

Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation

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ABSTRACT: We studied the year-round distribution and at-sea activity patterns of the sibling species, northern giant petrel *Macronectes halli* and southern giant petrel *M. giganteus*. Loggers combining light-based geolocators and immersion sensors were used to provide year-long data on large-scale distribution and activity of both species from the Crozet Islands (46° 25' S, 51° 51' E) and northern giant petrels from the Kerguelen Islands (49° 19' S, 69° 15' E) in the southern Indian Ocean. Argos platform transmitter terminals (PTTs) were used to track fine-scale movements of breeding adults and juveniles. Overall, adults remained within the Indian Ocean during and outside the breeding season, whereas juveniles dispersed throughout the Southern Ocean. In accordance with previous studies, differences in adult distribution and behaviour were greater between sexes than species: females dispersed more widely than males and also spent more time sitting on the water, particularly during the winter. Observed differences in distribution have important conservation implications: adults, especially males, overlap to a large extent with longline fisheries for Patagonian toothfish *Dissostichus eleginoides* in shelf areas within national Exclusive Economic Zones (EEZs), whereas adult females and juveniles are more likely to encounter high-sea longline fleets targeting tuna in subtropical waters. The circumpolar wide ranging behavior of naïve juvenile birds makes them particularly susceptible to interaction with a wide range of longline fisheries.

KEY WORDS: Year-round distribution · Giant petrels · Telemetry · Global location sensing · Longliners

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INTRODUCTION

Interactions with longline fisheries are a major concern for many seabirds (Weimerskirch et al. 1997, 2000, Gales et al. 1998). Assessing bycatch risks effectively requires the integration of both spatio-temporal distribution of seabird populations and fishing effort (Tuck et al. 2003, 2011). Albatrosses and petrels are amongst the species most affected by these fisheries (Croxall & Nicol 2004). Knowledge of at-sea distribution and behaviour is an essential

prerequisite for the development of appropriate conservation strategies, specifically for assessing overlap and hence potential susceptibility to bycatch in different fisheries.

Northern giant petrels *Macronectes halli* (hereafter NOGP) and southern giant petrels *M. giganteus* (hereafter SOGP) are sibling species of large, wide-ranging procellariiform seabirds, and have circumpolar breeding and at-sea distributions that show considerable overlap (Brooke 2004). Giant petrels are long-lived, with late sexual maturity, low fecundity,

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and high adult survival. As such, they are highly sensitive to additional mortality (Lebreton & Clobert 1991). Although categorised as Least Concern by the World Conservation Union (IUCN) since 2009 (Bird Life International 2012), both species are listed under the international Agreement for the Conservation of Albatrosses and Petrels (www.acap.aq). These 2 closely related and morphologically similar species breed with a 6 wk lag, which represents the main isolating mechanism between the 2 species (Hunter 1987). They show the highest sexual size dimorphism among seabird species — males are about 20% heavier than females — and the males in particular are dominant scavengers feeding extensively on land on penguins and seal carrion, and at-sea on dead cetaceans, although both sexes consume other prey such as crustaceans and fishes (Hunter 1983, Hunter & Brooke 1992, Ridoux 1994, González-Solís et al. 2002a,b). In the Atlantic Ocean, differences in foraging zones and habits are greater between sexes than between species (González-Solís et al. 2000a,b, 2007).

When giant petrels feed at sea, they are known to follow fishing boats (Cherel et al. 1996, Otley et al. 2007a) and are often caught incidentally by fishing gear, particularly in longline fisheries for Patagonian toothfish *Dissostichus eleginoides* during both the breeding and nonbreeding periods (Nel et al. 2002a, Delord et al. 2005, SC-CCAMLR 2010). Their populations show contrasting trends at different breeding sites (Delord et al. 2008, Ryan et al. 2009). Given their sensitive life history, it remains possible that incidental mortality in fisheries is a component of some of the observed population declines. Indeed, there is evidence for a decline of giant petrel populations linked to bycatch in longline fisheries in several localities (Nel et al. 2002a).

Information on the at-sea distribution of giant petrels is restricted largely to studies of breeding and nonbreeding adults or juveniles in the Atlantic and Pacific oceans (González-Solís et al. 2002a, 2007, Quintana & Dell'Arciprete 2002, Trebilco et al. 2008, Quintana et al. 2010). However, in the Indian Ocean, where current longline fishing effort is particularly high (Tuck et al. 2003), there are no published data on the year-round distribution of adults, nor that of juveniles and immatures, which represent almost half of the total population in these long-lived species (Warham 1996).

The aim of this study was to determine the foraging ranges, movements and activity patterns of the 2 sibling species of giant petrel throughout their annual cycle, and to estimate the relative potential overlap of

birds of different sex, breeding colony and life stage with longline fishing in the Indian Ocean.

MATERIALS AND METHODS

Species and study sites

NOGP and SOGP breed sympatrically on 4 sub-Antarctic archipelagos, including the French Southern Territories of the Crozet (46°S, 52°E) and Kerguelen islands (50°S, 70°E) in the southern Indian Ocean, although there are very few SOGP at the latter (ACAP 2010a,b). During the breeding season, NOGP were captured on their nest in the Pointe Morne colony (Courbet Peninsula, Kerguelen) and both species were captured in the mixed colony of Pointe Basse (Possession Island, Crozet). The 2 sites are referred to hereafter as 'Kerguelen' and 'Crozet', respectively.

Tracking

For the long-term study of giant petrel movements and activity patterns, we used Mk5 loggers (British Antarctic Survey) that combine archival light-based geolocators (global location sensing [GLS] units) and immersion sensors and provide low accuracy locations (Phillips et al. 2004). They were mounted on plastic leg bands and weighed 3.6 g, which is below the 3% limit recommended for flying birds (Phillips et al. 2003). Devices were deployed on breeding adults: 28 NOGP in early November 2008 during the early chick rearing period and 14 SOGP in late November 2008 during the incubation period (see Table 1).

The loggers measured light level intensity every 60 s and recorded the maximum intensity in each 10 min interval. Thresholds in the light curves were used to determine sunrise and sunset times, allowing an estimation of latitude based on day length and longitude based on the timing of local midday with respect to Universal Time (Phillips et al. 2004). In addition to light, the loggers also tested for salt water immersion every 3 s and stored the sum of positive tests in each 10 min interval (from 0 for continuously dry to 200 for continuously wet). When the immersion sensor was continuously wet for more than 20 min, a measure of water temperature was recorded.

To obtain information on finer scale movements, albeit for shorter periods, adults and juveniles of both species were tracked during their respective breed-

Table 1. *Macronectes halli* and *M. giganteus*. Deployment details for northern and southern giant petrels on the Crozet and Kerguelen islands, southern Indian Ocean, equipped with global location sensing (GLS)-immersion loggers in November 2008 and tracked throughout the annual cycle; or with Argos satellite platform transmitter terminals (PTTs) during breeding or post-fledging dispersal in 2008–2009

Population	Sex	Stage	Device	No. of birds tracked	Mean tracking duration (d)	No. of raw locations	No. of corrected/ filtered locations	Locations removed (%)
<i>M. halli</i> (northern giant petrel)								
Crozet	Female	Adult	GLS	9	250.58	6524	4750	27.19
			PTT	2	12.9	162	162	0
		Juvenile	PTT	2	136.17	1532	1531	0.07
	Male	Adult	GLS	8	300.34	6597	5082	22.96
			PTT	4	26.07	270	270	0
		Juvenile	PTT	3	83.01	1303	1303	0
Kerguelen	Female	Adult	GLS	4	221.95	2759	1928	30.12
			PTT	2	16.32	187	186	0.53
		Juvenile	PTT	5	131.99	4112	4112	0
	Male	Adult	GLS	7	221.15	4959	3556	28.29
			PTT	5	4.22	149	149	0
		Juvenile	PTT	1	58.03	367	367	0
<i>M. giganteus</i> (southern giant petrel)								
Crozet	Female	Adult	GLS	9	320.19	7157	4673	34.70
			PTT	4	13.31	266	266	0
		Juvenile	PTT	4	108.18	2355	2355	0
	Male	Adult	GLS	5	241.26	3498	2399	31.42
			PTT	5	9.52	337	337	0
		Juvenile	PTT	1	58.03	367	367	0

ing and post-fledging dispersal periods using Argos satellite tags or platform transmitter terminals (PTTs). We used PTTs with solar panels, programmed with a duty cycle of 12 h on: 24 h off (36 Solar PTT 100 weighing 18 g, and 1 Solar/GPS weighing 22 g; Microwave Telemetry), attached to back feathers with Tesa® tape. PTTs were deployed for a single foraging trip in November to December 2008 on adult NOGP at both Crozet and Kerguelen during the early chick rearing period and on adult SOGP at Crozet during incubation (Table 1). Juveniles of both species were equipped just before fledging: in January to February 2009 for NOGP at Crozet and Kerguelen; and in March 2009 for SOGP at Crozet ($n = 5$ juveniles in each case). Sex was determined by measurements of bill length and comparison of relative size when both partners were simultaneously at nest (Voisin 1968).

Band recoveries

A banding program for giant petrels started in 1951 on Kerguelen, and in 1960 on Crozet (Weimerskirch et al. 1985). Information on species, banding date, bird status, location and date of each recovery was collated for all banded giant petrels caught by fishing

vessels or found dead or alive on beaches and reported to our lab from 1956 to 2011 (see Weimerskirch et al. 1985 for details).

Analyses

GLS tracking data analysis

The light data were processed using TransEdit and Locator in the BASTrak software suite (British Antarctic Survey) to obtain 2 estimated locations per day. We removed unrealistic geolocation estimates (1) when light curves showed major interference at dawn or dusk, (2) when flight speeds were unrealistic ($>80 \text{ km h}^{-1}$) according to an iterative filter (McConnell et al. 1992) and (3) during the 1 wk period around the equinoxes (20–21 March and 22–23 September), when latitude cannot be estimated accurately (Wilson et al. 1992).

Positions provided by GLS loggers are typically associated with mean errors of 185 to 200 km (Phillips et al. 2004, Shaffer et al. 2005). Furthermore, a gradual seasonal drift in latitude was apparent from a comparison of estimated locations and records of birds ashore based on visual observations or immersion data. Hence, latitude estimates were refined

by matching temperature recorded by loggers with those obtained from NOAA CoastWatch satellite (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html>). Temperature was not available for all locations because of a malfunction of the GLS devices; hence locations not corrected using temperature that were beyond the known distribution range of each species were removed using ArcMap® 9.2. In addition, locations at the colony were removed.

For each bird, locations were assigned to the breeding or nonbreeding period. Breeding status of tracked birds was not monitored after deployment. Hence, breeding was divided into 3 stages: pre-laying, incubation and chick-rearing based on mean laying, hatching and fledging dates of each species (Paulian 1953, Voisin 1968, Warham 1990). However, these periods vary among species and individuals (depending on laying, hatching, fledging date or possible breeding failure). Birds that did not return to the colony according to immersion data were classified as shifting from the breeding to nonbreeding stage.

Kernel analysis was used to map density distributions according to breeding stage, species, population and sex. This approach does not require serial independence of the locations (De Solla et al. 1999) and has been recognized as a useful tool to highlight important areas used by seabirds (Tancell et al. 2013). Kernels were calculated using the kernelUD function in the 'adehabitat' package (Calenge 2006), with a smoothing parameter value of 2. Ninety-five percent density contours were considered to broadly represent the home range (Gallerani Lawson & Rodgers 1997, Brothers et al. 1998), and 50% and 25% density contours to indicate outer and inner core areas, respectively.

Monthly composite environmental variables from the NOAA CoastWatch satellite (chlorophyll *a*, sea surface temperature [SST], and bathymetry), were then extracted and averaged within the 50% kernel density polygon calculated for each individual trip in a given period, and then compared among species, sexes and breeding periods using linear mixed models.

Satellite tracking analysis

Raw Argos locations were also filtered using an iterative backwards/forwards filtering routine (McConnell et al. 1992) to remove those which exhibited unrealistic flight speeds ($>80 \text{ km h}^{-1}$). Total distance travelled, mean speed, maximum distance to

the colony, total trip duration and distance travelled per day were compared between species and sexes using Wilcoxon test. All values are mean \pm SD. To have sufficient sample sizes, data for NOGP from Crozet and Kerguelen were pooled.

Activity data

To investigate patterns in at-sea activity, the total amount of time spent on water each day was calculated and then averaged by month for each individual. To identify variables influencing the proportion of time spent on the water, general linear mixed models (GLMMs) were performed on the log-transformed monthly value, with a logit link function and a normal distribution using the 'lme' function implemented in the 'lme4' package (Bates et al. 2011). Species, sex, population and month were included as fixed effects, and individual as a random intercept term. Models including all combinations of variables were then tested and ranked using their Akaike information criterion (AIC) values and Akaike weights following the information-theoretic approach (Burnham & Anderson 2002). The model with the lowest AIC was considered as the best model. Two models separated by a difference in AIC values of less than 2 were assumed to fit the data similarly. To take into account uncertainty in model selection, parameters were estimated using a model averaging procedure (Burnham & Anderson 2002).

Overlap with fisheries

To quantify the overlap between the distributions of the tracked birds and longline fishing effort, we collated available data from the relevant regional fisheries management organisations (RFMOs), including the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), Inter-American Tropical Tuna Commission (IATTC), International Commission for the Conservation of Atlantic Tuna (ICCAT), Indian Ocean Tuna Commission (IOTC) and Western and Central Pacific Fisheries Commission (WCPFC). The pelagic longline fisheries target tuna, whereas the demersal longline fishery that occurs in the French Exclusive Economic Zones (EEZs) of Crozet and Kerguelen archipelagos targets Patagonian toothfish. We concentrated on longline fisheries since they are the main cause of seabird mortality, especially for giant petrels (Cherel et al. 1996). Fishing effort was reported as the sum of

hooks set within each $5 \times 5^\circ$ cell throughout 2008 to 2010, concurrent with the tracking study. The sum of these values was considered to be the cumulative risk for birds to interact with a fishing vessel. In order to facilitate interpretation (see below), fishing effort in each $5 \times 5^\circ$ cell was classified as follows: 0 for no fishing, 1 for <1.5 million hooks deployed, 2 for 1.5 to 5.0 million hooks, 3 for 5 to 10 million hooks, and 4 for >10 million hooks.

Based on the GLS locations of adult birds and Argos locations of juveniles, the proportion of time spent per square was calculated for each individual within a $5 \times 5^\circ$ grid using the R package 'trip'. Then, the mean proportion of time spent per square was calculated by species and sex to determine an overall distribution which was used to obtain a 'birds \times hooks' interaction index (Cuthbert et al. 2005, Tuck et al. 2011). Following these 2 studies, this index was calculated for each group by multiplication of fishing effort and time spent per square values which were log transformed to reduce variance. Finally, in order to obtain a weighted map of the overlap between birds and fishing effort, the value obtained for each $5 \times 5^\circ$ cell was multiplied by the number of birds for this cell, before dividing it by the total number of birds and weighting by the area of each cell, since this area is smaller at high latitudes.

In order to investigate relative risk of interaction between adults of each species and sex with long-liners, GLMMs were performed on time spent per square, with a normal distribution and a logit link function. Fixed effects were fishing effort classes, interaction between fishing effort classes and species, and interaction between fishing effort classes and sex. Individual was considered as a random effect. The model aimed at determining whether birds tend to visit cells showing high levels of fishing effort. However, according to their distribution pattern, birds of both species, sexes and populations were unlikely to reach the same zones of our study area, thus, a probability of presence index was estimated from kernels calculated for each group. This term was then integrated into the models as a fixed factor to free itself from deviance in time spent per square due to differences in distribution pattern, and to highlight differences due to presence or absence of fishing effort.

To examine whether the distribution of juveniles of giant petrels makes them likely to interact with long-line fisheries, GLMMs were performed on the standardised time spent per square as a proportion of the total trip duration spent in a given cell, with a normal distribution and a logit link. Fishing effort classes, sex and species were defined as fixed effects, and

individual as random term. Interactions between fishing effort classes and species were not significant according to AIC ranking and thus they were not considered in this analysis.

RESULTS

Patterns of at-sea distribution and activity of adults

Annual patterns of activity

The average daily time spent on the water by NOGP from Crozet and Kerguelen was influenced by population, sex, month and the interaction between sex and month, according to the best-fitting model. Although the Akaike weight of the second-best model was high (0.47) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m499p233_supp.pdf), the population \times sex interaction term for NOGP was difficult to interpret. The average daily time spent on the water by giant petrels from Crozet varied by species, sex and month (Fig. 1, Tables S2 & S3 in the Supplement). The effect of the month differed according to sex or species; SOGP spent less time on the water than NOGP, and males of both species and population spent less time on the water than females, especially during the nonbreeding period (Fig. 1). This difference between males and females indicates that males forage principally on land.

At-sea breeding season distribution

During the 2 breeding periods, males and females differed in their core areas, irrespective of the species or population. Ranges (the area included in the 95 % kernel contours) were larger during incubation (Fig. 2) than the early chick-rearing period (Fig. 3), with the exception of female SOGP. As suggested by the activity comparison, the GLS data confirmed that during incubation, females were distributed at sea whereas males foraged mainly on land, and when at sea, tended to move west from their colonies. As a result, the core areas of females of both populations and species were larger than those of males and their overall ranges included that of males. In terms of habitat used (bathymetry, SST and chlorophyll *a*), the only significant differences when comparing males and females was that male SOGP foraged over shallower waters than females (during the first breeding season, males: 3424.56 ± 147.53 m, females: 4063.48 ± 444.05 m, $p = 0.0096$).

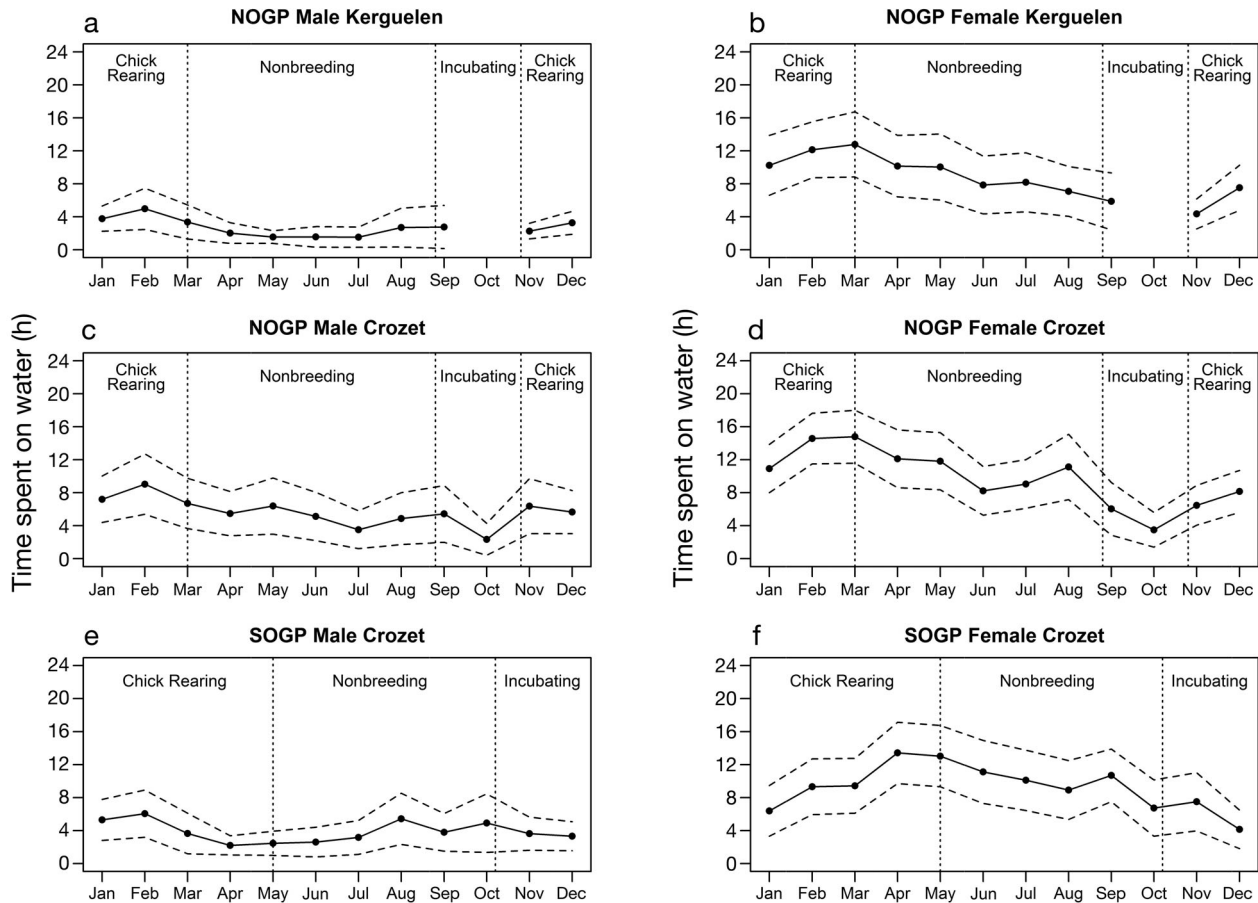


Fig. 1. *Macronectes halli* and *M. giganteus*. Annual activity patterns of adult giant petrels: time spent on the water in hours calculated from geolocator-immersion loggers for (a) male and (b) female northern giant petrels (NOGP) from Kerguelen, (c) male and (d) female NOGP from Crozet, and (e) male and (f) female southern giant petrels (SOGP) from Crozet. Solid lines are means; dashed lines are \pm SD

Female NOGP showed a sub-tropical distribution, especially those from Crozet which foraged to the north of the subtropical front, as far as the coast of South Africa. Female SOGP tended to use waters at lower latitudes than those of female NOGP from both populations, which did not cross the subantarctic front. Females of both populations and species foraged at lower latitudes in chick rearing than incubation. Female NOGP from Crozet and Kerguelen were mainly restricted to the subantarctic and polar frontal zones whereas female SOGP moved south of the Polar Front.

In addition, the analysis of habitat use indicated that during the breeding season, female SOGP foraged over deeper waters than female NOGP (all breeding seasons combined, NOGP: 2970.45 ± 518.65 m, SOGP: 3734.99 ± 515.59 m, $p < 0.007$), and over colder waters (SST during the second breeding period, NOGP: $0.28 \pm 0.03^\circ\text{C}$, SOGP: $0.33 \pm 0.04^\circ\text{C}$, $p = 0.0116$).

The range of males did not extend farther than the northern subtropical front. Male NOGP foraged mainly north of the polar front, whereas male SOGP foraged further south. During the chick rearing period, distributions were more restricted around colonies, with males remaining in waters close to the islands or on land. There was a significant difference in water depth within the 50% kernels of breeding males; SOGP were distributed in deeper water than male NOGP (NOGP: 2850.12 ± 585.08 m, SOGP: 3526.99 ± 282.91 m, $p < 0.045$) whereas there was no significant difference in the mean water temperature.

Finer-scale tracking using PTTs confirmed the results obtained from the GLS data (Fig. S1A in the Supplement). They clearly showed that male NOGP from Kerguelen foraged mainly on coasts or in shallow shelf waters (Fig. S1B). They performed extremely short foraging trips (Table 2). Conversely, females travelled west in long foraging trips to

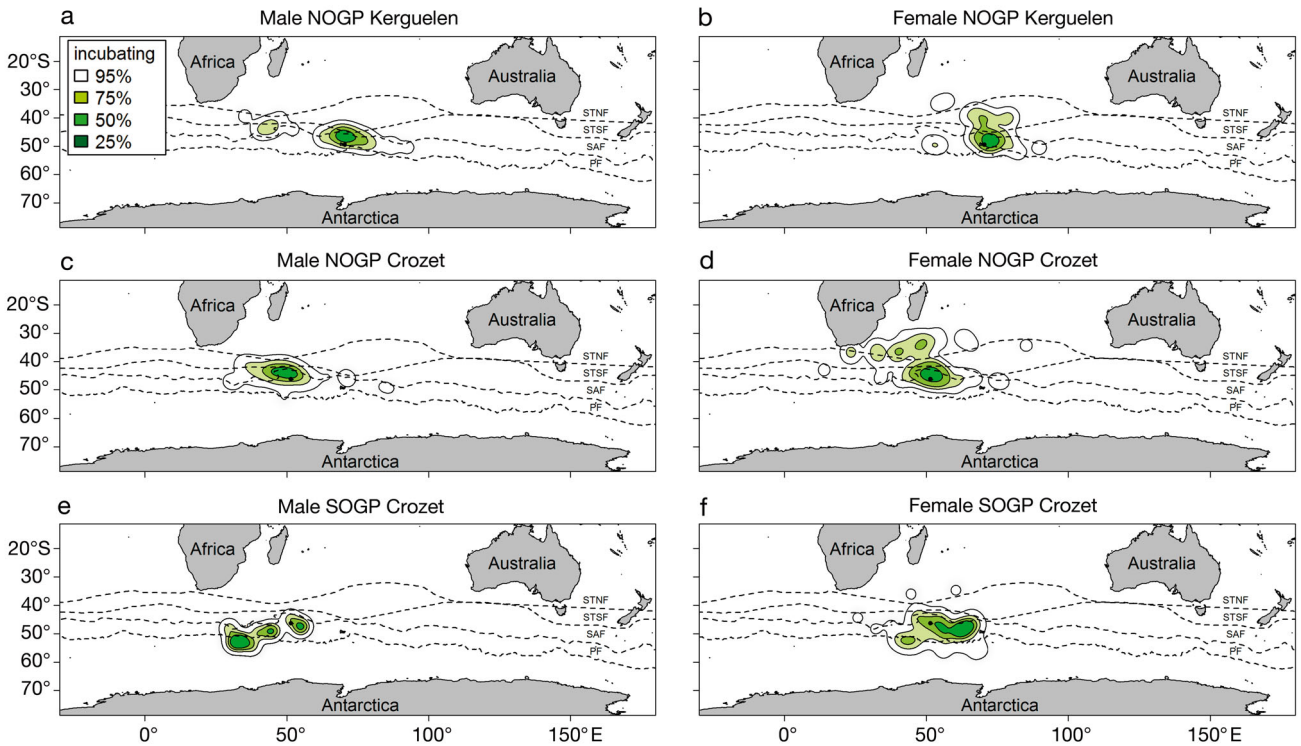


Fig. 2. *Macronectes halli* and *M. giganteus*. Kernel density contours (95, 75, 50 and 25%) from analysis of locations of giant petrels tracked by global location sensing (GLS) during the incubation period: (a) male and (b) female northern giant petrels (NOGP) from Kerguelen, (c) male and (d) female NOGP from Crozet, and (e) male and (f) female southern giant petrels (SOGP) from Crozet. Dashed lines show the subtropical north front (STNF), subtropical south front (STSF), subantarctic front (SAF) and polar front (PF)

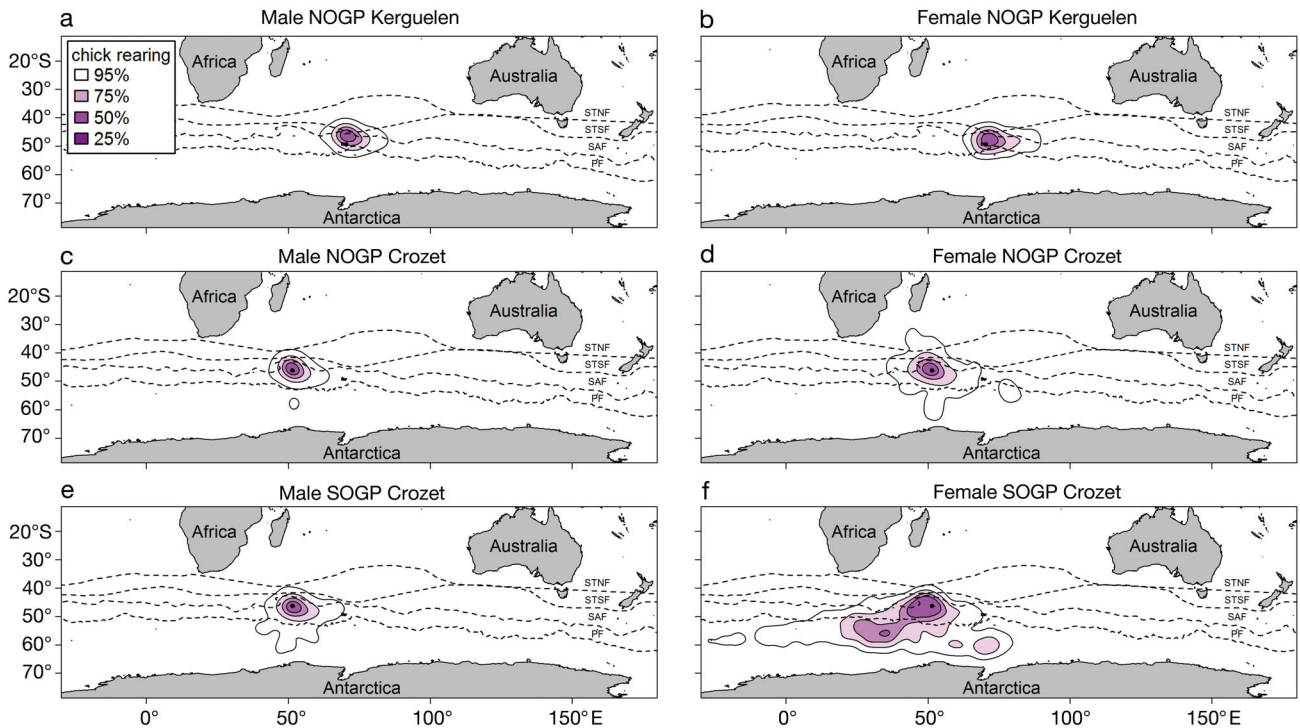


Fig. 3. *Macronectes halli* and *M. giganteus*. Kernel density contours from analysis of GLS locations of giant petrels tracked during the chick rearing period. Panels and symbols as in Fig. 2

Table 2. *Macronectes halli* and *M. giganteus*. Summary of foraging trip characteristics (mean \pm SD) of both sexes of northern giant petrels (NOGP) from Crozet and Kerguelen, and southern giant petrels (SOGP) from Crozet tracked during breeding

Species	Sex	Maximum distance to the colony (km)	Total distance travelled (km)	Distance travelled per day (km)	Total trip duration (d)	Mean speed (km h ⁻¹)
NOGP	Male	148.1 \pm 218.6	895.2 \pm 967.1	298.5 \pm 213.6	14 \pm 23	18.2 \pm 11.8
	Female	1288.5 \pm 876.6	5326.1 \pm 3134.5	635.6 \pm 89.2	15 \pm 4	34.3 \pm 9.6
SOGP	Male	999.7 \pm 748.5	2644.9 \pm 1607.5	586.3 \pm 256.5	10 \pm 5	33.4 \pm 13.8
	Female	1466.0 \pm 975.8	5043.1 \pm 3145.9	787.2 \pm 301.5	13 \pm 2	42.4 \pm 10.3

oceanic waters. At Crozet, males and females performed short as well as long trips. Male and female SOGP foraged in both coastal and pelagic areas but more birds undertook long trips than short trips and all were directed to the south, to Antarctic waters. Overall, male NOGP performed short trips, whereas females foraged farther away, in oceanic waters (Table 2; Wilcoxon test: $W = 3$, $p = 0.02$) and at higher flight speeds than males (Wilcoxon test: $W = 3$, $p = 0.02$).

There was no significant difference between male and female SOGP in foraging trip characteristics (Table 2). However, there were significant differences between males of the 2 species in maximum range (Wilcoxon test: $W = 5$, $p = 0.02$), and total distance travelled (Wilcoxon test: $W = 6$, $p = 0.03$), but not between female NOGP and SOGP.

At-sea nonbreeding season distribution

The distribution of giant petrels was wider during the nonbreeding than the breeding period, although birds remained restricted to the Indian Ocean (Fig. 4). Overall ranges (95% kernels) were large, especially in females. Female NOGP from Crozet had the smallest range, whereas female NOGP from Kerguelen and female SOGP were dispersed more widely (between 30 and 170°E for NOGP from Kerguelen and between 40°W and 80°E for SOGP). Female NOGP from Kerguelen foraged intensively in the Tasman Sea (Fig. 4b). Female NOGP from Kerguelen foraged in waters located between the northern subantarctic front and the polar front whereas female NOGP from Crozet dispersed over a large latitudinal range (from 30°S to 65°S). On the other

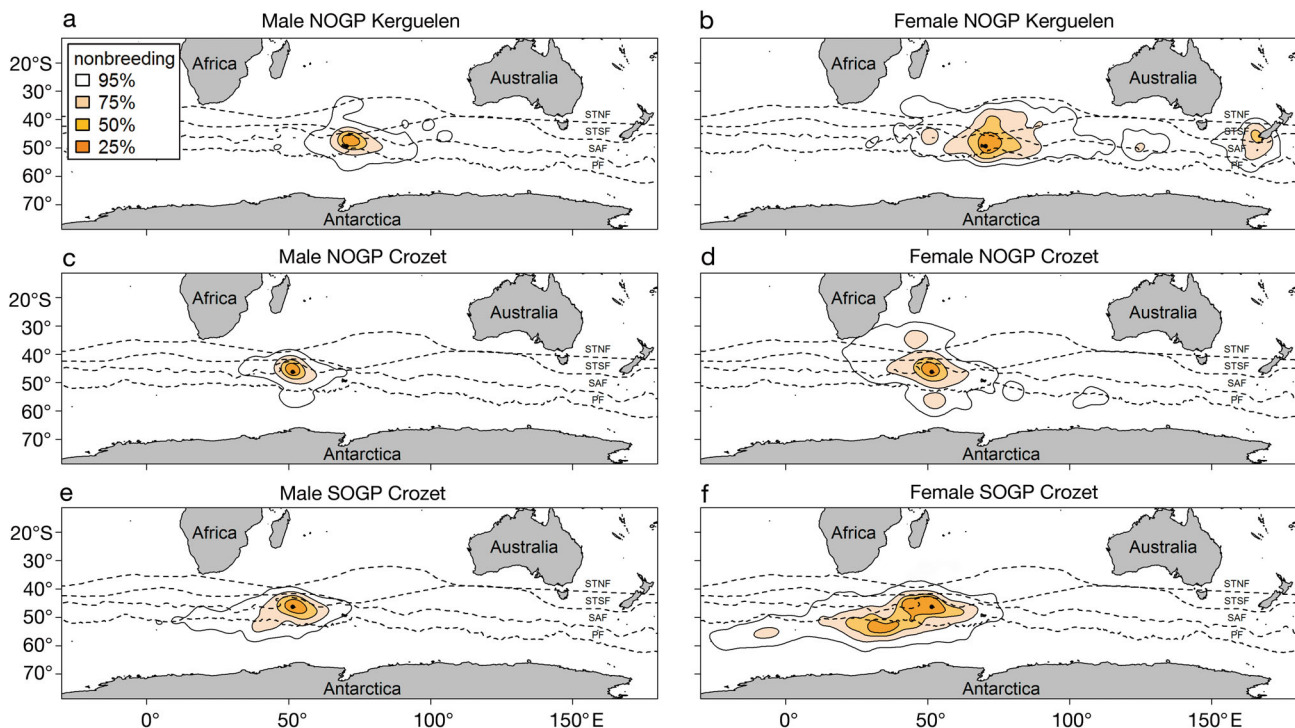


Fig. 4. *Macronectes halli* and *M. giganteus*. Kernel density contours from analysis of GLS locations from giant petrels tracked during the nonbreeding season. Panels and symbols are as in Fig. 2

hand, distribution of female SOGP was localised between the northern subantarctic front and the southern part of the polar front. Female SOGP foraged over significantly deeper waters than female NOGP ($p = 0.0043$), but there were no other differences in the oceanographic parameters studied here. Conversely, males tended to remain close to their colony during the nonbreeding period, as done during the breeding season (Fig. 4).

Post-fledging distribution

In contrast with adults, juveniles of both species performed long circumpolar journeys after fledging, in all cases following an easterly route (Fig. 5). During the initial dispersal period in the Indian Ocean, juvenile NOGP had a more northerly distribution than SOGP, whereas both species overlapped once birds had reached the Pacific Ocean.

Band recoveries

Band recoveries of juveniles and adults were consistent with the patterns observed for tracked birds. Recoveries of juveniles were distributed widely throughout the Southern Ocean (Fig. 5), over the coasts of Patagonia, South Africa, the Antarctic continent, Australia, New Zealand and the Indian Ocean. In contrast, recoveries of adults were restricted to waters relatively close to their breeding colonies.

Overlap with fisheries

There was extensive overlap between the at-sea distribution of giant petrels (defined as the contours of 95% kernel contours for the complete annual

cycle, i.e. breeding and nonbreeding stages) and fishing zones where longliners operated (Fig. 6). The overall ranges of females encompassed a larger number of cells comprising fishing operations compared to males, reflecting their wider distribution. However, NOGP showed a larger overlap with fisheries (Fig. 6a) than SOGP (Fig. 6b), including a higher number of cells with intensive fishing effort. Maximum value for the interaction index occurred in the Indian Ocean and coastal Antarctica for adults of both species and sexes (Fig. 7).

The interaction index for juveniles showed the highest values mainly in the neighbourhood of the breeding colonies (Fig. 8a,c,d). However, there were some high values for juvenile female NOGP around South Georgia (Fig. 8b), and close to the coast of Antarctica for SOGP (Fig. 8c,d).

The time spent per $5 \times 5^\circ$ cell for adult birds was influenced by sex and the interaction between fishing effort and species (Table S4 in the Supplement). The average model (more details in Table S5) shows that adults tended to spend more time in cells where fisheries were operating. The time spent per $5 \times 5^\circ$ square by juveniles varied according to sex, species, fishing effort class and the interaction between sex and species (Table S4). The average model (more details in Table S6) highlights that juvenile giant petrels tended to spend more time in cells with fishing effort, particularly female NOGP.

DISCUSSION

This study is the first to investigate year-round distribution and activity patterns of the sibling species of giant petrels in the Indian Ocean. Previously, the only information on distribution was an analysis of band recoveries reported up until the 1980s for giant petrels from Kerguelen and Crozet (Weimerskirch et

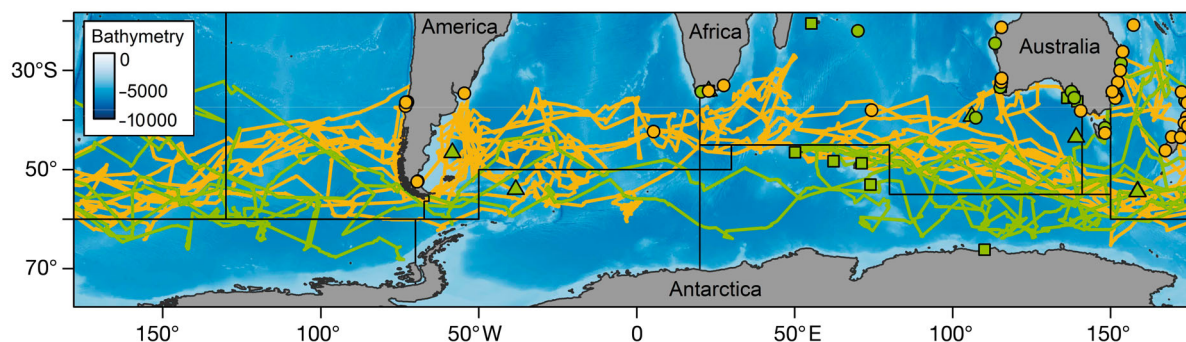


Fig. 5. *Macronectes halli* and *M. giganteus*. Tracks of satellite-tagged juvenile northern giant petrels (orange) and southern giant petrels (green) from Crozet and Kerguelen during the first months after fledging and band recoveries of adults (□) immatures (Δ) and juveniles (○)

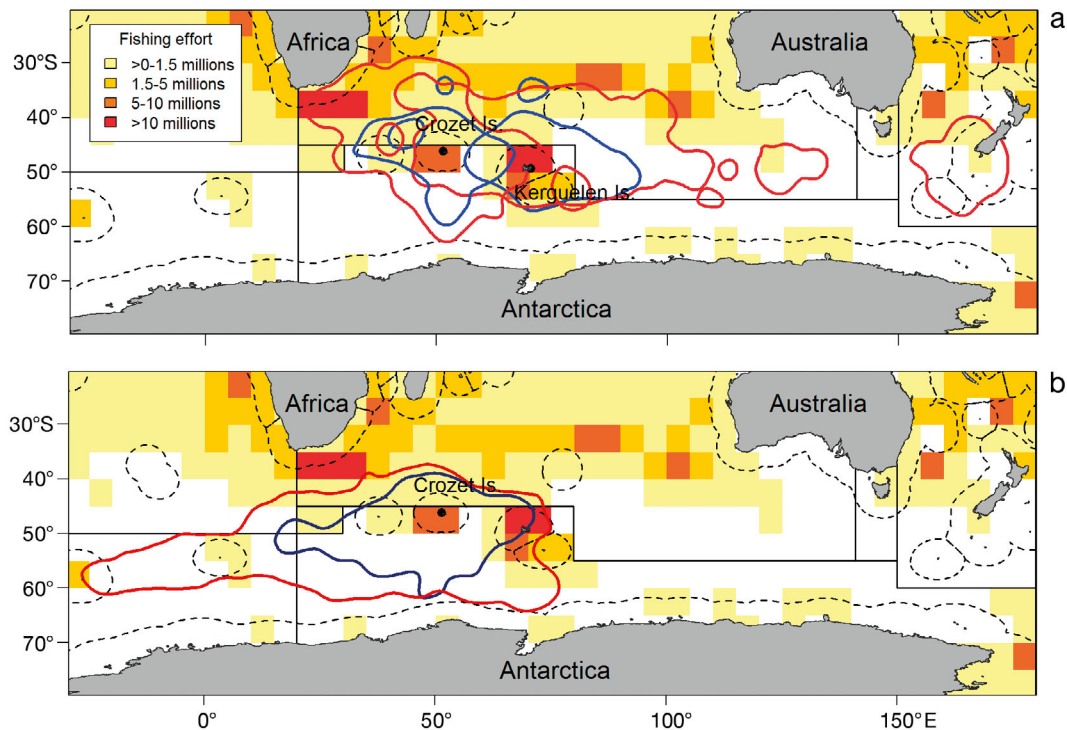


Fig. 6. *Macronectes halli* and *M. giganteus*. Spatial distribution of reported longline fishing effort class (total hooks deployed from 2008 to 2010, in millions). Data on fishing effort are reported for all regional fisheries management organisations (RFMOs, black solid lines) combined (see 'Materials and methods'). Overall ranges of (a) northern and (b) southern giant petrels are represented by the relevant 95% kernel density contours for males (blue) and females (red). Exclusive Economic Zones (EEZs) are represented as black dashed lines

al. 1985). Our study is also the first to quantify spatial overlap between giant petrel distribution and longline fishing effort, and to investigate differences in bycatch susceptibility between birds of different species, sexes and age class.

Differences in at-sea distribution according to species, sex and age class

Giant petrels are the most sexually dimorphic seabird species and the only procellariiforms that obtain a sizeable proportion of their food on land, from seal and penguin carrion (Ridoux 1994). For both species, throughout the year, tracked females were always distributed over a wider area than males, consistent with studies of giant petrels at others localities during the breeding season (South Georgia Island: González-Solís et al. 2000a, 2007).

Breeding season

During the breeding season, the maximum range of foraging trips by females was greater than that of

males. Trips by females also covered a much longer distance and involved higher mean flying speeds, particularly for NOGP. This is consistent with the logger activity data which show that males spent very little time on the water, presumably because their foraging was concentrated on land, although care is needed in interpreting this data because dry periods can also correspond to long flights. However, this accords with studies elsewhere reporting that females mostly feed on pelagic resources: in both species, their diet includes a high proportion of krill, cephalopods and fish (Hunter 1983, Hunter & Brooke 1992). However, female SOGP seem to forage in deeper waters than NOGP, according to results of linear mixed models comparing bathymetry within 50% kernel contours. Analysis of blood samples collected at South Georgia indicates that, during all breeding stages in NOGP, and during incubation in SOGP, the carbon isotope signature ($\delta^{13}\text{C}$) of females suggests a more pelagic diet than that of males (Phillips et al. 2011). Such differences are thought to result from intra-specific competition, with males taking advantage of their larger size and body mass to exclude females from access to carrion on land (Hunter 1983, González-Solís et al. 2000b, González-Solís 2004).

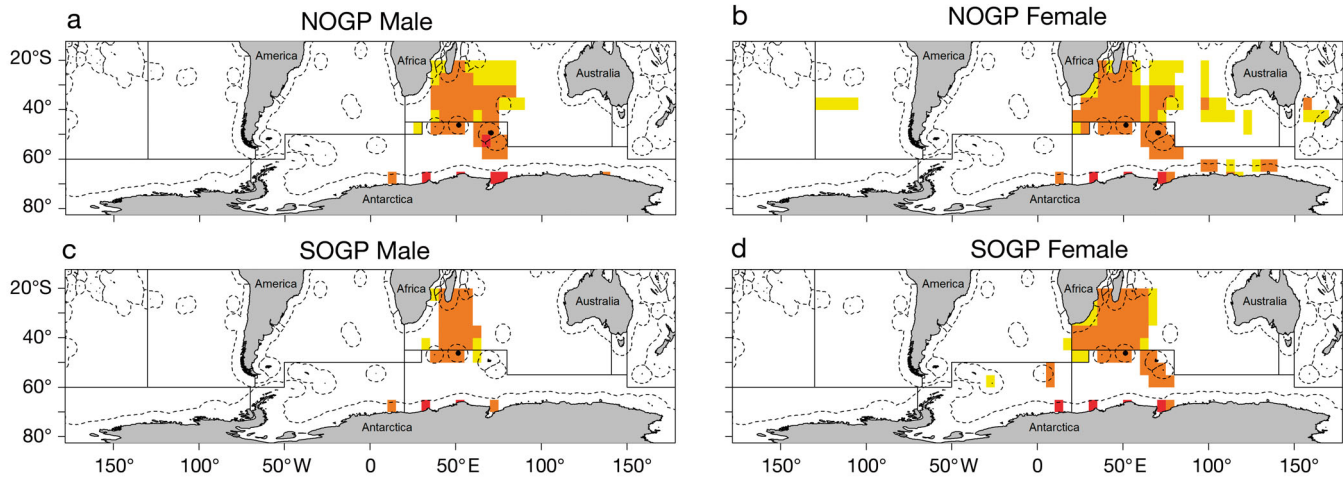


Fig. 7. *Macronectes halli* and *M. giganteus*. Spatial distribution of interaction index for adult giant petrels, as sum of hooks deployed (million hooks) by longline vessels from 2008 to 2009 multiplied by the log-transformed values of time spent per $5 \times 5^\circ$ grid square and weighted by the numbers of birds for (a) male and (b) female northern giant petrels (NOGP) and (c) male and (d) female southern giant petrels (SOGP). Low values are presented in yellow, medium in orange and high values in red. See Fig. 6 legend for explanation of solid and dashed lines on the map

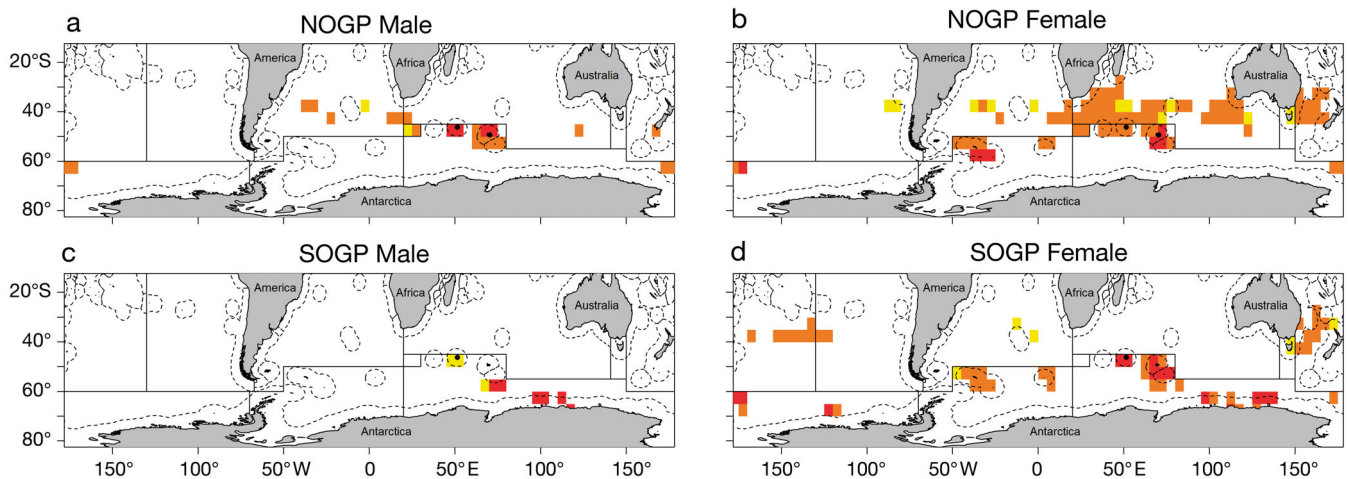


Fig. 8. *Macronectes halli* and *M. giganteus*. Spatial distribution of interaction index (see Fig. 7 legend) for juvenile giant petrels. Panels are as in Fig. 7; see Fig. 6 legend for explanation of solid and dashed lines on the map

During incubation, male giant petrels from both Crozet and Kerguelen tended to remain in shallow waters near the colony and probably fed on beaches on carrion, including elephant seals *Mirounga leonina* and king penguin *Aptenodytes patagonicus*, which are abundant around the breeding sites of the 2 species (Guinet et al. 1999, Delord et al. 2004). This is corroborated by visual observations and by analysis of stomach contents collected at the Crozet archipelago which highlight the predominance of carrion in the diet of both species (Ridoux 1994). However, our fine-scale satellite-tracking data indicate that male NOGP are more coastal than male SOGP, which is consistent with results of linear

mixed models performed on the core areas of males and with analyses of stomach contents showing a greater proportion of terrestrial food in the diet of male NOGP (Johnstone 1977, Ridoux 1994), and with tracking and isotopic studies at South Georgia and elsewhere (González-Solís et al. 2000a, Phillips et al. 2011).

Nonbreeding season

Unlike other large Procellariiformes that tend to disperse widely outside the breeding season (Mackley et al. 2010), our study shows that adult giant

petrels remain close to the colony during the non-breeding period. Furthermore, they appear to maintain the same sexual differences in foraging ecology that are evident during breeding. Males remained close to the island (also confirmed by activity data), probably feeding around colonies of king penguins (Le Bohec et al. 2003) or elephant seals (authors' pers. obs.). In contrast, the tracked females, particularly SOGP, typically made longer migration to winter in more distant areas (as far as the Tasman Sea). At South Georgia, tracking data indicate that although many individuals of both species remain in local waters or further south in the Scotia Sea, there are also substantial numbers of NOGP that winter on the Patagonian Shelf or in subantarctic waters (González-Solís et al. 2007). This is confirmed by values for $\delta^{13}\text{C}$ in feathers grown during the winter which indicate that SOGP are much more likely to have an isotope signature typical of Antarctic waters (Phillips et al. 2009). Wintering movements seem thus variable between giant petrel populations, presumably depending on the abundance of terrestrial resources and degree of intra- and inter-specific competition. However, for all giant petrel populations, when carrion availability decreases in the early to mid summer, males in particular switch to foraging over pelagic waters and thus extend their distribution (González-Solís et al. 2007, Phillips et al. 2009, this study).

Post-fledging period

The tracked juveniles of both species dispersed eastward from their colonies, and performed at least one, and for some individuals several circumpolar trips during the first year after fledging (Fig. 5). This very dispersive behaviour of juveniles confirms results of a previous tracking study at Macquarie Island (Trebilco et al. 2008) and the pattern of band recoveries of juveniles from the Indian Ocean and other colonies (van den Hoff 2011), which largely consists of birds found dead or dying on beaches of all major land masses bordering the Southern Ocean (Weimerskirch et al. 1985, Trivelpiece & Trivelpiece 1998, Patterson & Hunter 2000).

Although there was considerable overlap in the distribution of juveniles of both species, our results nevertheless suggest some sex- and species-specific differences in post-fledging dispersal. Only juvenile females (NOGP and SOGP) utilised the Tasman Sea, and only NOGP (both sexes) travelled to water off the Patagonian and Australian coasts as well as those surrounding South Georgia and Bouvet islands.

Juveniles of both species of giant petrels are often observed in coastal waters when exhausted after a long migration from their natal colony or forced ashore during severe storms. Furthermore they are known to restore their energy reserves by feeding on beached carcasses (Trivelpiece & Trivelpiece 1998, Petty et al. 2012).

Implication for conservation

By combining information on the overall distribution of giant petrels and longline fishing effort, we quantified the degree of overlap, and hence potentially the bycatch risk, at different stages. Our study highlights that this risk is very variable according to the age class, sex and species under consideration. For juveniles, and adults during the breeding and nonbreeding periods, there was extensive overlap with areas of high longline fishing effort. Overlap between giant petrels and vessels has also been recorded around Macquarie Island, South Georgia, Falkland Islands, Prince Edward Islands and New Zealand (Nel et al. 2002b, Robertson et al. 2003, Otley et al. 2007b, Trebilco et al. 2008, Copello & Quintana 2009).

Ship-based observations suggest that NOGP tend to follow fishing boats more than SOGP (Johnstone 1974). Based on recoveries of ringed birds, it appears that NOGP were more likely to be caught than SOGP in recent years in longline fisheries around the Crozet Islands (Delord et al. 2008). Moreover, our tracked female NOGP showed the greatest overlap with longliners (Fig. 6) and are therefore likely to be at a higher risk of being caught during fishing operations.

In general, NOGP are increasing worldwide, whereas SOGP breeding populations show differing trends (Nel et al. 2002a, Delord et al. 2008, Ryan et al. 2009). The few available data on incidental mortality indicate that SOGP appeared to be caught more frequently than NOGP in fisheries for both Patagonian toothfish (Nel et al. 2002b) and tuna (Gales et al. 1998, Bugoni et al. 2008). Although this could relate to differential application of mitigation measures, the observed variation in population trends of the 2 species seems more likely to relate to climatic and other environmental factors, although these are little known. Moreover, besides the potential bycatch risk, giant petrels may benefit from the additional food provided from fisheries, which can represent a large proportion of their diet (Copello et al. 2008). Additional studies are therefore necessary to explain the contrasting patterns between species and localities.

The sex ratio of birds recorded as bycatch or observed feeding on bait or discards indicates that female giant petrels are more likely than males to associate with longliners targeting Patagonian toothfish in waters off the Prince Edward Islands and the Falklands (Nel et al. 2002b, Otley et al. 2007a). This is in accordance with a recent review which concluded that sex biases in bycatch rates are due to differences in distribution rather than behavioural dominance of one sex behind vessels (Bugoni et al. 2011).

The apparent sex bias in previous bycatch studies at other sites contrasts with the interaction index calculated in our study for Crozet and Kerguelen birds: even if males of both species frequent areas of high fishing effort, it seems that females are at greater risk of bycatch because their distribution is more wide ranging, extending to tuna fisheries where use of mitigation measures is limited, whereas within the CCAMLR area (including French EEZs) effective bird bycatch mitigation has been implemented in recent years.

In terms of the potential risk of bycatch of juvenile giant petrels, their wide dispersal during the first months after fledging bring them to areas that overlap extensively with various major fisheries from subtropical to Antarctic waters (CCAMLR, WCPFC, IATTC and ICCAT). They move northward to areas of high tuna longline effort in both the Pacific and Atlantic oceans, and of high Patagonian toothfish effort around South Georgia and Bouvet islands. Although bycatch mitigation is very effective in CCAMLR waters, this is far from the case in most tuna fisheries (Anderson et al. 2011). Because of their naivety and especially during the first year when they are still inexperienced in both flying and foraging, juvenile birds are probably more likely to be caught in longlines than adults (Gales et al. 1998, Bregnballe & Frederiksen 2006). Moreover, the proportion of immature giant petrels caught incidentally in the French EEZs on longlines is higher than of adults (Delord et al. 2008). Previous studies have already highlighted the threat that tuna longline fishery represents for albatrosses and large petrels of all age classes (Gales et al. 1998), and this study confirms the high likelihood that juvenile giant petrel will interact with a wide range of longline fisheries (Watkins et al. 2008).

Based on the tracking data, males, in particular NOGP from both Crozet and Kerguelen, show extensive overlap with the local Patagonian toothfish fishery that occurs in shelf waters, whereas females, in particular NOGP, and juveniles overlap with tuna

fisheries operating in the high seas. These high-sea tuna vessels rarely have bird bycatch observers, nor any independent mechanism to monitor compliance with mitigation measures even if these are mandated by the relevant RFMO. Moreover, there is under-reporting of fishing effort by some countries, and consequently the effort values used in this study will be an underestimate. In addition, seabird bycatch is under-reported globally because of low observer coverage of legal fisheries, and no coverage of illegal, unreported and unregulated fishery (IUU) fisheries, which represent a major proportion of fishing activity worldwide (Agnew et al. 2009). In the CCAMLR area, the catch by IUU vessels was estimated to be up to 1615 t in 2009/2010 (SC-CCAMLR 2010). IUU vessels in this and other fisheries have no incentive to apply mitigation measures, and consequently are likely to cause major additional seabird mortality. Finally, longline fishing effort has been increasing since distant water fleets began operating in the Indian Ocean (Tuck et al. 2003), with associated increasing bycatch risks.

It is important to note one limitation of the current study, which was the relatively coarse temporal scale (1 yr) over which fisheries overlap was calculated, which does not take account of seasonal changes in fishing effort and distribution. A more comprehensive risk assessment would be provided by a detailed investigation of fine-scale overlap between birds and vessels (see e.g. Torres et al. 2013). However, this would require the use of more accurate tracking devices to avoid the error inherent in light-based geolocation.

Implications for giant petrel populations of the Indian Ocean

Female NOGP and juveniles of both species are at a higher risk of bycatch because of their at-sea distribution. However, the NOGP population at Crozet has been stable since the 2000s, and the SOGP population has increased slightly since the early 1990s (Delord et al. 2008, K. Delord et al. unpubl. data). This assessment seems to be paradoxical, but some studies suggested that fisheries may have a positive effect on giant petrel populations by providing extra food in the form of offal (Copello & Quintana 2003, Copello et al. 2008).

On the other hand, giant petrels of the Indian Ocean rely extensively on the availability of seals and penguins, and so are influenced by local changes in the populations of their prey (Patterson et

al. 2008). At South Georgia, the recent increase in the NOGP population has been linked to the exponential increase of the Antarctic fur seal population (González-Solís et al. 2000a), whereas on Heard Island, the marked decline in the numbers of fledglings of SOGP has been attributed to the decrease in elephant seal pup production (Woehler & Croxall 1991). Population trends of the 2 species therefore appear to be sensitive to bycatch risk in longline fisheries as well as changes in populations of their prey, especially seals.

Although populations of giant petrel in the Indian Ocean seem currently to be secure (Delord et al. 2008), improved uptake of mitigation measures in high seas tuna fisheries remains a top priority, given the overlap with the distribution of female and juvenile giant petrels, particularly NOGP. Moreover, it remains important to assess the actual interactions between giant petrels and fisheries by improving on-board observer programmes, including on trawl vessels where the risk is unknown.

By highlighting the potential threats posed by longline fisheries to giant petrels, and especially the contrasting susceptibility associated with species, sex, age class and life history stage, this study demonstrates the advantage of detailed information on foraging distribution for robust risk assessment and the development of effective strategies for conservation.

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