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Foraging behaviour of Magellanic Penguins during the early chick-rearing period at Isla de los Estados, Argentina

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Studies of the at-sea distribution and trophic ecology of penguins are essential to understand their role in the broader marine food web. Magellanic Penguins *Spheniscus magellanicus* have a wide distribution and their foraging behaviour varies across breeding sites and between sexes, among others. In this study, we characterized the at-sea areas, the diving strategies and the relative trophic level of Magellanic Penguins breeding at Isla de los Estados, Argentina, during the early chick-rearing period. In addition, we quantified the interannual, sexual and individual variability in those parameters during three breeding seasons (2011–2013) using devices recording position and dive depth, and obtained blood samples for stable isotope analysis. During the early chick-rearing period, Magellanic Penguins showed small differences between the sexes in their foraging behaviour and large overlap in the at-sea areas used, suggesting no intraspecific variation between sexes. Although there was interannual variability in the foraging behaviour and the trophic level of the penguins, most of the studied nests managed successfully to raise both chicks during the first stage of the breeding cycle (guard stage). The foraging ecology of Magellanic Penguins from this colony was comparable with results of past studies at other breeding colonies. This study contributes to the identification of important at-sea areas for Magellanic Penguins at the southern edge of their distribution and also to the identification of possible threats in the study area such as interaction with fisheries.

Keywords: at-sea distribution, diving behaviour, Isla de los Estados, *Spheniscus magellanicus*, stable isotope, trophic ecology.

Penguins are considered sentinels of the marine environment, with their population and dietary trends integrating changes occurring at lower trophic levels in the oceans (Boersma 2008). As such, studies of the at-sea distribution and trophic ecology of penguins are essential to understand their role in the broader marine food web. For example, the foraging behaviour of many penguin species is known to vary among colonies (Wilson *et al.* 2005, Boersma *et al.* 2009, Masello *et al.* 2010, Sala *et al.* 2012), between sexes (Clarke *et al.* 1998, Walker & Boersma 2003, Saraux *et al.* 2011, Raya Rey *et al.* 2012, Xavier *et al.* 2017) and also between breeding stages (Williams & Rothery 1990, Raya Rey *et al.* 2012). Among all stages of the life cycle, the reproductive stage is crucial because penguins are restricted to exploit resources within a given range around the colony and they need to maximize prey energy consumed while foraging to deliver food regularly to chicks (Costa 1991).

Magellanic Penguins *Spheniscus magellanicus* breed all along Patagonia Argentina, Malvinas/

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Falkland Islands and Chile (Schiavini *et al.* 2005, Boersma *et al.* 2013). Studies of this species using bio-logging technologies have allowed researchers to identify foraging areas and diving behaviour of penguins across multiple breeding sites (e.g. Radl & Culik 1999, Boersma *et al.* 2002, 2009, 2015, Pütz *et al.* 2002, Walker & Boersma 2003, Wilson *et al.* 2005, Raya Rey *et al.* 2010, 2012, Sala *et al.* 2012). These studies have found differences in foraging trip parameters across breeding sites, such as a longer trip duration or a larger distance travelled to foraging areas in the northern colonies than in the southern ones (Wilson *et al.* 2005, Boersma *et al.* 2009, Sala *et al.* 2012), and also how those parameters relate to the diving behaviour of penguins, such as deeper dive depths in the northern than in the southern colonies (Wilson *et al.* 2005). In addition, conventional and stable isotope dietary studies indicated differences in trophic levels (Forero *et al.* 2002, Weiss *et al.* 2009, Ciancio *et al.* 2015, Yorio *et al.* 2017) and prey items consumed (Thompson 1993, Frere *et al.* 1996, Radl & Culik 1999, Scolaro *et al.* 1999, Pütz *et al.* 2001, Scioscia *et al.* 2014) by Magellanic Penguins along their distribution, which reflects the availability of prey resources across their distribution range.

Recent studies have also revealed differences in diet composition (through stable isotope analysis) of Magellanic Penguins between sexes, ages (e.g. chicks, juveniles and adults) and stages of the life cycle (e.g. breeding, pre-moult; Forero *et al.* 2002, Silva *et al.* 2014, Yorio *et al.* 2017). Magellanic Penguins present a sexual dimorphism in body size, with males being 5–15% larger than females (Gandini *et al.* 1992, Agnew & Kerry 1995, Forero *et al.* 2001). In seabirds, dietary differences between dimorphic sexes (Clarke *et al.* 1998, Ratcliffe *et al.* 2013) and individual-level differences in foraging strategies (Dingemanse & Dochtermann 2013, Ceia & Ramos 2015) can act to reduce intraspecific competition. Some of those differences regarding sexual dimorphism were also observed in Magellanic Penguins (Walker & Boersma 2003, Scioscia *et al.* 2010, Raya Rey *et al.* 2012), but they may only arise when environmental conditions and prey availability are not favourable (Raya Rey *et al.* 2012). Although the foraging ecology of Magellanic Penguins has been relatively well studied, the high degree of variation both within and between breeding sites highlights the need for continued, site-specific and long-term studies on the different colonies.

Nesting Magellanic Penguins at Isla de los Estados, Argentina, at the southernmost edge of their distribution, increased over a period of more than 10 years (Raya Rey *et al.* 2014). In this study we performed a comprehensive survey of the trophic ecology of Magellanic Penguins during the early chick-rearing period at Isla de los Estados, over three consecutive breeding seasons. Specifically, we aimed to characterize the foraging areas and diving behaviour using bio-logging and to examine relative trophic level and habitat use through analysis of stable isotopes. We also aimed to quantify the degree of interannual, sexual and individual variability within these aspects of the foraging ecology of this species. Based on past studies, we would expect to find some differences between the sexes in diving parameters, such as the dive depth, and similarities in foraging behaviour, such as foraging trip distance and duration, with other colonies in southern Patagonia.

METHODS

Study area and sample collection

The study was carried out at the Magellanic Penguin colony located in the southwest of Bahia Franklin at Isla de los Estados (54°38′S, 63°48′W; Fig. 1). As of 2010 this breeding site holds around 1600 breeding pairs (Raya Rey *et al.* 2014). Isla de los Estados is separated by the 30-km-wide Le Maire Strait from Tierra del Fuego Island (Ponce & Fernández 2014 and references therein).

We collected data during three consecutive breeding seasons (2011, 2012 and 2013) from the end of November to mid-December (range of dates: 26 November to 20 December 2011; 4 December to 22 December 2012; 29 November to 17 December 2013). We randomly selected nests at the colony and equipped one individual per nest with GPS data loggers (GPS-TDlog, precision GPS and Temperature/Depth Recorder – Earth & Ocean Technologies, Kiel, Germany). We gently removed breeding adults from their burrows using a hook attached to a rod (Raya Rey *et al.* 2012). Then, we weighed them with a Pesola balance (to the nearest 100 g) and measured bill-depth and bill-length using callipers (to the nearest 0.02 mm) to determine sex of individuals, as these measurements are considered to be the most appropriate to sex the birds (Gandini *et al.* 1992). We attached the GPS data logger along the

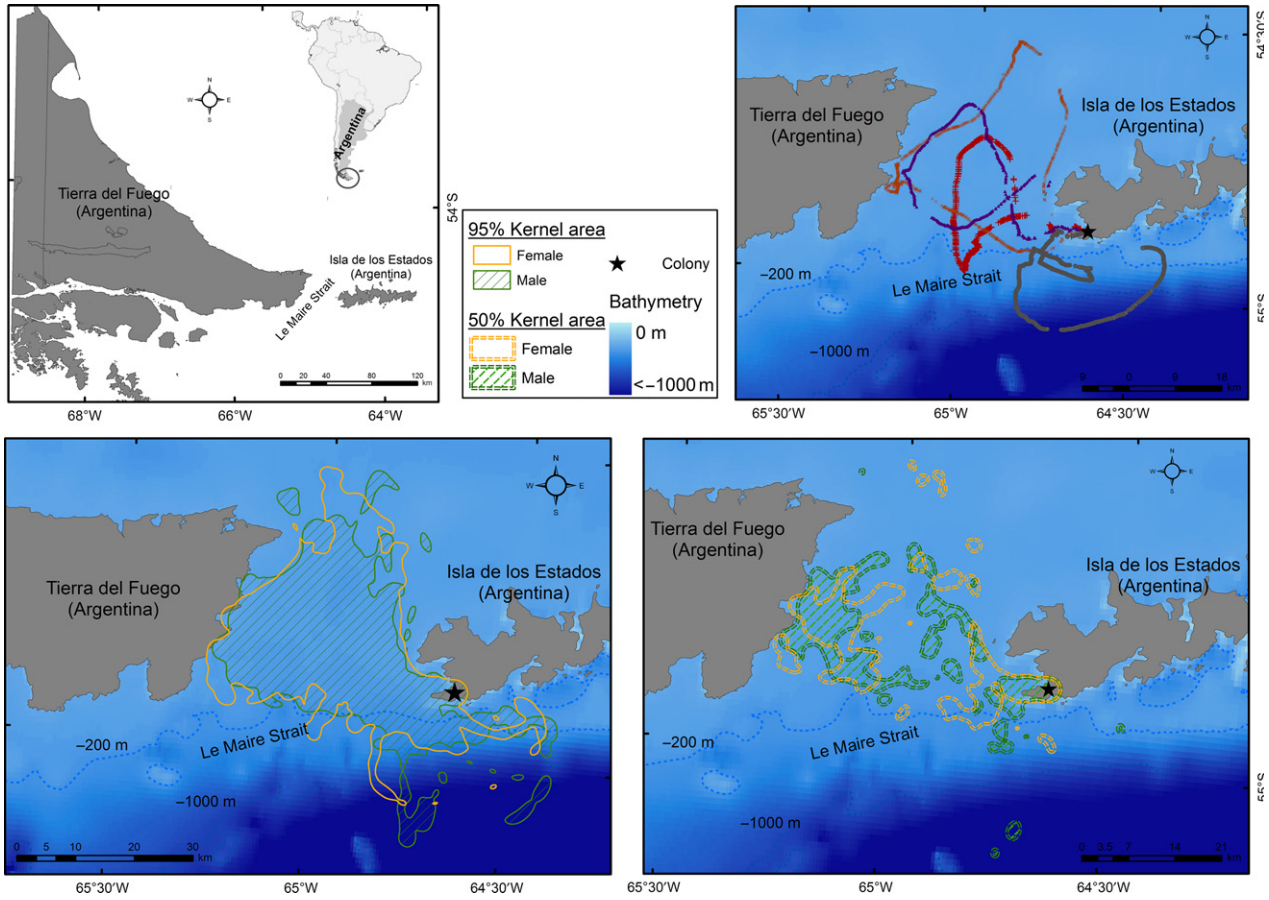

Figure 1. Study area and at-sea areas used by male and female Magellanic Penguins. Upper left, Tierra del Fuego Island and Isla de los Estados, Argentina. Upper right, examples of five tracks performed by five different Penguins, showing the loop-shape consistently seen on the foraging trips recorded. The lower maps show the 95% (left) and 50% (right) kernel density distribution that reflect the home-ranges and core areas, respectively, of the Penguins at sea for males and females encompassing the three breeding seasons studied (2011, 2012 and 2013).

midline of the Penguin's back using black tape (Tesa, Beiersdorf AG, Hamburg, Germany) covered with a layer of quick-drying epoxy glue to prevent the birds from removing the tape with their bills, following Wilson *et al.* (1997; method 2). The whole process took less than 20 min per bird. We programmed the GPS data loggers (size: 11.6 × 3.5 × 2 cm, 61 g, representing 1.3–1.6% of the individuals' mass) to record temperature and depth every 2 s, and latitude and longitude every 2 min. We weighed chicks while deploying the device on the adult as a proxy of chick age.

When devices were recovered (on average 3 ± 1 days after deployment), we collected whole blood samples from the tarsal vein of the Penguins into microcapillary tubes (~75 μL). Blood was preserved in 70% ethanol until later processing in the laboratory. Several studies in the past showed little effect of alcohol preservation on the stable isotope values of whole blood (Hobson *et al.* 1997, Halley *et al.* 2008, Therrien & Fitzgerald 2011, but see Bugoni *et al.* 2008). We checked nests of equipped Penguins every week until the end of the fieldwork to determine chick survival. We measured chick survival as the number of chicks per nest towards the end of December when fieldwork ended.

Diving and tracking analysis

We analysed temperature and depth data from the GPS-TDlog using MULTITRACE SOFTWARE (Jensen Software Systems, Kiel, Germany). We calculated diving parameters for each trip using dives

> 1 m following Raya Rey *et al.* (2012) and grouped these parameters into three categories for subsequent analysis: (1) *Feeding effort*: trip duration (h); percentage of time diving (%); dive rate (number of dives/h); (2) *Feeding activity*: bottom time per hour of dive (min/h; bottom time: the time a Penguin had a vertical speed ≤ 0.3 m/s while diving, detection criteria for the bottom phase 'Normal' in MULTITRACE); wiggle rate (number of wiggles/total time in bottom phase); (3) O*ther parameters*: average dive depth (m) and average dive duration (h) across all dives in a foraging trip. We analysed GPS data using ARCGIS 9.3.1 to calculate several foraging trip parameters, including: maximum distance to the colony (km), total distance covered (km), total area covered (km^2) calculated by the polygon covering all locations during the foraging trip, and sinuosity (maximum distance/total distance covered). When multiple foraging trips per individual were recorded, we evaluated the relative effects of year and individual for a subset of parameters listed above (dive rate, mean dive depth, trip duration, maximum distance to the colony and total trajectory) to quantify variation between and within individuals.

We used kernel density estimation analysis to compare foraging area use between sexes and among years. We calculated 95% and 50% kernel density areas, representative of the home-range and core areas, respectively, of the distribution at sea (Wood *et al.* 2000, Raya Rey *et al.* 2013), using the fixed kernel density estimator (Hawth's analysis tools; Beyer 2004) and the standardized smoothing factor (h = 1000) and a raster cell-size (100 m), which fitted the data well. We calculated the area and percentage overlap between males and females using the *Intersect tool* (*Analysis tools*) in ARCGIS 9.3 (ESRI). In addition, we characterized the foraging areas used by Penguins, using a bathymetric chart obtained from General Bathymetric Chart of the Oceans (GEBCO, 30 arc-second resolution; www.gebco.net), chlorophyll *a* (mg/m^3) and sea surface temperature (°C) satellite images obtained from Aqua-Modis (4 × 4 km cell resolution; http://oceancolor.gsfc.nasa.gov), and used the criteria of Hyrenbach *et al.* (2002) to characterize the foraging areas in terms of those environmental features (e.g. oligotrophic waters with chlorophyll concentrations < 0.1 mg/m^3; mesotrophic waters 0.1–0.3 mg/m^3; eutrophic (high productivity) waters 0.3–1 mg/m^3; and enriched waters with chlorophyll concentrations > 1 mg/m^3).

Stable isotope analysis

We first dried whole blood samples from Magellanic Penguins in an oven at 60 °C for 24 h and then freeze-dried samples in a lyophilizer. We weighed approximately 0.50-mg aliquots of each sample into tin cups that were flash-combusted (Costech ECS4010 or PDZ Europa ANCA-GSL elemental analysers) for $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$. Stable isotope abundances were expressed as δ in parts per thousands (‰), according to the following equation:

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

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 $\delta^{13}C$ values were normalized for the effects of lipid concentration on $\delta^{13}C$ methods following Post *et al.* (2007) as C : N ratio values indicated variable concentration of ^{13}C-depleted lipids (Cherel *et al.* 2005). As data on prey isotopic values in proximity to our study region were not available from the literature or other sources, we could not calculate Penguin diet composition using stable isotope mixing models. However, we calculated the trophic level (TL) for the individuals sampled to evaluate their position in the trophic chain and we also compared results between sexes and years. For TL calculation we used the equation modified from Hobson *et al.* (1994):

$$\text{TL}_{\text{predator}} = \text{TL}_{\text{baseline}} + \left(\frac{\delta^{15}\text{N}_{\text{predator}} - \delta^{15}\text{N}_{\text{baseline}}}{\Delta\text{N}_{\text{foodweb}}}\right),$$

where $\text{TL}_{\text{predator}}$ is the trophic level value of the individual being analysed, $\text{TL}_{\text{baseline}}$ the trophic level of the baseline chosen for the equation, $\delta^{15}\text{N}_{\text{baseline}}$ is its nitrogen isotope composition,

$\delta^{15}N_{predator}$ is the nitrogen isotopic composition of the individuals in the study, and $\Delta N_{foodweb}$ is the mean food web trophic fractionation factor, in this case 3.4‰, which is a robust value across multiple food webs (DeNiro & Epstein 1981, Minagawa & Wada 1984, Post 2002, Søreide *et al.* 2006, Brasso & Polito 2013). As a baseline value we used zooplankton (mostly copepods) TL = 2 $\delta^{15}N$ = 8.16‰ (sample taken on March 2014 in the Le Maire Strait: 54°41′17.58″S, 64°46′51.24″W; L. Riccialdelli unpubl. data). This approach allowed for qualitative comparisons of the trophic position of Penguins between Isla de los Estados and past studies at other breeding colonies.

Statistical analysis

We calculated the index of sexual dimorphism using the morphometric measurements from individuals equipped with GPS loggers following Forero *et al.* (2001). We also used regression analysis between diving and tracking parameters (trip duration, percentage of time diving and time in the bottom phase per hour of dive) and the sum of chick mass and its squared term (in case the relationship was not linear) at the time of the recorded foraging trip, to assess whether the foraging behaviour of parents changed with the age of chicks. We used linear models (LM) to assess differences between sexes and years in Magellanic Penguin diving and foraging trip parameters, stable isotope values, and trophic level. If the assumption of homogeneity of variance was not met using graphical diagnostics (Zuur *et al.* 2009) we fitted generalized least square models (GLS) with *varIdent* variance function (*nlme* package; Pinheiro *et al.* 2015) to estimate different variances per sex and/or year. We compared models using likelihood ratio tests (LR) and Akaike's information criterion (AIC; Pinheiro & Bates 2000, Zuur *et al.* 2009) and discarded sex × year interactions when not significant in order to simplify the model. When significant differences were found between sex and/or year, pairwise comparisons were examined (*lsmeans* package; Lenth & Herve 2015).

To assess individual variability among the diving and tracking parameters in the 15 individuals for which we recorded consecutive trips (13 individuals with two trips, one individual with three trips, and one individual with four trips) we fitted a linear mixed-effects model (LMM; Pinheiro *et al.* 2015). We considered the non-independence of trips within an individual and between individuals within year. We evaluated the nested effect of the individual (penguin) within year as random effects and sex as a fixed effect. We used variance component analysis to calculate the proportion of the variance explained by each random effect of the mixed-model (Zuur *et al.* 2009). We selected as response variables of the models those that were representative of foraging behaviour: trip duration (h), dive rate (dives/h), mean dive depth (m), maximum distance to the colony (km) and total trajectory covered (km).

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 ± standard deviation (sd).

RESULTS

We obtained tracking data and whole blood samples from 48 individuals (eight females and eight males in 2011; nine females and nine males in 2012; eight females and six males in 2013; mean per individual 1.4 ± 0.6 trips). However, we recovered diving data from only 35 individuals, as data from only two males and three females were obtained in 2012 due to logger failures (mean per individual 1.3 ± 0.6 trips). Body mass averaged 3.9 ± 0.4 and 4.7 ± 0.4 kg, bill length averaged 50.9 ± 2.5 and 54.8 ± 2.3 mm, and bill depth averaged 21.42 ± 1.03 and 25.1 ± 1 mm for females and males, respectively. Dimorphism indices were 84.2% for body mass, 92.7% for bill length and 85.2% for bill depth.

All but two pairs were still raising two chicks by the time fieldwork ended and the average brood size of all nests studied by the end of December was 1.90 ± 0.33, 2.00 ± 0.00 and 1.80 ± 0.53 in 2011, 2012 and 2013, respectively (1.9 ± 0.07 overall). Based on chick mass during the study period (Table S1) individuals were in the early chick-rearing period, with chick age ranging from 0 to 35 days after hatching (Scioscia *et al.* 2016). Regression analyses against chick mass were not significant for trip duration (2011: $F_{2,13} = 0.02$, $P = 0.98$; 2012: $F_{2,2} = 0.43$, $P = 0.70$; 2013: $F_{2,11} = 3.11$, $P = 0.09$), percentage of time diving (2011: $F_{2,13} = 1.78$, $P = 0.21$; 2012: $F_{2,2} = 5.76$, $P = 0.15$; 2013: $F_{2,11} = 1.45$, $P = 0.28$) or time in bottom phase/hour of dive (2011: $F_{2,13} = 3.48$, $P = 0.06$; 2012: $F_{2,2} = 3.85$, $P = 0.21$; 2013: $F_{2,11} = 1.67$, $P = 0.23$).

Diving data

The overall maximum dive depth observed was 95 m for females and 85 m for males, although most dives were shallow at between 5 and 15 m. Maximum dive duration was 160 s (2.67 min) and 138 s (2.3 min) for females and males, respectively, and mean dive duration ranged between 20 and 60 s. Foraging dives (dives deeper than 5 m) were observed during twilight and daylight hours, but never during the night. Colony departures occurred in the morning (02:00 to 12:00 h) and afternoons (14:00 to 20:00 h) and arrivals were in the morning (04:00 to 12:00 h), afternoon (13:00 to 18:00 h) and evenings (21:00 to 22:00 h) local time. Most Penguins performed overnight trips and only in 20% of the trips (12 trips) did individuals return to the colony within the same day. Trip duration did not differ between sexes ($F_{1,31} = 0.009$, $P = 0.93$) or years ($F_{2,31} = 2.36$, $P = 0.11$; Table 1) and on average individual trips lasted 19.10 ± 8.31 h. The percentage of time spent diving did not differ between sexes ($F_{1,31} = 0.04$, $P = 0.84$), although Penguins spent less time diving in 2011 than in other years ($F_{2,31} = 3.76$, $P = 0.03$; Table 1). Females had a higher dive rate (dives/h) than males across all years ($F_{1,31} = 876$, $P = 0.006$). Dive rates were significantly higher in 2013 than in 2012 or 2011 ($F_{2,31} = 12.75$, $P = 0.001$). Dive rate was more variable among females than males (*variance per sex* = 10.73 and 5.87, respectively) and dive rate in 2013 was more variable compared with 2011 and 2012 (*variance per year* = 9.23, 5.87 and 1.90, respectively; LR for different variances per sexes and years = 15.39, $P = 0.002$; Table 1).

Bottom time per hour of dive (min/h) did not differ between sexes ($F_{1,31} = 2.67$, $P = 0.11$) but was greater during 2013 and 2012 relative to 2011 ($F_{1,31} = 6.09$, $P = 0.006$; Table 1). This dive parameter was also more variable in 2013 compared with 2012 and 2011 (*variance per stratum* = 3.53, 1.69 and 1.40, respectively; LR = 11.21, $P = 0.004$). Wiggle rate was similar between males and females (wiggles/min in bottom phase; $F_{1,31} = 0.17$, $P = 0.68$), but was significantly lower in 2013 than in 2012 ($F_{2,31} = 4.1$, $P = 0.03$; Table 1). Males in 2011 showed the

Table 1. Mean (sd) foraging trip parameters for male and female Magellanic Penguins nesting in Isla de los Estados during the 2011, 2012 and 2013 breeding seasons. Sample sizes are given for each year and sex.

	2011		2012		2013	
Diving data	Males (n = 8)	Females (n = 8)	Males (n = 2)	Females (n = 3)	Males (n = 6)	Females (n = 8)
Foraging effort						
Trip duration (h)	22.71 (8.56)	22.03 (6.77)	21.99 (5.39)	21.85 (3.10)	18.42 (7.10)	15.87 (9.22)
% of time diving	27.25 (10.77)	21.90 (5.60)	34.84 (5.37)	42.61 (6.29)	31.94 (10.13)	30.41 (12.80)
Dive rate (dives/h)	18.51 (5.63)	20.37 (6.45)	28.35 (3.95)	33.36 (3.11)	34.30 (10.69)	35.69 (16.18)
Foraging activity						
Time in the bottom phase/hour of dive (min/h)	3.55 (1.18)	3.99 (1.37)	5.73 (1.79)	7.93 (1.96)	6.55 (2.77)	5.52 (3.42)
Wiggle rate (wiggles/min in bottom phase)	0.76 (0.55)	0.27 (0.16)	0.38 (0.12)	0.22 (0.09)	0.14 (0.09)	0.19 (0.18)
Other parameters						
Mean dive depth (m)	15.91 (6.32)	10.76 (2.60)	12.94 (5.54)	11.56 (4.59)	6.82 (1.70)	6.19 (2.05)
Mean dive duration (s)	46.01 (9.15)	45.53 (17.17)	44.51 (6.72)	46.21 (7.18)	31.66 (6.43)	30.99 (4.37)
Tracking data	Males (n = 8)	Females (n = 8)	Males (n = 9)	Females (n = 9)	Males (n = 6)	Females (n = 8)
Maximum distance to the colony (km)	34.48 (8.37)	36.49 (6.22)	28.74 (12.18)	34.46 (8.39)	21.6 (14.39)	26.97 (13.16)
Total trajectory (km)	109.79 (31.39)	111.57 (27.3)	83.24 (35.74)	106.46 (22.86)	65.93 (38.82)	97.69 (54.63)
Area (km^2)	277.93 (203.54)	176.69 (137.89)	166.88 (109.45)	229.79 (104.21)	95.97 (94.76)	185.59 (172.99)
Sinuosity (maximum distance/trajectory)	0.32 (0.06)	0.33 (0.05)	0.34 (0.04)	0.33 (0.06)	0.32 (0.07)	0.28 (0,06)

greatest variance in wiggle rate across groups (*variance per stratum* = 0.65 males in 2011, rest of the groups < 0.2; LR = 25.38, $P < 0.001$). Mean dive depth did not differ between sexes ($F_{1,31} = 0.09$, $P = 0.76$), but was shallower in 2013 than in 2011 ($F_{2,31} = 11.36$, $P = 0.0002$; Table 1). This dive parameter was also more variable in 2011 and 2012 relative to 2013 (*variance per stratum* = 5.73, 5.50 and 1.95, respectively; LR = 10.24, $P = 0.006$). Dive duration was similar between sexes ($F_{1,31} = 0.09$, $P = 0.77$) but was shorter in 2013 than in the other two years ($F_{2,31} = 8.97$, $P = 0.0008$; Fig. 2, Table 2). This dive parameter was also more variable in 2011 and 2012 than in 2013 (*variance per stratum* = 13.85, 7.31 and 5.38, respectively; LR = 11.14, $P = 0.004$; Table 1).

Tracking data

Seventy-five per cent of foraging trips were along the Le Maire Strait to the west-northwest of the breeding site, with the remaining directed south-southeast (Fig. 1). Maximum distance travelled to the colony ($F_{1,44} = 0.37$, $P = 0.55$), total trajectory covered ($F_{1,44} = 0.71$, $P = 0.40$), total area ($F_{1,44} = 0.07$, $P = 0.79$) and sinuosity ($F_{1,44} = 0.27$, $P = 0.61$) of trips were similar for both sexes, although there was a high interannual variability. Maximum distance was similar between years ($F_{2,44} = 3.09$, $P = 0.06$), although the model included different variances per year (LR = 5.49, $P = 0.06$; $AIC_{variance\ function\ year} = 351.85$ vs. $AIC_{no\ variance\ function} = 353.35$). Maximum distances were more variable in 2013, followed by 2011 and 2012 (*variance per stratum* = 13.46, 10.84 and 7.29, respectively; Fig. 2). The total trajectory covered was similar between years ($F_{2,44} = 1.14$, $P = 0.33$; Table 1), as on average Penguins travelled 31.02 ± 11.18 km from the colony (range: 4.61–45.11 km), covering a trajectory of 96.60 ± 37.78 km. The area covered was similar among years ($F_{2,44} = 1.08$, $P = 0.35$), although the greatest variance was seen in 2011, followed by 2012 and 2013 (*variance per stratum* = 182.99, 76.38 and 30.13, respectively; LR = 10.89, $P = 0.004$). Sinuosity also did not differ between years ($F_{2,44} = 2.54$, $P = 0.09$). Penguins performed foraging trips with a mean sinuosity value of 0.33 ± 0.05 (range 0.42–0.18), indicative of loop-shaped trips rather than direct-return trips to a preferred foraging zone (Fig. 1, Table 1) or even zig-zag movements during the inbound and outbound part of the trip.

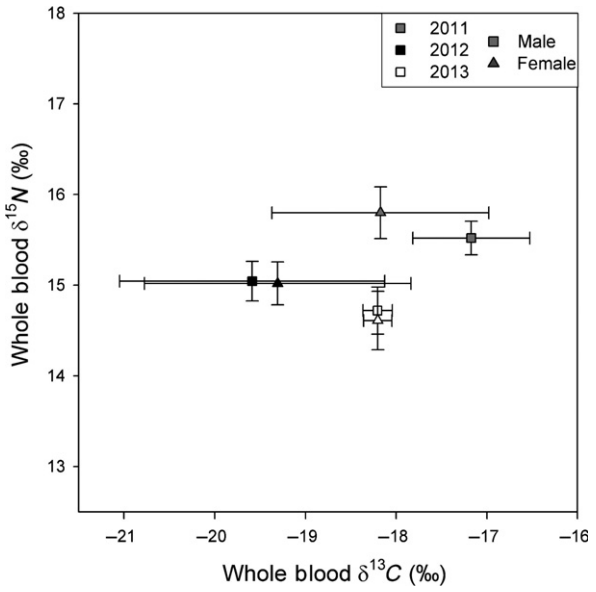

Figure 2. Whole blood stable nitrogen and carbon isotope values (mean ± sd) for Magellanic Penguins breeding on Isla de los Estados, during the early chick-rearing period. Males are represented by squares and females by triangles. Different breeding seasons are defined with different shading.

Kernel density areas were merged across years due to similarities in the areas used and the lack of interannual differences in maximum distance and trajectories. Home-ranges (95% kernel areas) were similar for males (1080 km^2) and females (1067 km^2), with an average overlap of 78% (Fig. 1). Core areas (50% kernel area) of males (258 km^2) and females (249 km^2) overlapped on average by 49% (Fig. 1). Due to this high overlap, we combined the sexes when characterizing the environmental features of foraging areas in each year. Descriptions of environmental characteristics of 50% and 95% kernel areas are detailed in Table 2. Individuals generally foraged in coastal waters and only in a few cases were water depths of 200–1000 m reached.

Individual variability and stable isotope data

We recorded tracking data from 33 consecutive foraging trips (12 males and three females) and diving data from 16 consecutive foraging trips (six males and two females). Foraging trip duration was as variable among individuals as within individuals, but dive rate varied more within

Table 2. Characterization of male and female Magellanic Penguin foraging areas in terms of bathymetry, productivity (chlorophyll *a*) and sea surface temperature (SST; °C). Mean values (sd) are provided for home-range (95% kernel areas) and core areas (50% kernel areas).

	Water depth (m)		Chlorophyll *a* (mg/m^3)		SST (°C)	
	Core area 50% kernel	Home-range 95% kernel	Core area 50% kernel	Home-range 95% kernel	Core area 50% kernel	Home-range 95% kernel
2011	87 (31)	82 (34)	1.68 (0.52)	1.46 (0.28)	8.2 (0.2)	8.1 (0.1)
2012	187 (333)	185 (270)	0.65 (0.14)	0.66 (0.09)	7.2 (0.2)	7.3 (0.1)
2013	69 (86)	121 (179)	1.14 (0.57)	1.26 (0.56)	7.1 (0.6)	7.2 (0.5)

individuals than among individuals (Table 3). The maximum distance to the colony and the trajectory covered was more variable between individuals than within individuals (Table 3). Differences among years explained the highest degree of interindividual variability in mean dive depth followed by the residual term (Table 3).

Whole blood δ^{13}C values did not differ between sexes ($F_{1,44} = 1.43$, $P = 0.24$) but were lower in 2012 relative to other years ($F_{2,44} = 7.16$, $P = 0.002$; Fig. 2). The model included different variances per year; 2012 was the most variable followed by 2011 and 2013 (1.5, 1.2 and 0.2, respectively; LR = 41.95, $P < 0.001$). Whole blood δ^{15}N values also did not differ between sexes ($F_{1,44} = 0.37$, $P = 0.55$) but differed among years ($F_{2,44} = 54.44$, $P < 0.001$), being highest in 2011 and lowest in 2013 (Fig. 2). Calculated trophic level did not differ between sexes ($F_{1,44} = 0.003$, $P = 0.96$), but differed among years ($F_{2,44} = 59.05$, $P < 0.001$). Trophic level was highest in 2011 and lowest in 2013 (Table S2).

DISCUSSION

Similar to results from previous studies, male Magellanic Penguins breeding on Isla de los Estados were 7–16% bigger than the females (Gandini *et al.* 1992, Agnew & Kerry 1995, Forero *et al.* 2001, Walker & Boersma 2003). Despite this, birds displayed only slight sexual differences in foraging behaviours, albeit with large interannual variation. These interannual differences were probably not a product of slight variation in the timing of data collection in each year, as both male and female foraging behaviours were not related to chick mass as a proxy of age. However, among the foraging effort parameters studied, female Magellanic Penguins showed a higher dive rate than males, indicating that they invested more effort than males during their foraging trips (e.g. Ryan *et al.* 2004, Petersen *et al.* 2006). Foraging effort parameters, such as trip duration and dive rate, were more variable among consecutive trips of the same individual than between individuals, at least in males. This low within-individual repeatability could indicate a high plasticity of foraging behaviour at the individual level.

There was large variability in specific diving parameters among years. In particular, during 2013, Penguins showed higher diving effort (e.g. percentage of time diving and dive rate) and spent more time in the bottom phase, thereby performing fewer wiggles per minute bottom phase. Also, they performed shallower and therefore shorter dives in 2013 compared with the other two years. These results could indicate a change in the prey distribution and/or availability in the area, a switch in Penguin diet or a change in the proportion of different prey items consumed during this particular year. Similarly, 2013 had the lowest δ^{15}N values and trophic level measured among years. Also in that year, the Penguins performed either long or short trips with a high variance in the maximum distances reached. Differences in diving parameters may therefore be associated with the type of prey consumed and foraging areas chosen in relation to the distance to the colony. A study on Adélie Penguins *Pygoscelis adeliae* did not reveal any differences in the diving parameters of penguins when foraging on different prey items (Ropert-Coudert *et al.* 2002). However, Magellanic Penguins breeding on Martillo Island, Beagle Channel, showed a relationship between the amount of Squat Lobster *Munida gregaria* consumed and deeper and longer dives, with more time spent during the bottom phase per hour and a higher number of wiggles (Scioscia *et al.* 2016).

Table 3. Components of variance in the diving and tracking parameters of Magellanic Penguin foraging trips, partitioned among years, among Penguins in a year, and within trips of an individual Penguin. Percentages of each component of variance are presented in bold, as well as significant results from an LR test when comparing between models with different random structure.

	F-test	*P*-value	
Trip duration (h)			
Effect			
Fixed			
Intercept	$F_{1,10} = 48.60$	< 0.0001	
Sex	$F_{1,7} = 0.01$	0.91	
Random	Variance (sd)	%	LRT
Year	$3.91e^{-07}$ (0.0006)	**0**	$L = 1.13e^{-08}$, $P = 0.9$
Penguin ID	38.75 (6.22)	**52**	$L = 2.92$, $P = 0.09$
Residual	35.77 (5.98)	**48**	
Dive rate (dives/h)			
Effect			
Fixed			
Intercept	$F_{1,10} = 171.98$	< 0.0001	
Sex	$F_{1,7} = 0.32$	0.59	
Random	Variance (sd)	%	LRT
Year	$2.89e^{-06}$ (0.002)	**0**	$L = 1.19e^{-08}$, $P = 0.9$
Penguin ID	39.11 (6.25)	**37**	$L = 1.3$, $P = 0.26$
Residual	67.22 (8.19)	**63**	
Average dive depth (m)			
Effect			
Fixed			
Intercept	$F_{1,10} = 6.34$	0.03	
Sex	$F_{1,7} = 0.73$	0.4	
Random	Variance (sd)	%	CV
Year	26.16 (5.11)	76	$L = 5.62$, $P = \mathbf{0.02}$
Penguin ID	1.27 (1.13)	4	$L = 0.19$, $P = 0.7$
Residual	7.19 (2.68)	21	
Maximum distance to the colony (km)			
Effect			
Fixed			
Intercept	$F_{1,18} = 35.31$	< 0.0001	
Sex	$F_{1,12} = 0.01$	0.91	
Random	Variance (sd)	**%**	LRT
Year	17.27 (4.16)	**8**	$L = 0.18$, $P = 0.68$
Penguin ID	134.04 (11.58)	**62**	$L = 10.64$, $\mathbf{P = 0.001}$
Residual	63.85 (7.99)	**30**	
Total trajectory (km)			
Effect			
Fixed			
Intercept	$F_{1,18} = 69.05$	< 0.0001	
Sex	$F_{1,12} = 0.39$	0.55	
Random	Variance (sd)	%	LRT
Year	$1.57e^{-05}$ (0.004)	**0**	$L = 2.51e^{-08}$, $P = 0.9$
Penguin ID	1198.09 (34.61)	**65**	$L = 9.43$, $\mathbf{P = 0.002}$
Residual	635.64 (25.21)	**35**	

Parameters such as distance to the colony and the trajectory covered in a foraging trip help researchers to understand how birds are distributed at sea and, indirectly, the type of prey they consume (Weimerskirch 2007). These parameters can also act as proxies of foraging effort during the breeding season when birds are central-place foragers. When compared with results from past studies, the trajectories and distances covered by Penguins in this study were similar to those at colonies in the central distribution of the species (Puerto San Julián: 97.5 ± 26.3 and 30.3 ± 14.8 km; Puerto Deseado: 182 ± 88.6 and 83 ± 19.7 km, trajectory and maximum distance, respectively; Sala *et al.* 2012), longer than those observed on Martillo Island (69.6 ± 32.4 and 24.3 ± 11.8 km, trajectory and maximum distance, respectively; Raya Rey *et al.* 2010, Sala *et al.* 2012), and much shorter than those observed in Penguins breeding in northern colonies (Punta Norte: 128.3 ± 39.8 and 45.4 ± 12.5 km, trajectory and maximum distance, respectively; Sala *et al.* 2012, Punta Tombo: 42–60 km mean distance, Boersma *et al.* 2015). Home-range areas in this study were considerably larger than those of Penguins at the Martillo Island colony (628 km^2; Raya Rey *et al.* 2010, Sala *et al.* 2012), similar to colonies in the central distribution (Puerto San Julián: 1063 km^2 and Puerto Deseado: 1188 km^2) and much smaller compared with northerly colonies (Sala *et al.* 2012, Boersma *et al.* 2015). These differences in distances travelled and home-range areas at sea might be related to the fact that Penguins nesting in Martillo Island are restricted to the waters of the Beagle Channel, whereas Penguins nesting in Isla de los Estados and Patagonia forage in the open sea.

Home-range areas extended all across the Le Maire Strait in all years studied and also off the south-eastern coast of Isla de los Estados. The chlorophyll *a* concentration in this area during the study period showed high levels of productivity, with some interannual variation. Previous studies showed an association with primary production (e.g. chlorophyll *a*) and at-sea foraging areas for Magellanic Penguins along their distribution (Boersma *et al.* 2009), in relation to the presence of frontal systems where prey species for penguins are concentrated. The Le Maire Strait is within the Patagonian cold estuarine zone, a front that extends along the Pacific and Atlantic coasts (from north of Chiloé Island, Chile, encompassing the

southern tip of South America and reaching the continental shelf of Atlantic Patagonia; Acha *et al.* 2004). This cold estuarine zone is not well known or studied, although it is assumed to play an important role as a transport system to carry organisms from one ocean to the other (Acha *et al.* 2004).

The shape of the track may reveal different search strategies in seabirds (e.g. Weimerskirch *et al.* 2005, Zavalaga *et al.* 2010, Harris *et al.* 2012), probably related to the distribution and predictability of prey or prey patches in the area (Weimerskirch 2007). It is possible that prey resources are more or less dispersed across the productive Le Maire Strait, encouraging Penguins in our study to perform loop-shaped trips to maximize the area covered in the search for food at a low energetic cost (Weimerskirch *et al.* 2005). In contrast, studies of this species at other colonies found direct return trips were more frequent than loop-shaped trips (Raya Rey *et al.* 2010, Sala *et al.* 2012). Energetic costs can be further reduced by using prevailing currents, as shown for Magellanic Penguins breeding at the Malvinas/Falkland and Martillo Islands (Pütz *et al.* 2002, Raya Rey *et al.* 2010).

Individual consistency was observed in other seabirds, including penguins, in parameters such as dive depth (e.g. Ropert-Coudert *et al.* 2003, Ratcliffe *et al.* 2013) or maximum distance to the colony (e.g. Harris *et al.* 2014). In those studies the consistent behaviour was associated with specific prey patches that individuals repeatedly used to forage, or age-dependent variation in diving capacity, although there might be many other reasons why animals specialize at the individual level, for instance to reduce intraspecific competition (Ceia & Ramos 2015). Although our results point towards high plasticity in the foraging behaviour in contrast to individual specialization, this could be associated with little intraspecific competition and widely dispersed prey in our study area. The sample size for intra-individual variability of foraging behaviour, however, was small and biased towards males. The reason for obtaining more multiple trips from males than females remains unclear. Magellanic Penguins at the southern edge of their distribution have widely variable schedules of colony departures and arrivals (Radl & Culik 1999, Scioscia *et al.* 2009, this study), in contrast to other penguin or seabird species, which have clearer patterns (e.g. Peters *et al.* 1998, Otley *et al.* 2004, Shiomi *et al.* 2012). This may have affected recapture at the end of the first foraging trip after device deployment. Therefore, conclusions about intra-individual variability may have to be drawn with caution and should be limited strictly to males.

Individuals in this study departed from and returned to the colony throughout the day, similar to Magellanic Penguins breeding in colonies in their southern distribution (Radl & Culik 1999, Scioscia *et al.* 2009, Raya Rey *et al.* 2012). Furthermore, in this and past studies at southerly colonies, overnight trips were the most common (Radl & Culik 1999, Scioscia *et al.* 2009, Raya Rey *et al.* 2012). Penguins are visual predators, but they can dive deep during the day (Wilson *et al.* 1993, Walker & Boersma 2003) where light levels are low, and penguins from colonies at higher latitudes are known to forage effectively during twilight (Schiavini & Raya Rey 2004, Raya Rey *et al.* 2012). Shoals of Fuegian Sprat *Sprattus fueguensis*, an important prey for southern Magellanic Penguin colonies (Radl & Culik 1999, Scioscia *et al.* 2014), exhibit a diel cycle, in which they disperse in superficial layers during night-time (5–10 m) and descend (maximum 70 m), whereas during the day they form compact shoals (Sánchez *et al.* 1995, Casarsa 2005). Overnight trips may allow Magellanic Penguins at these latitudes to forage throughout the twilight hours, accessing vertically migrating prey, returning with enough food to fulfil their own energetic needs and those of their chicks, similar to Chinstrap Penguins *Pygoscelis antarcticus* (Jansen *et al.* 1998).

Magellanic Penguins nesting at Isla de los Estados performed foraging trips of around 20 h, with a high degree of interannual variation and no differences between sexes. The reproductive success of the Penguins can be affected by the length of the foraging trips, as Penguins that stay away too long may not be able to deliver meals frequently enough to keep both chicks alive (Boersma & Rebstock 2009, Scioscia *et al.* 2010). Compared with other Magellanic Penguin colonies, the trip duration for Penguins breeding on Isla de los Estados was shorter than that recorded from colonies further north (Sala *et al.* 2012), but was slightly longer than trips performed by penguins in nearby colonies (Martillo Island < 20 h; Raya Rey *et al.* 2010, Scioscia *et al.* 2010). We observed higher chick survival and comparable or greater chick mass relative to those found in studies at other

Magellanic Penguin colonies (Boersma *et al.* 1990, 2015, Scioscia *et al.* 2016). Furthermore, due to the exclusively burrow-nesting habits of breeding pairs on Isla de los Estados (N. Rosciano, pers. obs) and the lack of mammal predators ashore, chicks in the study colony are exposed to lower predation risks compared with other colonies. However, due to the timing of fieldwork, we could not determine whether chicks fledged after the study period.

Isotopic data in this study integrate primarily the foraging history of the early chick-rearing period, but may also include a portion of the late incubation period, as blood tissue has a turnover rate of approximately 20 days (Barquete *et al.* 2013). δ^{15}N values reflect the trophic position of consumers due to a step-wise enrichment of ^{15}N between trophic levels (Minagawa & Wada 1984). In addition, inshore/benthic foraging areas have higher δ^{13}C values relative to offshore/pelagic areas (Hobson *et al.* 1994, France 1995, Cherel & Hobson 2007). The δ^{13}C values observed in this study suggested that the Penguins mainly foraged in inshore waters, and are in agreement with the tracking data showing positions along the Le Maire Strait and close to the coast of Tierra del Fuego. In this study, males and females did not differ either in δ^{15}N or δ^{13}C values during the study period. This contrasts with a previous study in northern Magellanic Penguin colonies that found higher δ^{15}N and δ^{13}C values in males than females, suggesting higher intake of fish and greater foraging in inshore habitats by males (Forero *et al.* 2002). The small variation between sexes observed in this study was in contrast to the more evident differences in foraging behaviour at colonies in the northern distribution. The colony at Isla de los Estados possibly has a higher availability of prey items nearby, whereas the lower prey availability and/or less favourable conditions at sea at the northern colonies increased competition, leading to a greater divergence between the sexes. In fact, Pozzi *et al.* (2015) suggested that the high growth rate of the colonies recently established in northern Patagonia may be related to an interaction between density dependence and environmental factors, with new colonies being established at locations where environmental conditions at sea may be stable and favourable. Our results suggest that a similar development may be occurring at Isla de los Estados, where conditions at sea might be favourable for breeding adults; thus intraspecific competition relaxes and differences between sexes disappear. However, the provenance of Magellanic Penguins at our study site is not known.

The trophic level (TL) values estimated for Magellanic Penguins in this study (4.0) were similar to penguins from northern Patagonian colonies (4.0; Forero *et al.* 2004) and Malvinas/Falkland Islands (Weiss *et al.* 2009) but lower than the ones calculated for the colonies in central Patagonia (Ciancio *et al.* 2015). TL calculated from the stomach contents of Magellanic Penguins breeding at the nearest colony, Martillo Island (Scioscia *et al.* 2014), using prey TL values from Riccialdelli *et al.* (2013, 2017), produced values of between 4.1 and 4.4 (females and males, respectively) with a diet composition of: 30.1% Fuegian Sprat (TL = 4.1), 38.3% squid *Loligo gahi* (TL = 3.8) and 11.1% Squat Lobster (TL = 2.7) for females and males that consumed a higher proportion of Fuegian Sprat (40.6%) and Squat Lobster (28.8%) but less *L. gahi* (25%). This similarity in TL values between sites suggests that Penguins from both colonies occupy the same position in the food web, and probably consume more or less the same prey types. Conventional dietary studies on Magellanic Penguin colonies near Isla de los Estados identified a diverse diet consisting of Fuegian Sprat as the most important prey type consumed and also squid (Radl & Culik 1999, Scolaro *et al.* 1999, Wilson *et al.* 2005) with, in some cases, crustaceans being of minor importance (Thompson 1993, Pütz *et al.* 2001). Further studies on isotopic signature for potential prey types in the study area would allow a better approximation of TL diets and allow for the use of mixing models to calculate penguin diet compositions.

Magellanic Penguin populations face several threats from interaction with human activities (e.g. fisheries), climate variation, etc., which may also vary among breeding colonies throughout their distribution (Boersma *et al.* 2013). This study contributes to the identification of important areas at sea for Magellanic Penguins in the southern distribution, and would also allow identification of possible threats in the study area such as interaction with fisheries, or how Penguins react to environmental variation. Further studies are strongly encouraged to increase our knowledge of the species in the southern part of its distribution.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Average and range of Magellanic Penguin chick mass (g) for each year sampled.

Table S2. Mean (±sd) $\delta^{13}C$ and $\delta^{15}N$ values and calculated trophic level for male and female Magellanic Penguins nesting on Isla de los Estados in the 2011, 2012 and 2013 breeding seasons.