


# Fine-scale interactions between boats and large albatrosses indicate variable susceptibility to bycatch risk according to species and populations

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## Keywords

albatross populations; biologging; bycatch assessment; ecological trap; fisheries; fishing boat bycatch; seabirds; bycatch risk.

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## Abstract

Many seabirds are attracted to fishing boats where they exploit foraging opportunities, often involving bycatch-related mortality. Bycatch risk is generally estimated by overlapping seabirds foraging ranges with coarse-scale monthly maps of fishing efforts, but a more direct estimation would be the time birds actually spend attending fishing boats. Here we matched data from Automatic Identification Systems from all declared boats in the Southern Ocean, with 143 simultaneous foraging trips from all populations of large albatrosses (*Diomedea amsterdamensis* and *Diomedea exulans*) breeding in the Indian Ocean (Marion, Crozet, Kerguelen, Amsterdam islands). We quantified and compared real-time co-occurrence between boats and albatrosses, at different scales (100, 30 and 5 km). We also examined to what extent co-occurrence at a large-scale ( $5 \times 5^\circ$  grid cell) predicted fine-scale attendance (5 km). Albatrosses on average spent about 3 h per trip attending fishing boats (<5 km) at both Amsterdam and Marion and about 30 h per trip at Kerguelen. In all populations, >90% of declared fishing boat attendances occurred within Economic Exclusive Zones (EEZ) where bycatch mitigation measures are enforced. Outside EEZs, birds from all populations to a large extent also attended non-fishing boats. Fishing boat density at a large scale ( $5 \times 5^\circ$ , 100 km) was a poor predictor of time spent attending fishing boats (<5 km) across populations. Our results indicate a large variation in fishing boat densities within the foraging ranges of different populations and in the time birds spent attending boats. We discuss the pros and cons of considering bycatch risk at a large geographical scale and methods that can be implemented to improve the estimation of seabird vulnerability to fishing activities when fine-scale data are available, particularly for the conservation of those highly threatened species.

## Introduction

In marine ecosystems, together with climate change, industrial fisheries constitute the main driver of ecological deterioration (Pauly *et al.*, 2002). Fisheries interact with marine predators mainly by competing for resources (Cury *et al.*, 2011; Grémillet *et al.*, 2018) and by inducing mortality through bycatch of non-target species (Lewison *et al.*, 2004). Fisheries can also facilitate access to prey for higher predators along the food chain or provide additional food resources (Oro *et al.*, 2013). As a result, many seabird species and marine mammals are attracted to fishing boats (Votier *et al.*, 2004; Read, 2008; Brothers *et al.*, 2010; Bugoni, McGill, & Furness, 2010) in search of foraging

opportunities associated with fishing bait or discards (Votier *et al.*, 2004; Bicknell *et al.*, 2013a). However, the associated bycatch is one of the primary threats for seabird populations around the world (Croxall *et al.*, 2012). Moreover, in some seabird populations the poor quality of these food resources negatively affect reproductive success (Grémillet *et al.*, 2008; Le Bot, Lescroël, & Grémillet, 2018a). Another concern is that populations heavily reliant on fishing vessels for food resources may be negatively impacted by changes in fishing policies (Bicknell *et al.*, 2013b).

Bycatch is the most important threat for albatrosses and large petrels while at sea with high levels of mortality often induced by longline fisheries (Delord *et al.*, 2005; Anderson *et al.*, 2011; Croxall *et al.*, 2012). In the Southern Ocean,

albatrosses overlap extensively with longline fisheries, targeting tuna in oceanic waters, and various species of bottom-dwelling fishes over shelves and shelf-edges, in international waters as well as the Economic Exclusive Zones (EEZ) of the respective countries. The extent of spatio-temporal overlap between different density of fisheries and albatross foraging grounds has been inferred to represent mortality risk for various populations (Bertrand *et al.*, 2012; Clay *et al.*, 2019; Heerah *et al.*, 2019). However, information on fisheries location is generally available at a large scale, especially in international waters. For example global fishing efforts provided by Regional Fisheries Management Organisations for tuna and billfishes are only available at a monthly and by  $5 \times 5^\circ$  cell resolution (Clay *et al.*, 2019; Heerah *et al.*, 2019). This approach overlooks the possibility that fisheries and seabirds could co-occur at a large scale without birds interacting with the fishing boats, particularly if they are not attracted to vessels (Clark *et al.*, 2020). To better estimate mortality risk, it is, therefore, necessary to complement these approaches with more direct information on the actual time birds spend attending fishing boats and how this varies spatially (Torres *et al.*, 2013). This has been hampered in the past by difficulties in obtaining fine-scale information on fishing vessel movements from fishing operators or authorities. This information can be made available through Vessel Monitoring Systems (VMS) but it is often confidential (Votier *et al.*, 2010) and restricted to confined EEZ territories. Several studies have combined VMS information and fine-scale tracking of seabirds to study interactions (Torres *et al.*, 2013; Collet, Patrick, & Weimerskirch, 2017a) but these have been restricted to specific small-scale geographical sectors.

In the Indian Ocean, large-scale active longline tuna fisheries in open waters and Patagonian toothfish *Dissostichus eleginoides* fisheries operating over sub-Antarctic shelf edges and seamounts overlap with the foraging ranges of the two large albatross species (wandering – *Diomedea exulans* and Amsterdam – *Diomedea amsterdamensis*) breeding in the region (Weimerskirch, Brothers, & Jouventin, 1997; Delord *et al.*, 2005). The past decline of the former species has been attributed to bycatch associated with longline fisheries (Brothers, 1991; Weimerskirch, Brothers, & Jouventin, 1997; Nel *et al.*, 2002). Despite mitigation measures that have been implemented by toothfish longline fisheries within the EEZs, which has resulted in a reduction in bycatch by this fishery (Delord *et al.*, 2005; Weimerskirch *et al.*, 2018), there are still concerns of bycatch risk from longline fisheries targeting tuna in international waters where no mitigation measures are implemented or from illegal or uncontrolled fisheries for toothfish without mitigation measures (Brothers, 1991; Weimerskirch, Brothers, & Jouventin, 1997; Weimerskirch *et al.*, 2020). Moreover, within more regulated EEZ waters it is important to estimate the extent to which albatrosses of different species and populations spend interacting with toothfish longliners, to better quantify potential sub-lethal issues of dependence and possibly poor forage quality (Bicknell *et al.*, 2013a; Le Bot, Lescroël, & Grémillet, 2018b).

In this study, we combined a large tracking dataset of foraging albatrosses (Weimerskirch *et al.*, 2020) with the locations and types of all declared boats from the Automatic Identification System (AIS) in the southern Indian Ocean. GPS tracking data were collected in 2018/2019 on breeding adults from all four major populations of large albatrosses in the Indian Ocean. We spatio-temporally matched these datasets to estimate the degree of co-occurrence at various scales from seascape ( $<100$  km from the tracked individual), through encounter ( $<30$  km) to attendance ( $<5$  km), following Weimerskirch *et al.* (2020). We particularly focused on the time spent attending fishing boats ( $<5$  km) as a potential proxy for bycatch and other boat-associated risks. We examined how it differed among individuals and populations, how it differed between different types of fishing and non-fishing boats, and how it differed between EEZs around subantarctic islands and international waters where different fisheries operate with different mitigation measures. Finally, to assess to what extent co-occurrence at a larger scale reflects co-occurrence at finer scale and could be used as a proxy for bycatch risk (exposure to bycatch risk), we compared the time spent attending fishing boats ( $<5$  km) to the encounter rate (30 km) and the density of boats in the seascape ( $<100$  km) as well as to the more widely used method of aggregating boat data from Regional Fisheries Management Organisations (RFMO:  $5 \times 5^\circ$  grid). We (1) hypothesized that there is a large variation in the levels of exposure to boats according to albatrosses' foraging zones and range, (2) tested to what extent it resulted in variation in the time spent attending boats and (3) tested whether large-scale  $5 \times 5^\circ$  grid methods provide an adequate reflection of the attendance to boats and therefore the exposure to the risk of bycatch. We then discuss implications for bycatch and sub-lethal risks to the different populations.

## Materials and methods

### Field sites

Fieldwork was carried out in French southern territories (Crozet, Kerguelen & Amsterdam) during the course of a large-scale Ocean Sentinel program between January and April 2019, during the breeding season of large albatrosses in the Southern Indian Ocean (Weimerskirch *et al.*, 2020). We deployed loggers for incubating wandering albatrosses at Possession Island (Crozet Islands) and at the Kerguelen Islands, and on Amsterdam albatrosses at Amsterdam Island. During the same season, incubation wandering albatrosses were fitted with GPS loggers at South Africa's Marion Island, Prince Edward Islands.

### Loggers

On Crozet, Kerguelen and Amsterdam, Centurion loggers (65 g) recording GPS location every 2 min were deployed on incubating birds for one or two successive foraging trips (Weimerskirch *et al.*, 2020). On Marion, GPS loggers (IgotU, 60 g) recording locations every 20 min were

deployed for several trips during the incubation and brooding period. The loggers were attached to the back feathers with Tesa® Tape (Germany), and represented between 0.5 and 0.85% of large albatross body mass, much less than the maximum 3% recommended for loggers attached to flying seabirds (Phillips, Xavier, & Croxall, 2003).

## GPS data and AIS dataset

A total of 143 trips on incubating albatrosses were recorded, with 57 trips from 27 individuals on Marion Island, 10 trips from eight individuals at Amsterdam, 49 trips from 49 individuals at Crozet and 27 trips from 24 individuals at Kerguelen.

After using speed filters ( $150 \text{ km h}^{-1}$ ; Weimerskirch *et al.*, 2020), we divided tracks by trips (removing location on land).

AIS data for all fishing and non-fishing boats (Fig. S1) were obtained from French satellite transmission society (*Collecte Localisation Satellites*) for the study period for the sector  $10^{\circ}\text{--}180^{\circ}\text{E}$ ,  $20^{\circ}\text{--}70^{\circ}\text{S}$  through the Ocean sentinel program (Weimerskirch *et al.*, 2020), providing a total of 120 million AIS locations. Through the AIS system, in addition to regular GPS locations (mean resolution of 10 min) we obtained continuous data on identification name, nationality, type of boat (fishing or not) and activity for all declared boats in the Southern Indian Ocean. AIS data and bird locations were spatio-temporally matched following Weimerskirch *et al.* (2020) to produce a dataset where all GPS locations of each bird from each population are associated with the presence/absence, number and types of boats transmitting AIS information within ranges of 100, 30 and 5 km from birds (Fig. 1).

These different radius distances from birds are used to characterize the ‘boat seascape’ (within 100 km around the tracked bird), the ‘boats encountered’ (30 km) and the ‘boats attended’ (5 km). The 30 km distance was used as it is the distance within which an albatross can visually detect a boat (Collet, Patrick, & Weimerskirch, 2015). The 5 km threshold

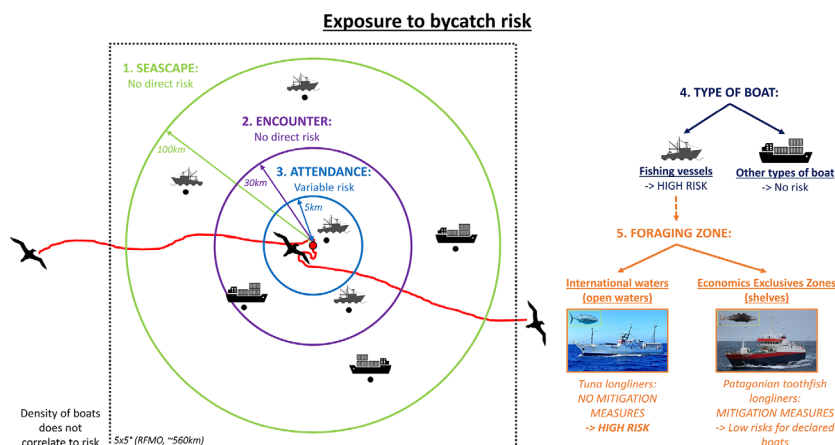
is the approximate distance within which wandering albatrosses are seen to engage in specific foraging behaviours around boats (3 km; Collet *et al.*, 2015) and is used to facilitate comparisons with previous studies that used radar detectors with a range detection of 5 km (Weimerskirch, Filippi, Collet, Waugh, & Patrick, 2018, 2020).

We defined ‘events’ (attendance and encounter events) as periods of consecutive bird locations within the respective distances of at least one boat with time intervals of less than 2 hours. To compare sites, and accommodate the relatively coarse-scale GPS sampling at Marion Island, we removed all events (attendance and encounter) lasting less than 20 min. This procedure also limits the effects of uncertainties on ‘instantaneous’ bird-boat distances (Weimerskirch *et al.*, 2020). We also removed the few incomplete trips for presenting trip statistics (Table 1).

To compare with other studies using large-scale  $5 \times 5^{\circ}$  of fishing effort provided by RFMOs (Clay *et al.*, 2019; Heerah *et al.*, 2019), we merged all AIS locations present during the study period within grid cells of  $5 \times 5^{\circ}$  (Fig. S1).

## Environmental variables

AIS data do not provide detailed information on the type of fishing gear used nor the mitigation measures employed by fishing boats. We tried to further infer this information from the waters they operated in. We added bathymetry data to each bird location (R package ‘marmap’, Pante & Simon-Bouhet, 2013), which was extracted from ‘ETOPO1 Global Relief Model’ from ‘National Oceanic and Atmospheric’. We used it to categorize bird locations as on a shelf or a shelf-edge (above  $-2000 \text{ m}$ ), where mainly benthic fish are targeted, or off the shelf, where tunas and billfishes are the main target. We also considered whether locations were within EEZ or not (data from <http://www.marinerregions.org>) and separately considered the time in attendance for specific EEZs with enforced mitigation measures within the range of our populations (Crozet, Kerguelen, Heard, McDonald Saint-Paul and Amsterdam Islands). Finally, from estimates of the



**Figure 1** Conceptual model illustrating the five points required to be checked to estimate exposure to bycatch risk applicable by species and populations.

**Table 1** Differences between each site: mean and standard deviation of parameters and significance letters of Tuckey tests (same letter in different site mean no difference and different letters mean significant differences)

	Amsterdam (trips: $n = 10$ , 10 complete)			Crozet (trips: $n = 49$ , 48 complete)			Kerguelen (trips: $n = 27$ , 23 complete)			Marion (trips: $n = 57$ , 53 complete)		
	Mean	Standard deviation	Significance letter	Mean	Standard deviation	Significance letter	Mean	Standard deviation	Significance letter	Mean	Standard deviation	Significance letter
PER TRIP ( $n = 143$ )												
Maximum distance from the colony (km)	1637.70	1281.10	AB	1177.90	813.90	AB	886.60	711.85	A	1424.70	660.54	B
Trip duration (day)	9.53	3.48	A	11.09	5.60	A	10.60	4.14	A	12.60	4.46	A
Ratio in EEZ	0.39	0.41	AC	0.57	0.35	AB	0.74	0.32	B	0.36	0.24	C
Ratio on shelf	0.20	0.29	AC	0.40	0.33	A	0.65	0.29	B	0.11	0.15	C
Ratio in Antarctic waters	0.00	0.00	A	0.07	0.20	A	0.19	0.30	A	0.12	0.26	A
Ratio in subantarctic waters	0.03	0.07	A	0.72	0.34	B	0.78	0.30	B	0.57	0.31	B
Ratio in subtropical waters	0.97	0.07	A	0.21	0.32	BC	0.02	0.13	B	0.31	0.32	C
Number of encounters	5.10	7.61	A	3.06	2.18	A	2.89	2.65	A	4.23	5.45	A
Time in encounter (h)	19.04	23.28	A	17.08	18.36	A	53.30	62.82	B	11.91	21.96	A
Number of attendances	1.80	2.20	A	1.71	1.57	A	3.59	4.41	A	1.72	2.70	A
Time in attendance (h)	4.31	6.97	A	6.75	11.00	A	31.14	38.22	B	3.21	10.20	A
Time in attendance with fishing vessels (h)	3.16	7.56	A	6.68	11.31	A	30.63	39.27	B	2.64	10.31	A
Time in attendance in EEZ (h)	2.90	6.71	A	5.84	11.14	A	28.37	38.60	B	2.46	10.24	A
Time in attendance out EEZ (h)	1.42	2.40	A	0.91	2.74	A	2.77	11.56	A	0.75	1.58	A
Time in attendance with fishing vessels in EEZ (h)	2.82	6.75	A	5.84	11.14	A	28.36	38.60	B	2.45	10.24	A
Time in attendance with fishing vessels out EEZ (h)	0.11	0.28	A	0.60	2.66	A	0.00	0.00	A	0.14	0.68	A
Ratio of fishing vessels attended (5 km)	0.64	0.43	AB	0.76	0.42	AB	0.95	0.23	A	0.22	0.37	B
Ratio of fishing vessels encountered (30 km)	0.63	0.36	AB	0.76	0.40	A	0.92	0.28	A	0.17	0.32	B
Ratio of fishing vessels in seascape (100 km)	0.43	0.27	A	0.75	0.36	B	0.92	0.23	B	0.16	0.29	A
PER LOCATION ( $n = 619631$ )												
Number of boats attended (5 km)	0.02	0.16	A	0.02	0.15	A	0.11	0.31	B	0.01	0.11	C
Number of boats encountered (30 km)	0.19	0.84	A	0.06	0.26	B	0.23	0.43	C	0.05	0.26	B
Number of boats in seascape (100 km)	1.99	5.08	A	0.29	0.60	B	0.40	0.60	C	0.35	1.11	D
Number of fishing vessels in seascape (100 km)	0.83	1.93	A	0.21	0.51	B	0.39	0.60	C	0.07	0.33	D
Ratio of number of boats 5 km/100 km	0.04	0.19	A	0.07	0.24	A	0.30	0.45	B	0.04	0.18	A

locations of the polar front (Moore, Abbott, & Richman, 1999) and the subtropical front (Belkin & Gordon, 1996) we further categorized bird locations into Antarctic, subantarctic and subtropical waters.

## Analyses

For visualization purposes, we used kernel Utilization Distributions (UDs 50 and 90%), using the R package ‘adehabitatHR’ (smoothing parameters,  $h = 1$  degree).

To compare different parameters (Table 1) between each population, we used linear mixed model or generalized linear mixed models (depending on the distribution, using R package ‘fitdistrPlus’). Negative binomial family were used for over-dispersed count data and binomial family for ratio data (R packages ‘lme4’ and ‘lmerTest’). Bird individual identities were used as random factors. We further used post hoc tests (Tukey tests, R package multcomp) and Holm–Bonferroni correction for  $P$  values. We used a  $\chi^2$  test to compare distributions of the number of trips with or without boat interaction between populations.

To compare the density of boat to the exposure to bycatch risk (time birds spent behind boat) per  $5 \times 5^\circ$  grid, we summed AIS locations (for all types of boat and only for fishing boats) per grid cell used by each study population during their respective incubation-period months (April for Amsterdam birds, January and February for Crozet and Kerguelen birds and February and March for Marion birds). We then used Pearson correlation to examine whether the density of boat is related to the time spent by birds in general, with boats in their seascape (<100 km), with boats encountered (<30 km) and with boats attended (<5 km) (exposure to bycatch risk) in the same  $5 \times 5^\circ$  grid cells used by birds.

## Results

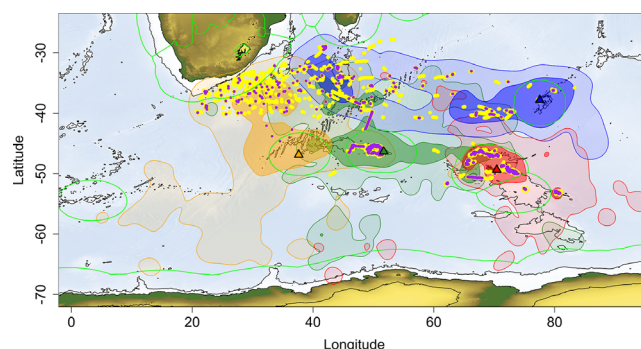
For the 143 trips recorded during incubation, there were no significant differences between populations in the duration of foraging trips. Mean maximum distance from the colony, however, differed between Kerguelen (shortest) and Marion (longest) (Table 1).

Birds from Kerguelen spent more time foraging within EEZs ( $74\% \pm 32$ , Table 1) than birds from Crozet ( $57\% \pm 35$ ), Amsterdam ( $39\% \pm 41$ ) and Marion ( $36\% \pm 24$ ). Amsterdam and Marion birds spent less time foraging over shelf waters ( $20\% \pm 29$  and  $11\% \pm 15$  respectively) as compared to Crozet ( $40\% \pm 33$ ) and Kerguelen birds ( $65\% \pm 29$ ) (Fig. 2) (Table 1 and Table S1 for test values).

Amsterdam albatrosses spent most of their time in subtropical waters ( $97\% \pm 07$ ). In contrast, the three wandering albatross populations foraged mainly in subantarctic waters ( $57\% \pm 31$  to  $78\% \pm 30$ ) (Fig. 2) (Table 1 and Table S1 for test values).

Among the 143 trips recorded, the percentages of trips with at least one boat within 100 km (boat seascape), were significantly different between populations, ranging from 68% to 100% ( $\chi^2$ , 3 = 24.9;  $P$  value =  $1.5e-05$ ) (Table 2). The percentage of trips with boats encountered (within 30 km) also varied significantly between sites, from 63 to 85% ( $\chi^2$ , 3 = 9.08;  $p$  value = 0.028) (Table 2). Finally, the percentage of trips with attendance (within 5 km) of boats was also significantly different between sites, varying from 47 to 73 % ( $\chi^2$ , 3 = 8.01;  $P$  value = 0.046) (Table 2).

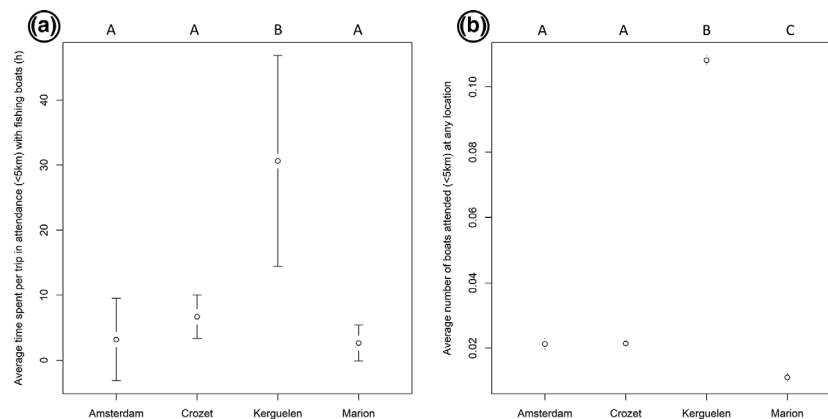
The number of encounters and attendance events per trip, when considering fishing boats and other boats together



**Figure 2** Map of the South Indian Ocean with kernel utilization distribution 50% (darker shade) and 90% (lighter shade) of birds for each site (triangles) (blue = Amsterdam, green = Crozet, red = Kerguelen, orange = Marion); yellow dots represent encounter events and purple dots, attendance events; isobaths: -2000 m (shelf), 0 m and +2000 m; light-green lines represent EEZ.

**Table 2** Number (and percentage) of trips per site with boats in seascapes (100 km), encountered (30 km) and attended (5 km)

	Amsterdam ( $n = 10$ )	Crozet ( $n = 49$ )	Kerguelen ( $n = 27$ )	Marion ( $n = 57$ )	TOTAL ( $n = 143$ )
With boats in seascape (100 km)	9 (90%)	48 (97.96%)	27 (100%)	39 (68.42%)	123 (86.01%)
With boats encountered (30 km)	8 (80%)	42 (85.71%)	23 (85.19%)	36 (63.16%)	109 (76.22%)
With boats attended (5 km)	6 (60%)	36 (73.47%)	18 (66.67%)	27 (47.37%)	87 (60.84%)



**Figure 3** Proxy of bycatch risk as (a) time spent per trip in attendance (within 5 km) with fishing boats (hours) and (b) Number of boat attended (within 5 km) at any location; Mean and confidence interval (95%) of each site. Letters represent a significant difference.

(transport, tankers, etc.) was broadly similar between populations (Table 1 and Table S1 for test values). Kerguelen birds nonetheless spent more time on average per trip within 30 km of all types of boats ( $53 \text{ h} \pm 62$ ), within 5 km of all type of boats ( $31 \text{ h} \pm 38$ ) and within 5 km of fishing boats ( $30.6 \text{ h} \pm 39$ ) (Fig. 3a) than birds from other populations (Table 1 and Table S1 for test values). Similarly, Kerguelen birds spent significantly more time attending boats inside EEZs (with mitigation measures) than birds from other populations. However, outside EEZs (where mitigation measures are less controlled) the different populations spent similar time attending AIS-recorded boats of all types, and similar time attending AIS-recorded fishing boats (Table 1 and Table S1 for test values).

Based on all location, Amsterdam birds on average had the greatest number of boats ( $1.9 \pm 5$ ) and the greatest number of fishing boats ( $0.83 \pm 1.9$ ) in their seascapes (<100 km), at least twice as much as other populations (Table 1 and Table S1 for test values). However, at Kerguelen, birds on average had the greatest number of boat encounters (<30 km:  $0.2 \pm 0.4$ ), the highest number of boats attended (<5 km:  $0.1 \pm 0.3$ , Fig. 3b) and the highest ratio of the number of boats attended relative to the number of boats in the seascape ( $0.3 \pm 0.5$ ), most of the time by a factor of 5–10 fold compared to other populations (Table 1 and Table S1 for test values).

Marion and Amsterdam birds had a smaller proportion of fishing versus non-fishing boats in their seascapes (<100 km) compared to other populations (Table 1 and Table S1 for test values). Marion birds had a significantly lower proportion of fishing boats among encountered boats (<30 km) than Crozet and Kerguelen and slightly less than Amsterdam. The proportion of fishing boats among attended boats (<5 km) was not different between Marion, Amsterdam and Crozet birds ( $0.22 \pm 0.4$ ,  $0.64 \pm 0.4$  and  $0.76 \pm 0.4$  respectively), but it was lower for Marion than for Kerguelen birds ( $0.95 \pm 0.2$ , Table 1 and Table S1 for test values).

Finally, we found that at all locations, birds attended only a small proportion of the total number of boats in their seascapes:  $30\% \pm 45$  for Kerguelen birds which were significantly

higher than for Crozet birds ( $7\% \pm 24$ ) and for Marion and Amsterdam birds ( $4\% \pm 0.19$ ; Table 1 and Table S1 for test values).

For all four populations, there were no significant correlations between the time spent by birds per  $5 \times 5^\circ$  grid cell (in general, with boats in their seascape, with boats encountered and with boats attended) and between the density of boat (the number of AIS signals) per  $5 \times 5^\circ$  grid cell used by birds. This applied when considering all types of boats as well as fishing boats only (Table 3, Figs. S1 and S2).

## Discussion

Our study clearly indicates strong differences between populations in the time spent attending boats, with different associated exposure to bycatch risks (Fig. 3a). Furthermore, we clearly show that these variations in time spent attending boats are not a simple function of the density of boats in the seascape, as previous methods aimed at assessing bycatch risk have assumed. Indeed, we have shown that using AIS data combined with fine-scale GPS tracking of seabirds can provide a considerably more reliable estimate of exposure to bycatch risks, through the documentation of the actual time birds spend interacting at a fine-scale with different types of declared boats (Fig. 1). Indeed, most previous studies used monthly maps of the number of hooks deployed within aggregated  $5 \times 5^\circ$  cells (around  $560 \times 560$  km in our region) to estimate risks incurred by foraging birds (Clay *et al.*, 2019; Heerah *et al.*, 2019), but here we show that analyses at this scale do not correlate at all with time spent interacting with boats.

Previous studies investigating fine-scale interactions with boats used VMS signals of fishing boats (Torres *et al.*, 2013; Collet, Patrick, & Weimerskirch, 2017b; Clark *et al.*, 2020), but VMS data are only available for declared boats inside EEZs, and are not always available for each fishing sector or country. Here we studied fine-scale seabird – boat interactions over a large oceanic basin covering several EEZs as well as extensive international waters, using AIS rather than VMS data. AIS data also have some limitations such as

**Table 3** Correlations (with p value of Pearson test) between the number of AIS signals (total and for fishing boats only) per 5×5° grid cells and the time spent by birds in same 5×5° grid cell (for a total time, for time with boats in seascape (<100 km), for time with boats in encounter (<30 km) and for time with boats in attendance (<5 km)) for the active months of the different populations of albatrosses

Analyses For 5×5° GRID	Amsterdam (n = 37 cells)		Crozet (n = 63 cells)		Kerguelen (n = 41 cells)		Marion (n = 54 cells)	
	Number of AIS signals (April)	Number of AIS fishery signals (April)	Number of AIS signal (January & February)	Number of AIS fishery signals (January & February)	Number of AIS signals (January & February)	Number of AIS fishery signals (January & February)	Number of AIS signals (February & March)	Number of AIS fishery signals (February & March)
Bird time spent in grid cell	-0.113 (P = 0.52)	-0.113 (P = 0.52)	-0.094 (P = 0.48)	-0.094 (P = 0.48)	-0.039 (P = 0.81)	-0.056 (P = 0.73)	-0.012 (P = 0.94)	-0.012 (P = 0.94)
Bird time spent with boat at 100 km	0.062 (P = 0.72)	0.062 (P = 0.73)	-0.021 (P = 0.87)	-0.021 (P = 0.88)	0.026 (P = 0.87)	0.008 (P = 0.96)	0.199 (P = 0.18)	0.199 (P = 0.19)
Bird time spent in encounter	0.194 (P = 0.27)	0.192 (P = 0.28)	-0.029 (P = 0.83)	-0.029 (P = 0.83)	0.025 (P = 0.88)	0.007 (P = 0.97)	0.164 (P = 0.28)	0.165 (P = 0.28)
Bird time spent in attendance	-0.050 (P = 0.78)	-0.052 (P = 0.77)	-0.038 (P = 0.78)	-0.037 (P = 0.78)	0.018 (P = 0.91)	0.002 (P = 0.99)	-0.014 (P = 0.93)	-0.014 (P = 0.93)

an unknown proportion of boats not continuously using their AIS (Weimerskirch *et al.*, 2020) as its use is not compulsory in international waters. However, to date, AIS data constitute the only source of boat locations at large geographical scales. Although previous studies have used AIS data (e.g. Natale *et al.*, 2015; Winnard *et al.*, 2018; Wong *et al.*, 2018; Burger *et al.*, 2019) to estimate fishing densities, here we provide a standardized comparison of fine-scale exposure to bycatch risk (boat by boat for each bird) on the scale of an ocean basin. Overall, we found that all four study populations spent considerably more time attending fisheries boats within EEZs (most boats using bycatch mitigation measures) than in international waters. On average, birds from all populations spent less than 1h per trip attending declared fishing boats outside EEZs where bycatch mitigation measures are not generally adopted potentially leading to high seabird mortality. Although at least three out of the four study populations are potentially at risk of bycatch from these declared fleets outside EEZs (where no bycatch mitigation measures are required), birds appear to spend limited time attending them. This result could be very different if non-declared boats (without AIS) could also be included. Indeed, illegal, undeclared and unregulated fleets may represent up to 30% of boat encounters for breeding large albatrosses (Weimerskirch *et al.*, 2020). The lack of information on these boats can partly be remedied using new loggers that can detect radar emission of boats up to 5 km away (Weimerskirch *et al.*, 2018). In sectors where fishing vessels use powerful lights to attract target species, satellite images of illumination could be used as an alternative method (Park *et al.*, 2020). However, AIS data provide additional information on boat characteristics and nationality on a global scale, so that more accurate results could be reached by combining them with other methods such as radar detectors (Weimerskirch *et al.*, 2020).

AIS data revealed that the four populations of large albatrosses breeding within the Indian Ocean foraged in very different boat seascapes. Yet, the time spent interacting with fishing boats within or beyond EEZs could not be predicted by the respective boat densities within the foraging ranges of the different populations. Fishing boats in the area mainly fall within two categories: toothfish longline fisheries operating on the edges of subantarctic shelves and tuna longlining fisheries operating in subtropical waters (Corbeau *et al.*, 2019). In addition, many non-fishing boats (cargo, tankers) transit through subtropical waters between Africa, Asia and Australia. Birds from Marion had the least contact with boats, with a large proportion of trips without boat encounters, yet most attended boats were not fishing boats. This can potentially be explained by the limited extent of shelf waters at the Prince Edward islands and the very small scale of the declared toothfish fishery in the region in comparison to Crozet and Kerguelen (Weimerskirch *et al.*, 2020). Furthermore, birds from Marion spent a relatively low proportion of their foraging time in subtropical waters (in contrast to Amsterdam birds). Conversely, Amsterdam birds were found within the densest boat seascape, both in terms of boat density and in terms of fishing boats density. This is of

particular concern for this endangered species with less than 60 pairs breeding annually on Amsterdam Island (Thiebot *et al.*, 2015; Heerah *et al.*, 2019). Yet, birds from Marion and Amsterdam populations eventually spent very similar average amounts of time with declared fishing boats both within or outside EEZs (with different bycatch mitigation measures). In contrast, compared to Marion and Amsterdam populations, Kerguelen birds spent considerably more time with fishing boats and mostly within EEZs with much lower boat densities and Crozet birds appeared to spend more time with fishing boats both outside and within EEZs. The larger productive shelf and EEZ of Kerguelen and the continuous presence of legal boats could explain this specialization of Kerguelen birds for fishing vessels (with mitigations measures and no-mortalities).

Moreover, we have shown that large-scale overlap analyses ( $5 \times 5^\circ$ ) of AIS data were not related to the proxy of fine-scale bycatch risk (Table 3). It is therefore very clear that the density of (fishing) boats within the foraging range does not linearly translate into time spent attending boats. This discrepancy between boat density in the foraging range of seabirds and the actual time birds spent attending fishing boats calls for caution when estimating bycatch risk from large-scale overlap data. AIS data are costly but it may be more easily accessible to researchers than the often confidential and geographically restricted VMS data (Votier *et al.*, 2010) to allow for fine-scale analyses. However, large-scale overlap analyses will still be needed in particular when bird tracking data are available at a lower resolution than that offered by GPS tracking devices (Clay *et al.*, 2019). This may be the case for many studies using GLS devices on non-breeding individuals (juveniles, failed breeders, adults in winter or on sabbatical, etc.) or for small species for which relatively large GPS device deployment could be problematic (Le Corre *et al.*, 2012; Delord *et al.*, 2014). It would thus be useful to understand why a higher boat density does not necessarily translate into more time spent by seabirds attending boats, and under what circumstances this applies, to improve bycatch risk estimation from large-scale data.

Boats may also cause other non-lethal issues beyond bycatch (nutritional and/or dependence issues), especially if they become an important part of birds' time budgets (Fig. 3b) and/or diet. To our knowledge, there are very few studies that have looked at how boats other than fishing boats may impact foraging success and behavior in seabirds. However, it seems that our studied birds spent a low fraction of their foraging time attending them. Of greater concern is the large amount of time Kerguelen birds seem to spend attending the toothfish longline fishery operating around their breeding ground. The nature, quality and amount of food albatrosses can obtain from these toothfish fisheries are unclear considering bycatch mitigation measures that are implemented, especially considering that discards should be released after maceration, and not during fishing operations, limiting the energetic advantage of attending fishing boats (Gremillet *et al.*, 2008). Yet, Kerguelen birds appear to spend considerable time attending fishing boats and to be more dependent on them than the Crozet population.

An important question about bycatch risk is whether the large differences we observe in the time incubating birds spent attending different types of fishing boats across populations may be related to differences in population trends. Amsterdam albatrosses have been increasing since the 1980s at such a high rate suggesting that they suffer limited if any mortality from fisheries (Weimerskirch *et al.*, 1997; Rivalan, Barbraud, Inchausti, & Weimerskirch, 2010). Although they forage in zones with high densities of both fishing and non-fishing boats, birds do not seem to be particularly attracted to fishing boats: the low interaction to boats may explain why this population has been able to increase steadily over the past four years. The three other populations have shown similar trends until about 15 years ago, with a steep decline in the 1970s and early 1980 followed by a partial recovery (Weimerskirch *et al.*, 1997; Nel *et al.*, 2002). Since then, the population on Marion has been increasing, whereas Kerguelen and Crozet populations are stable (Ryan, Jones, Dyer, Upfold, & Crawford, 2009; Weimerskirch *et al.*, 2018). This difference in population dynamics of the wandering albatross populations could be mainly related to the lower encounter and attendance rates of Marion birds compared to Crozet and Kerguelen birds.

Seabirds are one of the animal groups with the largest proportion of threatened species and there has been much effort globally to better understand causative mechanisms behind declining populations for conservation purposes. In this paper, we proposed a simple method for estimating fine-scale interactions between seabirds and boats with AIS (Fig. 1). This method is easily implemented through the combination of seabirds GPS tracks, now routinely collected globally (Burger & Shaffer, 2008; Le Corre *et al.*, 2012), and AIS data, which are readily available (International Maritime Organisation).

Combining AIS and fine-scale tracking data, we provided a more direct and comprehensive assessment to date of bycatch risk for large albatrosses breeding in the Indian Ocean, including for one of the most threatened bird species. We illustrated the pros and cons of using AIS data for such estimations, compared to other existing methods (large-scale overlap analyses and/or use of bird-borne radar detectors). Importantly, we showed that fishing boat density may not be a good proxy to predict time spent attending boats and bycatch risk for specific populations. Our results revealed extensive variations in the time and proportion of foraging time populations spent attending various types of boats, which may cause other non-lethal issues beyond bycatch risks, especially in the Kerguelen population. In particular, we provided evidence that the endangered Amsterdam albatross may not be at a high risk of bycatch despite its overlap with fisheries at a large scale. Thus, future studies investigating bycatch risks should favor when possible the use of fine-scale tracking and fisheries data to be able to provide robust estimates.

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## Authors' contributions

HW conceived the project, AC, JC, FO, HW and PP contributed data and/or did field work and prepared the data, JC merged AIS data to tracking data, AC performed all the other analyses, AC and HW wrote the original paper and all authors commented on earlier drafts.

## Data Availability Statement

Data are available in figshare at <https://doi.org/10.6084/m9.figshare.10289096> (Weimerskirch, Collet, Corbeau, Pajot, Hoarau, Marteau, Filippi, Patrick, et al., 2019).

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## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.