ARTICLE

Where's the best supermarket deal? Female Southern Rockhopper Penguins (*Eudyptes chrysocome*) show variable foraging areas during the guard stage at Isla de los Estados, Argentina

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Abstract: Understanding the spatial distribution of seabirds contributes to comprehending their ecological requirements and dispersion patterns. We studied the at-sea distribution of female Southern Rockhopper Penguins (*Eudyptes chrysocome* (J.R. Forster, 1781)) at Isla de los Estados colony during the early chick-rearing period. We used a clustering analysis approach to identify different groups according to the foraging trip (tracking and diving data from GPS and temperature and depth data loggers) and diet (δ^{15}N composition on blood samples) characteristics. Foraging trips differed in duration, location, and dive depths explored. Females in clusters 1 and 3 traveled longer distances and in opposite directions (36.3 ± 21.3 and 40.3 ± 14.0 km, respectively). Females in cluster 2 fed closer to the colony (16.8 ± 7.8 km). Dives occurred in pelagic habitats. Higher δ^{15}N values suggested a greater proportion of fish (e.g., the Fuegian sprat, *Sprattus fuegensis* (Jenyns, 1842)) consumption in the northern foraging areas (cluster 1). The variability observed in the spatial distribution suggests flexibility in the foraging behavior of Southern Rockhopper Penguins and availability of adequate foraging areas within the colony range during the early chick-rearing period, both important features for Southern Rockhopper Penguin population. These results contribute to understanding the use of the Southern Ocean by marine mesopredators and top predators and to the marine spatial planning in the area.

Key words: diving behavior, *Eudyptes chrysocome*, Southern Rockhopper Penguin, Isla de los Estados, at-sea distribution, stable isotopes, tracking.

Résumé : La compréhension de la répartition spatiale des oiseaux marins aide à mieux comprendre leurs exigences écologiques et les motifs de leur dispersion. Nous avons étudié la répartition en mer de gorfous sauteurs (*Eudyptes chrysocome* (J.R. Forster, 1781)) femelles dans la colonie de Isla de los Estados au début de la période de soin des oisillons. Nous avons utilisé une approche d'analyse typologique pour cerner différents groupes en fonction des caractéristiques des sorties de quête de nourriture (données de suivi et de plongée obtenues d'enregistreurs de données GPS et de température et profondeur) et du régime alimentaire (δ^{15}N d'échantillons de sang). Les sorties de quête de nourriture différaient sur le plan de la durée, du lieu et des profondeurs de plongée explorées. Les femelles des groupements 1 et 3 parcouraient de plus longues distances en directions opposées (36,3 ± 21,3 et 40,3 ± 14,0 km, respectivement). Les femelles du groupement 2 s'alimentaient plus près de la colonie (16,8 ± 7,8 km). Les plongées avaient lieu dans des habitats pélagiques. Des δ^{15}N plus élevés semblaient indiquer une plus grande proportion de consommation de poissons (p. ex. le sprat des îles Falkland, *Sprattus fuegensis* (Jenyns, 1842)) dans les lieux de quête de nourriture au nord (groupement 1). La variabilité observée de la répartition spatiale indiquerait une certaine souplesse du comportement de quête de nourriture des gorfous sauteurs et la disponibilité de lieux d'alimentation adéquats dans l'aire de répartition de la colonie au début de la période de soin des oisillons, deux caractéristiques importantes pour la population de gorfous sauteurs. Ces résultats améliorent la compréhension de l'utilisation de l'océan austral par des mésoprédateurs et des superprédateurs marins et sont utiles pour la planification d'aires marines dans cette région. [Traduit par la Rédaction]

Mots-clés : comportement de plongée, *Eudyptes chrysocome*, gorfou sauteur, Isla de los Estados, répartition en mer, isotopes stables, suivi.

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Introduction

Spatial distribution of seabirds is often determined by biological and physical attributes of the environment that determine appropriate foraging grounds. These areas can change through time according to modifications of the environment and prey distribution (Weimerskirch 2007), as well as the stage of the seabirds' annual cycle (Herman et al. 2017). Knowing the at-sea distribution of seabirds is important to comprehend their ecological requirements (Thiebot et al. 2012), their dispersion patterns (Carneiro et al. 2020), and possible threats in their foraging areas (Catry et al. 2013). Thus, it provides information that lead us to identify accurately areas to target conservation efforts and for marine spatial planning (Sansom et al. 2018).

During the breeding season, seabirds are central-place foragers that exploit resources within a foraging range around their colony, set by the trade-off of balancing time foraging and the need to regularly provision chicks (Costa 1991; Grémillet et al. 2004). Thus, prey depletion is likely to occur around the breeding sites, potentially leading to competition for food within easy commuting distances (Ashmole 1963; Birt et al. 1987). Seabirds may use different depths to forage (Masello et al. 2010; Wilson 2010), and (or) choose different at-sea areas, particularly those seabirds breeding in neighboring colonies, that usually spatially segregate within similar habitat types (Grémillet et al. 2004; Masello et al. 2010; Wakefield et al. 2011; Thiebot et al. 2012, 2013; Ratcliffe et al. 2014).

Direct tracking of seabirds provides location information on individuals through time and allows us to develop distribution maps that reflect individuals' use of space at a specific moment (Sansom et al. 2018). Moreover, some devices simultaneously record location and dive depth data, combining both the horizontal and the vertical movements of the birds, which is relevant for diving seabirds (e.g., Rosciano et al. 2016). Complementary, stable isotope analysis is a reliable tool that provides information on the trophic ecology and assesses patterns of habitat use by organisms (Hobson 2005; Newsome et al. 2012). In marine systems, stable isotope values of carbon ($\delta^{13}C$) reflect primary carbon sources within a food web and can be used to trace trends in marine habitat use by consumers (inshore or benthic vs. offshore or pelagic; Cherel and Hobson 2007). Stable isotope values of nitrogen ($\delta^{15}N$) reflect the trophic position of consumers due to a stepwise enrichment of ^{15}N between trophic levels (Minagawa and Wada 1984).

The largest colony of Southern Rockhopper Penguins (*Eudyptes chrysocome* (J.R. Forster, 1781); henceforth Rockhopper Penguins) is located at Isla de los Estados (Franklin Bay), Tierra del Fuego, Argentina (Schiavini 2000). It is home to approximately 130 000 breeding pairs stretching about 5 km along the western coast (Raya Rey et al. 2014). Rockhopper Penguins in this colony were tracked during different stages of their annual cycle (inter-breeding and incubation periods), and showed a wide range of use of the South Atlantic Ocean waters, even overlapping foraging ranges with conspecifics from the closest colonies at the Falkland/Malvinas Islands (~500 km; Pütz et al. 2002, 2006, 2009; Raya Rey et al. 2007). During the breeding season, after the chicks have hatched, female Rockhopper Penguins forage at sea and feed their offspring while males remain at the nest to guard them (Warham 1975).

Here, we aimed to investigate the at-sea distribution of breeding female Rockhopper Penguins during the guard stage. We evaluated this by exploring a multivariate clustering approach for statistically identifying different groups according to the foraging trip and diet ($\delta^{15}N$) characteristics of each female. Across three breeding seasons, we used a combination of tracking and diving data from GPS and temperature and depth (GPS–TD) data loggers to obtain the track and diving profile of the penguins (e.g., Rosciano et al. 2018), and $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis on whole blood samples to reveal the assimilated diet of the penguins for an extended period of time (Barquete et al. 2013).

Materials and methods

Study area and species

Isla de los Estados is a Natural Reserve (Reserva Natural Silvestre DN 929/16) located on the east side of Tierra del Fuego Province, separated by the 30 km wide Le Maire Strait (Fig. 1; Ponce and Fernández 2014 and references therein) that connects the Pacific and Atlantic oceans with the Cape Horn Current when it enters the continental shelf (Patagonian Cold Estuarine System; Acha et al. 2004). The study was conducted at Franklin Bay (54°38′S, 63°48′W; Fig. 1) where Southern Rockhopper Penguin subcolonies are patchily distributed along a coastal stretch of 5 km (Raya Rey et al. 2014). We randomly selected one subcolony for our study and sampled there over three consecutive breeding seasons (2011–2013).

Data collection

We collected data from early to mid-December (range of dates: 1–14 December 2011, 3–10 December 2012, and 2–15 December 2013), which corresponded to the early chick-rearing period between hatching (end of November to early December) and crèching (middle to end of December) (Warham 1975; Pütz et al. 2013). We randomly selected nests at the colony and equipped females with precision GPS–TD data loggers (GPS–TDlog; Earth & Ocean Technologies, Kiel, Germany). We only tagged females because during the initial chick-rearing period, they alone provision chicks with food while the males guard the chicks (Warham 1975; Pütz et al. 2013). When both adults were at the nest, we visually identified the females using bill size, gently removed them from their nest, and marked the nest with a numbered colored tape. We weighed the penguin with a Pesola balance (to the nearest 100 g) and measured bill depth and bill length using calipers (to the nearest 0.02 mm) to verify the sex of the individual (e.g., Hull 1996; Pütz et al. 2013). We attached the GPS–TD data loggers to the midline of the penguin's back using black tape (Tesa, Beiersdorf AG, Hamburg, Germany) following Wilson et al. (1997; method 2). Finally, the tape around the device was covered with a layer of quick-drying epoxy to prevent the birds from removing the tape with their bills. The whole process took less than 20 min per bird. We programmed the GPS–TD data loggers (size: 5.6 cm × 3.1 cm × 1.5 cm, 37 g, representing 1.7% of the mass of individuals) to record temperature and depth every 2 s, and latitude and longitude every 2 min, alternatively taking a position at each surfacing when birds were diving. Short-term logger attachment has been shown to have little effect on the breeding activities of Rockhopper Penguins (Ludynia et al. 2012).

We recaptured returning females to recover the device approximately 24–48 h after logger deployment (on average, 1.8 ± 0.6 days after deployment) and collected whole blood samples from the tarsal vein of the penguins into microcapillary tubes (~75 μL). Blood was preserved in 70% ethanol for later laboratory processing. Several studies have shown little effect of alcohol preservation on stable isotope values of whole blood (Hobson et al. 1997; Halley et al. 2008; Therrien et al. 2011; but see Bugoni et al. 2008).

We checked nests of equipped penguins every week until the end of each fieldwork season to monitor chick survival. We expressed these data as the number of chicks per nest studied towards the end of December, when crèche stage starts and chicks are no longer associated with nests (coinciding with the end of the fieldwork).

Ethics approval

Animal use was approved by Secretaría de Ambiente y Desarrollo Sustentable (Resolución SSCYT N° 08/11).

Fig. 1. At-sea distribution of female Southern Rockhopper Penguins (*Eudyptes chrysocome*) obtained from the clustering analysis. Individual tracks of each penguin are indicated by a sequence of black circles. Patterned squares highlight the cells where birds spent the maximum amount time during the foraging trip. Star indicates colony location. GCS: WGS 1984; Map Pojection: South Pole Lambert Azimuthal Equal Area, Central meridian −70. Base map Tierra del Fuego Island shape file, Instituto Geográfico Nacional (available from https://www.ign.gob.ar/NuestrasActividades/InformacionGeoespacial/CapasSIG). Base map Yaganes Marine Protected area shape flie, Administración de Parques Nacionales (available from https://mapas.apn.gob.ar/maps/38#category-more). Color version online.

Foraging trip analysis

We analyzed diving data from the depth sensor with Multitrace software (Jensen Software Systems, Kiel, Germany). We calculated diving parameters for each trip using dives >1 m following Raya Rey et al. (2012). For each data set, we obtained the following variables: trip duration (h), mean dive depth of all dives (m), and bottom time per hour underwater (min/h; with bottom time defined as the time a penguin had a vertical speed ≤0.3 m/s during the deepest phase of each dive, e.g., see Raya Rey et al. 2012).

We analysed GPS data using ArcGIS version 9.3.1 and the Spatial Analyst Tools and Hawth's Analysis Tools (http://www.spatialecology.com/htools). We first calculated the maximum distance traveled from the colony (km) by each female. Then, to identify the most used geographical locations by the penguins while at sea, we established a 156 km × 188 km grid including the entire area used by logger-equipped penguins for the 3 years combined. The grid was divided into 4 km × 4 km grid cells, which is the grid size of the satellite images used as input for environmental variables. By assuming that penguins swam in a straight line between two consecutive locations (latitude and longitude), the travel duration within each grid square could be allocated (e.g., Raya Rey et al. 2010). The procedure was repeated for each penguin to create a map of the relative time spent in each 4 km × 4 km cell for each female Rockhopper Penguin and for the 3-year study period. Finally, for each penguin, the cell with the greatest amount of time spent was considered the primary feeding area for each individual (Bost et al. 1997; Raya Rey et al. 2010). We superimposed those cells with a bathymetric chart (GEBCO (General Bathymetric Chart of the Oceans), 30 arc-second cell size; available from https://www.gebco.net/data_and_products/gridded_bathymetry_data/), chlorophyll *a* concentration (mg/m^3), and sea surface temperature (°C) satellite image from Aqua-MODIS (monthly or 32-day composite image according to the best resolution available for the period studied, 4 cell × 4 cell size resolution; available from https://oceancolor.gsfc.nasa.gov/data/aqua/) to characterize them environmentally. Finally, we calculated the distance from the central point of each grid to the 200 m isobath (maximum depth of the continental shelf) and to the Sub-Antarctic Front (determined by Orsi et al. 1995), as it was suggested in past studies that female Rockhopper Penguins foraged near this front (Schiavini and Raya Rey 2004).

Tissue analysis

We dried the whole blood samples in an oven at 60 °C for 24 h and then freeze-dried them in a lyophilizer. We weighed approximately 0.50 mg aliquots of each sample into 3 mm × 5 mm tin cups that were flash-combusted (Costech ECS4010 or PDZ Europa ANCA-GSL elemental analysers) for δ^{13}C and δ^{15}N analysis through an interfaced continuous-flow stable isotope ratio mass spectrometer (Thermo Scientific Delta V Plus or PDZ Europa 20-20). Sample precision based on repeated sample and reference material was 0.2‰ for δ^{13}C and 0.3‰ for δ^{15}N. Stable isotope abundances were expressed as δ in parts per thousands (‰), according to the following equation:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C:^{12}C or ^{15}N:^{14}N. The $R_{standard}$ values were based on the Vienna PeeDee Belemnite (VPDB) for ^{13}C and atmospheric N^2 for ^{15}N.

Whole blood δ^{13}C values were normalized for the effects of lipid concentration on δ^{13}C following Post et al. (2007), as C:N ratio values indicated variable concentration of ^{13}C-depleted lipids (Cherel et al. 2005).

Statistical analysis

We used the non-hierarchical cluster analysis *k*-means approach to identify groups according to the foraging behavior of female Rockhopper Penguins during their foraging trips at the guard stage. We included eight parameters considered important to group individuals presenting similar foraging behaviors: mean dive depth (m), time in bottom phase per hour (min/h), trip duration (h), δ^{13}C (‰), δ^{15}N (‰), bathymetry (m), distance to 200 m isobath (km), and distance to Sub-Antarctic Front (SAF; km).

The *k*-means clustering analysis is a method that finds a partition of the observations for a particular number of clusters by minimizing the total within-group sum of squares over all variables (Everitt and Hothorn 2010). We used the Euclidean distance as a method to minimize the within-group sum of squares. Variables were on different scales, so we standardized them prior to analysis (package "stats" from base R, "scale" function that centers and (or) scales the columns of a numeric matrix). To define the appropriate number of groups for the data set, we created a graph comparing the within-group sum of squares and the number of groups, and looked for the curve or elbow of the graph (following Everitt and Hothorn 2010). The curve occurred between groups (*k*) 3 and 4.

We then performed linear models to characterize each cluster. We used the diving (mean dive depth, time in bottom phase per hour), tracking (trip duration), and isotope (δ^{13}C, δ^{15}N) data as response variables, and cluster and year as explanatory variables, to study the differences among groups and the inter-annual variability. We first tested the cluster × year interaction and discarded it if it was not significant to simplify the model. If differences among clusters and (or) years were significant, then we examined them with pairwise comparisons ("lsmeans" package; Lenth and Herve 2015).

To characterize the foraging areas by its environmental features, we evaluated chlorophyll *a* (Chl *a*) concentration and sea surface temperature (SST) in terms of cluster and year by running linear models and pairwise comparisons if there were significant differences among clusters and (or) years (same as described above).

All statistical analyses were performed in R software version 3.2.3 (R Core Team 2015). Significance was assumed at the 0.05 level and all means are presented with standard deviations (±SD).

Results

We equipped a total of 36 female Rockhopper Penguins with GPS–TD data loggers over the 3-year study period (2011: *n* = 13; 2012: *n* = 10; 2013: *n* = 13). We obtained a complete data set covering one foraging trip (i.e., diving, GPS, and isotope data) from 24 female Rockhopper Penguins (9 in 2011, 4 in 2012, and 11 in 2013), and incomplete data sets (only GPS and isotope data) for 5 female Rockhopper Penguins in 2012. Differences in data recovered were due to logger failure (3 in 2011, 1 in 2012, and 1 in 2013), and loggers that were lost because penguins did not return to the colony (1 in 2011 and 1 in 2013).
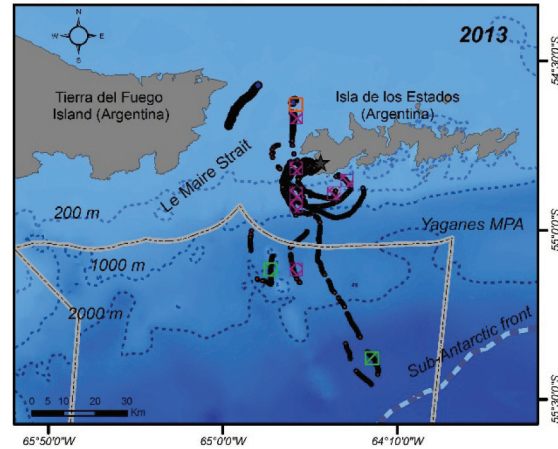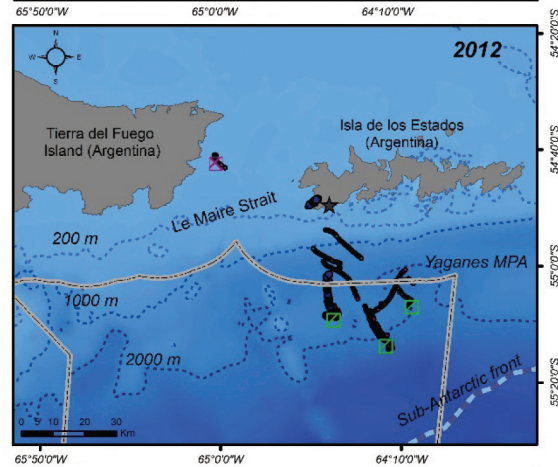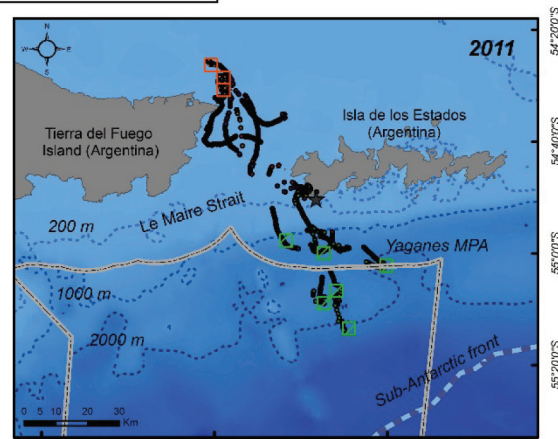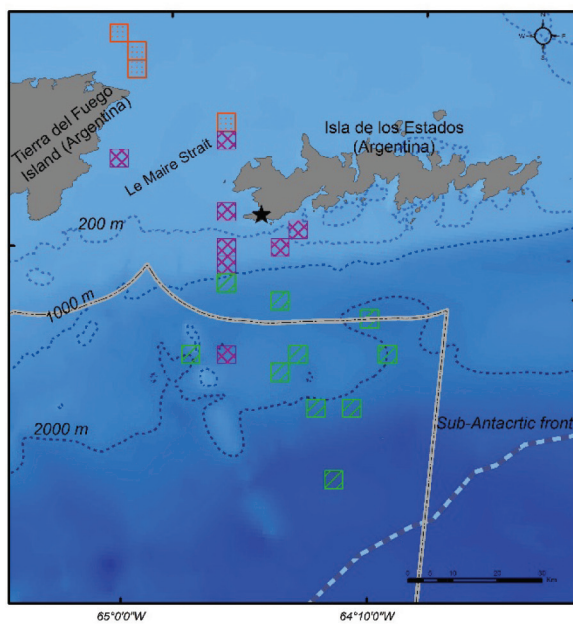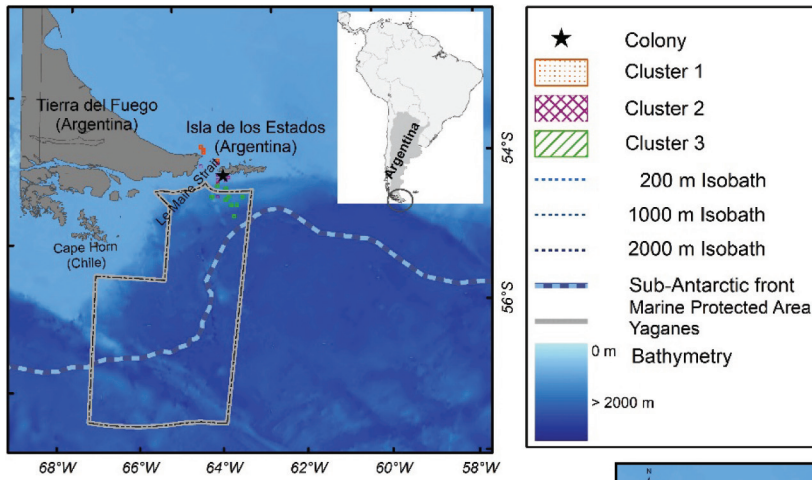
Table 1. Cluster characterization of female Southern Rockhopper Penguins (*Eudyptes chrysocome*) according to the results obtained from clustering analysis *k*-means with respect to diving, tracking, and stable isotope parameters.

	Cluster 1 "neritic" (n = 4)			Cluster 2 "neritic–oceanic" (n = 9)			Cluster 3 "oceanic" (n = 11)		
	Mean ± SD	Minimum	Maximum	Mean ± SD	Minimum	Maximum	Mean ± SD	Minimum	Maximum
Bathymetry (m)	99±4	93	103	589±628	92	2007	2209±631	1549	3764
Distance to 200 m isobath (km)	32±7	4	24	10±9	2	27	28±12	11	53
Distance to the Sub-Antarctic Front (km)	114±13	96	126	76±15	54	104	43±15	18	68
Maximum distance to the colony (km)	36.3±21.3ab	4.7	51.4	16.8±7.8a	5.4	34.4	40.3±14b	20.0	71.3
Trip duration (h)	22.1±8.8b	12.5	32.3	10.8±2.8a	6.8	14.2	24.0±9.2b	12.8	42.5
Mean dive depth (m)	10.6±2.3a	7.6	13.0	11.3±3.7a	6.9	19.1	21.3±6.2b	10.0	30.6
Time in the bottom phase per hour of trip (min/h)	7.6±1.5a	6.3	9.5	9.1±1.5a	6.2	11.1	11.5±2.3b	7.5	15.7
δ^{13}C (‰)	−22.0±0.5	−22.5	−21.4	−22.9±0.6	−24.0	−21.9	−22.6±0.8	−23.6	−20.4
δ^{15}N (‰)	9.9±0.3b	9.6	10.3	8.6±0.6a	7.7	9.4	9.2±0.5a	8.1	9.9

Note: Numbers of individuals (*n*), as well as the mean ± SD for each of the parameters used in the clustering analysis, are provided in the table. Across a row, different letters indicate significant differences after a post hoc test (α = 0.05).

Table 2. Distribution of female Southern Rockhopper Penguins (*Eudyptes chrysocome*) by cluster and by year.

	Year			
Cluster	2011	2012	2013	Total
1	3	0 (2)	1	4 (6)
2	0	1 (3)	8	9 (12)
3	6	3	2	11
Total	9	4 (9)	11	24 (29)

Note: Numbers in parentheses represent the birds that had incomplete data sets and were associated with the clusters obtained after the analysis (see the Results section).

The *k*-means cluster analysis using *k* = 3 fitted well to the data (within-group square sum per group: group 1 = 7.31 (*n* = 4), group 2 = 24.82 (*n* = 9), and group 3 = 59.18 (*n* = 11); within-groups square sum/total square sum = 50.4%). When comparing with the result of the grouping factor *k* = 4, we did not observe a substantial difference in the amount of variability explained (within-groups square sum/total square sum = 57.8%); thus, we chose to use the simplest cluster classification *k* = 3.

Based on the *k*-means cluster analysis, we mapped all individuals by group and identified three different recurrent foraging locations supporting the specified grouping number *k* = 3. Cluster 1 included the female Rockhopper Penguins that headed north towards the coast of Tierra del Fuego Island; cluster 2 consisted of individuals that foraged in areas around Isla de los Estados; and cluster 3 consisted of females that headed south towards the continental slope (Fig. 1). The three groups were well separated by the bathymetry of the respective foraging areas: while individuals in cluster 1 "neritic" remained in waters on the continental shelf (<200 m), individuals in cluster 2 "neritic–oceanic" used both shallow waters around the continental shelf and deeper waters around Isla de los Estados and individuals in cluster 3 "oceanic" foraged in more oceanic waters deeper than 1000 m (Fig. 1, Table 1). Females in cluster 1 "neritic" and cluster 3 "oceanic" traveled longer distances from the colony to feed (36.3 ± 21.3 km (cluster 1), 40.3 ± 14.0 km (cluster 3)), though in opposite directions, whereas females in cluster 2 "neritic–oceanic" fed near the colony (16.8 ± 7.8 km) (Table 1).

Although the incomplete data sets obtained in 2012 had to be excluded (*n* = 5) from the *k*-means analysis, the GPS data recorded allowed the calculation of the foraging trip duration and thus the association of those trips to the different foraging strategies obtained from the *k*-means cluster analysis. Overall, we observed that none of the females used the cluster 2 "neritic–oceanic" strategy in 2011, whereas 8 out of 11 females tracked were found in this cluster in 2013. In 2012, females used mostly the cluster 2 "neritic–oceanic" strategy (4 out of 9) and cluster 3 "oceanic" strategy (3 out of 9) (Table 2).

Foraging trip duration significantly differed between clusters ($F_{[2,19]}$ = 8.99, *p* = 0.002), with cluster 2 "neritic–oceanic" presenting the shortest foraging trips and cluster 1 "neritic" and cluster 3 "oceanic" revealing comparable foraging trip durations (Table 1). Females in cluster 3 "oceanic" dived deeper ($F_{[2,19]}$ = 4.05, *p* = 0.0002; Table 1) and spent more time in the bottom phase per trip hour ($F_{[2,19]}$ = 7.45, *p* = 0.004) compared with cluster 1 "neritic" and cluster 2 "neritic–oceanic" (Table 1). We did not obtain significant inter-annual differences for any of the variables mentioned above.

The δ^{13}C values were similar among clusters ($F_{[2,19]}$ = 2.31, *p* = 0.13) and all δ^{13}C values were lower than −20.0‰ (Fig. 2, Table 1). The δ^{15}N values were significantly higher in cluster 1 compared with cluster 2 and cluster 3 ($F_{[2,19]}$ = 11.92, *p* = 0.0004; Fig. 2, Table 1), and also differed significantly between years ($F_{[2,19]}$ = 4.82, *p* = 0.02) with

Fig. 2. δ^{13}C and δ^{15}N biplot in whole blood for female Southern Rockhopper Penguins (*Eudyptes chrysocome*). Mean values and standard deviations for each of the groups obtained with the clustering analysis are presented as follows: the circle (●) corresponds to females in cluster 1, the times symbol (×) corresponds to females in cluster 2, and the plus symbol (+) corresponds to females in cluster 3. The scattered data refers to each of the years sampled. Color version online.
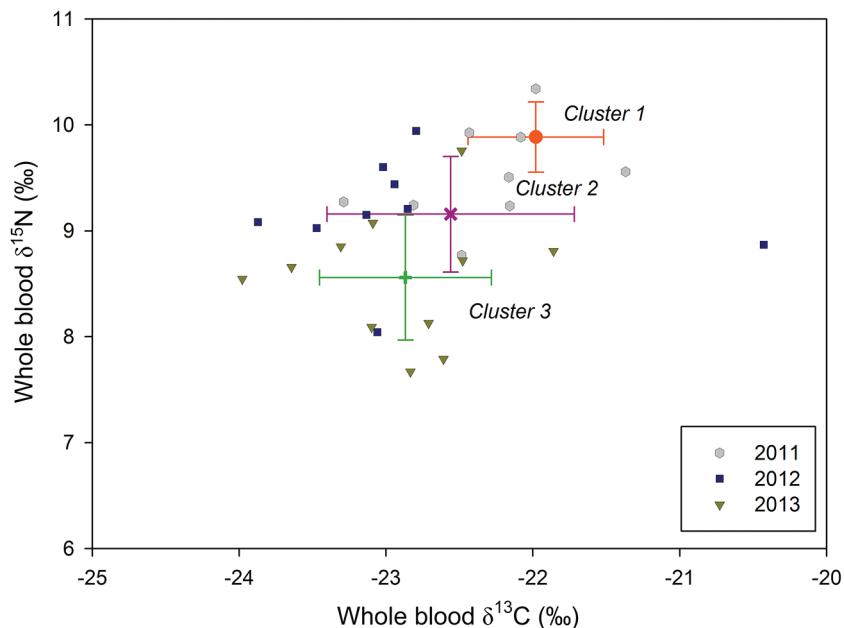

Table 3. Characterization of the areas where female Southern Rockhopper Penguins (*Eudyptes chrysocome*) spent the maximum amount of time based on chlorophyll *a* concentration (Chl *a*) and sea surface temperature (SST).

	Year			Cluster		
	2011 (*n* = 9)	2012 (*n* = 4)	2013 (*n* = 11)	1 (*n* = 4)	2 (*n* = 9)	3 (*n* = 11)
Chl *a* (mg/m^3)	0.6±0.2	0.4±0.2	0.8±0.4	0.7±0.3ab	0.9±0.4b	0.4±0.1a
SST (°C)	7.1±0.9	6.5±0.6	7.1±0.8	8.0±0.0b	7.2±0.7ab	6.5±0.7a

Note: Numbers of individuals (*n*), as well as the mean ± SD for each parameter, are provided in the table. Different letters indicate significant differences after a post hoc test (α = 0.05).

Table 4. Survival of Southern Rockhopper Penguin (*Eudyptes chrysocome*) chicks by year and by cluster.

	Year			Cluster		
	2011 (*n* = 9)	2012 (*n* = 4)	2013 (*n* = 11)	1 (*n* = 4)	2 (*n* = 9)	3 (*n* = 11)
Number of chicks/nest	1.1±0.3	0.8±0.4	0.9±0.3	0.8±0.5	1.0±0.0	1.0±0.5

Note: Numbers of individuals (*n*) and of chicks/nest (mean ± SD) are provided in the table. The nests were monitored from the moment that we deployed loggers on the females attending the nest until the beginning of the crèche period (when fieldwork ended) in all three seasons studied.

penguins in year 2013 (δ^{15}N = 8.6‰ ± 0.6‰) having lower values compared with penguins in year 2011 (δ^{15}N = 9.5‰ ± 0.5‰) and year 2012 (δ^{15}N = 9.4‰ ± 0.4‰). Chlorophyll *a* concentration (Chl *a*; mg/m^3) differed significantly between cluster 2 and cluster 3 ($F_{[2,19]}$ = 8.07, *p* = 0.003; Table 3). Similarly, sea surface temperature (SST; °C) was significantly different between cluster 2 and cluster 3 ($F_{[2,19]}$ = 9.37, *p* = 0.001; Table 3). Cluster 3 had the lowest Chl *a* concentrations and SST. No differences were observed between years either for Chl *a* ($F_{[2,19]}$ = 0.89, *p* = 0.43; Table 3) nor for SST ($F_{[2,19]}$ = 0.58, *p* = 0.58; Table 3) values. Finally, we observed that chick survival was similar between years ($F_{[2,19]}$ = 2.45, *p* = 0.11; Table 4) and clusters ($F_{[2,19]}$ = 0.88, *p* = 0.43; Table 4).

All the cluster × year interactions in the linear models were not significant and thus were discarded to simplify the models.

Discussion

Female Rockhopper Penguins breeding on Isla de los Estados, Argentina, exhibited differential at-sea distribution during their foraging trips at the early chick-rearing period with regards to trip duration, foraging location and associated bathymetry, and dive depth. Spatial segregation in seabirds can be beneficial within a large population as a strategy to relax intra-specific competition (Wakefield et al. 2011; Pütz et al. 2018), but may also be linked to environmental characteristics or prey distribution (Weimerskirch 2007). Furthermore, it could vary in relation to age, sex, reproductive condition and experience, and to some level of individual preferences (Masello et al. 2013; Pelletier et al. 2014; Ceia and Ramos 2015), although this is beyond the scope of this study.

Rockhopper Penguins in this study differed in the areas used to forage (horizontal axis) and in the depth ranges explored (vertical axis). The observed differences in the diving depths may be attributed to a different distribution of the prey and (or) prey sizes within the water column in the distinct foraging areas. Female Rockhopper Penguins that explored greater water depths spent more time in the bottom phase per hour of trip (cluster 3 "oceanic"). Although Bost et al. (2008) suggested that those parameters combined could be indicating a higher foraging success for those penguins, Scioscia et al. (2016) showed an association between a greater foraging effort of Magellanic Penguins (*Spheniscus magellanicus* (J.R. Forster, 1781)) during their foraging trips (e.g., greater % bottom time) for years in which the consumption of Fuegian sprat (*Sprattus fuegensis* (Jenyns, 1842)) (their main prey) decreased. Therefore, further exploration of the effects on the differences presented in the diving profile of female Rockhopper Penguins at the different locations used to forage are desirable (e.g., differences in chick growth and (or) food delivered to chicks). There is evidence for benthic foraging in Rockhopper Penguins (Ludynia et al. 2013; Pütz et al. 2018) and for female *Eudyptes chrysocome filholi* Hutton, 1879 (Tremblay and Cherel 2000) during incubation, suggesting that female Rockhopper Penguins may be able to explore the sea floor. However, and in agreement with previous studies at this location, the dives performed by female Rockhopper Penguins in this study were always pelagic (Schiavini and Raya Rey 2004), since they were too shallow to reach the sea floor, regardless of the foraging area.

The differential at-sea distribution observed (clusters) for female Rockhopper Penguins may also reflect different environmental conditions in the foraging areas and subsequently on the availability of different prey type. For instance, cluster 1 "neritic" and cluster 2 "neritic–oceanic" had similar values for both Chl *a* concentration and SST, which were higher than those in cluster 3 "oceanic". Differences in Chl *a* concentration and SST between years were not statistically significant, and cluster selection by penguins did not depend on year (interaction was not significant), which may indicate that the observed variation in the at-sea distribution of female Rockhopper Penguins during their foraging trips across years may not have been related to annual changes in those environmental characteristics. Moreover, though environmental conditions at sea can rapidly change, female Rockhopper Penguins that were equipped with loggers at the same time (e.g., same day) chose different areas to forage. For example, two females equipped with devices on 9 December 2011 grouped in cluster 1 and cluster 3. In another example, of three females equipped with loggers on 7 December 2012, two females grouped in cluster 3 and one female grouped in cluster 2. Both examples illustrate that the females departed from the colony the same day, but they chose different at-sea areas to forage. This revealed that the areas used to forage did not follow a daily pattern.

Small differences among clusters in δ^{15}N values suggest that the different foraging areas selected by female Rockhopper Penguin presented different availability of prey types and (or) sizes. Consumption of fish can be associated with higher δ^{15}N values compared with crustaceans (e.g., euphausiids; Dehnhard et al. 2016). Thus, the higher δ^{15}N values observed in cluster 1 "neritic" probably indicate higher consumption of fish (e.g., *S. fuegensis*), whereas the lower δ^{15}N isotope value in cluster 3 "oceanic" more likely indicate crustaceans as the main prey source (*S. fuegensis* usually presents higher δ^{15}N values compared with crustaceans, e.g., copepods and euphausiids; Ciancio et al. 2008; Riccialdelli et al. 2017, 2020). Accordingly, blood samples of Rockhopper Penguin chicks at the Falkland/Malvinas Islands showed that the higher δ^{15}N values were associated with greater consumption of fish and squid, and lower δ^{15}N values were associated with a higher prevalence of euphausiids (Dehnhard et al. 2016).

The available information on prey distribution, abundance, and availability in the study area confirm that it is very productive in terms of biodiversity (Sánchez et al. 1995; Hansen 1999; Ivanovic 2010; Padovani et al. 2012; Diez et al. 2016; Riccialdelli et al. 2020), mainly as a result of the frontal areas that occur in the region (Acha et al. 2004). For instance, swarms of swarming squat lobsters (*Munida gregaria* (Fabricius, 1793)) were recently reported occurring on the continental shelf possibly following a recent expansion process occurring throughout their distribution range (Diez et al. 2016). *Sprattus fuegensis* was also reported in the coastal region off southern Patagonia (Sánchez et al. 1995; Hansen 1999); moreover, both species (*S. fuegensis* and *M. gregaria*) usually overlap spatially and share an ecological niche (Diez et al. 2018). Some studies also showed high concentration of zooplankton south of 45° (Sabatini and Álvarez Colombo 2001; Sabatini et al. 2004; Romero et al. 2006) coupled with the higher productivity (Chl *a* concentration) that occurs during spring and summer (October–March). High heterogeneous densities of amphipods (e.g., *Themisto gaudichaudii* Guérin-Méneville, 1825) associated with the large abundance of zooplankton in the Southern Ocean were also reported for the study area (Padovani et al. 2012, 2015). The distribution pattern of these prey types is usually patchy and presents peaks according to productivity of the waters. Further studies that focus on prey distribution and availability specifically in the areas that female Rockhopper Penguin use to forage will contribute to our understanding of the differences in the isotope values observed in this study and if those areas actually present differential prey options for this predators.

Although the most parsimonious explanation to the variation in δ^{15}N values between clusters is related to different prey selected and (or) available in the different foraging areas, we do not fully discard the alternative hypotheses. For instance, the spatial, temporal, and (or) ontogenetic variation in stable isotope values at the base of the food web also has the potential to propagate up the food chain and influence the stable isotope values of marine predators (Polito et al. 2019). Thus, it may be possible that differences in δ^{15}N values in each cluster are related to differences in foraging habitats and their baseline δ^{15}N values. Recent information regarding the variation in the baseline of the food web in the area and the isotopic composition of the prey species for Rockhopper Penguins indicate some degree of spatial variation in δ^{13}C and δ^{15}N values at the base of the food web in the study area (Riccialdelli et al. 2020), thereby emphasizing the need for further studies to fully understand how it may propagate across the food web in the study area.

The δ^{13}C values in this study were low and similar among clusters, indicating that all individuals fed in pelagic and oceanic environments. This is not totally unexpected, because use of oceanic areas was observed, mainly in female Rockhopper Penguins grouped in cluster 3 "oceanic". However, we would have expected higher δ^{13}C values for female Rockhopper Penguins foraging in cluster 1 "neritic" using near-shore foraging habitats, because, for instance, Magellanic Penguins foraging in similar areas presented higher δ^{13}C values in comparison (Rosciano et al. 2018). Yet, the stable isotope data in this study integrate primarily the early chick-rearing period, so they may also include a portion from the late incubation period, during which female Rockhopper Penguins breeding at Isla de los Estados were located foraging to the south and east of the Island, reaching oceanic areas near the Polar Front and the Burwood Bank (Area Protegida Marina Namuncura), respectively (Pütz et al. 2006). These oceanic areas are most likely depleted in ^{13}C (Cherel and Hobson 2007; Lara et al. 2010).

Traveling farther to find food for the chicks can be a trade-off for parents: they will need more time to commute between the colony and the foraging areas, which may affect their reproductive success and hence chick survival (Boersma and Rebstock 2009). This constraint may be compensated with the possibility to prey on higher quality items and (or) more available prey in areas farther away from the colony (Burke and Montevecchi 2009). To have an overview of the breeding success of the female equipped with GPS loggers, we accounted for chick survival

through the early chick-rearing period, and numbers were similar among clusters and years. Therefore, during the guard stage, the length of the foraging trips, in terms of time and distance to the colony, had no effect on chick survival of the birds studied. However, the number of nests followed in our study was quite small; thus, we suggest increasing the sample size in further studies. For example, nesting Rockhopper Penguins at the Falkland/Malvinas Islands colonies showed a growth rate and survival of chicks during the early and late chick-rearing periods that were not affected by the distance from the colony traveled during their foraging trips (Dehnhard et al. 2016). Also, the quality of the adult breeders and their capacity to efficiently forage under harsh environmental conditions (e.g., prey depletion) can determine the efficiency in energy gain that can be translated into successful reproduction, as was demonstrated for Adélie Penguins (*Pygoscelis adeliae* (Hombron and Jacquinot, 1841)) (Lescroël et al. 2010). Future studies are warranted to further explore the observed pattern in this context.

Different foraging areas and diving patterns within a population can mitigate intra-specific competition (Grémillet et al. 2004). The high number of penguins nesting in the area (Schiavini 2000; Raya Rey et al. 2014) may suggest that choosing different foraging areas could act as a mechanism to reduce intra-specific competition as has been reported between neighboring colonies of the species at other locations (Masello et al. 2010) as well as other seabird species (Lewis et al. 2001; Grémillet et al. 2004). This study provides initial knowledge on the at-sea distribution of Rockhopper Penguins during the early chick-rearing period and allows to identify and to plan how the sample size needs to be increased to answer this question (Sequeira et al. 2019). Also, individual specialization and (or) consistency among Rockhopper Penguins may reveal other traits associated with the foraging behavior of the species. Individual consistency in seabirds was reported to reduce intra-specific competition (Ceia and Ramos 2015), revealing the possibility of individual-level differences in foraging strategies (Dingemanse and Dochtermann 2013). Further studies at the Rockhopper Penguin colony located on Isla de los Estados should focus in understanding this behavior, e.g., deploying loggers to record two or more foraging trips per penguin (e.g., Traisnel and Pichegru 2019).

Conclusions

This study provides important data on the spatial distribution of foraging female Rockhopper Penguins during one central phase of their annual cycle, the early chick-rearing period. It enhances our understanding of the distribution of Rockhopper Penguins in the Southwest Atlantic Ocean. It outlines the different foraging areas that female Rockhopper Penguins use during the early chick-rearing period, associated with dive depths explored and most likely different type of prey selected, which may reflect different strategies selected by female Rockhopper Penguins. Although the underlying mechanisms of this differential use of the water masses around Isla de los Estados remain unclear, the prospect of flexibility in the foraging behavior and the availability of several foraging areas within reach of the colony are important features in a scenario of constant environmental changes for a penguin population such as the Rockhopper Penguin (e.g., Pütz et al. 2018). Further studies are needed to fully explore individual specialization and (or) consistency among Rockhopper Penguins that may reveal other traits associated with the foraging behavior of the species. This study fills gaps in our knowledge of the spatial distribution of this penguin species during its complete annual cycle (Pütz et al. 2006, 2018; Raya Rey et al. 2007), strengthening that female Rockhopper Penguins foraged inside the northern limits of the recently created Marine Protected Area "Yaganes" (particularly, female Rockhopper Penguins in cluster 3 "oceanic"; Fig. 1) to protect the vast wildlife occurring in the area, preventing fisheries and (or) other extractive activities in the area (DNC/APN

2017). Thus, this study complements available information on the use of the Southern Ocean by marine mesopredators and top predators and contributes to marine spatial planning in the area.

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