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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.

Keywords: Diet; Krill; Crabeater seal; Diving patterns; Satellite telemetry; Spatial analysis

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