

Seascape modeling of southern giant petrels from Patagonia during different life-cycles

Gabriela S. Blanco¹ · Noela Sánchez-Carnero² · Juan Pablo Pisoni² · Flavio Quintana¹

Received: 30 August 2016 / Accepted: 1 February 2017
© Springer-Verlag Berlin Heidelberg 2017

Abstract Presence-only models such as Ecological Niche Factor Analysis (ENFA) compare distributions of environmental variables and species, generating habitat suitability (HS) maps. Here, we determined the factors affecting distribution of southern giant petrels (SGP) from northern Patagonian colonies (Isla Arce: 45° 00'S; 65°29'W, and Isla Gran Robredo: 45°08'S; 66°03'W) using ENFA, improving estimates of their potential year-round feeding habitats. Data on movements of 17 adult and 9 first-year juvenile SGP were gathered using satellite telemetry. Model ecogeographical variables (EGV) overlapped the tracked animals. The resulting HS maps included most of the tracking locations along the Argentinean Shelf and reflected characteristics that congregate procellariiformes elsewhere. Wind conditions and primary productivity shaped foraging HS of petrels over the year. However, different EGVs influenced this population differently depending on the requirements of their life stage. For example, juveniles showed high marginality (values of EGVs different from the mean values available). Breeding adults' HS was determined by a small range of values within those available, showing high specializations. Contrarily, wintering petrels showed

plasticity in the selection of their foraging environments being distribution of fisheries one of the variables influencing their distribution. This study highlights the importance of the Argentinean Shelf for conservation of the marine environment.

Keywords Seascape modeling · Ecological Niche Factor Analysis (ENFA) · Southern Giant Petrel · Argentinean Shelf

Introduction

The spatial distribution of threatened species and associated habitat suitability are key information in any management program of the marine environment (Catry et al. 2013; Monk et al. 2010). Habitat suitability models predict distribution beyond direct observations and may detect hotspots for conservation and spatial patterns within protected areas, helping to identify wildlife corridors, or forecasting how the distribution of a species might vary in response to environmental changes (Monk et al. 2011; Oppedal et al. 2012). Lately, habitat modeling has been used not only to predict current species' distribution but also to predict future and estimate past distributions (Brambilla and Saporetto 2014; Elith and Leathwick 2009; Legendre et al. 2016).

Ecological Niche Factor Analysis (ENFA) is a statistical method which identifies the environmental characteristics to which a species is best adapted (Hirzel et al. 2002). The ecological niche of a species is described by all of the characteristics of the geographical area (physical, chemical, and biological) that are suitable for the development and survival of the species (Hutchinson 1957; MacArthur 1972). The geographical distribution of these characteristics will

Responsible Editor: V. H. Paiva.

Reviewed by Lucas Krüger and Virginia Pujol.

✉ Gabriela S. Blanco
gblanco@cenpat-conicet.gob.ar

¹ Instituto de Biología de Organismos Marinos (IBIOMAR-CCT CONICET-CENPAT), Boulevard Brown 2915, Puerto Madryn, Argentina

² Centro para el Estudio de Sistemas Marinos (CESIMAR-CCT CONICET-CENPAT), Boulevard Brown 2915, Puerto Madryn, Argentina

be related to the geographical distribution of individuals of that species (Phillips et al. 2006b).

In particular, ENFA compares the distributions of environmental variables and species, defining parameters with an ecological meaning such as: (1) Marginality, which measures the distance between the global mean and the species distribution mean for a given variable (the higher the value of marginality the more the species departs from the average conditions within the study area); and (2) Specialization, which determines the width of a species niche by comparing the range of values the species selects from the range of values present in the area (the smaller the range of feature values the species selects from the range of values present in the area, the more specialized the species is (Sanchez-Carnero et al. 2016)). Given the marginality and specialization, ENFA generates habitat suitability maps that denote the level of *comfort* of the species in a cell of the study area in relation to the rest of it, which can be interpreted as a likelihood of encountering the species in each of those cells. These maps show the areas that contain suitable habitats based on the ecological requirements identified by ENFA (Bryan and Metaxas 2007; Monk et al. 2010; Skov et al. 2008). ENFA has been applied successfully in several studies showing that ecological niche analysis combined with tracking data provides suitable predictions of distribution patterns and feeding habitats for marine species (Skov et al. 2008).

Knowledge on animal movement has increased rapidly with the use of advanced technologies; satellite-linked data has represented a breakthrough in the field of spatial ecology. These data, together with the development of integrative systems such as Geographic Information Systems (GIS) for analyzing tracking data, allow for the possibility of linking biological and physical information to facilitate understanding the ecological requirements of wide-ranging species. For example, it has been demonstrated that highly migrant pelagic birds search for food in specific areas such as high productive shelf break waters (Croxall and Wood 2002; Gutowsky et al. 2014), rich productive upwelling waters (Péron et al. 2010), and oceanic fronts (i.e., Sub-tropical Front, Sub Antarctic Front, etc.) (Bost et al. 2009; Hyrenbach et al. 2002). Yet, several satellite telemetry studies have a limited sample size associated to the high cost of devices and/or the complexity of capturing the animals for their instrumentation. Presence-only models such as ENFA deal with constraints related to this type of data, and are designed to perform well even with small occurrence data sets (Monk et al. 2010).

The Southern Giant Petrel (SGP, *Macronectes giganteus*) is a procellariiform restricted to the Southern Ocean (Hunter 1984). Its breeding colonies are distributed among oceanic islands between 40°S and 60°S (ACAP 2011). In Patagonia Argentina, SGP breed at four colonies, two

of which are located in northern Patagonia separated by 47 km: Isla Arce and Isla Gran Robredo (Quintana et al. 2006). These colonies are characterized by temperate waters, in contrast to the rest of the colonies found in colder Antarctic and Sub-Antarctic waters (Patterson et al. 2008). SGP are central place foragers while breeding, exploiting environments near the colony with high availability of resources such as carrion from penguins and sea lions. Nonetheless, they also carry out longer foraging trips to the Argentinean Continental Shelf (Copello et al. 2011; Quintana et al. 2010).

During the non-breeding period, adult SGP from northern Patagonia feed on waters along the Argentinean Shelf and the shelf break, while first-year juveniles migrate to distant locations exploring environments with high chlorophyll a concentration associated to frontal waters (Blanco et al. 2015). As it has been shown, SGP from northern Patagonian colonies make use of areas with distinctive characteristics depending on the time of the year and on the age class. Identifying these sources of variation requires not only understanding major biological processes but also linking the species performance to the habitat characteristics (Gaillard et al. 2010). Thus, recognizing the processes that govern habitat use in different populations is particularly important.

At-sea distribution of the SGP from Isla Arce and Gran Robredo has been studied through the instrumentation of a limited number of individuals (Blanco et al. 2015). Based on previous knowledge we hypothesize that suitable habitats of SGP through their life cycle may be strongly influenced by environmental factors such as high productivity and distribution of carrion and fisheries. Moreover, we estimate that the habitat suitability index resulting from ENFA (during the breeding and non-breeding seasons and for different age classes) may indicate that high use areas would be similar to the ones previously described by the tracking of a small number of individuals. Here we intend to determine the factors that may affect the at-sea distribution of birds from these two northern Patagonian colonies using ENFA. We also expect to improve the estimates of potential at-sea distribution and feeding habitats of the SGP through the generation of habitat suitability maps.

Materials and methods

Tracking data

Data on the at-sea movements of SGP from Isla Arce and Gran Robredo were obtained through the instrumentation of 17 adults and 9 first year juveniles. Animals were deployed with satellite transmitters (PTTs-100, “Platform Terminal Transmitters”, Microwave

Telemetry, Columbia, MD, USA) during the breeding (11 adults) and non-breeding period (6 adults, 9 juveniles) from 1999 to 2013 (Table 1). Satellite transmitters were attached using Tesa tape to the mid-dorsal mantle feathers following Wilson et al. (1997) adapted in Quintana et al. (2010). Argos satellite data was filtered using *Argosfilter* 0.62 Package for the R software package (R Development Core Team 2015). Tracking data was then hourly resampled using the *adehabitat* package for R with *redistraj* function (Calenge 2006) to ensure that individual variation in daily transmission did not influence the analysis. Different at-sea stages were discriminated using the flying speed and turning angle (Awkerman et al. 2005). The normalized cumulative frequencies of flying speeds (resolution of 1 km h⁻¹) and turning angle (1° resolution) were calculated and two categories (residence and displacement) were depicted, where lower flying speeds and higher turning angles were indicative of residence behavior (for details see Blanco et al. 2015).

Only locations indicating residence behavior (as a proxy of foraging behavior) were included in this article.

Study area

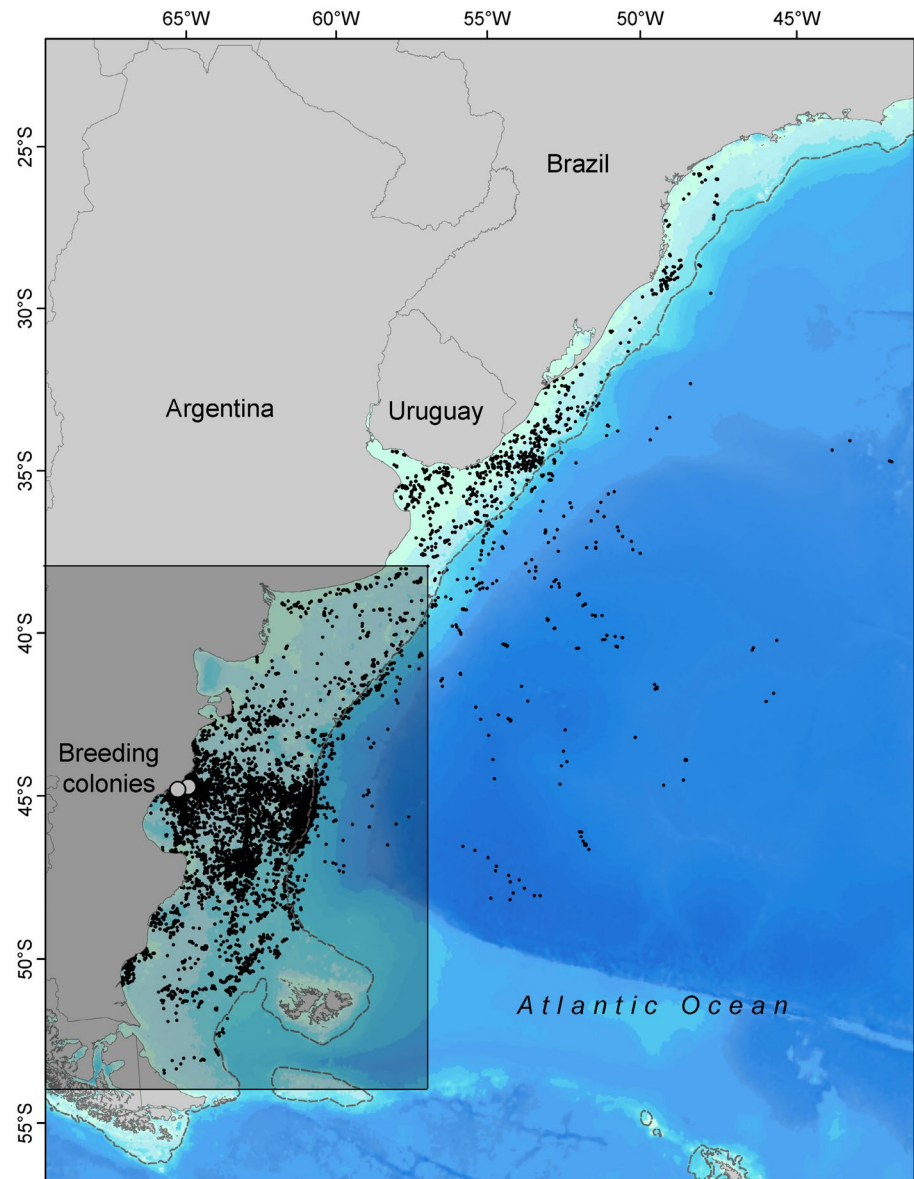
Giant petrels were instrumented on Isla Arce (45° 00'S; 65°29'W) and Isla Gran Robredo (45°08'S; 66°03'W) in Patagonia, Argentina. These two colonies host 80% of the Argentinean SGP population and represent the species' northernmost breeding colonies (Copello and Quintana 2009a; Quintana et al. 2005). The at-sea extension of the study area was determined by extrapolating the maximum distance from the colony recorded during the tracking period (for adults and juveniles) across all directions in space (see Blanco and Quintana 2014). Thus, for adults, we selected the area comprised between 38°S and 54°S and from the coast to 57°W. Similarly, the study area for juveniles ranged from 25°S to 55°S and from the coast to 40°W (Fig. 1).

Table 1 Southern giant petrels (*Macronectes giganteus*) instrumented with satellite transmitters included in the analysis

Individual	Sex	Colony	Breedingseason	Age	Stage	Start tracking	End tracking	Total tracking (days)	Days at sea post-fledging
5609	M	G. Robredo	1998	Adult	Breeding	9-Jan-99	31-Jan-99	22	–
5819	F	G. Robredo	1998	Adult	Breeding	9-Jan-99	22-Feb-99	44	–
25135	F	G. Robredo	1999	Adult	Breeding	26-Nov-99	23-Jan-00	58	–
25138	M	G. Robredo	1999	Adult	Breeding	27-Nov-99	20-Jan-00	54	–
10100	M	Arce	2001	Adult	Breeding	3-Jan-02	22-Feb-02	50	–
10102	M	Arce	2001	Adult	Breeding	3-Jan-02	28-Feb-02	56	–
10101	F	Arce	2001	Adult	Breeding	4-Jan-02	24-Feb-02	51	–
10103	M	Arce	2001	Adult	Breeding	4-Jan-02	14-Jan-02	10	–
56509	M	Arce	2004	Juvenile	Non-breeding	21-Apr-05	12-May-05	21	17
56505	F	Arce	2004	Juvenile	Non-breeding	21-Apr-05	6-Aug-05	107	105
56506	M	G. Robredo	2004	Adult	Non-breeding	22-Apr-05	8-Aug-05	108	–
56507	M	G. Robredo	2004	Adult	Non-breeding	22-Apr-05	20-Sep-05	151	–
56508	M	G. Robredo	2004	Adult	Non-breeding	22-Apr-05	8-Jul-05	77	–
44281	F	G. Robredo	2005	Adult	Non-breeding	24-Apr-06	23-Aug-06	121	–
56505	F	G. Robredo	2005	Adult	Non-breeding	24-Apr-06	5-Aug-06	103	–
39791	F	G. Robredo	2005	Adult	Non-breeding	24-Apr-06	31-Jul-06	98	–
39792	M	G. Robredo	2005	Juvenile	Non-breeding	24-Apr-06	13-Jul-06	80	79
44282	F	G. Robredo	2005	Juvenile	Non-breeding	24-Apr-06	25-May-06	31	29
56507	F	G. Robredo	2006	Juvenile	Non-breeding	17-Apr-07	18-May-07	31	26
56509	M	G. Robredo	2006	Juvenile	Non-breeding	17-Apr-07	18-Jul-07	92	83
56508	M	G. Robredo	2006	Juvenile	Non-breeding	17-Apr-07	22-Jun-07	66	61
79964	F	Arce	2007	Juvenile	Non-breeding	15-Apr-08	12-Jul-08	88	79
79965	M	Arce	2007	Juvenile	Non-breeding	15-Apr-08	1-Jun-08	47	45
105589	F	Arce	2012	Adult	Breeding	5-Jan-13	23-Apr-13	108	–
105590	F	Arce	2012	Adult	Breeding	5-Jan-13	2-Apr-13	87	–
105591	F	Arce	2012	Adult	Breeding	5-Jan-13	22-Feb-13	48	–

Days at sea post-fledging indicate number of days with location information after juveniles left the colony (from Quintana et al. 2010; Blanco and Quintana 2014)

Fig. 1 Tracking locations of 28 southern giant petrels (*Macronectes giganteus*) (17 adults and 9 juveniles) from Quintana et al. (2010) and Blanco and Quintana (2014). Extension of the study area was determined based on the maximum distance from the colony recorded (for adults and first year juveniles). Study area for juveniles ranged from 25°S to 55°S and from the coast to 40°W, shaded section indicates study area of adults



Eco-geographical variables (EGV)

Model eco-geographical variables comprised geographic, biological, and oceanographic parameters. All these variables were calculated to overlap at a spatial and temporal scale with the tracked animals (Table 2). All these variables were mapped with a spatial resolution of 4 km.

Geographic variables

Euclidean distance to the coast (km) and Euclidean distance to the colony (km) were calculated. To obtain depth gradients (m km^{-1}) we used bathymetry from the GEBCO data base (General Bathymetry Chart of the Oceans, <http://www.gebcos.org>), and then calculated the gradient for each

grid point. These variables were calculated using *Spatial Analyst tools* for ArcGis 9.3.

Biological variables

During the breeding period, SGP alternate foraging trips scavenging on Magellanic penguins (*Spheniscus magellanicus*) and South American sea lions (*Otaria flavescens*) carcasses within coastal areas, with long pelagic trips foraging mainly on squid (*Illex argentinus*) and fisheries discards (Copello and Quintana 2009b; Copello et al. 2008; Quintana et al. 2010). Therefore, we gathered information on distribution of penguin colonies (Falabella et al. 2009) and Sea Lion rookeries (Crespo et al. 2012; Thompson et al. 2005) along the coast of the study area, generated maps, and calculated the distance (km) from the closest

Table 2 Eco-geographical variables included in the analysis

	Breeding adults	Non-breeding adults	First year juveniles
Geographic	Distance to coast	Distance to coast	Distance to coast
	Distance to colony	Distance to colony	Distance to colony
	Depth gradient	Depth gradient	Depth gradient
Biological	Distance to penguin colonies	Squid distribution (Apr–Aug)	Squid distribution (Apr–Aug)
	Distance to sea lion rookeries		
	Squid distribution (Oct–Mar)		
Distribution of Fisheries	Trawlers	Trawlers	Trawlers
	Longliners	Longliners	Longliners
	Jiggers	Jiggers	Jiggers
Oceanographic	SST (Dec–Mar)	SST (Apr–Aug)	SST (Apr–Aug)
	SST gradient (Dec–Mar)	SST gradient (Apr–Aug)	SST gradient (Apr–Aug)
	Chl-a (Dec–Mar)	Chl-a (Apr–Aug)	Chl-a (Apr–Aug)
	Chl-a gradient (Dec–Mar)	Chl-a gradient (Apr–Aug)	Chl-a gradient (Apr–Aug)
	Wind speed (Dec–Mar)	Wind speed (Apr–Aug)	Wind speed (Apr–Aug)
	Wind direction (Dec–Mar)	Wind direction (Apr–Aug)	Wind direction (Apr–Aug)

All variables overlap at a spatial and temporal scale with Southern Giant Petrel (*Macronectes giganteus*) distribution. All variables were included in the analysis at a spatial resolution of 4 km

penguins and sea lions colony to the center each cell of the study area. Maps of squid stocks were created using records of abundance and distribution from Brunetti et al. (1998), Sacau et al. (2005), Chen et al. (2007), and Perez et al. (2009), adapting summer and fall/winter distribution of squid stocks. Distribution of fisheries operating along the study area were estimated from published literature; thus utilization maps were generated for trawlers (Copello and Quintana 2009b; Copello et al. 2014; Favero et al. 2011; Pezzuto et al. 2006; Seco Pon et al. 2013), jiggers (Copello and Quintana 2009b; Cozzolino 2014; Falabella et al. 2009), and longliners (Bugoni et al. 2009, 2011; Favero et al. 2013; Fossette et al. 2014; Gómez-Laich et al. 2006; Jiménez et al. 2009) along the study area.

Oceanographic variables

Sea surface temperature (SST, °C) data were obtained from MODIS/Aqua sensor (Physical Oceanography DAAC, <http://podaac.jpl.nasa.gov/>) for the period 2003 to 2013 (spatial resolution of 4 km) at monthly resolution. These monthly means were then averaged on each period (Breeding: Dec–Mar; Non-breeding: Apr–Aug, see Table 2). SST gradients (°C km⁻¹) were detected computing the SST derivatives using a centered difference scheme after smoothing with a Gaussian filter (Nixon and Aguado 2008). Chlorophyll a concentration (Chl-a) (mg m⁻³) monthly resolution images (2003–2013) at a spatial resolution of 4 km were obtained from <http://giovanni.gsfc.nasa.gov/>. Averages were calculated for each study period. To obtain the gradient of Chl-a, images were also smoothed,

and centered differences calculated as before (Nixon and Aguado 2008). Wind images (2003–2013, u and v monthly composites) were downloaded from <ftp://podaac.jpl.nasa.gov/OceanWinds/ccmp/L3.5a/monthly> at a spatial resolution of 25 km. Monthly means were averaged to obtain wind speed (m s⁻¹) and direction during each study period. Wind fields were linearly interpolated to resample data at 4 km.

All EGVs (geographic, biological and oceanographic EGVs) were normalized, linearly transforming them to zero-mean and unit-variance, before entering the analysis.

Statistical model: Ecological Niche Factor Analysis (ENFA)

The idea behind ENFA is to compare the global distribution of some relevant eco-geographical variables (EGV) in a given area with their distribution in locations where individuals of the target species have been spotted (Calenge and Basille 2008; Hirzel et al. 2002).

These EGV (e.g., depth, SST, Chl-a), that have known (or interpolated) values at all points in the study area, are interpreted as the coordinates of those geographical points in some abstract multidimensional space; a subset of those points corresponds to actual observations of individuals. ENFA is a factorial analysis that first computes the difference between the centers of mass of the observations subset and the entire area, what is called the species marginality. Afterwards, it finds a new set of axes defined in that abstract space, perpendicular to the marginality axis, and along which the variance of habitat coordinates becomes

maximal with respect to the variance of coordinates of observation points; this defines the specialization eigenvalues (the ratios) and axes. The new set of variables defined by these axes are linear combinations of the original EGVs, but concentrate the relevant information related to species distribution in the area. The weights of the old EGVs on each of the new coordinates ponders the importance of that EGV on the specialization of the species; irrelevant EGVs will have small weights along all specialization axes.

In particular, global marginality of a species (a numerical value) is computed as the length of the marginality vector, whose components are the differences between averages of the EGV at the positions of observed individuals and the mean values of those EGV on the study area. Global specialization is calculated as the square root of the sum of the principal ENFA eigenvalues; we have kept as many eigenvalues as axes in the Principal Component Analysis explaining 90% of the total EGV variability (specialization 1, 2, and 3, see Table 3). Regarding marginality and specialization mathematical computation, we can interpret that a species will be highly marginal when its marginality value is larger than 1.96 [to find the center of a species ecological niche at the center of the whole EGV, space will be less than 5% probable for every variable (Hirzel et al. 2002)]. A species will be specialized when its specialization value is higher than 1 (a specialization value about 1 means that the species can choose any of the EGV values in the study area).

The Habitat Suitability Index (HSI) stands for a distance from the environmental conditions at a given point to the optimal environmental conditions chosen by a given species. Here, we defined the HSI of a cell as the probability of finding a less suitable point than that cell in the entire study area (Sanchez-Carnero et al. 2016). We used the Mahalanobis distance along the marginality and specialization axes to assign to each cell in the study area the distance of the EGV to the species mean EGV values selected (Calenge and Basille 2008). Then these distances were ranked from smaller to larger and the ranks computed, so that each cell was given an HIS computed as the fraction of cells in the study area less suitable to the species than the cell itself based on the EGVs (Sanchez-Carnero et al. 2016).

To assess the accordance between an HSI map and the actual capture records we used Boyce index (BI) (Bryan and Metaxas 2007; Galparsoro et al. 2009), defining the

weighted Spearman rank correlation between HSI and the observed individuals per interval of HSI values over the HSI histogram to obtain a continuous BI (Sanchez-Carnero et al. 2016). Given that BI criterion is not related to ENFA hypotheses or mathematical model, the Boyce index plays the role of an independent quality assessment of the ENFA derived HSI map.

All analyses were performed using the Package *ade-habitat* (Calenge 2006) for R statistical software (R Core Team 2015) and costume-made scripts implementing algorithms described above to compute HSI and Boyce index and automating the processing of data. Analysis was performed based on the three stages of the animal's life cycle, considering the differential use of the study area during different periods and age classes (Blanco and Quintana 2014; Quintana et al. 2010): (1) breeding adults, (2) non-breeding adults, and (3) first-year juveniles.

In addition, the HSI obtained for non-breeding adults was introduced as a new EGV in the first-year juvenile stage, to assess the influence of adult's presence on juvenile's use of the area (see Blanco and Quintana 2014).

Results

Breeding adults

Application of ENFA to the at-sea distribution of foraging adults from northern Patagonian colonies depicted a high marginality component (8.42) which meant that, in general terms, adult birds preferred to forage in areas in which EGV values differed from those more frequent in the study area. Moreover, breeding SGPs showed a very small tolerance to variations in the foraging environment, as shown by the high values of specialization (9.43 to 27.09, Table 3). The HSI map obtained for adult breeders was highly accurate (BI=0.923, see Table 3).

Foraging suitable habitats (HSI>0.8) appeared in areas close to the coast, specifically at central Chubut and along Santa Cruz Province. This was not the case for the coast of the San Jorge Gulf, where HSI values ranged from 0 to 0.5. In addition, breeding adults found suitable areas in only a section of the study area (Fig. 2a). Interestingly, pixel values greater than 0.8 were also spread continuously along the 200 m isobath, indicating that the shelf break is among

Table 3 Marginality and specialization values for the three study cases

	Marginality	Specialization 1	Specialization 2	Specialization 3	Boyce index
Breeding adults	8.42	27.09	10.26	9.43	0.923
Non-breeding adults	1.74	9.1	6.63	4.74	0.927
First-year juveniles	13.321	15.92	7.26	3.75	0.971

Boyce index indicates the accuracy of the HSI for each group

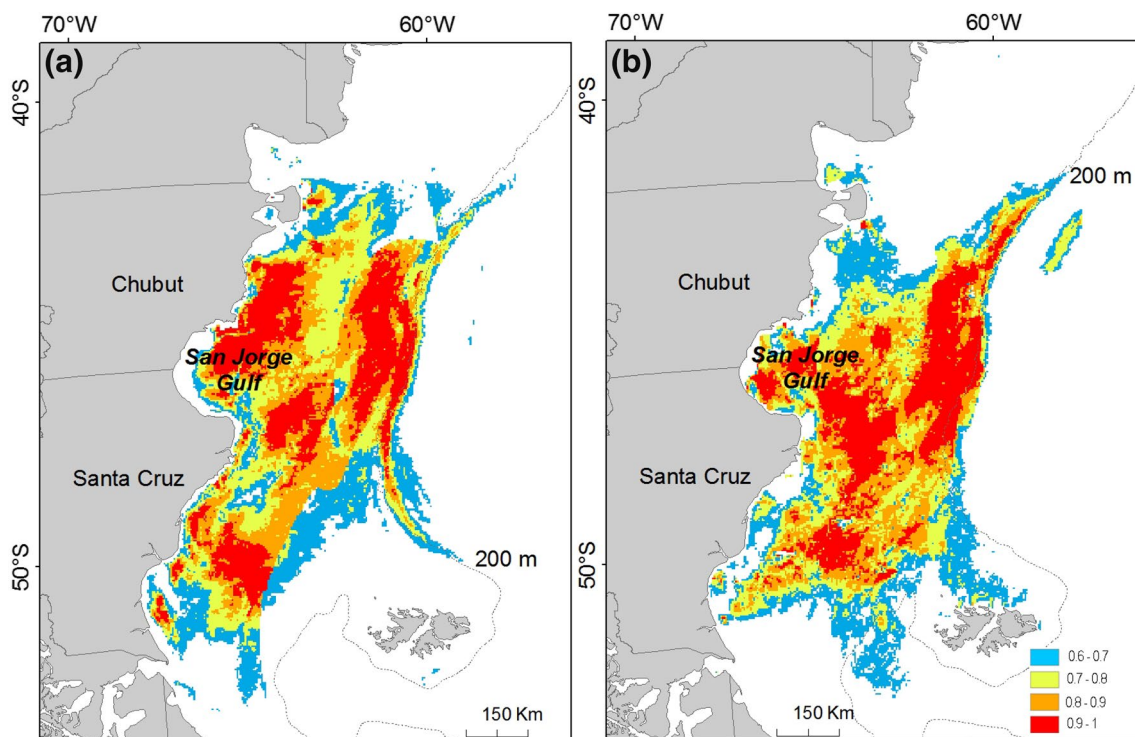


Fig. 2 Habitat Suitability Index (HSI) of southern giant petrels (*Macronectes giganteus*) obtained from ENFA for **a** adults during the breeding period (Nov–Feb) and **b** adults during the non-breeding period (Mar–Sept). The map shows HSI > 0.6

the most suitable environment for this group. The variables “distance to the coast” and distance to the colony, which was demonstrated by those variables large components along both marginality and specialization axes (Table 4), influenced habitat suitability areas of breeding adults. Moreover, this group showed strong consistency regarding variations in EGVs such as distances to penguin colonies and sea lion rookeries, as indicated by the high values of contribution to the overall marginality and specialization for these EGVs.

Regarding oceanographic variables, despite the fact that breeding SGP were shown to group in areas of high Chl-a concentration, this was not a strong requirement for them. On the contrary, breeding adults found suitable habitats within values different from the average temperature in the study area (i.e., they showed sensibility to SST). Finally, direction of wind was an important component of the specialization, indicating that breeding SGPs are very sensitive to that variable (see Table 4).

Non-breeding adults

In general, non-breeding SGP foraged in areas whose overall characteristics were closer to the average of the study area (marginality = 1.74). Habitat suitability of SGP during winter was determined by a specific range

of values from the ones available in the study area, as determined by the high specialization value (Table 3). Boyce index of 0.93 indicated the high accuracy of the HSI obtained for this stage of their life cycle (Table 3). Highly suitable habitats for foraging SGPs during winter (HSI > 0.8) were found in the middle continental shelf from 44°S to 51°S and along the shelf break (Fig. 2b). Noticeably, coastal areas were not suitable for non-breeding adults, showing HSI values lower than 0.6.

The habitat suitability seemed to be driven in part by distance to the SGP colony (marginality component -0.75) and within a narrow range (specialization component -0.28). As suggested by the high marginality values associated to the distribution of fisheries, an important proportion of the habitat suitability was explained by the areas where trawlers and jiggers commonly operate. In addition, EGV denoting primary productivity as Chl-a concentration and its gradient contributed largely to the overall marginality value for non-breeding SGPs (Table 4). In addition, foraging environments of this population were highly influenced by specific ranges of oceanographic EGVs, being determined by specific wind directions and wind speeds, in addition to high values of Chl-a concentration (those EGVs explained most of the specialization for this group, see Table 4).

Table 4 Summary of the ENFA axes for the Southern Giant Petrel (*Macronectes giganteus*) on three different stages of their life cycle

EGVs	Breeding adults			Non-breeding adults			Juveniles					
	Marginality	Spec 1	Spec 2	Spec 3	Marginality	Spec 1	Spec 2	Spec 3	Marginality	Spec 1	Spec 2	Spec 3
Geographical												
Distance to coast	-0.252	0.341	-0.092	0.299	0.006	-0.095	-0.182	-0.020	-0.316	0.487	-0.684	-0.346
Distance to the colony	-0.539	-0.273	0.197	0.183	-0.752	-0.163	-0.276	0.032	-0.285	-0.441	0.242	0.226
Depth gradient	0.083	-0.070	0.012	0.039	-0.160	0.011	-0.028	0.003	-0.164	-0.016	0.035	-0.035
Distance to penguin colonies	-0.425	-0.448	-0.105	-0.151	-	-	-	-	-	-	-	-
Distance to sea lion rookeries	-0.341	0.103	0.067	0.007	-	-	-	-	-	-	-	-
Squid distribution (Oct–Mar)	0.161	-0.029	-0.068	0.195	-	-	-	-	-	-	-	-
Squid distribution (Apr–Aug)	-	-	-	-	0.120	-0.040	0.102	-0.033	-0.347	0.089	-0.084	-0.089
Non-breeding adults (HST)	-	-	-	-	-	-	-	-	-0.310	0.013	-0.023	0.085
Trawlers	-0.167	0.082	-0.002	0.040	-0.201	-0.015	-0.009	0.072	-0.420	-0.058	-0.009	0.011
Longliners	0.059	-0.022	0.018	-0.028	-0.134	0.008	-0.114	0.009	-0.098	-0.058	-0.009	0.011
Jiggers	0.065	-0.005	0.007	0.048	-0.286	0.016	0.046	0.051	-0.263	-0.044	-0.005	-0.353
Chl-a (Apr–Aug)	-	-	-	-	0.335	-0.326	-0.231	0.006	0.402	-0.022	-0.400	-0.076
Chl-a (Dec–Mar)	0.251	-0.172	0.095	-0.028	-	-	-	-	-	-	-	-
Chl-a gradient (Apr–Aug)	-	-	-	-	0.282	-0.042	-0.003	0.016	0.346	-0.111	-0.144	0.015
Chl-a gradient (Dec–Mar)	0.262	-0.030	0.000	-0.006	-	-	-	-	-	-	-	-
SST (Apr–Aug)	-	-	-	-	0.179	-0.051	-0.620	-0.189	0.017	0.646	-0.476	0.495
SST (Dec–Mar)	0.165	-0.734	0.227	0.080	-	-	-	-	-	-	-	-
SST gradient (Apr–Aug)	-	-	-	-	0.026	0.004	-0.088	-0.036	0.078	-0.016	-0.076	-0.044
SST gradient (Dec–Mar)	0.274	-0.031	-0.044	0.040	-	-	-	-	-	-	-	-
Wind intensity E–W (Apr–Aug)	-	-	-	-	-0.031	-0.186	-0.563	0.668	-0.006	-0.164	-0.018	-0.005
Wind intensity E–W (Dec–Mar)	0.079	-0.115	0.670	0.642	-	-	-	-	-	-	-	-
Wind intensity N–S (Apr–Aug)	-	-	-	-	-0.115	0.624	0.252	-0.669	0.017	-0.005	0.054	0.016
Wind intensity N–S (Dec–Mar)	0.036	-0.041	-0.646	-0.593	-	-	-	-	-	-	-	-
Wind speed (Apr–Aug)	-	-	-	-	-0.128	-0.653	0.194	-0.243	-0.179	-0.309	-0.219	0.657
Wind speed (Dec–Mar)	-0.197	-0.003	0.050	-0.192	-	-	-	-	-	-	-	-

Higher weights of the old EGVs on each of the new coordinates (including three specialization axes) were highlighted to indicate influence of the variable on the marginality or specialization

First-year juveniles

Foraging areas of juvenile SGP were determined by values of EGVs particularly different from the mean EGVs values of the study area. This last group was the most marginal of all study cases (13.3). In addition, suitable habitats for this age class comprised a small range of features present in the study area as demonstrated by the high specialization coefficient (15.9, Table 3). As for the previous stages, BI=0.97 demonstrated the accuracy of the analysis. Juveniles' suitable areas were spread along almost the entire extension of the continental shelf (from 25°S to 50°S), expanding also to the east of the shelf break (Fig. 3).

During their first year at sea, suitable areas of juveniles were highly related to the presence of fisheries (trawlers and jiggers) and squid, where high productivity on nearby coastal areas had also influenced suitable areas (Table 4). Noticeably, suitable habitat of wintering SGP had an influence in the habitat suitability of foraging juveniles (Marginality: -0.310), suggesting that this last group selected areas where adults' HSI was lower than 0.5 (see Fig. 3).

This age class showed a high degree of specialization for geographical (distance to the coast and to the SGP colony)

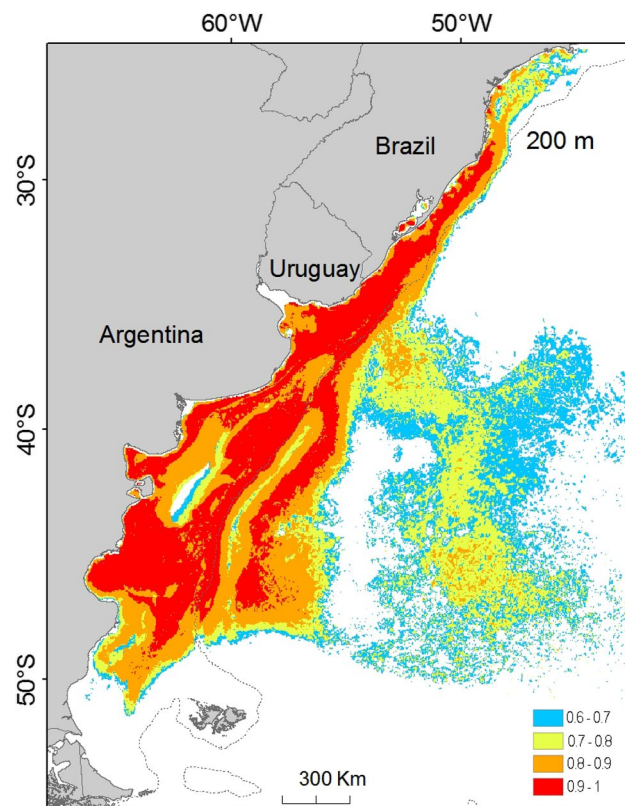


Fig. 3 Habitat Suitability Index (HSI) of the Southern Giant Petrel (*Macronectes giganteus*) obtained from ENFA for juveniles during their first months at-sea. The map shows HSI > 0.6

and oceanographic variables. Habitat suitability was determined by specific ranges of wind speed and SST values as these four variables contributed the most to the overall specialization (see Table 4). It is also worth noticing how values of HSI decreased south of 50°S, probably due to a decrease in SST.

Discussion

This study analyzed the habitat suitability of southern giant petrels from northern Patagonian colonies using presence-only ENFA models. This study overcomes limitations arising out of density analysis [where prediction of potential key habitats is not possible (Louzao et al. 2011)], by understanding the choices of resources that are unequally used when they are equally available. ENFA provided expected results of potential foraging grounds for this population, consistent with the ones described by a limited number of individuals (Blanco and Quintana 2014; Quintana et al. 2010). The HS maps included a high proportion of the foraging locations and represented a set of environmental characteristics (e.g., high primary productivity, strong wind conditions, fisheries distribution, etc.) which have been described to congregate procellariiformes elsewhere (Croxall and Wood 2002; Davies et al. 2010; Gutowsky et al. 2014; Phillips et al. 2006a). Furthermore, juvenile's habitat suitability area was also described to be a highly productive area where several species of other marine vertebrates such as sea turtles, albatrosses, and otariids gather (González Carman et al. 2016).

HSI for breeding petrels from northern Patagonian colonies indicated that suitable environments (>0.6) are found in coastal areas (probably related to the presence of carrion); for wintering adults, however, those areas were shown to be not suitable. The northern limit for both breeding and wintering period was approximately at 42°S; although, combination of EGVs depicted a smaller HS for wintering petrels. This is probably due to the absence of sexual segregation in foraging behavior during that period (Blanco and Quintana 2014; González-Solís et al. 2007a, b). This species is known to have sexual segregation (Forero et al. 2005; Thiers et al. 2014), where breeding males explore coastal areas foraging on carrion, and females exploit mostly pelagic environments (González-Solís et al. 2007; Quintana et al. 2010). During winter, carrion is not available, therefore males switch to also forage in oceanic environments (Blanco and Quintana 2014).

All these findings also illustrate the effective performance of our model. Previous studies suggested that some models failed to predict areas where individuals are observed due to the lack of fundamental variables included in the models (Doniol-Valcroze et al. 2012). We believe that

the high performance of ENFA in this study was in part due to the large number of EGVs included in the analysis.

Role of geographical and biological EGVs

The geographical variables (i.e., distance to the coast and to the SGP colony) showed a strong influence on the habitat suitability of adults SGP (large projections along the marginality and specialization axes). During the breeding period, individuals are constrained to the colony to deliver food to their chicks. In addition, this population in particular, remains in the vicinities of the breeding grounds all year round, visiting the colony periodically also during winter alternating foraging trips (approximately 12 days) with 3 days of permanence at the colony (Blanco and Quintana 2014). During their commutes, breeding SGP obtain their food from carrion of penguins and sea lions (Copello et al. 2008; González-Solís et al. 2000) and occasionally prey upon on live penguins. These EGVs were included in the analysis for breeding adults, and as expected, showed high values of marginality and specialization.

ENFA suggested that the potential at-sea distribution of foraging juveniles was also driven by the distance to the coast. Their initial flight may be influenced by adults' movements as indicated by Blanco and Quintana (2014), but after that, as specified by the high marginality value of the EGV HSI of non-breeding adults, juveniles elude areas where HSI of adults is higher than 0.5. To avoid competition with adults, particularly in this species where adults are present near the colony, juveniles move rapidly to different environments (de Grissac et al. 2016). This concurs what was proposed by Blanco and Quintana (2014) suggesting that dispersion of juveniles to more distant areas is caused in part to avoid competition with adults. Moreover, squid distribution seems to be an important factor influencing foraging behavior of these inexperienced birds, which may be indicative of the strategy to avoid competition, since juveniles must disperse to different locations to find prey (Åkesson and Weimerskirch 2014).

Interestingly, the EGV depth gradient was also included in the analysis, being the shelf break the steeper area. In contrast to the proposed for wandering albatrosses by Louzao et al. (2011), the variable depth gradient had no detrimental effect on petrels' foraging areas, nor did it have a strong influence on their habitat suitability.

Role of fisheries distribution

Distribution of fisheries (in particular trawlers and jiggers), may be significantly influencing the habitat suitability of wintering SGP. Considering that the carrion is not available during winter, SGP must obtain their food from other sources. As indicated by the high marginality values,

SGP shift their summer foraging behavior and probably obtain most of their food from interaction with fisheries. Seabird-fisheries interactions have been broadly described within the study area (González-Zevallos and Yorio 2006; González-Zevallos et al. 2007; Yorio et al. 2010). Recently, Krüger et al. (2016) described SGP from southern colonies foraging from jiggers operating along the Argentinean Shelf. There are some indications that during summer, seabird-fisheries interactions decrease significantly, which is attributed to lower bird abundance (Favero et al. 2011). Even though our analysis does not give enough evidence of what the animals are eating, it could be the case that SGP forage mainly from fishery discards during the post-breeding period, while during summer, more food from carrion is available in areas nearby the breeding grounds. It is important to consider that previous studies indicated that there is a high (> 64%) rate of marine debris ingestion, showing evidence that these anthropogenic items come from fisheries activities (Copello et al. 2008). More research needs to be done to reach further conclusions on this topic. In addition, several variables should be considered, such as the volume of discards, seasonal operation of fleets, etc.

The short-finned squid (*Illex argentinus*) is widely spread in neritic environments off Brazil, Uruguay and Argentina (Arkhipkin et al. 2015). Squid is one of the main prey items for Patagonian SGP (Copello et al. 2008) and also the target of jigging fisheries operating off Argentina (Arkhipkin et al. 2015). Considering that SGP are not diving birds and *I. argentinus* are attracted to the surface by the lights of this fishing fleet, we believe that, as suggested for adults (Copello and Quintana 2009b; Krüger et al. 2016), first year juveniles may be actively interacting with these fisheries, which could be an important part of their food sources. Furthermore, interaction between giant petrels and trawl and longline fisheries along the Brazilian, Uruguayan and Argentinean shelves have been previously described (Bugoni et al. 2011; Favero et al. 2011; Yeh et al. 2013).

Role of oceanographic EGVs

High primary productivity indicated by high concentrations of Chl-a and thermal fronts (SST gradients) appear to be one of the characteristics shaping foraging habitat suitability of petrels along the year. Seabirds rely extensively on frontal systems predictable in time and space (Åkesson and Weimerskirch 2014; Gutowsky et al. 2014), although special attention is needed because in some cases, the relation between primary productivity and prey availability in frontal areas is not yet well understood (Bost et al. 2009). Moreover, González Carman et al. (2016) modelled HS for different marine species (sea turtles, albatrosses, and otariids) and indicated that frontal areas had lower significance than

expected. Therefore, although our model points towards a relationship between the SGP and high Chl-a concentration, SST, and SST gradients, caution must be taken when drawing conclusions.

Wind conditions at the study area were also included in the model as a variable that may influence the foraging areas of this population. Animals in general alter their behavior to save energy, minimizing movement costs (Shepard et al. 2013); for some pelagic birds the energetic costs of flight may be mostly determined by wind (Elliott et al. 2014). For example, heart rates of wandering albatrosses (*Diomedea exulans*) during favorable wind conditions are close to basal levels (Weimerskirch et al. 2000). The wind energy is essential to achieve optimal gliding in procellariiformes species (Davies et al. 2010, and references within). However, wind will affect differently the flight of birds during different behaviors. When animals are traveling they may try to minimize energy expenditure by reducing the time to reach their destination, although during foraging, birds are also influenced by distribution of resources (Tarrow et al. 2016). In this sense, southern giant petrels from northern Patagonian colonies may be highly influenced by wind conditions. Our results suggested that specific wind intensity is influencing the habitat suitability of the SGP. During breeding, adults constrained to the colony may be taking advantage of the direction of wind (zonal and meridional) to minimize energy costs while moving within the foraging areas, as indicated by the high specialization values. Interestingly, during winter, wind speed also appears to shape SGP distribution. This group may be relying on both directionality and wind speed. Wintering adults perform longer foraging trips than breeding adults, spending more than 10 days at sea (Blanco and Quintana 2014; Quintana et al. 2010). During that time, they may be able to select beneficial wind speeds for flying, saving energy when moving towards and within foraging grounds. In addition considering that our analysis took into account only residence locations, favorable wind conditions may be a factor selected for this population to move while foraging, as it was also suggested for other procellariiformes (Weimerskirch et al. 2007).

Juveniles are helped by wind conditions during their initial flight out of the colony (Blanco et al. 2015). Moreover, some species have been documented to sit on water, waiting for the right wind condition to initiate their flight (Åkesson and Weimerskirch 2014). Our model suggested that wind speed may be a factor affecting distribution and foraging areas of first year SGP. This may be helpful for orientation, which suggests that despite lack of experience, these immature birds could use wind for orientation, an innate behavior that would help individuals to find areas to forage decreasing their energy costs (Riotte-Lambert and Weimerskirch 2013).

Final considerations

Overall, we believe that ENFA depicted a fair picture of the variables that influence SGP in their selection of foraging areas. Noticeably different eco-geographical variables influenced differently the distribution of this population, depending on the requirements of the different stages of their life cycle. For example, first year juveniles showed a high value of marginality; moreover, breeding adults' habitat suitability was determined by a small range of feature values from the range of values available, showing high specialization. In contrast, the model indicated that wintering petrels showed plasticity in the selection of their foraging environments, meaning that they may be best adapted to conditions spread along the study area. Likewise, when considering different colonies of the same species, we noticed that adult southern giant petrels breeding at Observatorio Island (54° 39' 25"S; 64° 08' 03"W) foraged between 50°S and 55°S (Quintana et al. 2010), and those from South Georgia also foraged in the southern portion of our study area along the year (González-Solís et al. 2007). Interestingly, neither of those defined foraging areas resulted in a suitable habitat for southern giant petrels from northern Patagonian colonies. Therefore, despite of the high performance of ENFA when applied to specific study cases, caution must be taken when applying this type of analysis to a single population and then extrapolating results at the species level in un-sampled areas. As indicated by our findings, results may vary not only from one population to another, but even within the same population during different life stages.

Conservation implications

The SGP is listed as *Least Concern* in the IUCN red list (BirdLife International 2012) and is also listed in Annex I of the Agreement on the Conservation of Albatrosses and Petrels (ACAP). As depicted by ENFA, main priority conservation areas for SGP from Islas Arce and Gran Robredo are located in the Argentinean Shelf from 42°S to 53°S extending to the west along the shelf break (HSI > 06). That area is currently exploited by fisheries, and although some mitigation measurements have been implemented (PAN-Aves 2010), seabirds are still at risk (Phillips et al. 2016). Habitat suitability of juveniles expanded from 25°S (Brazil) to 50°S in Argentina where the risk of by-catch increases, considering the extension of the area together with the strong influence that fisheries had in the habitat suitability of this age class. Currently, less than 0.5% of the Argentinean Sea is under some kind of regulation (i.e., Marine Park, Provincial Reserve, etc.) and all those protected areas are located along the coast. Although efforts to protect pelagic waters included the delimitation of

fishing closures for management of resources (Foro para la conservación del Mar Patagónico y áreas de influencia 2008), there are no Marine Protected Areas designed to protect seabirds where fisheries are banned (Alemany et al. 2013). The suitable habitats described for SGP in this study also congregate different species of seabirds and marine mammals (Croxall and Wood 2002; Falabella et al. 2009; González Carman et al. 2016), which highlights the importance of the Argentinean Shelf for conservation of the marine environment.

Based on our findings and the discussion above, we strongly recommend the use of presence-only models and determination of habitat suitability as a tool for conservation and management for albatrosses and petrels. This approach is particularly useful, considering that they are the most threatened group of seabirds and that due to the remoteness of their breeding colonies and foraging areas, data collection is difficult.

Acknowledgements We are grateful to Dr. Daniel Rodríguez-Pérez and reviewers for valuable comments and suggestions, and Amy Horton for English revision over the manuscript. We thank personnel of the Parque Interjurisdiccional Marino Costero Patagonia Austral for their support. We also thank Instituto de Biología de Organismos Marinos (IBIOMAR-CONICET) and Centro para el Estudio de Sistemas Marinos (CESIMAR-CONICET) for institutional support. The authors declare that they have no conflict of interest.

Compliance with ethical standards

All authors declare that there are no conflict of interest. All authors agree to this submission and approved this final version of the manuscript. Manipulation of animals occurred according to national legislation.

References

- ACAP (2011) Agreement on the conservation of albatrosses and petrels: report of the sixth meeting of the Advisory Committee. Guayaquil, Ecuador
- Åkesson S, Weimerskirch H (2014) Evidence for sex-segregated ocean distributions of first-winter wandering albatrosses at Crozet islands. *PLoS One* 9:e86779. doi:10.1371/journal.pone.0086779
- Alemany D, Iribarne OO, Acha EM (2013) Effects of a large-scale and offshore marine protected area on the demersal fish assemblage in the Southwest Atlantic. *ICES J Mar Sci* 70:123–134. doi:10.1093/icesjms/fss166
- Arkhipkin AI et al (2015) World squid fisheries. *Rev Fish Sci Aquac* 23:92–252
- Awkerman JA, Fukuda A, Higuchi H, Anderson DJ (2005) Foraging activity and submesoscale habitat use of waved albatrosses *Phoebastria irrorata* during chick-brooding period. *Mar Ecol Prog Ser* 291:289–300. doi:10.3354/meps291289
- BirdLife International (2012) *Macronectes giganteus*. In: IUCN 2012. IUCN Red List of Threatened Species Version 2012.2
- Blanco GS, Quintana F (2014) Differential use of the Argentine shelf by wintering adults and juveniles southern giant petrels, *Macronectes giganteus*, from Patagonia. *Estuarine Coastal Shelf Sci* 149:151–159
- Blanco GS, Pisoni JP, Quintana F (2015) Characterization of the seascape used by juvenile and wintering adult southern giant petrels from Patagonia Argentina. *Estuarine Coastal Shelf Sci* 153:135–144
- Bost CA et al (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376. doi:10.1016/j.jmarsys.2008.11.022
- Brambilla M, Saporetti F (2014) Modelling distribution of habitats required for different uses by the same species: implications for conservation at the regional scale. *Biol Conserv* 174:39–46
- Brunetti NE, Ivanovic ML, Rossi GR, Elena B, Pineda S (1998) Fishery biology and life history of *Illex argentinus*. Paper presented at the International Symposium on large pelagic squids, Marine Fishery Resources Research Center, Japan
- Bryan TL, Metaxas A (2007) Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. *Mar Ecol Prog Ser* 330:113–126
- Bugoni L, Alba L, Furness RW (2009) Marine habitat use of wintering spectacled petrels *Procellaria conspicillata*, and overlap with longline fishery. *Mar Ecol Prog Ser* 374:273–285. doi:10.3354/meps07750
- Bugoni L, Griffiths K, Furness RW (2011) Sex-biased incidental mortality of albatrosses and petrels in longline fisheries: differential distributions at sea or differential access to baits mediated by sexual size dimorphism? *J Ornithol* 152:261–268
- Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519. doi:10.1016/j.ecolmodel.2006.03.017
- Calenge C, Basille M (2008) A general framework for the statistical exploration of the ecological niche. *J Theor Biol* 252:674–685. doi:10.1016/j.jtbi.2008.02.036
- Catry P, Lemos R, Brickle P, Phillips RA, Matias R, Granadeiro JP (2013) Predicting the distribution of a threatened albatross: the importance of competition, fisheries and annual variability. *Prog Oceanogr* 110:1–10
- Chen C-S, Chiu T-S, Huang W (2007) The spatial and temporal distribution patterns of the Argentine short-finned squid, *Illex argentinus*, abundance in the Southwest Atlantic and the effects of environmental influences. *Zool Stud* 46:111
- Copello S, Quintana F (2009a) Breeding biology of the southern giant petrel (*Macronectes giganteus*) in Patagonia, Argentina. *Ornitol Neotrop* 20:269–380
- Copello S, Quintana F (2009b) Spatio-temporal overlap between the at-sea distribution of southern giant petrels and fisheries at the Patagonian Shelf. *Polar Biol* 32:1211–1220. doi:10.1007/s00300-009-0620-7
- Copello S, Quintana F, Pérez F (2008) Diet of the southern giant petrel in Patagonia: fishery-related items and natural prey. *Endanger Species Res* 6:15–23. doi:10.3354/esr00118
- Copello S, Dogliotti A, Gagliardini D, Quintana F (2011) Oceanographic and biological landscapes used by the Southern Giant Petrel during the breeding season at the Patagonian Shelf. *Mar Biol* 158:1247–1257. doi:10.1007/s00227-011-1645-3
- Copello S, Seco Pon JP, Favero M (2014) Spatial overlap of Black-browed albatrosses with longline and trawl fisheries in the Patagonian Shelf during the non-breeding season. *J Sea Res* 89:44–51. doi:10.1016/j.seares.2014.02.006
- Cozzolino E (2014) Uso de imágenes satelitales nocturnas NPP VIIRS/DNB para el monitoreo y cuantificación de flotas poteras extranjeras: desarrollo de un software específico. Instituto Nacional de Investigación y desarrollo pesquero-INIDEP, Informe Técnico Oficial
- Crespo E, Oliva D, Dans S, Sepúlveda M (eds) (2012) Current status of the South American sea lion along the distribution range. Universidad de Valparaíso Valparaíso

- Croxall JP, Wood AG (2002) The importance of the Patagonian Shelf for top predator species breeding at South Georgia. *Aquat Conserv: Mar Freshw Ecosyst* 12:101–118. doi:[10.1002/aqc.480](https://doi.org/10.1002/aqc.480)
- Davies RG, Irlich UM, Chown SL, Gaston KJ (2010) Ambient, productive and wind energy, and ocean extent predict global species richness of procellariiform seabirds. *Global Ecol Biogeogr* 19:98–110. doi:[10.1111/j.1466-8238.2009.00498.x](https://doi.org/10.1111/j.1466-8238.2009.00498.x)
- de Grissac S, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile albatrosses and petrels. *Sci Rep* 6:26103
- Doniol-Valcroze T, Lesage V, Giard J, Michaud R (2012) Challenges in marine mammal habitat modelling: evidence of multiple foraging habitats from the identification of feeding events in blue whales. *Endang Species Res* 17:255–268
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Syst* 40:677
- Elliott KH et al (2014) Windscape shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Mov Ecol* 2:17
- Falabella V, Campagna C, Croxall J (eds) (2009) Atlas del Mar Patagónico. Especies y espacios., Buenos Aires, Wildlife Conservation Society y BirdLife International
- Favero M et al (2011) Seabird mortality associated with ice trawlers in the Patagonian shelf: effect of discards on the occurrence of interactions with fishing gear. *Anim Conserv* 14:131–139
- Favero M et al (2013) Seabird bycatch in the Argentinean demersal longline fishery, 2001–2010. *Endanger Species Res* 19:187–199. doi:[10.3354/esr00478](https://doi.org/10.3354/esr00478)
- Forero MG, González-Solís J, Hobson KA, José A, Donazar MB, Blanco G, Bortolotti GR (2005) Stable isotopes reveal trophic segregation by sex and age in the southern giant petrel in two different food webs. *Mar Ecol Prog Ser* 296:107–113. doi:[10.3354/meps296107](https://doi.org/10.3354/meps296107)
- Foro para la conservacion del Mar Patagonico y areas de influencia (2008) Sintesis del estado de conservacion del Mar Patagonico y areas de influencia. Edicion del Foro, Puerto Madryn, Argentina
- Fossette S et al (2014) Pan-Atlantic analysis of the overlap of a highly migratory species, the leatherback turtle, with pelagic longline fisheries. *Proc R Soc B* 281:20133065 doi:[10.1098/rspb.2013.3065](https://doi.org/10.1098/rspb.2013.3065)
- Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Moorter BV (2010) Habitat–performance relationships: finding the right metric at a given spatial scale. *Philos Transac R Soc B: Biol Sci* 365:2255–2265. doi:[10.1098/rstb.2010.0085](https://doi.org/10.1098/rstb.2010.0085)
- Galparsoro I, Borja Á, Bald J, Liria P, Chust G (2009) Predicting suitable habitat for the European lobster (*Homarus gammarus*), on the Basque continental shelf (Bay of Biscay), using Ecological-Niche Factor Analysis. *Ecol Modell* 220:556–567
- Gómez-Laich A et al (2006) Environmental and operational variability affecting the mortality of black-browed albatrosses associated with long-liners in Argentina. *Emu* 106:21–28
- González Carman V et al (2016) Distribution of megafaunal species in the Southwestern Atlantic: key ecological areas and opportunities for marine conservation. *ICES J Mar Sci*. doi:[10.1093/icesjms/fsw019](https://doi.org/10.1093/icesjms/fsw019)
- González-Solís J, Croxall JP, Wood AG (2000) Foraging partitioning between giant petrels *Macronectes spp.* and its relationship with breeding population changes at Bird Island, South Georgia. *Mar Ecol Prog Ser* 204:279–288
- González-Solís J, Croxall J, Afanasyev V (2007a) Offshore spatial segregation in giant petrels *Macronectes spp.*: differences between species, sexes and seasons. *Aquat Conserv: Mar Freshw Ecosyst* 17:S22–S36
- González-Solís J, Croxall JP, Afanasyev V (2007b) Offshore spatial segregation in giant petrels *Macronectes spp.*: differences between species, sexes and seasons. *Aquat Conserv: Mar Freshw Ecosyst* 17:S22–S36. doi:[10.1002/aqc.911](https://doi.org/10.1002/aqc.911)
- González-Zevallos D, Yorio P (2006) Seabird use of discards and incidental captures at the Argentine hake trawl fishery in the Golfo San Jorge, Argentina. *Mar Ecol Prog Ser* 316:175–183. doi:[10.3354/meps316175](https://doi.org/10.3354/meps316175)
- González-Zevallos D, Yorio P, Caille G (2007) Seabird mortality at trawler warp cables and a proposed mitigation measure: a case of study in Golfo San Jorge, Patagonia, Argentina. *Biol Conserv* 136:108–116. doi:[10.1016/j.biocon.2006.11.008](https://doi.org/10.1016/j.biocon.2006.11.008)
- Gutowsky SE et al (2014) Divergent post-breeding distribution and habitat associations of fledgling and adult Black-footed Albatrosses *Phoebastria nigripes* in the North Pacific. *Ibis* 156:60–72. doi:[10.1111/ibi.12119](https://doi.org/10.1111/ibi.12119)
- Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-Niche Factor Analysis: How to compute Habitat-Suitability maps without absence data? *Ecology* 83:2027–2036. doi:[10.1890/0012-9658\(2002\)083\[2027:enfaht\]2.0.co;2](https://doi.org/10.1890/0012-9658(2002)083[2027:enfaht]2.0.co;2)
- Hunter S (1984) Breeding biology and population dynamics of giant petrels *Macronectes spp.* at South Georgia (Aves: Procellariiformes). *J Zool* 203:441–460. doi:[10.1111/j.1469-7998.1984.tb02343.x](https://doi.org/10.1111/j.1469-7998.1984.tb02343.x)
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbour. Symp Quant Biol* 22:415–427
- Hyrenbach KD, Fernández P, Anderson DJ (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Mar Ecol Prog Ser* 233:283–301. doi:[10.3354/meps233283](https://doi.org/10.3354/meps233283)
- Jiménez S, Domingo A, Brazeiro A (2009) Seabird bycatch in the Southwest Atlantic: interaction with the Uruguayan pelagic longline fishery. *Polar Biol* 32:187–196
- Krüger L, Paiva VH, Petry MV, Ramos JA (2017) Strange lights in the night: using abnormal peaks of light in geolocator data to infer interaction of seabirds with nocturnal fishing vessels. *Polar Biol* 40:221–226. doi:[10.1007/s00300-016-1933-y](https://doi.org/10.1007/s00300-016-1933-y)
- Legrand B, Benneveau A, Jaeger A, Pinet P, Potin G, Jaquemet S, Le Corre M (2016) Current wintering habitat of an endemic seabird of Réunion Island, Barau's petrel *Pterodroma baraui*, and predicted changes induced by global warming. *Mar Ecol Prog Ser* 550:235–248
- Louzao M, Pinaud D, Péron C, Delord K, Wiegand T, Weimerskirch H (2011) Conserving pelagic habitats: seascape modelling of an oceanic top predator. *J Appl Ecol* 48:121–132. doi:[10.1111/j.1365-2664.2010.01910.x](https://doi.org/10.1111/j.1365-2664.2010.01910.x)
- MacArthur RH (1972) Geographical Ecology: Patterns in the Distribution of Species. Harper & Row, New York
- Monk J et al (2010) Habitat suitability for marine fishes using presence-only modelling and multibeam sonar. *Mar Ecol Prog Ser* 420:157–174
- Monk J, Ierodiaconou D, Bellgrove A, Harvey E, Laurenson L (2011) Remotely sensed hydroacoustics and observation data for predicting fish habitat suitability. *Cont Shelf Res* 31:S17–S27
- Nixon MS, Aguado AS (2008) Feature Extraction and Image Processing. Academic Press, Elsevier, Oxford UK
- Oppel S, Meirinho A, Ramírez I, Gardner B, O'Connell AF, Miller PI, Louzao M (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biol Conserv* 156:94–104
- PAN-Aves (2010) Plan de accion nacional para reducir la interaccion de aves con pesquerias de la República Argentina. Consejo Federal Pesquero. Buenos Aires
- Patterson DL et al (2008) Breeding distribution and population status of the northern giant petrel *Macronectes halli* and the southern giant petrel *M. giganteus*. *Mar Ornithol* 36:115–124
- Perez JAA, Silva TN, Schroeder R, Schwarz R, Martins RS (2009) Biological patterns of the Argentine shortfin squid *Illex*

- argentinus in the slope trawl fishery off Brazil. *Lat Am J Aquat Res* 37:409–427
- Péron C, Delord K, Phillips RA, Charbonnier Y, Marteau C, Louzao M, Weimerskirch H (2010) Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island. *Mar Ecol Prog Ser* 416:267–284. doi:10.3354/meps08785
- Pezzuto PR, Perez JAA, Wahrlich R (2006) Deep-sea shrimps (Decapoda: Aristeidae): new targets of the deep-water trawling fishery in Brazil. *Braz J Oceanogr* 54:123–134
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V (2006a) Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biol Conserv* 129:336–347. doi:10.1016/j.biocon.2005.10.046
- Phillips SJ, Anderson RP, Schapire RE (2006b) Maximum entropy modeling of species geographic distributions. *Ecol Model* 190:231–259
- Phillips RA et al (2016) The conservation status and priorities for albatrosses and large petrels. *Biol Conserv* 201:169–183
- Quintana F, Schiavini A, Copello S (2005) Estado poblacional, ecología y conservación del petrel gigante del sur (*Macronectes giganteus*) en Argentina. *Hornero* 20:25–34
- Quintana F, Punta G, Copello S, Yorío P (2006) Population status and trends of southern giant petrels (*Macronectes giganteus*) breeding in North Patagonia, Argentina. *Polar Biol* 30:53–59. doi:10.1007/s00300-006-0159-9
- Quintana F, Dell’Arciprete O, Copello S (2010) Foraging behavior and habitat use by the Southern Giant Petrel on the Patagonian Shelf. *Mar Biol* 157:515–525. doi:10.1007/s00227-009-1337-4
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Riotte-Lambert L, Weimerskirch H (2013) Do naive juvenile seabirds forage differently from adults? *Proc R Soc B: Biol Sci* 280:20131434
- Sacau M et al (2005) The spatio-temporal pattern of Argentine short-fin squid *Illex argentinus* abundance in the southwest Atlantic. *Aquat Living Resour* 18:361–372. doi:10.1051/alr:2005039
- Sanchez-Carnero N, Rodríguez-Perez D, Counago E, Barzik FL, Freire J (2016) Species distribution models and local ecological knowledge in marine protected areas: the case of Os Minarzos (Spain). *Ocean Coast Manag* 124:66–77
- Seco Pon JP et al (2013) Seabird and marine-mammal attendance and by-catch in semi-industrial trawl fisheries in near-shore waters of northern Argentina. *Mar Freshwater Res* 64:237–248. doi:10.1071/MF12312
- Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB (2013) Energy landscapes shape animal movement ecology. *Am Nat* 182:298–312
- Skov H et al (2008) Application of habitat suitability modelling to tracking data of marine animals as a means of analyzing their feeding habitats. *Ecol Model* 212:504–512
- Tarroux A et al (2016) Flexible flight response to challenging wind conditions in a commuting Antarctic seabird: do you catch the drift? *Anim Behav* 113:99–112
- Thiers L, Delord K, Barbraud C, Phillips RA, Pinaud D, Weimerskirch H (2014) Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation. *Mar Ecol Prog Ser* 499:233–248
- Thompson D, Strange I, Riddy M, Duck CD (2005) The size and status of the population of southern sea lions *Otaria flavescens* in the Falkland Islands. *Biol Conserv* 121:357–367
- Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc R Soc Lond Ser B: Biol Sci* 267:1869–1874. doi:10.1098/rspb.2000.1223
- Weimerskirch H, Pinaud D, Pawlowsky F, Bost CA (2007) Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *Am Nat* 170:734–743
- Wilson RP, Puetz K, Peters G, Culik B, Scolaro JA, Charrassin JB, Roper-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull* 25:101–106
- Yeh YM, Huang HW, Dietrich KS, Melvin E (2013) Estimates of seabird incidental catch by pelagic longline fisheries in the South Atlantic Ocean. *Anim Conserv* 16:141–152
- Yorio P, Quintana F, Dell’arciprete P, González-Zevallos D (2010) Spatial overlap between foraging seabirds and trawl fisheries: implications for the effectiveness of a marine protected area at Golfo San Jorge, Argentina. *Bird Conserv Int* 20:320–334