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Stage-dependent distribution of the Critically Endangered Amsterdam albatross in relation to Economic Exclusive Zones

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ABSTRACT: Long-lived animals typically exhibit several stages throughout their life cycle during which their distribution may vary substantially, which may challenge the relevance of protection measures. Here we surveyed individual movements of the Critically Endangered Amsterdam albatross from Amsterdam Island, southern Indian Ocean, throughout its life cycle. Our goal was to identify, from the areas visited by the albatrosses, which coastal states share responsibility in regulating industrial fishing in their Exclusive Economic Zones (EEZs) in order to promote the preservation of this species. Using stage-relevant tracking techniques (satellite tags, GPS and GLS loggers), we surveyed 361 at-sea trips by 93 individuals over 9 yr, covering incubation, brooding, chick-rearing, sabbatical, failed-breeding, juvenile and immature stages. Our data show that Amsterdam albatrosses exhibit a wide and variable foraging radius (from 326 ± 193 km during brooding to 5519 ± 766 km for immatures) and at-sea distribution across stages, putting them beyond the French EEZ of Amsterdam Island for all or part of the trips surveyed in each stage, and even outside the Indian Ocean when breeding. In all, the breeding versus non-breeding albatrosses visited the EEZs of 1 to 3 versus 3 to 4 countries, respectively. Only breeders visited the EEZs of Madagascar and Mauritius, while only non-breeders visited the EEZs of Australia, South Africa and Namibia. This study stresses the relevance to conservation of obtaining synoptic information on the distribution of threatened species, especially regarding the breeding versus non-breeding categories of populations.

KEY WORDS: Seabird · Tracking · Global Location Sensing · GLS · Global Positioning System · GPS · Platform terminal transmitter · PTT · Fisheries · Non-breeding · Juvenile

INTRODUCTION

Long-lived animals are challenging to protect notably because they typically exhibit several stages throughout their life cycle, during which their ecology can be radically different (e.g. Andersen 1991, Péron et al. 2010). Comprehensive ecological surveys of these species are therefore required to implement relevant conservation measures. For the more endangered of these animals, this wide-scale approach becomes urgent, e.g. for seabirds, which represent one of the most threatened bird groups today (Croxall et al. 2012).

At-sea mortality induced by industrial fishing has been identified as the main factor currently affecting seabird populations worldwide (Tuck et al. 2001, 2003, Lewison et al. 2012). In this context, conservation efforts in fishing practice and regulatory meas-

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*Corresponding author: jbthiebot@yahoo.fr ures have been undertaken and/or proposed to mitigate incidental seabird capture at sea (e.g. Bull 2007) within each piece of the Regional Fisheries Management Organisations (RFMOs) world 'puzzle'. However, a specific legal regime applies within a coastal State's Exclusive Economic Zone (EEZ), a marine zone prescribed by the United Nations 1982 Convention on the Law of the Sea and stretching from the baseline out to 200 nautical miles (or ca. 370 km) from the coast. The Law of the Sea stipulates that in this EEZ, 'the coastal State has sovereign rights for the purpose of exploring and exploiting, conserving and managing the natural resources, whether living or non-living (…)'. Beyond this marine zone, fisheries are not legally required to report any seabird bycatch in international waters. EEZs therefore appear to be the very areas to focus on to develop the legal protection of endangered marine species, at the discretion of coastal states (Trebilco et al. 2008).

Albatrosses (family Diomedeidae) currently exhibit a particularly worrying conservation status among seabirds, with 17 out of 22 albatross species being listed today as threatened with extinction (IUCN 2012), mainly because of the impact of long-line fisheries (Brothers 1991, Tasker et al. 2000, Rolland et al. 2010). The rarest of all, the Critically Endangered Amsterdam albatross *Diomedea amsterdamensis* (BirdLife International 2013), may have suffered a severe toll from such fisheries in past decades (Weimerskirch et al. 1997), and still faces high risk of extinction today owing to the minute size of its sole population worldwide. Demographic studies have estimated that only 86 adults breed today on Amsterdam Island (southern Indian Ocean), and that an additional mortality of only 6 individuals per year would likely drive this small population to extinction over the short term (Rivalan et al. 2010). Consequently, the recently implemented National Plan of Actions to promote conservation of the Amsterdam albatross (Delord et al. 2011) has cited industrial long-line fishing as the most serious threat of bird mortality at sea.

In this study we aimed to determine, for conservation purposes, the at-sea distribution and movements of the Amsterdam albatross throughout its entire life cycle, with a special focus on its utilization of EEZs. In the southern Indian Ocean, considerable impact of industrial fishing on seabirds has been measured within the EEZ of several countries (e.g. Polacheck & Klaer 1997, Watkins et al. 2008), stressing the need to document the areas exploited by an endangered species such as the Amsterdam albatross. Moreover, the potential impact from artisanal coastal fishing on seabirds remains extremely difficult to estimate. Our survey aims to identify which countries share responsibility for the species' conservation at sea, where it is legally feasible to engage efforts. Little information was previously available on this species' distribution during breeding (Waugh & Weimerskirch 2003), and thanks to the tremendous development of telemetric approaches (Wilson & Vandenabeele 2012), we have been able to compile a unique data set of individual tracking records on all age- (juvenile, immature, adult) and breeding-related (incubation, brooding, chick-rearing, sabbatical, failed breeder) classes of the population, including prolonged phases the birds spend exclusively at sea (Weimerskirch & Wilson 2000, Croxall et al. 2005, Weimerskirch et al. 2006). Our study provides (1) one of the first tracking surveys of an albatross species covering its entire life cycle (see also Weimerskirch et al. 2014), and (2) the scientific basis for the implementation of conservation measures within EEZs. Similarly to the congeneric wandering albatross *D. exulans*, we expected the birds to show a wider distribution, and hence to visit more EEZs, with longer time at sea, especially outside of the breeding season and during the immature stages (Weimerskirch & Wilson 2000, Weimerskirch et al. 1993, 2006, 2014).

MATERIALS AND METHODS

Study site and species

Amsterdam Island (37° 50′ S; 77° 33′ E) is located in the subtropical part of the southern Indian Ocean (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n023p263_supp.pdf). In this oceanic region, the southern subtropical front (SSTF) delimits the warmer subtropical from the colder sub-Antarctic waters (Belkin & Gordon 1996). Few islands and great depths (generally >3000 m) characterize this region, in which 10 wide oceanic basins separated by seafloor ridges may be identified. EEZs in this area belong to 7 countries: Namibia, South Africa, Mozambique, Madagascar, Mauritius, Australia and France. The Amsterdam albatross, like other great albatrosses, is biennial (Roux et al. 1983, Jouventin et al. 1989): adults that raised a chick successfully do not start a new breeding cycle after chick fledging, but remain at sea for a sabbatical year (Table 1). However, early failed breeders may start to breed the following year. Immature birds may visit the colony when they are 4–7 yr old, but generally only start breeding at 9 yr old (Weimerskirch et al. 1997).

Table 1. *Diomedea amsterdamensis*. Chronology of life-cycle stages surveyed in this study. Dates are from Roux et al. 1983, Jouventin et al. 1989; the average age of first breeding attempt is taken from Weimerskirch et al. (1997)

Stage	Definition	Duration	Behaviour
Incubation[a]	From egg laying (~28 February) to hatching (~18 May)	79 d	One adult of each pair incubates the egg on the nest while the other is foraging at sea
Chick-brooding[a]	From hatching (~18 May) to chick left alone (~14 June)	27 d	One adult of each pair guards and feeds the chick on the nest while the other is foraging at sea
Chick-rearing[a]	From chick left alone (~14 June) to fledging (~15 January)	~7 mo	Both adults of each pair forage at sea and provision the chick
Sabbatical	Between two successive breeding periods (~15 January to the following 15 January)	1 yr	Adults leave the colony to forage at sea
Early failed breeding	Between breeding failure early in the season and the following breeding attempt (~15 January)	~7–11 mo	Adults leave the colony to forage at sea
Juvenile post-fledging dispersal	Following chick fledging in January	~1 yr	Chicks disperse at sea from the colony for the first time
Immature	After juvenile dispersal, until first breeding attempt (at 9 yr old on average)	~8 yr	Young birds forage at sea and occasionally visit the colony for mating

[a] Stage refers to the adult breeding period

Telemetric survey

Three types of tracking devices were used (Table 2), depending on the stage duration of the at-sea trip (known from observations of Roux et al. 1983), the feasibility of retrieving the device, the device autonomy and the spatial accuracy required.

ARGOS platform terminal transmitters (PTTs) emit signals to satellites allowing positioning with a fair spatial accuracy (expected range: <150 m to 1 km; ARGOS 2000). We used these devices to survey the incubation stage over 3 yr and collected data from 34 trips. The PTTs were retrieved after the birds made 1, 2 or 3 successive at-sea trips. The chick-rearing stage was also surveyed using PTTs in 2011 ($n = 10$ birds). For this latter stage, the PTTs remained on the birds for the whole rearing period from June to January (with the exception of 1 PTT that stopped emitting on 12 August, and another that was retrieved on 23 August after the adult was seen feeding the chick) and were lost during moult. We also used PTTs to track juvenile post-fledging dispersal during a 3 yr period. A total of 13 fledging birds were equipped in January before they dispersed. Post-fledging dispersal was tracked over periods of months until the tags stopped emitting; however, we acknowledge that these surveys do not fully depict the habitat used from fledging to the first return to the colony.

GPS loggers were used to survey the chick-brooding stage, when trips are the shortest (Roux et al. 1983, Jouventin et al. 1989). We collected data from 20 at-sea trips in 2011. GPSs recorded latitude and longitude with 5 to 10 m precision (according to the manufacturer), every 5 min.

Finally, Global Location Sensing (GLS) loggers were used to survey birds over periods of months to >1 yr. GLSs record the ambient light level every 10 min, from which we can infer local sunrise and sunset hours and estimate location every 12 h (Wilson et al. 1992). In addition, ambient sea temperature was recorded once during every 20 min period of continuous immersion with a resolution of 0.0625°C and an accuracy of ±0.5°C. Despite the higher mean spatial error of location estimates with these devices (over 100 km; Phillips et al. 2004), GLS loggers allowed us to follow the birds for prolonged periods with minimal disturbance to them. To date, we have retrieved 22 of the 30 GLS loggers deployed in total over 4 seasons, from which 19 tracks were estimated. These data are from a total of 12 adults surveyed throughout their sabbatical year, as well as from 2 early failed breeders and 5 immature birds. Immature birds were selected in the field and were classified as individuals aged no more than 9 yr that had never previously attempted breeding (known from individual banding and long-term monitoring, IPEV program 109, directed by H. Weimerskirch).

PTTs and GPSs were attached to the back feathers using black Tesa tape. GLS loggers were mounted with cable-ties to plastic rings attached to the bird's

Table 2. *Diomedea amsterdamensis*. Summary of individual movement metrics for each stage/year surveyed. Values are means ± SD (range). PTT: platform terminal transmitter; GLS: global location sensing logger

Stage	Year surveyed	No. of ind.	No. of trips	Device used	Max. foraging range (km)	Distance travelled (km)	Trip duration (d)
Incubation	1996	5	7	PTT[a]	1096 ± 971 (354–2583)	3029 ± 2568 (1019–7055)	6.3 ± 2.5 (3.7–10)
	2000	5	10	PTT[a]	672 ± 336 (340–1223)	3434 ± 1439 (1609–6668)	6.8 ± 2.1 (3.3–10.5)
	2011	14	17	PTT[c]	1000 ± 645 (312–2916)	2846 ± 1633 (975–7526)	6.5 ± 2.7 (2.4–11.2)
Brooding	2011	10	20	GPS[d]	326 ± 193 (37.1–759)	1414 ± 830 (244–3413)	2.5 ± 1.1 (0.9–5.0)
Chick-rearing: short trips	2011/ 2012	10	109	PTT[c]	147 ± 82 (25–328)	471 ± 323 (68–1383)	2.4 ± 1.6 (1.2–8.2)
Chick-rearing: long trips	2011/ 2012	10	160	PTT[c]	1196 ± 792 (342–3906)	3776 ± 2634 (765–14 203)	8.6 ± 5.0 (1.5–29.1)
Post-breeding	2012	8	8	PTT[c]	2772 ± 1333 (762–4199)	20 571 ± 20 345 (3335–67 543)	70.6 ± 62.6 (16.9–188.6)
Sabbatical	2006	2	2	GLS[e]	4569 ± 262 (4383–4754)	48 983 ± 6672 (44 265–53 701)	372 ± 20 (358–386)
	2007	3	3	GLS[e]	4827 ± 535 (4309–5377)	69 092 ± 15 436 (51 321–79 169)	378 ± 16 (360–390)
	2010	7	7	GLS[f]	5295 ± 636 (4381–6322)	59 340 ± 15 534 (37 877–85 027)	380 ± 12 (356–391)
Early failed breeding	2006	2	2	GLS[e]	4509 ± 481 (4169–4849)	46 258 ± 14 388 (36 084–56 432)	263 ± 9.9 (256–270)
Juvenile	2005	3	3	PTT[b]	4502 ± 1430 (2860–5483)	26 595 ± 3235 (23 068–29, 422)	108 ± 19 (92.4–129)
	2009	4	4	PTT[c]	2273 ± 2174 (389–5136)	6804 ± 5393 (1449–13 657)	37 ± 22 (20.8–68.0)
	2012	5	4	PTT[c]	4255 ± 250 (3972–4517)	61 385 ± 16, 134 (44 437–83 303)	239 ± 55 (190–295)
Immature	2006	1	1	GLS[e]	4628	38 788	369
	2011	4	4	GLS[g]	5742 ± 672 (5088–6682)	51 090 ± 8836 (38 449–58 961)	316 ± 35 (271–354)

[a] Microwave Telemetry PTT 100 (30–50 g); [b] Microwave Telemetry 50-g solar with duty cycles of 12 h on/24 h off; [c] Microwave Telemetrics 18-g solar with duty cycle 10 h on/24 h off; [d] i-GotU GT-120 (20 g) from Mobile Action Technology; [e] MK4 (5 g); [f] MK7 (4 g); [g] MK15 (2.5 g), from British Antarctic Survey

leg. Amsterdam albatrosses are large (>6 kg) seabirds, and tracking devices used always represented <1% of a bird's mass.

Birds of both sexes were surveyed; sex was known from our long-term database (males being larger and whiter than females within a pair), except for juvenile and immature birds.

Handling of tracking data

Unreliable ARGOS locations in the PTT data sets were removed using a speed filter algorithm (McConnell et al. 1992). We used the maximum travelling speed value measured with the more precise GPSs (99 km h^{-1}) to set up a specific speed threshold in this case. From GLS data sets, the most probable location estimates were generated following Thiebot & Pinaud (2010) with the package 'tripEstimation' in R 2.9.0 (R Development Core Team 2009, http://cran.r-project.org/web/packages/tripEstimation/index.html). This method is based on a combination of factors (including light level, time, sea-surface temperature, animal movement model and land mask) to generate the maximum likelihood distribution for the location estimates. This method bypasses the issue of the equinox periods, during which latitude estimation by light and time only is unreliable. The concurrent use of temperature recorded by the GLS loggers allowed us to estimate latitude continuously, with reference to sea-surface temperature data from satellite imagery (Reynolds data set, POET-PODAAC, http://podaac-tools.jpl.nasa.gov/las, spatial grid: 1°, time frame: 1 wk). We used average travelling speed calculated from the GPS surveys (22.6 km h^{-1}) to set up the specific movement model used to constrain location estimates. We summarized early model runs for this analysis following Thiebot & Pinaud (2010); however, proper implementation of these scripts should now involve summarizing from the posterior after running the chain for a large number of iterations (see Sumner et al. 2009). The current implementation nevertheless produced valid location estimates from the GLS loggers compared with the satellite tracks of the individuals surveyed during a similar stage (Fig. S2 in the Supplement).

To account for the fact that several tracks could be collected from a single individual during the breeding stages, we tested for temporal pseudo-replication in these datasets. This procedure followed the BirdLife International Marine Important Bird Areas toolkit (BirdLife International 2010). Polygons of 50% kernel density contours were drawn for each track and a series of variance tests (Mann-Whitney *U*-tests) were then conducted on inter-trips polygon overlap values. This would determine whether variance of foraging areas between trips of a single individual was significantly different from that between individuals. In our study, p-values were >0.28 for the 3 stages, indicating similar intra- versus inter-individual spatial variance of trips (i.e. all trips could be analyzed as from different individuals).

Quantifying at-sea distribution

From final location data sets, we derived movement metrics for each at-sea trip performed by the tracked birds: duration, the maximum foraging range reached from the colony (calculated from the great-circle distance of each location to the colony) and the total minimum distance travelled (i.e. the cumulated distance interpolated between successive locations). We also measured the spatial extent of the birds' home range for each stage, using the 95% kernel utilization distribution contour (sensu Fieberg & Kochanny 2005). To achieve this, we overlaid the latter contour on a bathymetry layer with a fine (10 nautical mile grid) resolution, and calculated the number of cells intersecting the contour's polygon. Hence, we could eliminate unlikely parts of the kernel area spreading on land. We set the search radius *h* according to the spatial accuracy of the tracking device used: 0.1, 0.5 and 2° for GPS, PTTs and GLS loggers, respectively, following BirdLife International (2004). Homogeneous sampling regime is required in kernel analyses (Wood et al. 2000); we thus re-sampled PTT fixes with constant linear interpolation of 1 h. Locations obtained from GPSs and GLS loggers were left unchanged at their original constant period of 5 min and 12 h, respectively.

Finally, we quantified the birds' relative occurrence in each EEZ versus international waters. We used global EEZ data from the standard geo-referenced website www.marineregions.org/downloads.php, and counted the proportion of constant-interpolated locations falling into each one of these areas, with respect to the total number of locations available for each stage.

We used parametric (1-way ANOVA, Student's *t*) and non-parametric (Wilcoxon and Kruskal-Wallis rank sum) tests to detect significant differences in distribution metrics between stages, sexes or years. However, a low sample size precluded statistical comparisons within early failed breeding and immature individuals. Data normality was systematically tested using the Shapiro-Wilk test. When significant differences were measured between more than 2 samples, we used Tukey's honestly significant difference multiple comparison of means test with a 95% family-wise confidence level to identify which sample(s) differed. For all tests, the significance threshold was set at p = 0.05. Values given are means ± SD unless otherwise specified.

RESULTS

Breeding adults

During incubation foraging trips, Amsterdam albatrosses generally headed westwards from their colony into the Crozet Basin area until reaching or crossing the Southwest Indian Ridge (Fig. 1). They ranged between 28.8 and 45.1° S, and performed anticlockwise looping trips (i.e. north on departure, south on return). A minor proportion of trips were directed eastwards to the South Australia Basin (14% in 1996 and 6% in 2011, but 50% in 2000). On average, birds had a foraging range of <1000 km, but this approached 3000 km for 1 long trip with a total distance covered of >7500 km (Table 2). Year, as well as sex, had no significant effect on average maximum range, distance travelled or trip duration (Table 3). During this stage, nearly half of the locations were within the French EEZ around Amsterdam Island, the remaining locations all being in international waters (Table 4).

During the brooding period, the birds contracted their distribution around Amsterdam Island, between 30.9 and 41.5° S, near the western slope of the Southeast Indian Ridge. The maximum foraging range reached up to 760 km for 1 individual. Foraging trips were directed either towards the north or southwest (55% versus 45% of trips, respectively), and some individuals made successive trips in both directions (data not shown). Sex had no significant effect on average foraging range, distance travelled or trip duration. During this stage, the French EEZ around Amsterdam encompassed >80% of the birds' locations, the rest being in international waters.

During chick rearing, each adult made 31 ± 4 at-sea trips over the entire stage, and there were no significant differences between sexes. We distinguished

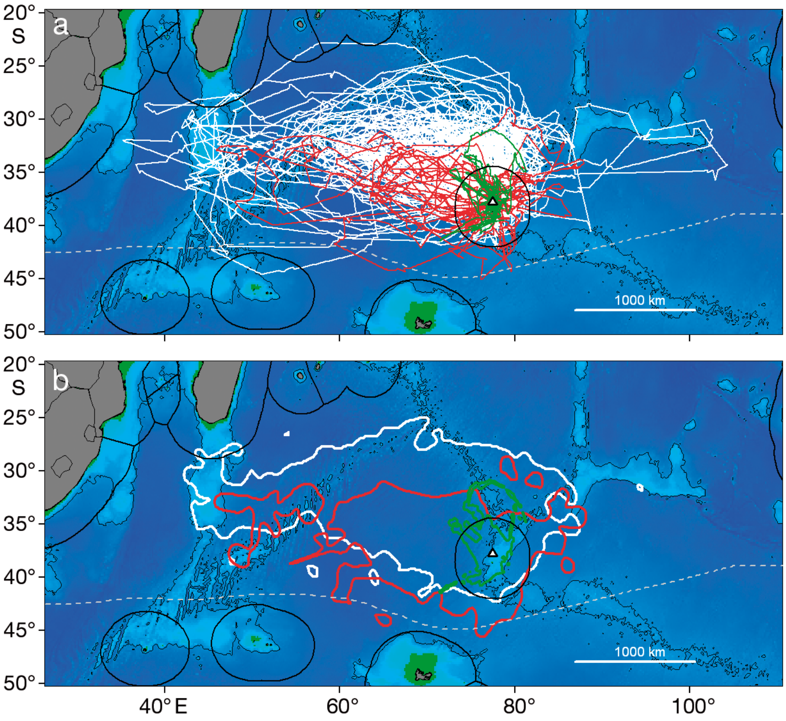

Fig. 1. *Diomedea amsterdamensis*. (a) Breeding adults' foraging trips and (b) home range (95% kernel contours) surveyed during incubation (red lines, n = 34 trips), brooding (green lines, n = 20) and chick-rearing (white lines, n = 269) stages. The white dashed line shows the average position of the southern subtropical front. Thin black lines delineate the 3000 m isobath (shallower areas appear in light blue), and areas shallower than 200 m appear in green. Bold black lines represent the extent of the Exclusive Economic Zones. The location of Amsterdam Island is shown by the triangle

short- versus long-range trips (41 versus 59% of all trips, respectively) based on the 2 modes in trip numbers found for ranges below and above 340 km, respectively (Fig. S3 in the Supplement), that suggested such a 2-fold foraging strategy. During the short-range trips, birds remained close to Amsterdam Island without dominant bearing. Long-range trips mainly consisted of anticlockwise loops

Table 3. Results of statistical tests (ANOVA, *F*; Wilkoxon rank sum test with continuity correction, *W*; Student's *t*; Kruskal-Wallis, χ^2; and Spearman's rank correlation, r_s) comparing the at-sea distribution metrics of *Diomedea amsterdamensis*. Significant effects are in **bold**

Stage	Factor	Dependent variable	Statistic
Incubation	Year	Maximum range	$F_2 = 1.1$, p = 0.35
		Distance travelled	$F_2 = 0.34$, p = 0.72
		Trip duration	$F_2 = 0.09$, p = 0.92
	Sex	Maximum range	$W = 20$, p = 0.16
		Distance travelled	$W = 19$, p = 0.13
		Trip duration	$W = 19$, p = 0.13
Brooding	Sex	Maximum range	$t = 0.90$, p = 0.38
		Distance travelled	$t = 1.41$, p = 0.18
		Trip duration	$t = 0.87$, p = 0.40
Chick-rearing	Sex	Number of trips	$t = -0.89$, p = 0.41 (excluding the two incomplete surveys)
		Maximum range (short-/long-range trips)	$t = 1.04$, p = 0.30; $t = 0.11$, p = 0.92
		Distance travelled (short-/long-range trips)	$t = -0.62$, p = 0.54; $t = -0.56$, p = 0.58
		Trip duration (short-/long-range trips)	$t = -1.27$, p = 0.21; $t = -0.83$, p = 0.41
Sabbatical	Year	Maximum range	$\chi^2 = 2.\ 5$, p = 0.29
		Distance travelled	$\chi^2 = 1.1$, p = 0.57
		Trip duration	$\chi^2 = 0.4$, p = 0.81
	Sex	Maximum range	$W = 25$, p = 0.31
		Distance travelled	$W = 20$, p = 0.82
		Trip duration	$W = 22$, p = 0.57
Juvenile	**Year**	Maximum range	$\chi^2 = 3.42$, p = 0.18
		Distance travelled	$\chi^2 = 8.91$, p = 0.01; Tukey's adjusted p = 0.0063 and 0.00021 for 2012 vs 2005 and 2009, respectively
		Tracking duration	$\chi^2 = 8.91$, p = 0.01; Tukey's adjusted p = 0.0046 and 0.00016 for 2012 vs 2005 and 2009, respectively
All	**Trip duration**	**Maximum range**	$r_S = 920892.2$, p < 0.001
	Stage	**Maximum range**	Kruskal–Wallis $\chi^2 = 82.8$, p < 0.001; Tukey's test adjusted p < 0.001 for all breeding versus non-breeding stages

Table 4. *Diomedea amsterdamensis*. Summary of the population's at-sea distribution metrics for each stage: home range area (95 % kernel utilization distribution contour) and repartitioning of individuals' locations with reference to neighbouring countries' Exclusive Economic Zones (EEZs). The portion of the French EEZ used by the birds was exclusively that around Amsterdam Island, except for chick-rearing adults (a), which used the EEZ around Amsterdam, Crozet and Réunion French Islands (51.4, 0.06 and 0.03 % of locations, respectively)

Stage	Home range area (km^2)	Locations in international waters (%)	Locations in EEZ (%)					
			France	Namibia	South Africa	Madagascar	Mauritius	Australia
Incubation	3 444 310	51.7	48.3	0	0	0	0	0
Brooding	299 088	15.7	84.3	0	0	0	0	0
Chick-rearing	5 154 803	48.3	51.5[a]	0	0	0.2	0.02	0
Sabbatical	17 102 873	73.4	8.4	0	8.7	0	0	9.5
Early failed breeding	13 550 522	72.4	6.5	0	12.1	0	0	9.0
Juvenile	9 464 477	75.8	19.6	0	2.5	0	0	2.2
Immature	17 199 597	55.6	21.2	0.06	12.8	0	0	10.4

with a wide latitudinal range (22.8 to 44.6° S), mostly directed westwards over the Crozet, the Madagascar and the Mozambique basins, with extreme foraging ranges of >3900 km. One individual also made 2 large eastward trips over the Broken Ridge region. Sex had no significant effect on range, duration or distance travelled within short- or long-range trips. Chick-rearing adults spent the majority of their time within the French EEZs. They also reached the EEZs of Madagascar and Mauritius and spent nearly half their time in international waters.

Non-breeding adults

After their last visit to the colony for chick-rearing, the 8 birds that were still tracked switched to their post-breeding sabbatical period. For comparison with the following complete surveys, we show these post-breeding tracks (Fig. 2, Fig. S2 in the Supplement). Birds moved widely (31.3 to 114.7° E) and mostly westwards to the Madagascar and Mozambique ridges, >4000 km from the colony.

The 12 birds followed throughout the complete sabbatical period showed even wider-scale dispersal in the southern Indian Ocean, over >130° of longitude. One individual reached the southern Atlantic Ocean (longitude <20° E), where it remained for 3 d, and another reached the Tasman Sea, where it remained for 2 d. In terms of latitude, the distribution of sabbatical albatrosses was rather narrow (27.3 to 45.0° S), reflecting the continuous exploitation of warm waters around 18°C (Fig. S4 in the Supplement). The birds exploited 2 main areas: (1) towards the southeastern African coasts (25 to 80° E), and (2) very locally (approximately 112° E) over the Naturaliste Plateau, west of Australia. At least one of these 2 marine sectors was used by every tracked albatross and both were sometimes used, even several times during their sabbatical period (Fig. 3a). Typically, birds did not show coherent seasonal movement in longitude (regardless of the year); however, more birds moved westwards in June and/or July and eastwards in November, so that the majority of them (8 out of 12) were distributed in the eastern sector between late November and early February, more so than at any other time of the year. During this long period at sea, movement metrics accordingly reached very high values (absolute maximum range from colony >6000 km) and were not significantly affected by year or sex. For sabbatical albatrosses three quar-

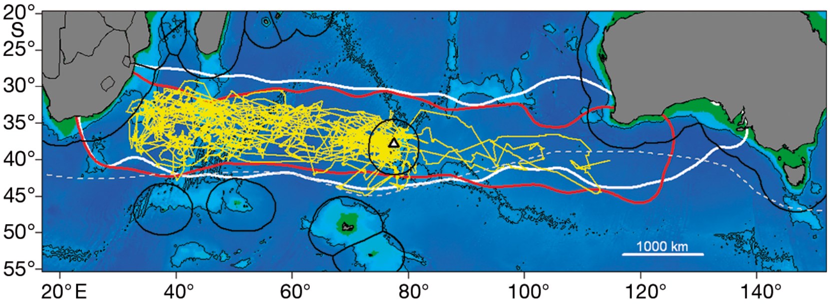

Fig. 2. *Diomedea amsterdamensis*. Non-breeding adults' home range (95 % kernel contours) surveyed in sabbatical (white lines, n = 12 birds) and early failed breeding (red lines, n = 2) periods. Tracks of post-breeding individuals (yellow lines, n = 8) are also shown. Symbols and colours as in Fig. 1

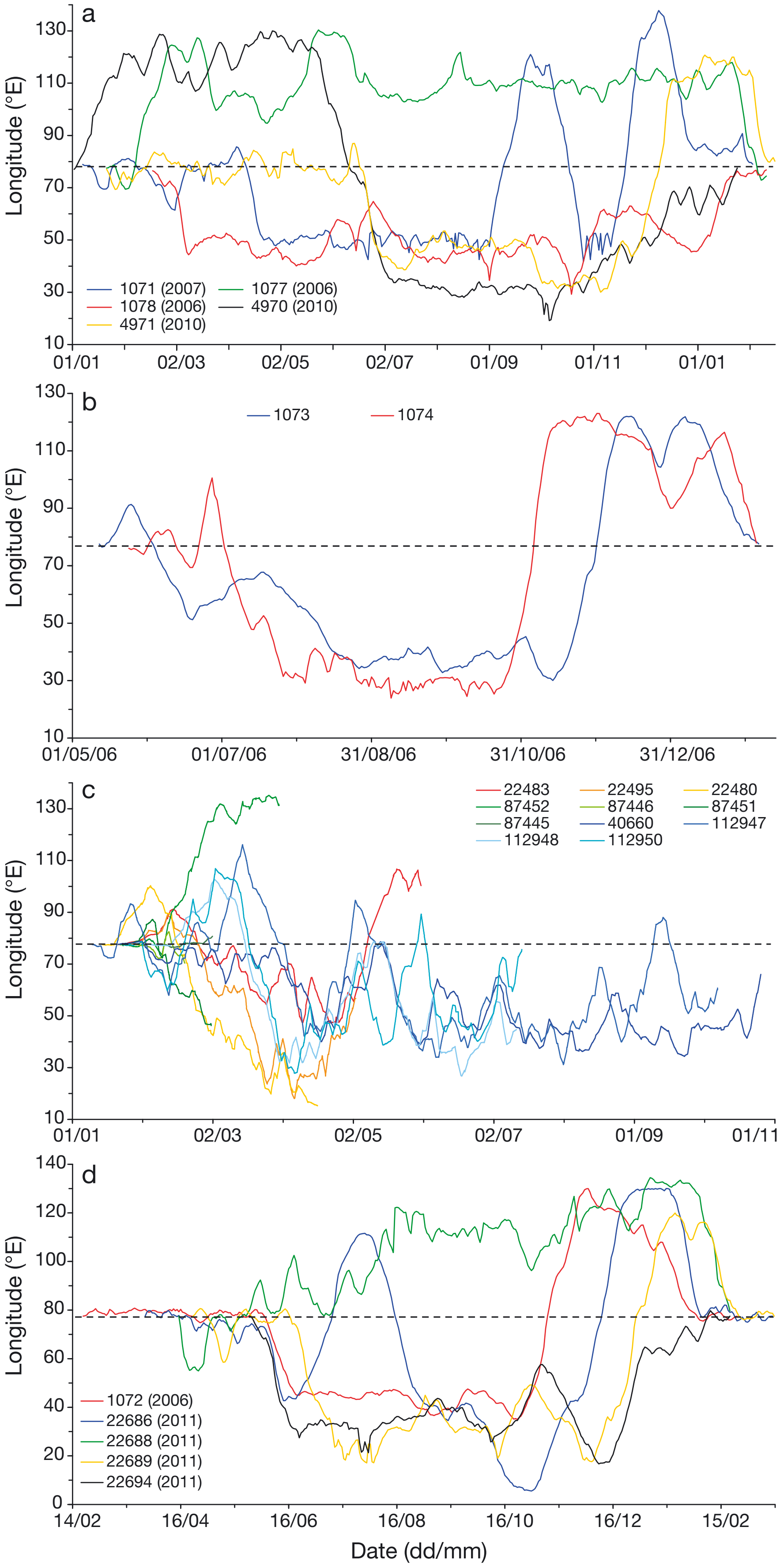

Fig. 3. *Diomedea amsterdamensis*. Longitudinal movement of the studied albatrosses (ID nos. shown in each graph) during the prolonged tracking surveys: (a) sabbatical individuals (5 contrasted individual strategies shown; year of survey is given in parentheses), (b) early failed breeders (2 individuals), (c) post-fledging juveniles (orange shades: individuals tracked in 2005, n = 3; green shades: individuals tracked in 2009, n = 4; blue shades: individuals tracked in 2012, n = 4) and (d) immature individuals (year of survey is given in parentheses). The horizontal dashed line shows the longitude of Amsterdam Island (locations below and above this line fall west and east of Amsterdam Island, respectively)

ters of location estimates occurred in international waters, and the remaining quarter was evenly distributed in the respective EEZs of Australia, South Africa and France.

The 2 early failed breeding birds dispersed between 25 and 125° E, that is from the Transkei to the South Australia basins. Latitudinal distribution was narrow (30.6 to 43.2° S), in agreement with the specific utilization of waters of ~18°C (Fig. S4 in the Supplement). Both birds ventured >4000 km from the colony. They first moved to the west in July until October (Fig. 3b), and then quickly flew eastwards in November until January. Similarly to the sabbatical birds, these 2 failed breeders were distributed mainly in international waters and reached the EEZs of South Africa, Australia and France, in decreasing order.

Juvenile and immature birds

Juvenile albatrosses dispersed on a very large scale over the southern Indian Ocean after fledging (Fig. 4), though their latitudinal range (27.1 to 47.4° S) seemed much constrained southward by the SSTF. To the west, juveniles were distributed mainly in the Crozet, Mozambique and Transkei basins (occasionally the Cape Basin), and in the east in the

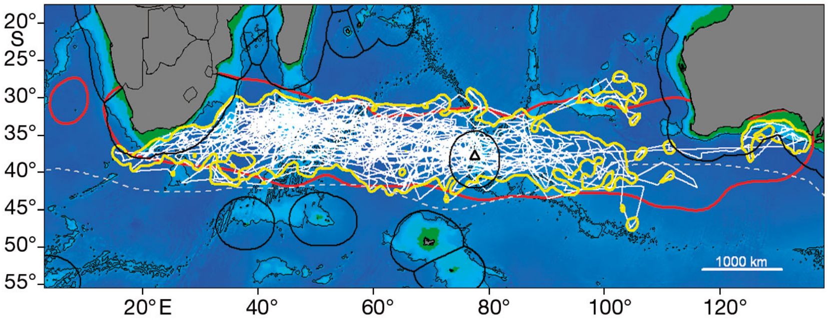

Fig. 4. *Diomedea amsterdamensis*. Juvenile albatrosses' movements (white lines, n = 11 birds) and home range (95% kernel contour: bold yellow lines), and immature birds' home range (95% kernel contour: red lines, n = 5). Symbols and colours as in Fig. 1

South Australia Basin and over the Broken Ridge (and occasionally the Australian continental shelf). In the 3 survey years, juvenile birds tended to disperse westwards first (Fig. 3c), so that there were more birds (4 out of 11) at western longitudes from late March to late April than at any other time of the year; only one flew markedly and durably eastwards. Some temporary, very synchronous individual movements were observed within cohorts. The birds were tracked for a significantly longer time in 2012 (up to 276 and 295 d) and the 2 longest surveys obtained in that year showed that after 5 mo at sea, juveniles were concentrated over the Southwest Indian and Madagascar ridges. Accordingly, distances covered by the birds were significantly larger in 2012, but the maximum range was not, which reflected dispersal capacities of ca. 4500 km. Of the received locations, 75% occurred in international waters and 20% only in the French EEZ; juvenile birds seldom used the EEZ of South Africa and Australia.

Finally, the 5 immature birds also ranged widely in longitude but not in latitude (26.1 to 43.8° S), reflecting exploitation of 17 to 18°C waters (Fig. S4 in the Supplement). In the west, these birds were concentrated from the Transkei Basin to the Madagascar Ridge, and 3 of them also reached the southern Atlantic Ocean. In the east, 4 birds were distributed in the South Australia Basin, occasionally close to the southwestern Australian coast. Each bird exploited the western, eastern or successively both sectors, but without coherent seasonal movement (Fig. 3d). Nonetheless, our limited samples suggest that more birds (4 out of 5) moved westwards in June and eastwards in November than at any other time of the year. Immature albatrosses reached extreme maximum ranges of >6600 km and could travel distances approaching 60 000 km over the survey duration. Nearly half of all location estimates for these young albatrosses were within the EEZs of France, South Africa, Australia and Namibia.

Breeding versus non-breeding distributions

Across stages, the birds spent differing amounts of time at sea. Trip duration and maximum foraging range were significantly correlated among stages and followed a logarithmic relationship (Fig. 5). Accordingly, maximum foraging range was different across stages, with significantly higher values for the non-breeding stages. Stage-specific time constraints for the birds affected their potential to be distributed in the different EEZs. Inevitably, they used the French EEZ around Amsterdam during all stages, but the proportions differed markedly between the breeding and non-breeding stages (range: 48.3–84.3% versus 6.5–21.2%, respectively), as did the number of countries hosting Amsterdam albatrosses in their respective EEZ (range: 1–3 versus 3–4, respectively). Conversely, both Madagascar and Mauritius EEZs were visited only by adult Amsterdam albatrosses during chick-rearing (both comprised <1% of locations). Australian and South African EEZs were reached by individuals during all the non-breeding stages (including >10% of individuals in 3 cases) and none of the breeding stages. Finally, Namibia's EEZ was also reached by non-breeding (immature) birds only, and was seldom visited. Mozambique's EEZ was the only one in the study region that was never visited by any of our tracked birds.

DISCUSSION

In this study we present the first comprehensive work on the distribution and movements of the Critically Endangered Amsterdam albatross over its complete life cycle. We show here that there was variation between life-cycle stages not only in the birds' foraging range, but also in the number of EEZs visited by the birds. Our study hence provides quantitative evidence of the importance of tracking the movements of long-lived animals over every life-cycle stage in order to obtain reliable knowledge on their distribution and to be able to develop conservation efforts at the relevant scale(s).

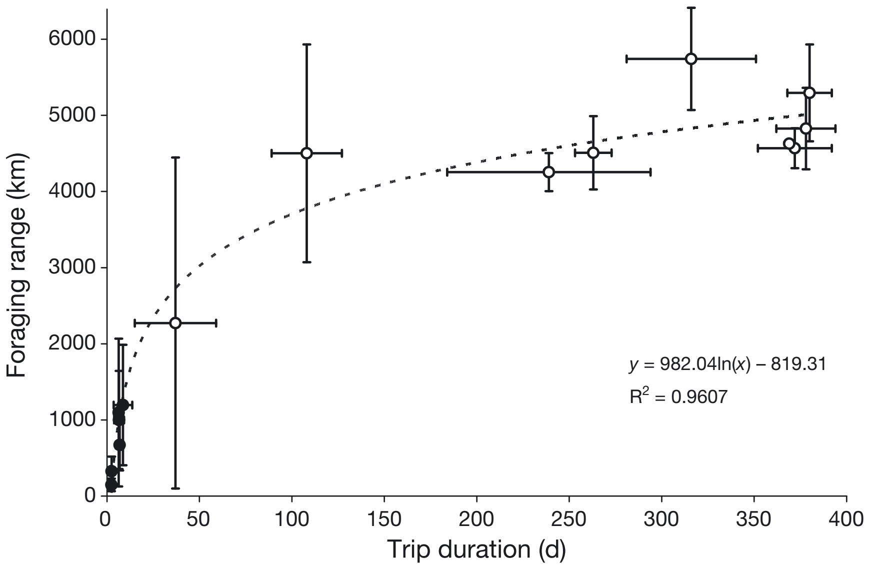

Fig. 5. *Diomedea amsterdamensis*. Logarithmic relationship between average time spent at sea and maximum foraging range reached from the colony by the individuals, for all stages/years/strategies shown in this study (see Table 1 for corresponding number of individuals). Filled and open symbols show breeding and non-breeding stages, respectively. Error bars represent standard deviation. The regression equation and coefficient of determination are given

Variability in distribution and movements

At-sea distribution and movements of the Amsterdam albatross were previously largely unknown (see fragmented information on adults in Inchausti & Weimerskirch 2001, Waugh & Weimerskirch 2003, Rivalan et al. 2010). Notably, both the apparent similarity of these birds with juvenile or immature birds of the more abundant wandering albatrosses and the extremely reduced population numbers precluded reliable ship-based surveys of their distribution (Roux et al. 1983, Weimerskirch et al. 1997).

The present study shows the following three clear results. First, this species is almost exclusively distributed in the southern Indian Ocean. However, our data show the first evidence that some non-breeding Amsterdam albatrosses may also reach the southern Atlantic Ocean and the Tasman Sea. This result is important as industrial long-line fishing for tuna-like species in the latter regions is managed by other RFMOs (International Commission for the Conservation of Atlantic Tunas, and Western and Central Pacific Fisheries Commission, respectively) rather than the RFMO of the southern Indian Ocean (Indian Ocean Tuna Commission), and hence these should now be required to include the Amsterdam albatross as a potential bycatch species.

Second, the main marine habitat exploited appears to comprise a very coherent latitudinal band, between 30 and 42° S, and to include all life-cycle stages. Surprisingly, the northernmost extension of this distribution (22.8° S) was reached by breeding birds. The southernmost extension (47.4° S) was reached by dispersing naïve juveniles. This distribution, mainly north of the SSTF, coincides with the use of a narrow, consistent thermal niche of generally 17 to 19°C warm surface waters, showing that the Amsterdam albatross is a typical subtropical species from the southern Indian Ocean.

Third, all non-breeding individuals (except dispersing juveniles) seem to more or less follow a similar large-scale movement pattern in time: westwards in June and/or July, and eastwards in November.

During the longer stages, the birds exhibited long-range movement ability, similar to other seabirds (e.g. Trebilco et al. 2008, Péron et al. 2010). On average, non-breeding Amsterdam albatrosses ventured further away from their colony than did the breeding birds, as previously observed in other albatross species (Weimerskirch & Wilson 2000, Croxall et al. 2005) with the exception of the neritic-slope foraging black-browed albatross *Thalassarche melanophrys* (Grémillet et al. 2000). Hence, our empirical study widely supports the concept that in central-place foraging animals (sensu Orians & Pearson 1979), the release of time constraints on foraging trips outside of the breeding season allows them to reach a greater foraging ambit (e.g. Thiebot et al. 2011). Nevertheless, chick-rearing adult Amsterdam albatrosses showed the greatest foraging radius of any breeding seabird so far, approaching a maximum distance of 4000 km from their colony (great shearwaters *Puffinus gravis* reached 3813 km, Ronconi et al. 2010; white-chinned petrels *Procellaria aequinoctialis* reached 2420 km, Catard & Weimerskirch 1999; and wandering albatrosses 2618 km, Weimerskirch et al. 1993). As found in the latter studies, these long-range trips measured here were part of a 2-fold foraging strategy typical of breeding Procellariiformes.

Looping trips performed by the breeding albatrosses were nearly always anticlockwise. Albatrosses are renowned to be proficient fliers, utilizing a dynamic soaring technique allowing them to cover large distances with low energetic cost (Richardson 2011, Sachs et al. 2012). Our results thus probably reflect the ability of these birds to take advantage of the easterly winds in the warmer oceanic zone to move westward, and then to come back quickly to the colony on a more direct trajectory using the stronger and fairly constant westerlies blowing in the cooler latitudes (Weimerskirch et al. 1993, 2000, 2012).

Our study shows that there are new concerns for the conservation of seabirds at sea, notably in the case of immature individuals. These birds may actually represent the most challenging category of the population to conserve adequately because of both their extremely large spatial distribution intersecting the highest number of countries' EEZs, and their inexperience in dealing with at-sea threats (Gales et al. 1998, Weimerskirch et al. 2006, Trebilco et al. 2008). Conversely, movement metrics were never significantly different between sexes, which may limit the complexity of conservation measures for this species. Also, year generally had no significant effect on birds' movements in each stage surveyed over multiple years (similarly to e.g. Phillips et al. 2005). Adjustment of the foraging strategies in response to the local, annual environment may, however, imply finer mechanisms, as suggested in our study by the inter-annual variation of bearings during incubation trips.

The paradox of contrasting foraging strategies in a minute population

Our comprehensive approach also provides an empirical opportunity to test a more theoretical ecological question: Why do central-place foraging animals in general, and seabirds in particular, move on a larger scale when they have the time for it, even though they can find sufficient food close to the colony when they do not have the time to travel greater distances?

Increased foraging ranges in seabirds are generally assumed to reflect an adaptive mechanism to mitigate intra-specific competition pressure that may constrain foraging success (e.g. Ashmole 1963, Ballance et al. 2009). More specifically, it has been assumed that progressively greater ranges during the breeding season reflect prey depression ('Ashmole's halo') in the vicinity of the large colonies, with the necessity for predators to travel further and further for provisioning (Birt et al. 1987). From these assumptions, we could expect that for Amsterdam albatrosses, because of the very small population size, intra-specific competition levels may be low (though from a broader perspective, inter-specific competition with similar species such as *Diomedea exulans* may occur). And thus we could expect a both lower and less variable foraging range between life-cycle stages in such a minute population compared with congeneric species with larger populations. However, our data do not support this scheme. Rather, the large and variable foraging ranges observed here (with greater range in the incubation stage, prior to the lowest range brooding stage) imply that intra-specific competition is not as important in wide-ranging central-place foragers such as albatrosses, or at least that birds do not respond quickly to modifications of their biotic pressures (assuming that the Amsterdam albatross population was formerly more abundant than at present; Weimerskirch et al. 1997, Inchausti & Weimerskirch 2001, Rains et al. 2011).

Moreover, great albatrosses (genus *Diomedea*) are generalistic and opportunistic feeders as well as biennial breeders (Warham 1991), which implies that they do not rely on a specific prey that would become seasonally depressed around the colony. The time-dependent variability in the foraging range of the Amsterdam albatross may thus be explained by a higher probability of encountering surface prey (under the hypothesis of unpredictable resources, Weimerskirch 2007) when travelling larger distances. Larger distances covered would likely imply a greater foraging range, as previously suggested by Weimerskirch et al. (1993). Potential inter-specific competition at sea with *D. exulans* may also produce a context similar to intra-specific competition regarding the foraging range variation. Both species' niches overlap extensively, with a limited segregation mechanism from the 2-mo shift in their breeding chronology (Roux et al. 1983).

Shared conservation responsibilities

France is currently involved in the 'National Plan of Actions for the Amsterdam albatross *Diomedea amsterdamensis* 2011–2015' (Delord et al. 2011), a 5-yr program aiming to promote conservation of this Critically Endangered seabird species both on its unique breeding site (the French Amsterdam Island) and at sea, with the support of a number of national and international organizations. Our results show that in any stage, Amsterdam albatrosses (1) exhibit a foraging range that brings them beyond the French EEZ of

Amsterdam Island, for all or part of the surveyed trips, and (2) may be distributed for substantial proportions of time in other countries' EEZs. Hence, effective conservation of the Amsterdam albatross at sea cannot rely exclusively on measures applying solely to the French EEZ.

Australian and South African EEZs were reached by albatrosses in all non-breeding stages. For example, nearly 13 % of location estimates for immature birds were within the South African EEZ. This implies a considerable responsibility for this country to preserve Amsterdam albatrosses, since immature birds represent a substantial fraction of the population (67 out of 167 individuals estimated for the whole species in 2007; Rivalan et al. 2010). Australia also hosted in its EEZ location estimates near or above 10 % for non-breeding birds. Previous studies have already highlighted the importance of these 2 countries' EEZs to hosting non-breeding endangered albatrosses (Phillips et al. 2005, Rolland et al. 2009), together with the considerable potential impact of industrial fishing on these birds within these areas (e.g. Polacheck & Klaer 1997, Watkins et al. 2008). However, our data precluded elucidating any clear-cut seasonal utilization pattern of these countries' EEZs by the Amsterdam albatrosses. It is noteworthy that both Australia and South Africa, together with 11 other countries, ratified the Agreement on the Conservation of Albatrosses and Petrels in 2005 (ACAP 2005), stressing the commitment taken by these nations to conservation efforts for endangered seabird species, including the Amsterdam albatross. Conversely, both Madagascar and Mauritius EEZs, visited only by chick-rearing adults, and Namibia's EEZ, seldom visited by immature birds, are not currently subject to such commitments.

From our surveys we recommend establishing an 'Amsterdam albatross special zone' encompassing all EEZs identified in our study (or at least those of France, Australia and South Africa, see previous paragraph), and in which we recommend that the sovereign states legally require the 2 following conservation measures to prevent catching Amsterdam albatrosses in long-line fisheries. First, to implement systematically and concomitantly the 3 best fishing practices advocated by conservation authorities in order to mitigate seabird bycatch (ACAP 2013, RSPB 2013). Regarding pelagic long-line fisheries, these are: (1) night-setting of the fishing lines, (2) use of streamer lines to keep the birds away from the fishing lines, and (3) weighting of the fishing lines so that they sink faster, away from the birds. Second, to maintain or reach a coverage rate of 100 % (or at least 50 % where it is now very low) by dedicated onboard observers of the fishing catches in these areas. This would (1) ensure the actual implementation of the above mitigation measures during fishing operations, and (2) allow for reporting of any potential albatross capture. France currently maintains a seabird bycatch coverage rate of 100 % in areas that are subject to potential albatross bycatch within its EEZs (Delord et al. 2010). This has provided evidence that no albatrosses are currently captured in these areas. However, our study showed that regulation solely within the French EEZ was insufficient to adequately protect the Amsterdam albatross at sea; further, we must acknowledge that these measures only apply to industrial fisheries, and the potential impact from artisanal coastal fishing remains extremely difficult to estimate.

In conclusion, our comprehensive study points out that Amsterdam albatrosses have contrasting ecology across life-cycle stages (similar to other seabirds), and that conservation of this species at sea should involve a consortium of different nations (mainly, France, South Africa and Australia) hosting several categories of the population in their respective EEZs. Further studies in progress will focus on the possibility of conservation measures in international waters, and specifically with respect to tuna long-line fisheries in the subtropical oceans, which may be the most serious threat to Amsterdam albatrosses there (Rivalan et al. 2010, Yeh et al. 2012). Hence, measuring the spatial overlap of the birds with reported fishing efforts, accounting for the birds' life-age cycle stage, the fleets nation of origin, and the fishing season, will represent further valuable progress in the conservation of this Critically Endangered species over its complete life cycle.

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