

# Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time

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**Abstract.** Ecological niche theory predicts segregation mechanisms that mitigate potential competition between closely related organisms. However, little is known outside the breeding season, when central-place foraging animals may move on larger scales. This study tested for segregation mechanisms within the same 2007 inter-breeding period on three neighboring populations of avian predators from the southern Indian Ocean: Eastern Rockhopper Penguins *Eudyptes filholi* from Crozet and Kerguelen and Northern Rockhopper Penguins *E. moseleyi* from Amsterdam. Using state-of-the-art geolocation tracking and stable isotope analysis techniques, we quantified and compared the ecological niches in time, space, and diet. The three populations showed large-scale movements over deep oceanic waters near the Subantarctic Front, with generally little individual variation. The two neighboring populations of Eastern Rockhopper Penguins showed strikingly distinct distribution in space, while foraging in similar habitats and at the same trophic level (crustacean-eaters). In contrast, Northern Rockhoppers showed marked spatial overlap with birds of the sibling Eastern species, but their temporal delay of two months enabled them to effectively avoid significant overlap. Our results highlight parsimonious mechanisms of resource partitioning operating at the population level that may explain how animals from neighboring localities can coexist during the nonbreeding period.

**Key words:** *Eudyptes filholi*; *Eudyptes moseleyi*; geolocation; habitat use; niche theory; nonbreeding period; penguins; resource partitioning; space segregation; stable isotopes; time segregation; trophic ecology.

## INTRODUCTION

Between two successive breeding periods, central-place foraging animals are no longer tied to their breeding grounds. They migrate or disperse to reach areas favorable to replenish their energetic reserves, where they may also face strong environmental constraints that may severely affect specific demographic categories, such as breeders (Fretwell 1972). How animals manage to mitigate competition on the favorable areas frequented during this inter-breeding period is poorly documented. These strategies may involve segregation mechanisms predicted by ecological niche theory (Hutchinson 1957), notably in space, time, and on food (Pianka 1981). Yet, the inter-breeding period has received little attention, especially in marine organisms, which are particularly challenging to study while at sea. Seabird foraging strategies at this time have consequently been inadequately described, and have mostly focused on coastal and neritic species (e.g., Grémillet et al. 2000): oceanic species remain the most challenging to study (e.g., Bost et al. 2009). Direct at-sea surveys may give valuable overviews of year-round habitat use for oceanic seabirds, but suffer from

important sampling issues, including the unknown origin and breeding status of individuals observed and low detection probabilities for diving animals such as penguins.

In this study we focus on the inter-breeding exodus of three neighboring populations of Rockhopper penguins *Eudyptes* spp. in the southern Indian Ocean. We investigated their activity schedule, habitat use, and trophic ecology during the complete inter-breeding period, in order to quantify their winter ecological niche in time, space, and diet. We carried out this investigation at the level of (1) individuals within a given population, (2) populations of the same species, namely the Eastern Rockhopper Penguin *E. filholi*, from the neighboring Crozet and Kerguelen Islands, and (3) populations of sibling species whose breeding schedules are shifted, namely Eastern Rockhopper from Kerguelen and Northern Rockhopper *E. moseleyi* from nearby Amsterdam Island. Our study was facilitated by recent developments in miniaturized light-based geolocation loggers (Gonzalez-Solis et al. 2007) and stable isotope analysis of animal tissues (Kelly 2000, Cherel et al. 2007) that enabled us to study penguin ecology at sea over extended periods and areas. Importantly, we had the unique opportunity to study all three neighboring populations during the same year.

At the population level, seabirds from a given colony generally distribute consistently at sea, while distribu-

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tions diverge between neighboring localities ("Hinterland model" [Cairns 1989]; see also Grémillet et al. 2004, Trathan et al. 2006). Our first prediction, therefore, was that individuals from given populations show a similar ecological niche during the inter-breeding period exodus. Our second prediction was that even in the case of long-range inter-breeding migration (e.g., Bost et al. 2009), there would be minimal spatial overlap in wintering areas for parapatric populations of conspecifics, which presumably have similar migration schedules and trophic ecology. Finally, we expected that spatial overlap could occur between neighboring populations of sibling species, as segregation mechanisms may already operate along other dimensions (at-sea activity schedule, diet).

## METHODS

### *Study area and species*

Our study took place in the southern Indian Ocean. This oceanic region is strongly influenced by the Antarctic Circumpolar Current (ACC), flowing eastward and comprising a succession of oceanographic fronts: from north to south the northern and southern boundaries of the Subtropical Front (NSTF and SSTF, respectively), the Subantarctic Front (SAF), the Polar Front (PF), and the southern boundary of the ACC. It is noteworthy that the location of these oceanographic fronts varies seasonally and their surface definition is not always absolute (Belkin and Gordon 1996, Park et al. 2009). These fronts delimit four water masses corresponding to different habitats in our study: from north to south, the Subtropical Zone (STZ), the Subantarctic Zone (SAZ), the Polar Frontal Zone (PFZ), and the Antarctic Zone.

Rockhopper penguins are small and sexually dimorphic penguins (Warham 1975). We studied Eastern Rockhopper Penguin populations on the Crozet and Kerguelen subantarctic archipelagos where, respectively, ~120 000–150 000 and 150 000–200 000 individuals breed (Jouventin et al. 1988). The Northern Rockhopper Penguin was studied on subtropical Amsterdam Island, where ~50 000 individuals breed (Guinard et al. 1998). These two sibling species show delayed at-land sojourns: late-July to mid-March for the Northern species vs. mid-November to mid-May for the Eastern Rockhopper Penguin (Warham 1975).

### *Type of data collected*

All three populations were studied during the same 2007 inter-breeding season. To track the animals during this entire period with minimal disturbance, we used miniaturized MK4 geolocators (British Antarctic Survey, Cambridge, UK) attached to specially designed leg bands, following Bost et al. (2009). These loggers record time and light level, allowing estimates of geographic position twice per day with an expected spatial accuracy of tens to hundreds of kilometers (Delong et al. 1992, Wilson et al. 2002). The loggers also record local

seawater temperature (accuracy: 0.5°C). We equipped 22 molting birds (11 males and 11 females) at Crozet (Possession Island) and 20 (10 males and 10 females) at Kerguelen (Mayès Island) in May 2007, as well as 20 (14 males and 6 females) at Amsterdam in late February 2007.

Following Cherel et al. (2007), animals were sampled on recapture ( $n=6, 14, 13$  plus control individuals:  $n=3, 20, 12$  at Crozet, Kerguelen, and Amsterdam, respectively) to determine the carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope signatures in whole blood. These values allowed foraging zone and trophic level to be estimated for the months preceding sampling (turnover of half markers in whole blood estimated to 27 days; Cherel et al. 2007), corresponding to the end of the inter-breeding period.

### *Analyses of tracks: description and comparison*

Geolocation data were analyzed following Thiebot and Pinaud (2010), allowing us to estimate the most probable movement pathways of individuals. We specified a mean speed of 2 km/h to constrain movement estimates, according to Raya Rey et al. (2007). Tracks were described and compared using a common set of parameters: (1) the start/end date of migration (corresponding to the first and last water temperature sensor record from each logger); (2) the total distance traveled; (3) the maximum distance reached from the colony (i.e., the "maximum range"); and (4) the proportion of time spent in the different water masses.

Population home ranges were evaluated from the 95% kernel density contour (Wood et al. 2000), with a consistent use of a smoothing parameter (search radius) of  $h=2^\circ$ , as needed for such data (BirdLife International 2004). Overlap between home ranges was quantified using the Utilization Distribution Overlap Index (UDOI), following Fieberg and Kochanny (2005). In order to calculate the maximum theoretical overlap among population pairs to compare with our data, we simulated an opposite bearing for trips. In this simulated situation, only longitude was modified in order to conserve the thermal preferendum of the species (i.e., latitude).

### *Habitat use during inter-breeding period*

In order to control that populations with mutually exclusive spatial distributions used similar marine habitats, we investigated the environmental niche used by each population during winter. Core use of a wintering area was distinguished from migration phases by relying on the period of the lowest mean travel speed of animals, which may reflect periods of intense prey search (Weavers 1992). The environmental characteristics of this winter habitat were extracted within the 95%, 75%, and 50% kernel density contours. The environmental variables investigated were bathymetry and its gradient, sea surface temperature (SST) and its gradient, SST anomalies, sea surface chlorophyll *a* concentration

(CHLA), mixed-layer depth (MLD), and eddy kinetic energy (EKE). The spatial grid of these variables was  $1^\circ$  in accordance with the geolocation technique accuracy, and the temporal resolution was 1 month, given the environmental variability in the study region (Clarke 1988). These data are *available online*: NOAA's ETOPO,<sup>4</sup> Bloomwatch 180,<sup>5</sup> AVISO,<sup>6</sup> and LOCEAN.<sup>7</sup> MLD was a mean of the annual data obtained since 1941.

## RESULTS

Minimal recovery rates of geolocation devices, depending on field possibilities to survey the colonies at the beginning of the next breeding season, were 55% at Crozet (12/22), 70% at Kerguelen (14/20), and 70% at Amsterdam (14/20). Finally, data could be extracted successfully from 11 loggers from Crozet (5 from males, 6 from females), 14 from Kerguelen (9 from males, 5 from females) and 11 from Amsterdam (7 from males, 4 from females).

### Overview of tracks

The home range of our study populations are shown in Fig. 1. This reveals large-scale movement of all birds (Table 1) over deep oceanic waters of the southern Indian Ocean, without any return to land. No bird went north of the NSTF, and virtually none south of the PF. All individuals followed a comparable at-sea pattern: during their first 2–3 months at sea they kept a fairly constant overall bearing, next they appeared much less mobile on one area during 1–2 months, and finally they exhibited a short, fast and linear return movement lasting  $\sim 1.5$  months. Individuals from Crozet all departed westward or northwestward, reached the edge of the Southwest Indian Ridge, and then moved slowly eastward along the SAF, north of the Crozet region. In contrast, individuals from Kerguelen all headed eastward to the Southeast Indian Ridge, in a linear and wider scale movement into the SAZ. Of the Kerguelen birds, five (two females and three males) showed a more northeasterly dispersal and temporarily reached the STZ. Individuals from Amsterdam all headed southeastward along the Southeast Indian Ridge and then moved eastward, with the majority south of the SSTF into the SAZ, before returning to their colony. Importantly, the home ranges of Kerguelen and Amsterdam birds overlapped spatially during their winter migration, whereas birds from Crozet foraged in a distinct area. In keeping with their breeding chronology, birds from Crozet and Kerguelen departed

later from their breeding colonies than did those from Amsterdam; this was later by  $\sim 2$  months (Table 1).

### Habitat use and spatial overlap between populations

In considering the proportion of time spent in each ocean water mass, birds from Crozet spent most of their inter-breeding period in the SAZ ( $52.6\% \pm 23.6\%$ , all values mean  $\pm$  SD; see Appendix D) and PFZ ( $47.2\% \pm 23.5\%$ ). The birds from Kerguelen also spent the majority of their time in the SAZ ( $43.2\% \pm 18.4\%$ ) and PFZ ( $34.6\% \pm 14.8\%$ ), and a minor fraction in the STZ ( $16.1\% \pm 24.2\%$ ). Animals from Amsterdam used almost exclusively the STZ ( $59.3\% \pm 24.4\%$ ) and SAZ ( $40.3\% \pm 24.2\%$ ). Overall, the three populations spent similar proportions of time into the SAZ (ANOVA,  $F_{2,33} = 0.95$ ,  $P = 0.397$ ).

The UDOI calculated between the 95% kernel density contours of paired localities was 0 for all except the Amsterdam–Kerguelen pair, for which it reached 0.33. During the four months of simultaneous presence at sea of populations from Kerguelen and Amsterdam, this overlap was maximal in July (UDOI = 0.28; Appendix E) and was nil to very weak for the other months (May, 0; June, 0.04; August,  $<0.01$ ). Water temperature recorded by loggers revealed two main facts about this overlap (Fig. 2). First, only the northerly heading birds from Kerguelen overlapped with birds from Amsterdam. Secondly, these two populations were concomitantly in waters of similar temperature during only one week of the whole inter-breeding period.

Maximum theoretical overlap was high in all cases: in our simulated situation, UDOI was 0.61 for the Crozet–Kerguelen pair and 0.31 for the Crozet–Amsterdam pair. Conversely, the simulated value for the Kerguelen–Amsterdam pair was the same as observed (UDOI = 0.33).

All populations showed significant variability in mean swimming speed by month, with the minimum speed consistently occurring two months before the birds were back on land (for Crozet, Kruskal-Wallis  $\chi^2_6 = 26.7$ ,  $P = 0.0002$ ; for Kerguelen, Kruskal-Wallis  $\chi^2_6 = 25.8$ ,  $P = 0.0002$ ; for Amsterdam, ANOVA,  $F_{5,50} = 8.96$ ,  $P < 0.0001$ ). This was in September for Crozet and Kerguelen birds, and in May for Amsterdam birds (Appendix F). During these months, each population used deep oceanic waters, mainly ranging between 3000 and 3500 m (Table 2), with apparently greater seafloor slope for animals from Crozet. SST and SST gradient values used by birds from Crozet and Kerguelen were variable but close, whereas birds from Amsterdam used warmer and less structured areas. All three populations were found in waters with highly heterogeneous SST anomalies and CHLA, although birds from Amsterdam tended to use areas with more negative anomalies. Birds from Kerguelen used waters with deeper mixed-layer depth, compared to birds from the two other populations. Finally, birds from Crozet used waters with the highest and most variable EKE values, compared with

<sup>4</sup> [http://www.ngdc.noaa.gov/mgg/gdas/gd\\_designagrid.html?dbase=GRDET2](http://www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html?dbase=GRDET2)

<sup>5</sup> <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp>

<sup>6</sup> <http://las.aviso.oceanobs.com/las/servlets/dataset>

<sup>7</sup> <http://www.locean-ipsl.upmc.fr/~cdblod/mlld.html>

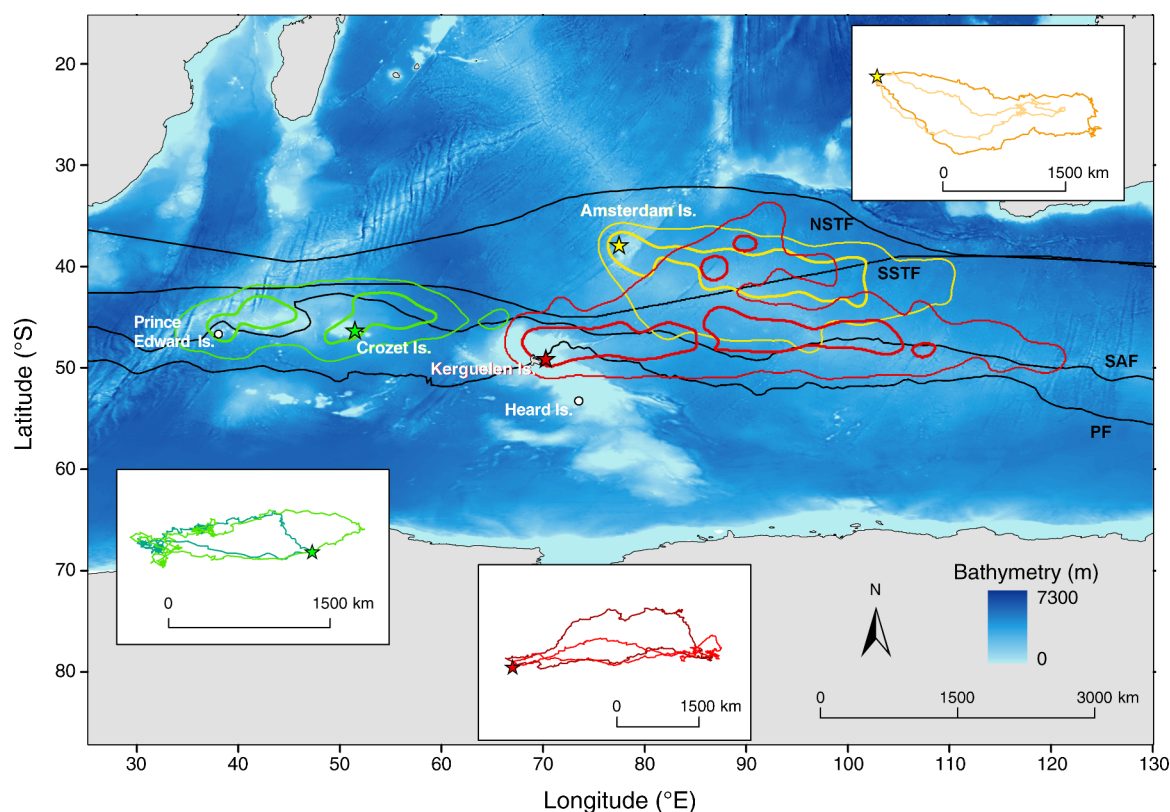


FIG. 1. At-sea distribution during the inter-breeding period of the three populations of Rockhopper Penguins (*Eudyptes* spp.) from Crozet (green colors), Kerguelen (red colors) and Amsterdam (yellow colors), with depth contours shown in the background (shallow areas such as seafloor ridges and peri-insular shelves appear in lighter blue); colored stars show the respective colony locations. The 95% (thin lines) and 50% (bold lines) kernel density contours are shown. The black lines represent the mean positions of the oceanographic fronts, from north to south the Northern and Southern boundaries of the Subtropical Front (NSTF and SSTF, respectively), the Subantarctic Front (SAF) and the Polar Front (PF); these boundaries delimit from north to south the Subtropical Zone, the Subantarctic Zone, the Polar Frontal Zone, and the Antarctic Zone. Inset boxes show details of two representative interpolated tracks of individuals from each study site.

TABLE 1. Winter migration parameters (mean  $\pm$  SD) of Rockhopper Penguins (*Eudyptes* spp.) from three tracked populations in the southern Indian Ocean.

Individuals ( <i>n</i> ), by locality	Peak departure date (range)	Peak return date (range)	Time at sea (d)	Minimal distance traveled (km)	Maximal distance from colony (km)
<b>Crozet</b>					
All (11)	13 May (10–15 May)	8 Nov (30 Oct–16 Nov)	179 $\pm$ 6	8237 $\pm$ 533	946 $\pm$ 264
Males (5)	13 May (10–15 May)	4 Nov (30 Oct–11 Nov)	175 $\pm$ 7	8058 $\pm$ 586	913 $\pm$ 332
Females (6)	13 May (11–13 May)	8 Nov (7–16 Nov)	183 $\pm$ 3	8387 $\pm$ 484	973 $\pm$ 222
<b>Kerguelen</b>					
All (14)	11 May (7–13 May)	25 Nov (11–26 Nov)	195 $\pm$ 5	10 127 $\pm$ 708	2520 $\pm$ 635
Males (9)	11 May (9–12 May)	17 Nov (11–26 Nov)	192 $\pm$ 5	9995 $\pm$ 801	2478 $\pm$ 697
Females (5)	11 May (7–13 May)	25 Nov (11–25 Nov)	198 $\pm$ 2	10 364 $\pm$ 487	2595 $\pm$ 571
<b>Amsterdam</b>					
All (11)	16 Mar (10–21 Mar)	25 Jul (17 Jul–06 Aug)	132 $\pm$ 5	7305 $\pm$ 693	2088 $\pm$ 421
Males (7)	16 Mar (10–16 Mar)	25 Jul (17–26 Jul)	131 $\pm$ 3	7540 $\pm$ 607	2199 $\pm$ 445
Females (4)	20 Mar (16–21 Mar)	31 Jul (26 Jul–6 Aug)	134 $\pm$ 7	6893 $\pm$ 713	1895 $\pm$ 342

Notes: For birds from Crozet and Kerguelen, time spent at sea tended to be longer for females than for males (*t* tests,  $P = 0.06$  and  $P = 0.006$ , respectively). Mean time spent at sea was greatest for Kerguelen birds and least for Amsterdam birds (Kruskal-Wallis  $\chi^2 = 30.3$ ,  $P < 0.0001$ ). The minimum distance traveled during the whole trip was also greatest for Kerguelen birds, and shortest for Amsterdam birds (ANOVA,  $F_{2,33} = 60.9$ ,  $P < 0.0001$ ). The maximum range reached from the colony was also greatest at Kerguelen, and smallest at Crozet (ANOVA,  $F_{2,33} = 33.8$ ,  $P < 0.0001$ ).



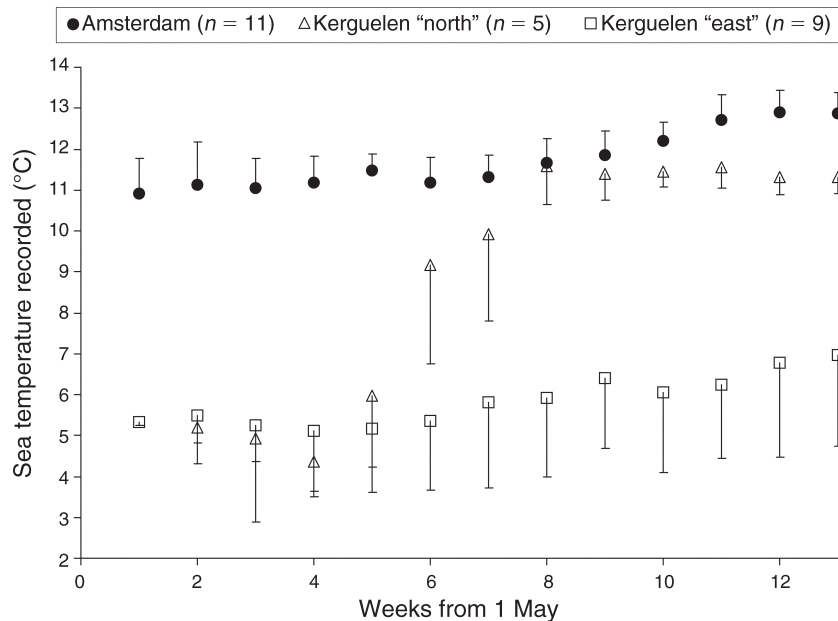


FIG. 2. Sea surface temperature recorded by the loggers deployed on Rockhopper Penguins from Amsterdam and Kerguelen, during their coincident time at sea: from early May (departure of the first animal from Kerguelen) to early August (return of the last animal from Amsterdam). Sea temperature is averaged over one-week intervals and is given as mean and SD. Animals from Kerguelen were divided into two groups, according to their bearing on leaving the breeding colony: northeastward ("north") or nearly eastward ("east").

birds from Amsterdam using waters with the lowest EKE values.

#### Isotopic ratios

At each locality, no significant differences in whole-blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were evident for instrumented penguins compared to control birds, or between males and females (Appendix A). Isotopic values for all birds from each locality were therefore pooled. Overall,  $\delta^{13}\text{C}$  showed low variances whatever the locality (Table 3; see Appendix B), as did the  $\delta^{15}\text{N}$  values. Eastern Rockhopper Penguins from Kerguelen showed lower blood  $\delta^{13}\text{C}$  values than Crozet birds ( $t_{10,4} = 4.08$ ,  $P = 0.002$ ), whereas their  $\delta^{15}\text{N}$  values were not significantly different ( $W = 94$ ,  $P = 0.081$ ). Between the two different

species, Kerguelen birds had lower blood  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than birds from Amsterdam (both  $W = 850$  and  $P < 0.0001$ ).

#### DISCUSSION

To our knowledge, this study is among the first to fully document the spatial distribution and trophic ecology of closely related populations of a seabird during the inter-breeding period (e.g., Thiebot et al. 2011), and the very first dealing with congeneric diving seabirds. A previous investigation showed that individual Cory's Shearwaters (*Calonectris diomedea*) breeding in different localities wintered in one or more of three areas associated with coastal upwellings, with birds from different colonies being mixed on their wintering

TABLE 2. Environmental variables (mean  $\pm$  SD) within three kernel density contours (95%, 75%, 50%) of each tracked population during the month when the mean speed of the individuals was lowest.

Environmental variable	Crozet (Sep)			Kerguelen (Sep)
	95%	75%	50%	95%
Bathymetry (m)	3389 $\pm$ 933	3166 $\pm$ 919	2946 $\pm$ 936	3499 $\pm$ 356
Bathymetry gradient	0.18 $\pm$ 0.18	0.23 $\pm$ 0.21	0.30 $\pm$ 0.25	0.06 $\pm$ 0.04
SST ( $^{\circ}\text{C}$ )	8.4 $\pm$ 4.0	8.4 $\pm$ 3.3	7.9 $\pm$ 2.6	8.4 $\pm$ 3.0
SST gradient	0.37 $\pm$ 0.16	0.39 $\pm$ 0.15	0.41 $\pm$ 0.15	0.24 $\pm$ 0.17
SSTA ( $^{\circ}\text{C}$ )	0.12 $\pm$ 0.92	-0.01 $\pm$ 1.06	-0.14 $\pm$ 1.32	-0.06 $\pm$ 0.67
CHLA ( $\text{mg}/\text{m}^3$ )	0.64 $\pm$ 1.52	0.62 $\pm$ 1.39	0.62 $\pm$ 1.35	0.42 $\pm$ 1.11
MLD (m)	124 $\pm$ 25	119 $\pm$ 22	114 $\pm$ 16	215 $\pm$ 76
EKE ( $\text{cm}/\text{s}$ )	316 $\pm$ 527	368 $\pm$ 585	380 $\pm$ 593	159 $\pm$ 185
Area ( $\text{km}^2$ )	1 818 506	856 796	428 398	3 829 354

Note: Variables are: SST, sea surface temperature; SSTA, sea surface temperature anomaly; CHLA, chlorophyll *a* concentration; MLD, mixed-layer depth; EKE, eddy kinetic energy), and area, total area inside the kernel density contours.

grounds (Gonzalez-Solis et al. 2007, Ramos et al. 2009). In contrast, Rockhopper Penguins show a completely different strategy. First, each individual penguin used only one of the wintering areas highlighted. Second, all individuals from a given locality generally followed the same overall migratory pattern, hence validating our first prediction. Third, all birds foraged in oceanic waters, and not in productive coastal areas (average ratio of primary production 1:10 between oceanic and coastal systems; Perissinotto and Walker 1998). Fourth, penguin populations segregated almost totally through either spatial or temporal mechanisms, thus minimizing potential competition between birds from different localities and validating our second prediction.

The SAZ was the main oceanic zone targeted east of Kerguelen and west of Crozet. Previously, inter-breeding at-sea distributions of Eastern and Northern Rockhopper Penguins were essentially unknown, and our results show marked contrast with the strategy of the Southern species *E. chrysocome*, which primarily targets shallow neritic waters during the winter months (Pütz et al. 2002, Raya Rey et al. 2007; in both these studies, birds could not be tracked during the whole inter-breeding period). This oceanic strategy of Eastern and Northern Rockhoppers is thus closer to that of the sympatric Macaroni Penguin *E. chrysolophus* (Bost et al. 2009). It can be assumed that this oceanic wintering strategy close to the SAF for both Eastern and Northern Rockhopper Penguins may be consistent from year to year. An adaptive strategy, especially for such flightless and long-lived predators during the breeding as well as the inter-breeding periods, is precisely to concentrate foraging effort in areas that were previously experienced as favorable (Fraser and Trivelpiece 1996, Trathan et al. 2006, Thiebot et al. 2011; see Appendix C).

#### Trophic niches

Blood isotopic signatures reflect the trophic niche of seabirds over the last roughly two months (Cherel et al. 2007), which in our case integrates time spent at both the wintering area and the short, fast, and linear return migration. The tracking and isotopic signatures strongly

TABLE 3. Isotopic signatures ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) measured on all individuals sampled; values are means  $\pm$  SD.

Locality	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Crozet	9	$-20.9 \pm 0.5$	$8.0 \pm 0.3$
Kerguelen	34	$-21.6 \pm 0.4$	$8.3 \pm 0.6$
Amsterdam	25	$-18.1 \pm 0.3$	$12.5 \pm 0.5$

support each other at the end of winter. Based on latitudinal variation in  $\delta^{13}\text{C}$  values in the Southern Ocean (Cherel and Hobson 2007), our data underline a spatial gradient between the southern and colder foraging zone of birds from Kerguelen ( $49^\circ\text{S}$ ) to the subtropical feeding area of those from Amsterdam Island ( $38^\circ\text{S}$ ), with birds from Crozet ( $46^\circ\text{S}$ ) having an intermediate position.

The Eastern Rockhoppers from Crozet and Kerguelen had identical  $\delta^{15}\text{N}$  values, indicating that both populations fed at the same trophic level in winter. Their  $\delta^{15}\text{N}$  values were slightly higher than those of crested penguins that mainly feed on crustaceans in summer, but much lower than those of larger penguins and fur seals that prey upon mesopelagic fish (Cherel et al. 2007). Taken together, the isotopic comparison strongly suggests that adult Eastern Rockhopper Penguins complemented a crustacean-based diet in winter by foraging on mesopelagic fish (i.e., myctophids). Finally, the Northern Rockhopper Penguin segregated isotopically from the Eastern species. Its higher  $^{15}\text{N}$  value potentially results from two nonexclusive explanations, first the elevated  $^{15}\text{N}$  baseline level evident in the subtropical zone compared to that in the subantarctic zone (Cherel and Hobson 2007), and second the different diets in warm and cold waters (Tremblay and Cherel 2003), as macrozooplanktonic and micronektonic species differ between water masses.

#### Resource partitioning

The concept of an ecological niche as a hyper-volume (Hutchinson 1957) allows one to understand how closely related organisms manage to coexist by exploiting different ranges of environmental resources. This

TABLE 2. Extended.

Kerguelen (Sep)		Amsterdam (May)		
75%	50%	95%	75%	50%
3516 $\pm$ 317	3497 $\pm$ 313	3370 $\pm$ 349	3227 $\pm$ 273	3114 $\pm$ 235
0.06 $\pm$ 0.03	0.06 $\pm$ 0.03	0.06 $\pm$ 0.03	0.07 $\pm$ 0.04	0.07 $\pm$ 0.03
7.9 $\pm$ 2.4	7.5 $\pm$ 1.8	11.8 $\pm$ 2.0	11.8 $\pm$ 1.3	11.8 $\pm$ 0.8
0.27 $\pm$ 0.15	0.31 $\pm$ 0.13	0.14 $\pm$ 0.10	0.10 $\pm$ 0.06	0.08 $\pm$ 0.03
0.03 $\pm$ 0.61	0.11 $\pm$ 0.53	-0.23 $\pm$ 0.38	-0.29 $\pm$ 0.28	-0.33 $\pm$ 0.25
0.41 $\pm$ 1.10	0.41 $\pm$ 1.09	0.48 $\pm$ 1.13	0.46 $\pm$ 1.12	0.46 $\pm$ 1.10
206 $\pm$ 67	206 $\pm$ 68	107 $\pm$ 21	110 $\pm$ 20	115 $\pm$ 20
173 $\pm$ 181	188 $\pm$ 173	87 $\pm$ 125	75 $\pm$ 101	77 $\pm$ 99
1 993 363	961 710	2 168 219	1 127 824	585 769

volume comprises three main axes: the trophic, spatial, and temporal dimensions. In our study, animals showed little individual specialization along these three axes within each population, including between sexes. These generally coherent at-sea distribution patterns observed for seabirds from a given colony have been attributed to better food localization and exploitation (Ward and Zahavi 1973, Clark and Mangel 1984) as well as possible cultural effects (e.g., Grémillet et al. 2004). Hence, mitigation of intra-population competition would occur through widening of ecological niches in comparison with the more favorable breeding period, as already observed for such species (Cherel et al. 2007).

At the population level, we showed that habitats exploited concomitantly by conspecific penguins from Crozet and Kerguelen were similar (including trophic niche). The model of Cairns (1989) predicts that, in this case, potential intraspecific competition is mitigated by complete spatial segregation. This latter phenomenon, observed in our study, indeed has scarcely been verified in the wild (e.g., Grémillet et al. 2004). It is noteworthy that these two neighboring colonies potentially overlap in their foraging range (see Table 1; distance between Crozet and Kerguelen is ~1300 km). In this situation, Cairns (1989) predicted that (1) the foraging area exploited by each population would be balanced by the need to minimize travel cost between the colony and the foraging area, and that (2) seabirds would forage closer to their own colony rather than closer to the neighboring colony. The strikingly opposite at-sea distribution patterns obtained for the Crozet and Kerguelen birds appear therefore as a standard illustration of these predictions. However, the generally high coherence of individual movements within a population suggests low levels of concurrence. It seems likely that two factors may contribute to this mutually exclusive distribution. Firstly, Rockhoppers are known to adjust their diet geographically (Tremblay and Cherel 2003). Thus the unexploited region between Crozet and Kerguelen suggests a very unfavorable winter feeding area, whereas more favorable areas are to be found elsewhere over the oceanic ridges (see Fig. 1). Secondly, the two populations may be responding to contrasting life history traits, with the emergence of divergent population-based cultural patterns. To support this latter hypothesis, it would be necessary to investigate: (1) the paleo-environmental conditions that each population experienced, and (2) whether the recent drop in prominent food competitors such as large whales may have led to a spatially skewed distribution of available food in this region (Conroy 1975).

Conversely, between neighboring populations of sibling species, the at-sea distribution of the birds from Amsterdam and Kerguelen overlapped spatially. The core winter habitats used by these two populations revealed contrasting environmental conditions (see Table 2), suggesting that the difference in migration onset between these two populations leads them to

different available habitats even in overlapping geographical areas. A major seasonal change in this geographic area is probably key to understanding this dynamic, allowing the area to support sequentially different migrating populations (Mueller and Fagan 2008). This temporal segregation in the use of overlapping areas thus provides a spectacular case of resource partitioning for populations of sibling species after the release of breeding constraints. Such a delay in activity schedules of both species is probably triggered by the different environmental conditions at their respective breeding localities (Warham 1975).

### *Conclusions and perspectives*

At the individual level, our study showed a low level of individual variation within each population. Conversely, at the population level, this study highlights a complete spatial segregation between parapatric populations of an oceanic predator during the inter-breeding period. Finally, at the species level, it documents that two sibling species with delayed activity schedules can exploit overlapping wintering areas. Using geolocation tags on penguins allows one to highlight the nutritional importance of vast oceanic areas that were not previously recognized as foraging hotspots for wintering animals (Bost et al. 2009). Yet, the world population of Rockhopper Penguins has declined throughout its range over the last century, although causes of this decline are not well understood (Hilton et al. 2006, Crawford et al. 2009, Cuthbert et al. 2009). One key factor appears to be the body condition of birds at the start of each breeding season, emphasizing the importance of both body reserves built up during the previous inter-breeding period and the availability of resources on the wintering grounds (Crawford et al. 2006). Monitoring secondary production levels within the hotspots delineated in this work may be a potentially useful step to better understand population declines.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Detail of isotopic signatures for control animals and for tracked males vs. females at Crozet, Kerguelen, and Amsterdam (*Ecological Archives* E093-012-A1).

##### Appendix B

Detail of isotopic signatures for Rockhopper Penguins from Kerguelen that showed divergent dispersion from the colony (northeastward vs. eastward (*Ecological Archives* E093-012-A2).

##### Appendix C

Overall mass gain for Rockhopper Penguins tracked from each locality (*Ecological Archives* E093-012-A3).

##### Appendix D

Time spent per water mass of the Southern Ocean for Rockhopper Penguins tracked from each locality (*Ecological Archives* E093-012-A4).

##### Appendix E

At-sea distribution of Rockhopper Penguins from Kerguelen and Amsterdam during the month of maximal overlap between these two populations (*Ecological Archives* E093-012-A5).

##### Appendix F

Monthly anomalies in the mean traveling speed of Rockhopper Penguins during the inter-breeding period (*Ecological Archives* E093-012-A6).