Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula

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Abstract

We quantified the winter and spring movement patterns and foraging behavior of adult crabeater seals (*Lobodon carcinophagus*), and the influence of sea ice and bathymetry on their foraging behavior. Thirty-four seals (16 M 18 F) were outfitted with Satellite Relay Data Loggers (SRDLs) in the Marguerite Bay Region of the Antarctic Peninsula (~67°S, 67°W) during the austral winters of 2001 and 2002. Tags transmitted position and dive information for between 4 and 174 days. Overall, winter activity patterns differed significantly from previously reported data collected during the summer: seals in this study dived deeper (92 ± 0.2 m, range 6–713 m) and longer (5.26 min ± 0.6, range 0.2–23.6 min), hauled out during the night rather than the day, and showed seasonal shifts in foraging patterns consistent with foraging on vertically migrating prey. While these patterns were more pronounced in 2001 than in 2002, there were no strong differences in patterns of habitat use between the 2 years. Some animals made long distance movements (furthest movements 664 km to northeast, 1147 km to southwest), but most seals remained within 300 km of their tagging location. Within the Marguerite Bay/Crystal Sound region, seals appeared to favor foraging locations on the continental shelf within the 50 to 450 m depth range, with a tendency to avoid depths of 600 m or greater. In both years, seals remained deep within the pack ice throughout the winter, and did not move into regions with less ice cover. Seals were more likely to be located in shallow water where the bathymetric gradients were greatest, and in areas of higher

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sea-ice concentration. In combination, these findings suggest that crabeater seals alter their behavior to accommodate seasonal and/or annual fluctuations in seasonal sea ice and associate with bathymetric features likely to concentrate prey patches.

1. Introduction

The pack ice region surrounding Antarctica is home to six species of pinnipeds (Antarctic fur seal, *Arctocephalus gazella*, crabeater, *Lobodon carcinophagus,* Weddell, *Leptonychotes weddellii*, Ross, *Ommatophoca rossii,* leopard, *Hydrurga leptonyx*, and Southern elephant, *Mirounga leonina,* seals) that account for much of the world's total pinniped biomass (Laws, 1977, 1985). As a group, these species are among the dominant predators in the Southern Ocean, and as such, changes in their abundance or distribution will likely influence the trophic structure of the Southern Ocean (Laws, 1985; APIS, 1995; Costa and Crocker, 1996; Hofmann et al., 2002). At the same time, shifts in the trophic structure of the Southern Ocean due to natural or anthropogenic impacts can influence the foraging behavior, reproductive success, and survival of these apex predators (Bengtson and Laws, 1985; Testa et al., 1991; Lunn et al., 1994; Guinet et al., 1994). Recent studies have focused on how researchers might use demographic or behavioral changes in apex predators as indications of ecosystem events (Boyd and Murray, 2001; Hindell et al., 2003), and linking shifts in predator and prey dynamics with environmental variability is a key goal of the US Southern Ocean GLOBEC (GLOBal ocean ECosystems dynamics) research program (Hofmann et al., 2002). However, for these efforts to be successful we must have information on how animals locate and utilize the resources available to them, and how such use varies temporally and spatially.

Marine mammals are not randomly distributed throughout the habitat, but instead are concentrated in more productive waters. As a result, predator distributions have been used as indices of resource availability (van Franecker, 1992; Ancel et al., 1992). However, not only do predator distributions track those of their prey, but for many species, regions of highly localized productivity appear critical for reproductive success and population growth (Costa, 1991; Trillmich et al., 1991; Guinet et al., 1994; Trathan et al., 1996; Boyd and Murray, 2001). Within Antarctic waters, higher predator densities are often seen in polynyas and local eddies (Trathan et al., 1993), at frontal systems and thermal layers (Boyd and Arnbom, 1991; Field et al., 2001), near sea mounts and the continental shelf break (McConnell et al., 1992; Guinet et al., 2001), and in association with certain characteristics of the marginal ice zone (Kawaguchi et al., 1986; Trathan et al., 1996; Ichii et al., 1998). Many of these oceanographic features physically aggregate prey, and therefore create areas where predator foraging efficiency can be increased. However, during the Antarctic winter, resident predators face reduced productivity, increased ice cover, altered hydrographic regimes, and concomitant changes in prey abundance and availability. The strategies marine mammals use to survive in this altered foraging landscape are poorly understood, but likely depend on the magnitude of the seasonal fluctuations and the diving capabilities of the predators.

Crabeater seals are well suited for investigations of relationships between seasonal variation in foraging behavior, habitat use, and environmental conditions. Crabeater seals are abundant, year-round residents of the Antarctic pack ice, and they forage primarily on Antarctic krill (*Euphausia superba*) (Laws, 1985). Krill is a patchily distributed prey resource that varies in abundance and energy content due to seasonal shifts in environmental conditions (Siegel, 1988; Sprong and Schalk, 1992; Trathan et al., 1993; Ichii et al., 1998; Lascara et al., 1999). Therefore, crabeater seal behavioral strategies are likely to change seasonally in response to the same factors that influence krill populations. Previous research has indicated that crabeater seal populations are sensitive to environmental fluctuations (Testa et al., 1991; Bester et al., 1995; APIS,

1995; Bengtson and Laws, 1985), and that individuals are often found in areas where krill abundance is higher (Nordøy et al., 1995; McMahon et al., 2002). However, most models of habitat selection rely on ship-based abundance surveys rather than individual movement patterns, and therefore focus on summertime patterns. To date, information on crabeater seal ecology during winter is largely absent.

Here, we characterize the wintertime diving and movement patterns of crabeater seals diving within the Marguerite Bay region of the Western Antarctic Peninsula (Fig. 1), with an emphasis on seasonal and spatial variation. We focus on seasonal shifts in the depth, duration, and timing of dives, and on how bathymetry and ice cover influence habitat use. We then relate seal behavior to data on prey abundance as determined by other Southern Ocean GLOBEC researchers. Our goal throughout is to determine how seals are selecting foraging locations and exploiting prey in a changing landscape. Because of their large numbers and high biomass, crabeater seals are perhaps the largest consumer of krill in the Antarctic

(Hewitt and Lipsky, 2002), and information on wintertime foraging tactics is critical for the ecosystem modeling efforts that are an ongoing component of the Southern Ocean GLOBEC program.

2. Methods

2.1. Animal handling

Crabeater seals were captured during four research cruises (23 April–6 June and 21 July–1 September 2001; 7 April–21 May and 29 July–19 September 2002) to the Marguerite Bay Region of the Antarctic Peninsula (~67°S, 67°W) by the *A.S.R.V. Lawrence M. Gould*. Seals were sighted from the bridge, approached on foot or by inflatable boat, and sedated by an intramuscular injection of Telezol (0.8–1.2 mg kg^{-1}, autumn 2001) or Midazolam (0.39–0.84 mg kg^{-1}; Hoffmann–La Roche Inc., NJ, USA, all subsequent cruises). Following induction, animals were restrained manually with a hoop net, and isoflurane
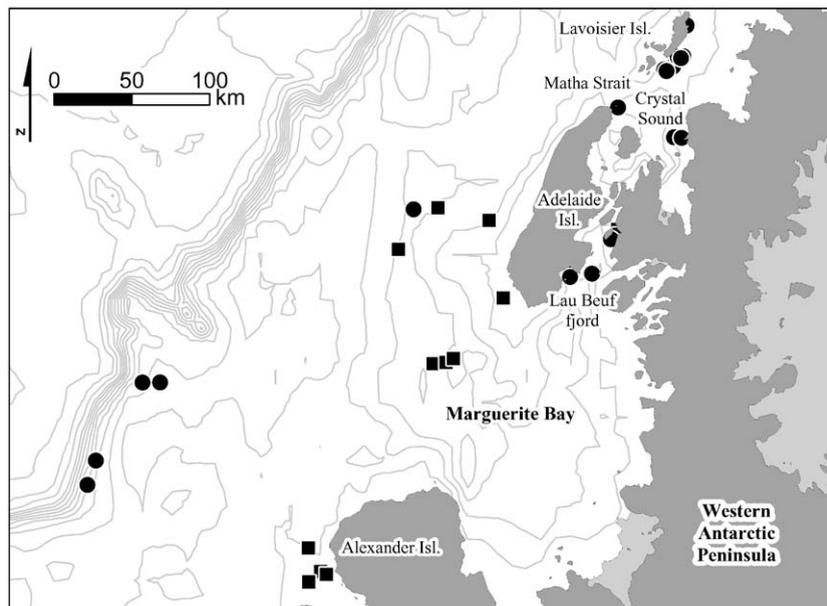
Fig. 1. Location of satellite tags deployed on crabeater seals within the Marguerite Bay study region in 2001 and 2002. Tags deployed in 2001 are indicated by ■, 2002 by ●. Key places mentioned in the text are also indicated, and contour lines are shown at 200 m intervals.

was delivered at 0.5–5% with 4–5 L min^{-1} oxygen flow using a non-rebreathing Bain circuit (LMG-01-04) or a circle rebreathing circuit (LMG 01-06, 02-03, 02-04) via gas mask or intubation (Gales and Mattlin 1998). Once animals were quiescent, morphometric measurements (mass $\pm$ 0.5 kg, length and girth $\pm$ 3 cm) were collected and a satellite-relay data logger (SRDL, manufactured by the Sea Mammal Research Unit, University of St. Andrews, Scotland) was attached to the head using Devcon^{TM} 5-min epoxy. After completion of all procedures, animals were allowed to recover from anesthesia and released. All animal handling protocols were authorized under US Marine Mammal Permit #1003-1665-00 and approved by Institutional Animal Care and Use Committees at University of Alaska Anchorage and University of California Santa Cruz.

2.2. Satellite relay data logger programming

The SRDL tags were programmed to collect data on a range of activity patterns. Tags recorded dive depth, start time, duration, and post-dive surface intervals (4 s sampling frequency), and the start time and duration of haulouts. In addition, for each four-h period of the day, tags recorded the percent time the animals spent hauled out, in water (<6 m depth), and diving (activities >6 m depth), the total number of dives made, and the average depth and duration of all dives in that period. Depth was transmitted with a resolution that increased from 3 to 24 m (3 m surface to 50 m; 24 m once dives exceeded 375 m), to a maximum depth reading of 712.5 m. Dive duration was transmitted with a resolution ranging from 6 s for dives shorter than 9 s, to 48 s once dives exceeded 741 s, with a maximum duration of 1413 s. Dive data were transmitted every 45 s when the animals were on the surface at sea, and at 80 s intervals during the first 2 h of each haulout. Tags then cycled 3 h 'off', 2 h 'on' for the remainder of the haulout, with a maximum of 500 transmissions per day. The ARGOS system calculated animal position from received transmissions (Service Argos, 1996). Since positions were time-referenced, it was possible to determine the approximate location of all dives. Additional tag

programming details have been previously published (Fedak et al., 2001, 2002). All time variables were collected in Greenwich Mean Time (GMT) and corrected for local time based on the geographic position of the seal at that time (local solar time = GMT + degrees longitude/15).

2.3. Activity patterns and dive frequency

Activity patterns and dive frequencies were determined only for those days when data were received from all 6-h periods. This summary information was then used to determine the percent time that individual seals spent in three different activity states: hauled out, in water but at the surface (<6 m) and diving (>6 m) each day. All proportions were arcsin transformed ($p' = $ arcsin $\sqrt{p}$) prior to analysis. Linear, mixed-effects, repeated measures analyses were used to determine the impact of period of day and month on the activity patterns of individual seals (SPSS$^{©}$ 11.5). Since light levels changed dramatically across the seasons, not all periods were similar (i.e. light levels 4–8 a.m. were lower in July than October). Therefore month was treated as the primary fixed factor and period was nested within month. Each year was treated separately due to the differential temporal coverage in 2001 (May–November) and 2002 (April–September). We used an autoregressive moving average covariance structure and a random intercept term. Bonferroni adjusted confidence intervals were used to compare the estimated marginal means for the modeled factors (significance assumed at $P < 0.05$).

2.4. Haulout patterns

The start and end time of all haulouts was determined, and the average haulout start, end, duration, and interval was then calculated for each seal in each month of the study. The average start and end time of all haulouts was determined using the circular statistics analysis package Oriana 1.0 (Kovach Computing Services, UK), and these data used to test the effect of month and year in a two-way analysis of variance (ANOVA).

2.5. Dive data analysis

To control for the abundance of short and shallow dives, and because dive depth and duration were bimodally distributed, dives were separated into two categories: dives $\leqslant 24$ m and dives > 24 m, where 24 m was the minimum value between the two depth distributions. This separation resulted in three positively skewed distributions: depth and duration of dives $\leqslant 24$ m, and depth of dives > 24 m. The duration of dives > 24 m was normally distributed. All skewed distributions were log-transformed prior to analyses. To remove internal data-processing errors that were present in a few of the 2002 tags, dives that required ascent or descent swim speeds in excess of $6 \, \mathrm{m \, s^{-1}}$ were removed from the data set. This cutoff speed is more than double the average swim speeds of most phocids (Williams, 2002), making it a highly conservative criterion.

To test for diel and seasonal effects on dive behavior, the average depth and duration of dives were determined for each individual seal in each hour of each month. As with activity patterns, these mean values were analyzed using a linear mixed-effects repeated measures model, with seal as the subject, an autoregressive moving average covariance structure, and a random intercept term. In these analyses, month was treated as the main term, hour was nested within month, and the measure was the mean value for each individual seal for that month and hour. Cases with fewer than five dives were omitted from the analyses, and separate analyses were run for each year and dive category. To identify significant differences within factors marginal means were compared, using Bonferroni adjustments of the confidence intervals to account for the number of internal comparisons (Sokal and Rohlf, 1995). All statistical analyses of dive data were carried out in SPSS 11.5 (SPSS Inc., USA).

2.6. Spatial analysis

Information received from the tags was integrated into Access databases, and exported into Interactive Data Language (IDL 5.0, Research Systems, Inc) and ArcGIS (ESRI, Inc., USA) for analysis. Locations were screened by an iterative forward/backward averaging filter that identified and excluded locations that would require rates of travel greater than $4 \, \mathrm{m \, s^{-1}}$ (Vincent et al., 2002). The maximum distance traveled was calculated as the difference between the original tagging location and the furthest average daily position.

Habitat-use patterns were assessed by determining the overall percent time that all seals spent in different regions of the study area, and then comparing this usage data with the physical characteristics of the habitat. To determine usage, the study area was divided into 5×5 km ($25 \, \mathrm{km^2}$) raster grid cells, and the time spent in each grid cell determined by interpolating between locations assuming constant average speed. This allowed us to determine the seal's putative time of entry and exit for each cell along the trajectory. A spatial grain of 5 km was chosen because (1) finer grains (i.e., < 5 km) would have made the summary of spatial data (water depth, sea ice concentration) difficult due to the different spatial scale between seal use and sea ice concentration, (2) finer grains would have made it impossible to determine the variance of depth and prevented the use of depth as a covariate in a general linear model, and (3) this scale provided a method of summarizing overall use from all sampled seals within a single spatial unit. Once entry and exit times were determined for each individual animal, the overall percent of time spent in each grid cell was determined for all animals combined, for each month of the study. All routines were processed in IDL (Bradshaw et al., 2002).

To determine if seals were actively selecting regions with particular depth or sea-ice characteristics, we examined the relationship between the percent time spent in each grid cell, and the depth and percent ice concentration. Bathymetry was determined using the ETOPO2 Global 2′ elevations, and there were a mean of 4.8 ETOPO2 bathymetry estimates per 5×5 km grid cell. This allowed both the mean and standard error of the depth per cell to be calculated. Data on the monthly sea-ice concentration were acquired from the Defense Meteorological Satellite Program (DMSP) Special Sensor Microwave/Imager (SSM/I) from the National Snow and Ice Data

Center (NSIDC) in Boulder, Colorado, and the bootstrap algorithm monthly sea-ice concentrations from the F13 instrument (Comiso, 1990) was used to obtain concentrations from 0% (open water) to 100% (closed ice cover) in every 25 km grid cell in the region surrounding Antarctica. Because the grain size for ice was larger than for seal use, 50 km × 50 km grid cells for sea ice were generated from the point data. Polygons of seal habitat usage were then overlaid onto the sea-ice polygons and the mean value of sea ice per grid cell of seal usage was calculated. Thus, many 5 × 5 km grid cells of usage had identical sea-ice concentration estimates (e.g., within cell variance in sea-ice could not be estimated).

Once the mean seafloor depth, most common sea-ice concentration, and the time spent in each grid cell were tabulated, the total time spent for all seals was determined within each pre-defined habitat class. These classes were based on the distribution of habitat types available. For bathymetry, we divided the habitat into 100-m depth classes (e.g., 0–49 m = '0' m class, 50–149 m = '100' m class, etc.), but because seals spent very little time in depth classes $\geqslant 700$ m, only those classes < 700 m were considered. For sea-ice concentration, we summarized the mean monthly sea-ice concentrations into classes of 10% cover (e.g., 0–19% ice cover, thereafter in 10% increments), and so considered a total of nine ice habitat classes. The amount of time that seals spent in each grid was the index of habitat use.

Habitat availability was determined by assuming that the distribution of all sampled seals represented the maximum dispersal capability within a specific time period (e.g., year; month). All grid cells occupied within a specific time period were outlined with a minimum convex polygon (MCP; White and Garrott, 1990). The resulting area was used to define the boundary of the 'available' environmental variable (bathymetry or sea ice) during that time period. For example, selection for sea-ice was determined by comparing the time spent per sea ice class to the mean sea ice available within the MCP area as defined for that month. For these analyses, the MCPs for the 2 years were combined so as to have the largest range of ice types available.

Habitat selection was determined by comparing modified Bonferroni-corrected 95% confidence intervals for the use and availability, as estimated for each depth and sea-ice concentration class (Neu et al., 2002). For each class, the 95% confidence intervals for both the proportion used and availability were calculated as

$$P_i \pm z_{\alpha/2k}\sqrt{\frac{P_i(1 - P_i)}{t}},$$

where P_i is the proportion of habitat type i (depth or sea-ice class) used or available, $z_{\alpha/2k}$ is the upper standard normal variate corresponding to a probability tail area of $\alpha/2k$, k is the number of habitat classes, and t is the total number of use hours estimated from the IDL output routines per month (sea-ice) or per year (bathymetry). When the lower 95% confidence interval for use exceeded the upper 95% confidence interval for availability, that habitat class was said to be significantly selected. When the upper 95% confidence interval for availability was less than the lower 95% confidence interval for use, that habitat class was said to be significantly avoided. When the 95% confidence interval for availability fell within the 95% use confidence interval, that habitat type was said to be used randomly with respect to its availability.

To determine if the amount of time that the seals spent in different areas of the habitat varied in response to physical characteristics of the environment, we examined the relationship between the time spent per 5 × 5 km grid cell, the study year, and the mean depth, standard error of depth, sea ice concentration using a generalized linear model (the GENMOD procedure in SAS 6.11 with a Poisson error model and a log link; McCullagh and Nelder, 1989; McMahon et al., 2002). This effort differs from that described above, as it focuses solely on the cells used by seals, and does not address the availability issue. The number of hours crabeater seals spent per grid cell and the mean depth per grid cell were log-transformed to normalize the data and reduce heteroscedasticity. For the estimated sea-ice concentrations, the angular transformation ($x' = \arcsin\sqrt{x}$) was used. The standard error of the depth estimate was used as a surrogate for bathymetric gradient. We chose

the most parsimonious model by examining all months together, and removing variables (year, depth, SE_{depth}, sea-ice) in a stepwise fashion. The change in deviance was assessed using χ^2 comparisons (McMahon et al., 2002). The resulting model was then applied to each winter month separately.

3. Results

3.1. Animal handling and tag performance

During the four Southern Ocean GLOBEC cruises we captured 46 crabeater seals (24 M, 22 F; 14 in 2001, 29 in 2002), and instrumented 34 seals (18 F, 16 M) with SRDLs (Fig. 1, Table 1). Animals ranged in mass from 113 to 413 kg, and all but the smallest female were judged to be 2 years or older based on mass and standard length (Laws et al., 2003). Animals were easily approached, and reacted well to handling procedures (mean handling time 114 ± 7 min). No adverse effects due to anesthesia protocols were noted. Scats collected from ice floes used by seals in 2001 contained only krill, while those from 2002 contained hard parts from both krill and fish, indicating that crabeater seals in the Marguerite Bay region were occasionally supplementing their zooplankton diet with fish.

The SRDL tags transmitted data for between 4 and 174 days (Table 1). In most cases, transmission failure could be attributed to antenna loss, as signal strength decreased and the proportion of successful transmissions declined prior to reception of the last transmission. Because tags deployed in autumn transmitted for longer than those deployed in winter (84.1 ± 14.7 vs. 47.7 ± 6.5 days), and tags deployed in the relatively lighter ice year (2001) lasted longer than those deployed in the heavier ice year (2002) ($72.6.1 \pm 9.4$ vs. 57.2 ± 12.6 days), we hypothesize that failure was due to antenna wear against the ice. When still functioning properly, we received an average of 21 (1–42) positions per day from the tags, of which an average of 15 (1–32) passed through the position screening algorithms. In total, we received information on 104–440 dives in 2001 and 46–751 dives in 2002. Data-processing errors resulted in the removal of 0.97% of the dives from the 2002 record.

3.2. Activity patterns

Overall, seals spent $29.7 \pm 8.8_{(SD)}\%$ of their time at the surface, $45.2 \pm 11.6\%$ diving, and $25.1 \pm 14.4\%$ hauled out. While all three activity patterns varied by month and period, the pattern was similar between years (Fig. 2). The proportion of time seals spent at the surface varied by month in both 2001 and 2002 (2001: $F_{6,104.6} = 5.370$, $P < 0.001$; 2002: $F_{6,51.7} = 3.129$, $P = 0.011$), with a decrease as the season progressed and ice formed. In addition, the proportion of time spent at the surface varied by time of day in both years (2001: $F_{35,94.3} = 1.948$, $P = 0.006$; 2002: $F_{35,81.3} = 2.596$, $P < 0.001$). The pattern was similar across months, with seals spending the least amount of time near the surface in midday, and the most at night.

The proportion of time spent hauled out increased significantly as the season progressed in 2001 but not in 2002 (month effect 2001: $F_{6,43.2} = 2.480$, $P = 0.038$; 2002: $F_{6,55.4} = 1.791$, $P = 0.118$). However, time of day significantly influenced time spent hauled out within each month in both study years (Period (month) 2001: $F_{35,87.3} = 2.115$, $P = 0.003$; 2002: $F_{35,102.1} = 2.959$, $P < 0.001$). Haulout was more common in early morning from May to July, and in late afternoon September to November. These effects were not solely due to the long haulout by seal G010 (discussed below) for they persisted when she was excluded from the data set.

The proportion of time spent diving (>6 m) varied by time of day in 2001 and 2002 (2001: $F_{35,125.9} = 3.516$, $P < 0.001$; 2002: $F_{35,105.4} = 2.042$, $P = 0.003$), with a greater proportion of dives around midday from April to June, and around midnight from September to November. Time spent diving also varied by month in 2001 (month: $F_{6,68.4} = 3.636$, $P = 0.003$) largely due to a decline in the proportion of time spent diving in October and November. There was no effect of month in 2002.

The mean number of dives made per day varied by year, month, and period of day. Overall, seals in 2001 made fewer dives than seals in 2002 ($119 \pm 40_{(SD)}$ vs. 188 ± 42 dives day^{-1}, $t_{31} = 4.854$,

Table 1
Summary information on crabeater seals outfitted with SRDL tags, showing sex, mass, and the first and last dates of data transmission for seal behavior or location

Seal ID	Sex	Mass (kg)	First transmission	Last transmission	Deployment days
G001	Female	—	5/7/2001	10/1/2001	147
G002	Male	287[a]	5/11/2001	10/22/2001	164
G003	Female	258[a]	5/11/2001	10/31/2001	173
G004	Male	342[a]	5/23/2001	8/26/2001	95
G005	Female	293[a]	5/23/2001	9/24/2001	124
G006	Female	413[a]	5/23/2001	9/6/2001	106
G007	Male	287[a]	5/23/2001	10/8/2001	138
G008	Female	355[a]	5/25/2001	6/18/2001	24
G009	Male	179.0	8/2/2001	9/23/2001	52
G010	Female	307.0	8/6/2001	11/29/2001	115
G011	Male	232.0	7/30/2001	11/18/2001	111
G012	Female	288.0	8/6/2001	9/14/2001	39
G013	Male	234.0	8/7/2001	10/24/2001	78
G014	Male	284.0	8/10/2001	11/18/2001	100
G015	Male	234.0	8/15/2001	10/21/2001	67
G016	Female	273.0	8/22/2001	10/18/2001	57
G017	Female	117.5	4/15/2002	5/23/2002	38
G018	Male	156.5	4/15/2002	04/27/02	12
G019	Female	155.5	4/15/2002	4/22/2002	7
G021	Male	270.5	4/17/2002	8/1/2002	106
G022	Female	268.0	4/20/2002	9/17/2002	150
G023	Male	174.0	4/23/2002	6/10/2002	48
G024	Female	256.0	4/27/2002	10/1/2002	157
G026	Female	266.0	4/27/2002	10/24/2002	180
G031	Female	385.0	8/6/2002	9/24/2002	49
G033	Female	267.5	8/6/2002	10/4/2002	59
G034	Female	294.5	8/6/2002	9/17/2002	42
G035	Female	238.0	8/7/2002	8/12/2002	5
G036	Female	207.0	8/7/2002	9/13/2002	37
G038	Male	273.0	8/9/2002	8/20/2002	11
G039	Male	246.5	8/12/2002	10/25/2002	74
G040	Male	301.5	8/13/2002	9/7/2002	25
G041	Male	269.0	8/13/2002	8/25/2002	12
G042	Male	224.0	8/17/2002	10/16/2002	60

[a]Due to equipment failure, mass was calculated based on length and girth following Laws et al. (2003).

$P < 0.001$). In both years, month had a significant impact on dive frequency (2001: $F_{6,61.9} = 2.673$, $P = 0.023$; 2002: $F_{6,53.7} = 2.850$, $P = 0.018$), with dive frequency higher in October and November in 2001, and lower in September 2002. While the diel pattern was similar in both years, the time of peak diving activity changed across the months (significant period by month effects 2001: $F_{35,90.1} = 3.202$, $P < 0.001$; 2002: $F_{35,89.6} = 2.092$, $P = 0.003$). Dives were more frequent around local noon between April and July, but least frequent around noon from September on. However the pattern was less evident in 2002 than in 2001 (Fig. 3).

3.3. Haulout patterns

During this study crabeater seals hauled out 1440 times. One haulout was unique: adult female G010 hauled out for 607 h from 14 October to 8 November 2001; this behavior likely reflects

parturition and lactation. Other than this single long haulout, most haulouts were shorter than 24 h (mean 8.0 ± 0.7 h, with only eight events lasting

longer than 24 h). On average, haulouts occurred once a day (mean interval 26.9 ± 1.7 h). There was no difference in haulout duration or intervals due to month or year. However, the timing of haulouts shifted during the study period. Before midwinter (April–July), seals hauled out in the late afternoon ($16:45 \pm 0:16$), and returned to the ocean in the early morning ($3:04 \pm 2:00$). After midwinter, the pattern shifted, with haulouts starting in the morning and ending in late afternoon ($07:17 \pm 1:41$ to $16:50 \pm 0:44$; Fig. 4).

3.4. Dive data

For all dives combined, the mean dive depth was $75.8 \, \text{m} \pm 33.9_{(SD)}$ (range for all dives 6–664.5 m) and the mean dive duration was $4.6 \, \text{min} \pm 1.5$ (range 0.2–23.6 min). Because dives longer than 23.6 minutes were assigned this maximum value, it is possible that seals made longer dives. When dives were separated into the two categories (shallow <24 m, or deep >24 m), deeper dives were more common: overall, 65.9% of dives were deeper than 24 m. Individually, the proportion ranged from 57.2–86.3% in 2001 to 10.9–78.4% in 2002.

In general, there was no seasonal or diel influences on the depth or duration of shallow dives. The only exception to this was in 2001, when dive duration varied by month ($F_{6,79.7} = 3.278$, $P = 0.006$), with dives in November significantly shorter than those in May–August. However, the mean difference was generally small (<5 s). Overall, dives averaged $11.0 \pm 5.3 \, \text{m}_{(SD)}$ and 89.5 ± 103.3 s.

In contrast, deeper dives ($\geqslant 24$ m) varied by time of day and season. In both 2001 and 2002 month
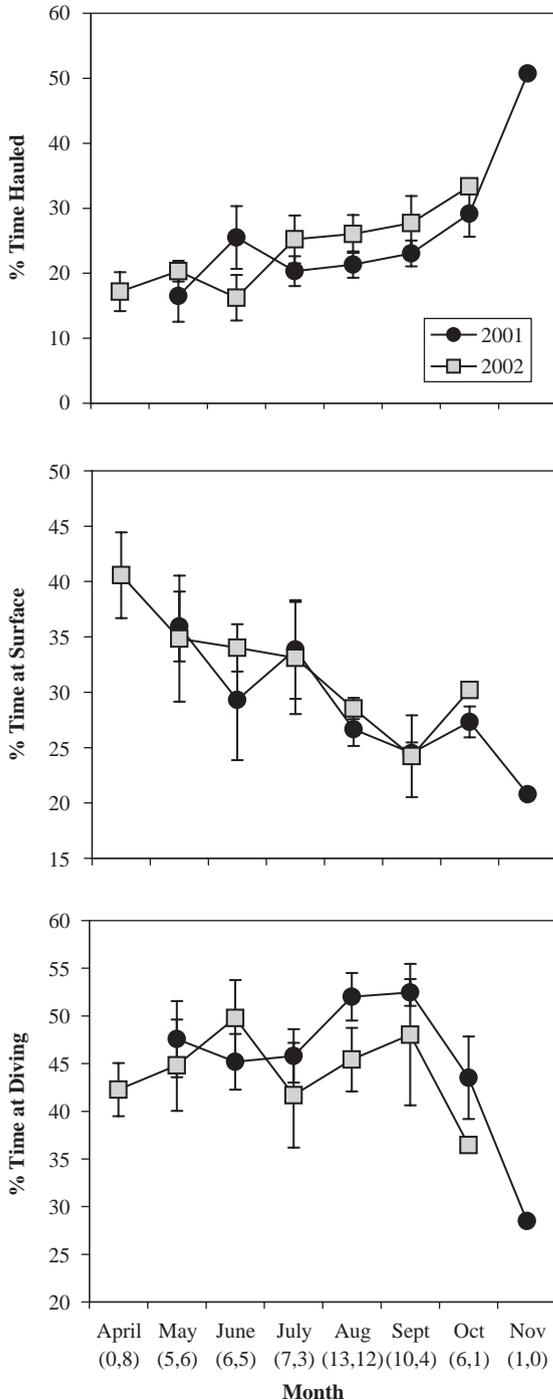
Fig. 2. Activity patterns of crabeater seals by month in 2001 and 2002. (A) mean $\pm$ SE time spent hauled out per day; (B) mean $\pm$ SE time spent in the water but at depths shallower than 6 m each day; (C) mean $\pm$ SE time spent diving per day. Monthly average values were calculated for each seal from only those days in which data were received from all six periods, provided that there were at least 3 days of data in the month. Each individual is represented once per month, and the number of seals is indicated below the month (n_{2001}, n_{2002}). The increase in time spent hauled out in November is associated with the long haulout made by female G010.
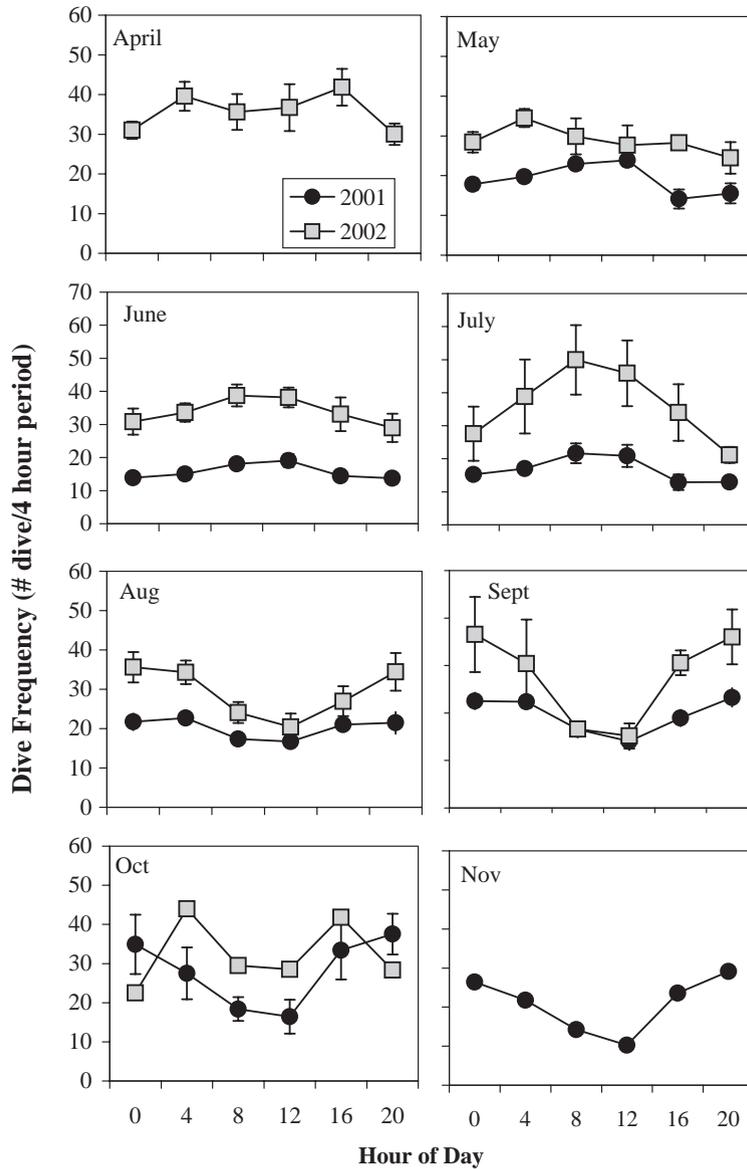
Fig. 3. Monthly mean±SE dive frequency (# dives/4-h period) for seals in 2001 and 2002. Daily averages were calculated for individual seals for those days in which data were received from all six periods. Monthly average values were calculated for each seal from only those days in which data were received from all six periods, provided that there were at least three days of data in the month. Each individual is represented once per month, and the sample sizes are as in Fig. 2.

and hour each accounted for a significant proportion of the overall variation in average depth and duration. Month effects were large: dive depth varied across months by 71% in 2001 and 81% in 2002, and dive duration varied by 94% in 2001 and 83% in 2002 (2001 logDepth $F_{6,83.8} = 4.278$,

$P = 0.001$; duration $F_{6,74.4} = 8.889$, $P < 0.001$; 2002 logDepth $F_{6,112.4} = 2.754$, $P = 0.016$; duration $F_{6,104.1} = 2.579$, $P = 0.023$). Post hoc tests demonstrated that average dive depth and duration increased through September, and then decreased in October and November.
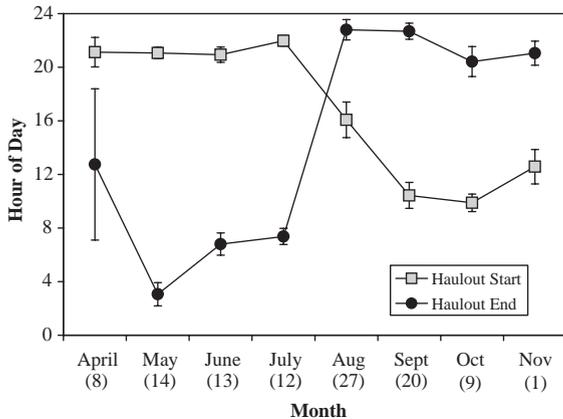
Fig. 4. Haulout patterns for seals in 2001 and 2002 combined showing the average (±SE) time that haulouts began and ended in each month of the study. Sample sizes are the number of seals that hauled out in each month for the two years combined. This number differs from that in Figs. 2 and 5 because haulout information was transmitted separately from diving or summary information.

However, within each month there was also a significant effect of time of day (nested ANOVA, hour by month effect: 2001 logDepth $F_{161,534.4} = 6.512$, $P < 0.001$; duration $F_{161,541.4} = 3.5089$, $P < 0.001$; 2002 logDepth $F_{161,442.6} = 3.766$, $P < 0.001$; duration $F_{161,466.8} = 1.187$, $P = 0.086$). Overall, dives were deeper and longer during midday, with the trend becoming more pronounced as the season progressed from April to September. However, in October and November, dive depth and duration declined, and the diel pattern became less evident. The diel pattern was more evident in 2001 than in 2002, perhaps because dives in 2001 tended to be slightly longer and deeper than those in 2002 (Figs. 5 and 6).

3.5. Movement patterns and spatial analysis

On average, seals remained within 231 ± 40 km of the site where they were tagged, and 26 of the 34 seals (76%) never traveled further than 300 km. However, the remaining seals did make longer movements. In 2001, adult male GG015 moved 1147 km to the southwest (final location 71.337°S, 98.055°W), while in 2002, female G017 traveled 664 km to the northern tip of the Antarctic Peninsula over a period of 30 days (Fig. 7).

Seals that remained within the study region were not distributed randomly throughout their habitat, but instead concentrated their activities in relatively few key areas (Fig. 8). These were the area south of Marguerite Bay off the northwest tip of Alexander Island (approx. 68°S 71°W), the northern portion of LauBeuf Fjord, and in the region of Crystal Sound bounded on the north by the northern end of Lavoisier Island, on the south by the southern end of Hanusse Bay, on the west by Matha Strait, and on the east by longitude 66° 30′W. For example, five seals that were tagged in Lazarev Bay in May 2001 used the Alexander Island region heavily. However, in July these seals, and those tagged in LauBeuf Fjord moved into Crystal Sound, and remained there for the rest of the winter months, along with most of the seals tagged in LauBeuf Fjord, Marguerite Bay, and the outer coast of Adelaide Island. Similarly, in April 2002, eight seals were tagged in Crystal Sound and LauBeuf Fjord, and half of these animals moved south to the same area off the northern tip of Alexander Island that was frequented in 2001. In addition, three seals tagged near Alexander Island and several seals tagged west of Adelaide Island in August later moved into Crystal Sound. Notably, in neither 2001 nor 2002 did seals spend much time the waters of Marguerite Bay proper.

The habitat use vs. availability analyses revealed that the areas where seals were most commonly found were shallower than the habitat as a whole (modified Bonferroni confidence intervals; $P < 0.05$ for significance tests). In 2001, seals were found more often than expected in depth classes 0–49, 50–149, 150–249, 250–349, and 350–449 m, and less often than expected in waters of 550–649 m (Table 2). Similarly in 2002, seals were found more often than expected in waters of 50–149, 150–249, 250–349, and 350–449 m, and less often than expected in waters of 550–649 m. When years were pooled, the combined results were identical to those in 2002 (Table 2).

Seals were also non-randomly distributed with respect to sea-ice, but the pattern was less clear due to the changing nature of the sea-ice and the extreme differences in ice cover in 2001 and 2002. When the average concentration of ice was low (<50%), seals selected areas of high ice cover and
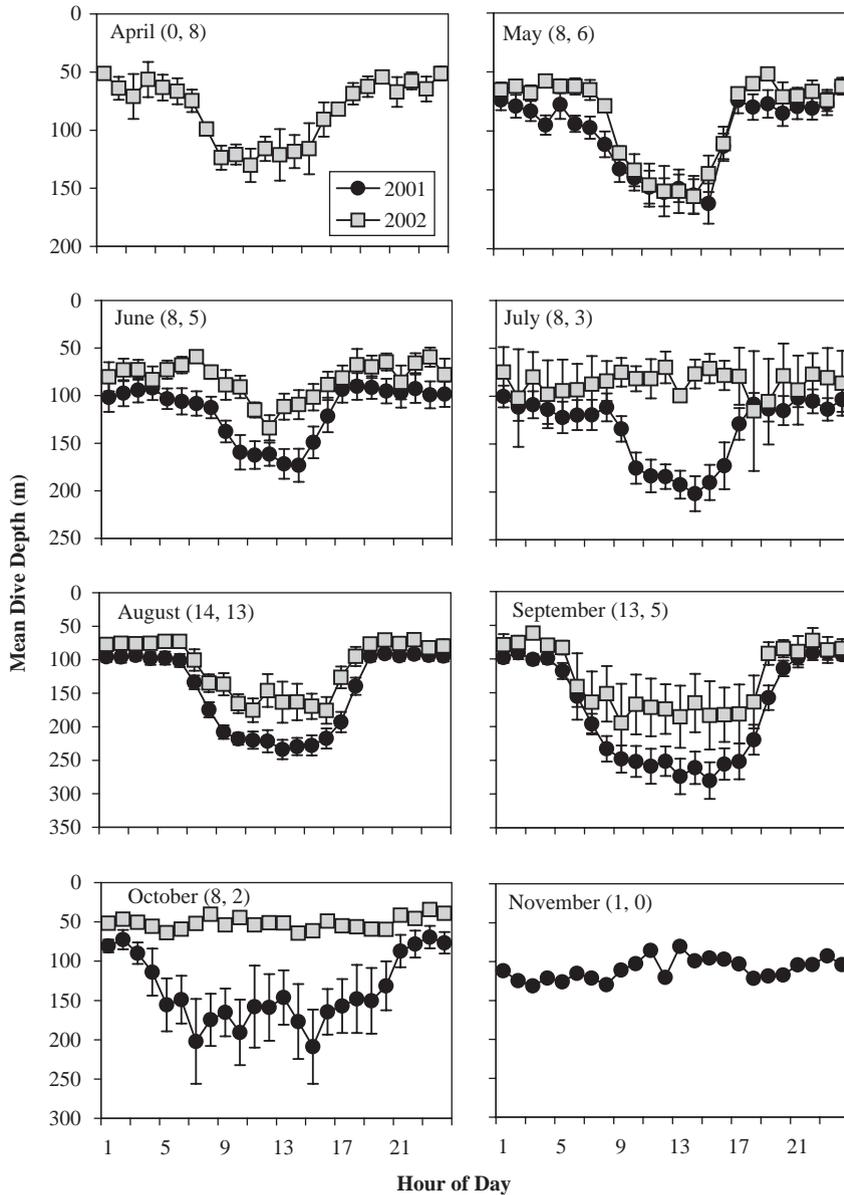
Fig. 5. Mean $\pm$ SE dive depth (m) by month and hour for seals in each year of the study. Each individual is represented once per month, and the number of seals is indicated (n_{2001}, n_{2002}). Sample sizes differ from those in Fig. 2 because data were included from all dives without ensuring complete daily coverage.

avoided region of open water. Once ice availability increased, seals remained within ice covered areas. As a result, there was a trend for animals to use areas of medium ice coverage (30–50%) earlier in the winter and to utilize areas of higher coverage (90%) later in the winter. However, in most late-

winter months complete ice coverage (100%) was significantly avoided (Table 3).

When we examined how physical features influenced the amount of time seals spent in the areas that they used, we found that the most parsimonious model that predicted crabeater seal
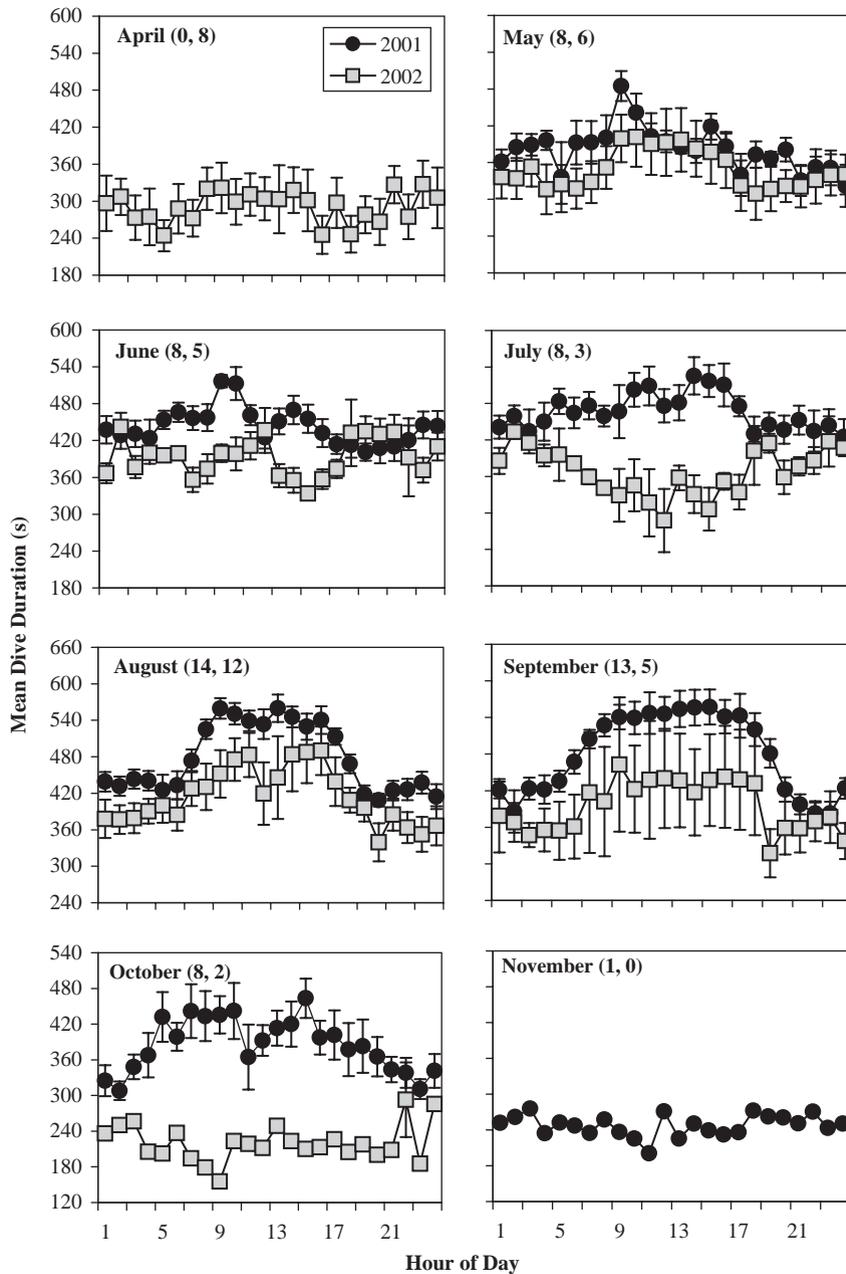
Fig. 6. Mean±SE dive duration (s) by month and hour for seals in each year of the study. Each individual is represented once per month, and the number of seals is indicated (n_{2001}, n_{2002}). Sample sizes differ from those in Fig. 2 because data were included from all dives without ensuring complete daily coverage.

habitat use (time spent per grid cell) was one that incorporated each of the modeled physical variables, but did not separate the 2 years (Table 4). This model was then applied to each month separately. Depending on the month, the relative significance of mean depth, standard error of depth, and mean sea ice concentration changed (Table 5). However, overall, there was a trend for
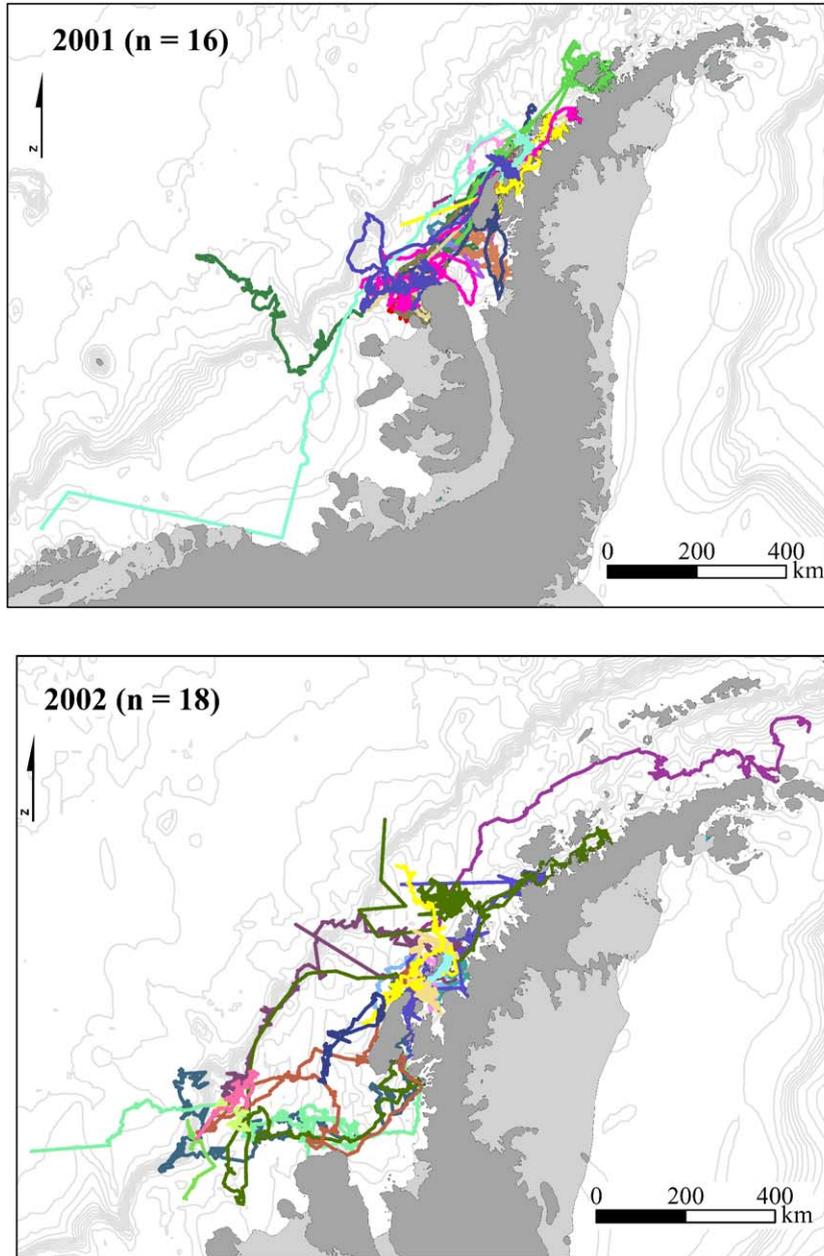
Fig. 7. Movement patterns of individual seals in 2001 and 2002. Lines were drawn between points that passed the location filtering algorithms.

habitat use to be positively related to sea-ice concentrations and standard error of depth, and negatively related to depth. This indicates that, on average, seals were selecting shallower areas, that had higher ice concentration and more varied depth. These results are in fundamental agreement with the results from the habitat selection analyses that used Bonferroni confidence intervals.
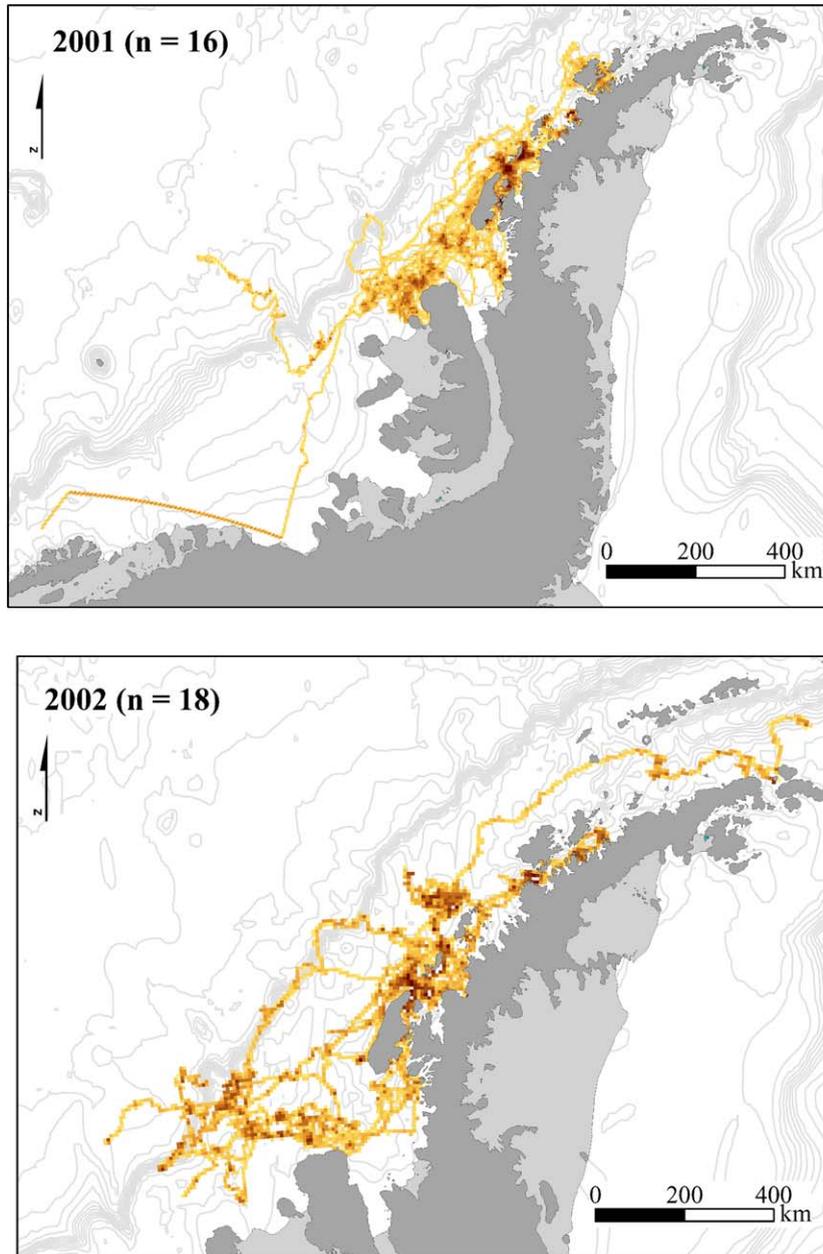
Fig. 8. Habitat use patterns for seals in 2001 and 2002. Deeper colors indicate a greater proportion of time was spent in that area.

4. Discussion

4.1. Diving behavior and activity patterns

Previous studies of crabeater seal diving patterns indicate that they, like most krill predators, primarily focus their foraging in the upper 50 m of the water column (Croxall et al., 1985; Costa et al., 1989; Bengtson and Stewart 1992; Boyd et al., 1994; Nordøy et al., 1995). However, in this study, crabeater seals made dives that were substantially longer and deeper than those in previous studies:

Table 2

Patterns of habitat use and availability for depth class.

Average depth available is the average coverage throughout the habitat, as determined from the ETOPO2 bathymetry data set. Average depth used is the weighted average depth in areas where seals were found, as defined by the annual MCPs. Modified Bonferroni confidence intervals for use and availability were used to assess whether seals were selecting or avoiding regions with particular depth classes (100 m increments from 0 to 600 m; depth bins rounded to nearest 100 m). Values for habitat use include all behavioral states

Year	Avg. depth available (mean $\pm$ SD)	Weighted avg. depth used ($\pm$ SE)	Selection for depth class	Avoidance of depth class
2001	1118.6 $\pm$ 1310.7	343.9 $\pm$ 44.6	0, 100, 200, 300, 400	600[a]
2002	1118.6 $\pm$ 1310.7	512.3 $\pm$ 66.0	100, 200, 300, 400	600
2001–2002 combined	1118.6 $\pm$ 1310.7	396.6 $\pm$ 53.8	100, 200, 300, 400	600

[a] Use of depth classes > 600 m was not modeled because of extremely low use of these areas.

Table 3

Patterns of habitat use and availability for sea ice concentration, calculated from monthly seal distribution for both years combined. Ice concentration (%) is the average coverage throughout the habitat, as determined from the NSIDC sea ice dataset. Average ice use is the weighted average ice cover in areas where seals were found ($\pm$ standard errors). Modified Bonferroni confidence intervals for use and availability were used assess whether seals were selecting or avoiding regions with particular ice densities. Values for habitat use include all behavioral states

Month	Year	Avg. ice concentration available	Weighted avg. ice used	Selection for % class ice cover	Avoidance of % class ice cover
April	2001	—	—	—	—
	2002	14.2 $\pm$ 1.6	30.1	40	0
May	2001	8.7 $\pm$ 1.0	35.8	30, 40	None
	2002	55.0 $\pm$ 2.6	55.8	40, 70	30, 60
June	2001	31.4 $\pm$ 1.7	44.6	40, 50, 60	0, 20
	2002	84.6 $\pm$ 1.2	70.6	30, 80	90
July	2001	77.0 $\pm$ 1.6	73.9	60	80
	2002	89.1 $\pm$ 1.1	67.9	50	100
August	2001	88.0 $\pm$ 0.9	85.9	90	100
	2002	86.4 $\pm$ 1.1	83.7	80	90, 100
September	2001	89.3 $\pm$ 0.8	86.9	90	80, 100
	2002	84.4 $\pm$ 1.1	90.1	90	80, 100
October	2001	80.1 $\pm$ 2.1	85.7	100	None
	2002	84.5 $\pm$ 0.9	75.8	60	None

55% of dives were deeper than 50 m, and 34% were deeper than 100 m. Similarly, two-thirds of all dives were longer than 3 min, and almost half (47%) were longer than 5 min. Thus, this study documented the deepest (664 m) and longest (23.6 min) dives ever recorded for crabeater seals, but more importantly, demonstrated that crabeater seals can utilize a much larger portion of the water column than previously recognized.

In part, differences between the diving behavior of seals in this study and those previously conducted are likely due to seasonal differences

Table 4
Results of the generalized linear model relating crabeater seal use (h) to three environmental variables: mean depth, standard error of depth, and sea ice concentration.
The most parsimonious model is Model 2 that included all three environmental variables, but excluded the *year* term. Any removal of the environmental variables resulted in a significant change in the deviance

Model	Variables	Deviance	Deviance/degrees of freedom	Difference in deviance (χ_1^2)	P
1	Year, depth, SE of depth, sea ice concentration	154.45	38.612	0.77	0.382
2	Depth, SE of depth, sea ice concentration	153.68	51.23	84.11	<0.001
3	Depth, sea ice concentration	69.57	34.79	43.76	<0.001
4	Sea ice concentration	25.81	25.81		

Table 5
Results of the monthly generalized linear modeling using GENMOD (SAS 6.11) with a Poisson error model and a log link.
The dependent variable was the $\log_e$-transformed total seal use (h) per $5 \times 5\,\text{km}^2$ grid cell. Independent model terms include the $\log_e$-transformed mean depth (D), the untransformed standard error of depth (D_{SE}) and the angular-transformed sea ice concentration (SI). Term coefficients and standard errors (SE) are also shown. Significant terms ($P<0.05$) and terms approaching significance ($P<0.10$) for each monthly model are shown in italics

Month	Scaled deviance	Df	Model significance (P)	Coefficient $\pm$ SE	Coefficient P
April				D: -0.0447 ± 0.0303	0.1406
	7.64	3595	0.054	D_{SE}: 0.0016 ± 0.0019	0.4101
				SI: 0.2027 ± 0.1178	*0.0852*
May				*D: -0.0441 ± 0.0188*	*0.0188*
	11.36	31,263	0.0099	D_{SE}: -0.0018 ± 0.0012	0.1355
				SI: -0.0162 ± 0.1009	0.8722
June				*D: -0.0755 ± 0.0140*	*< 0.0001*
	28.08	31,308	< 0.0001	D_{SE}: 0.0012 ± 0.0009	*0.1723*
				SI: 0.1981 ± 0.0752	*0.0084*
July				*D: -0.0487 ± 0.0234*	*0.0369*
	5.86	31,131	0.1187	*D_{SE}: 0.0033 ± 0.0015*	*0.0375*
				SI: 0.2420 ± 0.1533	0.1144
August				D: 0.0020 ± 0.0198	0.9216
	44.71	31,496	< 0.0001	*D_{SE}: 0.0050 ± 0.0008*	*< 0.0001*
				SI: -0.0951 ± 0.1554	0.5405
September				*D: -0.0845 ± 0.0223*	*0.0002*
	29.51	3791	< 0.0001	*D_{SE}: 0.0044 ± 0.0009*	*< 0.0001*
				SI: 0.6635 ± 0.1920	*0.0005*
October				*D: -0.0552 ± 0.0304*	*0.0699*
	26.32	3752	< 0.0001	*D_{SE}: 0.0075 ± 0.0019*	*< 0.0001*
				SI: -0.1636 ± 0.2170	0.4508
November				D: -0.1813 ± 0.1152	0.1156
	2.71	3221	0.4385	D_{SE}: 0.0086 ± 0.0090	0.3369
				SI: -0.5188 ± 0.4236	0.2207

in when the studies were carried out. Most studies of krill predators have taken place during summer and fall, when adult krill are abundant in the upper 50 m of the water column, and are generally accessed there (Croxall et al., 1985; Bengtson and Stewart 1992; Hunt et al., 1992; Veit et al., 1993; Boyd et al., 1994). However, during the Southern Ocean GLOBEC cruises, adult krill and large zooplankton were largely absent from the surface waters, and instead were most abundant in deep waters and close to the bottom (Ashjian et al., 2004; Lawson et al., 2004; Zhou and Dorland, 2004). In addition, large zooplankton were less abundant in winter than fall, and more biomass was observed at depth later in the season (Lawson et al., 2004). Crabeater seals were likely diving deep to access these prey resources, and the downward shift in the prey distribution likely explains the increased depth of dives later in the winter. However, fish were also more prevalent in deeper waters, and it is possible that the deeper diving later in the winter reflects an increased reliance on fish as zooplankton biomass declined over winter (Øritsland, 1977; Green and Williams, 1986; Lowry et al., 1988; Lawson et al., 2004). Ongoing studies of crabeater seal diet should help resolve this issue. Regardless of the diet composition, the absence of prey in the upper water column in late fall and early winter likely required crabeater seals to dive deeply in order to access sufficient food resources.

Another notable feature of the diving patterns of crabeater seals in this study was the strong diel pattern in dive depth and duration. From autumn to midwinter, seals were more active during the daylight hours, with dives around midday more frequent, deeper, and longer than those around midnight. This pattern differs substantially from that previously observed, and from the activity patterns of the Antarctic fur seal, another krill specialist. Prior work with both species has indicated that animals generally rest during the day and forage mainly at night when krill are close to the surface and easily accessed (Croxall et al., 1985; Costa et al., 1989; Bengtson and Stewart 1992; Boyd et al., 1994; Nordøy et al., 1995). The pattern we observed more closely resembles that of king and Adélie penguins, which forage at depth

during the day and haulout during the night (Kooyman et al., 1992; Wilson et al., 1993). For these species, daytime prey capture rates are higher because birds could more easily capture krill when they were aggregated along the seafloor than when dispersed throughout the water column (Wilson et al., 1993). Similar conditions could be present within Marguerite Bay: krill are known to migrate vertically (Kalinowski, 1978; Tomo, 1983; Siegel et al., 1998), and diel vertical migrations were observed within the coastal fjords frequented by seals (Zhou and Dorland, 2004). In addition, large zooplankton were most abundant and in denser swarms closer to the bottom (Ashjian et al., 2004; Lawson et al., 2004), and previous research has suggested that krill overwinter at depth (Kawaguchi et al., 1986; Gutt and Siegel 1994). In combination it appears likely that crabeater seals were improving foraging success by focusing activities in areas where the seafloor could constrain prey escape movements.

However, this explanation does not account for the seasonal changes in activity patterns. In both 2001 and 2002, seals shifted to daytime haulout and nighttime foraging by the end of August, and from that date forward their behavior was more similar to, although still deeper and longer than, that recorded during summer studies (Bengtson and Stewart, 1992; Nordøy et al., 1995). Possible explanations for this shift include changes in seal diet, prey behavior, or seal foraging tactics. While we cannot assess midwinter diets or prey behaviors directly because there were no late winter cruises, several lines of evidence suggest that this behavioral shift reflects both changes in prey behavior and seal foraging tactics. For example, many vertically migrating prey species descend until the ambient light levels reach some minimum set point (Wilson et al., 1993; Nybakken, 2001; Zhou and Dorland, 2004), and it may be that as day length increased, zooplankton moved into areas of deeper water and became less accessible to foraging seals. Deep troughs and depressions are common in Marguerite Bay and the coastal areas, and may serve as refuges from predation by seals (Zhou and Dorland, 2004). Indeed, as day length and light levels increased, the depth and duration of midday dives also increased, until more than half the dives

were longer than 8 min. Since dives longer than 9 min were followed by extended post dive surface intervals, if krill moved into deeper waters, seals may have switched to nighttime midwater feeding as a result of increased recovery costs associated with such long and deep dives (Fedak and Thompson, 1993).

Alternatively, seals may have switched foraging tactics as a result of increased prey abundance in the surface water in early spring (O'Brien, 1987; Siegel, 1988). Support for this hypothesis comes from the fact that as behavioral patterns shifted, neither dive frequency nor time in water increased, as would be expected if prey were more dispersed or harder to capture (Costa et al., 1989; Trillmich et al., 1991; Boyd et al., 1994). Instead, as light levels increased and nighttime diving became more common, average dive depth and duration declined, and the proportion of time spent hauled out increased. In combination, this suggests that as seals shifted to focus their foraging effort into the upper water column, they were able to obtain sufficient prey with less effort than when foraging at depth (Costa et al., 1989; Boyd et al., 1994). However, deep midday dives did not disappear completely from the behavioral repertoire, indicating that seals within Marguerite Bay continued to utilize deep prey patches even once prey availability in the surface waters increased. Nor does deep, water foraging appear to negatively impact condition. Seals handled in this study were significantly heavier (246 kg) than those handled in March in LauBeuf fjord (Laws et al., 2003) and along Queen Maud Land (182.5 kg; Nordøy et al., 1995), in October off Enderby Land (220 kg; Shaughnessy, 1991), and between late December and early February in the Ross Sea (183.6 kg, M. Castellini pers comm.). This pattern suggests that winter foraging is associated with mass gain, and that seals are lightest at the end of the summer season. Unfortunately, without serial measurements of individuals it is impossible to tell if the above pattern is due to seasonal, annual, or geographic differences.

In combination, these data indicate that crabeater seals, like many Antarctic predators, show seasonal differences in diving patterns, and suggest that differences result from interactions between zooplankton behavior and predator diving capacity. However, not only can diving seals track krill over a much larger segment of the water column than was previously appreciated, they might also influence it. Vertical shifts in zooplankton biomass were not observed farther offshore where seals and other predators were less abundant (Lawson et al., 2004), and within the coastal fjords vertically migrating zooplankton descended further than expected based on light levels alone (Zhou and Dorland, 2004).

4.2. Habitat use patterns

In this study, we found that seals showed habitat selection at both broad- and finer-scales, and with respect to both bathymetric features and ice characteristics. At the broad scale, we identified several areas within the Marguerite Bay area where tagged seals were commonly found in both study years. These regions were the northwest tip of Alexander Island, LauBeuf fjord, and Crystal Sound, all areas where zooplankton abundance was high, bathymetry varied (Lawson et al., 2004; Zhou and Dorland, 2004), and apex predator densities high (Chapman et al., 2004; Thiele et al., 2004; Zhou and Dorland, 2004). While coastal regions were heavily utilized, areas such as the middle of Marguerite Bay, the offshore shelf, and the shelf break were not frequented by seals. During the research cruises, these were regions of lower zooplankton and predator abundance (Ashjian et al., 2004; Chapman et al., 2004; Lawson et al., 2004; Thiele et al., 2004). Thus, crabeater seals, like other aquatic predators appear to be selecting regions of their habitat where prey are locally concentrated (Croxall et al., 1985; McConnell et al., 1992; Wilson et al., 1993; Crocker et al., 2004).

Our next question was whether these areas of local concentration shared particular habitat characteristics that might help explain habitat use patterns at times when information on zooplankton abundance was not available. To address this issue we examined both how seals were distributed with respect to range of habitat types available, and how time spent in areas varied based on the physical characteristics at that

location. The two sets of results were similar and complimentary. We found that areas of local concentration and higher than expected seal usage were characterized by shallower than average bathymetry, bathymetry that was discontinuous, and/or areas with higher than average ice density. One reason that seals might select shallower coastal regions would be to exploit prey residing at or near the bottom that in deeper waters would be less accessible (as discussed above). However, shallower coastal zones could have higher zooplankton abundance due to hydrographic features that serve to retain zooplankton, or to active habitat selection by zooplankton themselves.

Within Marguerite Bay hydrographic features likely play a key role. Drifter studies (Beardsley et al., 2004) identified small gyres off Alexander Island and in LauBeuf fjord that may have retained krill in these areas, and there was a persistent mesoscale cyclonic gyre within Marguerite Bay (Klinck et al., 2004) that may have retained krill inshore (Lawson et al., 2004). Similarly, visual surveys conducted by other researchers (Chapman et al., 2004; Thiele et al., 2004) indicate that seals and seabirds were often seen in association with particular water masses and fronts, areas that may be preferred by krill due to their generally enhanced productivity. Gyres, currents, frontal systems, and varied bathymetry are often associated with increased productivity (McConnell et al., 1992; Ichii et al., 1998; Field et al., 2001), and studies on krill movements and swimming speeds suggest that krill could have been actively selecting these inshore and coastal habitats (Lawson et al., 2004; Zhou and Dorland, 2004). From the predator perspective, relying on foraging areas that are correlated with physical features of the environment offers the significant advantage that they are likely highly predictable. Certainly, regions of high seal abundance and use were remarkably similar across the two study years, and seals made very directed movements between LauBeuf fjord and Alexander Island, suggesting previous familiarity with these regional 'hotspots'.

However, bathymetry and currents are not the only physical variables of importance to crabeater seals. Seasonal changes in sea-ice abundance and distribution impact all marine species, but particularly air breathing predators (Lunn et al., 1994; Costa and Crocker 1996; Ainley et al., 1998). As predicted, seals were not randomly distributed with respect to ice. In both years when ice was scarce, seals used areas of open water, but spent a disproportionate amount of time in areas where sea-ice was present, such as Crystal Sound and the coast along Alexander Island. Then, as the season progressed and ice thickened, seals remained within the pack ice but selected regions with high but not complete ice cover, such as was found in Crystal Sound and off the coast of Adelaide Island. This change in habitat selection criteria as the season progressed likely explains the inconsistent monthly results produced by our generalized linear modeling effort. It also may explain why previous studies on how seals are distributed with respect to ice have produced conflicting results (Gilbert and Erickson, 1977; Joiris, 1991; Bengtson and Stewart, 1992; Bester et al., 1995).

In part, crabeater seals may have been selecting regions with ice cover to improve foraging success. Krill are often associated with ice edges and ice algae (O'Brien, 1987; Stretch et al., 1988; Brierley and Watkins, 2000), and water currents may have retained krill along with ice in Crystal Sound and the coastal fjords (Beardsley et al., 2004; Klinck et al., 2004). However, even though adult krill have been observed to aggregate under the ice during winter (Marschall, 1988; Spiridonov, 1992), they were rarely abundant under the ice surface during the Southern Ocean GLOBEC cruises. Therefore, habitat selection for ice was probably not solely due to ice-related increases in krill density. Instead, our modeling results suggest that seal habitat use patterns reflect the interaction between the seals' reliance on regions of high zooplankton abundance, such as occurred near the bottom, at water mass boundaries, over varied topography, and (perhaps) under stable sea ice, and their need to access air to breath and ice to rest.

As a result, crabeater seal densities in Marguerite Bay did not decline throughout the winter as the pack ice expanded (Bester et al., 1995; Chapman et al., 2004), but instead became locally concentrated in areas of suitable ice, bathymetery, and prey availability. In this, our results are

qualitatively similar to those of Nordøy et al. (1995) who found that crabeater seals near Queen Maud Land spent considerable time in very deep (>2000 m) waters along the shelf break and near seamounts, and McMahon et al. (2002) who found that seals in the Mertz Glacier region (∼66°S, 144°E) were associated with shallow water and thick sea ice. Seals in all three studies selected regions of higher than average prey availability, as determined by the local physical and hydrographic conditions. Thus, crabeater seals, like other krill predators, appear to forage at the depths and in areas where prey are locally abundant, and perhaps predictably found, provided that the substrate is suitable for both prey access and haulout (Croxall et al., 1985; Costa et al., 1989; Wilson et al., 1993; Ainley et al., 1998; Guinet et al., 2001). Our challenge now is to determine how seals locate new hot spots, should environmental conditions change.

In this endeavor, we offer one note of caution. Our analysis of habitat selection was based on where seals spent their time, and did not distinguish between time in water and time hauled out. In contrast, visual survey records are biased towards areas where seals haul out, and areas of daytime activities. Because crabeater seals do not always haul out during the day, are capable of extensive use of ice free waters, and can go for long periods without hauling out (23 days for seal G017 in this study), interpretation of overall habitat use patterns based on observational data may be significantly biased. This is particularly true in low ice conditions, when sighting probabilities are low. For example, in fall 2001, tag data indicated that seals were active in LauBeuf Fjord, but few seals were ever sighted there due to the absence of ice suitable for haulout.

Furthermore, interpretation of habitat use patterns also can be confounded by the occurrence of highly seasonal events. For example, one adult female (G010) hauled out for the entire period between 14 October and 8 November 2001, during which time she moved (drifted) farther offshore and over deeper water than any other crabeater seal in the study, and thus 'used' very different habitat classes. This long haulout was coincident with observations by Rothera Base (67° 35S, 68°

10W) personnel of a female crabeater seal that hauled out, gave birth on 11 October and nursed her pup until 6 November (Rothera Base, unpublished science records). In combination with prior research (Shaughnessy and Kerry, 1989; Green et al., 1993), these observations suggest that crabeater seals select highly stable substrates for reproduction, in part due to the long lactation period (approximately 24 days). Further, they indicate that crabeater seal females fast for the entire nursing period. Seasonal models of krill predation by crabeater seals should take the timing and duration of this fasting period into account.

5. Conclusions

Crabeater seals foraging during the winter in the Marguerite Bay region were locally concentrated in areas where adult krill and large zooplankton are abundant, and these regions were characterized by shallower-than-average depths, and greater-than-average ice cover. These findings suggest that seal densities need not decline during winter as more sea ice becomes available, but instead might increase as seals become concentrated in regions with suitable ice concentrations and prey densities. The highly localized habitat use, in combination with the deep diving pattern, likely serves to concentrate predation pressure on adult krill and large zooplankton found in the deeper waters inside the coastal fjords. If seals are able to continue to specialize on krill throughout the winter, then the impact of the crabeater seal population on overwintering krill will be substantial, albeit localized, and may account for much of the observed reduction in larger zooplankton biomass. However, even a small percentage of fish in the diet would reduce the impact on krill populations, and cannot yet be ruled out as an alternative foraging strategy.

Seals in this study did not exploit surface waters at night as has been previously reported, but instead demonstrated a nocturnal haulout pattern, used deeper depths, and possibly included benthic foraging in their repertoire. While wintertime growth and acquisition of lipid reserves suggest that this strategy was effective, as summer

approached, seals returned to daytime haulout and nocturnal foraging. These findings indicate that despite their high degree of specialization on a single prey resource, crabeater seals have the behavioral plasticity to forage successfully under a wide range of environmental conditions. Further, they suggest that there are complex interactions between seal movement and diving patterns, krill abundance and distribution, sea-ice extent and seafloor depth, and seasonal light levels.

Acknowledgements

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