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Gauging the threat: exposure and attraction of sooty albatrosses and white-chinned petrels to fisheries activities in the Southern Indian Ocean

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Bycatch risk assessments typically rely on spatial overlaps between seabirds and fishing vessels but should also consider seabirds' position in the attraction spectrum. Investigating seabird-fishery interactions in relation to habitat use is vital for species-specific risk assessments. To address this, we studied interactions between sooty albatrosses (SA) and white-chinned petrels (WCP) with fisheries. GPS data from 20 SA and 18 WCP individuals from Marion Island were analysed alongside Automatic Identification System-derived boat locations over two breeding seasons. We calculated encounter and attraction rates and correlated them with marine habitat characteristics. SA interactions occurred in deeper, warmer waters compared to their foraging habitat when vessels were absent, with 20% of individuals encountering and only 5% being attracted to boats. In contrast, WCP interactions occurred in shallow, warm South African shelf waters, consistent with their typical foraging habitats, with 72% encountering and 56% attracted to boats. These results highlight the need for continued reinforcement of mitigation measures for WCP. Despite the low attraction rates for SA, ongoing vigilance is required due to their smaller population size, which heightens the potential impact of illegal fisheries. The comparison of species along an attraction spectrum contributes to refining risk assessments and informs species-specific conservation strategies.

Keywords: attraction spectrum, Marion Island, seabird-fishery interactions, sooty albatross, white-chinned petrel.

Introduction

Occupying the upper-trophic level of marine ecosystems, seabirds perform many important ecosystem functions and services, such as the maintenance of food web structure (e.g. Ferretti *et al.*, 2010) and nutrient cycling (Ratnarajah *et al.*, 2018). Because of their trophic position and ability to identifiably respond to changes in climatic conditions and ecosystem dynamics, they have been recognized as climate and ecosystem sentinels (Hazen *et al.*, 2019). Thus, they are not only an important ecosystem component, but also important providers of ecological information useful for conservation. However, a large proportion of seabirds are threatened with extinction (IUCN, 2020), with fisheries mortality being one of the leading causes (Dias *et al.*, 2019).

The relationship between seabirds and fisheries entails competition for the same prey resources (Anderson *et al.*, 2011; Grémillet *et al.*, 2018), and potential seabird fatalities, when the appeal of bait, discards, and offal exposes seabirds to bycatch risk in drift nets, set-nets, trawls, and longlines (Baker *et al.*, 2007; Žydelis *et al.*, 2009; Anderson *et al.*, 2011; Croxall *et al.*, 2012; Žydelis *et al.*, 2013; Lewison *et al.*, 2014; Pott and Wiedenfeld 2017). The outcome of this attraction has several consequences, including reduced foraging efficiency

(Cianchetti-Benedetti *et al.*, 2018), decreased breeding success due to the low nutritional value of discards (Grémillet *et al.*, 2008), fishing gear-related injuries (Berón and Seco Pon 2021), and fishing gear-related mortality (Croxall *et al.*, 2012; Phillips *et al.*, 2016). The previously reported annual bycatch estimates of over 400000 seabirds by gillnet fisheries (Žydelis *et al.*, 2013), between 160000 and 320000 by longline fisheries (Anderson *et al.*, 2011), and an annual average of over 800000 shearwaters for 49 years by drift-nets (Uhlmann *et al.*, 2005), clearly show how fisheries mortality is contributing to the present decline of many seabird species. As such, fisheries interactions pose important present and potential future implications for seabird behaviour, demography, and conservation (Grémillet *et al.*, 2019).

Bycatch risk is governed by the level of attraction to fishing vessels and the time birds spend interacting with fishing activities in their boatscape, which depends on the level of fishing activity within a bird's foraging range. Fishing fleets often operate on a large spatio-temporal scale, which leads to their overlap with seabirds' foraging ranges. This overlap is frequently used to estimate bycatch risk (e.g. Schoombie *et al.*, 2017; Clay *et al.*, 2019; Heerah *et al.*, 2019). However, at a finer scale, during their foraging trips, seabirds often

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perform “Area Restricted Search” (ARS) behaviour in particular areas or habitats, where they reduce speed and increase sinuosity (Kareiva and Odell, 1987; Hill *et al.*, 2000; Corbeau *et al.*, 2019), enhancing the likelihood of encountering prey within these areas (Benhamou, 1992). If boats operate where seabirds perform ARS, encounters and interactions between them will be more likely than if birds and boats target different areas or habitats. Estimating bycatch risk through the level of overlap between ARS behaviour and fishing areas is further complicated because seabirds can also exhibit ARS-like behaviour during fishing boat interactions (Torres *et al.*, 2011; Bodey *et al.*, 2014; Corbeau *et al.*, 2019). For instance, black-browed albatrosses *Thalassarche melanophris*, a ship-following species, has shown strong attraction to fishing boats encountered outside its foraging habitat (Collet *et al.*, 2017a). Moreover, seabirds do not necessarily interact with all boats that enter their detection range (e.g. Collet *et al.*, 2017b). To clearly estimate the risks of bycatch, it is therefore important to assess fine-scale seabird movement data in relation to co-occurring fisheries’ activity data (Votier *et al.*, 2010; Torres *et al.*, 2013; Corbeau *et al.*, 2021a). It is only recently that such data has been made widely available, especially in international waters (Kroodsma *et al.*, 2018; Weimerskirch *et al.*, 2020). As a result, fine-scale bycatch risk estimation is only available for a handful of species and/or areas, and there is still a limited quantitative understanding of the extent of variation in seabird-fisheries interactions among species (Collet *et al.*, 2017a; Corbeau *et al.*, 2021a; Orben *et al.*, 2021).

In the Southern Ocean, the white-chinned petrel (*Procellaria aequinoctialis*, WCP) is generally regarded as strongly attracted to fishing vessels and is often the most abundant species attending fishing vessels and the most numerous in bycatch estimates (Cherel *et al.*, 1996; Nel *et al.*, 2002; Robertson *et al.*, 2006). This is consistent among populations (Weimerskirch *et al.*, 2000; Delord *et al.*, 2005; CCAMLR, 2021). This species—whose extinction risk is categorized as Vulnerable (BirdLife International, 2018a) on the IUCN *Red List of Threatened Species*—is the most abundant among the large petrels and albatrosses attracted by vessels and to date, no study has quantitatively estimated how frequently individual WCP encounter boats or how strongly they are attracted to the boats they encounter. High numbers of WCP behind boats may indeed partly reflect high densities and/or co-occurrence of WCP and boats at sea rather than strong attraction *per se*, but these hypotheses cannot easily be disentangled with onboard or bycatch data only.

Conversely, the sooty albatross (*Phoebastria fusca*, SA) is much more rarely observed flying towards fishing vessels (Griffiths, 1982), and anecdotal onboard observations suggest it may not be strongly attracted to boats. Nonetheless, several breeding population declines have been at least partly attributed to fisheries bycatch mortality (Gales, 1998; Cuthbert and Sommer, 2004; Delord *et al.*, 2005; Rolland *et al.*, 2010; Schoombie *et al.*, 2016) and the species is in danger of extinction (*Endangered*; BirdLife International, 2018b). This means their total world population is low compared to WCP. Like WCP, there is a knowledge gap on individual SA-fishery interactions in terms of large-scale exposure through distributional overlap and strength of behavioural attraction to encountered boats. Presenting bycatch and onboard observation data as total numbers, rather than as proportions of the affected populations, fails to account for the bycatch risk at the individual level. Overlapping large-scale distribution is also insufficient

to quantify fine-scale seabird-fishery interactions that are required to assess bycatch risk (Delord *et al.*, 2010a; Torres *et al.*, 2013; Corbeau *et al.*, 2021a). A fine-scale evaluation is therefore needed to comprehensively determine the extent of interaction between fisheries and these two seabird species. Moreover, examining the distinct behavioural responses and attraction to boats between these two species—one known to follow boats and the other not—may aid in estimating a quantitative “behavioural attraction spectrum” that can be applied to other seabird species worldwide.

Fine-scale analysis of seabird-fishery interactions has previously been performed using data from Vessel Monitoring Systems (VMS) (Votier *et al.*, 2010; Granadeiro *et al.*, 2011; Torres *et al.*, 2011, 2013). However, VMS have a limited geographic range and data are publicly unavailable or otherwise challenging to acquire (Kroodsma *et al.*, 2018; Weimerskirch *et al.*, 2020). Automatic Identification Systems (AIS) are an alternative monitoring system that make information such as boat identity, position, and speed available to those nearby, and is effectively used for navigation to prevent collisions (Kroodsma *et al.*, 2018). This generates a wealth of continuous fine-scale distributional data, which is an improvement on VMS that are mainly used in national EEZ waters. As such, AIS data is optimal for assessing fine-scale interactions with seabirds, as recently demonstrated for wandering albatrosses (*Diomedea exulans*; Weimerskirch *et al.*, 2020).

In this study, we used a combination of seabird GPS tracking and vessel AIS data to investigate the extent of Marion Island-breeding SA and WCP-fishery interactions in the Southern Indian Ocean—to facilitate a better understanding of fishery impacts on their populations. Bird locations and boat locations were spatio-temporally matched to quantify their co-occurrence at 100 (seascape scale), 30 (encounter), and 5 km (attendance). The number of fisheries interactions and attraction to fishing boats were then assessed. Additionally, the habitat associated with fisheries interactions was evaluated in relation to ARS behaviour inferred from seabird tracks when fishing boats were present or absent.

It was hypothesized that both species will interact with fisheries, but SA to a lesser extent as WCP are more often seen in the vicinity of fishing boats (e.g. Cherel *et al.*, 1996; Weimerskirch *et al.*, 2000). A greater level of interaction is expected north of the Subtropical Front (STF; Figure 1) and in shelf waters where fishing activity is high (Phillips *et al.*, 2006; Huang and Liu, 2010).

Methods

Study location

Sample collection was carried out at sub-Antarctic Marion Island (46°52' S; 37°51' E; Figure 1) in the Southern Indian Ocean. The island is situated between the Sub-Antarctic Front to the north and the Antarctic Polar Front to the south (Lutjeharms and Anson, 2008). Ethics approval was granted by the Nelson Mandela University Research Ethics Committee (A14-SCI-ZOO-012). Fieldwork was permitted by the Prince Edward Islands Management Committee.

Study design

SA and WCP breeding at Marion Island were tracked during their incubation period over two breeding seasons. Subsequently, AIS-derived boatscape data and satellite-derived

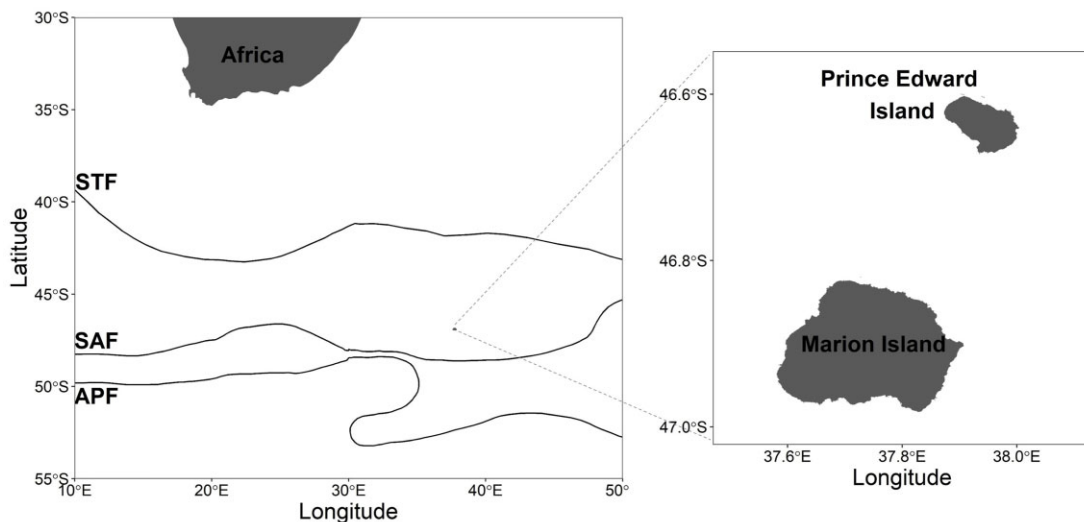


Figure 1. Location of the study site, Marion Island, within the Southern Indian Ocean. STF denotes the Subtropical Front, SAF the Sub-Antarctic Front, and APF the Antarctic Polar Front. Frontal estimations in the map were obtained from Orsi *et al.* (2019).

environmental data (including bathymetry, sea surface temperature, and windspeed) were collected for the period when tracking took place to investigate seabird-fishery interactions.

Bird tracks

GPS loggers were deployed on adult SA (October 2018–January 2019 and October 2019–January 2020) and WCP (November 2018–December 2018 and November 2019–February 2020) to record their at-sea distribution and movement patterns (Supplementary Figure S1).

Birds were caught on their nest and waterproof Tesa tape (Beiersdorf, AG, GmbH, Hamburg, Germany) was used to attach the GPS loggers to their back feathers. Deployments took <15 min to complete. SA were equipped with either I-gotU (Mobile Action, Taiwan) (60 g) or CatLog (22 g) loggers (Perthold Engineering LLC, USA), representing c. 0.8–2% of their mass, and CatLog Gen2 loggers (16 g) were used on WCP, representing less than c. 1.5% of their mass. During the 2018/19 and 2019/20 breeding seasons, GPS locations were recorded every 10 min and 30 min, respectively, for SA, and every 2 h and 1 h, respectively, for WCP.

Boatscape data

AIS data for all declared boats (fishing and non-fishing) operating in the Southern Ocean for the periods between 29/11/2018–31/01/2019 and 24/11/2019–29/02/2020 (160 days) were obtained through the Ocean Sentinel Programme (Weimerskirch *et al.*, 2020). This data includes information on the name, type, nationality, location, and activity of boats.

Fisheries interactions

On-land locations were removed from GPS tracks, which were then divided into trips at sea and interpolated using the R package “crawl” (Johnson *et al.*, 2008; Johnson and London, 2018) with a time step of 20 min for comparability. The GPS data was filtered to match the period for which AIS data was available; GPS data that extended beyond the AIS period was removed. Bird locations from the tracking data

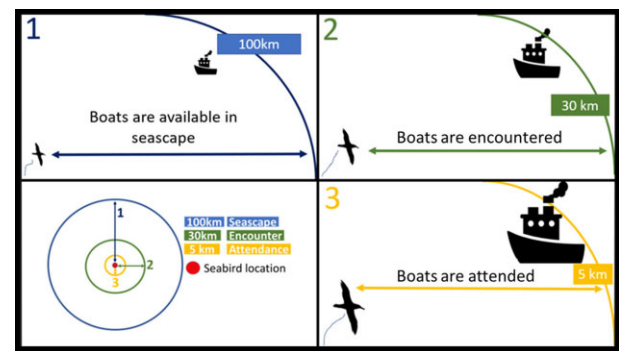


Figure 2. The distance categories used (100, 30, and 5 km) to represent seabird-fishery interaction scenarios. In order of decreasing distance between a seabird location and a boat, a boat within 100 km is available in the seascape (1), a boat within 30 km is encountered (2), and a boat within 5 km is attended (3).

and boat locations from the AIS data were spatio-temporally overlapped following Weimerskirch *et al.* (2020) and Corbeau *et al.* (2021a), generating a dataset from which the number and type of boats within 100, 30, and 5 km of each bird location was computed. These distances are used for different ecological and behavioural interpretations (Figure 2). A distance of 30 km was chosen to characterize encounters because it is the estimated maximum distance at which birds can visually detect boats (Thiebault *et al.*, 2014; Collet *et al.*, 2015; Collet *et al.*, 2017b). The 5 km distance was used to characterize boat attendance because seabirds perform specific foraging behaviours within this proximity of vessels (Collet *et al.*, 2015; Weimerskirch *et al.*, 2020).

Encounter and attendance events were classified as periods when bird locations were within the associated distances (30 km and 5 km) of at least one boat and departed without return for at least 2 h. Birds attracted to fishing boats usually stay within their range for at least a couple of hours (Collet *et al.*, 2017b), allowing the reasonable assumption that a bird leaving an interaction range for >2 h has exited the interaction event.

Environmental data

Bathymetry data from the “ETOPO1 Global Relief Model” was obtained from the National Oceanic and Atmospheric Administration (NOAA) and added to bird tracks using the R package “marmap” (Pante and Simon-Bouhet, 2013) to determine whether bird locations were on the shelf (>2000 m) or oceanic. Bird locations were also categorized as inside or outside an EEZ (shape files from <http://www.marineregions.org>). Bird locations were further categorized into Antarctic, sub-Antarctic, and subtropical waters based on updated estimations of the Antarctic Circumpolar Current fronts (Park *et al.*, 2019). These fronts separate waters with different characteristics (Chapman *et al.*, 2020) and are themselves often important seabird foraging areas (Baduini and Hyrenbach, 2003; Bost *et al.*, 2009). Lastly, hourly sea surface temperature (SST, °C) was added to each bird location (data from <https://www.copernicus.eu>). Foraging habitat was characterized using SST (°C), bathymetry (m), and windspeed (km/h).

Area restricted search

ARS behaviour, which is characterized by low speeds and high turning angles (Kareiva and Odell, 1987), was estimated using a speed filter of <10 km/h and a turning angle filter of >10° based on visually determined thresholds (Supplementary Figure S2). These thresholds were used because procellariiforms cannot sustain straight flights at such low speeds, and water current drift could not explain such high turning angles between successive bird locations when resting on water. Accordingly, these low flight speeds and high turning angles strongly suggest an active intensification of searching over a restricted area. Turning angles were calculated from bird tracks using the R package “adehabitatLT” (Calenge, 2006).

Interaction scenarios

To compare boat and non-boat-related habitat use, four “interaction scenarios” were defined for each bird location based on the presence/absence of ARS behaviour during either an encounter or an attendance event. A fifth, non-interaction scenario, was defined as “natural ARS”, where ARS was conducted in the absence of boats within 30 km of the bird. The R package “dplyr” (Wickham *et al.*, 2023) was used to identify these scenarios by characterizing each location according to its ARS and boat conditions.

Data analysis

The R statistical software version 4.0.0 (R Core Team 2020) was used for all data preparation and analyses.

Both species spent a similar amount of time at sea during the AIS period (256 and 219 days), enabling a reasonable comparison. Given that some trips were rendered incomplete after filtering the GPS data to match the AIS period, events rather than trips were compared between species. Comparisons of the number of boats available per distance category, interaction scenarios, proportions, ocean/shelf use, and water masses (Antarctic, sub-Antarctic, or subtropical) used were performed using Kruskal-Wallis tests due to the non-normality of the residual distributions of ANOVA (verified using Shapiro-Wilk normality tests) and low sample size (Jenkins and Quintana-Ascencio, 2020). No pairwise tests were run when one side had less than $n = 4$.

Linear mixed-effects models (R package “lme4”; Bates *et al.*, 2015) and “lmerTest” (Kuznetsova *et al.*, 2017) were used to assess the relationship between environmental variables and the various interaction scenarios. Individual identities were used as random intercepts to take into account repeated measurements per individual (Zuur *et al.*, 2009). Following this, post-hoc tests (R package “emmeans”; Lenth, 2021) were conducted to identify where significant differences occurred between the groups compared.

Results

A total of 6149 at-sea hours, equivalent to about 256 days, were recorded from 20 SA, and 5257 h, equivalent to about 219 days, from 18 WCP. SA travelled a mean maximum distance of 1007 ± 389 km from their nests, with trips lasting 307 ± 163 h during which time they conducted looping trips to and from the north of the Subtropical Front (Figure 3). WCP travelled further than SA ($1925 \text{ km} \pm 509$), spent 292 ± 164 h at sea and mostly commuted to and from the South African shelf (Figure 3).

Boatscape description

For SA, 90 different boats were identified within 100 km of bird locations, of which 17 were classified as fishing boats. For WCP, 510 different boats were identified within 100 km of their locations. Of these boats, 157 were fishing boats and boat activity was mostly found north of 40°S (Figure 3).

Comparison of interactions with boats at the population level

The average duration with at least one fishing boat within 100 km was not significantly different between species (Kruskal-Wallis test, $X^2 = 2.63$, $p = 0.10$), unlike the average duration with a fishing boat within 30 km, which was significantly shorter for SA (Kruskal-Wallis test, $X^2 = 10.05$, $p < 0.05$; Table 1). Only one SA attended a fishing boat, and it spent a total of 30 min in attendance, compared to the 10 WCP that attended fishing boats and spent 15.75 ± 11.46 h on average. Thus, SA virtually spent no time attending fishing vessels (0.008% of their time at sea), whereas WCP spent 3.3% of their time at sea in attendance. For non-fishing boats, the average duration with a boat within 100 km was significantly higher for SA (Kruskal-Wallis test, $X^2 = 5.20$, $p = 0.02$), in contrast to the duration with a boat within 30 km (Kruskal-Wallis test, $X^2 = 1.68$, $p = 0.19$) and 5 km (Kruskal-Wallis test, $X^2 = 1.23$, $p = 0.27$) that were not significantly different between species (Table 1).

The ratio of the number of locations with a boat in the seascape relative to the number with a boat attended was much higher for WCP (Kruskal-Wallis test, $X^2 = 87.13$, $p < 2.2 \times 10^{-16}$) (Table 2). Likewise, the ratios between locations with fishing boats at 5 and 30 km, as well as between 30 and 100 km, differed significantly between the two species, with SA being much lower in all comparisons (Table 2, Supplementary Table S1 for test values).

Comparison of parameters between individuals that encountered fisheries

Out of 20 SA individuals, 20% encountered fishing boats, compared to 72% of 18 WCP (Table 3). The total time spent at sea by these individuals was not significantly different

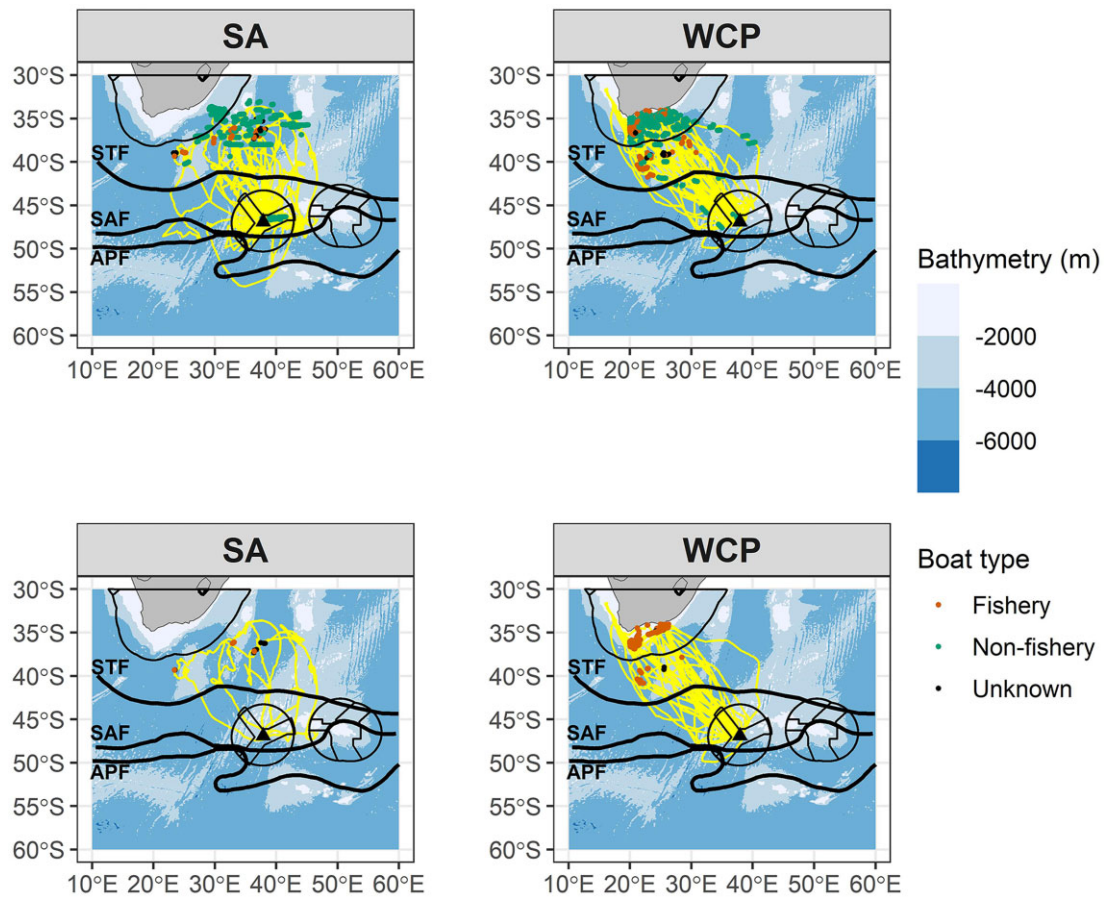


Figure 3. Tracks of SA and WCP from Marion Island, with the positions of all boats available within the seascape (100 km radius from each bird location; above, all tracks shown), and boats encountered (<30 km; below, only the tracks of individuals with encounters) categorized by boat type. STF denotes the Subtropical Front, SAF the Sub-Antarctic Front, and APF the Antarctic Polar Front. The circular shapes are Economic Exclusion Zones (EEZs), and the polygons within them are Marine Protected Areas (MPAs). The position of Marion Island is represented by the triangle. Frontal estimations in the map are from Orsi *et al.* (2019).

Table 1. The mean and standard deviation of hours with boats in seascape (100 km), detection range (30 km), and attraction range (5 km), per species.

Species	Fishing boats		Non-fishing boats	
	SA	WCP	SA	WCP
Available in seascape (100 km)	6.79 ± 4.53 (N = 6)	27.30 ± 23.55 (N = 16)	17.90 ± 10.95 (N = 13)	8.07 ± 5.69 (N = 15)
Encountered (30 km)	1.00 ± 0.35 (N = 4)	24.50 ± 21.91 (N = 13)	3.50 ± 2.07 (N = 8)	2.20 ± 2.00 (N = 15)
Attended (5 km)	0.50 (N = 1)	15.75 ± 11.46 (N = 10)	0.45 ± 0.28 (N = 5)	2.06 ± 3.43 (N = 13)

Based on Kruskal-Wallis test results, light grey is significant ($p < 0.05$), dark grey is not significant ($p > 0.05$), and white is when the sample size was too low for a statistical test. *N* is the number of individuals represented.

Table 2. Ratios of fishing boats encountered and attracted towards relative to availability, per location, and individual.

	SA (<i>n</i> = 15318 locations)	WCP (<i>n</i> = 8306 locations)
	Mean ± SD	Mean ± SD
Ratio 5 km/100 km	0.005 ± 0.04	0.06 ± 0.11
Ratio 5 km/30 km	0.09 ± 0.27	0.24 ± 0.30
Ratio 30 km/100 km	0.08 ± 0.25	0.22 ± 0.21

Ratios range from 0 to 1. Based on Kruskal-Wallis test results, all cases of significance ($p < 0.05$) are indicated in light grey.

between species (Table 3), but the maximum distance travelled by SA (1264.1 km ± 131.7) was significantly lower than WCP (1828.1 km ± 174.7; Table 3).

The number of fishing boat encounter and attendance events by these individuals was significantly lower for SA than

WCP (Table 3). WCP individuals also spent more time in encounter and attendance of fishing boats than SA (Table 3).

WCP with fishing boat encounters, encountered more fishing boats relative to non-fishing boats than SA (Table 3). The proportion of fishing boats attended after being encountered,

Table 3. Mean and standard deviation of parameters for individuals that encountered fisheries (Figure 3), and Kruskal-Wallis test values.

Species (Number of individuals)	SA (N = 4)	WCP (N = 13)	Chi-squared value	<i>p</i> value
Percentage of individuals with fisheries encounters	20% (N = 4/20)	72% (N = 13/18)		
Total at-sea duration (days)	25.13 ± 14.31	35.92 ± 27.45	0.13	0.72
Maximum distance from the colony (km)	1264.1 ± 131.7	1828.1 ± 174.7	8.01	<0.005
Number of fishing boat attendances	0.25	16.9 ± 14.4	5.80	<0.02
Time in attendance with fishing boats (hours)	0.5 (N = 1)	3.95 ± 3.37	NA	NA
Number of encounters with fishing boats	1 ± 0	7.9 ± 10	5.52	<0.02
Time in encounter with fishing boats (hours)	1.21 ± 0.33	23.9 ± 39.3	3.77	0.05
Ratio of encounters in EEZ	0.17 ± 0.29	0.81 ± 0.22	1.64	0.2
Proportions of encounters, attendances, and attraction				
Proportion of encounters with fishing boats (locations 30 km fishing/locations 30 km all boats)	0.19 ± 0.37	0.63 ± 0.30	81.05	<2.2e-16
Proportion of non-fishing boats attended (5 km after being encountered (30 km) (locations 5 km non-fishing/locations 30 km non-fishing)	0.06 ± 0.27	0.03 ± 0.11	2.82	0.09
Proportion of fishing boats attended (5 km after being encountered (30 km) (locations 5 km fishing/locations 30 km fishing)	0.09 ± 0.27	0.24 ± 0.30	7.74	<0.006
Proportion of fishing boats encountered (30 km) relative to their availability (100 km) (locations 30 km fishing/locations 100 km fishing)	0.09 ± 0.27	0.22 ± 0.21	121.71	<i>p</i> < 2.2e-16
Proportion of non-fishing boats encountered relative to their availability (100 km) (locations 30 km non-fishing/locations 100 non-fishing)	0.09 ± 0.26	0.03 ± 0.11	0.02	0.88
Waters and ocean/shelf use				
Ratio in Antarctic waters	0.02	0.00	NA	NA
Ratio in sub-Antarctic waters	0.21	0.03	6.67	0.009
Ratio in subtropical waters	0.77	0.97	6.49	0.01
Ratio on shelf	0.04	0.80	7.16	<0.008
Ratio in oceanic waters	0.96	0.20	8.47	<0.004

NA represents when the sample size was too low for a statistical test, and italicized *p*-values indicate a significant difference.

and the proportion of fishing boats encountered relative to their availability in the seascape were also significantly higher for WCP. The only non-significant differences between the two species were the proportion of non-fishing boats encountered relative to availability and of non-fishing boats attracted to after encounter (Table 3).

Habitat selection

SA that encountered fisheries spent less time foraging over shelf waters and therefore more time in oceanic waters, compared to WCP (Table 3 and Supplementary Table S2 for test values). These SA spent more of their time in subtropical waters than sub-Antarctic waters, and a negligible amount in Antarctic waters (Table 3). WCP also spent most of their time in subtropical waters, and minimal time in Antarctic waters (Table 3). Between species, SA spent significantly more time in sub-Antarctic waters, and WCP spent significantly more time in subtropical waters (Table 3 and Supplementary Table S2 for test values). The ratio of encounters within EEZs also did not differ significantly between species but was 80% lower for SA (Table 3 and Supplementary Table S2 for test values).

There were very few individuals and locations for SA with boat interaction scenarios, and most locations were in scenarios without ARS, in contrast to WCP. Overall, the ARS of both species—when no vessels were present—occurred in significantly warmer waters than their fisheries interactions (SA: $z = -4.08$, $p < 0.05$; WCP: $z = 13.2$, $p < 0.0001$). For SA, bathymetry and windspeed were not significantly different between non-boat-associated ARS and boat interactions (Supplementary Table S2 for test values; Figure 4).

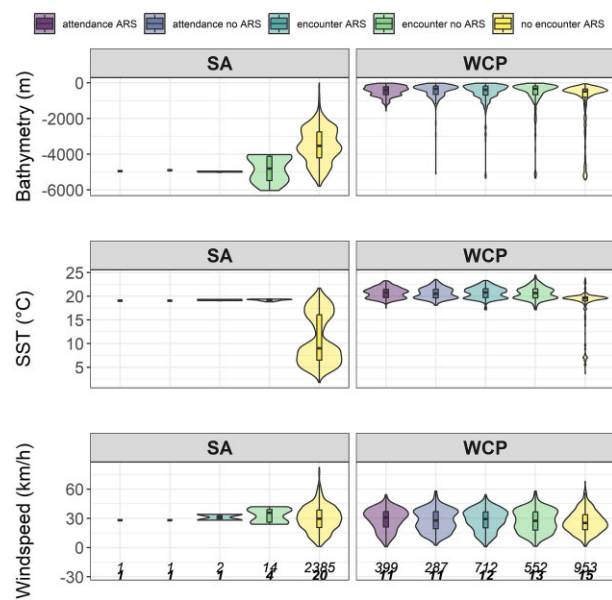


Figure 4. Violin plots showing values of the habitat—bathymetry, SST, and windspeed—of ARS during the five interaction scenarios for SA and WCP breeding on Marion Island. The numbers in italics (above) are the number of locations per scenario, and the numbers in bold (below) are the number of individuals.

Compared to their ARS without boats present, WCP boat-associated ARS occurred in significantly shallower waters ($z = 13.67$, $p < 0.0001$) and higher windspeed, which was

marginally non-significant ($z = 3.41$, $p = 0.051$). Additionally, the SST and bathymetry of WCP interactions without ARS behaviour were higher than their non-boat-associated ARS (Supplementary Table S2 for test values; Figure 4). Both species performed ARS over a wide geographical range, but WCP was more concentrated over shelf waters (Supplementary Figure S1).

For both species, there were no significant differences between the habitat of boat-associated ARS and where boats were encountered but no ARS was performed (Supplementary Table S2 for test values; Figure 4).

Discussion

This study showed a distinct contrast in the presence of boats within the foraging range, number of encounters, and subsequent boat attraction of incubating SA and WCP breeding on Marion Island. SA had lower fishing boat encounters and attractions. Differences in boat availability and encounters between the two species were largely based on them using different foraging habitats. When the habitat where birds encountered boats differed from the non-encounter foraging habitat, the WCP, which is more attracted to boats, still exhibited ARS behaviour in the vicinity of fishing vessels. By comparing these two species with varying degrees of attraction to boats, our findings contribute to a better understanding of the behavioural attraction spectrum in seabirds and inform future conservation efforts.

Foraging range and exposure to boats

The location of encounters is important because bycatch risk is generally higher in open waters where tuna and Patagonian toothfish (*Dissostichus eleginoides*) longliners may not employ the mitigation measures that are required in national shelf waters within the EEZ (FAO, 2018). Although SA mainly foraged in oceanic subtropical open waters that tuna longline boats are presumed to frequent (Huang and Liu, 2010), they did not have many boats available within their seascape, leading to very few encounters. Mention must be made of the possible underestimation of this boatscape due to the inability to account for illegal, unreported, and unregulated (IUU) fishing that is occurring (CCAMLR, 2021; Park *et al.*, 2020; Weimerskirch *et al.*, 2020; Supplementary Figure S3). In contrast, WCP which mainly foraged over subtropical shelf waters where trawl, purse seine, and longline fisheries operate (FAO, 2018), had a higher number of boats within their seascape, followed by many encounters. For both species, the movement from 100 km to 30 km of fishing boats is likely attributed to their use of the same foraging habitat because they are unaware of boats' presence at that distance (Thiebault *et al.*, 2014; Collet *et al.*, 2015; Collet *et al.*, 2017b). As such, foraging distribution played the primary role in determining both the availability of boats within the seascape and the probability of availability leading to encounter.

Boat attraction and foraging habitat selection

Given that foraging distribution influences the available boatscape, which in turn affects the likelihood of encounters, it is crucial to investigate how seabirds respond to these encounters and identify the underlying factors driving their behaviour. SA showed low boat attraction and spent considerably more time within encounter distance than attendance

distance. Similarly, early accounts of SA responses to boats reported more individuals being further from (30–100 km) than closer to (0–30 km) boats and a tendency to fly past them (e.g. Griffiths, 1982). This, in addition to SA not performing searching behaviour when the SST of an encounter was different from where they normally engage in ARS, suggests higher interest in favourable habitats rather than fishing activity.

Based on our results, we estimate that 1 in 20 SA individuals interact with a fishing boat and are at risk of bycatch over a period of 160 days. Then, for a population of 1838 breeding pairs (Schoombie *et al.*, 2016), this translates to a predicted daily bycatch risk rate of 1.15 individuals per day. The contribution of bycatch mortality to the previous Marion Island population decline (Schoombie *et al.*, 2016) is therefore possible. Despite the bycatch risk, the tendency for birds within the population to be attracted to boats continues to persist, indicating an ongoing issue with bycatch mortality. It is, however, important to note that our sampling was limited to the incubation period. Attraction may be higher during brooding and chick-rearing due to the increased energetic requirement of parenting chicks. Reduced natural food availability, and periods of higher energetic requirements, are additional factors that could influence seabirds to opt for high-risk choices, such as approaching boats, in search of food (Bateson, 2002).

As expected, WCP was more likely to attend fishing boats after an encounter compared to SA. This species is well known for being attracted to and following boats (Cherel *et al.*, 1996; Weimerskirch *et al.*, 2000; Delord *et al.*, 2010b), and this is supported by them spending more time within attendance distance than encounter distance. Arriving at a foraging habitat and proceeding to target the fishing boats present there strongly implies attraction to fishing activity regardless of the specific characteristics of the habitat itself. Abundance trends for the WCP Marion Island population have not been recently updated but the last population estimate was 24000 breeding pairs (Ryan *et al.*, 2012), which is much higher than the sympatric SA population size (1838 breeding pairs, Schoombie *et al.*, 2016). This illustrates how the higher bycatch estimates of WCP compared to SA in literature can be due to both WCP being more abundant and having a higher attraction to boats.

Determinants of attraction

Seabirds and fisheries might both target the same foraging habitat, resulting in encounters. However, a seabird's behaviour during an encounter determines if the interaction is accidental or intentional. Intentional encounters involve seabirds attending boats due to their attraction towards them after detection. A significant behavioural indicator of seabird attraction to boats would be a seabird returning to a location of a previously encountered boat (Collet and Weimerskirch, 2020).

Given the bycatch risk associated with this attraction, it is crucial to comprehend the factors influencing the varying likelihood of seabirds moving towards a fishing boat. Larger, more dominant, and generalist species are intuitively expected to have a higher attraction to anthropogenic food sources (Bicknell *et al.*, 2013; Corbeau *et al.*, 2021b). However, smaller and less generalist species have been shown to be more attracted to boats than larger counterparts (Collet *et al.*, 2017a),

elucidating how size and diet may play more secondary rather than primary roles in attraction. Logically, the more specialized a diet is, the lower the chances of being attracted to a non-preferred food source. Both SA and WCP are known to feed on cephalopods and fish (Cooper and Klages, 1995; Cherel and Klages, 1998; Connan *et al.*, 2007; Croxall *et al.*, 2009; Connan *et al.*, 2014), with SA also feeding on carrion (Ridoux, 1994) and WCP on Antarctic krill (Croxall *et al.*, 2009). Thus, the two species both have varied diets and could be expected to exhibit similar attraction to the food available at fishing boats. Indeed, the two species have been bycaught by the same fishing fleets (Gales *et al.*, 1998; Huang and Liu, 2010), showing that from a dietary perspective, food sources at fishing boats are desirable to them. Still, a higher proportion of WCP individuals are attracted to fishing boats.

The influence of seabird body size on boat attraction is related to the presence or absence of diving ability and the consequent ability to be competitive within the seabird aggregation (Zhou *et al.*, 2019). Diving species, whether large or small, can catch sinking bait and therefore forage successfully unless caught in fishing gear (Nel *et al.*, 2002). However, for non-diving species, which normally scavenge for prey at the surface, large size increases competitive ability to acquire space and prey. SA is a medium-sized, surface-feeding seabird that is larger than the proficient diving WCP. Although SA may be less efficient within a seabird aggregation at a boat compared to larger seabirds (e.g. wandering albatross), their presence in bycatch shows that some individuals are still attracted. Thus, once again, both species satisfy a requirement of boat attraction.

Considering diet, physical attributes, and foraging modes, many seabirds should be attracted to fishing boats, and based on onboard observations and bycatch estimates, many are (Anderson *et al.*, 2011; Żydelis *et al.*, 2013; Dias *et al.*, 2019). However, as shown in several studies, the extent of attraction varies substantially between species and individuals (e.g. Collet *et al.*, 2017a; Corbeau *et al.*, 2021a; Corbeau *et al.*, 2021b). Even after fisheries have reduced natural prey, a preference for switching prey rather than attending fisheries for discards has been observed (Grémillet *et al.*, 2019). Thus, while prey scarcity can lead to fishery attraction (Tew Kai *et al.*, 2013) with detrimental consequences (Grémillet *et al.*, 2008), it may not necessarily result in it.

A similarity between the most ship-attracted species, WCP and the black-browed albatross is their foraging over productive shelf waters (Cherel and Weimerskirch, 1995; Berrow *et al.*, 2000; Huln, 2002; Phillips *et al.*, 2006; Wakefield *et al.*, 2011, 2012). This has, and continues to, expose them to a higher overlap with fishing activity (e.g. Clay *et al.*, 2019), even though they do not depend on it for subsistence. The WCP population in this study has presumably been commuting to and foraging over the south African shelf since before the advent of fishing activity there (early 1960s; Cooper and Ryan, 2005). Their subsequent and relatively prolonged exposure to fishing activity could be a possible explanation for their strong behavioural attraction to fishing boats. This could be a case of habituation initiated by co-occurrence in a productive environment and maintained by the competitive ability to obtain predictable anthropogenic food sources. Thus, the behavioural differences observed between species imply a relationship between exposure to boats and the development of boat attraction.

Conservation implications

There are several approaches available for studying seabird-fisheries interactions (Le Bot *et al.*, 2018) and two were combined in this study, identifying areas of encounter and analysing behaviour at a fine scale. This study demonstrates the value of quantifying the boatscape and individual fine-scale boat attraction of seabird species to provide an accurate estimation of fisheries interactions and their associated risks. By comparing different seabird species, the study has demonstrated the significance of assessing relative risks. The results support the need to minimize encounter chances between fishing boats and seabirds, to limit the potential development of strong attraction where it has not yet occurred. In addition to marine protected areas, many mitigation measures are in place (Croxall, 2008; Delord *et al.*, 2010b; Anderson *et al.*, 2011; Maree *et al.*, 2014; FAO, 2018) with room for improvement in ensuring the fishing activity occurring at any time is responsibly permitted. Effective mitigation in the form of streamed and weighted lines was able to reduce longline bycatch mortality significantly, including in the French EEZ around Crozet and Kerguelen (Delord *et al.*, 2010b), where WCP mortality was previously high and impacting on population growth (Delord *et al.*, 2005; Barbraud *et al.*, 2008, 2009). This shows the stark contrast between the effect of fishing activity with and without mitigation measures. Overlapping use of the same fine-scale habitat with unmitigated fisheries could lead to a consequent change in behaviour, which inherently increases the chance of mortality. This would be detrimental for large, long-lived species whose populations are especially vulnerable to increases in adult mortality (Hall *et al.*, 2000; Lewison *et al.*, 2004).

The comparison between SA and WCP has shown that SA have lower exposure and attraction to the fishing boats they encountered. Nonetheless, due to the SA population being smaller, the current level of attraction may still qualify fisheries as a threat. Additionally, non-breeding SA utilize sub-tropical waters (Schoombie *et al.*, 2021), where encounters were highest. Thus, non-breeding adults have possibly higher exposure to fishing activity and bycatch risk than breeding SA. Therefore, management decisions should consider not only the risks to a particular species but also the differences in risk between species to ensure the protection of vulnerable populations.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

Author contributions were as follows: conceptualization—PP and FO; data curation—DZK, AC, JC, AP, SB, and FO; methodology—JC, AC, and HW; investigation and formal analysis—SB and FO; visualization—SB; writing of the

original draft—SB; review and editing—PP, FO, SB, JC, AC, and HW; supervision—PP and FO.

Conflict of interest

The authors have no conflicts of interest to declare.

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Data availability

The GPS data underlying this article can be requested from Pierre Pistorius (Pierre.Pistorius@mandela.ac.za) and the boat data can be requested from Henri Weimerskirch (henri.weimerskirch@cebc.cnrs.fr).

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