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Ecological niche modeling of sympatric krill predators around Marguerite Bay, Western Antarctic Peninsula

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ABSTRACT

Adélie penguins (*Pygoscelis adeliae*), carabeater seals (*Lobodon carcinophagus*), humpback (*Megaptera novaeangliae*), and minke whales (*Balaenoptera bonaernsis*) are found in the waters surrounding the Western Antarctic Peninsula. Each species relies primarily on Antarctic krill (*Euphausia superba*) and has physiological constraints and foraging behaviors that dictate their ecological niches. Understanding the degree of ecological overlap between sympatric krill predators is critical to understanding and predicting the impacts on climate-driven changes to the Antarctic marine ecosystem. To explore ecological relationships amongst sympatric krill predators, we developed ecological niche models using a maximum entropy modeling approach (Maxent) that allows the integration of data collected by a variety of means (e.g. satellite-based locations and visual observations). We created spatially explicit probability distributions for the four krill predators in fall 2001 and 2002 in conjunction with a suite of environmental variables. We find areas within Marguerite Bay with high krill predator occurrence rates or biological hot spots. We find the modeled ecological niches for Adélie penguins and crabeater seals may be affected by their physiological needs to haul-out on substrate. Thus, their distributions may be less dictated by proximity to prey and more so by physical features that over time provide adequate access to prey. Humpback and minke whales, being fully marine and having greater energetic demands, occupy ecological niches more directly proximate to prey. We also find evidence to suggest that the amount of overlap between modeled niches is relatively low, even for species with similar energetic requirements. In a rapidly changing and variable environment, our modeling work shows little indication that krill predators maintain similar ecological niches across years around Marguerite Bay. Given the amount of variability in the marine environment around the Antarctic Peninsula and how this affects the local abundance of prey, there may be consequences for krill predators with historically little niche overlap to increase the potential for interspecific competition for shared prey resources.

1. Introduction

The structure and function of ocean ecosystems are affected in large part by spatial and temporal variability in the physical environment, which produces areas of enhanced biological activity. These areas, where critical linkages between trophic levels exist, are considered ‘biological hot spots’ (Sydeman et al., 2006). These regions attract higher trophic level organisms, as a result of physical features (static) and forcing (episodic) mechanisms that act in concert to enhance prey availability (Ainley et al., 1998; Bost et al., 2009). At evolutionary time scales, species have adopted life history strategies and foraging behaviors to take advantage of particularly persistent and profitable regions (Costa, 1993; Etnoyer et al., 2004). Biological hot spots have been described across a broad range of spatial scales: from broad upwelling zones to meso-scale frontal boundaries and smaller episodic eddies (see Palacios et al., 2006). In fact, it could be argued that the entire Southern Ocean below the Polar Front is in and of itself an entire biological hot spot (Tynan, 1998; Bost et al., 2009).

Within the Southern Ocean, physical, biological, and chemical processes combine to create an ecosystem dominated by the annual advance and retreat of sea ice and seasonal primary productivity (Knox, 2007). This in turn has lead to a zooplankton community dominated by abundant euphausiids, particularly Antarctic krill (*E. superba*). The Southern Ocean supports an unprecedented number of upper trophic-level predators, including

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whales, seals, penguins, seabirds, and fish, which feed primarily on the large biomass of Antarctic krill (Knox, 2007). Baleen whales (humpback (*M. novaeangliae)*, minke (*Balaenoptera bonaerensis)*), crabeater seals (*L. Carcinophagus)*, and Adélie penguins (*P. adeliae)* are all abundant in the nearshore waters along the Western Antarctic Peninsula (WAP). They all feed primarily on Antarctic krill, and yet have extremely varied foraging strategies and abilities to access prey (Costa and Crocker, 1996; Fraser and Trivelpiece, 1996; Ducklow et al., 2007). Humpback whales are seasonal residents, migrating between tropical breeding and calving grounds to feed along the WAP in summer and autumn months (Laws, 1985). Minke whales have been observed throughout winter months around the WAP, indicating that they are year-round residents (e.g. Thiele et al., 2004). Some portion of the minke whale population may migrate seasonally, but little is known regarding this behavior and what proportion of the population this represents. Crabeater seals are resident to the Antarctic and are pagophilic; they rarely come to shore, and use sea ice as their primary haul-out platform and breeding and pupping substrate (Siniff, 1991). Adélie penguins breed on rocky shores along the WAP (Fraser and Hofmann, 2003). They are considered central-place foragers that they must come and go to their breeding colonies to provision chicks while they are being raised in spring and summer months. They also utilize sea ice as a haul-out substrate throughout the year between foraging bouts.

Given the broad size ranges and energetic requirements of these krill predators, each has developed unique foraging behaviors and feeding strategies to maximize efficiency (Costa, 1991). While Adélie penguins feed mainly in the upper 100 m of the water column (Chappell et al., 1993), crabeater seals forage as deep as 450 m (Burns et al., 2004). And while both penguins and seals feed on individual krill, baleen whales (including humpback and minke whales) engulf large quantities of krill-rich water to consume as many prey as possible at once. Considering these feeding and life history constraints, the distributions of each species should reflect locations that offer the ability to satisfy both their physical and energetic requirements for survival.

Over the past 50 years, significant climate warming has been detected along the WAP (Vaughan et al., 2003). This warming is believed to have affected the amount of sea ice and its interannual variability (Murphy et al., 2007; Stammerjohn et al., 2008) and the abundance of Antarctic krill around in the region (Atkinson et al., 2004; Ducklow et al., 2007). These changes have, in part, led to decrease in population trends in some krill predator populations (e.g. Adélie penguins, see Fraser and Hofmann (2003), Ducklow et al. (2007) and Forcada et al. (2008)). Given the changes in both the physical environment and availability of prey resources, assessing the likelihood or degree of ecological interactions between krill predators is necessary to better understand future impacts of climate-driven changes to the Antarctic marine ecosystem (Costa et al., 2010). The purpose of the present study is to: (1) better understand how physical and biological features, and variability among these as observed in 2001 and 2002, affect the distribution of sympatric krill predators around Marguerite Bay, WAP; and (2) describe the amount of niche overlap among and between krill predators during autumn months and how these relationships are affected by environmental variability. We address these objectives by determining the combination of environmental variables (derived largely from data collected during the Southern Ocean Global Ecosystems Dynamics (SO GLOBEC) field seasons in 2001 and 2002) that best predict the habitat and account for the distribution of different krill predators using a presence-only habitat modeling technique called maximum entropy modeling, Maxent. Maxent estimates a species' probability distribution by finding the probability distribution of maximum entropy (i.e., closest to uniform), subject to a set of constraints derived from available information about the species' environmental relationships (Phillips et al., 2006). We also explore the extent of ecological overlap and niche partitioning of these habitat models across predator taxonomic groups and between years using established niche overlap assessment techniques.

2. Materials and methods

2.1. Time frame, study region and data sources

We use data collected as part of the Southern Ocean GLOBEC program in April–May 2001 and 2002 (Julian days 90–150) in and around Marguerite Bay, WAP (see Hofmann et al., 2004; Fig. 1). We integrate a suite of physical and biological environmental variables collected by a combination of underway continuous and station-based sampling, as well as remotely sensed imagery. Hydrographic data were collected from the RVIB *Nathaniel B. Palmer* in both 2001 and 2002. The hydrographic variables in this study are described in greater detail in Friedlaender et al. (2006). These measures include chlorophyll *a* concentrations, as well as the deep temperature maximum below 200 m that has been shown to relate to episodic intrusions of nutrient-rich circumpolar deep water on to the continental shelf and into the Marguerite Bay (Beardsley et al., 2004; Klinck et al., 2004). We use sea ice edge information from Chapman et al. (2004) and bathymetric information from Bolmer et al. (2004). Quantitative hydro-acoustic surveys were conducted in both 2001 and 2002 using the Bio-Optical Multi-frequency Acoustical and Physical Environmental Records (BIOMAPER-II) (Wiebe et al., 2002), which were used to investigate whales–prey interactions (Friedlaender et al., 2006) and zooplankton distribution and abundance in relation to environmental conditions (Lawson et al., 2004, 2006, 2008). For the current research, we use acoustic backscattering information averaged along the ship's trackline as a measure of the relative abundance of prey throughout the water column. Lawson et al. (2004) discuss confounding influences to be considered when using backscattering to examine patterns in zooplankton and micronekton biomass that make generating actual abundance estimates difficult. We specifically use information from 120 kHz echosounders as this frequency is optimal for detecting larger zooplankton such as krill (reviewed by Lawson et al. (2004)). In regions where predator presence does not overlap directly with acoustic measurements of prey, we use methods described in Friedlaender et al. (2006) to interpolate volume backscatter into a continuous surface grid. Finally, we use occurrence data for a suite of krill predators – Adélie penguins, crabeater seals, minke whales, and humpback whales – generated from a combination of visual survey sampling and remote satellite telemetry techniques as described. Our study area is defined by the margins of the SO GLOBEC study area (Hofmann et al., 2004).

2.2. Crabeater seal satellite telemetry data

As part of four Southern Ocean GLOBEC cruises we instrumented 34 crabeater seals (18 F, 16 M) with satellite-relay data recorders (SRDLs). 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 the mass and the standard length (Laws et al., 2003). Seals were sedated by an intramuscular injection of Midazolam (0.39–0.84 mg kg^{-1}; Hoffmann-La Roche Inc., NJ USA), followed by isoflurane gas anesthesia (see Gales et al. (2005) for more details). Once anaesthetized, SRDLs (Model 7000, Sea Mammal Research Unit, St. Andrews, Scotland, 300 g) were attached to the fur on the top of the head of each animal using Devcon$^{\mathrm{TM}}$ 5 min epoxy (ITW Devcon, Danvers MA). After completion of all procedures, animals were monitored as they recovered from anesthesia and released.

The SRDLs collect information on instrument depth (pressure transducer) and immersion status (wet or dry conductivity sensor)

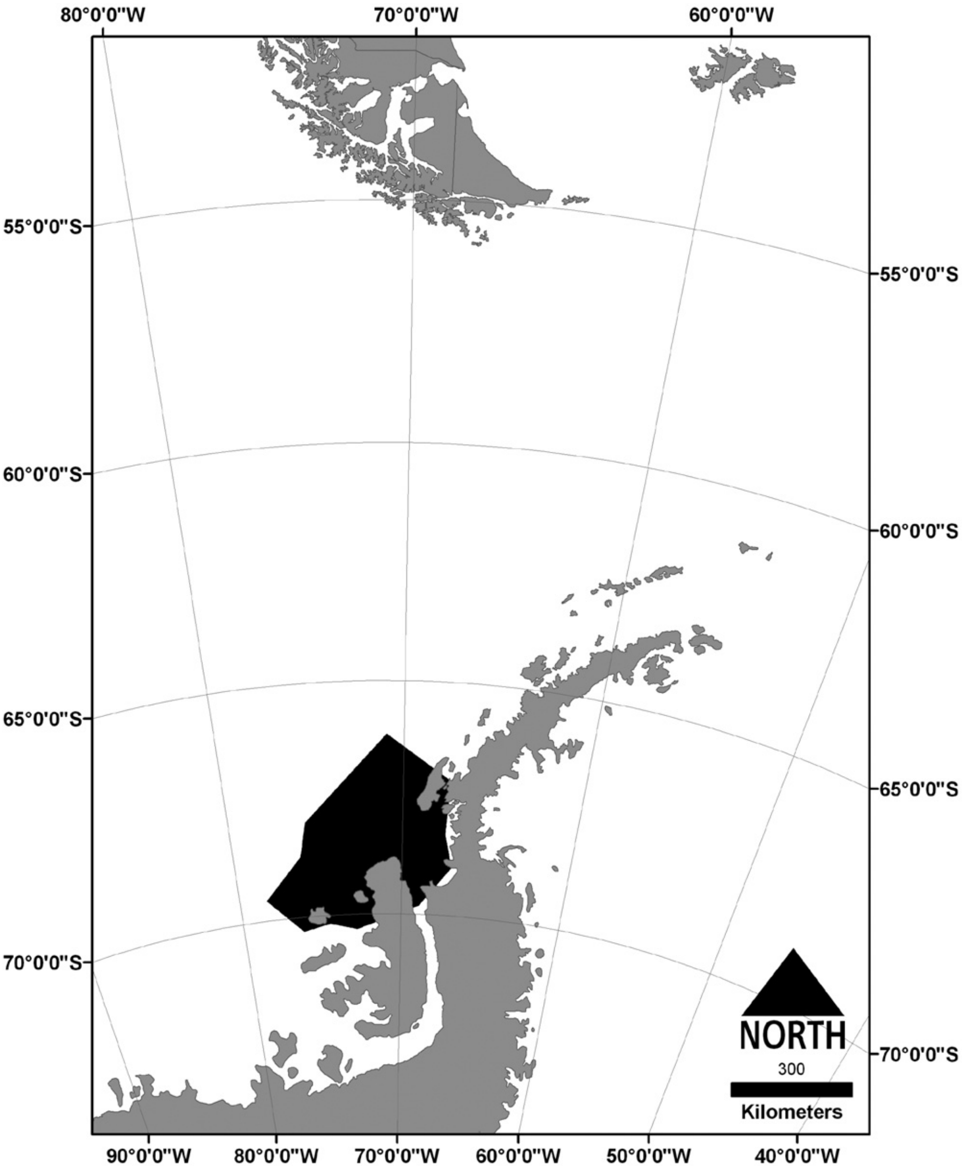

Fig. 1. Southern Ocean GLOBEC study area around Marguerite Bay, Western Antarctic Peninsula.

every 4 s. These data are aggregated into measures of diving behavior (Fedak et al., 2001), and stored in on-board memory prior to transmission to the Argos satellite data-relay system (Service Argos, 1996). Animal locations received from Service Argos are screened by an iterative forward/backward averaging filter that identified and excluded locations that would require rates of travel greater than 4 m/s (Vincent et al., 2002). These positions are then used to reconstruct a trackline of animal movements and to estimate the position of each dive. During this study the SRDL tags transmitted data via the ARGOS system for between 4 and 174 days. 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. 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. Additional tag programming and transmission schedule details have been published previously (Fedak et al., 2001, 2002; Burns et al., 2004). We use a single satellite-fixed location as close to local noon-time as possible for each seal located in the study area during the study period between Julian days 90–150 in 2001 and 2002. This time was chosen as it coincided the most with when visual observations of whales were made.

2.3. *Adélie penguin satellite telemetry data*

Twenty-five Adélie penguins were outfitted with smart position and temperature transmitting (SPOT) (58 g) and SDR-T16 (satellite depth recording) (105 g) series (Wildlife Computers, Redmond, WA) tags in 2001 and 2002 over the course of the SO GLOBEC study. The tags were attached using standardized methods (Wilson et al., 1997) including a gel epoxy platform, waterproof tape, and cable ties to secure the tag to the penguin's feathers. The SPOT tag provided satellite-linked locations through an ARGOS system while the SDR-T16 included information on diving performance. In this paper we use only location data for our analysis. We use a single daytime location for each bird that was located within the study area each day during the study period (Julian days 90–150) in both 2001 and 2002. While locations are classified into 7 categories intended to reflect decrease in accuracy, we use only locations that were from the 3 most accurate categories. Further quality control for position validity (BirdLife International, 2004) was run using a 7 km/h maximum speed species-specific biological threshold filter to determine whether or not consecutive locations could in fact be biologically possible given the known swim speeds of Adélie penguins (e.g. Ainley, 2002; Erdman et al., 2011). There is considerable variability in the number of locations provided by each individual penguin. In order to diminish the effects of individual birds that may be over-represented, and to ensure that birds with fewer data points were not lost, we calculate the mean and standard deviation number of locations per bird per year. Birds with fewer locations than the standard deviation were not used in our analysis. Likewise, birds that had more locations than the standard deviation were randomly sub-sampled at a rate that placed them within one standard deviation of the mean.

2.4. *Cetacean visual survey data*

Visual surveys for cetaceans were conducted on 5 cruises: 3 in 2001 between 1 April and 31 May, and 2 in 2002 between 12 April and 18 May. The platforms used include the ARSV *Laurence M Gould*, the RVIB *Nathaniel B Palmer*, and the RV *Polarstern*. Trained observers worked while the vessel was underway during daylight hours within the study area. Specific protocols are described in Friedlaender et al. (2006). Our dataset included all positively identified sightings of humpback and minke whales made during the aforementioned SO GLOBEC cruises. The location of each sighting was calculated based on the ship's position and the range and bearing to each sighting.

2.5. *Presence only ecological niche modeling*

Initially, we generated a map showing the overall distribution of occurrence for penguins, seals, and whales based on the observations collected for analysis in the study. We plotted these in the geographic information system software package ArcGIS using a kernel density approach commonly employed to creation utilization surfaces for marine species (e.g. Johnston et al., 2005) to create a qualitative map, indicating where areas of high predator occurrence (hot spots) were, if at all, found.

We developed ecological niche models (ENMs—see Bentlage et al. (2009)) for Adélie penguins, crabeater seals, humpback whales, and minke whales using a Maxent approach commonly applied to terrestrial species (e.g. Lozier et al., 2009) and only recently applied to marine predators (see Edren et al., 2010). This technique produces a geographic model of a species' environmental requirements from a set of known occurrences (presence-only data from sightings or wildlife telemetry) combined with measures of environmental factors that contribute to the suitability of the environment for the species (Phillips et al., 2006). The Maxent algorithm estimates the probability distribution of a species by creating a probability distribution across a study region that approaches maximum entropy (or a uniform distribution) as constrained by the availability of 'suitable' habitat for that species (Phillips et al., 2006). The species locations are taken as representing known suitable habitat and are employed as sampling points for each environmental variable used to develop constraints for the Maxent algorithm as it is applied to the entire study region (Phillips et al., 2006). During a model run, the "gain" represents the probability distribution of the model and starts at 0 and increases with every model iteration until the difference between model iterations is below the convergence threshold. The gain can be thought of as a measure of how much better the distribution fits the sample points in comparison to the uniform distribution as iterations are conducted. In geographic space, each pixel of the study area is part of the probability distribution derived by the Maxent algorithm and the model outputs spatially explicit geographic predictions of suitable habitat for each species (Phillips et al., 2006, Phillips and Dudik, 2008).

In the present study, we use the software program Maxent (ver. 3.3.3) to develop ENMs using continuous surfaces of several physical and biological parameters believed to be important in defining suitable habitat for Antarctic krill predators in both 2001 and 2002 separately. Because we are interested in assessing changes in the modeled ecological niches of each krill predator over time and with varying ecological conditions, we choose to perform our analyses for 2001 and 2002 separately. From Julian day 90–150 in 2001 and 2002 we use a single daytime location from each of the tagged crabeater seals and Adélie penguins that were contained within the Marguerite Bay study region. Likewise, we use all of the visual sightings of humpback and minke whales collected within the study region during the same period.

We chose physical and biological variables that are known to affect the distribution and abundance of the avian and mammalian krill predators in our study region (sensu Burns et al., 2004; Chapman et al., 2004; Thiele et al., 2004; Friedlaender et al., 2006; Burns et al., 2008, Ribic et al., 2008). The specific physical factors we employ are bathymetry (m), bottom slope (%), distance to shore (km), distance to ice edge (km), and deep temperature maximum (°C). The biological factors are: measures of integrated water column chlorophyll a (g/m^3) and two acoustic measures of prey availability: krill biomass (g/m^3) in the top 100 m of the water column and krill biomass (g/m^3) in the deeper portion (100–300 m) of the water column.

Grids of all environmental surfaces were created using an inverse distance weighting function in the spatial analyst extension to ArcGIS 9.3 (as in Friedlaender et al. (2006)) if they were not already available as a continuous surface. All grids were resampled to the same geographic extent and a cell size of 1 km^2 and then clipped to eliminate portions of the study area not sampled by cruises or by animals fitted with telemetry packages. The resultant study region is a polygon with an area of 149,758 km^2 and perimeter of 3793 km that spans 78.282°S and 67.456°S and 65.486°W and 69.781°W (Fig. 1).

Maxent modeling commonly splits occurrence datasets into training data and test data. Training data are used to create ENMS for a species, and the remaining test data are used to assess the accuracy of the training model. To address any residual effects of spatial autocorrelation after sub-sampling the telemetry data to only daily occurrences, we use the replication function in Maxent to randomly sample occurrences from each dataset for training runs and use the remaining occurrences to test the model. Specifically, we use the cross-validation technique in Maxent 3.3.3, where the occurrence data is randomly split into a number of equal-size groups called "folds", and training models are created by eliminating each fold in turn. The eliminated folds are then used to test the performance of the training models. This is often referred to as a 'K-folds' cross-validation approach (e.g. Kohavi, 1995). Cross-validation is preferable to using a single training/test split in the dataset as it uses all of the data for validation, thus making better use of small datasets. For our models, we ran 25 model replications for each species. Table 1 indicates the number of training and test occurrences used for replication in Maxent modeling. In 2001, for example, 33 Adélie penguin occurrences were used for training and 11 for testing in each model run. This procedure also provides for a sampling and modeling framework that is consistent across different types (telemetry data versus survey data) of occurrence data. We also lowered the Maxent regularization multiplier to 0.5 to better fit the model distributions more closely to our observations. This parameter interacts with regularization parameters for each feature used in the model (Phillips and Dudik, 2008).

The resulting output provides spatial models of the mean probability of presence for each predator, as well as models of the error associated with this mean (1 standard deviation), the minimum model, the maximum model, and the lower 95% confidence interval model.

The performance of each Maxent model is assessed using the area under the curve (AUC) metric of the receiving operator characteristic (ROC) curve (Fielding and Bell, 2002). In a Maxent ROC curve, all sensitivity values (true positives) are plotted on the *y*-axis against specificity (false positive) values on the *x*-axis. The AUC value provides a threshold-independent metric of overall accuracy, and ranges between 0.5 and 1.0. To illustrate how much each variable contributed to the Maxent run, the increase in regularized gain is added or subtracted (if the change is negative) to the contribution of the corresponding variable during each iteration of the training run. This provides an overall estimate of how each variable contributes to the model. We also obtain alternative estimates of variable importance for our Maxent models by conducting a jackknife analysis on their AUC values. In our case, the jackknife analyses systematically recomputed the AUC for each model leaving out one environmental variable at a time. This provides the ability to assess the extent to which each variable contributes to the model individually, and how well the model performed when that variable was omitted from the analysis entirely.

2.6. Niche overlap

To quantitatively assess the overlap of SO GLOBEC krill predator ENMs (amongst species and between years), we use a niche overlap index that compares our mean predicted probability distributions defined over geographic space, in which pX,i (or pY,i) denotes the probability assigned by the ENM for species X (or Y) to cell i. The overlap metric employed (Eq. (1)) comes from the ecological literature; Schoener's (1968) statistic for niche overlap (D):

$$D(pX,pY) = 1 - \frac{1}{2}\sum_{i} \left| pX,i - pY,i \right| \tag{1}$$

This metric was recently applied to Maxent-generated ENM data to re-explore niche overlaps of several closely related organisms (Warren et al., 2008). For the present analysis, we used the software package ENM Tools Version 1.0 (Warren et al., 2010) to assess overlaps amongst mean ENMs of Adélie penguins, crabeater seals, minke whales, and humpbacks whales and between 2001 and 2002 for each of these species. Schoener's niche overlap metric (D) ranges from 0 (niche models have no overlap) to 1 (niche models identical). Schoener's D is typically applied with values of pX,i that reflect relative use of particular microhabitats and/or prey items.

Table 1
The number of training and test occurrences used for each species for each year for replicated Maxent models of Antarctic krill predators including average area under the curve (AUC) values.

2001	Occurrences Training (test)	Average test AUC	AUC St. Dev.
Adélie penguins	33 (10)	0.97	0.01
Crabeater seals	44 (14)	0.97	0.02
Humpback whales	23 (7)	0.76	0.10
Minke whales	27 (8)	0.86	0.07
2002			
Adélie penguins	193 (64)	0.93	0.01
Crabeater seals	129 (43)	0.83	0.02
Humpback whales	42 (14)	0.89	0.04
Minke whales	12 (3)	0.77	0.15

3. Results

3.1. Ecological niche modeling

The number of observations or occurrences for each species in each year is shown in Table 1. Initial plots of predator occurrence reveal several "hot spots" (Fig. 2). In 2001, the area along the southeastern corner of Adelaide Island and near the northwestern corner of Alexander Island had the highest rates of occurrence. In 2002, the same general area around Adelaide Island (as well as along the northern coast of the island) contained the most predator occurrences. Predator occurrence is spread more throughout Marguerite Bay in 2002 than in 2001.

An example of diagnostic output of replicated Maxent modeling is provided (Fig. 3). Both the testing and training dataset omission rates versus predicted area (as a function of cumulative threshold) for a single Adélie penguin model are presented in Fig. 3A. The average model derived from 25 replication runs is presented in Fig. 3B. These plots illustrate the predictive performance of the model over a range of thresholds of suitable habitat, provide details on the uncertainty associated with omission rates in the replicated model, and illustrate the replicated models performance in relation to what a random prediction would generate. In this case both the test and training omission rates are close to the predicted, and do not lie well below the predicted omission line.

The Maxent receiver operator characteristic curve for the replicated Maxent Adélie penguin model is presented in Fig. 3C. The AUC value is high for this model and the standard deviation is low, indicating some level of uniformity amongst replications.

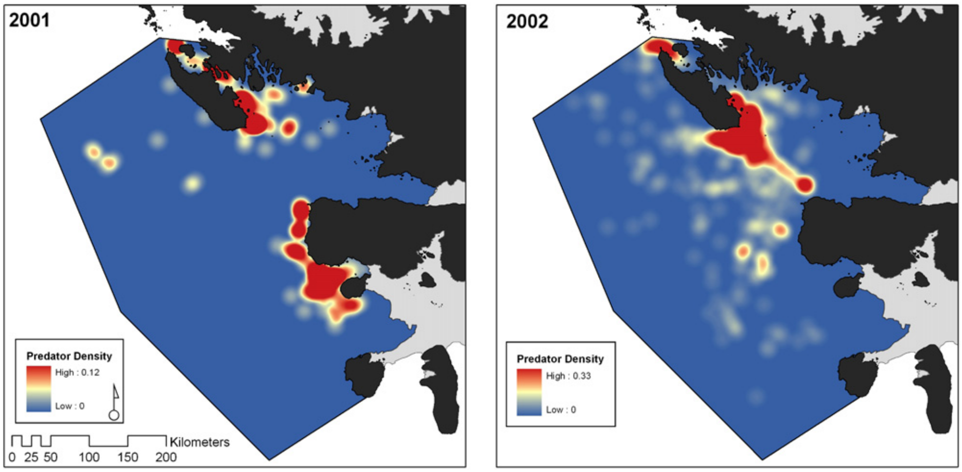

Fig. 2. Occurrence patterns of krill predators in the Marguerite Bay study area for 2001 and 2002.

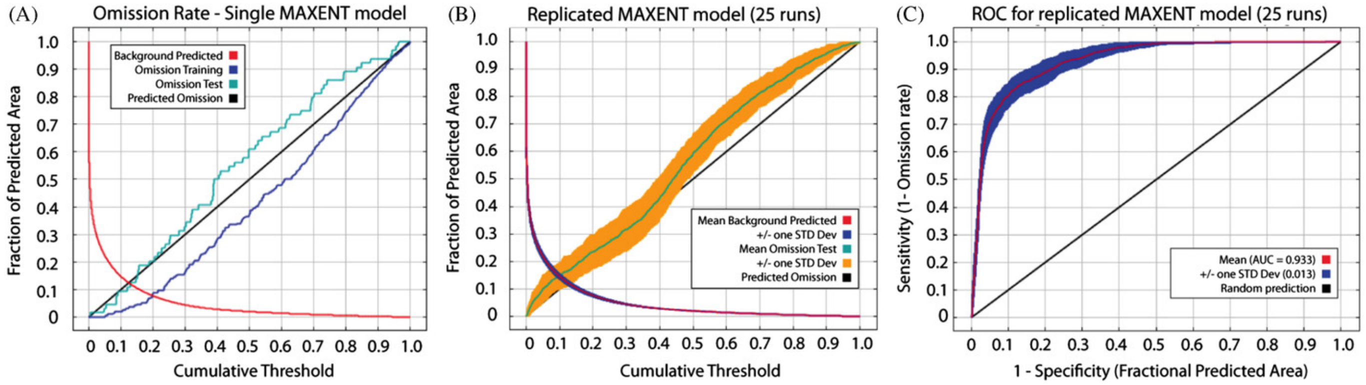

Fig. 3. Diagnostic plots for Maxent modeling of Adélie Penguins in Marguerite Bay, 2001. Plot 3A indicates omission rates for both training and test model runs, as a function of the fraction of background habitat predicted and the cumulative threshold of suitable habitat. Plot 3B indicates the omission rates for the mean Maxent model, as in Plot 3A. Plot 3C represents the Maxent receiver operator characteristic (ROC) curve for the 2001 Adélie penguin model.

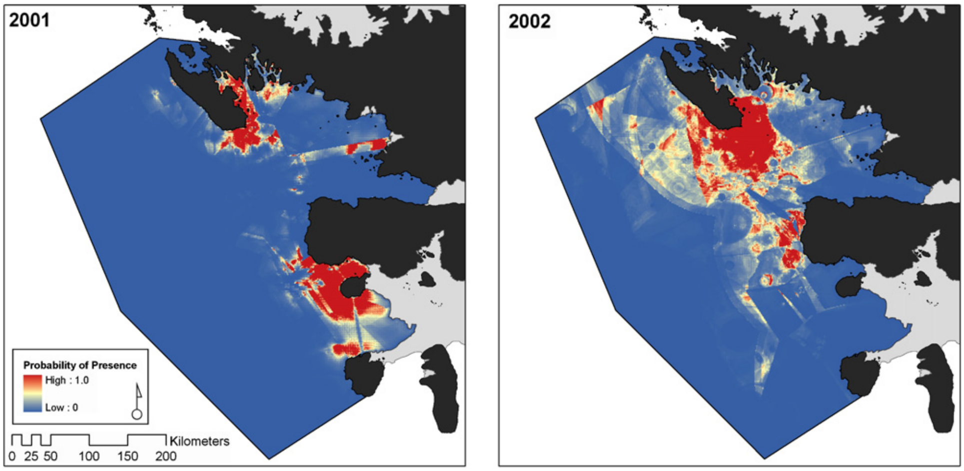

Fig. 4. Maxent predictions of suitable habitat for Adélie penguin distribution in 2001 (left panel) and 2002 (right panel).

Both Adélie penguin and crabeater seal models did not reveal any effects of spatial autocorrelation. In these cases, when the test or training data are not independent, the omission line often lies well below the predicted omission line. In all cases our test and training lines approximated the predicted omission rate (see Fig. 3A).

Maxent modeling of Antarctic predator niches performed well, with AUC values for replicated models ranging from 0.76 to 0.97. These AUC values indicate that for our models, over 76% of the time a random selection of specificity values from the model (where sensitivity is the conditional probability that the occurrence is correctly classified) will have a score greater than a random selection of specificity (the inverse of sensitivity) values from the model (Fielding and Bell, 2002). The model AUC values for each replicate are presented in Table 1.

For Adélie penguins in 2001, distance to coast is the largest overall contributor to the Maxent model (30.8%) by a factor of 2 (Figs. 4 and 5). The next greatest contributors to the model are depth (16.1%) and prey in the upper 100 m (13.3%). The AUC Jackknife results for this model confirmed the importance of these variables and illustrated that both slopes contributed the least to the 2001 Adélie model. During 2002, distance to the ice edge (24.5%) and distance to coast (21.6%) are the strongest contributors to the ENM. The AUC jackknife test revealed that slope again contributed the least to the model.

For crabeater seals in 2001 distance to shore is the largest overall contributor to the model (47.4%), followed by deep prey (13.3) (Figs. 6 and 7). The jackknife AUC test confirmed the importance of these variables, and revealed that prey in the lower portion of the water column contributed the least to the model. In 2002, deep temperature maximum contributed most strongly to the ENM (34.3%), followed by chlorophyll a (14.6%), prey in the upper 100 m of the water column (14%), and distance to ice edge (12.8%). The AUC jackknife test reflects these results.

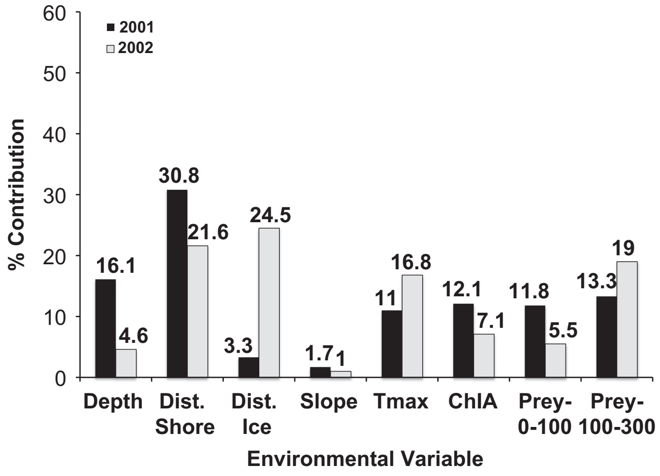

Fig. 5. Environmental niche model output for Adélie penguins in 2001 and 2002. The values represent the percent contribution for each variable to the overall model for each year.

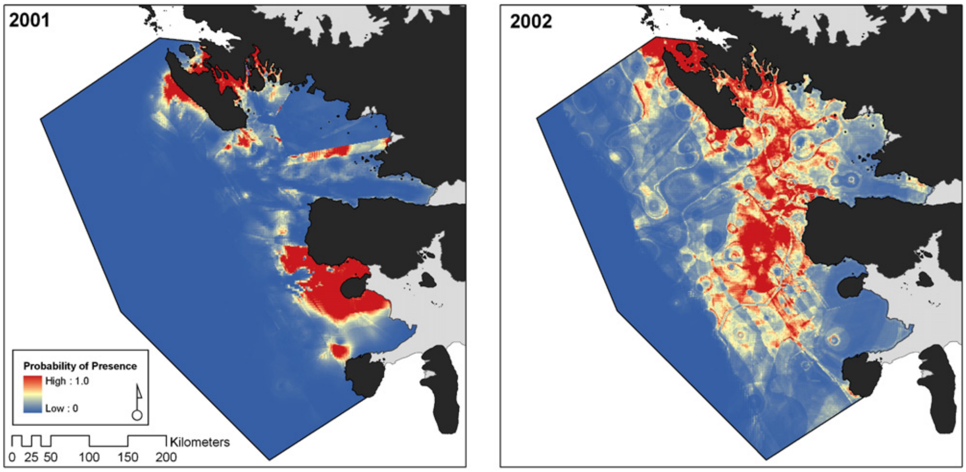

Fig. 6. Maxent predictions of suitable habitat for crabeater seal distribution in 2001 (left panel) and 2002 (right panel).

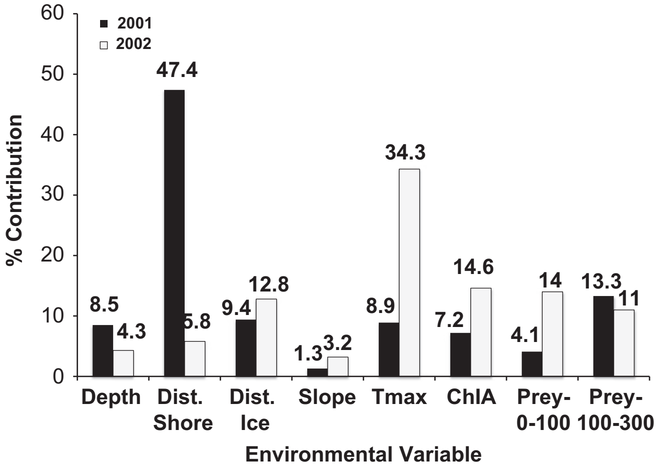

Fig. 7. Environmental niche model output for crabeater seals in 2001 and 2002. The values represent the percent contribution for each variable to the overall model for each year.

For humpback whales in 2001, the strongest contributors to the model are deep prey (31.2%), slope (17.6%), depth (13.7%), and prey in the upper 100 m of the water column (13.2%) (Figs. 8 and 9). The AUC jackknife reveals that deep prey contributed the most to the model if used in isolation (AUC greater than 0.74). In 2002, distance to ice edge is the greatest contributor to the model (35.9%) followed by prey in the upper water column (30.2%). The AUC jackknife test indicates that distance to coast contributed most to the model if used in isolation (AUC > 0.77).

For minke whales in 2001, the strongest contributor to the model is distance to the coast (55.5%), followed by deep prey (13.9%) (Figs. 10 and 11). The AUC jackknife test demonstrates that distance to coast is the strongest contributor if used in isolation (AUC > 0.89), and decreased the AUC of the model the most if excluded to below 0.83. In 2002, distance to coast is again the strongest contributor to the model (33.4%), followed by distance to the ice edge (18.9%) and deep prey (18.5%). The AUC jackknife test shows that distance to coast (AUC > 0.77) alone has the greatest effect on AUC values if used in isolation.

3.2. *Niche overlap*

In 2001, the average niche overlap across krill predator species is 0.37, ranging between 0.25 and 0.55 (Fig. 12). Adélie penguins have the most niche overlap with crabeater seals (0.55), and a similar overlap with humpback whales (0.25) and minke whales (0.26). Crabeater seals have less overlap with whales in general than with Adélie penguins: 0.31 overlap with humpback whales and 0.38 overlap with minke whales. Minke whales have the greatest amount of niche overlap with humpback whales (0.47).

In 2002, the ranges in the amount of niche overlap are smaller (0.42–0.56) than in 2001, and the average overlap is greater (0.49) (Fig. 13). Adélie penguins have less overlap with crabeater seals (0.42) in 2002 than in 2001. However, they have greater overlap with humpback (0.47) and minke whales (0.45) in 2002 than in 2001. Crabeater seals have greater overlap with humpback (0.50) and minke whales (0.56) in 2002 than in 2001. And the overlap between humpback and minke whales (0.54) is similar in 2001 and 2002.

We then compare the niche overlap for each species against itself from 2001 to 2002. If there is no variability in the environment (including prey), and the distribution of each species remained constant, we expect the niche overlap for each species to be 1 when comparing 2001 to 2002. Generally, we find this not to be the case, and each species has a niche overlap between years ranging from 0.25 to 0.39 (Fig. 14). Adélie penguins have the least amount of niche overlap between years (0.25) followed by crabeater seals (0.29). Humpback whales (0.39) showed the highest amount of niche overlap across years followed by minke whales (0.37).

4. Discussion

The results of our analyses indicate several important and novel aspects of the distribution and amount of niche overlap between krill predators in Antarctica. We use presence-only data to generate ecological niche models, which (1) describe the concurrent habitat preferences, (2) model the amount of niche overlaps between, and (3) measure variability in modeled ecological niches in 2 years for several major groups of krill predators in autumn around Marguerite Bay, WAP. We find that there are areas within Marguerite Bay with high krill predator occurrence rates that can be considered biological hot spots. At least one of these areas, at the northern extent of Marguerite Bay near the southeastern end of Adelaide Island (Fig. 2), is a hot spot for krill predator occurrence between years regardless of the changes in both the physical environment (e.g. Klinck et al., 2004, Costa et al., 2008, Hyatt et al., 2011) and prey distribution (Lawson et al., 2008). We also find that the modeled ecological niches for Adélie penguins and crabeater seals may be

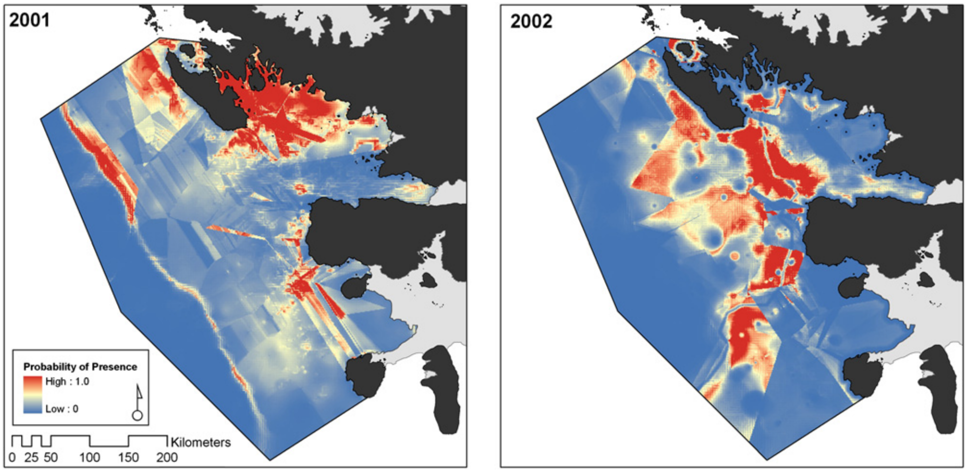

Fig. 8. Maxent predictions of suitable habitat for humpback whale distribution in 2001 (left panel) and 2002 (right panel).

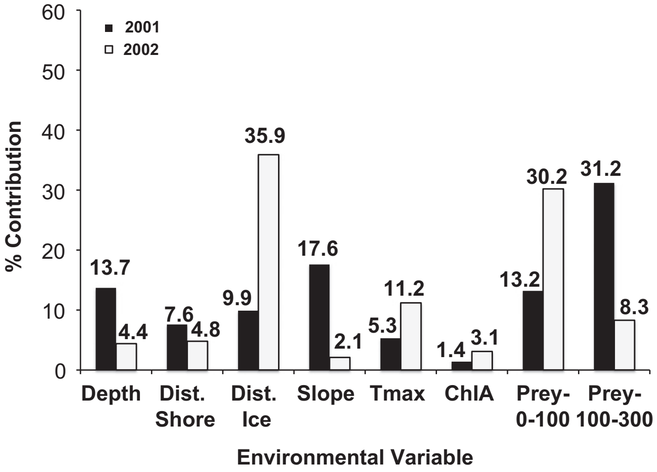

Fig. 9. Environmental niche model output for humpback whales in 2001 and 2002. The values represent the percent contribution for each variable to the overall model for each year.

affected by their physiological needs to return to land or sea ice as a haul-out substrate. Because of this limitation, their distributions may be less dictated by direct proximity to their prey and more so by physical features that over time provide adequate access to prey resources. Humpback and minke whales, not being constrained in the same manner and having greater energetic demands due to their larger sizes, occupy ecological niches more directly proximate to their prey (Friedlaender et al., 2006, 2008a).

The most important environmental variables affecting the modeled distribution of Adélie penguins are proximity to the coast, and when present, proximity to sea ice. Our modeling exercise indicates that in 2001 when little sea ice was present, penguin distribution is more closely associated to land, while in 2002 when more sea ice was available in the study area, the penguins shift their distribution to take advantage of this substrate. In 2001, when penguins associate close to land, their distribution is more related to the amount of prey in the upper 100 m of the water column than the following year. In both years, the distribution of penguins is also affected by the distribution of prey deeper than they are known to forage. In 2002, penguin distribution is more related to deep krill than shallow krill. Similarly, Ribic et al. (2008) found that Adélie penguin distribution was related to prey in the upper 100 m of the water column (and deeper) during winter months, which suggests consistency in the relationship between predators and prey during ice formation when the physical structure of the marine ecosystem changes dramatically.

Crabeater seal distribution is most related to the distance to shore in 2001 and the deep temperature maximum in 2002. Regions of warmer water below 200 m reflect intrusions of Circumpolar Deep Water on to the continental shelf (Klinck et al., 2004) and may signify areas of enhanced vertical mixing biological production (Prezelin et al., 2000, 2004), thus increasing access to prey. However, in 2001 when sea ice was less prevalent, crabeater seals are found in areas closer to shore (bays and fjords) than in 2002 when sea ice covered a greater portion of the study area and their distribution is more affected by sea ice cover. In 2001, seal distribution is more closely related to the amount of prey below 100 m in the water column, while in 2002 they prey throughout the water column had similar impacts on seal distribution. Geographically, these distributions correspond with those presented by Burns et al. (2004), who found preference to areas of increased ice cover in generally shallow, coastal regions.

The modeled ecological niches for the humpback and minke whales support the previous findings by Friedlaender et al. (2006, 2008a,b). Humpback whales occupy coastal waters with rugged topography and increased changes in bottom depth over short distances, where the abundance of prey in the water column is high. In 2002 when ice cover was more prevalent, humpback whales were found in proximity to the ice edge and where preys were more abundant in the upper 100 m of the water column. Minke whales occupy an ecological niche greatly defined by proximity to shore and with prey abundance deeper in the water column. In 2001 when less sea ice was available, minke whale distribution is more tied to proximity to shore and shallow water where prey was available, whereas in 2002 when more ice was present, minke whales aggregate in regions more associated with sea ice and increased prey availability. While the amount of modeled ecological niche overlap is relatively high between whale species, the likelihood that these species are in competition for prey resources is low. Our results and those of Friedlaender et al. (2008a) show that each species is generally distributed relative to krill that are vertically segregated in the water column. Furthermore, the relationship between humpback whales (seasonally migrant) and prey is more explanatory of their distribution than minke whales, some portion of which are known to overwinter in Antarctic waters. With respect to interspecific comparisons of niche overlap, Schoener (1968) explains that the greater the amount of spatial overlap in habitat, the lower the maximum overlap in prey size, and

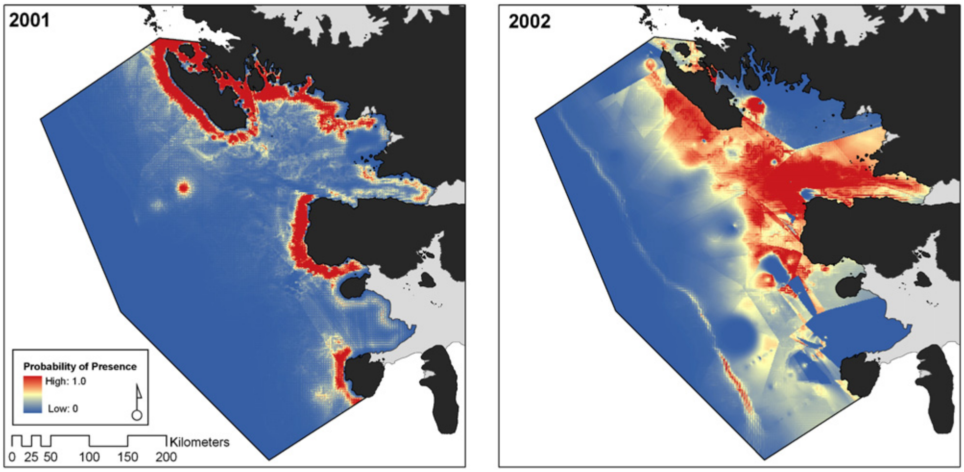

Fig. 10. Maxent predictions of suitable habitat for minke whale distribution in 2001 (left panel) and 2002 (right panel).

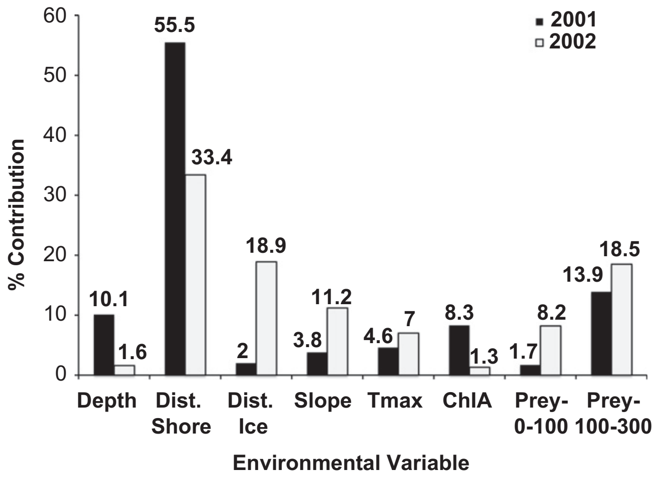

Fig. 11. Environmental niche model output for minke whales in 2001 and 2002. The values represent the percent contribution for each variable to the overall model for each year.

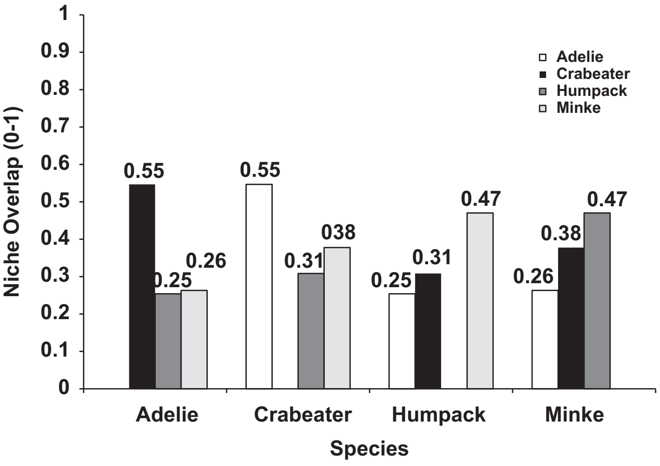

Fig. 12. Niche overlap (using Schoener's niche overlap metric 0–1) between krill predators, 2001.

vice versa. Thus, competition for similarly sized prey is avoided if spatial overlap is greater, but may or may not occur if spatial overlap is slight (Schoener, 1968).

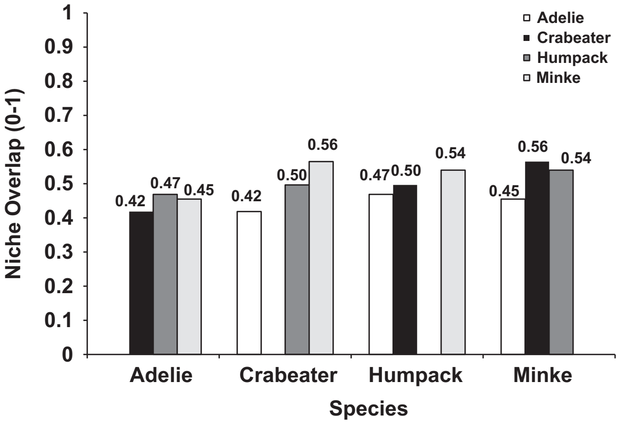

Fig. 13. Niche overlap (using Schoener's niche overlap metric 0–1) between krill predators, 2002.

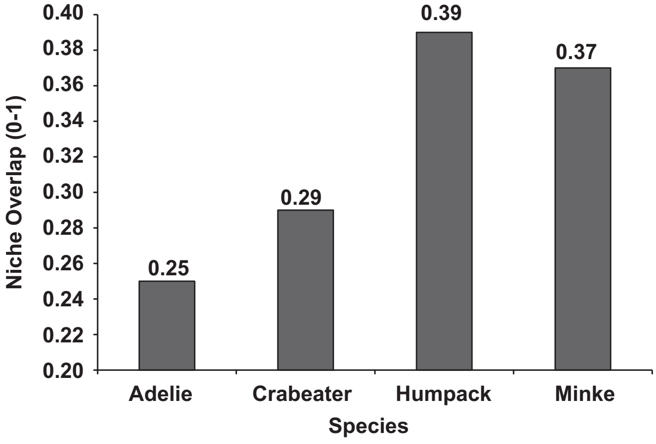

Fig. 14. Interannual niche overlap for each krill predator species between 2001 and 2002 using Scheoner's niche overlap metric (0–1).

In 2001, the greatest amount of modeled ecological niche overlap occurs between Adélie penguins and crabeater seals, and between humpback and minke whales. As stated above, the higher amount of modeled overlap between these pairs of species may indicate that competition for similarly sized prey between these sympatric krill predators is largely absent. The relatively high amount of modeled niche overlap between minke and humpback whales may reflect their energetic needs and ability to access areas with increased prey abundance. Similarly, access to haul-out substrate (coastal regions and sea ice) may relate to a similarly increased amount of niche overlap between Adélie penguins and crabeater seals. In a year with less sea ice in the study region, minke whales and Adélie penguins have a greater amount of modeled niche overlap across all predators than humpback whales and crabeater seals.

Conversely, in 2002, there is generally greater overlap but less variability in modeled niche overlap between all of the krill predators. It is interesting to note that the amount of modeled niche overlap between humpback and minke whales is generally consistent (0.47 and 0.54) across years irrespective of changes in the physical environment in the study area (Massom et al., 2006). While slightly smaller in 2002, the amount of modeled niche overlap between Adélie penguins and crabeater seals does not vary substantially across years either. The greatest changes from 2002 to 2001 are, in fact, increases in overlap between both Adélie penguins and crabeater seals and the two cetacean species. Thus, the pair-wise modeled ecological niche relationships between the land/ice-based krill predators and between the more mobile cetacean species may be more stable over time in this area, given how little they change between years with dramatically different physical conditions.

Further niche separation may result from the minimum viable krill patch that different sized predators can utilize. Larger predators have absolutely greater energy requirements. Adélie penguins should be able to utilize the smallest most ephemeral krill patch as their small size and thus absolute energy requirements are the lowest (Costa, 1991). While the threshold for a viable krill patch would be larger for crabeater seals than required by penguins, it would still be substantially smaller than that required by a minke and humpback whale. Larger predators would also have an advantage accessing deeper krill swarms. Large body size provides both a greater breath-hold diving capability as well as a faster ability to descend to depth. For example, a penguin diving to 200 m must descend many more body lengths then a humpback whale. While krill swarms are preyed upon throughout the water column, they may be most efficiently consumed during the daylight hours when they remain at depth in dense swarms avoiding diurnal fish predators (Croxall et al., 1985; Croll et al., 1998; Fiedler et al., 1998; Burns et al., 2004). Previous studies have hypothesized that competition between krill-eating predators cannot be assumed based simply on diet preferences (Croxall et al., 1985), and that there are several factors that relate to foraging niche overlap (Fraser et al., 1992). Previous modeling efforts (Murphy et al., 1988) predicted that reductions in baleen whale numbers from commercial whaling would most benefit similarly sized krill predators, and not smaller predators like penguins. Ainley et al. (2006) provide evidence to suggest that in some cases the presence of baleen whales can affect the availability of krill to the point that penguins must switch their prey in order to successfully acquire enough energy for survival. Along similar lines, Friedlaender et al. (2008b) found significant relationships between humpback whale abundance and the size-frequency distribution of krill targeted by Adélie penguins, as well as the foraging success of these penguins. Based on Schoener's (1968) explanation of how dissimilarity in niche overlap relates to similarities in prey, our findings of less niche overlap between humpback whales and Adélie penguins suggest that both krill predators share common prey resources in the upper portion of the water column and that the potential for interspecific competition in some years is increased.

Between top predators along the WAP, a common link is their reliance on Antarctic krill as a staple of their diets. It is reasonable then to assume that stability in the modeled ecological relationship between predators and prey exists, and each species has limitations and restrictions on their energetic requirements and life history demands, such that their ecological niches should remain constant over time. From 2001 to 2002, we found little consistency in the amount of modeled niche overlap for each species in the study area and during the season of the research. The two species reliant on land or sea ice, Adélie penguins and crabeater seals, had less overlap between years than the baleen whales that have no such requirements. Rather than suggesting that these values between years indicate species that are very flexible in their ability to change ecological niches to suite their environment (which would result in an interannual niche overlap value of 1), we suggest that variability in the physical and biological environment around the Antarctic Peninsula creates such different conditions from year to year that some animals (penguins and crabeater seals) may have very little adaptability to change, while baleen whales may have better mechanisms to cope.

Fraser and Hofmann (2003) discuss how changes in sea ice cover around the Antarctic Peninsula and concurrent changes in the standing stock and recruitment of Antarctic krill available for Adélie penguins have affected their population growth. Over recent time, fewer years with enough sea ice to successfully recruit new age classes of krill have contributed to decreases in prey availability and subsequent negative population trends for these penguins in the region. Such bottom-up or physical control of krill predator populations has been discussed recently by Ainley et al. (2009), especially in reference to the difficultly in understanding the myriad effects of the many physical forces that structure ecosystems. While there are no reliable population trend estimates for crabeater seals (Southwell et al., 2008) in the region, and declining populations were suggested for continental populations in some regions (Erickson and Hanson, 1990), it is generally thought that their numbers have increased over the past century as nearly all of the baleen whales were extirpated from the Antarctic during commercial whaling ventures (Laws, 1985; Clapham and Baker, 2001) and competitive release between krill predators had occurred (see Ballance et al., 2006) . Among the cetaceans, humpback whale populations have shown consistent positive population increases since the cessation of commercial whaling (Branch, 2009). Confounding factors in the ability to accurately estimate the number of minke whales (see Branch, 2006) in the region have clouded attempts to determine, with any measure of accuracy, their population numbers (although there is evidence to suggest they are stable, e.g. Branch, 2006).

Ainley et al. (2009) provide examples for the role of cetaceans in penguin population change, concluding that both top-down and bottom-up forcing are contributing, and interrelated factors. The results of our analysis provide additional information to better understand these relationships. We have modeled different evidences to suggest that the amount of overlap between modeled niches for two years is relatively low, even for species with similar energetic requirements. In a rapidly changing and variable environment, our modeling work shows little indication that krill predators maintain similar ecological niches across the two years of our study around Marguerite Bay. The baleen whales, whose distributions are more directly linked to prey availability, may be better suited to maintain this relationship as conditions change, while Adélie penguins and crabeater seals that rely more basically on sea ice and land substrate change their modeled ecological niches by up to 85% between years in our study. Given the amount of variability in the marine environment around the Antarctic Peninsula and how this affects the local abundance of prey, there may be consequences for krill predators with historically little niche overlap to increase the potential for interspecific competition for shared prey resources (Ducklow et al., 2007; Siniff et al., 2008; Costa et al., 2010).

4.1. Caveats and limitations

Our analyses are not meant to be final definitive descriptions of the realized niches of different krill predators in the Antarctic.

Rather, our work should be viewed as an important initial modeling effort to assess and describe ecological dissonance and overlap between krill predators in a single place over time using a relatively new technique. As such, these models should be considered by other researchers as null models of the niches of krill predators in Marguerite Bay, to be tested against future studies of the foraging ecology of these animals in other locations around Antarctica and beyond.

Our study makes quantitative analytical connections between data collected by two disparate mechanisms. Combining different observational methods (satellite-linked locations and visual surveys) in a meaningful way can be challenging, but previous studies that compare Maxent models of occurrences collected through disparate means suggest that these issues are not significant (e.g. Kuemmerle et al., 2010). As such we would not suspect that our comparisons are biased using different types of occurrence data. Furthermore, we suspect that employing the model cross-validation replication techniques in Maxent uniformly across our datasets would limit the effects of any residual biases that could be associated with different data structures. Further research is required to fully assess the utility of Maxent on different data types.

There is debate in the scientific community regarding the effects of spatial autocorrelation in geostatistical analyses (see for example Dormann et al. (2007), Betts et al. (2009) and Dormann (2009)). In the case of Maxent, a comprehensive retrospective analysis of spatially autocorrelated data indicates that it can indeed affect model performance (Veloz, 2009). In some cases the descriptive power of Maxent models can be reduced where spatial autocorrelation is significant (Veloz, 2009). However, the actual relationships amongst predicator variables in models appear to be conserved (Veloz, 2009). In our case, the employment of data decimation techniques (sensu Johnston et al., 2005) and cross-validation replication in Maxent modeling (similar to bootstrapping replication conducted by Edren et al. (2010)) appear to have reduced any biases due to spatial autocorrelation. If any remains, it would likely reduce the AUC values of our models marginally, but not change the actual relationships predicted.

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References

Ainley, D.G., Jacobs, S.S., Ribic, C.A., Gaffney, I., 1998. Seabird distribution and oceanic features of the Amundsen and southern Bellingshausen seas. Antarctic Science 10, 111–123.

Ainley, D.G., 2002. The Adélie Penguin: Bellwether of Climate Change. Columbia University Press, New York.

Ainley, D.G., Ballard, G., Dugger, K.M., 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea. Ecology 87, 2080–2093.

Ainley, D.G., Ballard, G., Blight, L.K., Ackley, S., Emslie, S.D., Lescroel, A., Olmastroni, S., Townsend, S.E., Tynan, C., Wilson, P., Woehler, E., 2009. Impacts of cetaceans on the structure of Southern Ocean food webs. Marine Mammal Science. doi:10.1111/j.1748-7692.2009.00337.x.

Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432, 100–103.

Ballance, L., Pitman, R.L., Hewitt, R.P., Siniff, D.B., Trivelpiece, W.Z., Clapham, P.J., Brownell, R.L., 2006. The removal of large whales from the Southern Ocean: evidence for long-term ecosystem effects?. In: Estes, J.A., Demaster, D.P., Doak, D.F., Williams, T.E., Brownell, R.L. (Eds.), Whales, Whaling and Ocean Ecosystems. University of California Press, Berkeley, CA, pp. 215–230.

Beardsley, R.C., Limeburner, R., Owens, R.B., 2004. Drifter measurements of surface currents near Marguerite Bay on the Western Antarctic Peninsula shelf during austral summer and fall 2001 and 2002. Deep-Sea Research II 51, 1947–1964.

Bentlage, B., Peterson, A.T., Cartwright, P., 2009. Inferring distributions of chirodropid box-jellyfishes (Cnidaria: Cubozoa) in geographic and ecological space using ecological niche modeling. Marine Ecology Progress Series 384, 121–133.

Betts, M.G., Lisa M. Ganio, M.P., Huso, M.M.P., Som, N.A., Huettmann, F., Bowman, J., Wintle, B.A., 2009. Comment on "Methods to account for spatial autocorrelation in the analysis of species distributional data: a review". Ecography 32, 374–378.

BirdLife International, 2004. State of the World's Birds: Indicators for our Changing World. BirdLife International, Cambridge.

Bolmer, S.T., Beardsley, R.C., Pudsey, C., Mooris, P., Wiebe, P.H., Hofmann, E.E., Anderson, J., Maldonado, A., 2004. High-resolution bathymetry map for the Marguerite Bay and adjacent West Antarctic Penginsula shelf for the Southern Ocean GLOBEC programs. Woods Hole Oceanographic Institution Technical Report WHOI-2004-02, 76pp.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G., Weimerskirch, H., 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. Journal of Marine Systems 78, 363–376.

Branch, T.A., 2006. Abundance estimates for Antarctic minke whales from three completed circumpolar sets of surveys, 1978/79 to 2003/04. IWC SC Paper SC/58/ IA18.

Branch, T.A., 2009S. Humpback whale abundance south of 60S from three completed sets of IDCR/SOWER circumpolar surveys. Journal of Cetacean Research and Management.

Burns, J.M., Costa, D.P., Fedak, M.A., Hindell, M.A., Bradshaw, C.J.A., Gales, N.J., McDonald, B., Trumble, S.J., Crocker, D.E., 2004. Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. Deep Sea Research II 51, 2279–2303.

Burns, J.M., Hindell, M.A., Bradshaw, C.J.A., Costa, D.P., 2008. Fine-scale habitat selection by crabeater seals diving within Marguerite Bay, Antarctica. Deep Sea Research II 55, 500–514.

Chapman, E.W., Ribic, C.A., Fraser, W.R., 2004. The distribution of seabirds and pinnipeds in Marguerite Bay and their relationship to physical features during austral winter in 2001. Deep-Sea Research II 51, 2261–2278.

Chappell, M.A., Shoemaker, V.H., Janes, D.H., Maloney, S.K., Bucher, T.L., 1993. Energetics of foraging in breeding Adélie penguins. Ecology 74, 2450–2461.

Clapham P.J., Baker, C.S., 2001. How many whales were killed in the Southern Hemisphere during the 20th century? Report to the International Whaling Commission, vol. 53, p. 3.

Costa, D.P., 1991. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. American Zoologist 31, 111–130.

Costa, D.P., 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. In: Boyd, I.L. (Ed.), Marine Mammals: Advances in Behavioural and Population Biology. Oxford University Press, Symposium Zoological Society of London, pp. 293–314.

Costa, D.P., Crocker, D.E., 1996. Marine mammals of the Southern Ocean. In: Ross, R., Hofmann, E., Quentiin, L. (Eds.), Foundations for Ecological Research West of the Antarctica Peninsula. American Geophysical Union, pp. 287–301.

Costa, D.P., Klinck, J.M., Hofmann, E.E., Dinniman, M.S., Burns, J.M., 2008. Upper ocean variability in West Antarctic Peninsula continental shelf waters as measured using instrumented seals. Deep Sea Research II 55 (3–4), 323–337.

Costa, D.P., Huckstadt, L.A., Crocker, D.E., McDonald, B.I., Goebel, M.E., Fedak, M.A., 2010. Approaches to studying climatic change and its role on the habitat selection of antarctic pinnipeds. Integrative and Comparative Biology 50, 1018–1030.

Croll, D.A., Tershy, B.R., Hewitt, R.P., Demer, D.A., Fiedler, P.C., Smith, S.E., Armstrong, W., Popp, J.M., Kiekhefer, T., Lopez, V.R., Urban, J., Gendron, D., 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea Research Part II 45, 1353–1357.

Croxall, J.P., Everson, I., Kooyman, G.L., Ricketts, C., Davis, R.W., 1985. Fur seal (*Arctocephalus gazella*) diving behavior in relation to vertical distribution of krill (*Euphausia superba*). Journal of Animal Ecology 54, 1–8.

Dormann, C.F., Mcpherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609–628.

Dormann, C.F., 2009. Response to comment on "Methods to account for spatial autocorrelation in the analysis of species distributional data: a review". Ecography 32, 379–381.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M., Fraser, W., 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 67–94.

Edren, S.M.C., Wisz, M.S., Tellmann, J., Deitz, R., Soderkvist, J., 2010. Modelling spatial patterns in harbour porpoise satellite telemetry data using maximum entropy. Ecography 33, 698–708.

Erdman, E.S., Ribic, C.A., Patterson-Fraser, D.L., Fraser, W.R., 2011. Characterization of winter foraging locations of Adélie Penguins along the Western Antarctic Peninsula, 2001–2002. Deep-Sea Research II 58 (13-16), 1710–1718.

Erickson, A.W., Hanson, M.B., 1990. Continental estimates and populations trends in Antarctic ice seals. In: Kerry, K.R., Hempel, G. (Eds.), Ecological Change and The Conservation of Antarctic Ecosystems. Proceedings of the 5th SCAR Symposium on Antarctic Biology, Hobart, August–September 1988. Springer, New York, pp. 253–264.

Etnoyer, P., Canny, D., Mate, B., Morgan, L., 2004. Persistent pelagic habitats in the Baja California to Bering Sea (B2B) ecoregion. Oceanography 17, 90–101.

Fedak, M.A., Lovell, P., Grant, S.M., 2001. Two approaches to compressing and interpreting time-depth information as collected by timed-depth recorders and satellite linked data loggers. Marine Mammal Science 17, 94–110.

Fedak, M.A., Lovell, P., McConnell, B.J., Hunter, C., 2002. Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. Integrative and Comparative Biology 42, 3–10.

Fiedler, P.C., Reilly, S.B., Hewitt, R.P., Demer, D., Philbrick, V.A., Smith, S., Armstrong, W., Croll, D.A., Tershy, B.R., Mate, B.R., 1998. Blue whale habitat and prey in the California Channel Islands. Deep-Sea Research Part II 45, 1781–1801.

Fielding, A.H., Bell, J.F., 2002. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38–49.

Forcada, J., Trathan, P.N., Murphy, E.J., 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. Global Change Biology 14, 2473–2488.

Fraser, W.R., Trivelpiece, W.Z., Ainley, D.G., Trivelpiece, S.G., 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming. Polar Biology 11, 525–531.

Fraser, W.R., Trivelpiece, W.Z., 1996. Factors controlling the distribution of seabirds: winter–summer heterogeneity in the distribution of Adélie penguin populations. In: Ross, R.M., Hofmann, E.E., Quetin, L.B. (Eds.), Foundations for Ecological Research West of the Antarctic Peninsula. American Geophysical Union, Washington, DC, pp. 257–272.

Fraser, W.M., Hofmann, E.E., 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Marine Ecology Progress Series 265, 1–15.

Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D., Read, A.J., 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Marine Ecology Progress Series 317, 297–310.

Friedlaender, A.S., Lawson, G.L., Halpin, P.N., 2008a. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. Marine Mammal Science 25, 402–415.

Friedlaender, A.S., Fraser, W.R., Patterson, D., Qian, S.S., Halpin, P.N., 2008b. The effects of prey demography on humpback whale (*Megaptera novaeahngliae)* abundance around Anvers Island, Antarctica. Polar Biology 31, 1217–1224.

Gales, N.J., Barnes, J., Chittick, E., Robinson, S., Burns, J.M., Costa, D.P., 2005. Effective, field-based inhalation anesthesia for ice seals. Marine Mammal Science 21, 717–727.

Hofmann, E.E., Wiebe, P.H., Costa, D.P., Torres., J.J. (Eds.), 2004. Deep-Sea Research II, 51; 2004, pp. 1921–2344.

Hyatt, J., Beardsley, R.C., Owends, W.B., 2011. Characterization of sea ice cover, motion and dynamics in Marguerite Bay, Antarctic Peninsula. Deep-Sea Research II 58 (13-16), 1553–1568.

Johnston, D.W., Westgate, A.J., Read, A.J., 2005. Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy. Marine Ecology Progress Series 295, 279–293.

Klinck, J.M., Hofmann, E.E., Beardsley, R.C., Salihoglu, B., Howard, S., 2004. Water-mass properties and circulation on the west Antarctic Peninsula continental shelf in austral fall and winter 2001. Deep-Sea Research II 51, 1925–1946.

Knox, G.A., 2007. Biology of the Southern Ocean, 2nd edition CRC Press/Taylor & Francis, Boca Raton, FL.

Kohavi, R., 1995. A study of cross-validation and bootstrap for accuracy estimation and model selection. In: Mellish, C.S. (Ed.), Proceedings IJCAI-95 Montreal, Que. Morgan Kaufmann, Los Altos, CA, pp. 1137–1143.

Kuemmerle, T., Perzanowski, K., Chaskovsky, O., Ostapowicz, K., Halada, L., Bashta, A.-T., Kruhlov, I., Hostert, P., Waller, D.M., Radeloff, V.C., 2010. European Bison habitat in the Carpathian Mountains. Biological Conservation 143, 908–916.

Laws, R.M., 1985. The ecology of the Southern Ocean. American Scientist 73, 26–40.

Laws, R.M., Baird, A., Bryden, M.M., 2003. Size and growth of the crabeater seal *Lobodon carcinophagus* (Mammalia: Carnivora). Journal of Zoology London 259, 103–108.

Lawson, G.L., Wiebe, P.H., Ashjian, C.J., Gallager, S.M., Davis, C.S., Warren, J.D., 2004. Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. Deep-Sea Research II 51, 2041–2072.

Lawson, G.L., Wiebe, P.H., Ashjian, C.J., Chu, D., Stanton, T.K., 2006. Improved parameterization of Antarctic krill target strength models. Journal of the Acoustical Society of America 119, 232–242.

Lawson, G.L., Wiebe, P.H., Ashjian, C.J., Stanton, T.K., 2008. Euphausiid distribution along the Western Antarctic Peninsula—Part B: distribution of euphausiid aggregations and biomass, and associations with environmental features. Deep-Sea Research II 55, 412–431.

Lozier, J.D., Aniello, P., Hickerson, M.J., 2009. Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modelling. Journal of Biogeography 36, 1623–1627.

Massom, R.A., Stammerjohn, S.E., Smith, R.C., Pook, M.J., Iannuzzi, R.A., Adams, N., Martinson, D.G., Vernet, M., Fraser, W.R., Quetin, L.B., Ross, R.M., Massom, Y., Krouse, H.R., 2006. Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in Austral Spring and Summer 2001/02, and its profound impact on sea ice and biota. Journal of Climate 19, 3544–3571.

Murphy, E.J., Watkins, J.L., Reid, K., Trathan, P.N., et al., 1998. Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. Fisheries Oceanography 7, 381–390.

Murphy, E.J., Trathan, P.N., Watkins, J.L., Reid, K., Meredith, M.P., Forcada, J., Thorpe, S.E., Johnston, N.M., Rothery, P., 2007. Climatically driven fluctuations in Southern Ocean ecosystems. Proceedings of the Royal Society B—Biological Sciences 274, 3057–3067.

Palacios, D.M., Bograd, S.M., Foley, D.G., Schwing, F.B., 2006. Oceanographic characteristics of biological hot spots in the North Pacific: a remote sensing perspective. Deep-Sea Research II 53, 250–269.

Phillips, S.J., Anderson, R.P., Schapire., R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190, 231–259.

Phillips, S.J., Dudik, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Prezelin, B.B., Hofmann, E.E., Mengelt, C., Klinck, J.M., 2000. The linkage between upper circumpolar deep water (UCDW) and phytoplankton assemblages on the west Antarctic Peninsula continental shelf. Journal of Marine Research 58, 165–202.

Prezelin, B.B., Hofmann, E.E., Moline, M., Klinck, J.M., 2004. Recognizing physical forcing of phytoplankton community structure and primary production in continental shelf waters of the western Antarctic Peninsula: synthesis and analysis of five seasonal cruises. Journal of Marine Research 62, 419–460.

Ribic, C.A., Chapman, E., Fraser, W.R., Lawson, G.L., Wiebe, P.H., 2008. Top predators in relation to bathymetry, ice and krill during austral winter in Marguerite Bay, Antarctica. Deep Sea Research Part II 55, 485–499.

Schoener, T.W., 1968. The anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49, 704–726.

Service Argos, 1996. User's Manual, 2 ed. Argos/CLS, Landover, MD, pp. 1–174.

Siniff, D.B., 1991. An overview of the ecology of antarctic seals. American Zoologist 31, 143–149.

Siniff, D.B., Garrott, R.A., Rotella, J.J., Fraser, W.R., Ainley, D.G., 2008. Opinion projecting the effects of environmental change on Antarctic seals. Antarctic Science 20, 425–435.

Southwell, C., Paxton, C.G.M., Borchers, D., Boveng, P., de la Mare, W., 2008. Taking account of dependent species in management of the Southern Ocean krill fishery: estimating crabeater seal abundance off east Antarctica. Journal of Applied Ecology 45, 622–631.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X., Rind, D., 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Nino-Southern Oscillation and Southern Annular Mode variability. Journal of Geophysical Research—Oceans 113.

Sydeman, W.J., Brodeur, R.D., Grimes, C.B., Bychkov, A.S., McKinnell, S., 2006. Marine habitat "hotspots" and their use by migratory species and top predators in the North Pacific: introduction. Deep-Sea Research II 53, 247–249.

Thiele, D., Chester, E.T., Moore, S.E., Sirovic, A., Hildebrand, J.A., Friedlaender, A.S., 2004. Seasonal variability in whale encounters in the Western Antarctic Peninsula. Deep-Sea Research II 51, 2311–2325.

Tynan, C.T., 1998. Ecological importance of the southern boundary of the Antarctic circumpolar current. Nature 392, 708–710.

Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J., Turner, J., 2003. Recent rapid regional climate warming on the Antarctic Peninsula. Climate Change 60, 243–274.

Vincent, C., McConnell, B.J., Ridoux, V., Fedak, M.A., 2002. Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. Marine Mammal Science 18, 155–166.

Veloz, S.D., 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. Journal of Biogeography 36, 2290–2299.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62, 2868–2883.

Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33, 607–611.

Wiebe, P.H., Stanton, T.K., Greene, C.H., Benfield, M.C., Sosik, H.M., Austin, T., Warren, J.A., Hammar, T., 2002. BIOMAPER II: an integrated instrument platform for coupled biological and physical measurements in coastal and oceanic regimes. IEEE Journal of Oceanic Engineering 27, 700–716.

Wilson, R.P., Putz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.B., Ropert-Coudert, Y., 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildlife Society Bulletin 25, 101–106.