



# Differences in foraging habitat result in contrasting fisheries interactions in two albatross populations

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**ABSTRACT:** Albatrosses attend fishing boats to feed on fishing discards but are often at risk of accidental bycatch. To examine whether populations (same species) and sexes differ in their overlap with fisheries due to differences in habitat use, we combined the use of recently developed loggers equipped with GPS and boat radar detectors with Automatic Identification System (AIS) data. Our study indicates that incubating wandering albatrosses *Diomedea exulans* from Crozet and Kerguelen foraged in different habitats although the duration of trips was similar. Both female and male Kerguelen birds took advantage of the large and productive surrounding shelf, whereas Crozet birds used the small shelf around the islands to a lesser extent. In Crozet, there was segregation between males and females, the latter favouring deeper and warmer waters. The 2 strategies of habitat use led to different overlap and attraction to boats, with Kerguelen birds encountering and attending boats for longer and at closer proximity to the colony than Crozet birds. Crozet females encountered boats at greater distances from the colony than males. Because of their different habitat use and foraging outside exclusive economic zones (EEZ) and further from the colony, Crozet birds attended more non-declared boats (without AIS) than Kerguelen birds. Albatrosses were more attracted by fisheries than cargo vessels and were especially attracted by fishing discards that led them to attend vessels for longer periods for both sexes and populations. The differences found between populations and individuals in terms of habitat specialization and encounter rate of fisheries should be considered for future assessments of risk of bycatch.

**KEY WORDS:** Boat attraction · Fisheries · Fisheries discards · *Diomedea exulans* · Crozet · Kerguelen

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## 1. INTRODUCTION

Fisheries are operating over the world oceans, affecting the long-term sustainability of many fish stocks (Pauly et al. 2002). Non-declared and illegal fisheries have a significant impact on marine ecosystems which is difficult to estimate (Weimerskirch et al. 2020). In addition to the impact on fish stocks, legal and illegal fisheries impact marine ecosystems through the bycatch of non-target species such as sharks, sea turtles or seabirds (Finkbeiner et al. 2011,

Croxall et al. 2012, Worm et al. 2013, Lewison et al. 2014, Gianuca et al. 2017). Among seabirds, albatrosses are one of the most threatened groups, mainly because of bycatch in longline fisheries (Votier et al. 2004, Delord et al. 2005, Anderson et al. 2011, Croxall et al. 2012, Phillips et al. 2016). Albatrosses have been attracted to boats for centuries, and over the last decades they have attended fishing boats in large numbers to feed on fishing discards, but also on baits of longlines where they can be drowned (Weimerskirch et al. 1997a, Delord et al.

2005, Anderson et al. 2011). This accidental mortality due to fisheries is considered to be the major cause of decline for many albatross populations (Paleczny et al. 2015, Weimerskirch et al. 2018a).

The difference in demographic trends observed between species (Weimerskirch et al. 2018a) and populations of the same species (e.g. between the Indian and Atlantic Oceans; Ryan et al. 2009, Pardo et al. 2017) could be due to a difference in susceptibility to bycatch. The latter could be explained either by differences in overlap between fisheries and the natural foraging habitat of albatrosses (Clay et al. 2019, Heerah et al. 2019) or by differences in the level of attraction to boats (Collet et al. 2017), or both. It is therefore important to consider the potential variations in the foraging habitats used by different populations and their overlap with fisheries to better assess their susceptibility to bycatch. Over 25 yr, measures to reduce incidental mortality of albatrosses and petrels (e.g. night setting of line, line weighting, bird-scaring devices) have been progressively implemented in the demersal fisheries in the economic exclusive zones (EEZ) of the subantarctic islands, leading to reduced mortality (Weimerskirch et al. 2018a). In addition to reduced bycatch risk, it has been recommended for 20 yr that fishing discards are not released during longline setting in the subantarctic zone (Waugh et al. 2008). Instead, they should be kept onboard and only later released between fishing operations. Very little is known about the role of such fishing discard practices in the attraction of albatrosses to fishing boats. Although it is likely that the greatest factor is the fishing practices and mitigation measures employed by the fisheries, differences in attendance and attraction between populations and species could be an important factor explaining risks of bycatch.

Wandering albatrosses are large seabirds, with a strong sexual dimorphism, that are attracted in large numbers by fishing vessels (Weimerskirch et al. 2020). In the Indian Ocean, they favour shelf edge habitats and seamounts (Louzao et al. 2011) and, to a lesser extent, oceanic waters. They are potentially in contact with 2 types of fisheries that can put them at risk of bycatch. Pelagic longline fisheries for tuna operate in subtropical international oceanic waters, and do not use mitigation measures. Demersal longline fisheries for Patagonia toothfish *Dissostichus eleginoides* operate over shelf edges in subantarctic waters, mainly within the EEZ around subantarctic islands, where mitigation measures are compulsory for licensed vessels (Waugh et al. 2008).

Populations breeding on 2 archipelagos of the Indian Ocean—Crozet and Kerguelen (separated from each other by 1300 km)—have contrasting surrounding habitats. The Kerguelen Islands are surrounded by a vast shelf (1 310 000 km<sup>2</sup>), whereas the Crozet Islands sit within a small-sized shelf (37 000 km<sup>2</sup>).

The 2 populations, although genetically very close (Milot et al. 2007), have contrasting spatial distributions and strategies during migration: Kerguelen birds migrate to distant shelf areas in the Pacific, whereas Crozet birds stay in oceanic waters in the Indian Ocean (Weimerskirch et al. 2015). Little is known about the foraging movements of Kerguelen birds during the breeding season, in contrast with the better-studied Crozet birds (Weimerskirch et al. 2015). In Crozet, breeding birds forage over a mix of oceanic and shelf waters (Weimerskirch et al. 2014). Crozet birds overlap with fisheries over shelf areas as well as over oceanic waters (Weimerskirch et al. 2018b, Corbeau et al. 2019) and they are strongly attracted by Patagonian toothfish longliners operating over shelf edges (Collet et al. 2017). Until very recently, no studies had been performed on these behaviours among Kerguelen birds.

Here, the aim of the study was to (1) compare the foraging habitats of the 2 populations during the breeding season, (2) compare the overlap with fisheries between the 2 populations and their attraction to boats, especially fishing boats (including non-declared and illegal boats), and (3) estimate the role of fishing discards in the attraction of birds to fishing boats and determine whether this attraction provided benefits in terms of breeding success. We used loggers with a GPS and a boat radar detector (Weimerskirch et al. 2018b) along with Automatic Identification System (AIS) data from all declared boats in the studied area (Weimerskirch et al. 2020). In addition, we used data on release of fishing discards from 7 declared French longliners operating around the Crozet and Kerguelen Archipelagos during the study period. In our analyses, we further controlled for suspected factors affecting attraction to boats, such as competition due to sexual size dimorphism (Weimerskirch et al. 2014), fishing practices (Collet et al. 2017) or fishing discards presence (Cherel et al. 1996), and how they could vary between the 2 populations.

Wandering albatrosses have significant sexual dimorphism with noticeably larger body size among males that coincides with different use of habitats (Weimerskirch et al. 2014, Pereira et al. 2018). These differences in space use might also translate into differences in overlap with fisheries. However, a previ-

ous study showed no differences in the attraction to longline boats on the shelf around the breeding grounds between males and females in the Crozet population (Collet et al. 2017).

In this study, we compared the foraging movements and overlap with fishing boats (declared and non-declared or illegal) of breeding Kerguelen and Crozet wandering albatrosses. Those 2 populations follow the same demographic trend (Weimerskirch et al. 2018a) although the colonies are surrounded by very different habitats. To compare the habitat use, foraging strategies and interactions with boats between these 2 populations, we tested whether differences in interactions with boats were attributable to differences in foraging habitats and/or to differences in behavioural responses to boats: either differences in attraction of birds to boats and/or in time spent with boats encountered once attracted. We further controlled for suspected factors of attraction to boats such as competition due to sexual size dimorphism (Weimerskirch et al. 2014), fishing practices (Collet et al. 2017), or presence of fishing discards (Cherel et al. 1996) and how they could vary between the 2 populations. To reduce bycatch risk, it is recommended that fishing discards are not released during longline setting in the subantarctic zone (Waugh et al. 2008). Instead, they should be kept onboard and only later released between fishing operations. Very little is known about the role of such fishing discard practices in the attraction of albatrosses to fishing boats.

To achieve these aims and study the overlap between albatrosses and fisheries, including non-declared fisheries, we combined the use of recently developed loggers equipped with a GPS and boat radar detectors (Weimerskirch et al. 2018b) with AIS data from all declared boats in the study area (Weimerskirch et al. 2020). In addition, we used original data of the release of fishing discards from 7 declared French longliners operating around the Crozet and Kerguelen Islands during the study period.

## 2. MATERIALS AND METHODS

We performed all analyses using the R software and environment (v 3.5.2; R Core Team 2020)

### 2.1. Fieldwork

Fieldwork was carried out in the Crozet and Kerguelen Archipelagos, Southern Indian Ocean, be-

tween January and April 2019 (see details of the program in Weimerskirch et al. 2020). Wandering albatrosses have been studied for 60 and 25 yr at Crozet and Kerguelen, respectively. The sex and breeding success (defined as flight of the chick during the breeding cycle in 2019) of individuals were derived from these long-term studies (Weimerskirch et al. 2018a).

### 2.2. Loggers

Centurion loggers (65 g) recorded GPS locations approximately every 2 min and recorded radar emissions every 5 min of every boat at less than 5 km for 1 min (all logger details are in Weimerskirch et al. 2020). Loggers were deployed on incubating birds for 1 or 2 successive foraging trips. The loggers were attached to the back feathers with Tesa® tape, and represented between 0.5 and 0.85% of the body mass of wandering albatrosses, much less than the maximum 3% recommended for loggers attached to flying seabirds (Phillips et al. 2003). The deployment procedures and logger sizes are similar to those employed in previous studies that showed no negative effects on trip duration or breeding success (Weimerskirch et al. 1995, Barbraud & Weimerskirch 2012).

### 2.3. Albatross and boats dataset

We deployed loggers on 69 incubating wandering albatrosses: 45 at Crozet (24 females and 21 males) and 24 at Kerguelen (10 females and 14 males). We obtained 71 complete trips (48 trips from 44 individuals at Crozet and 23 trips from 21 individuals at Kerguelen; 1 logger failed to record trips, and 3 incomplete trips, due to battery issues, were removed; see Table 1).

All the data were speed filtered ( $150 \text{ km h}^{-1}$ ) and tracks were divided by trips (removing locations on land). In order to link boat presence and individual GPS tracks, we followed the procedure described by Weimerskirch et al. (2020) using (1) the radar detection recorded on the centurion logger and (2) cross-matching it with AIS. AIS data provide the identification, name, nationality, type of boat (fishery or cargo mainly), location and activity for all declared fishing and non-fishing boats in the Southern Indian Ocean. AIS data were spatio-temporally matched with bird-borne GPS and radar detection data to produce a dataset in which 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 30 and 5 km from birds. The presence/absence of declared or non-declared boats within a range of 5 km was determined from the radar detectors (Weimerskirch et al. 2018b), a boat is considered non-declared (and illegal inside the EEZ, where AIS is required) when radar detector receives a signal without AIS within 5 km.

These different radius distances from birds were used to characterise the 'boat encountered' (bird tracked within 30 km from a boat with AIS), the 'boats attended' (bird within 5 km from a boat with AIS) and the 'radar events' (boats detected by radar detector). The 30 km threshold chosen for encounters was the distance within which an albatross can visually detect a boat (Collet et al. 2015, Pirotta et al. 2018). The 5 km threshold is close to the distance at which albatrosses have been seen to engage in specific foraging behaviour associated with vessels (Collet et al. 2015) and is used to facilitate comparisons with studies using embarked radar detectors (included in the loggers) with a detection range of 5 km (Weimerskirch et al. 2018b, 2020, Corbeau et al. 2019). We defined 'events' (encounter, attendance and radar events) as periods of consecutive bird locations (with time gaps of less than 2 h) within the respective distances of at least 1 boat.

## 2.4. Discard data

Discard data for the studied period were obtained from fisheries observers onboard the 7 French legal longliners operating in the EEZ around Crozet and Kerguelen. The time and location of each discard release, considered as a 'discard event', were matched to the seabird tracking data. We considered a 'discard event' to encompass the following 6 h within a range of 5 km from the location of a discard release.

## 2.5. Environmental variables

The bathymetry, water masses, sea surface temperature (SST) and whether birds were inside or outside an EEZ were added to the dataset for each bird location. Bathymetry was extracted from the ETOPO1 Global Relief Model from the National Oceanic and Atmospheric Administration using the R package 'marmap' (Pante & Simon-Bouhet 2013). We considered bird locations to be over a shelf (shelf and shelf break) for depths above -2000 m or over oceanic

waters (deeper than -2000 m). From estimations of the locations of the Polar Front (Moore et al. 1999) and the Subtropical Front (Belkin & Gordon 1996), we further categorized bird locations into water masses: Antarctic (south of Polar Front), subantarctic (between Polar and Subtropical Fronts) and subtropical waters (North of Subtropical Front). Finally, we added hourly SST for each bird location, extracted from Copernicus data ([www.copernicus.eu](http://www.copernicus.eu)). We also considered whether locations were within all EEZ or not (data from [www.marineregions.org](http://www.marineregions.org)).

## 2.6. Analysis

Bird behaviours throughout their trips were inferred with hidden Markov models (HMMs), and the tracking data were linearly interpolated to obtain strictly regular 2 min time steps. We then computed step length and turning angles, to identify the hidden behavioural modes that could be revealed through these 2 observed variables. Like Clay et al. (2020), who analysed the tracking data from the same species, we expected to find 3 types of behaviour in albatross foraging trips: travel (or directed flight, with high speeds and shallow turning angles), search (with moderate speeds and turning angles, considered as foraging behaviour) and rest (with low speeds and shallower turning angles). Thus, a 3-state HMM (Morales et al. 2004) was fitted to the interpolated tracks. Gamma and von Mises distributions were used to model the conditional distributions of step lengths and angles (the observed variables) to the states. The initial values for the parameters of the HMMs are shown in Tables S1–S3 and Figs. S1 & S2 in the Supplement at [www.int-res.com/articles/suppl/m633p197\\_supp.pdf](http://www.int-res.com/articles/suppl/m633p197_supp.pdf). The state sequences were reconstructed via the Viterbi algorithm (Rabiner 1989). This analysis was performed using the R package 'momentuHMM' (McClintock & Michelot 2018). The results were validated through expert judgement: based on the biological knowledge of the foraging behaviour of the species, A. Corbeau validated visual representations of the tracks with the inferred sequences (more details in Fig. S3 in the Supplement).

To compare different variables between populations of Crozet and Kerguelen, and between sexes of the 2 populations, we used linear mixed models (*t*-test) and generalised linear mixed models (*z*-value) (R package 'lme4', 'lmerTest' and 'glmmTMB') (Table S4 in the Supplement). The negative binomial distribution was used for over-dispersed count data,



the binomial distribution for ratio data, and the Gaussian distribution for all others. We used the R package 'fitdistrPlus' for residual diagnostics (Table S4). For each variable (see Tables 1 & S4 for test values), we made a model to compare the 2 populations, then another model to compare sexes for Crozet birds and another for Kerguelen birds. In each model, bird ID was used as a random factor.

First, we compared the SST and bathymetry at each fixed and interpolated bird location, and then only bathymetry identified as 'search' via HMMs (see Tables 1 & S4). Second, we used each complete trip to compare their range, duration, proportion of time (ratio) on shelf, proportion of time in different waters, proportion of time in the EEZ and proportion of time in the 3 different HMM states (and within those states, we considered 3 conditions: in general, above shelf or in oceanic waters). Then, we used the radar detector as the most reliable measure of contact with boats, for comparisons of trip ratio in contact with boats (general, declared and non-declared) and for radar event comparison of distance to the nest and duration of this 'event' (in general, for declared and for non-declared boats) (see Tables 1 & S4). Third, we used AIS data and encounter events to define the encounter duration and the 'attraction' to boats as the time spent in attendance (<5 km from boats) and sitting in the water (speed <10 km h<sup>-1</sup>; Weimerskirch et al. 2002) divided by the time within encounter range (<30 km from boats). Then, for each encounter, we compared the distance to the nest, the attraction and the duration. For the attraction and encounter duration models based on discard data,

we only used data (encounter events) from the 7 declared French fishing boats, the only ones with recorded fishing discards (see Tables 1 & S4).

### 3. RESULTS

#### 3.1. Trip description

Foraging trip ranges and duration were similar between Crozet and Kerguelen. At Crozet (Fig. 1), females travelled further but with similar duration as males. At Kerguelen (Fig. 2), females and males had similar foraging ranges and duration (Table 1, see Table S4 for averages and test values).

The proportion of time birds spent in 'search' mode per trip was not significantly different between Crozet and Kerguelen and between sexes for Crozet. The proportion of time spent in 'travel' mode was similar between Crozet and Kerguelen, and between sexes at Kerguelen, but females from Crozet spent more time travelling than males. Crozet birds spent more time resting than Kerguelen birds, and Crozet males spent more time resting than Crozet females (Fig. 3a,d,g, Table S4).

#### 3.2. Habitat use

Kerguelen birds used colder waters than Crozet birds. Males and females from Kerguelen foraged in similar water temperatures, while females from Crozet foraged in warmer waters than males

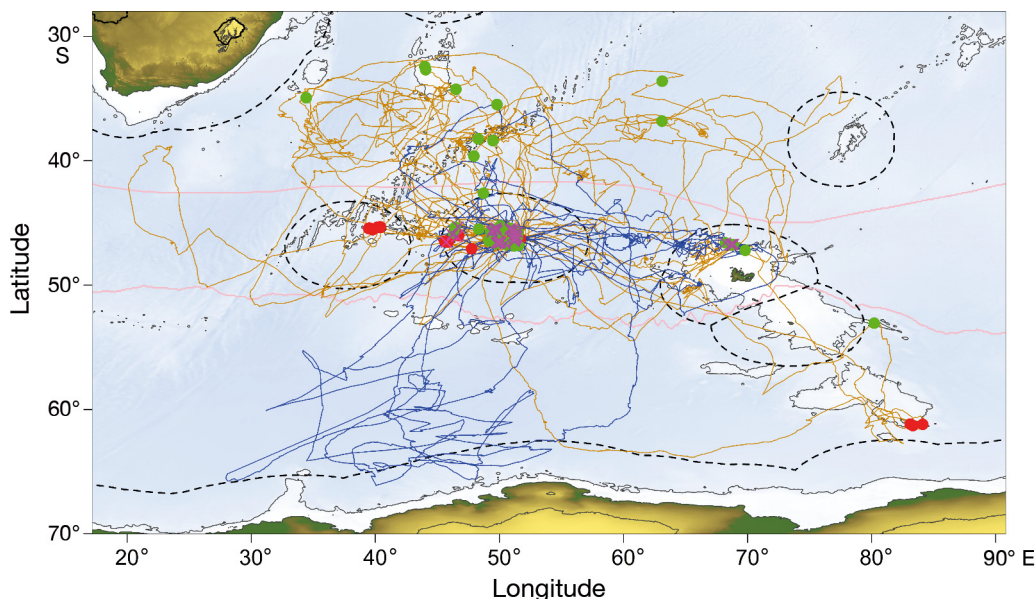


Fig. 1. South Indian Ocean with tracks of Crozet wandering albatrosses — blue: males; orange: females; red dots: contact with non-declared boat; green dots: contact with declared boat; purple cross: release of fishing discard by 7 French longliners; iso-baths: -2000 (shelf), 0 and +2000 m; pink lines: Subantarctic and Polar Fronts; dashed black lines: exclusive economic zones

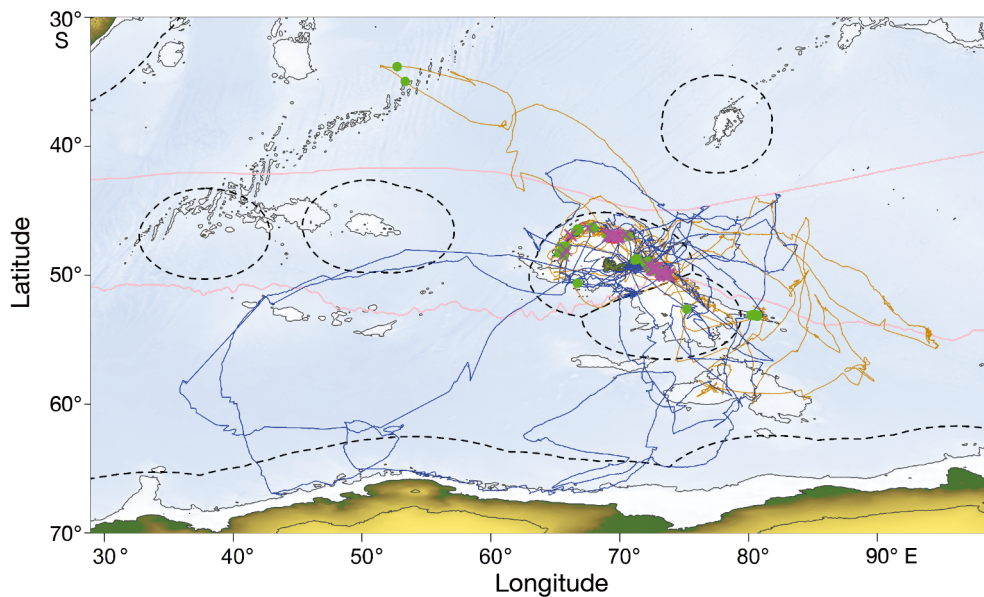


Fig. 2. South Indian Ocean with tracks of Kerguelen wandering albatrosses. See Fig. 1 legend for definition of lines and symbols

(Tables 1 & S4). Crozet albatrosses foraged over deeper waters than Kerguelen birds, which spent more time over shelf edges. Crozet females foraged over deeper waters than males, whereas there were no differences between sexes at Kerguelen (Tables 1 & S4). Therefore, Kerguelen birds spent more time in 'search' and 'travel' modes over shelves than Crozet birds, with females from Crozet travelling more and resting less over oceanic waters than males (Fig. 3, see Table S4 for test values).

We also found that Kerguelen and Crozet birds foraged over Antarctic, subantarctic and subtropical waters in similar proportions. Crozet females foraged in a larger proportion over subtropical waters than males, which favoured subantarctic waters (Fig. 1, Tables 1 & S4). Finally, Kerguelen birds spent more time in the EEZ and over shelves than Crozet birds, with no significant differences between sexes at Kerguelen, whereas Crozet males spent more time in the EEZ and over shelves than females (Figs. 1 & 2, Tables 1 & S4). Some Crozet birds foraged over the Kerguelen Shelf (Figs. 1 & 2)

### 3.3. Interactions with boats (from radar data)

The analysis of radar detector data showed that Crozet birds contacted more (27.78%;  $n = 25/90$ ) non-declared boats than Kerguelen birds (14.56%;  $n = 15/103$ ) ( $\chi^2 = 4.3$ ,  $df = 1$ ,  $p = 0.02$ ) but spent the same proportion of time per trip in contact with boats

(declared and non-declared) and there was no difference between sexes (Tables 1 & S4).

When considering all boats from radar detector data and separating declared boats from non-declared (no AIS) boats, we found no differences between birds from Crozet and Kerguelen and between sexes within each population. Equally, we found no differences between populations and sexes in the durations of the radar events for declared and non-declared boats. We found that Crozet females encountered boats further from the colony than males (Tables 1 & S4). The duration of the contacts (defined by radar detection) with declared boats ( $n = 153$ , mean duration =  $207.82 \pm 224$  min, mean  $\pm$  SD) and non-declared boats ( $n = 40$ , mean duration =  $222.33 \pm 245$  min) was similar (slope<sub>GLMM estimate</sub> =  $-0.20 \pm 0.24$ ,  $z$ -value =  $-0.83$ ,  $p = 0.408$ ).

### 3.4. Behaviour associated with boats (from AIS data)

We found that Crozet birds encountered boats with AIS (<30 km from boats with AIS) at a greater distance from the colony than Kerguelen birds, with Crozet females encountering boats further than males and Kerguelen females slightly further than males (Tables 1 & S4). Moreover, Crozet birds were less attracted by boats and spent less time behind boats than Kerguelen birds inside and outside the French EEZ. In Crozet, males spent more time within 30 km of boats than females. (Tables 1, S4 & S5).

Table 1. Differences (mean  $\pm$  SD) between sexes for each population of wandering albatrosses: mean  $\pm$  SD of variable and slope value (estimate of linear mixed models [LMM] or generalised linear mixed models [GLMM]) and p-value (*t*- or *z*-test). Differences between populations: \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001. EEZ: exclusive economic zones; SST: sea surface temperature

	Crozet		p	Kerguelen		p	Difference between Crozet and Kerguelen p
	Female (n = 24)	Male (n = 21)		Female (n = 10)	Male (n = 14)		
<b>Per location (n = 537522)</b>							
Bathymetry (m)	-3218.3 (±1413.01)	-2754.91 (±1703.37)	0.08.	-1942.14 (±1483.74)	-2152.22 (±1540.73)	0.67	0.001**
Bathymetry in 'search' (m)	-3032.12 (±1490.88)	-2367.46 (±1831.37)	0.001**	-1546.60 (±1429.72)	-1552.13 (±1525.28)	0.91	0.002**
SST (°C)	13.35 (±6.69)	7.61 (±3.96)	0.002**	6.18 (±4.26)	4.98 (±3.61)	0.39	6.0 × 10 <sup>-5</sup> ***
<b>Per trip (n = 71)</b>							
Range (m)	1496784.04 (±744155.70)	825029.54 (±750857.18)	0.002**	871555.91 (±722680.07)	998357.58 (±784426.58)	0.72	0.31
Duration (h)	300.19 (±130.32)	232.1 (±133.42)	0.11	255.74 (±117.98)	253.15 (±133.09)	0.96	0.64
Ratio on shelf	0.3 (±0.27)	0.51 (±0.36)	0.02*	0.71 (±0.32)	0.56 (±0.29)	0.41	0.002**
Ratio in Antarctic waters	0.06 (±0.17)	0.09 (±0.24)	0.67	0.13 (±0.25)	0.22 (±0.34)	0.33	0.41
Ratio in subantarctic waters	0.60 (±0.34)	0.86 (±0.26)	0.02*	0.82 (±0.27)	0.74 (±0.34)	0.69	0.51
Ratio in subtropical waters	0.34 (±0.36)	0.05 (±0.13)	0.03*	0.05 (±0.17)	0.04 (±0.13)	0.84	0.13
Ratio in EEZ	0.44 (±0.31)	0.72 (±0.31)	0.01*	0.74 (±0.36)	0.69 (±0.30)	0.54	0.04*
Ratio in contact with boat	0.03 (±0.07)	0.04 (±0.06)	0.92	0.11 (±0.14)	0.04 (±0.05)	0.51	0.51
Ratio in contact with declared boat	0.03 (±0.05)	0.05 (±0.07)	0.77	0.11 (±0.14)	0.06 (±0.05)	0.75	0.47
Ratio in contact with non-declared boat	0.03 (±0.07)	0.01 (±0.01)	0.64	0.00 (±0.00)	0.01 (±0.02)	0.81	0.74
<b>Per encounter (n = 248)</b>							
Distance from the nest (m)	1094907.41 (±711969.48)	316393.09 (±424445.4)	0.004**	387662.43 (±432637.75)	197838.16 (±192929.04)	0.06	0.03*
Attraction	0.12 (±0.24)	0.16 (±0.20)	0.49	0.30 (±0.28)	0.21 (±0.32)	0.32	0.02*
Duration (min)	200.19 (±251.65)	489.45 (±558.3)	2.1 × 10 <sup>-5</sup> ***	1130.74 (±1435.45)	752.41 (±1670.65)	0.17	2.0 × 10 <sup>-4</sup> ***
Attraction in French EEZ	0.17 (±0.19)	0.17 (±0.20)	0.63	0.31 (±0.28)	0.22 (±0.32)	0.51	0.03*
Duration encounter in French EEZ (min)	468.58 (±506.28)	484.04 (±526.94)	0.02*	1207.44 (±1527.13)	753.56 (±1711.05)	0.12	0.04*
Attraction fisheries	0.16 (±0.21)	0.18 (±0.20)	0.281	0.31 (±0.28)	0.23 (±0.33)	0.68	0.02*
Duration encounter fisheries (min)	326.68 (±344.77)	533.84 (±576.28)	0.006**	1166.49 (±1501.31)	747.77 (±1743.73)	0.12	0.03*
Attraction to fishing discard	0.27 (±0.21)	0.32 (±0.22)	0.60	0.42 (±0.26)	0.46 (±0.43)	0.79	0.11
Duration encounter with fishing discard (min)	683.8 (±557.38)	881.05 (±806.11)	0.45	2107.69 (±1777.83)	1237.36 (±3142.28)	0.23	0.19
Attraction without fishing discard	0.12 (±0.18)	0.11 (±0.15)	0.89	0.27 (±0.28)	0.19 (±0.25)	0.55	0.03*
Duration encounter without fishing discard (min)	287.22 (±278.87)	352.64 (±266.22)	0.19	429.05 (±456.05)	630.61 (±643.2)	0.35	0.03*
<b>Per radar event (n = 193)</b>							
Distance from the nest (m)	788763.53 (±688158.86)	244832.17 (±307186.42)	0.01*	259313.67 (±134639.16)	220825.69 (±186285.07)	0.743	0.90
Duration (min)	181.81 (±212.09)	192.32 (±190.65)	0.80	271.11 (±279.3)	173.69 (±185.97)	0.14	0.47
Duration for declared boat (min)	120.87 (±150.57)	187.29 (±191.56)	0.11	287.04 (±275.00)	178.92 (±193.84)	0.12	0.18
Duration for non-declared boat (min)	251.9 (±252.02)	234.6 (±198.35)	0.89	198.72 (±300.74)	124.00 (±74.98)	0.42	0.32

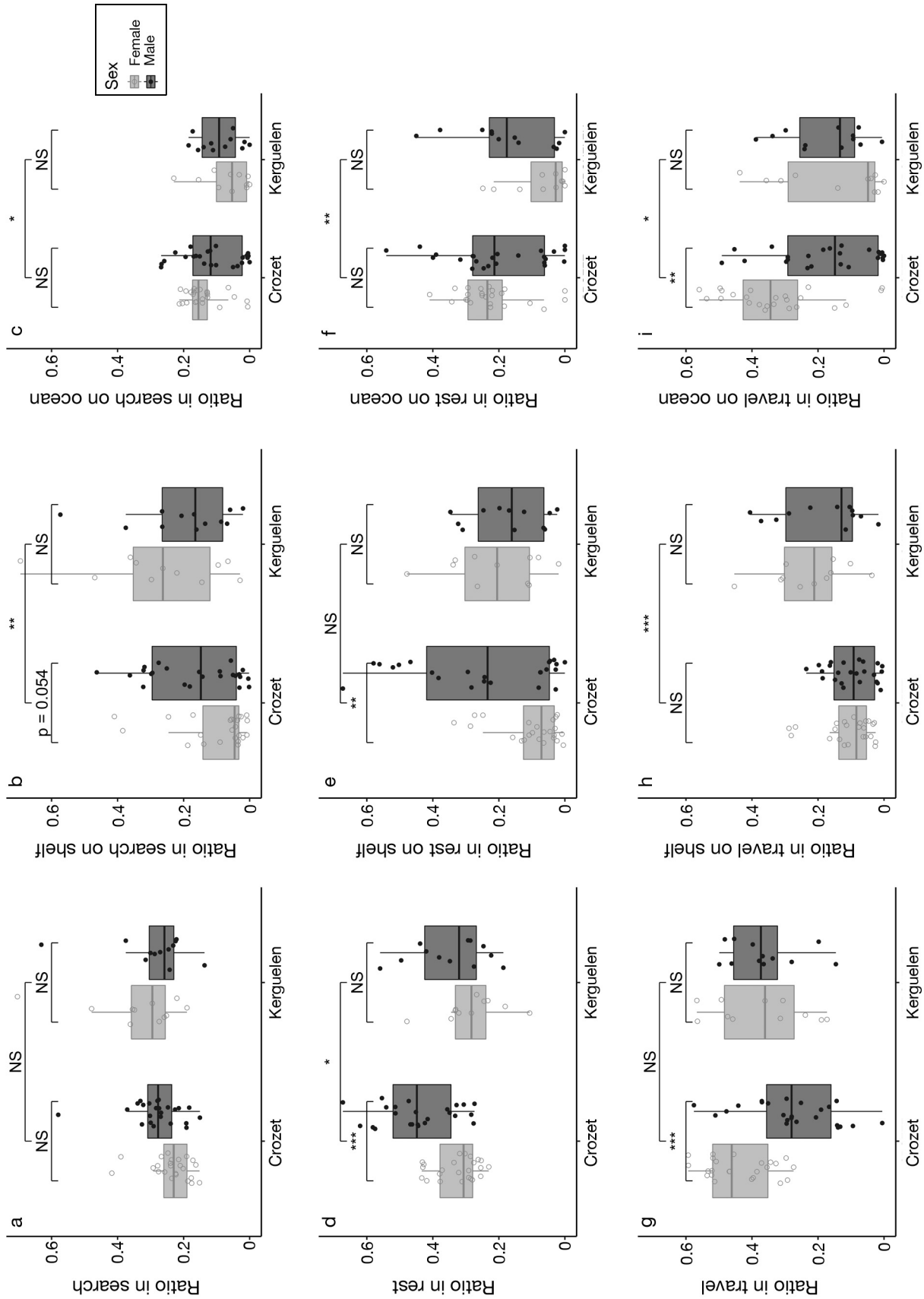


Fig. 3. Proportion of time spent in each of the 3 behaviours, (a,b,c) search, (d,e,f) rest and (g,h,i) travel, for each population and sex of wandering albatross (a,d,g) in general, (b,e,h) on the shelf and (c,f,i) over the ocean. NS: not significant, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001



However, birds from Crozet and Kerguelen spent the same proportion of time per trip behind boats (declared and non-declared) and there was no difference between sexes (Tables 1 & S4).

Attraction and duration of encounters were higher and longer, respectively, for fishing boats ( $n = 174$ , mean attraction =  $0.22 \pm 0.26$  [41 % of encounter without attendance]; mean duration =  $686.81 \pm 1188$  min) than for cargo vessels ( $n = 55$ , attraction =  $0.09 \pm 0.25$  [84 % of encounter without attendance]; mean duration =  $105.82 \pm 81$  min; attraction: slope =  $1.06 \pm 0.51$ ,  $z$ -value = 2.07,  $p = 0.038$ ; encounter duration: slope =  $1.49 \pm 0.27$ ,  $z$ -value = 5.42,  $p = 6.12 \times 10^{-8}$ ) (Fig. S4 in the Supplement). When considering only fishing boats, attraction and duration were higher and longer for Kerguelen birds than Crozet birds. There was no difference between sexes in attraction and duration in Kerguelen, whereas for Crozet, male birds had similar attraction rates but stayed within the encounter range of fishing boats for longer periods of time than females (Tables 1, S4 & S5).

We found no evidence that the attraction rate or the duration of encounter affected the breeding success during the breeding season (successful breeders:  $n = 152$ , mean attraction =  $0.19 \pm 0.27$  [51 % of encounter without attendance]; mean duration =  $564.91 \pm 1104$  min; failed breeders:  $n = 33$ , mean attraction =  $0.11 \pm 0.16$  [55 % of encounter without attendance]; mean duration =  $446.64 \pm 511$  min; attraction: slope =  $1.72 \pm 1.03$ ,  $z$ -value = 1.66,  $p = 0.096$ ; encounter duration: slope =  $-0.26 \pm 0.40$ ,  $z$ -value =  $-0.65$ ,  $p = 0.515$ ). We also found no difference in the breeding success of Crozet (0.75; successful breeders:  $n = 410$ ; failed breeders:  $n = 102$ ) and Kerguelen (0.80; successful breeders:  $n = 60$ ; failed breeders:  $n = 12$ ) populations ( $\chi^2 = 0.04$ ,  $df = 1$ ,  $p = 0.84$ ).

### 3.5. Fishing discards of French longliners

Attraction and duration of boat encounters (<30 km from AIS, for the 7 French longliners) were higher and longer, respectively, when fishing discards were released (within 5 km) (with fishing discards:  $n = 52$ , mean attraction =  $0.38 \pm 0.29$  [13 % of encounter without attendance]; mean duration =  $1314.89 \pm 1856$  min; without fishing discards:  $n = 98$ , mean attraction =  $0.16 \pm 0.22$  [49 % of encounter without attendance]; mean duration =  $404.71 \pm 415$ ) (attraction: slope =  $1.18 \pm 0.40$ ,  $z$ -value = 2.95,  $p = 0.0032$ ; encounter duration: slope =  $1.12 \pm 0.20$ ,  $z$ -value = 5.48,  $p = 4.14 \times 10^{-8}$ ).

The attraction and the duration of encounters were not different between populations and sexes in the

presence of discards. In the absence of discards, attraction and duration of encounters (for the 7 French longliners) were higher for Kerguelen birds compared to Crozet birds, with no sex differences (Tables 1, S4 & S5).

## 4. DISCUSSION

### 4.1. Differences in habitat use between populations and sexes

Our study indicates that, although the duration of foraging trips was similar for birds from Kerguelen and Crozet, incubating wandering albatrosses from these 2 populations foraged in different habitats. Kerguelen birds took advantage of the large and productive surrounding shelf (Dulaiova et al. 2009, Cavagna et al. 2014), whereas Crozet birds used the small shelf at Crozet to a lesser extent, but travelled to other shelves such as the Del Cano Rise or the Kerguelen Shelf. These results are also confirmed by the analysis of behaviours inferred by the HMMs showing that Kerguelen birds travel and search more over the shelf, whereas Crozet birds travel, search and rest more in oceanic waters (Fig. 3). In particular, Crozet females foraged over deep waters in the subtropical waters. Kerguelen wandering albatrosses hence appeared to be highly specialized in foraging over shelf areas during the breeding season, as well as outside the breeding season when they migrated to spend their sabbatical year over shelves off Chile and New Zealand (Weimerskirch et al. 2015). In contrast, Crozet birds foraged more over deeper waters during and outside the breeding season. A possible explanation is that Crozet is farther north, making it more viable for females to travel to subtropical waters.

Wandering albatrosses have similar population sizes in Crozet and Kerguelen (2200 pairs) (Weimerskirch et al. 2018a). In Kerguelen, we found no differences in foraging parameters and habitats between males and females, whereas we confirmed segregation between males and females for Crozet (Weimerskirch et al. 1993, 1997b, 2014), with females favouring deeper and warmer waters than males. This difference between sites may be explained by the presence of the large productive shelf around Kerguelen that could reduce competition between sexes, whereas the smaller shelf around Crozet may force the smaller females to forage at greater distances in less productive waters. Indeed, the Kerguelen Shelf is not only larger but also more productive than the small Crozet Shelf (Dulaiova et al. 2009, Cavagna et al. 2014).

#### 4.2. Overlap and attraction to boats

The strong differences in foraging habitats between the 2 populations and sexes have consequences on their overlap with fishing boats (exhaustive from radar detector) and on their behaviour behind boats (from AIS data). In this study, we estimated attraction as the time spent in attendance (<5 km) and sitting on the water behind boats divided by the time within encounter range (<30 km, when bird can see boats), quantifying the extent to which being within potential perceptual distance of a boat led to higher interactions. Overall, wandering albatrosses from both populations and both sexes spent an equivalent time per trip in contact with all types of boat (from radar detector data), declared and non-declared. We found no differences in the duration of contact with boats (estimated from radar detector data) between populations and sexes. However, at Crozet, more than 25% of contacts with boats were associated with non-declared boats, whereas at Kerguelen, this happened less than 15% of the time.

However, the 2 strategies of habitat use led to different overlap with and attraction to boats, with Kerguelen birds encountering more boats than Crozet birds. Kerguelen birds encountered and attended boats for longer periods and closer to the colony, with no sex-specific differences. Conversely, Crozet females encountered boats at greater distances from the colony than males, because of their propensity to forage in subtropical waters. On the other hand, since old males from Crozet foraged in Antarctic waters where there was reduced boat traffic and fishing activity (Weimerskirch et al. 2014), the average number of males attending boats was reduced. We found the same result when we considered boat encounters inside the French EEZ, which reinforces our suggestion that even if the birds are in the presence of the same boats (exactly the same 7 French longliners for the EEZ of Crozet and Kerguelen and a small fraction of non-declared boats; Weimerskirch et al. 2020), the birds of Kerguelen are still more attracted and forage for longer periods behind boats than Crozet birds. For Crozet birds, although attraction is similar between males and females, we found that males encounter boats closer to the colony and for longer durations. Females foraging in subtropical waters were more likely to encounter tuna longliners in oceanic waters (leading to shorter interactions or Area Restricted Search, ARS), and males foraging more over shelves were likely to encounter toothfish longliners closer to the colony, and these were characterized by longer interactions and ARS (Corbeau et al. 2019).

Although we found important differences between populations and individuals in terms of encounters of fishing boats, we found no consequences in terms of breeding success. The contact rate of individuals did not affect the individual breeding success, and the breeding success of the Crozet and Kerguelen populations was similar. Over the long term, the differences in attraction and time spent in encounter between populations did not affect the trends in population size, which are similar in the 2 populations (Weimerskirch et al. 2018a).

A couple of studies have assumed that seabirds are attracted by fishing boats (Wahl & Heinemann 1979, Skov & Durinck 2001), and a recent study showed that seabirds can also be attracted by other types of boats (Weimerskirch et al. 2020). Here we demonstrate for the first time that albatrosses are more attracted to and forage for longer periods associated with fishing boats compared to cargo vessels.

#### 4.3. Role of fishery discards

Fishery discards are a source of food for many seabird populations (Votier et al. 2004), although in some cases they might be of lower food quality than 'natural' food (Grémillet et al. 2008). Our study suggests that the release of fishing discards clearly attracted wandering albatrosses and led them to stay longer within sight of boats, compared to boats that were not releasing discards. Both sexes from the 2 populations were more attracted by boats when discards were released. Fishing discards appear as a significant source of food for scavenging birds, especially albatrosses (Bugoni et al. 2010), and it has been suggested that the release of fishing discards should be controlled to decrease bycatch risk (Waugh et al. 2008). Indeed, a new study in the North Atlantic has shown that the banning of fishing discards led gannets *Morus bassanus* to no longer be attracted to boats (Clark et al. 2020). In the EEZ around Crozet and Kerguelen, French authorities now require fishers to not release discards during line setting to avoid bycatch. However, the disappearance of this source of food may have a significant impact (Bicknell et al. 2013) on those populations that have adapted to this new food source. In order to assess this impact, future studies should focus on quantifying the proportion of the total food intake that fishing discard represents compared to natural food.

In conclusion, our study shows that for the same species, populations and even sexes can differ extensively in their foraging habitat, and such differences

have important implications for their overlap with fisheries and consequently for their susceptibility to bycatch risks. Future studies of risk assessments should take into account this additional complexity.

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