance and quality, but are characterized by a lower risk of predation than those exploited by males (Campagna et al. 1998, 1999, Le Boeuf et al. 2000). Some sexual segregation was

observed among postbreeding grey seals from Sable Island (Canada), with males using deeper waters near the continental shelf and larger home ranges, while females use the mid-shelf region with higher prey availability (Breed et al. 2006). However, considerable horizontal overlap is observed among grey seals from the Gulf, with males preferring deeper waters than females, suggesting some vertical separation (Harvey et al. 2008). Hooded seals seem to closely resemble grey seals of the Gulf, with considerable horizontal overlap in distribution and defined vertical separation in dive depths. Separation between sexes in mean dive depths would reduce intraspecific competition at the vertical scale (Baird et al. 2005). Detailed information on the diet as well as on the distribution and abundance of potential prey of hooded seals in our study area are lacking, but in other areas they feed on capelin *Mallotus villosus* and Greenland halibut *Reinhardtius hippoglossoides*, which are known to be abundant during summer in the area (Gascon 1995, Hammill & Stenson 2000, Bourdages et al. 2002, Haug et al. 2007). Since larger fish generally occur at deeper depths than smaller fish (Macpherson & Duarte 1991, Chouinard & Swain 2002), larger males may feed on larger prey than females.

Female grey seals lose significantly more mass than males during the breeding season (36 vs. 25%; Tinker et al. 1995, Haller et al. 1996). After breeding, females spend more time diving and perform longer dives than males as they begin to increase in mass earlier in the season than males and also forage more selectively on higher quality prey than males (Beck et al. 2003b, 2007). Hooded seals appear to have a lower reproductive effort than grey seals, and both sexes lose similar proportions of body mass during the breeding season (approximately 16%; Kovacs & Lavigne 1992, Kovacs et al. 1996). With the exception of the longer female foraging period in the Gulf prior to migration and vertical separation between the sexes, little difference was observed in diving activity between the 2 sexes, suggesting that both sexes might seek to replace some reserves prior to undertaking the long migration ( $>2000$  km) to Greenland.

Continued diving behaviour during migration, instead of swimming at the surface, has been proposed as a means of reducing drag, while increasing the probability of encountering prey (Williams & Kooyman 1985). The observation that females and males showed diurnal variation in dive depth in migration suggests that both sexes continued to forage while in transit. Once seals had reached the east coast of Greenland, a reduction in diving effort and depth was observed among both males and females, although separation between the 2 sexes was still observed, with females diving to deeper depths than males. The change in

dive depths may be related to changes in prey species as animals began feeding on ice-associated prey such as polar cod *Boreogadus saida*, capelin *Mallotus villosus*, or young squid *Gonatus* sp. that are known to occur in the upper part of the water column in this region (Folkow & Blix 1999, Haug et al. 2007). Upon arrival in Greenland, females and males spent less time overall diving and shifted diving effort to nighttime. The reduction in diving effort and shift to nocturnal dives may be related to animals profiting from warmer daytime temperatures to facilitate moulting (Rasmussen 1960, Ashwell-Erickson et al. 1986).

In summary, intersexual differences in distribution and diving activity among hooded seals were principally characterized by a longer foraging period of females in the Gulf of St Lawrence and significantly deeper dives for males in the Gulf immediately following breeding. Vertical separation between sexes continued, with females performing longer and deeper dives in the moulting area off Greenland, but diving activity of both sexes declined in this area. Given the distances that these animals are capable of covering in a relatively short time, the greater overlap in the spatial distribution of males and females compared to grey seals and northern elephant seals suggests that the limited extent of the channel slope area in the Gulf reduces opportunities for extensive geographic spatial separation, resources may be relatively abundant and widely distributed in the Gulf area, and/or both sexes must undergo some replacement of energy resources before undertaking the long migration to Greenland. Future studies should consider postmoulting individuals in order to determine whether sex differences in foraging behaviour occur during the months leading up to the subsequent breeding season.

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#### LITERATURE CITED

- Ashwell-Erickson S, Fay FH, Elsner R (1986) Metabolic and hormonal correlates of molting and regeneration of pelage in Alaskan harbor and spotted seals (*Phoca vitulina* and *Phoca largha*). *Can J Zool* 64:1086–1094
- Austin D, McMillan JI, Bowen WD (2003) A three-stage algorithm for filtering erroneous Argos satellite locations. *Mar Mamm Sci* 19:371–383
- Austin D, Bowen WD, McMillan JI (2004) Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* 105:15–30
- Baird RW, Hanson MB, Dill LM (2005) Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. *Can J Zool* 83:257–267
- Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar Ecol Prog Ser* 311:157–164
- Beck CA, Bowen WD, Iverson SJ (2003a) Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *J Anim Ecol* 72:280–291
- Beck CA, Bowen WD, McMillan JI, Iverson SJ (2003b) Sex differences in diving at multiple temporal scales in a size-dimorphic capital breeder. *J Anim Ecol* 72:979–993
- Beck CA, Bowen WD, McMillan JI, Iverson SJ (2003c) Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Anim Behav* 66:777–789
- Beck CA, Iverson SJ, Bowen WD, Blanchard W (2007) Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *J Anim Ecol* 76:490–502
- Bininda-Emonds ORP, Gittleman JL (2000) Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses. *Evolution* 54:1011–1023
- Boness DJ, Bowen WD (1996) The evolution of maternal care in pinnipeds. *Bioscience* 46:645–654
- Bourdages H, Archambault D, Morin B, Fréchet A, Savard L, Grégoire F, Bérubé M (2002) Preliminary results from the groundfish and shrimp multidisciplinary survey from August 2002 in the northern Gulf of St. Lawrence. DFO Can Sci Advis Res Doc 2002/090, Canadian Science Advisory Secretariat, Ottawa
- Bowen WD, Oftedal OT, Boness DJ (1985) Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Can J Zool* 63:2841–2846
- Bowen WD, Myers RA, Hay K (1987) Abundance estimation of a dispersed, dynamic population: hooded seals (*Cystophora cristata*) in the Northwest Atlantic. *Can J Fish Aquat Sci* 44:282–295
- Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *J Mammal* 85:1039–1052
- Breed GA, Bowen WD, McMillan JI, Leonard ML (2006) Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc R Soc Lond B Biol Sci* 273:2319–2326
- Burns JJ, Castellini MA (1998) Dive data from satellite tags and time-depth recorders: a comparison in Weddell seal pups. *Mar Mamm Sci* 14:750–764
- Campagna C, Quintana F, Le Boeuf BJ, Blackwell S, Crocker DE (1998) Diving behaviour and foraging ecology of female southern elephant seals from Patagonia. *Aquat Mamm* 21:1–11
- Campagna C, Fedak MA, McConnell BJ (1999) Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. *J Mammal* 80:1341–1352
- Chouinard GA, Swain DP (2002) Depth-dependent variation in condition and length-at-age of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Can J Fish Aquat Sci* 59:1451–1459
- De Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *J Anim Ecol* 68:221–234
- Folkow LP, Blix AS (1999) Diving behaviour of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. *Polar Biol* 22:61–74

- Folkow LP, Mårtensson PE, Blix AS (1996) Annual distribution of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. *Polar Biol* 16:179–189
- Gascon D (1995) Collected stock status reports for 1994: fish stocks in the Gulf of St Lawrence assessed by the Laurentian Channel. *Can Manuscr Rep Fish Aquat Sci* 2335:1–89
- Haley MP, Deutsch CJ, Le Boeuf BJ (1994) Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim Behav* 48:1249–1260
- Hall AJ, McConnell BJ, Barker RJ (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *J Anim Ecol* 70:138–149
- Haller MA, Kovacs KM, Hammill MO (1996) Maternal behaviour and energy investment by grey seals (*Halichoerus grypus*) breeding on land-fast ice. *Can J Zool* 74:1531–1541
- Hammill MO (1993) Seasonal movements of hooded seals tagged in the Gulf of St Lawrence, Canada. *Polar Biol* 13:307–310
- Hammill MO, Stenson GB (2000) Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. *J Northwest Atl Fish Sci* 26:1–23
- Hansteen TL, Andreassen HP, Ims RA (1997) Effects of spatiotemporal scale on autocorrelation and home range estimators. *J Wildl Manag* 61:280–290
- Harvey V, Côté SD, Hammill MO (2008) The ecology of 3-d space use in a sexually dimorphic mammal. *Ecography* 31:371–380
- Haug T, Nilssen KT, Lindblom L, Lindström U (2007) Diets of hooded seals (*Cystophora cristata*) in coastal waters and drift ice waters along the east coast of Greenland. *Mar Biol Res* 3:123–133
- Hooge PN, Eichenlaub B (2000) Animal movement extension to Arcview, Ver 2.0. Alaska Science Center—Biological Science Office, US Geological Survey, Anchorage, AK
- Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78:57–66
- Kovacs KM (1990) Mating strategies in male hooded seals (*Cystophora cristata*)? *Can J Zool* 68:2499–2502
- Kovacs KM, Lavigne DM (1992) Mass-transfer between hooded seal (*Cystophora cristata*) mothers and their pups in the Gulf of St. Lawrence. *Can J Zool* 70:1315–1320
- Kovacs KM, Lydersen C, Hammill MO, Lavigne DM (1996) Reproductive effort of male hooded seals (*Cystophora cristata*): estimates from mass loss. *Can J Zool* 74:1521–1530
- Kvålseth TO (1985) Cautionary note about  $R^2$ . *Am Stat* 39:279–285
- Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PM, Houser DS (2000) Foraging ecology of northern elephant seals. *Ecol Monogr* 70:353–382
- Lewis R, O'Connell T, Lewis M, Campagna C, Hoelzel A (2006) Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*). *Proc R Soc Lond B Biol Sci* 273:2901–2907
- Lidgard DC, Boness DJ, Bowen WD, McMillan JI (2005) State-dependent male mating tactics in the grey seal: the importance of body size. *Behav Ecol* 16:541–549
- Lindenfors P, Tullberg BS, Biuw M (2002) Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behav Ecol Sociobiol* 52:188–193
- Loseto LL, Richard P, Stern GA, Orr J, Ferguson SH (2006) Segregation of Beaufort Sea beluga whales during the open-water season. *Can J Zool* 84:1743–1751
- Macpherson E, Duarte CM (1991) Bathymetric trends in demersal fish size: Is there a general relationship? *Mar Ecol Prog Ser* 71:103–112
- Main MB, Weckerley FW, Bleich VC (1996) Sexual segregation in ungulates: new directions for research. *J Mammal* 77:449–461
- Mysterud A (2000) The relationship between ecological segregation and sexual body size dimorphism in large herbivores. *Oecologia* 124:40–54
- Pistorius PA, Bester MN, Lewis MN, Taylor FE, Campagna C, Kirkman SP (2004) Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *J Zool (Lond)* 263:107–119
- Pomeroy PP, Fedak MA, Rothery P, Anderson S (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *J Anim Ecol* 68:235–253
- Rasmussen B (1960) On the stock of hood seal in the northern Atlantic. *Fisken Havet* 1:1–23
- Rode KD, Farley SD, Robbins CT (2006) Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87:2636–2646
- Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085
- Seaman DE, Millsbaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. *J Wildl Manag* 63:739–747
- Sergeant DE (1976) History and present status of populations of harp and hooded seals. *Biol Conserv* 10:95–118
- Tinker MT, Kovacs KM, Hammill MO (1995) The reproductive behavior and energetics of male gray seals (*Halichoerus grypus*) breeding on land-fast ice substrate. *Behav Ecol Sociobiol* 36:159–170
- Tucker S, Bowen WD, Iverson SJ (2007) Dimensions of diet segregation in grey seals *Halichoerus grypus* revealed through stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ). *Mar Ecol Prog Ser* 339:271–282
- Weckerley FW (1998) Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J Mammal* 79:33–52
- Williams TM, Kooyman GL (1985) Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiol Zool* 58:576–589
- Zar JH (1996) *Biostatistical analysis*. Prentice Hall, London

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