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Post-moult movements of sympatrically breeding Humboldt and Magellanic Penguins in south-central Chile

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ABSTRACT

Ten Humboldt (*Spheniscus humboldti*) and eight Magellanic Penguins (*S. magellanicus*) were successfully equipped with satellite transmitters in March 2009 on Islotes Puñihuil in central south-Chile to follow their post-moult dispersal. Overall, Humboldt Penguins could be followed for a mean period of 49 ±18 days (range: 25–93) and Magellanic Penguins for 57 ±12 days (range 35–68). Irrespective of species and sex, seven study birds remained in the vicinity of their breeding ground throughout the transmission period. All other penguins moved northwards, either only a relatively short distance (max 400 km) to Isla Mocha at 38°S ($n = 3$) or further north beyond 35°S ($n = 8$). However, eight of these birds (73%) turned south again towards the end of the individual tracking periods. The total area used by both species during the tracking period was restricted to a coastal area stretching from the breeding site at 42°S about 1000 km to the north at about 32°S. The area used by Humboldt penguins overlapped by 95% the area used by Magellanic penguins, whereas the area used by the latter species was much larger and overlapped only by 45% with the area used by Humboldt penguins. Overall, our results indicate that Magellanic Penguins in the Pacific Ocean are probably less migratory than their conspecifics on the Atlantic side, while Humboldt Penguins appear to be more migratory than previously anticipated. In general, there was a poor relationship between preferred foraging areas and chlorophyll-a, as a proxy for primary productivity, indicating the limitations of using remote-sensed primary productivity as a proxy to interpret the foraging behaviour of marine predators. In addition, there was also no clear relationship between the preferred foraging areas and the amount of regional fish catches by artisanal fishery.

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1. Introduction

Improving our knowledge on animal movements during the breeding and non-breeding periods have largely enhanced our understanding of individual behaviours and physiological constraints. In addition, these data are essential for conservation measures implemented to prevent species extinction, preserve biodiversity and to accomplish ecosystem-based management of living resources. Especially the management of endangered species requires spatially-explicit information on their distribution and its variation over time.

Humboldt and Magellanic Penguins are classified by the IUCN as vulnerable and near threatened, respectively (IUCN, 2015). Both species inhabit the coast and islands of South America, but the Humboldt Penguin population of an estimated 15,000–20,000 breeding pairs (De la Puente et al., 2013) is far outnumbered by two orders of magnitude by the 1.2–1.6 million Magellanic Penguin breeding pairs (Boersma et al., 2013). There is only a marginal overlap in distribution of the two species on the Pacific side of South America, and the Islotes Puñihuil, located at the north-western tip of Isla Grande de Chiloé in south-central Chile, are one of the few places where both species breed in sympatry (Cursach et al., 2009; Simeone and Hucke-Gaete, 1997; Wilson et al., 1995).

Until 1999, tourists were landed by boat on Islotes Puñihuil and moved around without supervision (Simeone and Schlatter, 1998). Also, wild goats roamed on the islets. The damage created by tourists and goats was significant, ranging from disturbances during the breeding phase to destruction of the breeding burrows by trampling (Simeone, 2005), with Humboldt penguins likely to have been more affected than Magellanic Penguins due to the fact that they may respond more strongly to human presence than any other penguin species (Ellenberg et al., 2006). In 1999, the islets were declared a nature reserve, goats were removed and landing on the islets only allowed by special permission for scientific purposes (Skewgar et al., 2009). Since 1999, the number of breeding burrows has increased and the number of collapsed burrows decreased, indicating an improved utilization and potentially breeding success of the penguin populations on the islets (Reyes-Arriagada et al., 2013; Simeone, 2005). Nowadays, local fishermen earn some extra income by driving tourists by boat around the islets, thereby offering views on the abundant wildlife, including penguins, pelicans, other seabirds and sea otters (Skewgar et al., 2009). However, these conservation measures affected only the terrestrial habitat and left the surrounding waters unprotected. Fishing activities in the area constantly result in accidentally catching and drowning of penguins and other seabirds, particularly in gillnet fishing for Corvine (*Cilus gilberti*) (Pütz et al., 2011; Simeone et al., 1999; Suazo et al., 2013). Thus, the establishment of a Marine Reserve was requested to protect natural resources and local economy (Skewgar et al., 2009).

A recent study investigated the dive characteristics and foraging areas of both species during the breeding period and found both, inter-specific and sex-related differences in the utilization of the marine habitat, although the differences between species were more pronounced than between sexes (Raya Rey et al., 2013). Furthermore, following moult, the most common area used by five Magellanic Penguins was located 600–800 km north in the highly productive Gulf of Acrauco, while one bird swam 300 km to waters inland of Chiloé, Chile (Skewgar et al., 2014).

Magellanic Penguins from colonies in the Atlantic Ocean are known to migrate north, usually in coastal waters (Pütz et al., 2000, 2007; Stokes et al., 1998). Only Magellanic Penguins from the Falkland Islands may also make use of the slope of the Patagonian Shelf during their winter migration (Pütz et al., 2000). In contrast to the migratory Magellanic Penguin, Humboldt Penguins are considered sedentary (Croxall and Davis, 1999; Williams, 1995), although there are indications that Humboldt Penguins may travel several hundreds of kilometres during El Niño events (e.g. Culik, 2001; Culik and Luna-Jorquera, 1997; Culik et al., 2000; Wallace et al., 1999).

In general, more information on the movements of both penguin species during the non-breeding period is essential to elucidate their migration patterns, inter-specific competition and potential anthropogenic threats in their preferred foraging areas and migration corridors. The aim of this study was (1) to simultaneously investigate the post-moult dispersal of Magellanic and Humboldt Penguins from the Islotes Puñihuil, (2) to identify any inter-specific differences in the post-moult movements of the two closely related penguin species, (3) to identify oceanographic features characterizing the preferred foraging grounds, and (4) to investigate potential threats from the local artisanal fishery in the preferred foraging grounds.

2. Material and methods

2.1. Field work

The study was conducted at the Natural Monument "Islotes Puñihuil" (41° 55.4′S, 74° 2.3′W), located off the northwest coast of Isla Grande de Chiloé, south-central Chile. The islets consist of three small islands with a total area of ca. 9 ha, where ca. 90 Humboldt and ca. 480 Magellanic penguin breeding pairs nest sympatrically between September and April (Reyes-Arriagada et al., 2013; Simeone, 2005). On 10 and 11 March 2009, ten adult Humboldt and eight adult Magellanic penguins that had moulted recently were captured in their burrows and equipped with ARGOS satellite transmitters. Although age and breeding experience of the study birds was unknown, we assumed that they were residents in the breeding colony. After capture, the penguins were at first masked to reduce stress levels, and then bill depth and length measured to determine their sex (Bertellotti et al., 2002; Vanstreels et al., 2011; Wallace et al., 2008).

All satellite transmitters were mounted on the dorsal mid-line of the back with waterproof black tape (Tesa, Beiersdorf AG, Hamburg, Germany) and 2-component glue following the method of Wilson et al. (1997). All devices were covered with a layer of quick epoxy (Loctite® 3430, Loctite Deutschland GmbH, München, Germany) to prevent the birds from removing the tape with their beaks. The attachment process took less than 15 min per bird. As the site of equipment could not be monitored during the study period, no transmitters were recovered but are assumed to have become detached and subsequently fallen off after varying time periods.

2.2. Device details

The KiwiSat 202 satellite transmitters (Sirtrack, New Zealand) weighed about 100 g (incl. attachment material), corresponding to less than 3% of the mean penguin body mass, and measured 80 × 35 × 27 mm. To reduce hydrodynamic drag and potential impacts on the behaviour (Bannasch et al., 1994; Wilson et al., 2004), devices were hydrodynamically shaped and the flexible antenna (185 mm long and 2 mm in diameter) was positioned at an angle of 60° at the rear of the device. A saltwater switch prevented transmission while under water. Devices were programmed to transmit with a duty cycle of 5 h on/19 h off with a repetition period of 60 s between 2300 and 0400 local summer time (GMT minus 3 h). This period was chosen because penguins are optically orientated predators and thus more likely to be less active at night (e.g. Wilson et al., 1993), thereby increasing the likelihood of successful transmissions while the penguin was resting at the sea surface.

2.3. Data analysis

Positional data obtained from ARGOS (CLS, Toulouse, France) were classified according to the quality of the location fix provided by Argos (1996). Data within one transmission period were filtered for biologically unrealistic speeds and onshore locations. Only one position with a high accuracy (95% of positions had location classes 1, 2 or 3, translating into 68% of positions associated with errors <1 km (e.g. Boyd and Brightsmith, 2013)) was processed per duty cycle and individual. A more detailed analysis of the locational data received was not feasible, because fixes were obtained only during a limited time period at night when penguins were usually resting at the water surface, which resulted in clusters of positional fixes very close to each other. The foraging parameters calculated from the resulting daily positions were maximum distance to the colony, minimal distance covered (= sum of distances between two consecutive daily positions) and mean daily distance during the individual study periods. Mann–Whitney tests were performed using Minitab 13, means are given ±SD.

For each penguin species (sexes pooled) and each month (March, April, May) we calculated a utilization grid with the kernel density from the density function in the spatial analysis extension in ArcGIS 9.3 with a search radius of 8000 m and an output cell-size of 800 m, both chosen due to the foraging range of the species and the maximum distance reached (Hemson et al., 2005; Falabella et al., 2009). We categorized kernel density grids into two separate percentile regions corresponding to the 50% and 95% density of position estimates, where the 95% kernel was representing the dispersion range and the 50% was the kernel with the highest density (Wood et al., 2000). To assess the overlap of the foraging areas between species, we quantified the percentage of the kernel area (50% and 95%) that overlapped with the other species. Furthermore, to characterize the habitat utilized during post-moult dispersion, we overlaid the foraging kernel polygons with bathymetry data, sea surface temperature (SST) and chlorophyll-a (chl-a) concentration as a proxy for productivity. Bathymetry data (ETopo Digital Maps, see http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html, accessed 12 May 2014) were obtained at a spatial resolution of 2′ latitude and longitude. Chl-a data were obtained from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) Ocean (4.5-km resolution, see http://oceancolor.gsfc.nasa.gov/, accessed 7 May 2014) as monthly composite images from March, April, May 2009. SST data were obtained from NASA MODIS Aqua L3 products (4.5 km resolution, see http://podaac.jpl.nasa.gov/dataset/MODIS_AQUA_L3_SST_THERMAL_MONTHLY_4KM_DAYTIME, accessed 7 May 2014) as monthly composite images from March, April and May 2009. We used the Marine Geospatial Ecology Tools (Roberts et al., 2010) in ArcGIS 9.3 to handle the oceanographic data.

Data on fish catches in artisanal fisheries were obtained from Servicio Nacional de Pesca (SERNAPESCA) from https://www.sernapesca.cl/index.php?option=com_remository&Itemid=246&func=select&id=2.

3. Results

Overall, the movements of Humboldt Penguins could be monitored for a mean period of 49 ± 18 days (range 25–93) and Magellanic penguins for 57 ± 12 days (range 35–68) (Table 1). No significant inter-specific differences were found in the parameters calculated to characterize the movement patterns (Table 1). Maximum distance to the colony ranged between 6 and 1036 km in Humboldt and between 17 and 927 km in Magellanic penguins. The minimal distance covered (= sum for all individuals of each species) was 8014 km in Humboldt penguins and 9247 km in Magellanic penguins ($W = 130$, $p = 0.92$). The mean minimal daily distance covered was 22 km in both species, the maximal daily distance covered was 106 km in Humboldt and 115 km in Magellanic penguins ($W = 98$, $p = 0.97$; and $W = 130$, $p = 0.95$, respectively). Due to the limited sample sizes and the lack of significant differences in the movement patterns, sex data were pooled for further analysis.

The area used by both penguin species extended from the study site about 1000 km northwards along the coast (Fig. 1, Table 1). Seven birds performed only local movements and remained within 100 km from the colony (Fig. 1(a)); these

Table 1
Summary of parameters characterizing the migratory behaviour of Humboldt and Magellanic Penguins from Islotes Puñihuil in south-central Chile. Section 1 contains birds foraging locally during the transmission period, the second contains birds migrating to Isla Mocha and back, and the third contains birds migrating further north. Species and Sex: Humboldt Penguin = H, Magellanic Penguin = M, Female = F, Male = M.

Penguin name	Species and sex	Date of departure	Date of return	Tracking duration (days)	Maximum distance to colony (km)	Minimal distance covered (km)	Daily distance	
							Mean (km/day)	Maximum (km/day)
India	HF			93	18	298		20
Lativami	HM			33	6	42		6
Pedro	HM	15-Mar		25	55	158	7.9	40
Quin	HM	27-Mar	14-Apr		46	220	12.2	40
		22-Apr	29-Apr	52	45	87	12.4	40
Trippi	HM	28-Mar	13-Apr	43	56	141	8.8	49
Aklipoti	MF	23-Mar		35	62	433	19.7	42
Vandem	MF	30-Mar	2-Apr		24	30	10.0	14
		3-Apr		58	92	596	17.0	68
Mean ± SD				**48 ± 23**	**45 ± 26**	**223 ± 190**	**13 ± 4**	
Bo	HF	20-Mar	23-Apr	49	405	957	28.1	82
Valdivia	HF	11-Mar	25-Apr	47	403	948	21.1	106
Birma	MM	20-Mar		48	407	1035	27.2	92
Mean ± SD				**48 ± 1**	**405 ± 2**	**980 ± 48**	**25 ± 4**	
Carla	HF	12-Mar		62	733	2075	34.0	96
Cora	HF	13-Mar		47	1036	1661	36.9	94
Lucy	HF	10-Mar		40	923	1427	35.7	88
Ella	MF	29-Mar	2-Apr		17	50	12.5	17
		3-Apr		53	616	711	23.7	87
Ormella	MF	6-Apr		68	910	1432	34.1	115
Susanne	MF	19-Mar		68	735	1643	27.8	96
Gonzo	MM	13-Mar		61	913	1377	23.7	73
Gus II	MM	14-Mar	17-Mar		17	37	12.3	17
		17-Mar	27-Mar		93	224	22.4	45
		27-Mar		67	927	1679	33.6	83
Mean ± SD				**58 ± 11**	**849 ± 139**	**1120 ± 730**	**31 ± 5**	

movements included trips to the exposed ocean as well as the interior waters in the Gulf of Ancud. Three birds travelled to Isla Mocha, about 400 km to the north of the breeding site, and then returned to the colony (Fig. 1(b)). The remaining eight birds moved along the coast up 33°S, about 1000 km to the north of the colony (Fig. 1(c)). However, five of these birds then turned south again until transmissions ceased. During the northbound movement, the maximum distance to the coast increased from ca. 50 km in the southern part to ca. 150 km in the northern part.

A kernel analysis revealed that the area used by Humboldt penguins overlapped by 95% with that used by Magellanic penguins, whereas the latter species overlapped only by 45% of the area used by Humboldt penguins (Fig. 2). The core area (50%) used by Humboldt penguins completely overlapped with that of Magellanic penguins (100%), but only 15% of the area used by Magellanic penguins was shared with that of Humboldt penguins (Fig. 2).

Fish catches from artisanal fisheries over a 8-year period (from 2007 to 2014) in the area utilized by post-moult Humboldt and Magellanic Penguins, separated according to geographical region, are added in Fig. 2. Region VIII reported the highest catches in all years, followed by regions X and XIV with catches at least one magnitude lower. Catches in the remaining regions VI, VII and IX were at least further two magnitudes lower. Especially in the latter years, there was a decreasing trend in catches in the most prolific regions VIII, X and XIV. Irrespectively of region and year, the artisanal fish catches during the 3-months study period represented between half and two thirds of the annual reported catch. When separated according to month, it became evident that the months March, April and May were always among the four months with the highest catches.

In association with mean monthly chl-a concentration, SST and water depth, the positions of Humboldt (Fig. 3(a)) and Magellanic Penguins (Fig. 3(b)) appeared to be mostly associated with, or in the vicinity of, areas with a high chl-a concentration. In general, chl-a concentrations and SST decreased over the study period in the 50% and 95% kernels of both species, while deeper waters were preferred in April and May (Table 2). For Humboldt Penguins in the 50% kernel, chl-a concentrations decreased from 4.2 to 2.7 $\mathrm{mg/m^3}$ and SST from 14 °C to 12 °C, while water depths increased from 94 to 275 m during the study period. For Magellanic Penguins, chl-a concentrations decreased from 5.2 to 1.6 $\mathrm{mg/m^3}$, SST ranged between 14 °C to 13 °C and water depths between 111 m and 187 m (Table 2).

4. Discussion

The movements of sympatrically breeding Humboldt and Magellanic Penguins in the Pacific Ocean were tracked simultaneously for the first time. During the tracking period, both sexes and species showed different movement patterns

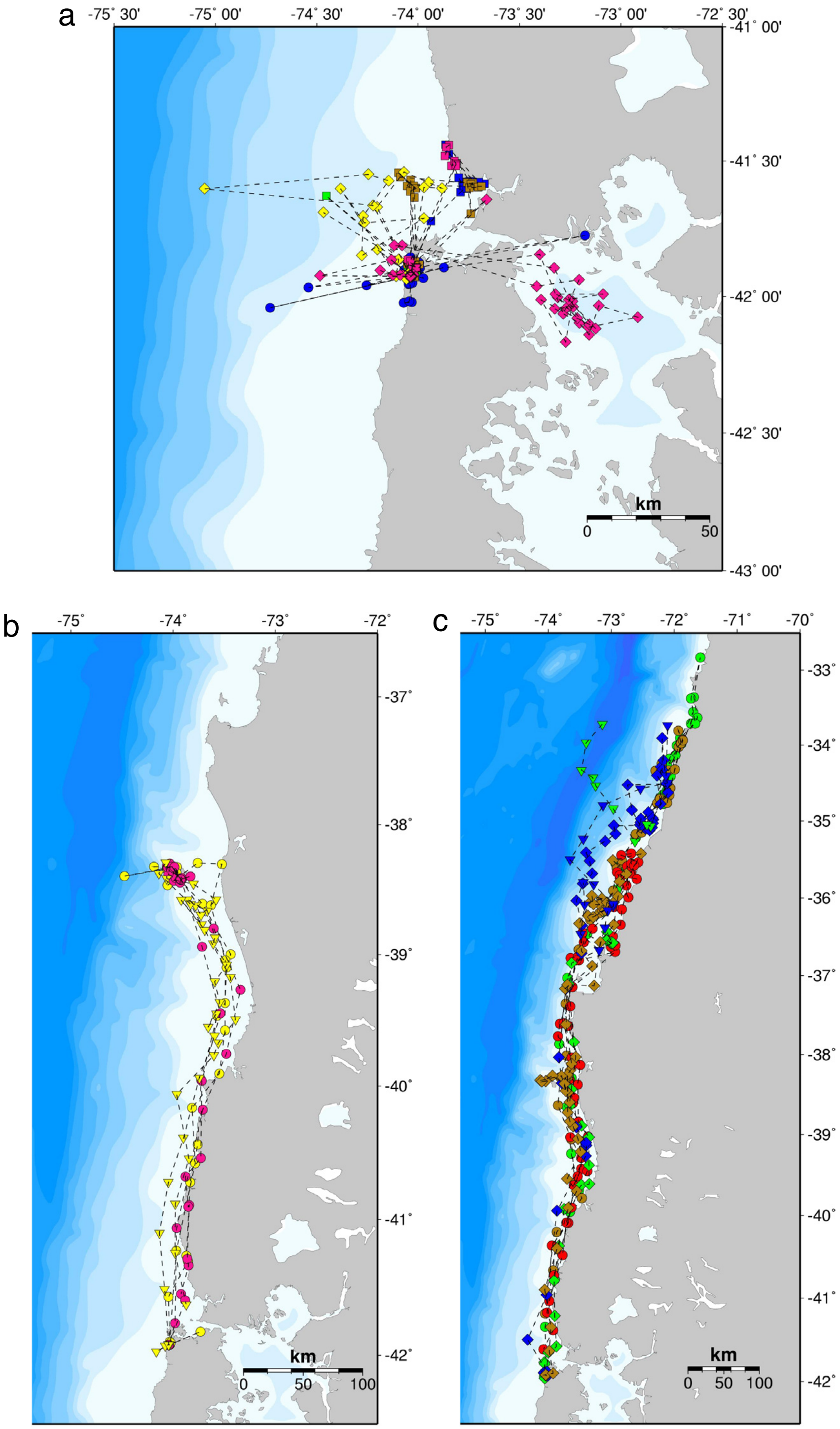

Fig. 1. Movements of Humboldt (males = squares, females = circles) and Magellanic Penguins (males = triangles, females = diamonds) from Islotes Puñihuil. Given the different spatial scales during the respective tracking periods, data for both species were pooled in relation to the maximum distance from the colony. Movements separated according to birds (a) foraging locally, (b) travelling up to Isla Mocha and (c) further north. Symbols are: (a) India = blue circle, Lativami = green square, Pedro = blue square, Quin = golden square, Trippi = red square, Aklipoti = yellow diamond, Vandem = red diamond; (b) Bo = yellow circle, Valdivia = red circle, Birma = yellow triangle; (c) Carla = red circle, Cora = green circle, Lucy = golden circle, Ella = green square, Ormella = blue diamond, Susanne = golden diamond, Gonzo = green triangle, Gus II = blue triangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

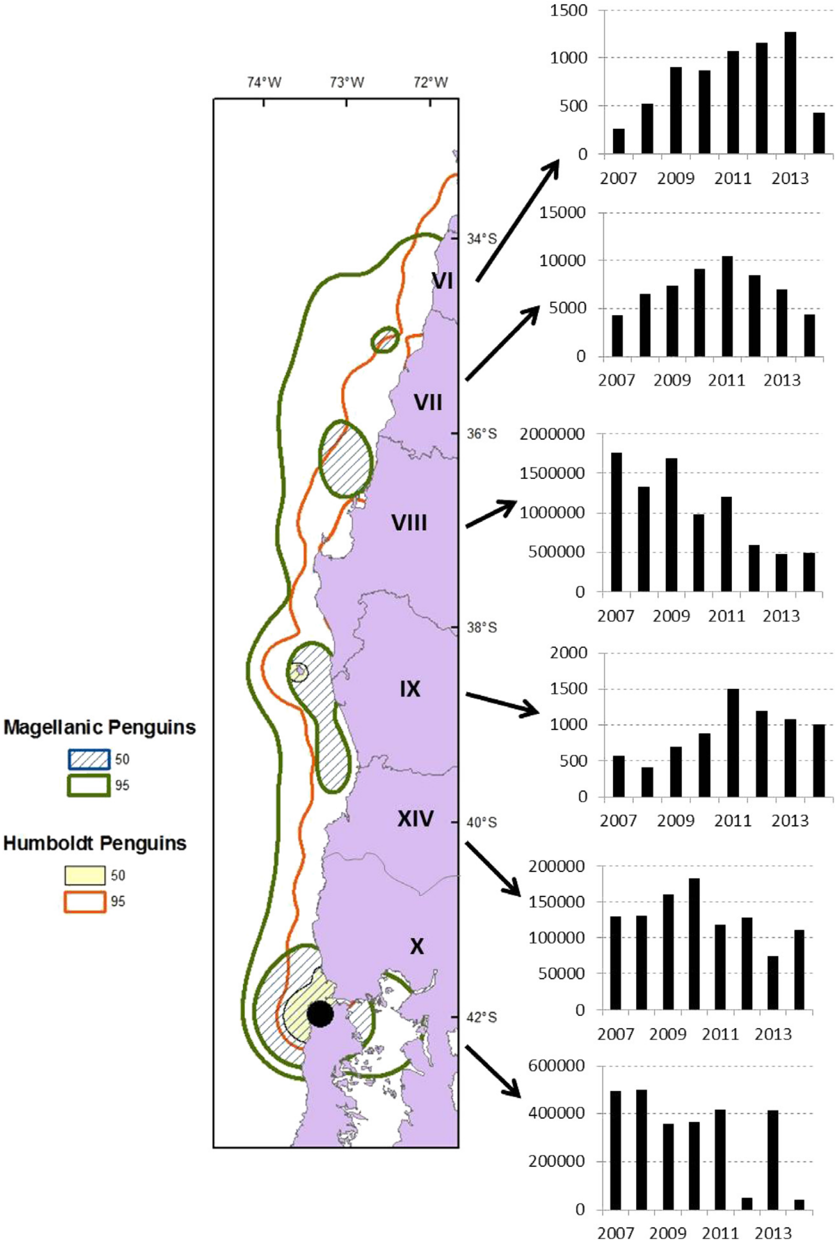

Fig. 2. At-sea distribution maps (50% and 95% kernel contours) of the post-moult dispersal of Humboldt and Magellanic Penguins from Islotes Puñihuil. Yearly artisanal fish catches (t) are given according to region for the years 2007–2014.

and either remained in the vicinity of the study site or moved northwards, with most penguins returning after varying time periods (Fig. 1, Table 1). However, the lack of any significant sex- or species-related differences in the observed movement patterns may be due, at least partly, to the limited sample sizes, which may have masked any differences. For example, all male Humboldt Penguins remained in the vicinity of the study site during the tracking period, but the same behaviour was observed in one Humboldt and two Magellanic Penguin females. Thus, more data are needed to elucidate any potential species- or sex-related differences in the winter migration patterns of the two species. The absence of any species-related differences is especially noteworthy, because dive characteristics and foraging areas were shown to differ between species from the same site during the breeding season (Raya Rey et al., 2013). Probably the lack of both, the time-constraints imposed on birds having to provision their offspring with food, and competition in an environment with sufficient food supply, is, at least partly, responsible for the absence of inter-specific differences in the foraging behaviour of the two penguin species during the post-moult period. The only difference in the dispersal patterns was that Magellanic Penguins appeared to use a significant larger foraging area than Humboldt Penguins (cf. Fig. 2).

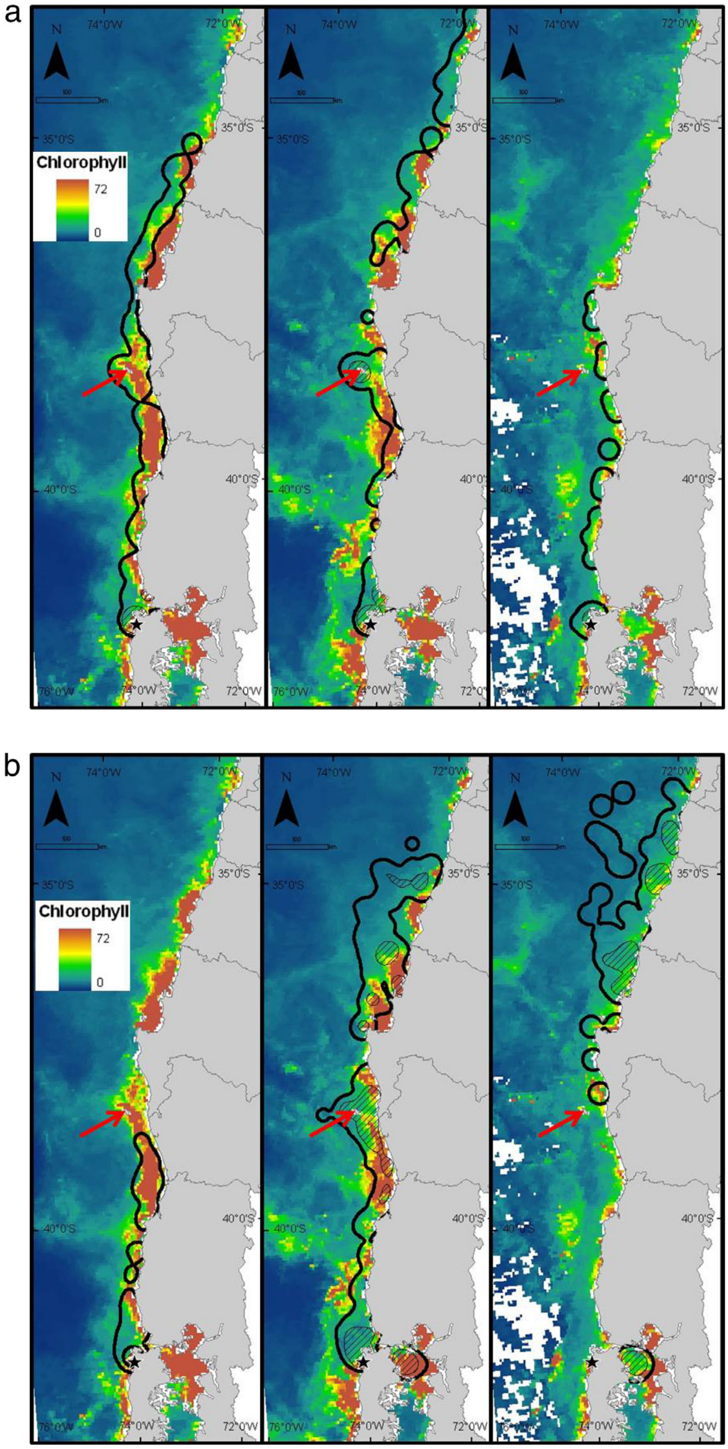

Fig. 3. Monthly at-sea distribution maps (50% and 95% kernel contours, hatched areas and solid lines, respectively) for March (left), April (centre) and May (right) for Humboldt (a) and Magellanic Penguins (b) from Islotes Puñihuil in relation to chlorophyll-a concentration (mg/m^3). The location of the breeding colony is marked by a black asterisk, the red arrow indicates Isla Mocha. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Our results confirm previous findings by Skewgar et al. (2014) on the winter migration of Magellanic Penguins from the same site, where five out of six birds travelled northwards and frequented the same areas while one bird moved up to 300 km south. This indicates, in general, a consistent use of the same wintering areas, at least by Magellanic Penguins. However,

Table 2
Mean monthly chlorophyll-a concentration, sea surface temperature and depth in the Kernel density areas of post-moult Humboldt and Magellanic Penguins from Islotes Puñihuil in south-central Chile.

Month	Kernel			
	Humboldt		Magellanic	
	50	95	50	95
Chlorophyll-a concentration (mg/m^3)				
March	4.2	4.3	5.2	3.6
April	2.5	3.4	3.9	2.6
May	2.7	1.8	1.6	1.2
Sea surface temperature (°C)				
March	14	13.9	13.7	13.9
April	13.5	13.8	14	14
May	12	12.4	13	13.4
Depth (m)				
March	94	284	111	122
April	275	345	187	604
May	139	238	164	1228

in contrast to the findings of Skewgar et al. (2014), where no return movements were recorded among the Magellanic Penguins, and despite comparable tracking periods, the frequent return not only of Magellanic but also Humboldt Penguins is noteworthy. Magellanic Penguins have been reported to reach coastal areas up to Peru, about 2000 km to the north of their nearest breeding site (Zavalaga and Paredes, 2009). This pattern mirrors the behaviour observed in Magellanic Penguins breeding in the Atlantic Ocean, where, irrespective of their breeding site, birds move north after their moult (Pütz et al., 2000, 2007; Stokes et al., 1998). It is, however, surprising that Humboldt Penguins also moved considerable distances northwards away from their breeding site, albeit some of them also turned south after varying time periods. This raises the question, whether Humboldt Penguins can be really considered as sedentary (Croxall and Davis, 1999; Williams, 1995), or whether the extensive travels observed during El Niño events (e.g. Culik and Luna-Jorquera, 1997; Culik et al., 2000; Wallace et al., 1999) are more common than previously anticipated. However, in comparison with the simultaneously tracked Magellanic Penguins, Humboldt Penguins used more coastal waters (cf. Fig. 2), which is supported by the preferred water depths in the 50% and 95% kernels (cf. Table 2).

The post-moult foraging area of both species is located within the upwelling system of the Humboldt Current, which is considered as one of the most productive marine areas in the world (Daneri et al., 2000; Thiel et al., 2007). Obviously, this enabled some birds to forage successfully in local waters throughout the tracking period, which is supported by the high chl-a concentrations in the area (cf. Fig. 3). Others, however, migrated north, either as far as Isla Mocha or even beyond. Isla Mocha itself supports no penguin colonies (AS, personal observation), but on neighbouring islets a few Magellanic Penguin burrows were found (Schlatter et al. unpubl. data). However, the surrounding waters and those located north at the Gulf of Arauco are highly productive, supporting several industrial and artisanal fisheries (Thiel et al., 2007). This is also mirrored in the chl-a concentrations recorded (cf. Fig. 3) and the observation of large numbers of Pink-footed Shearwaters *Puffinus creatopus* (Guicking et al., 2001) and Black-browed Albatrosses *Thalassarche melanophrys* (Birdlife International, 2004) in the area during winter. Wallace et al. (1999) reported at least one Humboldt Penguin from the Algarrobo colony (33°S), located about 600 km north, that was found dead on Isla Mocha.

As can be seen from Fig. 3, chl-a concentrations, widely accepted as a proxy for primary productivity, were patchy, and both species were not clearly associated with areas of highest chl-a concentrations, but were frequently located in the vicinity of these hot spots (cf. Fig. 3). Dispersion range (95%) and the most utilized area (50%) for both species were characterized by a mean level of up to 5 mg Chl-a/m^3, which decreased over the study period (Table 2). Areas with high chl-a contents of up to 70 mg Chl-a/m^3 were frequented only occasionally (cf. Fig. 3), which could be due to a temporal mismatch between monthly averages of chl-a and the penguin locations. However, a discrepancy between the preferred foraging areas of an predator and chlorophyll concentrations has also been observed in the Benguela upwelling system in the South East Atlantic for Cape Gannets *Morus capensis* (Gremillet et al., 2008). This was explained by the fact that marine predators do not feed directly on phytoplankton but at higher trophic levels, and highlights the limitations of using primary productivity to interpret the foraging behaviour of marine predators (Gremillet et al., 2008). This is further substantiated by the fact that artisanal fish catches on a regional scale were also not clearly correlated to a high primary productivity (cf. Figs. 2 and 3). For example, highest fish catches were reported from region VIII, where chl-a concentrations were also high, but not from the coast of region IX, where chl-a concentrations were equally high. The latter area also corresponded to an hot spot for Magellanic Penguins, indicated by the 50% kernel (cf. Fig. 2). These observations support the fact that high primary production and the distribution of animals feeding at higher trophic levels may not always match.

Unfortunately, our knowledge on the winter diet of Humboldt and Magellanic Penguins along the Chilean coast is scarce to non-existent. During the breeding season, however, Humboldt Penguins from the Puñihuil Islets feed mostly on Anchovy (*Engraulis ringens*), Araucanian Herring (*Clupea bentincki*) and Silverside (*Odontesthes regia*), whereas conspecifics from more northerly colonies consume predominantly Atlantic Saury (*Scomberesox saurus*) (Herling et al., 2005). Also, only indirect evidence is available for the winter diet of Magellanic Penguins from Atlantic populations. However, during the breeding season there was a latitudinal gradient with birds from more northerly colonies preying mainly upon Argentine Anchovy (*Engraulis anchoita*) whereas birds from southern locations feed on a mixture of squid (*Loligo* spp. and *Illex* spp.), Fuegian Sprats (*Sprattus fuegensis*) and hagfish (*Myxine* spp.) (Scolaro et al., 1999). Given the catch rates of the artisanal small-scale fishery, it can be assumed that also during the study period shoaling fish constituted a major part of their diet, which has been confirmed by the presence of Araucarian Herrings in the stomachs of Magellanic penguin carcasses incidentally caught in gill nets (Schlatter et al., 2009).

As mentioned above, shoaling fish are also heavily exploited along the Chilean coast by small-scale fishery mainly using gill nets (cf. Fig. 2). Apart from an indirect competition for food resources, this fishing method poses a direct threat to penguins, because frequent mortalities involving one or the other species have been observed in central Chile (Pütz et al., 2011; Simeone et al., 1999, 2009; Suazo et al., 2013; Wallace et al., 1999) and Perú (Majluf et al., 2002). It is usual practice for fishermen to return drowned penguins to the sea after cutting them open to support their descent, so many incidental catches remain unreported (AS, unpubl. data; Pütz et al., 2011). Even one mass mortality, coinciding with our study period, occurred in March 2009 when nearly 1400 penguin carcasses were washed ashore in a bay near Queule (39° 23′S), about 300 km to the north of Puñihuil. Clinical examination of a number of carcasses revealed that the most likely cause of death was drowning, which was confirmed by several reports from fishermen (AS unpubl. Data; Schlatter et al., 2009). It is quite likely that the real extent of this mass mortality was even higher because many carcasses may either have sunk before being washed ashore or drifted somewhere else (Schlatter et al., 2009). Fortunately, while some of our study birds were in the specific area affected by the mass mortality during the time the mortality occurred, none was killed. This shows that (a) the area is a favourable foraging ground for penguins during this time of the year, and (b) that mortalities occurring in one specific area can have significant effects on penguin populations breeding somewhere else, due to their migratory behaviour. Accordingly, it has been proposed to separate fishermen and penguins, either by spatial or temporal means (Trathan et al., 2014; Yorio et al., 2010), to reduce the incidental capture of penguins in fishing nets. However, while this appears to be manageable during the breeding season, when penguins are restricted in their foraging range due to the necessity to provision their offspring with food on a regular basis, the development of exclusion devices that stop penguins entering fishing gear needs to be promoted to reduce incidental capture of penguins outside the breeding season when they roam over much larger areas.

5. Conclusion

Humboldt and Magellanic penguins breeding in southern Chile (Puñihuil islets) make use of coastal areas extending up to 1000 km north from their breeding site during the post-moult period and early winter. In their foraging grounds birds benefit from the high productivity of the Humboldt Current but are also threatened by artisanal fisheries. It would be desirable to develop, in conjunction with local fishermen, adequate conservation measures to protect migrating penguins and other seabirds. However, while conservation measures have been partially established on a local scale, more efforts must be made to also install marine protected areas in the wintering grounds, e.g. around Isla Mocha or in the Gulf of Arauco. On a local scale, successful conservation will require, for example, a termination of the replacement of local fishermen engaging in ecotourism by fishermen from other areas in Chile, whereas many more stakeholders, including government and NGO's, have to become involved on regional or even larger scales.

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