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Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories

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Abstract. In the Southern Ocean, wide-ranging predators offer the opportunity to quantify how animals respond to differences in the environment because their behavior and population trends are an integrated signal of prevailing conditions within multiple marine habitats. Southern elephant seals in particular, can provide useful insights due to their circumpolar distribution, their long and distant migrations and their performance of extended bouts of deep diving. Furthermore, across their range, elephant seal populations have very different population trends. In this study, we present a data set from the International Polar Year project; Marine Mammals Exploring the Oceans Pole to Pole for southern elephant seals, in which a large number of instruments ($N = 287$) deployed on animals, encompassing a broad circum-Antarctic geographic extent, collected *in situ* ocean data and at-sea foraging metrics that explicitly link foraging behavior and habitat structure in time and space. Broadly speaking, the seals foraged in two habitats, the relatively shallow waters of the Antarctic continental shelf and the Kerguelen Plateau and deep open water regions. Animals of both sexes were more likely to exhibit area-restricted search (ARS) behavior rather than transit in shelf habitats. While Antarctic shelf waters can be regarded as prime habitat for both sexes, female seals tend to move northwards with the advance of sea ice in the late autumn or early winter. The water masses used by the seals also influenced their behavioral mode, with female ARS behavior being most likely in modified Circumpolar Deepwater or northerly Modified Shelf Water, both of which tend to be associated with the outer reaches of the Antarctic Continental Shelf. The combined effects of (1) the differing habitat quality, (2) differing responses to encroaching ice as the winter progresses among colonies, (3) differing distances between breeding and haul-out sites and high quality habitats, and (4) differing long-term regional trends in sea ice extent can explain the differing population trends observed among elephant seal colonies.

Key words: foraging behavior; *Mirounga leonina*; physical oceanography; population status; sea ice; Southern Ocean water masses.

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Introduction

The Southern Ocean controls the mixing of the world's deep and upper water masses and thereby regulates the capacity of the ocean to store and transport heat and carbon as well as having major influences on global biogeochemical cycles (Rintoul 2011). These processes dictate where primary and secondary production occur (Olonscheck et al. 2013), and consequently where higher trophic level species focus their foraging in order to maximize energy acquisition at minimum cost, thereby maximizing fitness (Murphy et al. 2012). Consequently, monitoring animal behavior and population trends in relation to *in situ* habitat structure provides spatio-temporally explicit information on changes in the distribution of predator aggregations and foraging behavior, which are essential for understanding ecological processes (Block et al. 2011). Moreover, coupling the diving behavior of marine predators with characteristics of their ocean habitats is a particularly powerful way to understand biophysical interactions and enhance our ability to quantify and understand ecological patterns and processes in marine environments (Melbourne-Thomas et al. 2013). The Southern Ocean has a unique predator fauna as a result of its isolation and extreme environmental conditions. To be successful, species have evolved diverse life-history patterns adapted to extensive seasonal and interannual fluctuations in both the physical and biological environment. Quantifying where and when predators concentrate their foraging effort contributes to resolving a number of important ecological issues, such as the distribution and availability of resources along with their spatial and temporal variability.

Variation in prey availability leads predators to shift their foraging locations and modify foraging behavior, which can affect their foraging success, which in turn influences survival, breeding success, and eventually population abundance, all of which are readily measurable (New et al. 2014). An important first step in understanding these complex processes is to quantify patterns of habitat use and foraging ecology of top predators such as seals. Ocean properties are the fundamental determinant of habitat suitability for marine predators, and in many ways are analogous to the way that terrain or vegetation types determine habitats for terrestrial predators. However, in marine systems such data are often incomplete or totally lacking, because animals use areas of ocean that are generally inaccessible or difficult to monitor. Furthermore, the marine environment is highly dynamic. Primary productivity can be transported over vast areas due to advection and predators need to track the shifts. In polar regions seasonally dynamic sea ice cover adds further to the complexity (Charrassin et al. 2008).

The development of miniaturized logging and satellite-linked monitoring equipment that can be attached to marine animals has revolutionized how we gather information in extreme environments like the Southern Ocean (Aarts et al. 2008). Biologists can now monitor *in situ* oceanographic conditions simultaneously with animal behavior (Biuw et al. 2007, Charrassin et al. 2008), creating a vital link in understanding animals' responses to local changes in food availability and how they use different habitats (Costa et al. 2010).

The world's oceans are heterogeneous and comprise a variety of different water masses. Functionally, these water masses can be regarded as different marine habitats. Water masses are large-scale, three-dimensional features, sharing common water temperature, salinity and density ranges, where unique combinations of these variables define each individual water mass's evolution and physical structure (Herraiz-Borreguero and Rintoul 2011). The geo-chemical and