



Important areas and conservation sites for a community of globally threatened marine predators of the Southern Indian Ocean



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ABSTRACT

In the Southern Ocean, the impact of environmental changes and increasing human encroachment is causing declines in several populations of seabirds. Amsterdam island (77°33'E; 37°50'S) hosts some emblematic but globally threatened seabird species with alarming population trends. In 2017, concerns about Amsterdam Island's marine biodiversity led to the extension of a marine reserve to the boundaries of the exclusive economic zone (EEZ). Nevertheless, it is unknown whether this protected area is sufficiently large to encompass the most important foraging hotspots of the threatened seabirds, particularly during key stages of their life cycle (e.g. breeding period). We analysed movements of four threatened seabird species using a tracking dataset acquired over several breeding seasons from Amsterdam Island: Amsterdam albatross *Diomedea amsterdamensis*, sooty albatross *Phoebastria fusca*, Indian yellow-nosed albatross *Thalassarche carteri* and northern rockhopper penguin *Eudyptes moseleyi*. Our objectives were threefold: (1) characterise the at-sea distribution of the above-mentioned populations and delineate the marine Important Bird and Biodiversity Areas (mIBAs) triggered by them; (2) assess the potential threat at-sea by quantifying the overlap between seabird distribution and longline fishing efforts; (3) evaluate the coverage of identified mIBAs by marine protected areas and suggest complementary conservation actions. The identified important areas fell within the boundaries of the EEZ, but vastly exceeded the former reserve. Thus, our results reinforce the justification of the recent expansion of the reserve to the boundaries of the EEZ. However, overall seabird distributions extended beyond the EEZ (5 to 50% of the locations) and we found substantial overlap with longline fishing in the high seas. Our results provide a spatio-temporal envelope of where and when bycatch mitigation and observer coverage of longline fisheries should be mandated and enforced.

1. Introduction

Seabirds are key consumers in marine food webs and serve a critical role as bioindicators of the state of oceanic ecosystems (Bost et al., 2009; Brooke, 2004a, 2004b; Hindell et al., 2003; Trathan et al., 2007). However, they are among the most threatened group of birds worldwide (Croxall et al., 2012). Species such as albatrosses (Diomedidae) and penguins (Spheniscidae) are particularly at risk, and in both families > 50% of the species are threatened with extinction (BirdLife International, 2018; Phillips et al., 2016; Trathan et al., 2015). Most of these species breed and inhabit the Southern Ocean (Brooke, 2004a; Trathan et al., 2015). However, the Southern Ocean is undergoing rapid environmental change and faces increasing human encroachment (such as commercial fisheries, introduction of invasive species or alterations

in oceanographic conditions driven by climate change), which all potentially impact biodiversity (Constable et al., 2014; Phillips et al., 2016; Trathan et al., 2007, 2015).

The Southern Ocean is a vast area of water with few islands suitable for breeding for seabirds (Holmes et al., 2018). Among these, Amsterdam Island is part of the French Southern Territories in the southwestern Indian Ocean, located in the sub-tropical zone (77°33'E; 37°50'S). Despite its small area (58 km²), Amsterdam island hosts several emblematic and threatened seabird species, including the endemic and endangered Amsterdam albatross (*Diomedea amsterdamensis*), with a population of only ~40 breeding pairs (Thiebot et al., 2014; Weimerskirch et al., 2018a). Amsterdam Island hosts three other endangered seabird species: the Indian yellow-nosed albatross (*Thalassarche carteri*), the Sooty albatross (*Phoebastria fusca*), and the

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Table 1

Population estimates of four threatened seabird species from Amsterdam Island (37°50'00" S, 77°31'00" E) considered to identify important areas for conservation in the Southern Indian Ocean. Population estimates were calculated from numbers of breeding pairs (most recent counts at Amsterdam Island) and population dynamics coefficients from Dillingham and Fletcher (2011). Percentages of world population estimates are from Delord et al. (2013) and Jaeger et al. (2018). IUCN status from BirdLife International (2018).

Species	Breeding pairs	Latest count	Total population estimate	% of world population	IUCN status
Amsterdam albatross	51	2018	617	100%	Endangered
Indian yellow-nosed albatross	22,000	2015	132,000	65%	Endangered
Sooty albatross	400	2012	5040	4%	Endangered
Northern rockhopper penguin	12,000	2015	48,000	12%	Endangered

Northern rockhopper penguin (*udyptes moseleyi*) (Delord et al., 2013). Notably, numbers of Indian Yellow-nosed albatross breeding on Amsterdam Island account for 65% of the world population (Delord et al., 2013; Jaeger et al., 2018). Furthermore, it is the only breeding site for the Northern rockhopper penguin (Delord et al., 2013) besides the Tristan archipelago and Gough Island (37°07'S–12°16'W and 40°18'S–9°57'W, respectively) in the Southern Atlantic Ocean (Robson et al., 2011). Amsterdam Island is thus a critical breeding ground for four globally threatened seabird species.

Ongoing monitoring of these seabird populations at Amsterdam Island since the early 1980s has revealed an alarming overall status (Jaeger et al., 2018; Weimerskirch et al., 2018a). While the population of Amsterdam albatross is stable to increasing, it is still facing a very high risk of extinction owing to the very small size of its sole population (Rivalan et al., 2010; Thiebot et al., 2014). In addition, Jaeger et al. (2018) and Weimerskirch et al. (2018a) showed that the demographic situation of the three other seabird species has worsened dramatically during the past decade, with extremely low reproductive success and declining populations for all three species.

The main causes of decline of the seabirds breeding in Amsterdam Island have been identified as incidental mortality associated with longline fisheries and infectious diseases (Delord et al., 2013; Jaeger et al., 2018). Other important threats include the potential impacts arising from competition with humans for the same marine resources, the introduction of invasive alien species at breeding colonies (Brooke et al., 2018; Croxall et al., 2012; Phillips et al., 2016; Trathan et al., 2015), and changing environmental conditions. Seabird foraging sites are associated with specific oceanographic features (Bost et al., 2009) that are shifting as the Southern Ocean oceanography is warming, freshening, decreasing in oxygen and acidifying (Constable et al., 2014; IPCC, 2014). Consequently, these seabirds may not be able to shift their foraging location to respond to environmental change or resource overexploitation by commercial fisheries (e.g. Krüger et al., 2018; Desprez et al., 2018). The association with specific foraging sites is especially important during the breeding season, when adults must maximize resource acquisition in a limited time to ensure their survival and breeding success (Weimerskirch, 2007).

Areas with a high abundance or diversity of foraging predators are regarded as ecologically important areas (Dias et al., 2017; Hindell et al., 2011; Reisinger et al., 2018). As such, collecting quantitative information on the spatial distribution of marine predator assemblages is a crucial step to understand and protect marine systems. Data collected using tracking devices have become a fundamental tool in this process (Augé et al., 2018; Burger and Shaffer, 2008; Heylen and Nachtshiem, 2018). Following this approach and the need for a multi-species generic procedure to inform on relevant conservation sites at the population level, BirdLife International developed a protocol to identify marine Important Bird and Biodiversity Areas (hereafter “mIBAs”) (Dias et al., 2017; Lascelles et al., 2016).

The unique biogeography and seabird community assemblage at Amsterdam Island led to the extension of the former marine reserve to the boundaries of the French Exclusive Economic Zone around Amsterdam Island (EEZ) resulting in a protected area of 513,222 km² (<http://www.taaf.fr>). Although, it is unknown whether this protected

area is sufficiently large to cover the most important foraging hotspots of this seabird community. Thus, information on their movement are still needed.

In this study, we analysed a tracking dataset for four threatened species from Amsterdam Island acquired over several breeding seasons. Our objectives were to: (1) characterise the at-sea distribution of the species and identify potential mIBAs; (2) assess the potential risk of bycatch by quantifying the overlap between seabird distribution and longline fishing efforts; (3) evaluate whether the existing marine protected area covers an adequate spatial extent to effectively conserve the most important marine areas for the threatened seabirds of Amsterdam Island.

2. Material and methods

2.1. Study site and species

Amsterdam Island lies between the northern and southern boundaries of the subtropical front, which delimits the warmer subtropical from the colder sub-Antarctic waters (Belkin and Gordon, 1996; Bost et al., 2009). Its remoteness (3400 km from Western Australia, 4200 km from Eastern Africa and 3100 km from Antarctica) and great depths of the surrounding waters (> 3000 m) characterise this region (Jaeger et al., 2018; Thiebot et al., 2014).

Most breeding seabirds concentrate on the Entrecasteaux cliffs (Southwest Amsterdam Island), with over 22,000 pairs of Indian yellow-nosed albatross, ~400 pairs of sooty albatross and 12,000 pairs of Northern rockhopper penguin (Table 1). In contrast, the very small population of the endemic Amsterdam albatross (Table 1), is found on the Plateau des Tourbières (in the centre of the island). Changes in breeding population size have been monitored since the 1980s and 1990s, depending on the species considered (Jaeger et al., 2018). Overall, the latest population estimates show that Amsterdam Island hosts 4–100% of the global population of these four endangered species (Table 1).

The four study species are asynchronous breeders, and their combined breeding season extends throughout the year (Fig. S1). Overall, most breeding occurs during the austral summer (first and fourth quarters of the year). The first quarter (YQ1, January–March), includes chick-rearing for Indian yellow-nosed albatross and Sooty albatross and incubation for Amsterdam albatross. YQ2 (April–June) encompasses chick-rearing for Amsterdam albatross. YQ3 (July–September) is mostly characterised by chick-rearing for Amsterdam albatross and by Northern rockhopper penguin incubation starting in September. YQ4 (October–December) includes incubation and early chick-rearing for Indian yellow-nosed albatross, encompasses almost the entire breeding season for Northern rockhopper penguin and incubation for Sooty albatross.

2.2. Tracking data

We compiled all tracking data available for the four study species from Amsterdam Island during their respective breeding season (Table 2). We attached ARGOS Platform Terminal Transmitters (PTTs)

Table 2

Summary of individual movement metrics after pre-processing the tracks. Data are presented for each species and breeding stage surveyed. Values are means \pm SE (range). AMS: Amsterdam albatross, YNA: yellow nosed albatross, SOAL: sooty albatross, NRP: northern rockhopper penguin, CHR: chick-rearing, Inc.: incubation, PTT: platform terminal transmitter (providing Argos locations).

Species	Stage	Departure months	Year surveyed	No. of ind.	No. of trips	Device	Trip duration (days)	Max. dist. from colony (km)
AMS	Inc. ^a	Feb–Apr	1996, 2000, 2011	12	62	PTT	3 \pm 0.4 (0.2–11)	487 \pm 79 (5–2884)
	CHR ^b	Apr, Jun–Jan	2011, 2012	8	69	PTT	13 \pm 2 (0.25–60)	1040 \pm 121 (10–3854)
YNA	Inc. ^a	Sep–Jan	2000–02, 2006, 2009, 2011, 2013, 2016	63	67	PTT, GPS	10 \pm 1 (0.2–23)	1206 \pm 94 (25–2911)
	CHR ^b	Nov–Jan	2001, 2005–06, 2011–14	62	109	PTT, GPS	3 \pm 0.2 (0.12–14)	366 \pm 26 (8–1901)
SOAL	Inc. ^{a,b}	Dec	2008	2	2	PTT	4 \pm 1 (3–5)	710 \pm 113 (597–822)
	CHR ^b	Jan–March	2009	4	17	PTT	10 \pm 3 (0.04–31)	302 \pm 80 (11–1075)
NRP	Inc. ^{a,b}	Sep	2011	4	6	PTT	8 \pm 2 (0.4–12)	138 \pm 36 (18–234)
	CHR ^b	Oct–Nov	2011, 2017	9	28	PTT	8 \pm 2 (0.3–38)	125 \pm 34 (6–632)

^a Corresponds to the breeding stage observed at tag deployment but can include both successful and failing breeders.

^b Datasets excluded from marine Important Bird and Biodiversity Area (mIBA) identification because of small sample sizes.

that were battery (working continuously) or solar (duty cycled) powered to adults of all species to track their movement across different breeding stages (incubation vs. chick-rearing) and years (Table 2). In addition, GPS loggers were deployed on adult Indian yellow-nosed albatross during the incubation and chick-rearing stages. The resulting dataset includes data for 164 birds with locations sampled at irregular time intervals and associated with different spatial errors (i.e. ARGOS location classes in increasing order of accuracy: Z, B, A, O, 1, 2, 3 vs. GPS location error \sim 50 m). To overcome this heterogeneity, for all species and breeding stages tracks of $>$ 15 locations were retained and processed with (1) a displacement speed filter with maximum speeds set to 50 km/h for albatrosses and 10 km/h for Northern rockhopper penguin; (2) a Kalman filter, which accounted for location error according to their assigned ARGOS location class (R package *crawl*; Johnson, 2013). The resulting correlated random walk models were used to predict a location (and estimated uncertainty) at a regular hourly time step interval (Johnson et al., 2008). Finally, tracking datasets for each individual were divided into foraging trips, with all locations within 5 km from the deployment site considered as the bird having returned to the colony and subsequent locations $>$ 5 km from the colony were therefore regarded as a separate foraging trip (Table 2).

2.3. Identification of marine Important Bird and Biodiversity Areas (mIBAs)

A marine IBA is generally defined as a site known to regularly hold significant numbers of a globally threatened species, or a site that supports $>$ 1% of the global population of a congregatory seabird species (Donald et al., 2018; Lascelles et al., 2016) (usually calculated as a marine area corresponding to \geq 20% of a colony, providing that this corresponds to $>$ 1% of the global population; Lascelles et al., 2016). The four seabird species included in our analyses are all classified as endangered (Table 1), thus, their important foraging sites meet the criteria to be designated as global IBAs (Lascelles et al., 2016).

We analysed each dataset following the procedures developed by BirdLife International to identify marine IBAs (mIBAs) using tracking data (see (Lascelles et al., 2016)). Briefly, datasets were compiled for each breeding stage and species in order to account for the variability in space-use among different life history stages (Lascelles et al., 2016). For each dataset, we first estimated the 50% (i.e. core area) kernel utilisation distributions for every individual trip. We used a smoothing factor that corresponded to the scale of interaction of the birds with the environment estimated from the peak of variance in first passage time, which assesses the time taken by an individual to cross the area of a circle of 5–200 km around each location (see (Fauchald and Tveraa, 2003; Lascelles et al., 2016; Suryan et al., 2006; Weimerskirch et al., 2007); Table 3, Fig. S2). Using individual trips as independent samples carries the risk of pseudo-replication if individuals perform multiple trips to the same area. Therefore, we tested for pseudo-replication bias

by comparing within-and between-individual variance. Because the variance between individuals was not significantly greater than within individuals, we retained single trips as independent samples (Lascelles et al., 2016). We then assessed the representativeness of each dataset to make population-level inferences (Fig. S2), and finally calculated the proportion of each population using each 0.1° grid cell by counting the number of core areas overlapping with each cell. We defined mIBAs as sites used by a proportion of the population above a threshold that depended on the representativeness of each dataset (Table 3, Fig. S2), and merged all species-specific mIBAs to delineate a single mIBA for all threatened seabirds of Amsterdam Island. A more detailed description of this process can be found in Lascelles et al. (2016).

Finally, to assess the adequacy of the spatial extent of existing protected areas for the seabirds of Amsterdam Island, we calculated the percentage of seabird locations occurring within (i) the former TAAF (French Antarctic and Sub-Antarctic territories) marine reserve; (ii) the recently established marine protected area in the EEZ; and (iii) the final mIBA for all species pooled together. As locations were interpolated on a regular time-step, the proportion of locations was equivalent to assessing the relative time spent by each species in the considered areas.

2.4. Data for longline fishing effort

To assess the potential threat posed by bycatch in longline fisheries, we quantified the fishing effort in the areas highlighted by our analysis described above. Within the known range of occupancy of the four study species during the breeding season, longline fishing effort for tuna-like fisheries operating in the Indian Ocean are freely available online as the monthly number of hooks set in $5 \times 5^\circ$ grid cells (<http://www.iotc.org/>). We retained only data (with quality indices of 2 and 3 corresponding to reliable catch and effort estimates (see <http://www.iotc.org/>)). For each species and breeding stage, we summed the total number of hooks deployed per year while the birds were at sea (corresponding to the years and months between the birds' departure and return, i.e. Table 2) for each $5 \times 5^\circ$ grid cell. We retained the maximum cumulative number of hooks deployed among all years for each grid cell (hereafter “fishing effort value”), because the maximum cumulative number of hooks provides a more realistic overview of the threat birds have been exposed to over several breeding seasons.

Finally, we estimated the 50% (i.e. core areas) and 90% (i.e. overall distribution) kernel utilisation distributions for each species and breeding stage, and extracted the fishing effort values associated with these distributions as well as within the EEZ for the corresponding years and months using the packages *sp* and *raster* in R software (Hijmans, 2014; Pebesma and Bivand, 2005).

All analyses were performed using R v. 3.4.1 (R Core Team, 2017) and QGIS software (version 2.18.22) (QGIS Development Team, 2018).

Table 3

Outputs from analyses performed to identify core areas (50 and 90% kernel home range) and marine Important Bird and Biodiversity Areas (mIBAs) for each species per breeding stage. The percentages of locations of the four threatened species falling within Amsterdam Island and Exclusive Economic Zones (EEZ) as well as the TAAF (French Antarctic and sub-Antarctic Territories) former marine reserve are also presented. AMS: Amsterdam albatross, YNA: Indian yellow nosed albatross, SOAL: sooty albatross, NRP: northern rockhopper penguin, CHR: chick-rearing, Inc.: incubation.

Species	Status	h value (km)	Representativeness	Core use thr.	mIBA (km ²)	% of loc. in final mIBA	% of loc. in EEZ	% of loc. in former TAAF marine reserve
AMS	Inc.	40	0.5%	NA	NA	94%	95%	92%
	CR	40	99%	10%	125,398	48%	56%	29%
YNA	Inc.	45	73.00%	20%	NA	71%	73%	12%
	CR	55	94%	10%	75,883	49%	71%	17%
SOAL	Inc.	38	NA	NA	NA	21%	50%	4%
	CR	75	92.40%	20%	141,988	83%	92%	28%
NRP	Inc.	15	NA	NA	NA	97%	100%	25%
	CR	15	72%	20%	3731	52%	89%	38%
All species					166,155			

3. Results

3.1. Seabird movements and core areas

The at-sea areas, trip durations and distances travelled by our four species from Amsterdam Island varied across species, breeding stage and season (Fig. 1, Table 2).

During incubation, Amsterdam albatrosses travelled only half as far compared to the chick-rearing stage, resulting in a relatively small core area around the colony (Fig. 1, Table 2). In contrast, during chick-rearing they mostly performed extended westward trips from the colony.

Similar distance ranges and areas were used by Indian yellow-nosed albatrosses compared to Amsterdam albatross. However, they performed overall shorter trips and the opposite pattern was observed in terms of breeding status, with individuals travelling four times larger distances during chick rearing compared to incubation.

Sooty albatrosses travelled intermediate distances from the colony, and mainly targeted areas around and south of the colony during chick-rearing and incubation, respectively. Similar to Indian yellow-nosed albatrosses, they travelled larger distances during incubation compared to chick-rearing.

Northern rockhopper penguins had the smallest distance ranges of all four species (Fig. 1, Table 2). While trip duration and distances travelled were quite similar during incubation and chick-rearing stages, there was a spatial segregation during the breeding season. Individuals mostly targeted areas around and north-east of the colony during incubation, whereas core areas were essentially west and south-east of the colony during chick-rearing.

3.2. Characterisation of mIBAs

The scales of interaction with the environment differed across species, but were similar between breeding stages, except for sooty albatrosses (Table 3). Overall, the tracks of the four species during the incubation stage were insufficient to meet mIBA criteria for several reasons: data for Northern rockhopper penguin, sooty albatross and Amsterdam albatross were not representative of the wider population (i.e. < 70% representativeness, Table 3). Data for the Indian yellow-nosed albatross were representative but did not result in sufficient overlap of individual core areas for any grid cell to meet the threshold of 20%.

However, mIBA were successfully identified for each species during the chick-rearing stages. While polygon sizes of the species-specific mIBA differed (Table 3), they all overlapped with each other and were included in the EEZ around Amsterdam and St Paul Islands (Fig. 2A–D).

The combined mIBA was eight times larger than the TAAF marine reserve area before its recent extension. Our tracking data therefore justify the recent expansion of the protected area to encompass the EEZ. In addition, on average $31 \pm 10\%$ (range: 4–92%), $64 \pm 9\%$ (range:

21–97%) and $78 \pm 7\%$ (range: 50–100%) of seabird locations were within the former TAAF marine reserve, combined mIBA and EEZ, respectively (Table 3). This means that the recent decision to expand the TAAF marine reserve resulted in an additional cover of on average 47% of the locations.

3.3. Overlap between seabird core areas and longline fishing

Overall, except for Amsterdam albatross during chick-rearing, fishing effort was on average smaller within the EEZ and our seabirds' core areas compared to the whole region regulated by the Indian Ocean Tuna Commission (Fig. 3, Table 4). Nonetheless, an average of $23,000 \pm 100$ to $1,018,000 \pm 7900$ hooks (max: 18 millions) were set per year within the core areas of the four study species. Fishing effort varied between core areas used by different species and at different breeding stages as well as within and outside the EEZ for the corresponding periods. The largest fishing effort was reported for areas targeted by Amsterdam and Indian yellow-nosed albatross during the chick-rearing and incubation stages, respectively, corresponding to periods during which their home ranges extended far beyond the EEZ. Fishing effort data were not available within the areas used by Northern rockhopper penguin and sooty albatross (incubation stage only), either corresponding to an absence of hooks set at this time of the year or an absence of reported fishing effort.

4. Discussion

We quantified the area used by four globally threatened seabird species in the Southern Indian Ocean and delineated areas that were used consistently by a large proportion of each population during the breeding season. The identified important areas fell within the boundaries of the French EEZ, but vastly exceeded the former TAAF reserve. Thus, our results reinforce the justification of the recent expansion of the reserve to the boundaries of the EEZ. However, overall seabird distributions extended beyond the EEZ (up to 50% of locations) and we found substantial overlap with longline fishing effort in the high seas.

4.1. Seabird at-sea distribution and core areas

Demographic parameters of wild animals are often closely associated with their foraging distribution and behaviour (Stearns, 1992; Weimerskirch, 2018). For seabirds, successful foraging depends on the spatio-temporal distribution of their prey and is particularly important during the breeding season, when adults are spatially constrained as they must commute between the colony and their feeding grounds (Weimerskirch, 2007). Overall, the French EEZ around Amsterdam Island encompassed over 70% of birds' locations and core areas during the breeding season. Yet, Amsterdam and sooty albatrosses travelled beyond the EEZ in international waters half of their time during chick rearing and incubation stages, respectively.

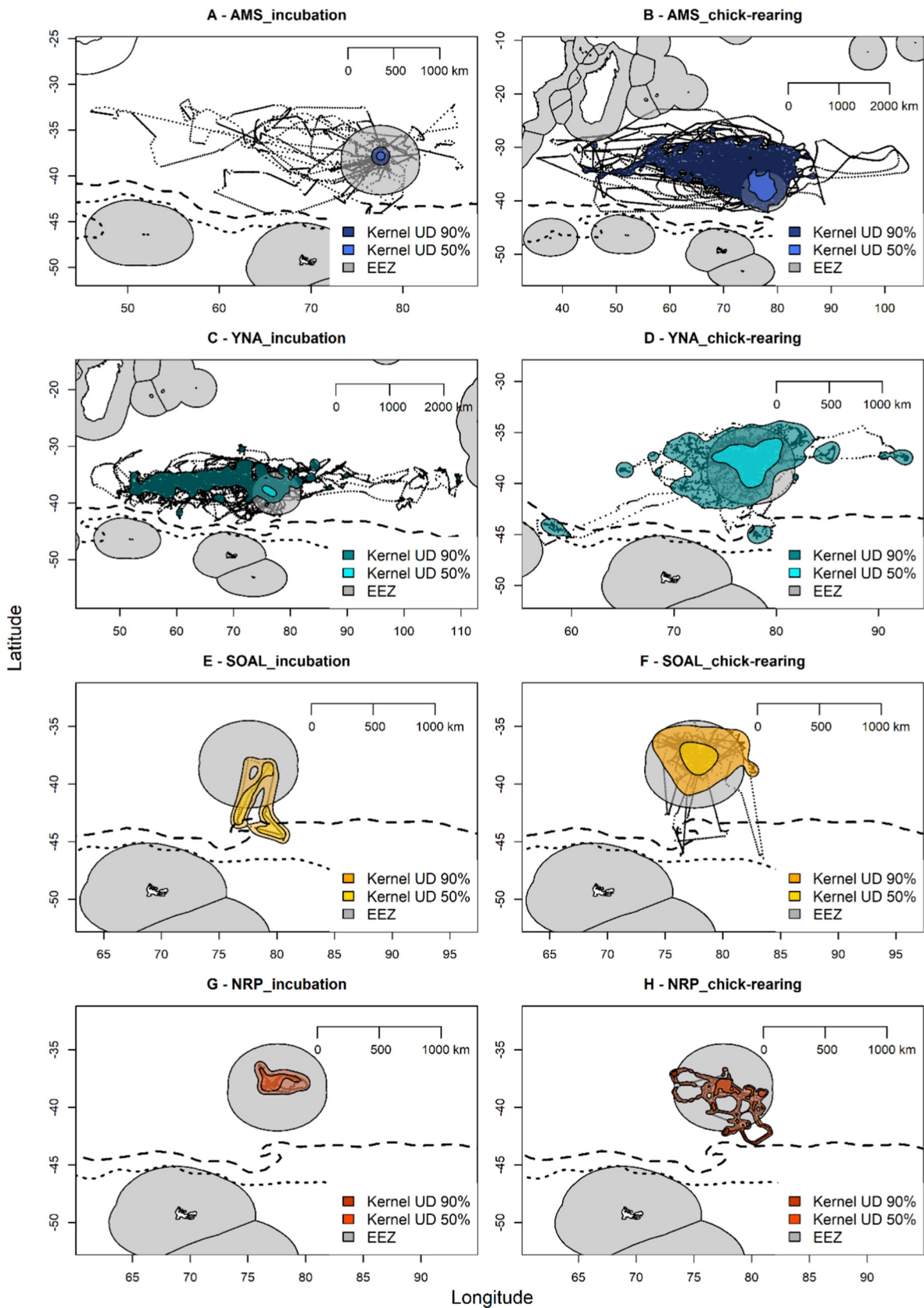


Fig. 1. Tracks and home ranges (kernel 50 and 90% utilisation distributions – individuals pooled together) for Amsterdam (AMS), yellow-nosed (YNA), sooty (SOAL) albatrosses and northern rockhopper penguins (NRP) from Amsterdam Is. during each breeding stage (CHR: chick-rearing, Inc: incubation). The values of the h smoother included in the kernel analyses (Table 3) corresponded to the scale of interaction with the environment defined by first passage time (FPT, Fauchald and Tveraa, 2003) analyses (Lascelles et al., 2016). Dashed and pointed lines correspond to sub-tropical and sub-Antarctic fronts, respectively. The exclusive economic zones (EEZ) are also presented (grey polygons).

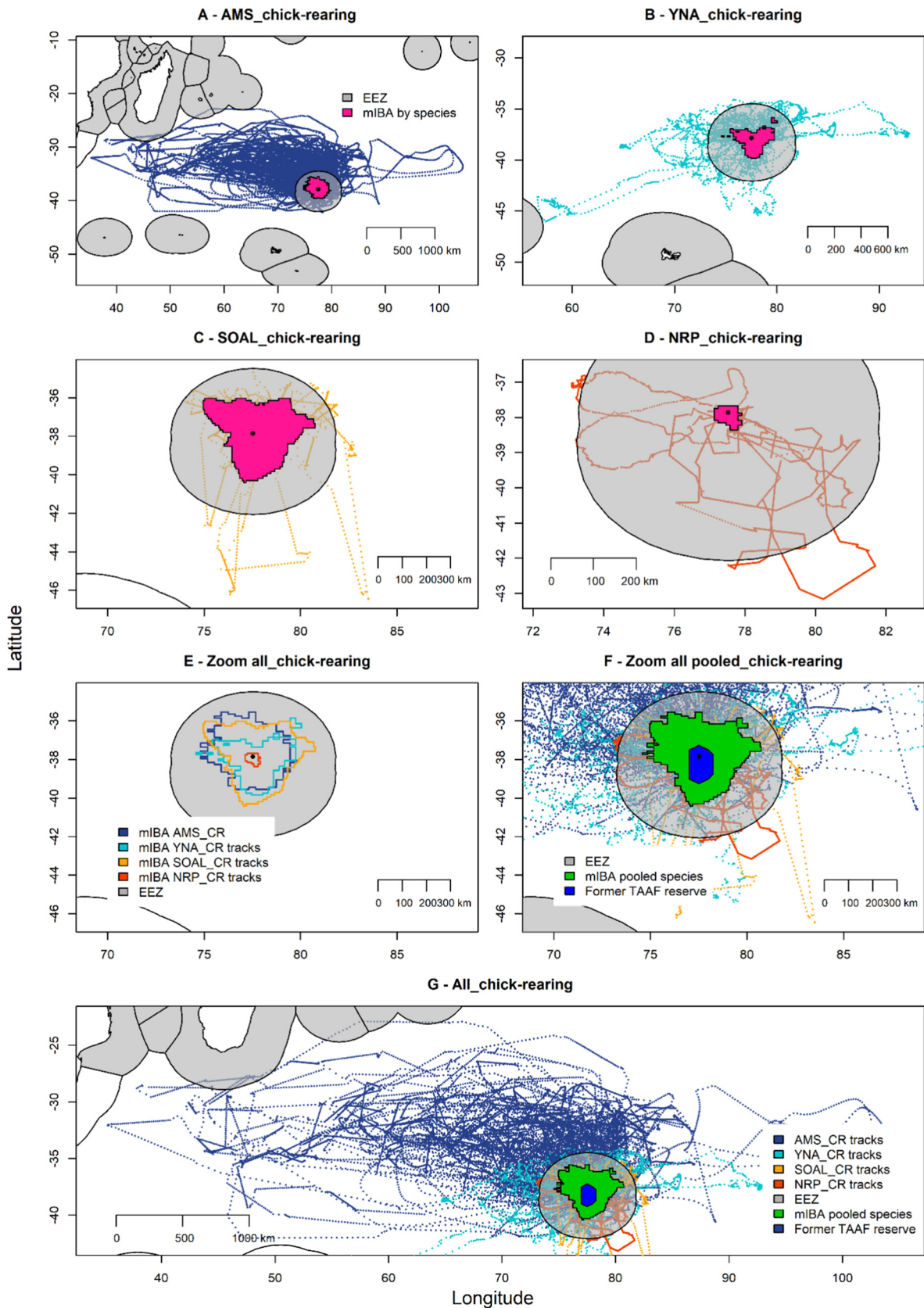


Fig. 2. mIBAs used by > 10 to 20% of the tracked population (Table 3) of Amsterdam (AMS), yellow-nosed (YNA), sooty (SOAL) albatrosses and northern rockhopper penguins from Amsterdam Is. Important areas were successfully identified for each species during chick-rearing (A to D) and merged into one for the four pooled species (D and E). The exclusive economic zones (EEZ, grey polygons) as well as the TAAF (French Antarctic and sub-Antarctic Territories) former marine reserve are also presented.

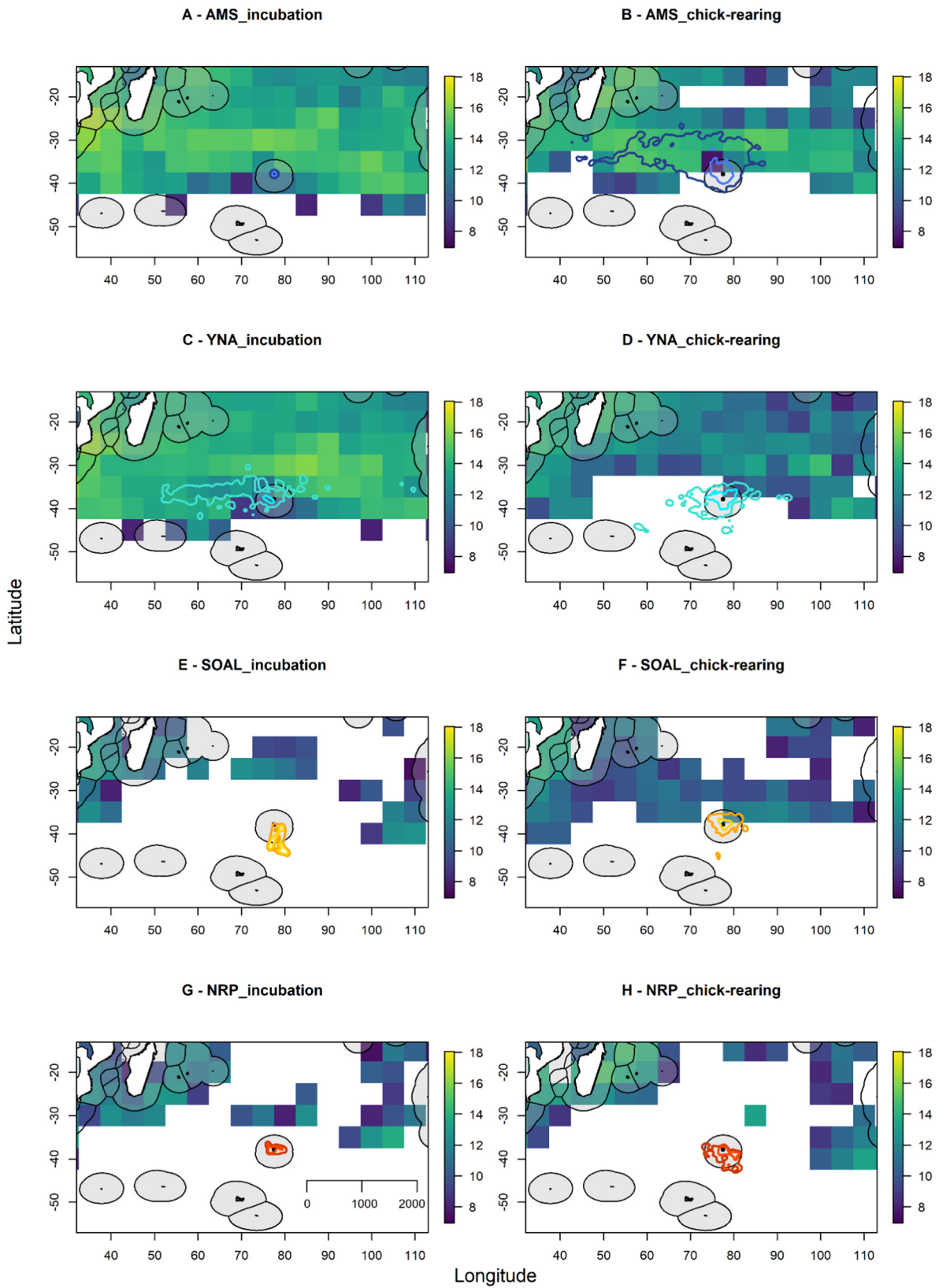


Fig. 3. Overlap between the four threatened species in Amsterdam Is. core areas (50 and 90% kernel home ranges – individuals pooled together) and fishing effort. Fishing effort is expressed as the log-transformed maximum cumulated number of hooks set per year (long line fishing, monthly data, $5 \times 5^\circ$ cell grid) deployed while the birds were at sea (corresponding years and months), according to species and breeding stages. Fishing data were obtained from the Indian Ocean Tuna Commission (IOTCA, www.iotc.org). The exclusive economic zones (EEZ) are also presented in grey.

Table 4

Overlap between the four threatened species in Amsterdam Is. core-used areas (50 and 90% kernel home range – individuals were pooled together), French Exclusive Economic Zone and reported fishing effort. Fishing effort corresponds to the maximum values between cumulative number of hooks set per year (mean \pm se (range) $\times 10^3$, long line fishing, monthly data, $5 \times 5^\circ$ cell grid) deployed while the birds were at sea (corresponding years and months), according to species and breeding stages. Fishing data were obtained from the Indian Ocean Tuna Commission (IOTC, www.iotc.org). AMS: Amsterdam albatross, YNA: yellow nosed albatross, SOAL: sooty albatross, NRP: northern rockhopper penguin, CHR: chick-rearing, Inc.: incubation.

Species	Stage	HR 50	HR90	EEZ	Overall IOTC region
AMS	Inc.	64 \pm 0.1 (64–2395)	66 \pm 0.3 (64–2395)	79 \pm 0.8 (63–6357)	2511 \pm 258 (0.9–28,282)
	CHR	64 \pm 1.3 (1.8–880)	1018 \pm 7.9 (1.8–4093)	64 \pm 0.9 (1.8–134)	1110 \pm 121 (1.8–10,085)
YNA	Inc.	23 \pm 0.1 (12–75)	178 \pm 1.8 (6.6–9213)	54 \pm 0.9 (12–1204)	2579 \pm 296 (1.1–30,708)
	CHR	18	22 \pm 0.3 (4.9–51)	18	573 \pm 70 (0.8–5744)
SOAL	Inc.	NA	NA	NA	250 \pm 32 (0.5–1576)
	CHR	99	99	99	583 \pm 97 (0.6–7520)
NRP	CHR	NA	NA	NA	429 \pm 62 (1.3–3213)
	Inc.	NA	NA	NA	141 \pm 22 (1.3–1192)

As is typical for most seabirds, Indian yellow-nosed and sooty albatrosses travelled greater distances and spent longer time at sea during incubation than during chick-rearing (Oppel et al., 2018). This resulted in our inability to define mIBAs during incubation, because the tracked birds were too far dispersed at sea. There was little overlap between breeding Indian yellow-nosed albatrosses from Amsterdam Island and birds breeding at the Prince Edward Islands, suggesting possible space partitioning to reduce competition (Makhado et al., 2018; Wakefield et al., 2013). Interestingly, sooty albatrosses from Amsterdam Island seem to target similar oceanographic features (sub-tropical and sub-Antarctic fronts) than their counterparts from Tristan, Gough and Prince Edward Islands (Schoombie et al., 2017).

Amsterdam albatrosses travelled longer distances during chick-rearing than during incubation, which is an untypical pattern for seabirds (Oppel et al., 2018). During the chick-rearing stage, two main patterns were evident: (1) colony centred short (< 340 km) versus (2) westward looping long-range trips; while the chicks were younger versus older, respectively; also suggesting a dual foraging strategy (Thiebot et al., 2014). The very long trips in our dataset likely corresponded to birds which failed breeding, and no longer had to return to feed a chick (see Thiebot et al., 2014). Similarly, while Northern rockhopper penguins mainly stayed within the French EEZ exploiting small areas east or north-west of the colony, long trips to the south, toward the sub-tropical front, were likely undertaken by failed breeders in 2017, when no chicks survived in the colony (C-A Bost, pers. obs.).

Except for Indian yellow-nosed albatross, relatively few birds were tracked due to the difficulty to obtain tracking data on these species breeding at remote locations. We therefore performed analyses based on individual trips to increase sample sizes, which may have reduced the representativeness of the samples and consequently our ability to identify mIBAs (i.e. during the incubation stage). However, the critical demographical decline (except for AMS) these seabird populations undergo (Jaeger et al., 2018; Weimerskirch et al., 2018a) also highlights the relevance of using outcomes for these species as baseline reference to define priority biodiversity conservation sites and mitigation actions.

4.2. Overlap with longline fishing effort

Industrial fisheries represent one of the most serious threats to seabird conservation worldwide (Delord et al., 2008; Croxall et al., 2012; Thiebot et al., 2016; Weimerskirch et al., 2018b).

We found high overlap between longline fishing effort and the distribution of breeding Amsterdam (both stages) and Indian yellow-nosed albatrosses (mostly during incubation stage). Indian yellow-nosed albatrosses are known to interact with fisheries across their range, and birds from Amsterdam Island have been incidentally caught in fisheries targeting Patagonian toothfish *Dissostichus eleginoides* near the Prince Edward Islands (Ryan and Boix-Hinzen, 1999), in tuna

longline fisheries (Huang and Liu, 2010) and in demersal longline fisheries off the West coast off New-Zealand (Delord et al., 2013). Given the evidence for additional mortality due to bycatch in this species, the high overlap with longline fisheries is a major concern that will require appropriate management. We recommend regulations that mandate best available bycatch mitigation techniques and complete observer coverage for all longline fisheries operating in areas where and at times when Indian yellow-nosed albatross typically occur in an area (Fig. 3).

Despite extensive overlap with longline fisheries, the Amsterdam albatross population is increasing (Jaeger et al., 2018; Weimerskirch et al., 2018a) and no incidental catch for this species has been reported (Thiebot et al., 2016). While these patterns could be interpreted as low or non-existing threat of bycatch to Amsterdam albatross individuals, we caution that Amsterdam albatross range widely outside the EEZ (Fig. 3) and bycatch could occur outside of EEZs where fisheries are not required to have observers or report bycatch (Huang, 2011). In addition, due to the extremely small population size of Amsterdam albatross, vulnerable individuals may have already been killed leaving only individuals that avoid fishing vessels (Barbraud et al., 2013). Previous studies suggested that the population could have been reduced by longline fishing activity around Amsterdam Island between the mid-1960s and mid-1980s (Inchausti and Weimerskirch, 2001). Our results provide a spatio-temporal envelope where and when bycatch mitigation and observer coverage of longline fisheries should be mandated and enforced to ensure no negative effects on the endangered Amsterdam albatross population (Rivalan et al., 2010).

There appears to be little overlap between sooty albatrosses during their breeding season and longline fishing effort in the Southern Indian Ocean (this study; Schoombie et al., 2017), which is partly due to their limited range within the EEZ where there is lower fishing effort (Tuck et al., 2011, 2003). While sooty albatross populations are stable at Gough Island and increasing at the Prince Edward Islands (Cuthbert et al., 2014; Schoombie et al., 2017), the populations of this species on Crozet and Amsterdam islands are decreasing (Delord et al., 2008; Jaeger et al., 2018), which have been related to low survival in immature and adult individuals, supposedly resulting from bycatch in longline fishing operations (Jouventin et al., 1984; Weimerskirch and Jouventin, 1998). This mortality, however, is more likely to occur during the non-breeding season (not analysed in our study), given the large subtropical range covered by sooty albatrosses during this stage (from both Crozet and Amsterdam Islands; range between 20 and 140°E; Delord et al., 2013), which coincides with longline fishing activity (Huang and Liu, 2010; Tuck et al., 2003). We should also highlight that the sample sizes for this species were considerably lower (mostly due to the logistic difficulties in tracking the species (Delord et al., 2013; Weimerskirch and Guionnet, 2002)), which might have affected our capacity to detect potential areas of overlap.

In summary, available data on the distribution of the albatross study species and longline fishing operations indicate that the Southern

Indian Ocean is an area with a very high rate of potential seabird bycatch (Delord et al., 2013; Huang and Liu, 2010; Lewison et al., 2014), despite the low observer coverage and therefore likely incomplete reporting of seabird bycatch in international waters. Although the use of novel radar detector tags is promising to obtain new insights in seabird-longline fishing interactions (Weimerskirch et al., 2018b), our results identify key areas in which bycatch mitigation and complete observer coverage should be prioritised to reduce incidental mortality of globally threatened seabirds.

Overall, the priority sites for conservation identified in this study justify the extension of the marine reserve to the EEZ boundaries. Fishing activity within the French EEZ is highly regulated by the French administration and only one commercial vessel can set demersal vertical longlines between November and April within the EEZ. Therefore, we recommend a reinforced protected area using our mIBA boundaries, such as the ones established at Kerguelen and Crozet Islands during the 1st and 4th quarters of the year (see <http://www.taaf.fr/Perimetre-et-statuts-de-protection>). In addition, we would recommend the mandatory adoption of at least two of the three most efficient mitigation measures for albatross bycatch (branchline weighting, tori lines, night-setting; Jiménez et al., 2018) as a minimum to reduce seabird bycatch, and enforce complete observer coverage on all commercial fishing vessels to improve systematic bycatch reporting (Melvin et al., 2013, 2014; Robertson et al., 2018; Sullivan et al., 2018; <https://www.acap.aq/>).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.03.037>.

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