Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin

Francisco Ramírez,[1,†] Isabel Afán,[2] Keith A. Hobson,[3] Marcelo Bertellotti,[4] Guillermo Blanco,[5] and Manuela G. Forero[1]

[1]Estación Biológica de Doñana–Consejo Superior de Investigaciones Científicas (EBD-CSIC),
Departamento de Biología de la Conservación, Avda. Américo Vespucio s/n, 41092-Sevilla, Spain
[2]Estación Biológica de Doñana–Consejo Superior de Investigaciones Científicas (EBD-CSIC),
Laboratorio de SIG y Teledetección, Avda. Américo Vespucio s/n, 41092-Sevilla, Spain
[3]Environment Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan S7N 3H5 Canada
[4]Centro Nacional Patagónico, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Brown 2915 U9120ACD,
Puerto Madryn, Chubut, Argentina
[5]Department of Evolutionary Ecology, National Museum of Natural History,
Consejo Superior de Investigaciones Científicas (CSIC), José Gutiérrez Abascal 2, 28006 Madrid, Spain

Abstract. Understanding how top predators respond to natural and anthropogenically induced changes in their environment is a major conservation challenge especially in marine environments. We used a multidisciplinary approach to explore the mechanisms through which a typical central-place forager, the Magellanic penguin (*Spheniscus magellanicus*) from the Chubut province of Argentina, responds to variations in oceanic conditions and prey resources. We combined habitat and species distribution modeling with isotopic dietary reconstructions based on blood $\delta^{13}C$ and $\delta^{15}N$ values to quantify the role of bathymetry, sea-surface temperature and chlorophyll-*a* concentration, abundance of conspecifics, and extent of fisheries activities in explaining the foraging and feeding ecology of individuals breeding at different colonies. The at-sea distribution of penguins was tightly coupled with the spatial distribution of their staple prey species, anchovies (*Engraulis anchoita*), especially in areas over the continental shelf (>200 m depth), with relatively warm water (from 16° to 21°C), and moderate abundances of conspecifics (from 50 to 250 individuals). Competition with conspecifics and human fisheries were also identified as important factors explaining penguin diet with decreasing relative contributions of anchovies with increasing abundance of conspecifics and fishing activity. Our multifactorial approach allowed us to simultaneously explore different physical, biological and anthropogenic features likely affecting marine resource availability, and, consequently, driving the feeding and foraging ecology of this central-place forager. Our approach can be extended to a large suite of central-place foragers, thus providing important advances in the way we investigate how to effectively conserve and manage these species.

† **E-mail:** ramirez@ebd.csic.es

INTRODUCTION

Top-predators integrate sources of nutrients and trophic interactions throughout entire food webs and so can be ideal indicators of overall ecosystem functioning (Frederiksen et al. 2006, Fauchald 2009). The utility of such indicators would be enhanced if variation in key environmental features could be linked with subsequent changes in predator feeding ecology. Such information would also increase our understanding of ecosystem responses to natural or human-induced environmental changes. In marine systems, top predators are confronted by highly dynamic and spatially heterogeneous prey resources and so are forced to fine-tune their diet and foraging distribution in response to variations in food resource availability both in space and time. Thus, marine top predators may be particularly appropriate for investigating the consequences of changes to food-web composition and function (Furness and Camphuysen 1997).

Marine productivity is patchily distributed, and marine predators that are also central-place foragers tend to distribute themselves according to oceanographic features (e.g., frontal systems, shelf edges or upwellings) surrounding their breeding sites where their prey aggregates (Hunt et al. 1992, Weimerskirch et al. 2005). Moreover, strong breeding and foraging site fidelity exhibited by these predators indicates that experienced individuals are able to consistently locate adequate food to raise young and the occurrence of predictable food resources or seasonally productive areas are important cues for selecting foraging areas (Weimerskirch 2007, Cama et al. 2012, Louzao et al. 2012). In addition to these oceanographic features, human fisheries or the abundance and distribution of conspecifics are known to affect the diet and foraging behavior of marine predators in a variety of ways, including facilitation (Henkel 2009, Bartumeus et al. 2010, Cama et al. 2012) or competition for resources (Crawford 2007, Weimerskirch et al. 2009, Masello et al. 2010, Bertrand et al. 2012). Understanding how top predators respond to variations in such physical, biological and anthropogenic features is a major conservation challenge in marine environments.

Recent advances in the fields of modeling habitat and species' distributions (Louzao et al. 2011a, Louzao et al. 2012), animal tracking (Hobson and Wassenaar 2008, Boersma et al. 2009, Navarro et al. 2009) and the use of endogenous tracers of diet including fatty acids and stable isotopes (Navarro et al. 2009, Ramos et al. 2011, Karnovsky et al. 2012) offer a unique opportunity to investigate the feeding response of central-place foragers to spatiotemporal variations in the availability of marine food resources. In particular, remote sensing data on oceanographic features for the last decades are now available (e.g., Acha et al. 2004, Boersma et al. 2009, Louzao et al. 2012), thus providing valuable information on marine productivity patterns at large spatial and temporal scales. In addition, spatially explicit information derived from monitoring programs of fishing vessels provides a unique opportunity to investigate the interaction between marine predators and fishing activities (Yorio et al. 2010, Bertrand et al. 2012). Furthermore, the recent development and widespread application of bio-logging techniques have revolutionized our knowledge on the movement ecology and spatial distribution of marine predators (Weimerskirch et al. 2009, Masello et al. 2010, Louzao et al. 2012). Based on this previous information, predictive modeling of species' distribution has provided a popular analytical framework for relating geo-located observations of occurrence to environmental variables that contribute to a species distribution (Monk et al. 2012).

We evaluated the role of several environmental factors, including physical, biological and anthropogenic features, likely driving the availability of marine food that in turn constrains the feeding behavior and reproductive performance of a typical central-place forager, the Magellanic penguin (Spheniscus magellanicus), breeding at the Chubut province of Argentinean Patagonia. This species has been studied extensively because it constitutes 84% of the breeding seabird community in this region (Yorio et al. 1998), is near threatened (IUCN 2012; IUCN Red List of Threatened Species; Version 2012.2. www.iucnredlist.org; accessed on December 2012), and interacts with humans through fisheries and ecotourism (Yorio et al. 2001, 2010, Villanueva et al. 2012). Magellanic penguins have been the subject of several studies aimed at investi-

gating the link between prey availability and diet (e.g., Forero et al. 2002a, 2004, Wilson et al. 2005), spatial distribution of conspecifics (e.g., Wilson et al. 2005, Boersma et al. 2009, Yorio et al. 2010) and reproductive performance (e.g., Tella et al. 2001, Forero et al. 2002a). However, most previous studies have not addressed large-scale ecological mechanisms in an integrative way. We combined and reanalyzed previous information in light of recent advances in habitat and species distribution modeling and Bayesian isotopic approaches to diet reconstructions in order to quantify the importance of several factors influencing the foraging ecology and reproductive success of Magellanic penguins. Our approach was based on key predictions associated with the expected effects of environmental and anthropogenic factors on penguin foraging movements and diet and ultimately on reproductive performance. Our proposed approach could be also extended to a large suite of central-place foragers, thus providing important advances in the way we tackle investigations into the feeding ecology of these organisms.

MATERIALS AND METHODS

General approach

Diet and foraging distribution of Magellanic penguins were expected to be coupled with the abundance and spatial distribution of the richest and most predictable prey patches available within their foraging range. In addition, the abundance and distribution of conspecifics and fishing vessels were expected to influence the diet and foraging distribution of penguins through a density-dependent depletion of optimal (i.e., high-protein) prey types (Tella et al. 2001, Forero et al. 2002a). We used remote sensing and geographic information systems (GIS) to derive several explanatory variables likely informing marine productivity patterns (Acha et al. 2004), fishing pressure (Skewgar et al. 2007, Yorio et al. 2010), and intra-specific competition (Tella et al. 2001, Forero et al. 2002a). A species distribution model was used to quantitatively infer the role of different environmental features in explaining the at-sea distribution of penguins and general linear models were used to evaluate the effect of food availability on different dietary metrics (inferred from penguin

blood δ^{13}C and δ^{15}N values). Given that food quality and availability is positively correlated with animal reproductive output, inter-colony dietary differences were finally expected to influence penguin reproductive performance, with penguins feeding on suboptimal prey likely showing poorer reproductive output (Tella et al. 2001, Forero et al. 2002a). Accordingly, we finally investigated the relationship between inferred dietary estimates and penguin breeding success.

Magellanic penguins in Chubut province

Magellanic penguins occur at Argentinean Patagonia in 29 colonies on the mainland and islands from about 42° S to almost 55° S (Yorio et al. 1998, Wilson et al. 2005). Our study area extended along ~1000 km of the coast of Chubut province (from 42° S to 46° S latitude; Fig. 1). Colony size is highly variable (Yorio et al. 1998) and adjacent marine areas exhibit considerable heterogeneity in marine productivity at the meso-scale, mostly driven by the spatial distribution of frontal systems (Acha et al. 2004). In particular, marine areas surrounding southern colonies (those located near the Golfo de San Jorge; see Fig. 1) are strongly influenced by the cold and low salinity water of the northward flowing Patagonian current that reaches the southern boundary of the Golfo de San Jorge during austral summers producing a highly productive extension of waters north (Acha et al. 2004, Boersma et al. 2009). North of Golfo de San Jorge, tidal mixing fronts dominate the coastal oceanography, being visible along the coast from Cabo dos Bahías to Península Valdés. Finally, the cooler and more saline waters of the Malvinas Current meet the sub Antarctic shelf waters in the offshore along the continental shelf-break, resulting in a thermohaline front where nutrients from the Malvinas Current reach the euphotic zone and enhance marine productivity (Acha et al. 2004).

Previous dietary investigations of breeding Magellanic penguins at our study area indicated that diet remained stable across years (Wilson et al. 2005). However, inter-colony dietary differences were also reported and these differences followed a latitudinal gradient (Scolaro et al. 1999, Wilson et al. 2005, Boersma et al. 2009) related to the abundance of anchovy (Engraulis anchoita; Scolaro et al. 1999, Hansen et al. 2001,
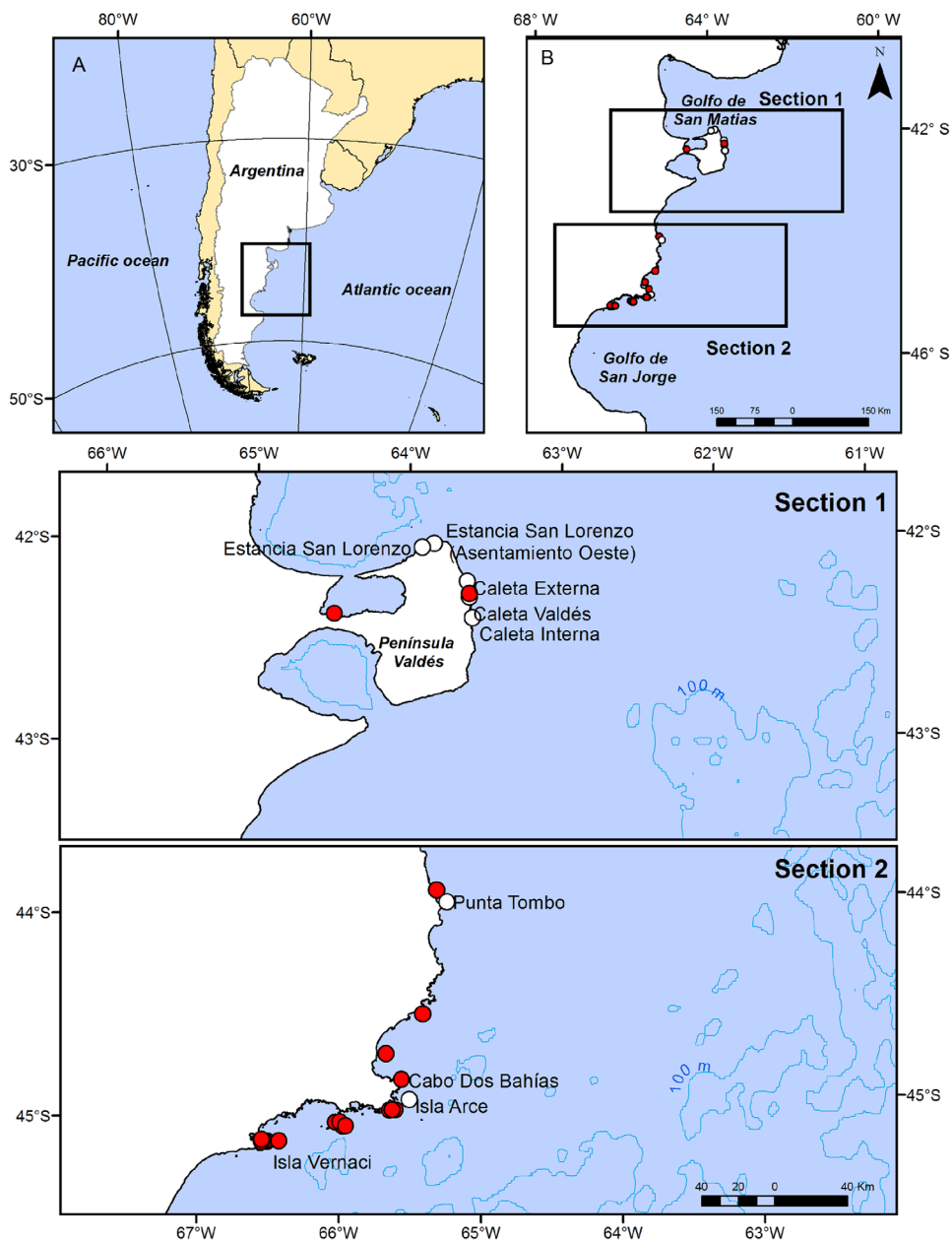
Fig. 1. Geographical location of the study area and breeding colonies of Magellanic penguins (dots). White dots represent penguin colonies that were sampled for stable isotope determinations (white dots for Cabo dos Bahías and Isla Vernaci are not visualized as they are hidden by red dots of neighboring colonies).

Wilson et al. 2005, Boersma et al. 2009). At northern colonies penguins consume anchovy almost exclusively, whereas squid (*Loligo* spp. and *Illex* spp.) or hake (*Merluccius hubbsi*) become much more important in penguin diet at southern colonies (i.e., North Puerto Deseado; Scolaro et al. 1999, Forero et al. 2002*b*, Wilson et al. 2005).

In addition to natural variability in food supplies, inter-colony dietary differences could also be explained by a density-dependent reduction in food resource availability due to a heterogeneous distribution in the abundance of

conspecifics (Tella et al. 2001, Forero et al. 2002*a*) and fishing pressure (see Skewgar et al. 2007, Yorio et al. 2010). Indeed, increasing densities of conspecifics may increase competition for common resources among penguins and deplete more optimal prey types such as anchovy (Tella et al. 2001, Forero et al. 2002*a*). Competition may contribute to observed inter-colony differences in diet, but also result in poorer reproductive performance at those colonies experiencing high levels of competition (Tella et al. 2001, Forero et al. 2002*a*). Similarly, fishing activities may also affect diet, distribution and, ultimately, penguin reproductive performance since anchovy, hake and squid are important target species for commercial fisheries in the area (Argentinean "Ministerio de Agricultura, Ganadería y Pesca," www.minagri.gob.ar; accessed on September 2012), suggesting high competition between fisheries and penguins (see Skewgar et al. 2007, Yorio et al. 2010).

Penguins breeding at the Chubut province typically forage up to 450 km from their colonies (Wilson et al. 2005, Boersma et al. 2009, Yorio et al. 2010). Foraging trips typically show a commuting pattern (sensu Weimerskirch 2007) where individuals depart the colony and meander toward their foraging area where they stay before swimming rapidly and directly back to colony. However, individuals from the northern and central colonies spend most of their time within 150 km from the focal colonies, with a peak in abundance at ca. 120 km (Wilson et al. 2005).

Identifying features driving penguin feeding locations

Information on foraging distribution of penguins breeding at the Chubut province was extracted from Boersma et al. (2009) who, during the 2003–2004 breeding season, placed 37 satellite transmitters (Platform Transmitter Terminals, PTT) on individuals from six colonies spanning most of the latitudinal range of the species in Argentina, and including three colonies enclosed within our study area (i.e., La Ernestina, 42°07′ S, 63°43′ W; Punta Tombo, 44°02′ S, 65°12′ W; and Cabo dos Bahías, 44°51′ S, 65°32′ W). Boersma et al. (2009) used a fixed-kernel analysis on foraging locations (once excluded commuting locations) to show main foraging areas. We considered previ-

ously defined areas encompassing 50% isopleths (i.e., 50% kernel contours; Boersma et al. 2009: Fig. 5) as main foraging grounds for Magellanic penguins (see Seaman and Powell 1996). We randomly drew ten different points within each of the 12 defined foraging areas to extract potential foraging locations for individuals breeding at colonies located within the Chubut province (see below for the appropriateness of considered sample size).

Environmental predictors

1. Marine productivity.—Among different oceanographic features commonly used for identifying highly productive hotspots, chlorophyll-*a* concentrations (mg/m^3), sea-surface temperature (°C) and bathymetry (m) are widely considered as the most biologically relevant and readily measured. In particular, chlorophyll-*a* can be considered a reliable surrogate of marine productivity and, consequently, of prey abundance, whereas sea-surface temperature and bathymetry may provide relevant information on physical processes or oceanographic features driving prey distribution (Acha et al. 2004, Yen et al. 2004, Pinaud et al. 2005, Louzao et al. 2011*b*, Louzao et al. 2012). Here, we used Aqua MODIS (4 × 4 km resolution) derived winter composites (i.e., austral summers) to extract information on chlorophyll-*a* and sea-surface temperature for the area and breeding season (2003–2004) of interest. Bathymetry was downloaded from the ETOPO web site (http://www.ngdc.noaa.gov/mgg/global/global.htm), as a binary product at a spatial resolution of 0.01° (approximately 1 km). For analysis purposes, bathymetry was adjusted to match the spatial resolution for the Aqua MODIS imagery data by averaging depth values for pixels enclosed within a 4 × 4 km cell grid.

Key marine areas associated with sea fronts were identified by exploring the spatiotemporal component of sea-surface temperature gradients. In particular, we used the longest time series (2002–2012) of Aqua MODIS sea-surface temperature derived winter seasonal composites. For each one of these composites, and following Louzao et al. (2012), we estimated a dimensionless metric Proportional Change (PC) expressing the magnitude of change in sea-surface temperature, within a moving window of a 3 × 3 cells and following the equation: PC = [(maximum
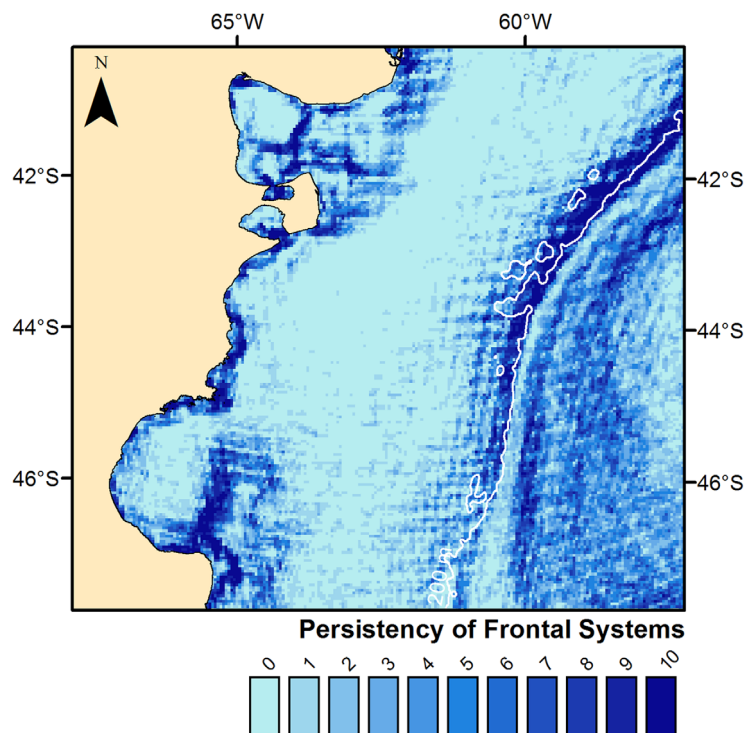
Fig. 2. Spatiotemporal heterogeneity of key marine areas associated with sea fronts at the marine area surrounding the Chubut province and based on sea-surface temperature gradients. Colors represent the persistency of such key marine areas according to the number of years in which each pixel was defined as frontal system (see *Materials and Methods* for information on criteria used to define each pixel as frontal system). Values range from 0 (minimum persistence) to 10 (maximum persistence), according to the time period for which imagery data on sea surface temperature is available, i.e., 10 years (2002–2003 to 2011–2012). White line represents the 200 m isobaths.

value − minimum value) × 100]/(maximum value). Frontal systems were identified as areas with PC values within the 75th percentile, whereas the persistence of these areas was quantified by counting in how many years each cell was identified as a frontal system (values ranged from 0 to 10 corresponding to the sea-surface temperature time series; Fig. 2).

2. Penguin abundance.—Following Grecian et al. (2012), we combined available information on colony sizes and locations (Yorio et al. 1998), and frequencies of foraging distances (Wilson et al. 2005), to generate a predicted distribution of penguins in the marine area around the Chubut province. In particular, the penguin abundance distribution (Fig. 3) was generated by uniformly distributing the total number of individuals reported at each colony within their foraging range (i.e., 450 km from the focal colony; Wilson

et al. 2005, Yorio et al. 2010), based on calculations of the Euclidean distances from each colony, and on the average frequency of distances provided by Wilson et al. (2005) for the northern and central colonies (Fig. 3).

3. Fishing pressure.—The spatial distribution of fishing vessels operating within our study area for the 2001–2005 period were grouped as cold store and freezer vessels differing in their main target species and fishing areas based on the On-board Observer Program of Chubut Province (Secretaría de Pesca de la Provincia de Chubut; Fig. 4). In addition, long-term (1999–2010) fish landing data obtained from the Argentinean "Ministerio de Agricultura, Ganadería y Pesca" (www.minagri.gob.ar; accessed in November 2012) was used to estimate the relative contribution of main fishing fleets to total landing of anchovies. Extraction of environmental variables
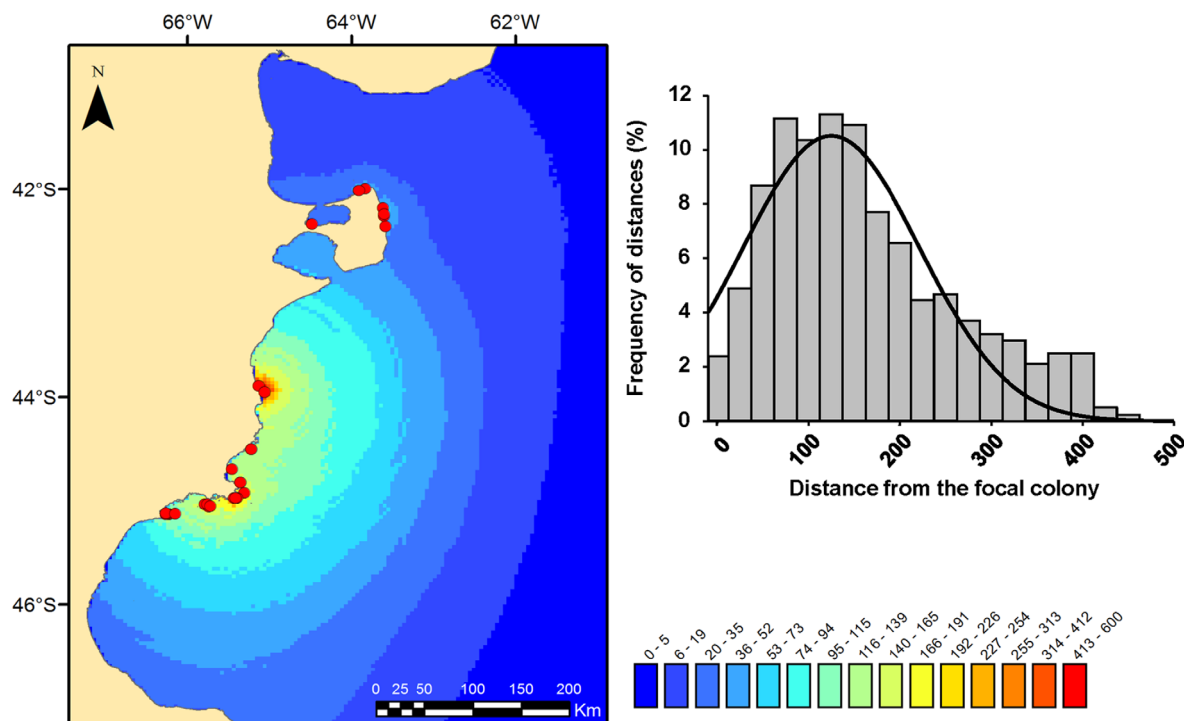
Fig. 3. Spatial distribution of abundances of Magellanic penguins within the marine area surrounding the Chubut province (left side). Individuals from each colony (information on colony sizes were obtained from Yorio et al. 1998) were uniformly distributed within their home range (i.e., 450 km; Wilson et al. 2005), based on calculations of the Euclidean distances from the focal colonies, and on the average frequency of distances provided by Wilson et al. (2005) (right side).

and spatial analyses were performed with ArcGis 10 (Environmental Systems Research Institute [ESRI], Redlands, California, USA).

Species distribution modeling

Penguin distribution (Fig. 5) was performed using Maximum Entropy (MaxEnt) modeling (version 3.3.3; http://www.cs.princeton.edu/~schapire/maxent/) based on presence data obtained from Boersma et al. (2009), and the above-mentioned explanatory variables. Among different modeling methods, MaxEnt has been proposed as the strongest because it remains fairly stable in both prediction accuracy and the total area predicted present across all sample size categories (Hernandez et al. 2006, Pearson et al. 2007). Thus, we considered that ten randomly chosen points within previously defined foraging areas (Boersma et al. 2009) would provide us with an appropriate representation of the spatial distribution of penguins while foraging. Regard-

ing explanatory variables, we considered chlorophyll-*a* and sea-surface temperature for the 2003–2004 winter season, along with bathymetry as integrative measures of marine productivity and physical features driving prey distribution. The persistence of frontal systems was considered as a proxy for the predictability of prey patches. Penguin abundance distribution was also considered to account for the degree of intra-specific competition for food. Finally, distribution of cold store and freezer vessels were used to account for potential interaction between penguins and human fisheries.

MaxEnt procedure was used to estimate relationships between estimated probability of presence of penguins and the above-mentioned explanatory variables. Although MaxEnt can fit complex relationships between estimated probabilities of presence and different environmental variables, we exclusively fitted linear and quadratic relationships due to the difficulty of
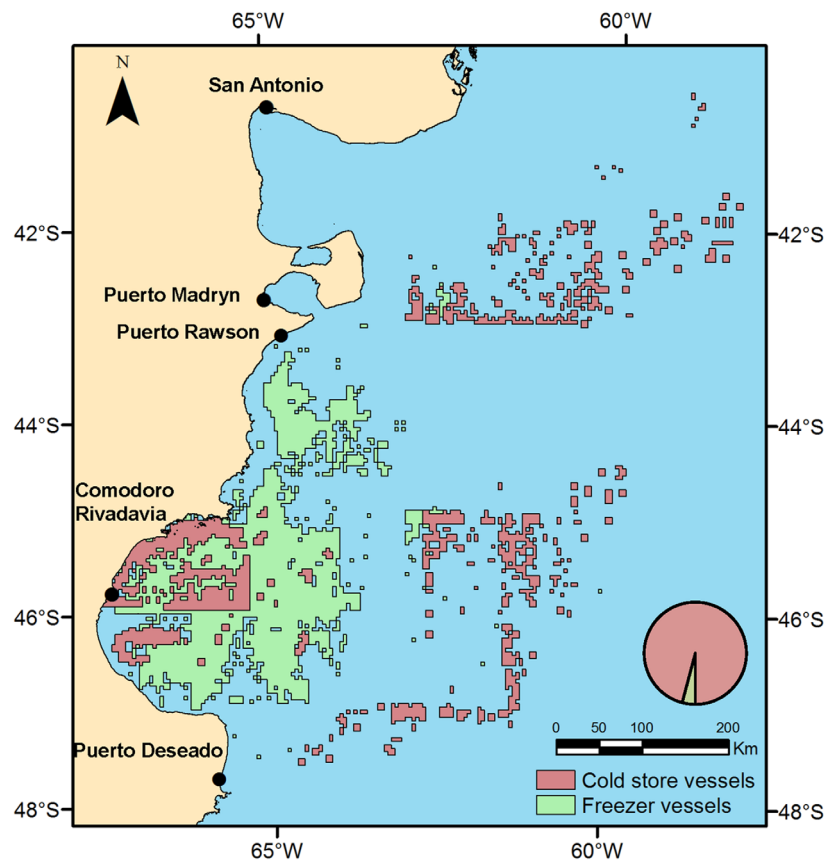
Fig. 4. Spatial distribution of main fishing vessels (grouped in cold store and freezer vessels) for the 2001–2005 period obtained from the On-board Observed Program of Chubut Province (Secretaría de Pesca de la Provincia de Chubut). Black dots represent main fishing ports at the area. The relative contribution of main fishing fleets (i.e., cold store and freezer vessels) to total landing of anchovies are represented by a pie chart.

interpreting other more complex associations. For internal validation, obtained models were tested using 30% of potential foraging locations randomly selected. One hundred replicates of the model were run to obtain an average prediction and a coefficient of variation for predictions. To assess the predictive performance of our model, we evaluated each MaxEnt prediction using the Area Under the Receiver Operating Characteristic (ROC) Curve (hereafter AUC; ranging from 1, perfect predictive performance, to 0, perfect reversed predictive performance, and with 0.5 values denoting null predictive ability; Fielding and Bell 1997). AUC values were also used to evaluate the predictive performance of each explanatory variable when used in isolation. Finally, we tested for spatial autocorrelation in model residuals by calculating the Moran's I

values (ranging from −1, perfect dispersion, to +1, perfect autocorrelation, with zero values denoting random spatial distribution) for 20 equal-distance classes, and using the Spatial Analysis in Macroecology (SAM, v.4.0) software (Rangel et al. 2010). We used this test because significant spatial patterning in the residuals might reflect missing environmental effects that are geographically patchy or reflect the effect of disturbance-related processes that are independent of environment (Barry and Elith 2006).

Features affecting penguin feeding habits

Dietary metrics.—Dietary information was based on stable isotope measurements extracted from Forero et al. (2004). These authors provided blood $\delta^{13}C$ and $\delta^{15}N$ values for penguins ($n = 246$ and 153 for adults and fledglings, respectively)
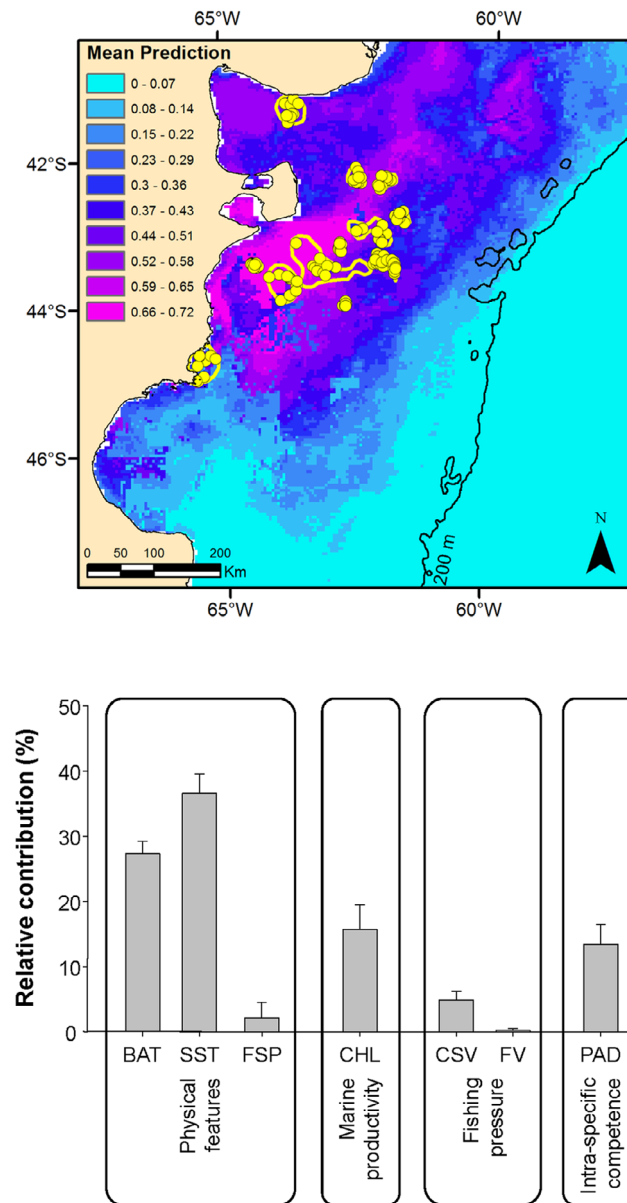
Fig. 5. Species distribution modeling output for Magellanic penguins (top). Potential foraging locations were extracted by randomly drawing 10 different points (yellow dots) within main foraging areas (50% contours from a fixed-kernel analysis, yellow lines) defined by Boersma et al. 2009. Explanatory variables considered and their relative contributions to the MaxEnt model (mean ± SD) have been also represented (bottom). Explanatory variables have been grouped according to their ecological significance. In particular, bathymetry (BAT), sea surface temperature (SST) and the persistence of frontal systems (FSP) were included as physical features likely driving prey distribution and their persistence/predictability. Chlorophyll-*a* concentrations for the 2003–2004 (CHL) winter period were included as a surrogate of marine productivity. Spatial distributions of cold store (CSV) and freezer vessels (FV) for the 2001–2005 period (On-board Observed Program of Chubut Province, Secretaría de Pesca de la Provincia de Chubut) were included as a proxy to fishing pressure. Estimated distribution of penguin abundances (PAD) was also incorporated to account for the degree of intra-specific competence for food.

Table 1. Isotopic composition (δ^{13}C and δ^{15}N, mean ± SD) of Magellanic penguins breeding at different colonies at the Chubut province (Argentinean Patagonia). Based on isotopic variability ascribed to different colonies, and the recent isotopic Bayesian framework developed for R (Parnell et al. 2008), we generated multivariate ellipse-based metrics (SEA.B; median, and low and high 95% Bayesian credibility interval [95% BCI]) which were taken as a reliable proxy to trophic niche width. Localities are listed from north to south.

Locality	δ^{13}C (‰) (mean ± SD)	δ^{15}N (‰) (mean ± SD)	SEA.B (‰^{2}) 95% BCI	Median
Estancia San Lorenzo	−17.16 ± 0.48	18.84 ± 0.26	0.38–0.58	0.47
Estancia San Lorenzo†	−17.22 ± 0.33	19.08 ± 0.24	0.28–0.48	0.37
Caleta Externa	−16.58 ± 0.17	18.65 ± 0.32	0.43–1.65	0.91
Caleta Valdés	−16.49 ± 0.37	18.85 ± 0.51	0.55–1.21	0.84
Caleta Interna	−16.62 ± 0.36	18.97 ± 0.46	0.43–0.76	0.59
Punta Tombo	−16.48 ± 0.48	18.51 ± 0.41	0.52–0.84	0.67
Cabo dos Bahías	−16.36 ± 0.61	18.76 ± 0.6	0.88–1.34	1.09
Isla Arce	−17.01 ± 0.44	18.43 ± 0.45	0.52–1.11	0.79
Islas Vernaci	−16.13 ± 0.36	19.16 ± 0.23	0.45–1.58	0.9

† Asentamiento Oeste.

sampled during three consecutive breeding seasons (from 1999 to 2001) and at nine different breeding colonies distributed across the Chubut province (Table 1 and Fig. 1). Bird diet was reconstructed using dual-isotope (δ^{13}C and δ^{15}N) Bayesian mixing models (SIAR; Parnell et al. 2008). Dietary endpoints included in these models were isotopically clustered (mean ± SD) by grouping main potential prey species defined by previous dietary reports at this area (i.e., anchovy, hake and squid), and adjusted to account for diet-blood isotopic discrimination factors (ΔX) linking diet with consumers' tissues (Δ^{13}C: 1.1‰; Δ^{15}N: 2.9‰; see Caut et al. 2009). The robustness of derived inter-colony dietary estimates was tested through sensitivity analysis in which different diet to blood discrimination factors (Δ^{13}C: ranging from 0.7‰ to 1.5‰; Δ^{15}N: ranging from 2.5‰ to 3.3‰) and error terms (SD ranging from 0.1‰ to 0.6‰) were incorporated in our multisource isotope mixing models.

We also used isotopic variability ascribed to different colonies, and the recent isotopic Bayesian framework, to generate multivariate ellipse-based metrics (area of the multivariate ellipses, hereafter referred as SEA.B, expressed as ‰^{2}; Table 1) following methods from Jackson et al. (2011) and the R package SIAR (Parnell et al. 2008). These metrics were taken as a reliable proxy to trophic niche width for each colony (Bearhop et al. 2004, Jackson et al. 2011).

Linking dietary metrics with environmental features.—General linear models (GLM) with normal error and identity link functions of PROC GENMOD in SAS (SAS Institute, Cary, North Carolina, USA) were used to explore the effect of derived explanatory variables on median percentages of anchovy and median values for SEA.B for each sampled colony. Marine productivity and fishing pressure associated with a given colony was estimated by adding chlorophyll-*a* concentrations and presences of cold store and freezer vessels (i.e., 4 × 4 km pixels in which fishing activity was reported) respectively for the marine area enclosed within penguin foraging range (450 km; Wilson et al. 2005). As estimates of intra-specific competition, we considered the total number of penguins within different buffer areas from the focal colonies. In particular, we extracted, from the predicted distribution of penguins, the total number of individuals within buffers of 150, 300 and 450 km from the focal colonies, to account for areas in which penguins spend ~50%, 90% and 100% of their time (Wilson et al. 2005). Each explanatory variable and their potential interactions were tested following a forward-step procedure to finally obtain a set of models that only retained variables with significant (or nearly significant) effects. Model parsimony was evaluated based on the Akaike information criterion corrected for small sample sizes (AIC$_C$; Johnson and Omland 2004) and the corresponding AIC$_C$ weights. All tests were two tailed. QQplot and a scatterplot of the residuals plotted against fitted values indicated no obvious deviations from the assumptions of normally distributed and homogeneous residuals.

Diet and penguin reproductive performance

Reproductive performance was based on average brood size and fledgling body condition. Brood size was measured as part of a previous study (1999–2000) at six of the sampled colonies (Forero et al. 2002a) and was based on the average number of siblings at fledging time in nests located within a transect (2 m wide) perpendicular from each focal nest to the sea ($n = 3220$, range = 204–1138 nests per colony). Empty nests were excluded from analysis because of the impossibility of distinguishing unoccupied nests from those resulting from breeding failure. Chicks were measured (flipper length ± 1 mm) and weighed (± 10 g) during the 1999–2000 and 2000–2001 breeding seasons at seven different colonies where blood samples were taken (Forero et al. 2002a, b). Here, we used these morphometrics to estimate fledgling body condition by averaging residuals from the linear regression between flipper length and body mass ($F_{1, 213} = 84.98$, $p < 0.001$). Season was included in the model as a fixed factor to account for observed differences in fledglings' body conditions among breeding events ($F_{2, 213} = 18.27$, $p < 0.001$).

The effect of diet on penguin reproductive performance was explored through Pearson correlation tests between estimated relative median contribution of anchovy to the diet of penguins from different colonies and the corresponding mean values of brood size and fledgling body condition. For this latter relationship, we exclusively considered fledglings' isotopic data when applying Bayesian mixing models for dietary reconstructions. Our predictions of the influence of anchovy to reproductive success were directional and so one-tailed tests were used. Statistical analyses were done using SAS (SAS Institute, Cary, North Carolina, USA) and SPSS 18.0 software (SPSS, Chicago, Illinois, USA).

RESULTS

Spatiotemporal heterogeneity in marine productivity, fishing pressure and penguin abundance

Long-term information on sea-surface temperature was used to explore the spatiotemporal distribution of key marine areas surrounding the Chubut province (Fig. 2). This approach revealed several highly productive marine areas that occurred consistently along the coast and following the continental shelf-break (200 m isobath). The at-sea distribution of main fishing vessels in this area suggested that fishing pressure was particularly high within the Golfo de San Jorge. However, fishing activity was also detected in the nearshore between Cabo dos Bahías and Península Valdés and following the continental shelf-break. Freezer vessels aggregated in the nearshore, whereas cold stores were clearly associated to the continental shelf-break where they were responsible of more than 90% of anchovy captures (Fig. 3).

Penguin abundance, and consequently the assumed degree of intra-specific competition for food, was higher in areas close to Punta Tombo where the largest colony occurred, but also in the northern part of Golfo de San Jorge and Peninsula Valdés, where a number of smaller colonies aggregate in relatively small coastal areas. In contrast, northern and southern inshore areas (i.e., marine areas within the Golfo de San Jorge and Golfo de San Matías), and offshore marine areas (nearby the continental shelf-break) had the lowest penguin densities.

Physical, biological and anthropogenic features driving penguin feeding ecology

Penguin distribution.—The distribution model for penguins performed reasonably (mean AUC $\pm$ SD = 0.84 ± 0.02, for the model and the internal validation), with model residuals showing a moderate but non-significant spatial autocorrelation at any distance class (mean Moran's $I \pm$ SD = 0.35 ± 0.23; $p > 0.0025$ once adjusted through Bonferroni procedure). Penguins were more likely to forage in the nearshore between Cabo dos Bahías and Península Valdés thus overlapping with key marine areas associated with tidal mixing fronts. In contrast, key marine areas located at the southern boundary of the Golfo de San Jorge and over the continental shelf-break were not considered as suitable foraging areas. Penguin distribution was best explained by sea-surface temperature and bathymetry, with a moderate contribution of chlorophyll-*a* concentration and penguin abundance (Fig. 5). However, sea-surface temperature, the distribution of penguin abundance and bathymetry were the best predictive variables when considered indi-
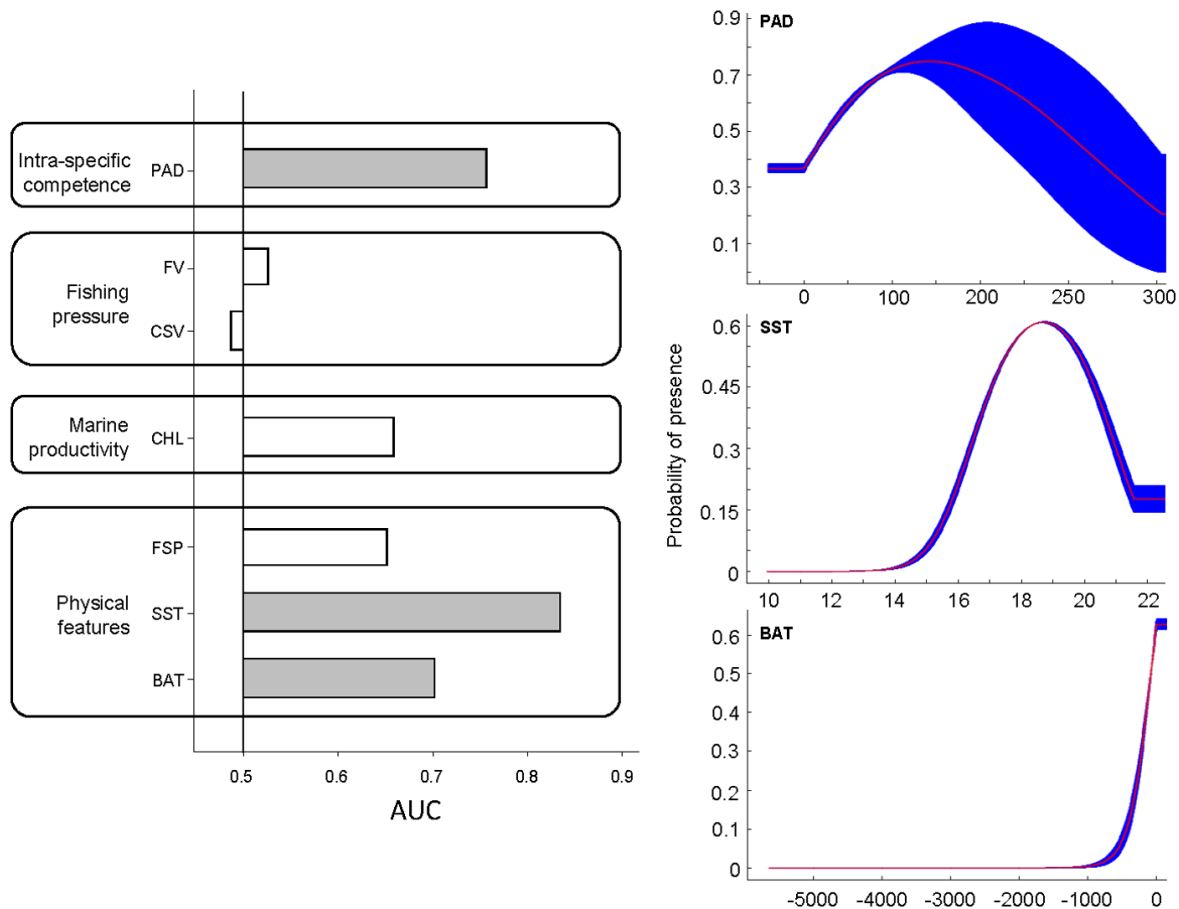
Fig. 6. Predictive performance of single explanatory variables (see Fig. 5 for acronyms) as indicated by the Area Under the ROC (Receiver Operating Characteristic) Curve (AUC, right side). AUC values range from 1, perfect predictive performance, to 0, perfect reversed predictive performance, and 0.5 values denote null predictive ability). Best predictive variables (AUC > 0.7) are shown in grey. Response curves illustrating the relationship between best predictive variables and the probability of presences for penguins are also shown (left side).

vidually (AUC = 0.83 ± 0.02, 0.75 ± 0.02 and 0.7 ± 0.03, respectively, see Fig. 6). Based on obtained response curves for best predictors (Fig. 6), penguins were more likely to forage over the continental shelf (>200 m depth) and in areas of relatively warm water (sea surface temperature values ranging from 16° to 21°C) and with moderate penguin abundances (abundances ranging from 50 to 250 individuals).

Penguin diet.—Overall, isotopic analysis of penguin diet indicated it was mainly composed of anchovy, followed by hake and squid. However, diet composition differed slightly among colonies (see Table 2), with inter-colony dietary differences quite consistent regardless of varia-

tions in considered discrimination factors (Fig. 7 and 8). In particular, Northern colonies were characterized by a greater contribution of anchovy to penguin diet (ranging from 46% in Caleta Externa to 73% in Estancia San Lorenzo-Asentamiento W). In contrast, hake (ranging from 19% to 48%) and squid (ranging from 10% to 33%) became more prevalent at central colonies (North of Golfo de San Jorge; Fig. 1, Section 2). Indeed, inferred dietary estimates suggested that hake was the most consumed prey type for penguins breeding at Cabo dos Bahías, with an average relative contribution of 48%, followed by anchovy (27%) and squid (25%). Derived dietary estimates from our multisource isotope mixing

Table 2. Relative contribution (%, median, and low and high 95% Bayesian credibility interval [95% BCI]) of main food resources (anchovy, hake and squid) to penguin diet. Dietary reconstructions were performed through a double isotope (δ^{13}C and δ^{15}N) Bayesian mixing model (Stable Isotope Analysis for R [SIAR]; Parnell et al. 2008). Localities are listed from north to south.

Locality	Anchovy (%)		Hake (%)		Squid (%)	
	95% BCI	Median	95% BCI	Median	95% BCI	Median
Estancia San Lorenzo	55.13–75.66	65.4	3.37–18.5	11.0	19.92–27.46	23.6
Estancia San Lorenzo†	60.85–83.53	72.5	0.75–17.21	9.1	13.91–23.04	18.4
Caleta Externa	22.49–74.67	46.9	7.85–46.84	28.4	12.47–36.79	24.7
Caleta Valdés	29.2–70.08	48.7	16.44–46.04	32.1	10.89–27.36	19.3
Caleta Interna	44.02–74	59.0	13.58–35.31	24.5	11.03–22.02	16.5
Punta Tombo	24.45–49.03	36.5	23.78–43.68	34.0	24.84–34.11	29.4
Cabo dos Bahías	14.86–39.22	26.9	38.01–56.78	47.7	20.72–30.34	25.4
Isla Arce	29.38–68.11	48.0	3.75–32.78	18.6	26.26–40.44	33.4
Islas Vernaci	27.65–80.07	52.9	15.58–56.24	336.9	0.08–20.57	10.2

† Asentamiento Oeste.

model were most useful in a comparative sense (since we lacked diet-tissue discrimination factors specific for Magellanic penguins) and only considered as an approximation of the actual diet.

When investigating the effect of environmental variables driving food resource availability on inferred contribution of anchovies to the diet of penguins, the best supported model (see Table 3) included a negative effect of fishing pressure by cold store vessels (explaining up to 67.9% of original deviance). However, penguin diet was also affected by the number of conspecifics feeding near the colony, as indicated by penguin abundance within 150 (explaining up to 61.4% of original deviance) and 300 km (explaining up to 53.5% of original deviance) buffer areas, with decreasing relative contributions of anchovies to penguins' diet as the abundance of conspecifics increased. Regarding isotopic niches (SEA.B), the null model (including intercept) was best supported (Table 4). However, the model including penguin abundance within a 450 km buffer also showed good support (AIC$_C$ increments, ΔAIC$_C$ = 0.8; explaining up to 35.9% of original deviance) with wider isotopic niches as the number of conspecifics within penguins' foraging ranges increased.

Dietary constraints on penguin reproductive performance

A positive relationship was found between the relative contribution of anchovy to fledgling diet and their body condition (Pearson's $r = 0.685$, $p = 0.045$, $n = 7$; Fig. 9A). Similarly, we found a positive, but non-significant, relationship between estimated relative contribution of anchovy to penguins' diet and brood size (Pearson's $r = 0.652$, $p = 0.8$, $n = 6$; Fig. 9B). Just one colony, Caleta Interna, strayed from this general trend, showing smaller brood sizes relative to estimated dietary consumption of anchovy and fledglings' body condition (Fig. 9C).

Discussion

Seabirds forage in diverse and stochastic environments that are influenced strongly by natural and anthropogenic processes (Zimmer et al. 2011). The complexity of these systems has seriously limited our ability to understand how these central-place foragers respond to such processes and especially how they adapt their foraging strategies to cope with their environments spatially and temporally. However, through the combined use of several analytical tools, it is now possible to model responses of predators to variation in food availability at various scales. Here, we combined remote sensing, animal tracking, species distribution modeling and isotopic dietary reconstructions to provide deeper insights into the mechanisms through which these top predators adapt to variation in critical resources. As expected, penguin foraging distributions were tightly coupled to the spatial distribution of their staple prey species (driven, in turn, by oceanographic features) but other biological and anthropogenic features, such as the abundance of conspecifics or the presence of fishing vessels, also played an
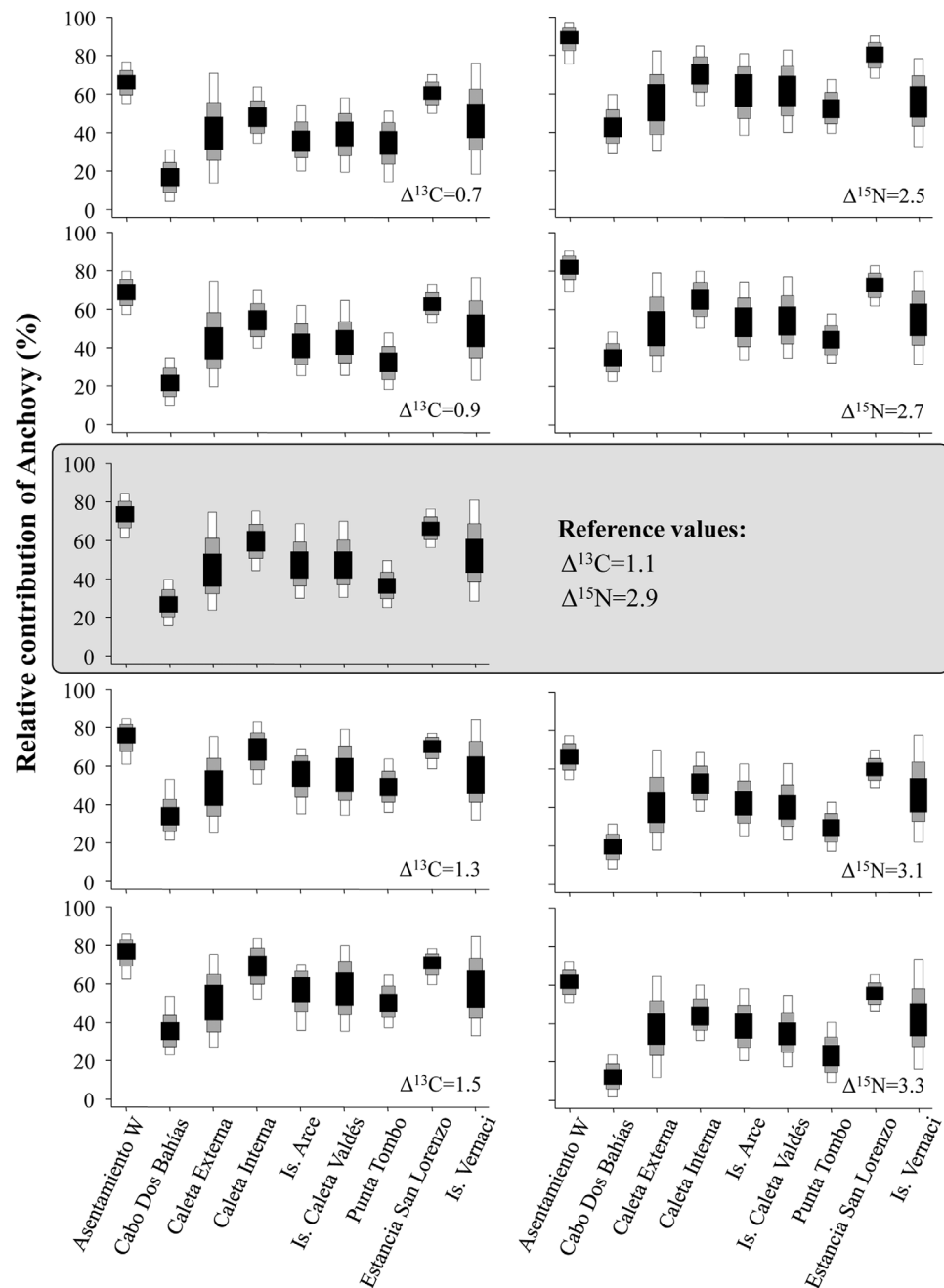
Fig. 7. Sensitivity analysis for estimated contributions of anchovy to penguin diet. Isotopic discrimination factor for $\delta^{13}C$ ($\Delta^{13}C$) ranged from 0.7‰ to 1.5‰, whereas that one for $\delta^{15}N$ ($\Delta^{15}N$) ranged from 2.5‰ to 3.3‰ (while the other factor was kept constant).

important role in explaining the foraging and feeding preferences of Magellanic penguins. Given the observed relationship between penguin diet and reproductive output, such physical, biological and anthropogenic features should be considered as important drivers of Magellanic penguin breeding parameters and population dynamics.
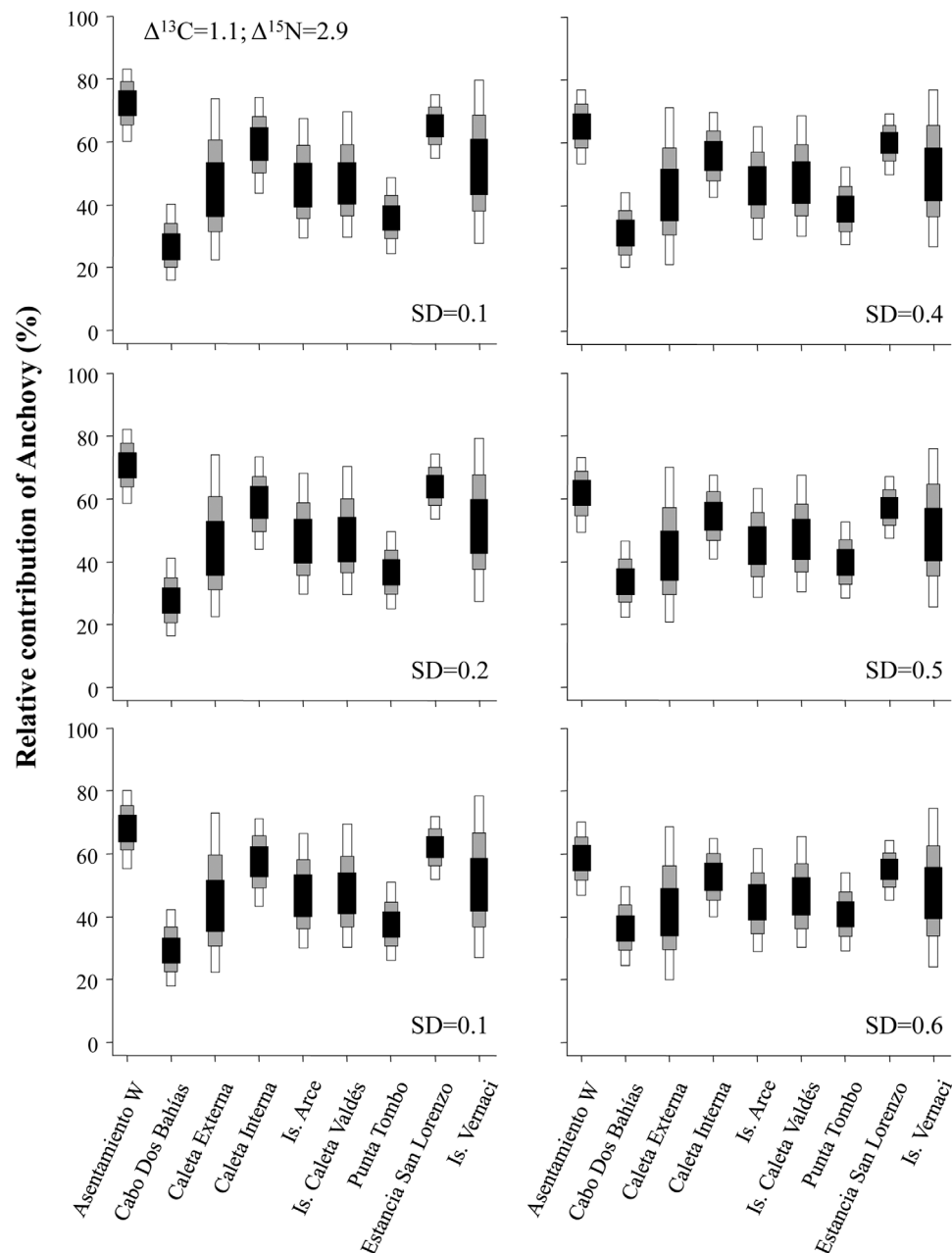
Fig. 8. Sensitivity analysis for estimated contributions of anchovy to penguin diet. The error term for considered discrimination factors ($\Delta^{13}C = 1.1‰$ and $\Delta^{15}N = 2.9‰$) ranged from 0.1 to 0.6.

Features driving the at-sea distribution of penguins

As expected, Magellanic penguins concentrated their foraging effort in highly productive marine areas, commonly characterized by high chlorophyll-*a* concentrations and sea-surface temperature and bathymetry gradients (Acha et al. 2004), where prey species also tend to aggregate (see Boersma et al. 2009). However, their foraging range was restricted to areas surrounding breeding colonies and this constraint resulted in many prey patches being out

Table 3. Set of models that retained variables with significant (or nearly significant) effects to fit the data corresponding to estimated relative contributions of anchovy (%) to the diet of Magellanic penguins from different colonies. Associated measures of information (corrected AIC [AIC$_C$]; AIC$_C$ increments [ΔAIC$_C$]; and AIC$_C$ weights [AIC$_C$ Wgt]) are shown to evaluate their parsimony. Best supported models (i.e., the most parsimonious) appear in boldface.

Models	Residual deviance	AIC$_C$	ΔAIC$_C$	AIC$_C$ Wgt	df	χ^2	p
Null model	0.156	−4.966	5.423	0.033	8		
Marine productivity							
Chlorophyll-a	0.073	−7.025	3.364	0.094	7	6.86	0.0088
Fishing pressure							
Cold store vessels	**0.05**	**−10.389**	**0**	**0.503**	**7**	**10.22**	**0.0014**
Freezer vessels	0.076	−6.642	3.747	0.077	7	6.48	0.0109
Intra-specific competence							
Penguin abundance at 150 km	0.06	−7.869	2.52	0.143	7	7.7	0.0055
Penguin abundance at 300 km	0.072	−7.057	3.332	0.095	7	6.89	0.0087
Penguin abundance at 450 km	0.082	−5.933	4.457	0.054	7	5.77	0.0163

of reach (see Hunt et al. 1992). Penguins in our study area tended to forage on tidal mixing fronts occurring consistently near the shore and between Cabo dos Bahías and Península Valdés (see also Boersma et al. 2009), whereas other key marine areas, such as those associated with the continental shelf-break front, were likely out of their foraging range (see Figs. 2 and 5).

Despite the spatial linkage between productivity and foraging distribution of penguins, our results suggested that the at-sea distribution of penguins was primarily a reflection of physical oceanographic features driving the distribution of their staple prey species. In particular, sea-surface temperature and bathymetry were the most important explanatory variables within our species' distribution model. Indeed, individuals preferentially selected foraging habitats within a 16–21°C sea-surface temperature range over

shallower waters. These attributes also described the distribution of penguin prey such as anchovies, hake and squid (Acha et al. 2004, Hansen et al. 2001).

Penguins distributed themselves in areas with moderate abundance of conspecifics. As in many other colonial seabirds, intra-specific competition for food resources can be strong for Magellanic penguins due to a lack of dietary segregation (Masello et al. 2010). Ecological theory predicts that animals with similar feeding strategies should not coexist without segregating either in space, time or diet. Indeed, intra-specific competition for food can drive the neighboring populations of the same species to spatial segregation of foraging areas (e.g., Boersma et al. 2009, Masello et al. 2010), but also can lead to segregation of foraging areas by sex, foraging periods, dive depth, or prey choice (Weimer-

Table 4. Set of models that retained variables with significant (or nearly significant) effects to fit the data corresponding to the multivariate ellipse-based metrics (SEA.B), which were taken as a reliable proxy to trophic niche width. Associated measures of information (corrected AIC [AIC$_C$]; AIC$_C$ increments [ΔAIC$_C$]; and AIC$_C$ weights [AIC$_C$ Wgt]) are shown to evaluate their parsimony. Best supported models (i.e., the most parsimonious) appear in boldface.

| Models	Residual deviance	AIC$_C$	ΔAIC$_C$	AIC$_C$ Wgt	df	χ^2	p
Null model	**0.427**	**4.099**	**0**	**0.261**	**8**		
Marine productivity							
Chlorophyll-a	0.292	5.477	1.378	0.131	7	3.42	0.0643
Fishing pressure							
Cold store vessels	0.348	7.056	2.957	0.06	7	1.89	0.1746
Freezer vessels	0.287	5.324	1.225	0.142	7	3.57	0.0587
Intra-specific competence							
Penguin abundance at 150 km	0.301	5.759	1.66	0.114	7	3.14	0.0764
Penguin abundance at 300 km	0.299	5.7	1.601	0.117	7	3.2	0.0737
Penguin abundance at 450 km	**0.273**	**4.899**	**0.8**	**0.175**	**7**	**4**	**0.0455**
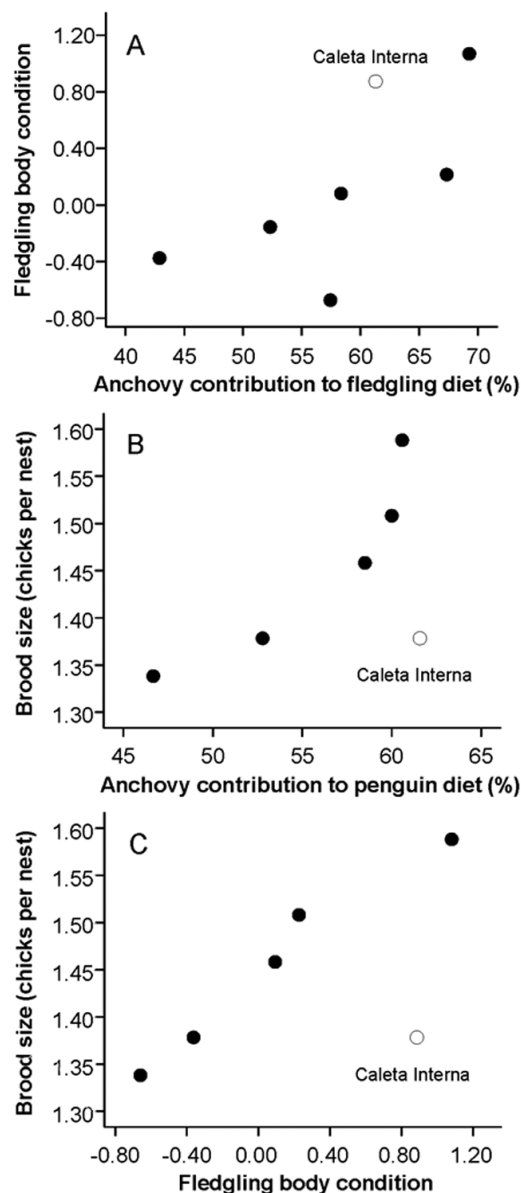
Fig. 9. Observed relationship between (A) estimated relative contribution of anchovies to the diet of fledglings (in %) and their body condition (residuals of the relationship between body size and weight); (B) estimated relative contribution of anchovies to the diet of penguins and their brood size (average number of chicks per nest); and (C) estimated body condition and brood size.

skirch et al. 2009, Navarro et al. 2010). Individual penguins may reduce the degree of intra-specific competition by avoiding areas with higher

densities of conspecifics. However, deleterious effects of interference competition for food must be traded against the benefits of feeding in flocks (Henkel 2009). Thus, penguins may preferably concentrate at areas with moderate penguin abundances, where the benefits of flock-foraging likely outweighed any cost of competition.

Features driving penguin dietary composition and trophic niche breadth

In agreement with previous dietary reports for Magellanic penguins breeding in Argentinean Patagonia (e.g., Scolaro et al. 1999, Forero et al. 2002*b*, Wilson et al. 2005, Boersma et al. 2009), our isotope approach reveled a latitudinal dietary segregation which could reflect the abundance and distribution of anchovies, which are widespread North of 43° S latitude (Hansen, Martos and Madirolas 2001, Wilson et al. 2005, Boersma et al. 2009). However, interactions with human fisheries may also affect penguin diet. Localized depletions of prey by fisheries, even if occurring at reasonably large scales, may affect seabird feeding strategies due to local prey depletions (Bertrand et al. 2012). Our models suggested that the occurrence of cold store vessels, which are responsible for the vast majority of anchovy captures, within penguins' foraging ranges negatively affected the consumption of anchovies by penguins. Finally, inter-colony dietary differences could also be explained by food depletion mechanisms mediated through intra-specific competition (Tella et al. 2001, Forero et al. 2002*a*). Consistent with this latter hypothesis, our models suggested that the abundance of conspecifics feeding near the focal colonies (up to 300 km, where penguins spend up to 90% of their time; Wilson et al. 2005) was negatively correlated with the relative contribution of anchovies to individual diet. In addition to this effect, higher densities of conspecifics within penguins' foraging ranges also resulted in wider trophic niches (i.e., SEA.B median values), suggesting certain intra-specific segregation in prey choice likely directed to reduce the degree of competition among conspecifics. However, it is necessary to be aware of the several assumptions and limitations associated with the use of isotopic variability as a proxy to dietary niche width. Isotopic variability not only depends on inter-individual trophic segregation, but also on
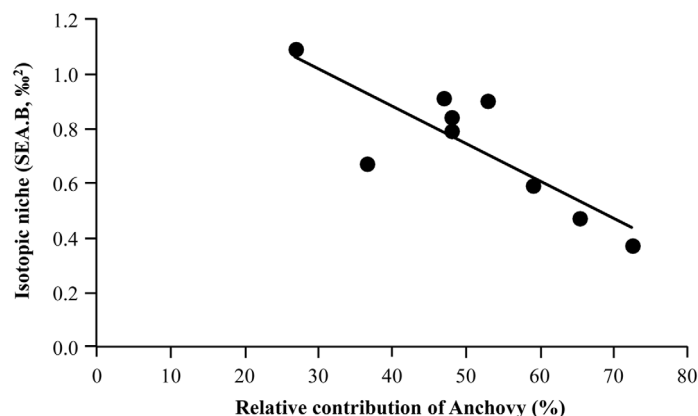
Fig. 10. Observed relationship between the relative contribution on anchovy to penguin diet and derived metrics for isotopic niche breadth (SEA.B, ‰^{2}).

the amount of isotopic variation among different food sources (Newsome et al. 2007). This may hamper the use of isotopic approaches for comparisons of dietary niche width between species or populations exploiting isotopically different food resources (Newsome et al. 2007). Alternatively, total isotopic variability can be composed of among- and within-individual components (Carrasco et al. 2010). Here, we compared isotopic variability among neighboring colonies of the same species which are expected to share foraging areas and trophic resources, thus minimizing potential biases in observed inter-colony differences in estimated isotopic niche breadths. Further, and provided there are only three main prey species for Magellanic penguins (anchovy, hake and squid), the observed negative relationship between the contribution of anchovy to penguin diet and derived SEA.B values supported the use of this metric as a reliable proxy to penguins' trophic niche breadth since the less diverse diets resulted in the narrower isotopic niches (Fig. 10).

Effect of diet on reproductive performance

Previous studies have suggested that depletion of high-protein prey may result in poorer reproductive performance of Magellanic penguins (Tella et al. 2001, Forero et al. 2002a). Our isotopic models support this idea since those colonies relying mainly on anchovies showed higher brood sizes and raised fledglings with better body condition (see Fig. 9). Just one colony, Caleta Interna, strayed from this general trend.

That colony showed smaller mean brood size than predicted based on estimated consumption of anchovy and fledgling body condition. Possibly the high levels of human disturbances and more frequent predation episodes noted at this colony could be factors causing higher breeding failure (Yorio et al. 2001). In general, marine productivity patterns, along with spatiotemporal variations in fishing pressure and intra-specific competition constrain the availability and accessibility of optimal prey types for Magellanic penguins during the breeding period, modulating breeding parameters and population dynamics.

Concluding remarks and future considerations

Previous approaches to investigating responses of marine predators to spatiotemporal variations in marine productivity patterns have focused on feeding responses of key top predators (e.g., Pinaud et al. 2005, Weimerskirch 2007, Boersma et al. 2009, Louzao et al. 2012). However, for penguins, few have considered other effects on foraging such as social or competitive interactions among conspecifics (Forero et al. 2002a) or with fishing activities (Bartumeus et al. 2010, Yorio et al. 2010, Cama et al. 2012). Ours is the first to explore simultaneously the role of these different physical, biological and anthropogenic features likely affecting marine resources availability, and, consequently, driving the feeding and foraging ecology of this central-place forager. Accordingly, we provide a useful framework for evaluating

and predicting the potential impact of currently undergoing fishing policies such those aimed at developing a trawler fishery for anchovy as an alternative to the overfished hake (Skewgar et al. 2007 and references therein) on Magellanic penguin populations. Consequently, this work supposes an important advance in the way we tackle the management and conservation of this species. However, further investigation should additionally contemplate other potential explanatory variables likely affecting the feeding ecology of this central-place forager, such as the at-sea distribution of competitive species (e.g., South American sea lion, *Otaria flavescens*; Koen-Alonso and Yodzis 2005, Drago et al. 2010) and predators (e.g., the killer whale, *Orcinus orca*; Guinet 1992), or additional geographic features, such as marine currents, that can directionally impede or facilitate animal movements, thus affecting their distribution (Elith and Leathwick 2009).

Acknowledgments

Literature Cited

Acha, E. M., H. W. Mianzan, R. A. Guerrero, M. Favero, and J. Bava. 2004. Marine fronts at the continental shelves of Austral South America: Physical and ecological processes. Journal of Marine Systems 44:83–105.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. Journal of Applied Ecology 43:413–423.

Bartumeus, F., L. Giuggioli, M. Louzao, V. Bretagnolle, D. Oro, and S. A. Levin. 2010. Fishery discards impact on seabird movement patterns at regional scales. Current Biology 20:215–222.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: A novel approach using stable isotope analysis. Journal Animal Ecology 73:1007–1012.

Bertrand, S., R. Joo, C. A. Smet, Y. Tremblay, C. Barbraud, and H. Weimerskirch. 2012. Local depletion by a fishery can affect seabird foraging. Journal of Applied Ecology 49:1168–1177.

Boersma, P. D., G. A. Rebstock, E. Frere, and S. E. Moore. 2009. Following the fish: Penguins and productivity in the South Atlantic. Ecological Monographs 79:59–76.

Cama, A., R. Abellana, I. Christel, X. Ferrer, and R. Vieites. 2012. Living on predictability: Modelling the density distribution of efficient foraging seabirds. Ecography 35:912–921.

Carrasco, J. L., C. Sanpera, M. García-Tarrasón, F. Ramírez, K. Skaltsa, and L. Jover. 2010. Distinguishability, isotopic variance and niche width. VII International Conference on Applications of Stable Isotope Techniques to Ecological Studies (IsoEcol), Fairbanks, Alaska, USA, August 9–13.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (delta N-15 and delta C-13): The effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

Crawford, R. J. M. 2007. Food, fishing and seabirds in the Benguela upwelling system. Journal of Ornithology 148:S253–S260.

Drago, M., L. Cardona, A. Aguilar, E. A. Crespo, S. Ameghino, and N. García. 2010. Diet of lactating South American sea lions, as inferred from stable isotopes, influences pup growth. Marine Mammal Science 26:309–323.

Elith, J. and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: Review and synthesis. Marine Ecology Progress Series 391:139–151.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Forero, M. G., J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. 2002a. Conspecific food competition explains variability in colony size: A test in Magellanic penguins. Ecology 83:3466–3475.

Forero, M. G., K. A. Hobson, G. R. Bortolotti, J. A.

Donázar, M. Bertellotti, and G. Blanco. 2002b. Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: Segregation by sex and age and influence on offspring quality. Marine Ecology Progress Series 234:289–299.

Forero, M. G., G. R. Bortolotti, K. A. Hobson, J. A. Donazar, M. Bertelloti, and G. Blanco. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: A multiscale approach. Journal of Animal Ecology 73:789–801.

Frederiksen, M., M. Edwards, A. J. Richardson, N. C. Halliday, and S. Wanless. 2006. From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. Journal of Animal Ecology 75:1259–1268.

Furness, R. W., and C. J. Camphuysen. 1997. Seabirds as monitors of the marine environment. ICES Journal of Marine Science 54:726–737.

Grecian, W. J., M. J. Witt, M. J. Attrill, S. Bearhop, B. J. Godley, D. Grémillet, K. C. Hamer, and S. Votier. 2012. A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern Gannets breeding in the North East Atlantic. Biological Conservation 156:43–52.

Guinet, C. 1992. Comportement de chasse des orques (Orcinus orca) autour des îles Crozet. Canadian Journal of Zoology 70:1656–1667.

Hansen, J. E., P. Martos, and A. Madirolas. 2001. Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, Engraulis anchoita, and sea temperatures during late spring to early summer. Fisheries Oceanography 10:193–206.

Henkel, L. A. 2009. Co-occurrence and aggregation of marine birds and mammals in Monterey Bay, California, USA. Marine Ecology Progress Series 387:295–303.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modelling methods. Ecography 29:773–785.

Hobson, K. A., and L. I. Wassenaar. 2008. Tracking animal migration with stable isotopes. Elsevier, Amsterdam, The Netherlands.

Hunt, G. L., J. Priddle, M. J. Whitehouse, R. R. Veit, and R. B. Heywood. 1992. Changes in seabird species abundance near South Georgia during a period of rapid change in sea-surface temperature. Antarctic Science 4:15–22.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Karnovsky, N. J., K. A. Hobson, and S. J. Iverson. 2012. From lavage to lipids: Estimating diets of seabirds. Marine Ecology Progress Series 451:263–284.

Koen-Alonso, M., and P. Yodzis. 2005. Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. Canadian Journal of Fisheries and Aquatic Sciences 62:1490–1512.

Louzao, M., K. Delord, D. García, A. Boué, and H. Weimerskirch. 2012. Protecting persistent dynamic oceanographic features: Transboundary conservation efforts are needed for the critically endangered Balearic shearwater. PLoS ONE 7:e35728.

Louzao, M., D. Pinaud, C. Perón, K. Delord, T. Wiegand, and H. Weimerskirch. 2011a. Conserving pelagic habitats: Seascape modelling of an oceanic top predator. Journal of Applied Ecology 48:121–131.

Louzao, M., J. Navarro, M. G. Forero, J. M. Igual, M. Genovart, K. A. Hobson, and D. Oro. 2011b. Exploiting the closest productive area: Geographical segregation of foraging grounds in a critically endangered seabird. Marine Ecology Progress Series 429:291–301.

Masello, J. F., R. Mundry, M. Poisbleau, L. Demongin, C. C. Voigt, M. Wikelski, and P. Quillfeldt. 2010. Diving seabirds share foraging space and time within and among species. Ecosphere 1:19.

Monk, J., D. Ierodiaconou, E. Harvey, A. Rattray, and V. L. Versace. 2012. Are we predicting the actual or apparent distribution of temperate marine fishes? PLoS ONE 7:e34558.

Navarro, J., D. Oro, A. Bertolero, M. Genovart, A. Delgado, and M. G. Forero. 2010. Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. Marine Biology 157:2453–2459.

Navarro, J., M. G. Forero, J. González-Solís, J. M. Igual, J. Bécares, and K. A. Hobson. 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. Biology Letters 5:545–548.

Newsome, S. D., C. M. del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and Environment 5:429–436.

Parnell, A., R. Inger, S. Bearhop, and A. L. Jackson. 2008. Stable isotope analysis in R (SIAR). http://cran.r-project.org/web/packages/siar/index.html

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102–107.

Pinaud, D., Y. Cherel, and H. Weimerskirch. 2005. Effect of environmental variability on habitat

selection, diet, provisioning behaviour and chick growth in Yellow-nosed albatrosses. Marine Ecology Progress Series 298:295–304.

Ramos, R., F. Ramírez, J. L. Carrasco, and L. Jover. 2011. Insights into the spatiotemporal component of feeding ecology: An isotopic approach for conservation management sciences. Diversity and Distributions 17:338–349.

Rangel, T. F., J. A. F. Diniz-Filho, and L. M. Bini. 2010. SAM: A comprehensive application for spatial analysis in macroecology. Ecography 33:46–50.

Scolaro, J. A., R. P. Wilson, S. Laurenti, M. Kierspel, H. Gallelli, and J. A. Upton. 1999. Feeding preferences of the Magellanic penguin over its breeding range in Argentina. Waterbirds 22:104–110.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:1197–1207.

Skewgar, E., P. D. Boersma, G. Harris, and G. Caille. 2007. Anchovy fishery threat to Patagonian ecosystem. Science 315:45.

Tella, J. L., M. G. Forero, M. Bertellotti, J. A. Donázar, G. Blanco, and O. Ceballos. 2001. Offspring body condition and immunocompetence are negatively affected by high breeding densities in a colonial seabird: A multiscale approach. Proceedings of the Royal Society B 268:1455–1461.

Villanueva, C., B. G. Walker, and M. Bertellotti. 2012. A matter of history: Effects of tourism on physiology, behaviour and breeding parameters in Magellanic penguins at two colonies in Argentina. Journal of Ornithology 153:219–228.

Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? Deep-Sea Research Part II 54:211–223.

Weimerskirch, H., M. Le Corre, S. Jaquemet, and F. Marsac. 2005. Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. Marine Ecology Progress Series 288:251–261.

Weimerskirch, H., S. A. Shaffer, Y. Tremblay, D. P. Costa, H. Gadenne, A. Kato, Y. Ropert-Coudert, K. Sato, and D. Aurioles. 2009. Species and sex specific differences in foraging behaviour and foraging zones in Blue-footed and Brown boobies in the Gulf of California. Marine Ecology Progress Series 391:267–278.

Wilson, R. P., et al. 2005. How do Magellanic penguins cope with variability in their access to prey? Ecological Monographs 75:379–401.

Yen, P. P. W., W. J. Sydeman, and K. D. Hyrenbach. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation. Journal of Marine Systems 50:79–99.

Yorio, P., F. Quintana, P. Dell'arciprete, and D. González-Zevallos. 2010. Spatial overlap between foraging seabirds and trawl fisheries: Implications for the effectiveness of a marine protected area at Golfo San Jorge, Argentina. Bird Conservation International 20:320–334.

Yorio, P., E. Frere, P. Gandini, and A. Schiavini. 2001. Tourism and recreation at seabird breeding sites in Patagonia, Argentina: Current concerns and future prospects. Bird Conservation International 11:231–245.

Yorio, P., E. Frere, P. Gandini, and G. Harris. 1998. Atlas De La Distribución Reproductiva De Aves Marinas En El Litoral Patagónico Argentino. Fundación Patagonia Natural, Puerto Madryn, Argentina.

Zimmer, I., Y. Ropert-Coudert, N. Poulin, A. Kato, and A. Chiaradia. 2011. Evaluating the relative importance of intrinsic and extrinsic factors on the foraging activity of top predators: A case study on female Little penguins. Marine Biology 158:715–722.