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Fine-scale habitat selection of crabeater seals as determined by diving behavior

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Abstract

Previous studies within the Marguerite Bay region of the Antarctic Peninsula (~67°S, ~67°W) demonstrated that during winter, crabeater seals (*Lobodon carcinophagus*) were not randomly distributed across available habitat, but instead were more likely to be located in nearshore waters where bathymetric gradients and ice concentrations were high. Here, we investigate how the diving patterns of crabeater seals vary in response to these habitat characteristics, and interpret seal behaviors in light of information on the distribution of their primary prey, krill (*Euphausia superba* or *Euphausia crystallorophias*). Diving and movement patterns were obtained from 34 seals (16 male, 18 female) fitted with satellite-relayed data loggers (SRDLs) during the 2001 and 2002 Southern Ocean GLOBEC cruises. Tags transmitted position and dive information for 4–174 days, during which time we received an average of 21 positions/day, and information on a total of 124,681 dives. A series of generalized linear mixed-effect models (GLMM) were used to evaluate the relationship between diving behavior and temporal and physical features of the habitat, and models contrasted using AIC_c and BIC weights. Overall, we found that the most parsimonious models included year, month, and period (day, dusk, night). In general, seals dived deeper (158 vs. 73 m) and longer (432 vs. 360 s) during the day than at night. In addition, daytime dives included slightly more time at the foraging depths (142 vs. 102 s), and were slightly more efficient (24% vs. 21% of the dive cycle spent at the bottom). When dive patterns were examined with respect to bathymetry, models indicated that seals were foraging in shallower waters (366 vs. 410 m) and closer to the bottom (dives were 50.3% vs. 26.3% of bathymetric depth) during the day than at night. In combination, these findings suggest that crabeater seals foraging during the day exploited zooplankton schools compressed along the bottom. At night, when zooplankton were dispersed and light levels low, foraging activity was less frequent and seals concentrated their diving closer to the surface over a broader range of habitat depths. As individual seals moved an average of only 4.1 ± 1.4 km between daytime and nighttime positions, these results suggest that crabeater seals diving along the Western Antarctic Peninsula select areas of high bathymetric gradients so that they can maximize foraging success over a 24-h cycle without the need to travel long distances. However, annual differences in behavior and the generally low amount of deviation explained by models also suggests that seals vary their diving behavior in response to finer-scale biological, temporal, and/or physical features that were not monitored as part of this study.

1. Introduction

There is a growing interest in understanding how natural and anthropogenically induced changes in ecosystems will impact marine predators (van Franecker, 1992; Ancel et al., 1992; Hindell et al., 2003; Reid et al., 2005). In polar regions, small changes in ambient temperature are having large effects on the duration, extent, and predictability of ice cover and the resulting patterns of primary and secondary productivity (Constable and Nichol, 2003; Moline et al., 2004; Smetacek and Nichol, 2005). Along the Western Antarctic Peninsula, the extent of winter sea-ice has decreased significantly over the past 35 years

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(Moline et al., 2004; Smetacek and Nichol, 2005), and such changes can directly impact upper trophic level predators such as penguins, seals, and whales by altering their access to critical habitats, or indirectly through bottom-up influences (Boyd et al., 1994; Ainley et al., 1998; Croxall et al., 2002; Burns et al., 2004). For example, annual abundance and recruitment success of krill, *Euphausia* spp., are broadly linked to the extent and timing of ice formation and melt (Constable and Nichol, 2003; Atkinson et al., 2004; Siegel, 2005; Smetacek and Nichol, 2005). Along the Antarctic Peninsula, reduced winter ice extent and increased freshwater runoff have been correlated with declines in krill and shifts in the abundance and distribution of other zooplankton species (Constable and Nichol, 2003; Moline et al., 2004; Siegel, 2005).

Changes in the structure of the food web along the Western Antarctic Peninsula may particularly affect those marine mammal and seabird species that rely on large and predictable seasonal aggregations of krill (Laws, 1977; Croxall et al., 2002; Fraser and Hofmann, 2003; Hindell et al., 2003). Crabeater seals, *Lobodon carcinophagus*, are one such species, for they remain within ice-covered Antarctic waters throughout the year, they rely on pack ice as a platform for resting, molting, and reproduction, and they feed almost exclusively on krill and other large zooplankton (Øritsland, 1977; Laws, 1977; Lowry et al., 1988). In fact, due to their large population size (Erickson et al., 1971; Gilbert and Erickson, 1977) and circumpolar range, crabeater seal are an important consumer of krill biomass in Antarctic waters (Hewitt and Lipsky, 2002). This reliance on krill suggests that seal distribution and behavior may be a good indicator of the abundance and distribution of krill swarms in the short term (Burns et al., 2004; Hofmann et al., 2004; Reid et al., 2005). Longer-term changes in krill populations also may be reflected in seal population demographics (Bengtson and Laws, 1985; Testa et al., 1991; Reid et al., 2005). As a result, crabeater seals have been recognized as potentially important indicators of ecosystem change by a variety of scientific organizations (APIS, 1995; Agnew, 1997; Hindell et al., 2003; Hofmann et al., 2004).

While characterization of crabeater seal habitat use patterns is important, it has been difficult to link seal distribution and abundance to fine-scale shifts in prey abundance and distribution (Nordøy et al., 1995; Burns et al., 2004; Southwell et al., 2005), although see (Costa et al., 1989, 2000; Boyd et al., 1994; Mori and Boyd, 2004). In part, this is because there are few studies that have collected data on marine predator and prey distributions simultaneously over periods longer than a few days. Instead, most work in this area has focused on correlating observed or remotely sensed information on abundance and habitat use with static or remotely sensed physical features of the habitat hypothesized to influence prey, such as bathymetry and sea-ice type and extent (Boyd and Arnbom, 1991; Ainley et al., 1998; Goebel et al., 2000; Field et al., 2001; Guinet et al., 2001; Burns et al., 2004;

Bradshaw et al., 2004; Pinaud and Weimerskirch, 2005; Campagna et al., 2006). Other physical or biological features such as sea-surface temperature, sea-surface height anomalies, and chlorophyll *a* that may be more closely correlated with lower trophic level productivity are rarely available for ice-covered waters. Thus, apart from a few specific studies (Ackley et al., 2003; Chapman et al., 2004; Thiele et al., 2004; Wall et al., 2007), surrogate measures of primary productivity have yet to be incorporated into long-term studies of marine mammal habitat selection in the Antarctic.

Most studies that have been conducted on crabeater seals have demonstrated that individuals are not distributed randomly throughout the pack ice, but are instead associated with regions of enhanced productivity (Ackley et al., 2003; Burns et al., 2004; Southwell et al., 2005). However, the physical features that characterize these regions vary considerably around the continent; seals therefore may be associated either with deeper *or* shallower areas of the water column, and more *or* less complete ice cover (Joiris, 1991; Nordøy et al., 1995; Bester et al., 1995; McMahon et al., 2002; Ackley et al., 2003; Wall et al., 2007). As a result, models that attempt to predict areas of high seal abundance based solely on physical features generally perform poorly (Southwell et al., 2005). This has complicated the design and implementation of broad-scale surveys, and may be one of the reasons behind the large confidence intervals surrounding crabeater seal population estimates (Erickson et al., 1971; Gilbert and Erickson, 1977; Southwell, 2005).

A clear understanding of the broad-scale habitat selection by crabeater seals has been elusive because it is not yet clear why certain areas are selected, or whether there are different habitat requirements at different times of the year (Bengtson and Stewart, 1992; Nordøy et al., 1995; Burns et al., 2004; Bengtson and Cameron, 2004; Southwell et al., 2005; Southwell, 2005; Wall et al., 2007). We must move beyond simple examination of haul-out probabilities and instead focus on determining how seals use their underwater habitats and on identifying the key components of the habitats on which they rely (Bengtson and Stewart, 1992; Nordøy et al., 1995; Guinet et al., 2001; Burns et al., 2004; Pinaud and Weimerskirch, 2005). In particular, given the ongoing reliance on physical habitat features for predicting seal abundance, it is important to understand how crabeater seal foraging behavior is influenced by both the dynamic and static environmental features with which they are associated. Such influences may be direct (e.g. ice that provides or limits access to air, or provides haul-out substrata near desired foraging areas) or indirect (e.g. bathymetric gradients or current structures that enhance local primary productivity). Examining the diving and foraging behavior of seals in these areas and correlating them with physical features and prey distribution should improve our understanding habitat selection. Because such information is necessary to predict how changes in krill dynamics might influence the population

dynamics of apex predators, these are key goals of the US Southern Ocean GLOBEC (GLOBal ocean ECosystems dynamics) research program (Hofmann et al., 2004), and have formed the basis for our research on crabeater seals in the Western Antarctic Peninsula.

Our initial work in this area (Burns et al., 2004) found that seals dived much longer and deeper during the winter than had previously been documented (Bengtson and Stewart, 1992; Nordøy et al., 1995), and that they foraged more during the day than at night. Seasonal shifts in behavior suggested that seals were foraging on vertically migrating prey species, and that they were spending more time in regions with relatively high ice cover, shallow depths, and steeper bathymetric gradients (Burns et al., 2004). In this paper, we extend that work to determine how habitat variation influences diving behavior. We focus on seasonal (i.e. weeks to months) and temporal (i.e. days) shifts in the seals' use of the water column, and on how monitored individuals track the behavior of their primary prey, krill, and schooling fishes. We also model behavioral patterns to determine which physical features most strongly correlate with diving patterns. Our goal throughout is to determine how seals are selecting foraging locations and exploiting prey in a changing landscape.

2. Methods

2.1. Animal handling and tagging

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 Western Antarctic Peninsula ($\sim$67 °S, 67 °W). Details of the capture and handling procedures are reported in Burns et al. (2004). Each captured seal was fitted with a satellite-relayed data logger (SRDL, manufactured by the Sea Mammal Research Unit, University of St. Andrews, Scotland) that was attached to the head using Devcon^{TM} 5-min epoxy (ITW Devcon, Danvers, MA). All animal handling protocols were authorized under US Marine Mammal Permit #1003-1665-00 and approved by Institutional Animal Care and Use Committees at the University of Alaska Anchorage and University of California Santa Cruz.

The SRDL tags determined whether the seal was at the surface or submerged at depth at 4-s intervals throughout the deployment. These depth time-lines were aggregated into several measures of diving behavior, of which two are analyzed: (1) detailed dive profiles with information on dive shape as determined from four internal depth-at-time points that represented the largest changes in dive trajectory (Fedak et al., 2001); and (2) summary dive profiles that consisted of the start time of the dive, maximum dive depth, dive duration, and post-dive surface interval. Due to the limited bandwidth available with the Argos system, depth and duration values, while measured accurately, were not relayed with the same detailed precision (Fedak

et al., 2002). Near the surface (from 6 to 50 m), dive depth was transmitted to the nearest 3 m, but this precision decreased with depth such that once dives exceeded 375 m, depth was relayed to the nearest 24 m. Similarly, for short dives (from 8 to 90 s), dive duration was relayed to the nearest 6 s, but precision decreased thereafter so that for dives longer than 741 s were relayed with a precision of 48 s. The maximum recording limits for the tags were 712.5 m and 1413 s. In addition, the ARGOS system calculated animal position from received transmissions (Service Argos, 1996). Because positions were time-referenced, the approximate location of all dives could be determined following (Fedak et al., 2002). Additional tag programming and transmission schedule details have been published previously (Fedak et al., 2001, 2002; Burns et al., 2004).

2.2. Behavioral data

Dives were separated into two categories based on depth as reported in Burns et al. (2004). Category 1 dives were 24 m deep or less, and Category 2 dives were deeper than 24 m. To render the distributions Gaussian, dive depth and duration for Category 1 dives were log-transformed; for Category 2 dives, only dive depth was log-transformed because raw dive duration data were already normally distributed. For all dives, the maximum depth, dive duration, and post-dive surface interval were determined.

For those dives for which detailed dive profiles were received, a smoothed dive profile was calculated so that the proportion of time spent at the bottom of the dive could be determined. To determine bottom time, 100 equally spaced depth-time points were linearly interpolated between the four internal depth-time points and the surface at the start and the end of the dive (Rehberg, 2004). These points were then standardized to a proportion of the total dive depth and duration, and *percent bottom time* was calculated as the number of these interpolated depth-time points that were at depths $\geqslant$80% of the maximum dive depth. This value was then multiplied by dive duration to produce an estimate of bottom time in seconds. Dive efficiency, the proportion of each dive cycle that an animal was able to spend at the foraging depths, was calculated from the estimated bottom time and the reported dive duration and post-dive surface intervals, as (bottom time × [dive duration + post-dive surface interval]$^{-1}$) (Ydenberg and Clark, 1989).

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). To examine the effect of time of day on behavioral metrics, the angle of the sun above or below the horizon was used to divide the day into three periods based on the definitions for civil twilight: day (sun above horizon); twilight (sun 0–12° below horizon); night (sun > 12° below horizon). This was done to control for the different light levels experienced at any given hour of the day between April and October.

2.3. Habitat associations and movement patterns

Seal locations were screened by an iterative forward/backward averaging filter that identified and excluded locations that would require rates of travel greater than $4 \, \mathrm{m \, s^{-1}}$ (McConnell et al., 1992). Positions were then integrated into Interactive Data Language (IDL 5.0, Research Systems, Inc.) and ArcGIS (ESRI, Inc., USA) so that dives could be associated with ice cover and bathymetry where the dive was estimated to occur. Sea-ice cover (0–100%) at the location of each dive was determined based on the average monthly sea-ice concentration reported by the National Snow and Ice Data Center (NSIDC) in Boulder, CO, and interpolated for the study area following (Burns et al., 2004). Bathymetric data used in this analysis were the Southern Ocean GLOBEC Bathymetric dataset, which is the local area-improved version (ETOPO8.2A) of the Sandwell and Smith ETOPO2 2-min digital gridded bathymetry for the SO GLOBEC study area, as improved by using bathymetric data collected from a wide variety of sources (Bolmer et al., 2004). For these analyses, the dataset was interpolated for a grid of 15 in. intervals.

Dives were associated with their nearest-neighbor bathymetric value, and an index of seafloor slope (bathymetric gradient) was calculated as the standard error of depth within 5×5-km grid around each position (Burns et al., 2004). To determine if crabeater seals were diving close to the seafloor bottom, the distance between the bottom of the dive and the seafloor was calculated for all dives for which there was a seafloor depth value available. To account for difficulties in correctly assigning seafloor depth nearshore, the depth of the seafloor was treated as a missing value if it was less than or equal to 10 m. To address issues of precision in the measured depth of the dive, a buffer of twice the depth precision was added to the dive depth. The distance between the bottom of the dive and the seafloor was set to zero (i.e. the seal was judged to be at the ocean floor) if the difference between the seafloor depth and the buffered dive depth was less than the buffer value. This distance to seafloor was set to missing if the dive depth was deeper than the seafloor depth plus the buffer value, or if the distance between the seafloor and dive bottom was greater than 1000 m. Distance to the seafloor was also calculated on a relative scale as (1−[distance to the bottom × seafloor depth^{-1}]). Thus, relative depth is 100% when seals were at the seafloor bottom, regardless of actual seafloor depth.

To examine the distances over which individual seals moved between nighttime and daytime diving, the filtered location for each seal for each day and period was calculated as the average of all positions within that period and day. Then, the straight-line distance between the average daytime and nighttime positions for that day was calculated, provided that there were more than three locations within each time period. For comparative purposes, the average daily travel rate was calculated as the distance between the average daily positions for each animal over all periods combined.

2.4. Statistical approach

To determine the relationship between the temporal (*year*, *month*, *period* and their interactions) and physical features of the habitat (*seafloor depth*, *bathymetric slope*, and *sea-ice cover*) and diving behavior, we fitted a series generalized linear mixed-effect models (GLMM) to the data using the *lmer* function implemented in the R Package (R Development Core Team, 2004). Most variables were pre-transformed prior to analysis to correct for non-Gaussian distributions (log for maximum dive depth and seafloor depth, arcsine square-root for sea-ice concentration). Each model was constructed using either a Gamma or Gaussian error distribution, with an identity link function. The amount of variance in the response variables captured by each model considered was assessed as the percent deviance explained (Brook et al., 2006).

Given the repeated-measures structure of the model, we first calculated the mean of model responses over successively increasing intervals (1, 2, 3, …, h) and applied an autocorrelation function to determine at which temporal resolution most autocorrelation disappeared. We determined that a 6-h average removed most temporal autocorrelation in *maximum dive depth*, *dive duration*, *post-dive surface interval*, *bottom time*, and *distance to bottom*, so we averaged the dataset over this interval for these terms. However, there was little autocorrelation apparent for dive efficiency, likely because many of the dives (23,768 or 37%) did not have estimates of bottom time available. Thus, no binning procedure was necessary for the analysis of *dive efficiency*. There was insufficient replication using the 6-h interval summaries to evaluate the interaction between *year* and *month*.

Our model-building strategy was based on a logical set of term combinations hypothesized to explain variance in each response considered. We first applied the term *dive duration* as a control variable for the dive-depth analysis to account for the observation that the log of dive depth increases approximately linearly with increasing dive duration (log-linear relationship, data not shown). We applied different combinations of the three habitat variables, with and without considering the effects of *year* and *period*. In all cases, we coded *individual* as a random effect in the model to account for random differences among seals, with *month* nested within *individual* to account for temporal shifts in habitat use. The full model set comprised 25 models.

We used an index of Kullback–Leibler (K–L) information loss to assign relative strengths of evidence to the different competing models (Burnham and Anderson, 2002), Akaike's information criterion corrected for small sample sizes (AIC$_c$), and the dimension-consistent Bayesian Information Criterion (BIC) (Burnham and Anderson, 2002). These indices of model parsimony identify those model(s) from a set of candidate models that minimize

K–L information loss (AIC$_c$; Burnham and Anderson, 2004) or identify the probability that a model is truth given that truth is in the model set (BIC; Link and Barker, 2006). The relative likelihoods of candidate models were calculated using AIC$_c$ and BIC weights (Burnham and Anderson, 2002), with the weight (wAIC$_c$ and wBIC) of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set. However, the K–L prior used to justify AIC$_c$ weighting can favor more complex models when sample sizes are large (as was the case for our dataset), so we considered BIC weighting to determine the contribution of the most important major correlates of extinction, and AIC$_c$ weighting to identify the most parsimonious models for maximizing prediction accuracy (Burnham and Anderson, 2004; Link and Barker, 2006).

3. Results

Over the four Southern Ocean GLOBEC cruises (Hofmann et al., 2004) 34 adult crabeater seals (18 female, 16 male) were fitted with SRDLs. Tags transmitted position and dive information for 4–174 days, during which time an average of 21 positions/day were received. Tags transmitted information on 124,681 dives for the periods April–October 2001 and 2002, and bottom time and dive efficiency could be calculated for 97,384 of these dives. There was no effect of month or period of day on the average dive depth, post-dive surface intervals, or dive efficiency for dives ⩽24 m (these dives averaged 11.0 ± 5.3 m ($\pm$S.D.) and 89.5 ± 103.3 s throughout). These shallow dives are not considered throughout the rest of the analyses presented here, although more details can be found in Burns et al. (2004). The following results and discussion deal only with dives >24 m.

3.1. Temporal variation in dive behavior

All dive measures analyzed showed important differences between the 2 years examined (i.e. the *year* term was

included in the top-ranked models with wBIC = 0.937, 0.999, 0.980, 0.964, 0.976, 0.620 for *maximum dive depth*, *dive duration*, *dive efficiency*, *post-dive surface interval*, *bottom time*, and *distance to the bottom*, respectively, Table 1). Likewise, the *month* and *period* terms were present in the top-ranked models for all responses except *post-dive surface interval* which had only weak evidence for a *month* effect (wBIC of the second-highest ranked model = 0.017). Finally, there was good evidence for the interaction between *year* and *period* for the responses of *dive duration*, *dive efficiency*, and *bottom time* (interaction term present in top-ranked models), suggesting the daily variation in diving behavior as measured by these variables changed between years.

Given the relatively uniform importance of *year*, *month*, and *period*, we further investigated how diving behavior varied with respect to these features. For both *maximum dive depth* and *dive duration*, the most parsimonious models included all three main terms, but not *month-by-period* interaction effects (Table 1). While daytime dives tended to be longer and deeper than those made at night, this pattern was much more apparent in 2001 than in 2002. Similarly, seasonal changes in both *maximum dive depth* and *dive duration* were more prominent in 2001 than 2002 (Fig. 1). Dives made during dusk were intermediate in their depth and duration to those during day and night.

How seals budgeted their time in each dive cycle (a dive plus the associated *post-dive surface interval*) was explored by examining variation in the *post-dive surface interval*, *bottom time*, and *dive efficiency*. Unlike most other behavioral metrics, there was no effect of month on the *post-dive surface intervals*, although there was an effect of *year* and *period*, with *post-dive surface intervals* being longer in 2001 vs. 2002, and slightly longer during the day than during dusk or night (Fig. 2). In contrast, the most parsimonious models for *bottom time* and *dive efficiency* included *year*, *month*, *period*, and *year-by-period* interactions but failed to account for much of the observed deviance (Table 1). There was no clear directional pattern of change in *bottom time* (as measured on either the

Table 1
The most parsimonious generalized linear mixed-effects models investigating the habitat and temporal correlates of diving behavior for 34 crabeater seals (full dataset, $n = 4050$ 6-h binned dive periods) according to the Bayesian Information Criterion (BIC)

Model	k	LL	wBIC	wAIC$_c$	%DE
DEP–YR + MON + PER	12	−769.693	0.937	<0.001	3.62
DUR–YR + MON + PER + YR × PER	14	−24367.700	1.000	<0.001	1.22
PDSI–YR + PER	6	1357.499	0.965	<0.001	4.16
BOT-T–YR + MON + PER + YR × PER	14	−17439.780	0.976	<0.0010	1.81
EFFIC–YR + MON + PER + YR × PER	14	−14523.530	0.980	<0.001	3.06
DIST-BOT–YR + MON + PER	12	−2275.406	0.621	0.02	8.05
REL-BOT–YR + MON + PER	12	−217.520	0.999	0.00	8.65

Diving behaviors considered are maximum dive depth (DEP), dive duration (DUR), post-dive surface interval (PDSI), bottom time (BOT-T), dive efficiency (EFFIC), distance to the seafloor (DIST-BOT), relative distance to the seafloor (REL-BOT). Temporal variables considered in the models were year (YR), period of day (PER), month (MON), and their interactions. Seal ID was coded as a random effect in the model to account for differences among different individuals. Also shown is the number of parameters (k), the maximum log-likelihood (LL), the AIC and BIC weights (wAIC and wBIC) and the percent deviance (%DE) in the dependent variable explained by the model under consideration.
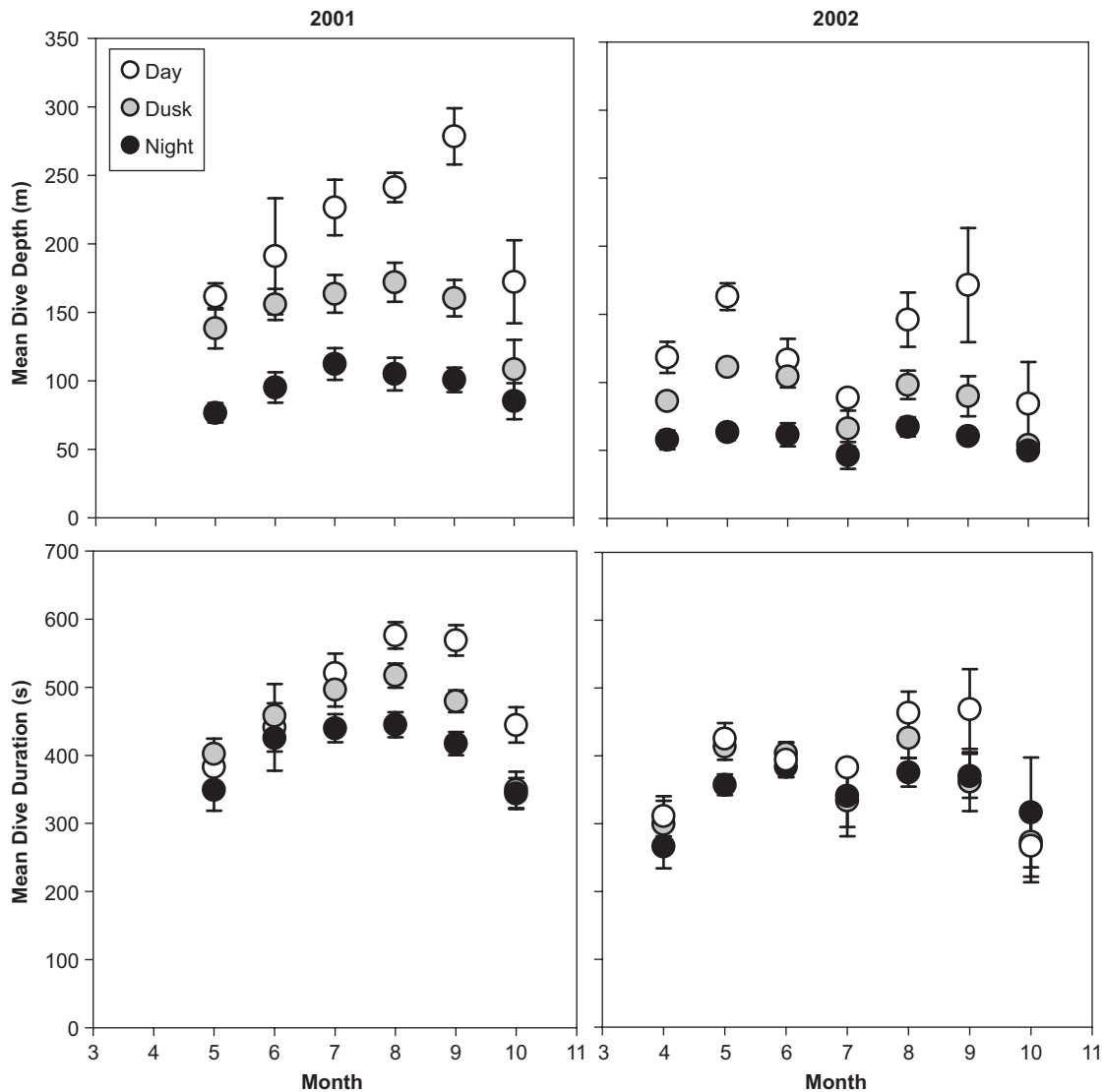
Fig. 1. Mean ($\pm$S.E.) maximum dive depth (m) and duration (min) for dives made by crabeater seals in each month and year, during the day, dusk, and night periods of the day. These figures only include dives that were >24 m.

absolute scale or as a percentage of dive duration) due to *month*, but in most months and both years, *bottom time* was lowest during the night (Fig. 2). *Dive efficiency*, the ratio of *bottom time* to *dive duration* plus the *post-dive surface interval*, followed the same pattern—there was no clear pattern with respect to *month*, but it was generally lower at night than during the day (Fig. 2). In contrast to *maximum dive depth* and *dive duration*, the annual differences in these parameters was much larger than the diel differences, with dives in 2001 having significantly longer *post-dive surface intervals*, *bottom time* (both on a percentage and absolute scale), and *dive efficiency* than dives in 2002.

Several interesting patterns emerged from the examination of how the distribution of dives within the water column changed with *year*, *month*, and *period*. Dives were closer to the seafloor bottom in both absolute (*distance to*

seafloor) and relative terms (*relative distance to seafloor*) during autumn as compared to spring, during the day as compared to night, and in 2001 as compared to 2002. In addition, the effect of *month* was much stronger in 2001 (Fig. 3). As with all other behavioral metrics, dives that occurred at dusk were intermediate in characteristic to those during the day or night. These effects were not only due to changes in the depth of dives, but also to the depth of the seafloor over which dives occurred, as dives at night occurred over waters that were approximately 60 m, or 17%, deeper than daytime dives (Fig. 3). This difference results from seals using the full range of habitats available at night, but a shallower subset of the habitat during the day (Fig. 4). Seals moved an average of 4.2 ± 1.1 km between their average day and average night positions, in all months except April, during which time they moved an average of 11.0 ± 1.1 km. In contrast, seals moved twice as
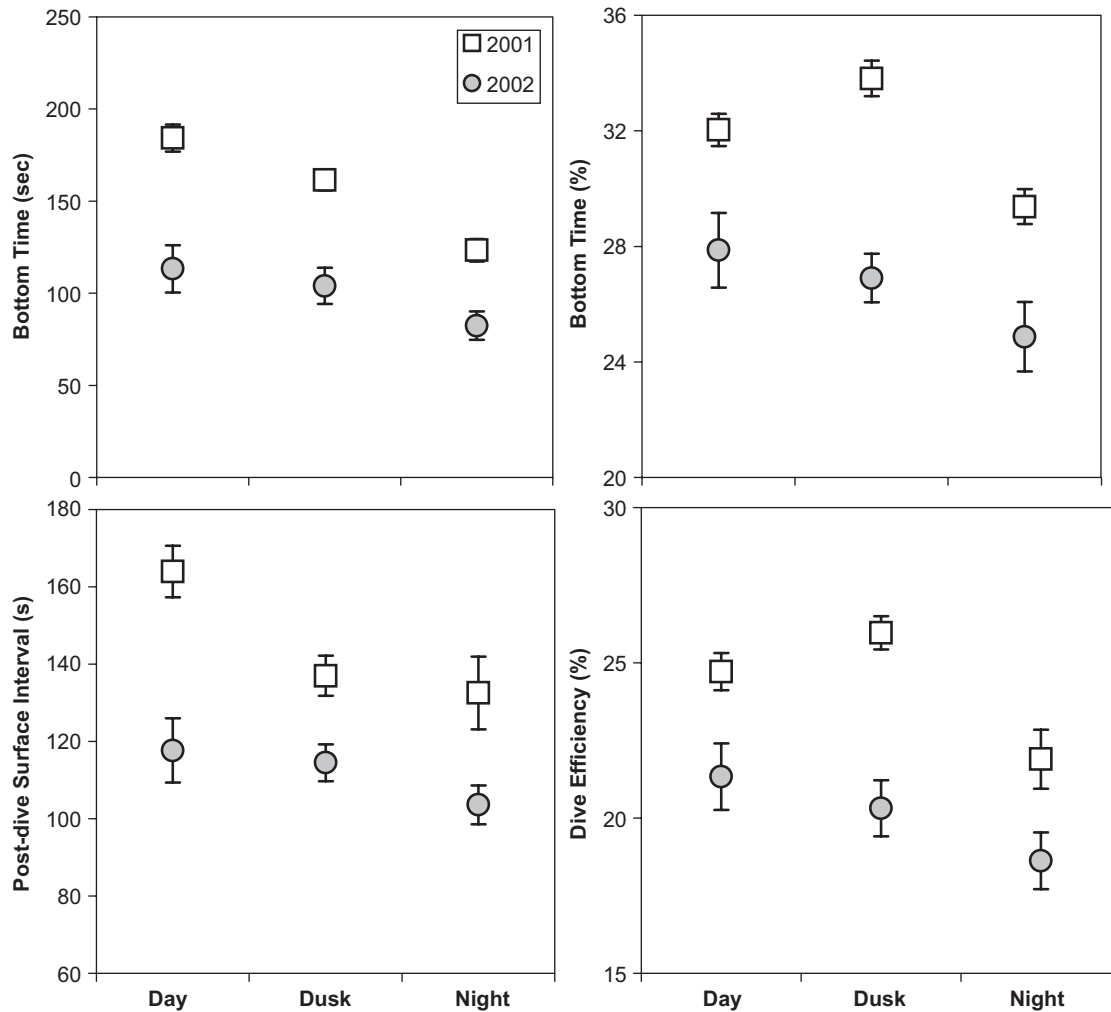
Fig. 2. Mean (±S.E.) bottom time, percent bottom time, post-dive surface interval, and dive efficiency for dives made by crabeater seals between April and October 2001 and 2002, during the day, dusk, and night periods of the day. These figures only include dives that were >24 m.

far between sequential days (an average of 8.0 ± 1.1 km for all months except April, Fig. 5). The most parsimonious model did not include a *year* term.

3.2. Environmental analysis

We also examined the impact of physical features of the habitat on diving behavior directly, by including *bathymetric slope*, *seafloor depth*, and *sea-ice concentration* in the models evaluated. We limited this examination to *maximum dive depth* and *dive efficiency* only, as we felt these two parameters would shed the most light on habitat use patterns. After accounting for temporal autocorrelation and the random effect of *individual*, *dive duration* accounted for >45% of the deviance in *maximum dive depth*, with a small contribution of *bathymetric slope* (2.5%), *seafloor depth* (2.2%) and *sea-ice concentration* (<1.0%) to the relationships (ranked models 2, 3, and 5 with approximately equal $w\mathrm{BIC} \sim 0.03$–0.06; Table 2). The model ranking according to $w\mathrm{AIC_c}$ indicated approximately equal

support for these physical correlates; however, the addition of *year* and *period* improved the deviance explained in *maximum dive depth*. For *dive efficiency*, there was some evidence for a correlation with the physical variables considered according to $w\mathrm{BIC}$ and $w\mathrm{AIC_c}$ and rankings; however, these explained only a small proportion of the deviance in the response (Table 3). Most of the deviance in *dive efficiency* was explained by differences among *periods* (%DE = 1.93), with some additional variation explained by *year* and *seafloor depth* (Table 3). This lack of goodness-of-fit suggests poor explanatory power in the terms considered and suggests that *dive efficiency* was more a function of behavioral and biological factors not considered here (e.g. prey availability).

4. Discussion

Previous studies investigating the diving behavior of crabeater seals have shown that most dives are short and shallow (Bengtson and Stewart, 1992; Nordøy et al., 1995;
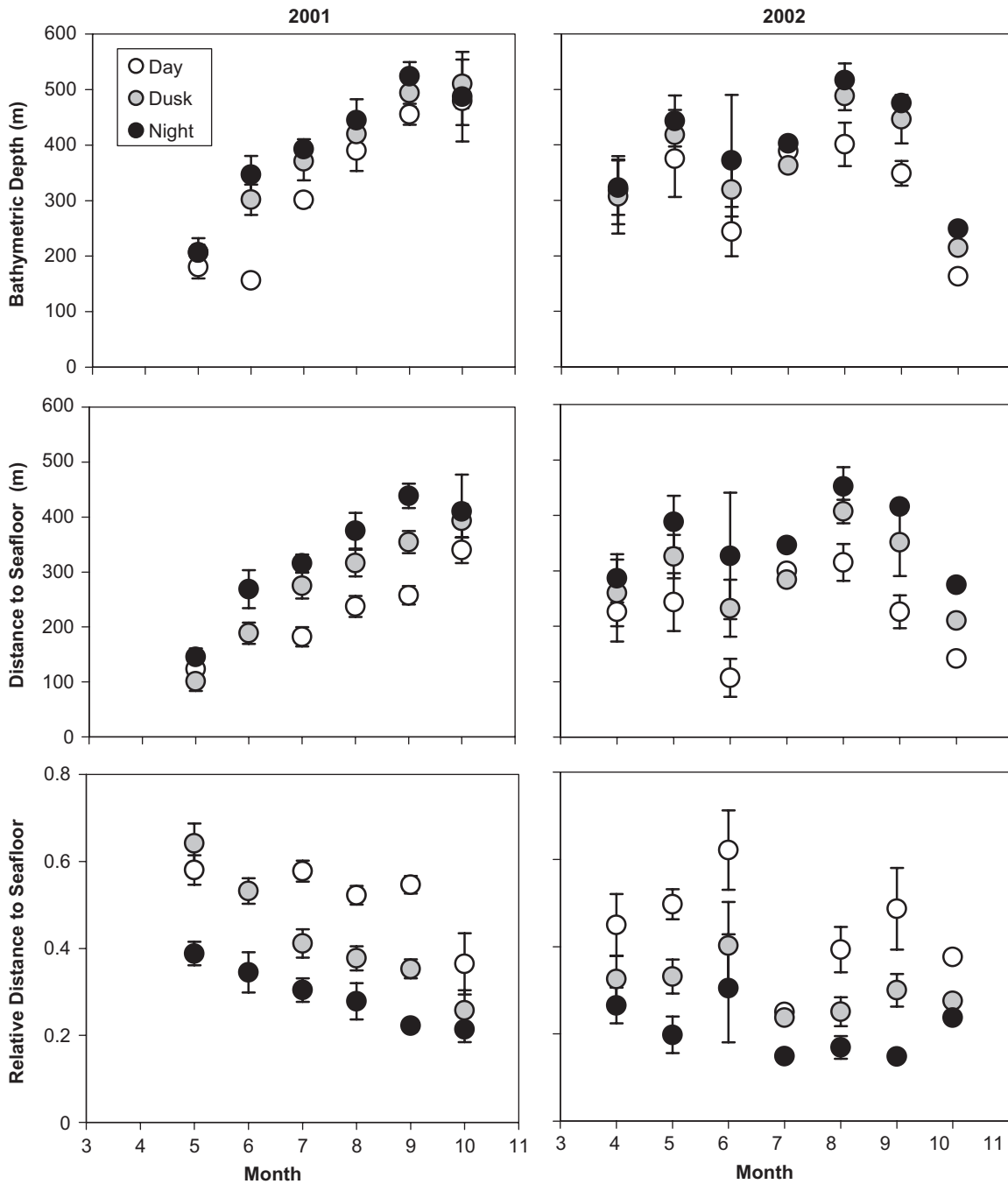
Fig. 3. Mean ($\pm$S.E.) seafloor depth (m) over which dives were occurring, distance of dives to the seafloor (m), and relative distance to the seafloor (larger values indicate that dives were closer to the bottom) for dives made by crabeater seals between April and October 2001 and 2002, during the day, dusk, and night periods of the day. These figures only include dives that were >24 m.

Wall et al., 2007); however, the individuals tracked in this study frequently made relatively long, deep dives (Gales et al., 2004; Burns et al., 2004), and dive depths coincided with the modal depths of krill aggregations (Lawson, 2006). In both years, dives were on average deeper and longer during daylight hours compared to night. Crepuscular dives were always intermediate in characteristic to day and night dives, suggesting that light level may ultimately drive foraging behavior. This pattern suggests that crabeater seals were foraging on a vertically migrating

prey resources, although most predators having a diurnal foraging pattern concentrate their diving activity during the night when prey are believed to be more accessible and nearer to the surface (Wilson et al., 1993; Boyd et al., 1994; Horning and Trillmich, 1999). However, unlike in previous studies (Bengtson and Stewart, 1992; Nordøy et al., 1995; Ackley et al., 2003; Southwell, 2005), the individuals we tracked dived more frequently during the day when dives were longer and deeper, and spent more time hauled out on ice floes during the night (Burns et al., 2004).
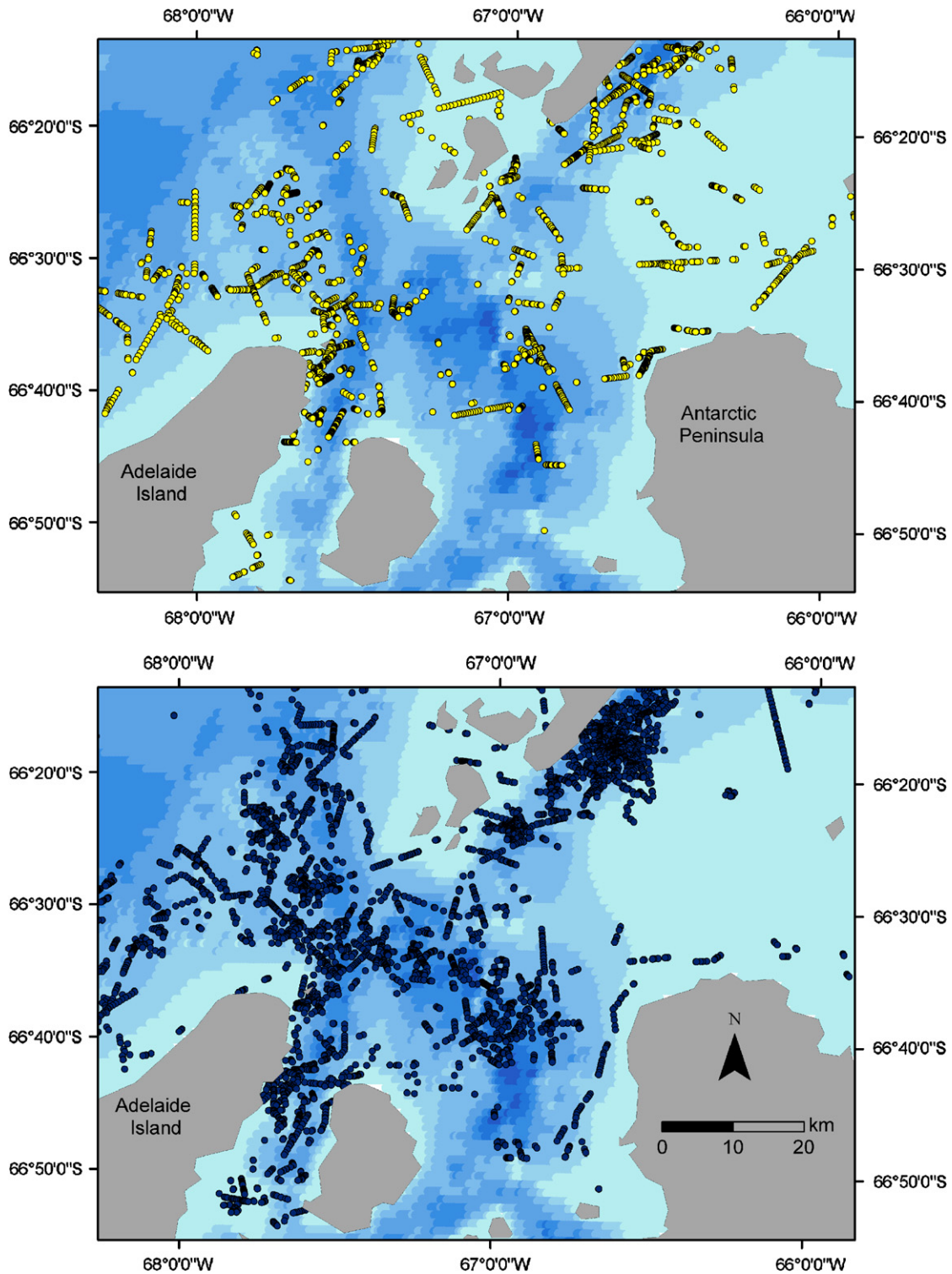
Fig. 4. Locations of crabeater seal dives during day (upper panel) and night (period) dives in the Crystal Sound area, just to the north of Marguerite Bay.

Under the predictions of optimal foraging theory (Stephen and Krebs, 1986), air-breathing marine predators should opt to forage closer to the surface if prey are available and thereby reduce travel and recovery costs (Ydenberg and Clark, 1989; Carbone and Houston, 1996). This is the pattern seen in most previous studies of crabeater seal diving: dives are typically short (<5 min), shallow (<50 m), and occur predominantly at night (Bengtson and Stewart, 1992; Nordøy et al., 1995). However, if deep-residing prey are easier to capture or are of higher energetic value, then deeper foraging strategies can be more efficient than shallow dives, even if

they require anaerobic metabolism (Ydenberg and Clark, 1989; Carbone and Houston, 1996). Dive depth can also be limited by physiological or sensory constraints such as oxygen stores or light levels; as a result, the selected foraging depth range integrates features of both predator and prey (Castellini, 1991; Wilson et al., 1993; Burns, 1999; Horning and Trillmich, 1999). For crabeater seals, the deeper daytime foraging activities that occurred during winter do not appear to reflect a switch to non-krill prey given the predominance of krill in the diet during the entire

year (Øritsland, 1977; Green and Williams, 1986; Lowry et al., 1988; Burns et al., 2004). Therefore, the pattern we observed most likely tracks the vertical migrations of large zooplankton and krill (*Euphausia superba* and/or *Euphausia crystallorophias*) observed in interior fjords surrounding Marguerite Bay (Zhou and Dorland, 2004; Siegel, 2005; Lawson, 2006). Along the Western Antarctic Peninsula and in the Marguerite Bay region, krill descents are limited in depth by the continental shelf. Thus, the differences in dive patterns across regions may be influenced by prey behavior and local bathymetric features.

The diel variation in post-dive surface interval, bottom time, and dive efficiency sheds light on how seals allocate their time when foraging, and all metrics support the hypothesis that nighttime foraging is less effective than daylight foraging. For example, dives made at night were characterized by the shortest bottom time, even though the relatively shallow depths to which these dives occurred should have allowed seals to spend more time the bottom searching for prey due to the reduced time required to reach foraging depths. Instead, seals spent a smaller fraction of the dive cycle at depth during the night, such as might be expected if nighttime foraging activities were associated with higher diving metabolic rates, or reduced foraging success (Thompson and Fedak, 2001; Hastie et al., 2006). Conversely, daytime foraging dives were associated with increased bottom time, which would allow for greater prey contact time, and potentially higher prey capture rates, given that daytime krill aggregations were of higher biomass density (Lawson, 2006). Still, it must be noted that the diel variation in these parameters was relatively small compared to intra-annual differences in dive depth, duration, and dive frequency (Burns et al., 2004), suggesting that within each year seals were shifting how time was
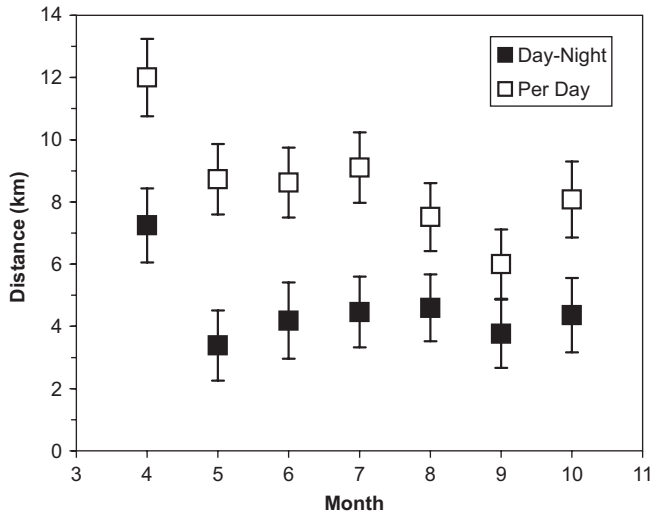

Fig. 5. Mean ($\pm$S.E.) distance traveled (km) by crabeater seals between April and October 2001 and 2002. Distance traveled per day is the average strait line distance between sequential average daily positions for each seal. Distance traveled day–night, is the average strait line distance between the average position during the day and the night for each day and seal. Distances traveled between day and dusk, and between dusk and night intermediate to day–night distances.

Table 2
The five most parsimonious generalized linear mixed-effects models investigating the habitat and temporal correlates of *maximum dive depth* for 34 crabeater seals (full dataset, $n = 4050$ 6-h binned dive periods) according to the Bayesian Information Criterion (BIC) (a) and Akaike's Information Criterion corrected for small sample size (AIC$_c$) (b)

Model	k	LL	ΔBIC	wBIC	ΔAIC$_c$	wAIC$_c$	%DE
(a) BIC-ranked							
DEP–DUR	5	−20.107	0.000	0.778	2.825	0.039	45.73
DEP–DUR + SLP	6	−19.179	5.095	0.061	2.993	0.035	48.23
DEP–DUR + BTH	6	−19.297	5.333	0.054	3.229	0.031	47.92
DEP–DUR + YR	6	−19.325	5.389	0.053	3.286	0.031	47.84
DEP–DUR + ICE	6	−19.856	6.469	0.031	4.347	0.018	46.41
(b) AIC$_c$-ranked							
DEP–DUR + YR + PER	8	−15.653	11.976	0.002	0.000	0.158	57.75
DEP–DUR + YR + PER + SLP	9	−14.798	17.224	<0.001	0.323	0.134	60.06
DEP–DUR + YR + PER + BTH + SLP	10	−14.210	23.010	<0.001	1.186	0.087	61.65
DEP–DUR + YR + PER + ICE	9	−15.356	18.331	<0.001	1.440	0.077	58.55
DEP–DUR + YR + PER + BTH	9	−15.396	18.413	<0.001	1.520	0.074	58.44

The five most highly BIC-ranked models accounted for >96% of the information-theoretic weight (wBIC) of the total of 26 models considered. Terms shown areas follows: DEP, maximum dive depth; DUR, dive duration; SLP, bathymetric slope; BTH, bathymetric depth; YR, year; ICE, sea-ice concentration; and PER, period of day (day, twilight or night). Also shown is the number of parameters (k), the maximum log-likelihood (LL), the difference in BIC and AIC$_c$ for each model from the most parsimonious model (ΔBIC and ΔAIC$_c$), the AIC and BIC weights (wAIC and wBIC), and the percent deviance explained in maximum dive depth by the model under consideration.

Table 3

The five most parsimonious generalized linear mixed-effects models investigating the habitat and temporal correlates of dive efficiency (bottom time $\times$ [dive duration + post-dive surface interval]$^{-1}$) for 31 crabeater seals (full dataset, $n = 41276$ dives) according to the Bayesian Information Criterion (BIC) (a) and Akaike's Information Criterion corrected for small sample size (AIC$_c$) (b)

Model	k	LL	ΔBIC	wBIC	ΔAIC$_c$	wAIC$_c$	%DE
(a) BIC-ranked							
EFFIC–YR + PER + BTH	8	−14319.11	0.000	0.954	1.623	0.147	2.13
EFFIC–YR + PER + BTH + ICE	9	−14317.30	7.004	0.029	0.000	0.331	2.14
EFFIC–YR + PER + BTH + SLP	9	−14317.82	8.043	0.017	1.039	0.197	2.14
EFFIC–YR + PER + BTH + SLP + ICE	10	−14316.31	15.660	<0.001	0.029	0.326	2.15
EFFIC–PER	6	−14340.29	37.112	<0.001	55.990	<0.001	1.93
(b) AIC$_c$-ranked							
EFFIC–YR + PER + BTH + ICE	9	−14317.30	7.003	0.029	0.000	0.331	2.14
EFFIC–YR + PER + BTH + SLP + ICE	10	−14316.31	15.660	<0.001	0.029	0.326	2.15
EFFIC–YR + PER + BTH + SLP	9	−14317.82	8.043	0.017	1.039	0.197	2.14
EFFIC–YR + PER + BTH	8	−14319.11	0.000	0.954	1.623	0.147	2.13
EFFIC–YR + PER + ICE	8	−14340.16	42.107	<0.001	73.730	<0.001	1.99

The five most highly BIC-ranked models accounted for >96% of the information-theoretic weight (wBIC) of the total of 25 models considered. Terms shown are as follows: EFFIC, dive efficiency; DUR, dive duration; SLP, bathymetric slope; BTH, bathymetric depth; YR, year; ICE, sea-ice concentration; and PER, period of day (day, twilight or night). Also shown is the number of parameters (k), the maximum log-likelihood (LL), the difference in BIC and AIC$_c$ for each model from the most parsimonious model (ΔBIC and ΔAIC$_c$), the AIC and BIC weights (wAIC and wBIC), and the percent deviance explained in dive effort by the model under consideration.

allocated within the dive cycle in order to maintain relatively constant prey encounter rates, despite diel variation in the depths at which the prey were encountered.

Within each year, the diel shifts in bottom time and dive efficiency indicate that seals adjusted their dive patterns to spend more time at depth during the day without incurring substantially increased recovery costs. Given that the average daytime dive duration (7.2 ± 0.4 min, range $3.5-10.7$ min by individual) was close to the estimated ADL ($6.1-11.8$ min, calculated using measured oxygen stores and a diving metabolic rate of $2 \times$ Kleiber, unpublished data); further increases in bottom time were likely not possible without an increased reliance on anaerobic metabolism. When placed within the context of simultaneously monitored krill behavior, findings suggest that seals were targeting krill during the day when adults were aggregated at depth closer to the seafloor (Zhou and Dorland, 2004; Lawson et al., 2004; Ashjian et al., 2004; Lawson, 2006). Foraging at depth on densely aggregated krill swarms as opposed to more broadly dispersed individuals closer to the surface has been correlated with increased foraging efficiency in a variety of krill predators (Wilson et al., 1993; Tremblay and Cherel, 2000; Croll et al., 2005). In addition, the shift from nighttime foraging during summer to the deeper, daylight foraging patterns observed in this study are in agreement with research indicating that adult krill within the study area vertically migrate and can be found in large aggregations at depths in excess of 200 m (Zhou and Dorland, 2004; Lawson, 2006). This suggests that crabeater seals improve winter foraging success by focusing their diving close to the seafloor in areas where bathymetry constrains prey-escape movements. As crabeater seals

maintain mass and body condition throughout the winter (Laws et al., 2003; Burns et al., 2004; McDonald et al., This issue), this strategy is apparently successful.

Within this context, the large annual differences in dive metrics suggest that foraging conditions were different in 2001 as compared to 2002. Dives were significantly longer and deeper in all periods in 2001, and yet these longer dives were associated with more bottom time and higher dive efficiency. If dives with higher bottom time and dive efficiency are indeed associated with improved foraging success, then it would appear that krill were more available to seals in 2001, either due to differences in absolute abundance, aggregative behaviors, or accessibility. Fall and winter krill surveys found inter- and intra-annual differences in krill aggregation size, biomass density, and depth distribution, with more krill present in fall than winter, and krill more abundant, but more deeply distributed in 2002 than 2001 (Lawson, 2006). Indeed, if krill were deeper, more dispersed and/or more difficult for seals to capture in 2002 (due to either krill behavior or ice conditions), then many of the annual differences fit with optimal foraging predictions: deeper dives with their increased travel time would not have been as profitable, seals would have targeted krill with shorter, shallower dives, and the diel pattern would have been less marked-all patterns which we observed. The alternative explanation, that dives were shorter and associated with lower bottom time and dive efficiency in 2002 because krill were easier to capture, is not as supported by survey data (Lawson, 2006), nor by the observation that seals spent similar amounts of time hauled out in 2001 and 2002 (Burns et al., 2004). Rather, the similarities across years in activity budgets (Burns et al., 2004), and the absence of differences in seal mass between

the years (McDonald et al., This issue) suggests that seals can and do alter their foraging strategies to compensate for variations in prey availability.

Predators can increase foraging success by targeting prey at appropriate depths and times, but also by foraging selectively in habitats where prey are more abundant or easier to capture. Within Antarctic waters, higher predator densities are often seen in polynyas and local eddies, at frontal systems and thermal layers, near sea mounts and the continental shelf break, and in association with the marginal ice zone (Boyd and Arnbom, 1991; McConnell et al., 1992; Field et al., 2001), and these are all features that aggregate adult krill (Siegel, 1988; Trathan et al., 1993; Siegel, 2005). Our results indicate seals along the Western Antarctic Peninsula make hierarchical foraging decisions across broad temporal and spatial scales. Seals select mesoscale (hundreds of km) areas that have predictably elevated productivity due to particular fixed habitat features. Individuals then select foraging locations within these areas based on finer-scale (tens of km) habitat features that increase the probability of finding prey (Trathan et al., 1993; Fauchald et al., 2000; Bradshaw et al., 2002; Fritz et al., 2002; Pinaud and Weimerskirch, 2005; Vlietstra, 2005).

At the mesoscale, crabeater seals within Marguerite Bay spent more time than expected in the shallow (<600 m) nearshore habitats characterized by heavy ice cover, varied bathymetry, and eddies and small gyres (Burns et al., 2004; Beardsley et al., 2004; Klinck et al., 2004) that retain krill (Hofmann and Murphy, 2004; Lawson et al., 2004). However, once within these areas, seal behavior was correlated with a much smaller subset of physical features. For example, ice cover influenced mesoscale habitat selection but inside these areas, ice cover ceased to have a consistent effect on dive behavior (i.e. ice cover only accounted for $<1\%$ of the variation in *maximum dive depth* and none of the variation in dive efficiency). This selectivity for heavy but not complete cover at the mesoscale level has been seen before (Ribic et al., 1991; Joiris, 1991; Bester et al., 1995; McMahon et al., 2002; Southwell et al., 2005) and may reflect selection for habitat with suitable haul-out substrata that also allow for easy access to available prey. Seals also demonstrated meso-, but not fine-scale habitat selection with respect to bathymetric slope. At the mesoscale, seals spent more time in regions of higher-than-average bathymetric slope (Burns et al., 2004), but at the fine scale (<1 km), slope did not account for large or consistent differences in behavior. We note, however, that the temporal and spatial resolution of sea-ice concentration, and bathymetric depth were coarse relative to that of the measured behavior, and this mismatch may account for our failure to find evidence for associations at the finer scales.

Once within areas of suitable depth, ice and slope, seals made daily fine-scale movements between deeper and shallower areas. The movements needed to achieve this were small, in part because the seals were already in an area

where the bathymetry was variable (high gradient, Burns et al., 2004). However, as a result of these small-scale movements, seals were able to dive closer to the seafloor during the day, resulting in a three-fold increase in benthic dives. This fine-scale habitat selection likely allows for a more effective targeting of krill swarms during daylight hours when swarms were compacted along the seafloor, while still retaining the ability to forage with minimal travel costs when krill ascended into shallower waters at night (Zhou and Dorland, 2004; Lawson et al., 2004; Ashjian et al., 2004; Lawson, 2006). In deeper waters off the continental shelf, this strategy would not be as effective because krill could descend to depths greater than seals could efficiently exploit given their physiological constraints (Costa et al., 2001, 2004). This interaction between prey behaviors, local bathymetry and the physiological limits of diving may explain why previous studies, conducted in oceanic waters have found that seals confine their foraging to upper water column at night (Nordøy et al., 1995; McMahon et al., 2002; Ackley et al., 2003; Southwell et al., 2005). In deep-water habitats, both the scale and identity of the physical features to which seals behavior responds may be different, and models that predict seal distributions within coastal environments such as the Western Antarctic Peninsula might not be broadly applicable to off-shelf habitats.

The generalized linear models demonstrate that crabeater seal diving behavior responds to temporal and physical variables associated with shifts in the distribution of their primary prey, Antarctic krill. That the models could not account for the majority of the variance in behavior should be expected because seals are unlikely to vary their behavior in direct response to these static features, but rather respond to the abundance, density, and behavior of Antarctic krill at spatial and temporal scales finer than those examined here (Trathan et al., 1993; Vlietstra, 2005). The decoupling between physical and biotic factors represented by the as yet unexplained variance is probably due to krill swarms only being loosely tied to ice extent, slope, or bathymetry, and instead varying with respect to smaller scale features such as eddies, primary productivity, and even predator exposure (Zhou and Dorland, 2004; Hofmann and Murphy, 2004; Siegel, 2005; Lawson, 2006). This suggests that models designed to predict how seals will allocate time within dives should incorporate biotic features of the habitat measured at finer temporal and spatial scales as well as detailed information on local prey behavior and distribution. Conversely, simple models such as those presented here may be useful at revealing broader-scale patterns, and benefit from the ease with which information on bathymetry and ice cover can be collected.

5. Conclusions

This study revealed that crabeater seals diving during the winter along the Western Antarctic Peninsula employed a scale-dependent use of their habitat. At the meso-scale,

seals selected areas of the habitat with shallower-that-average depths and greater-than-average ice cover, and these were areas where krill were most abundant. Once within these areas, seals showed fine-scale habitat selection based on depth, with daytime dives occurring over shallower waters than those at night. This increased the proportion of efficient, benthic dives during the day and allowed seals to effectively target krill when swarms were more densely aggregated and closer to the bottom of the continental shelf (Lawson, 2006). These results suggest that seals selected areas of high bathymetric gradients so that they could maximize foraging success over a 24-h cycle without the need to travel long distances. However, features that were important at the meso-scale were not always influential at the finer scale, and the relative importance of different features varied annually, seasonally, and diurnally. This indicates that developing behavioral models with reasonable predictive power will rely on selecting relevant physical and biological features at the appropriate spatial and temporal scales. For example, GLMMs that incorporated only a few physical oceanographic variables were able to account for a reasonably large amount of the variance in dive depth, likely due to the large size of the krill swarms and the inability of krill to escape predation in the coastal fjords. However, models were unable to account for much of the variance in dive efficiency, probably because no information on prey abundance or behavior at scales relevant to single dives or even groups of dives was included. This suggests that using information on seal diving, movement, and haul-out patterns to assess broad-scale changes in the underlying prey fields will be difficult, and studies that focus on demographic variables may prove more successful. However, within limited areas, changes in seal distribution and behaviors may still prove useful for understanding shifts in lower trophic levels that are likely to accompany environmental change.

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