

Influence of depredating cetaceans on albatross attraction and attendance patterns at fishing boats

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ABSTRACT: Human fisheries inadvertently attract and provide food for a range of wild organisms worldwide with important ecological consequences. Some animals directly feed on human catch ('depredators', e.g. killer whales), causing economical losses and calling for wildlife management. However the impact of depredation (and its potential management) on the behaviour of the other scavengers attracted to vessels (e.g. seabirds) is unknown. We examined how the fine-scale behavioural response of wandering albatrosses to a toothfish longline fleet was influenced by the presence of depredating killer and/or sperm whales. We hypothesized that the presence of depredating whales might facilitate detection of and/or access to food at fishing vessels for surface-feeding albatrosses. We used seabird GPS tracking together with a vessel monitoring system (GPS vessel tracking) coupled with systematic onboard records of depredator numbers during 3 fishing seasons. We found that when albatrosses 'encountered' vessels (n = 254), they had the same probability to start attending vessels whether or not cetaceans were present. However, once attracted, they attended the vessel longer when depredators were present. We conclude that birds are attracted to vessels independently of the presence of cetaceans, but that depredating whales probably facilitate access to food for surface-feeding birds such as the wandering albatross. Scavenging behaviour of seabirds does not appear to be strongly dependent on the presence of depredating cetaceans and is likely minimally affected by changes in cetacean behaviour. This type of data is rare and we discuss how these results for wandering albatrosses could be generalized for other seabird species.

KEY WORDS: Fisheries interactions · Seabird foraging · Depredation · Longliners · Trophic interactions · GPS tracking · Sub-Antarctic · Toothed whales

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INTRODUCTION

Human fishing activities are now important elements of marine ecosystem functioning (Gislason et al. 2000, Pikitch et al. 2004). They directly impact targeted species stocks (Pauly et al. 2002, 2005) and often have further indirect 'domino' effects on the food web (Votier et al. 2004, Ainley & Blight 2009, Smith et al. 2011) and/or direct impacts on non-targeted species through bycatch (Crowder & Mu-

rawski 1998, Lewison et al. 2004, Harrington et al. 2005). Fisheries also serve as a substantial source of food for a range of organisms that scavenge near fishing vessels (e.g. seabirds, marine mammals, benthic invertebrates; Garthe et al. 1996, Ramsay et al. 1997, Catchpole et al. 2006, Read 2008). The ecological impacts of fisheries on scavenging populations should be accounted for when making fisheries management decisions in a sustainable ecosystem-based context (Pikitch et al. 2004). In particular, some ani-

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mal populations may be dependent upon fishing activities, and they could be severely impacted by changes in fishing practices (Furness et al. 2007, Bicknell et al. 2013, Heath et al. 2014).

Among these fisheries scavengers, some large sub-surface predators directly eat human captures before they are hauled onboard, a case termed 'depredation', and types of predators with this behaviour termed 'depredators'. Depredation, which is increasingly being reported worldwide, can have serious economic and ecological consequences (Gilman et al. 2008, Read 2008, Hamer et al. 2012). Additionally, some organisms, such as seabirds and benthic invertebrates, feed on discards, offal and baits or lost captures generated by fishing activities, with much lower direct economic consequences (Garthe et al. 1996, Ramsay et al. 1997, Catchpole et al. 2006). Among these, albatrosses and petrels are natural scavengers often attracted to fishing vessels. The conservation status of albatrosses and petrels today is of global concern (Croxall et al. 2012); the primary threat is often their incidental capture on longlines (Anderson et al. 2011, Croxall et al. 2012, Pardo et al. 2017). Ecological and/or socio-economic considerations call for management of these interactions between vessels and wildlife; however, little is known about the interactions between scavengers and depredators. If the presence of depredators influences the behaviour of scavengers like seabirds, measures aimed at reducing depredation may indirectly affect seabird populations.

Foraging associations between marine predators, including human fishermen, are frequent (Johannes 1981, Scott et al. 2012, Thiebot & Weimerskirch 2013) and often linked to facilitation of food access. Many seabirds, in particular, naturally rely on sub-surface predators to access their prey (Thiebot & Weimerskirch 2013), where they approach and follow cetaceans swimming at the surface (Ridoux 1987, Sakamoto et al. 2009, Tremblay et al. 2014). The presence of deep-living species of cephalopods in albatross diet has suggested that these birds occasionally feed on cetacean vomit (Clarke et al. 1981, Imber 1992, Croxall & Prince 1994). The depredation behaviour of cetaceans is being increasingly studied (Hamer et al. 2012, Guinet et al. 2015), but very little information is available on the importance of depredation to scavengers. Anecdotal observations onboard vessels suggest close associations between depredators and seabirds (Ashford et al. 1996, Tixier 2012). However we know of no studies that have attempted to quantify the influence of depredators on overall seabird behaviour at vessels.

Regardless of cetacean presence, the behaviour of seabirds interacting with vessels can be broken down into 2 (facultative) phases (Collet et al. 2015): a detection and approach phase followed by an 'attendance' phase. The detection/attraction of seabirds to vessels can happen from distances up to ca. 30 km, as estimated from bird flight directions biased towards vessels in several species of procellariiforms tracked by GPS (Collet et al. 2015, 2017a, Pirotta et al. 2018). In many cases however, individual birds within detection range of a vessel never approached vessels at closer distances and did not directly interact with them (Tew Kai et al. 2013, Bodey et al. 2014, Collet et al. 2017b). The probability of attraction once within detection range varies with different factors potentially affecting the detection probability (e.g. weather) and/or the bird's motivation to interact (e.g. Weimerskirch et al. 2000, Bodey et al. 2014, Collet et al. 2017b). The presence of depredating cetaceans may increase seabird motivation to approach vessels if they facilitate food access to birds. Moreover, their depredation activity and/or the seabird aggregations around depredators may further increase the probability for nearby seabirds to detect vessels.

Once birds have approached and are close to vessels ('attendance phase'), they can engage in feeding attempts. They also spend a lot of time simply sitting on the water close to vessels, resting or waiting for opportunities, with or without interaction with conspecifics and other species (e.g. Hudson & Furness 1989, Chérel et al. 1996). We will here refer to this complex mix of activities as 'attendance behaviour', i.e. behavioural patterns clearly influenced by vessel presence. Some individuals within detection range of vessels might be 'naturally foraging' independently of vessels (Torres et al. 2011, 2013, Collet et al. 2017a). However, observations from telemetry data have shown clear changes in movement patterns when seabirds are very close to vessels (Torres et al. 2011, Bodey et al. 2014, Collet et al. 2015). For instance, wandering albatrosses *Diomedea exulans* within 3 km of vessels have largely reduced apparent speeds compared to when they are further away from vessels, consistent with the above description of 'attendance behaviour' (Collet et al. 2015, 2017a). The presence of depredating cetaceans may affect how long birds keep attending the vessel. In addition, birds that appear to attend vessels may, in fact, at very fine spatial scales, be more attracted to cetacean depredators than to the vessel itself (G. Richard & A. Janc pers. obs.), and we predict that birds may be at slightly larger distances from vessels when depredators are present.

Here we examined the case of wandering albatrosses interacting with the longline fleet targeting Patagonian toothfish *Dissostichus eleginoides* off Crozet and Kerguelen Islands, Southern Indian Ocean. This fleet has been experiencing increasing depredation levels by killer whales *Orcinus orca* and sperm whales *Physeter macrocephalus* in the past decades (Roche et al. 2007, Tixier et al. 2010, Guinet et al. 2015). Fishermen, scientists and authorities are currently searching for management solutions (Guinet et al. 2015, Tixier et al. 2015, Janc et al. 2018). Several species of seabirds are also attracted to this fishery (Cherel et al. 1996, Weimerskirch et al. 2000, Delord et al. 2005). The fleet complies with mitigation measures introduced by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) in 1992 to reduce seabird bycatch (Delord et al. 2005), including nocturnal line setting. A previous study showed that attraction of breeding wandering albatrosses to this fleet reached its highest levels during hauling operations (Collet et al. 2017b). However, no discarding occurs during hauling, complying with mitigation measures which are enforced by onboard observers. Moreover, the lines are hauled in rapidly and their access is prevented by the use of tori lines deterring birds, so that few birds attempt to directly feed around hooks during hauling (Cherel et al. 1996). Therefore, only occasional drops of fish from the hooks or the vessel's deck are available to seabirds during hauling (G. Richard & A. Janc pers. obs.), and it is unlikely that enough food is provided for all the seabirds aggregated around the vessel. The frequent presence of depredating cetaceans during hauling may, however, facilitate access to food for seabirds and explain the strong attraction of wandering albatrosses to vessels during hauling operations.

Our objective in the present study was to determine how behavioural responses of wandering albatrosses to the toothfish longlining vessels around Crozet are impacted by the presence of depredating killer and sperm whales. To address this, we used GPS movement data collected on incubating birds during 3 consecutive breeding seasons. We intersected these tracks with Vessel Monitoring System (VMS; vessel GPS tracks) data combined with onboard cetacean census data performed each time a line was hauled. Specifically, we first tested whether birds flying within the detection range of vessels were more likely to be attracted when cetacean depredators were present (H1). Second, we tested whether bird attendance behaviour at vessels (time spent attending vessels, distance from vessels when attending) was affected by the presence and number of cetaceans (H2).

MATERIALS AND METHODS

Bird movement data

Fieldwork was carried out during the incubation period of wandering albatrosses (January to March) in 2011, 2012 and 2013 on Possession Island, Crozet Archipelago (46° S, 52° E). GPS devices (I-GotU mobile technology) encased in heat-shrinking tubing (final mass ~30 g, <0.5% of body mass) were attached to the back feathers using Tesa tape on breeding adults captured on the nest. Tags recorded foraging trips at a frequency of one location every 15 min. Birds were captured a second time to recover devices, generally after the bird had completed 1 trip, but several consecutive trips were recorded in some cases. Further details can be found in Collet et al. (2017b).

Here we restrict our analysis to the 117 trips from 100 different incubating adult birds that encountered fishing vessels (see below) during their foraging trip. Age and sex of all birds were known from the population long-term monitoring database (Weimerskirch et al. 2014, Collet et al. 2017b).

Longline vessel data

All data on fishing vessel movements and operations and on cetacean presence was provided by the Pecheker database hosted by the Museum National d'Histoire Naturelle de Paris (Martin & Pruvost 2007). This database has records of all legal fishing operations within the Crozet and Kerguelen exclusive economic zones (EEZ). While illegal fishing can occur within these EEZ, it is rare and does not represent a significant proportion of albatross interactions with vessels (Weimerskirch et al. 2018). Incubating wandering albatrosses from Crozet forage from South Africa to Antarctica well beyond the limits of the EEZ (Weimerskirch et al. 2014). There they interact with vessels in various areas within the Indian Ocean (Weimerskirch et al. 2018), for which no vessel tracking data was available to us in the present study.

Each year, 7 demersal longline fishing vessels targeting mainly Patagonian toothfish are allowed to operate in the Kerguelen and Crozet EEZ (Pruvost et al. 2015). In January–March 2013, only 4 vessels operated in the EEZ, not all simultaneously, and each vessel operated for a reduced amount of time compared to other years. We treated this year separately from the other 2 years (2011 and 2012) in our models following observations that wandering albatrosses

spent less time attending vessels per encounter in 2013, and that in 2013, younger birds appeared to remain further from vessels than older birds when attending vessels (Collet et al. 2017b). All these vessels complied with the VMS, recording their GPS location every 1 hour. Moreover, the date, time and spatial coordinates of longlines at the beginning and the end of both setting and hauling operations were available. These were combined with VMS data to recreate fishing vessel tracks. During hauling operations within the Crozet EEZ, vessels cruised at $2.8 \pm 1.4 \text{ km h}^{-1}$. Longlines were $7.5 \pm 3.1 \text{ km}$ long, and hauling of a longline lasted $3.1 \pm 1.9 \text{ h}$, with sets of neighbouring lines often operated in blocks (Richard et al. 2018).

Vessels were not continuously fishing, but were sometimes travelling for extended periods in-between fishing events. Therefore, after inserting fishing event locations into VMS tracks, the sampling frequency appeared locally variable (once per hour when there was no fishing, more frequently if there were fishing events in-between VMS locations). To allow for a more accurate description of bird–boat distances, we linearly interpolated locations of longliners in between ‘real’ recorded locations, assuming straight line and constant speed, to obtain 1 location every 10 min. This allowed matching all bird GPS locations with a concurrent vessel location within a 5 min interval. Concurrent distances between bird and fishing vessel locations were then calculated for each bird GPS location. In previous studies of seabird interactions with fishing trawlers, it has been recommended to account for spatial inaccuracy in interpolated boat locations by creating circular ‘buffers of location’ of a radius size increasing with the time to the closest ‘real’ recorded location (Torres et al. 2011, 2013). This method is employed to avoid assumptions on the real path of trawlers which can be circuitous and backtracking between locations when the boat is operating. Here we did not use such a method, because we think longliners have a much more linear behaviour both when they operate at fine scale and when they move between line sets. Therefore, we believe that our linear interpolation is probably more accurate in this case than a circular buffer assumption. Analyses of interactions based on these interpolated vessel tracks are shown in the ‘Results’. See the Supplement at www.int-res.com/articles/supp/m605_p049_supp.pdf for a discussion on this choice of linear interpolation and a simplified analysis based on ‘real’ recorded vessel locations only, confirming that our conclusions are not a spurious effect of the error in interpolated vessel locations.

Cetacean data

Every time a longline was hauled, fisheries observers onboard each vessel recorded the presence or absence of (presumably depredating) killer and sperm whales, and, when present, their number and time of arrival relative to the beginning of hauling operations (minutes after the hauling started, 0 min if depredators were already present before hauling started). Cetacean presence was not assessed outside hauling events, and we treated these periods separately in the analyses. The presence and number of cetaceans were assessed from observations of fins and tails emerging from the surface (Tixier et al. 2010, Tixier 2012). Since all individuals do not necessarily surface simultaneously, observers were asked to provide estimates of the minimum and maximum group size of each cetacean species present. For our analyses we used the average of these 2 estimates.

Probability of albatross attraction to vessels (H1)

Wandering albatrosses can detect and be attracted to vessels from the studied fleet at up to 30 km (Collet et al. 2015). However it is only at much closer distances (3 km, see next section) that they show clear changes in behaviour (‘attendance’) consistent with albatrosses trying to obtain food from vessels (Collet et al. 2015). When albatrosses are between 3 km and 30 km from vessels, it is therefore challenging to know whether their behaviour is influenced by vessels or not.

Anytime an albatross entered the 30 km buffer around a vessel, we defined the whole period where it remained in this area as one ‘encounter’ (Collet et al. 2017b). When birds left the 30 km buffer for less than 1 h before re-entering it, we considered it as a single encounter (Collet et al. 2017b). This 1 h threshold is the minimum duration that ensures that at least 1 bird location is matched with a recorded, non-interpolated boat location at a distance > 30 km. We thus recorded 469 ‘encounters’ of wandering albatrosses with toothfish longline vessels over the 3 studied seasons. In 44% of encounters (including ca. 35% of encounters that took place during hauling operations), birds were within 30 km but never sat on the water within 3 km of vessels (Collet et al. 2017b, see also Weimerskirch et al. 2018). In these cases, it is most likely that no direct interactions with boats occurred during the encounter, revealing variations in attraction and/or detection. Here we first tested whether part of this variation could be linked to the presence/absence of depredating cetaceans (H1).

For each encounter, we assessed whether or not there was at least one bird location classified as 'vessel attendance behaviour' (see next section). We could then examine whether the probability for birds to start attending vessels during an encounter increased with depredator presence. In a relatively large number of encounters of vessels by birds, we had no data on whale presence/absence. In most cases, this absence of data occurred when birds encountered boats outside of hauling operations and thus were more likely to indicate whale absence than presence. In some cases however, depredator presence/absence was not assessed during a hauling operation, mostly due to poor weather conditions and visibility (A. Janc & G. Richard pers. obs.). These encounters were not included in statistical models; however, we report on them in the 'Results' section as a potential source of noise in our analyses. We believe however this does not affect our conclusions.

Statistically, for each encounter we used the variable 'attendance or not' as a response in a binomial generalized linear mixed model (GLMM) with bird identity and trip number as random factors. Depredator presence/absence was included as an explanatory variable. We only accounted for depredator presence/absence at the beginning of the encounter, i.e. before the bird started attending the vessel or before it left detection range without attendance. In other words, if the bird started attending the vessel whilst no cetaceans were present, and depredators arrived later, i.e. while the bird was still attending the vessel, we considered this an encounter with no depredators. This allowed us to focus on the information available to the bird on depredator presence/absence when 'making the decision' to start attending the vessel or not.

Previous analyses revealed no influence of age, sex or year on this response (Collet et al. 2017b). We nevertheless included these covariates in the model and tested for the interaction between depredator presence and bird sex. Indeed, female wandering albatrosses are smaller than males, which could hypothetically affect their respective abilities to access food within seabird aggregations around boats (see Collet et al. 2017b). The time elapsed between the start of an encounter and the closest hauling operation was also included in the model, as birds were shown to be much more attracted during or soon before or after hauling operations (Collet et al. 2017b).

Attendance behaviour (H2)

Attendance behaviour was defined as birds displaying speeds $<10 \text{ km h}^{-1}$ within 3 km of a vessel.

These low speeds are consistent with birds sitting on the water for a large proportion of the 15 min interval between GPS locations, which is what is expected from onboard observations of surface-seizing albatrosses either waiting for opportunities or making feeding attempts (Cherel et al. 1996). At such low distances, it is unlikely that this behaviour is independent of vessel presence (i.e. simple 'overlap' sensu Torres et al. 2013); and indeed the proportion of bird GPS locations with apparent speeds $<10 \text{ km h}^{-1}$ dramatically increased within 3 km compared to when birds were further away from vessels (Collet et al. 2015; see also the Supplement).

When birds were not attending vessels (beyond 3 km and/or with speeds $>10 \text{ km h}^{-1}$) but within 30 km of a vessel and thus potentially detecting it, it could not be reliably determined whether their behaviour was linked to vessel presence and/or whether it represented independent foraging or resting (Collet et al. 2015, 2017a,b). Encounters (see previous subsection) containing attendance behaviour lasted longer ($14.0 \pm 12.5 \text{ h}$, mean \pm SD, median 10.4 h, range 1.0–82.2 h) than encounters without attendance behaviour ($2.0 \pm 2.7 \text{ h}$, median 1 h, range 15 min–15.3 h; Collet et al. 2017b).

For each encounter event, we established the proportion of locations that were classified as 'attendance behaviour'. This can be interpreted as the time spent attending vessels (while being within detection/attraction distance). We then examined the influence of depredator presence and number on this proportion. To calculate this proportion, we used only bird locations concurrent to vessels locations where depredator presence/absence had been assessed (i.e. only during hauling operations). We modelled this proportion with negative binomial GLMMs, including as an offset the total number of bird locations during the encounter with available data on whale presence/absence. We expected a higher proportion of locations classified as attendance behaviour when depredators were present rather than absent, and/or with an increasing number of depredators being present.

In addition, we also examined the average distance of birds from vessels when they were attending vessels (i.e. within 3 km of them). The average was calculated for each encounter using only bird locations concurrent to vessel locations where depredator presence/absence had been assessed (i.e. only hauling operations). The average distance from boats when birds were 'attending them' was necessarily bounded between 0–3 km, following our definition of attendance behaviour. However, observed values of average distances were not concentrated close to

these bounds, so we used Gaussian linear mixed models to analyze their variance. We expected that birds would be further from boats when depredators were present and/or in higher numbers if they were staying around cetaceans rather than waiting close to the vessel deck to obtain food.

For each of these response variables, we proceeded in 2 steps: first, a binary variable assessing cetacean presence was included in the model ($n = 221$), then the average number of cetaceans (killer and sperm whales pooled) was included in a model applied only to a subset of data where cetaceans were present ($n = 163$). We also checked whether including killer whale presence or sperm whale presence alone influenced the results. For each model, bird identity and trip number were included as random factors.

We included as covariates the same factors as in a previous study by Collet et al. (2017b): age, sex and year; and we tested for the interaction between depredator presence and bird sex. For the models on the attendance distance, we also included the interac-

tion between year and age, as this was found to be significant in the previous study (Collet et al. 2017b). On average in 2013, the younger the birds, the further from boats they stayed when attending those boats; however, this was not the case in other years. Because depredator presence/absence was only assessed during hauling, we did not include any covariate for fishing activity. All analyses were conducted in the R environment (R Version 3.2.2, 2015-08-14; R Core Team 2015) using packages lme4 (Bates et al. 2015) and nlme (Pinheiro et al. 2015) for statistical analyses and the geosphere package (Hijmans et al. 2015) for the calculation of geographic distance and directions.

RESULTS

We recorded 355 albatross–fishing vessel encounter events where killer and/or sperm whale presence/absence was assessed, leaving 114 events where whale presence/absence data was not recorded (Fig. 1). Of these 114 events, 32 (28.1%) occurred within 1 h of a hauling operation, of which only 3 triggered bird attendance (9.4%, Fig. 1). The remaining 82 events with no whale data contained bird attendance in 23.2% of cases ($n = 19$, Fig. 1).

Of the 355 encounter events where whale presence/absence was assessed, the assessment was made only after the bird had started attending the vessel in 101 cases (28.5%; Fig. 1), so we could not reliably assess whether the initial attraction decision was influenced by depredators. The presence/absence of whales was assessed before the bird left the attraction range and before it started attending the vessel for the remaining 254 encounter events (from 82 different individuals and 95 different foraging trips). Whales were present in 50.4% of these encounters ($n = 128$ out of 254, Fig. 1), and attendance occurred in 54.0% of these 128 encounters ($n = 68$, Fig. 1). Conversely, attendance started in 40.5% of encounters where no whales were present (51 out of 126 encounters, Fig. 1). Whether whales were present or not at the start of these encounters did not influence the probability that the bird attended the vessel ($z = -1.160$, $p = 0.25$; Fig. 1), and this was not dependent on sex ($z = 0.034$, $p = 0.97$). There was no detected effects in control variables (time to hauling operation: $z = 0.433$, $p = 0.67$; sex: $z = 0.488$, $p = 0.63$; age: $z = -0.719$, $p = 0.472$; year 2013: $z = 1.265$, $p = 0.21$).

When whales were present at the beginning of the encounter (before the bird left the attraction range and before it started attending the vessel, $n = 128$), the killer:sperm whale ratio was not different be-

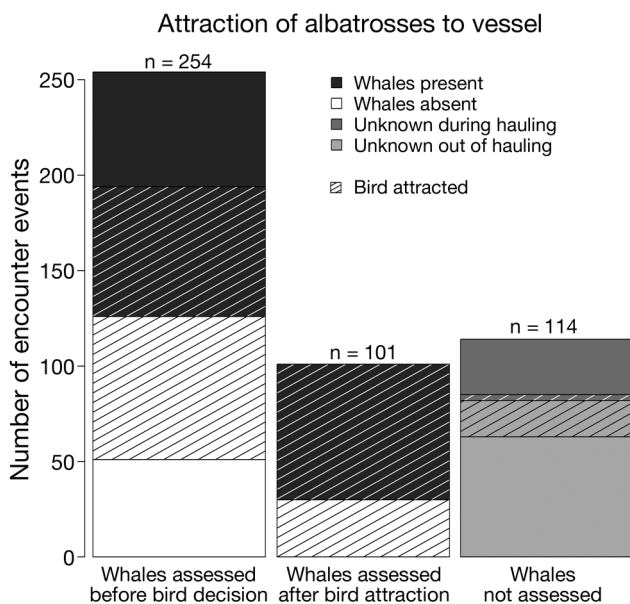


Fig. 1. Whale presence/absence and bird attendance or lack of attendance during vessel encounter events. Hatching indicates encounter events where birds attended vessels. Different shades indicate whale presence, absence or missing data. For the latter, we further categorized events where vessels were in hauling operation ('unknown during hauling', where both bird and cetacean attractions are more likely) or not ('unknown out of hauling', >1 h before or after any hauling operation). Only the events from the first bar are reliable to use for analyzing the attraction probability, whereas shaded encounters from both the first and second bars were used to analyze bird behaviour while attending vessels (Fig. 2)

tween encounters with or without bird attendance ($F_{1,67} = 1.006$, $p = 0.32$). Sperm whales were present without killer whales in 101 of these 128 encounters (78.9%; 51 out of 101 contained bird attendance: 50.5%), both killer and sperm whales were present in 23 of them (18.0%; 15 out of 23 contained bird attendance: 65.2%), and only killer whales were present in 4 encounters (3.1%; 2 out of 4 contained bird attendance).

Birds spent a higher proportion of time attending vessels per encounter when cetaceans were present (model estimator: $+10.3 \pm 1.7\%$, $z = 2.023$, $p = 0.04$; Fig. 2A). The interaction of whale presence and bird sex was marginally significant, with a tendency for a larger proportion of time spent attending vessels during whale presence in males than in females (interaction: $z = 1.692$, $p = 0.09$). The effects were not detectable when looking separately at the presence/absence of killer whales ($z = -1.027$, $p = 0.30$) or sperm whales ($z = 1.515$, $p = 0.13$). Control variables had no noticeable effects on this time spent attending vessels per encounter (sex alone: $z = -1.465$, $p = 0.14$; age: $z = 1.112$, $p = 0.27$; year 2013: $z = -0.537$, $p = 0.59$). When whales were present, group size had no effect on the proportion of time birds spent attending vessels ($z = -0.688$, $p = 0.49$; Fig. 2B).

When birds did attend vessels, they were at the same distance from vessels whether or not cetaceans were present ($t = -1.647$, $df = 135$, $p = 0.10$; Fig. 3A), with no interacting effects with sex ($t = -1.614$, $df = 134$, $p = 0.11$). However, when cetaceans were present, birds attended vessels from increasing distances with increasing numbers of cetaceans (model estimator: $+23.7 \pm 7.4$ m whale⁻¹, $t = 3.216$, $df = 89$, $p < 0.01$; Fig. 3B). This effect of increased distances with increased number of cetaceans was also detected when looking only at killer whale presence/absence ($t = 2.167$, $df = 89$, $p = 0.03$), or only at sperm whale presence/absence ($t = 3.190$, $df = 89$, $p < 0.01$). Among control variables, as noted in Collet et al. (2017b), older birds interacted closer

to vessels in 2013 (but not in other years) compared to younger birds ($t = 1.973$, $df = 80$, $p = 0.05$); but there was no effect of sex ($t = 1.496$, $df = 80$, $p = 0.14$).

DISCUSSION

Our study is the first to examine whether the presence of depredated cetaceans affects the scavenging behaviour of seabirds at fishing vessels. We showed that cetacean presence and/or number modified bird behaviour attending vessels at close distances (H2), but not the initial bird attraction to vessels (H1).

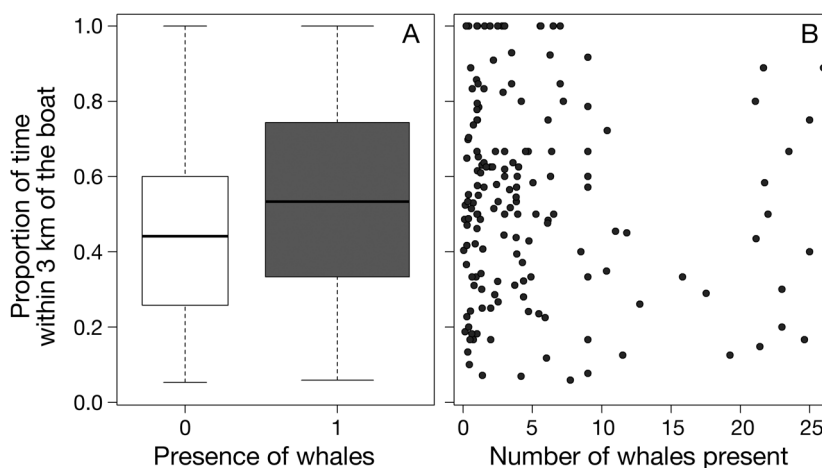


Fig. 2. Time spent by birds attending vessels (relative to total time within detection range of vessels) as a function of depreducer (A) presence (1) or absence (0) or (B) number when present. Only periods where depreducer presence/absence was assessed were retained to calculate the proportion of time. Boxplots—midline: median; box: interquartile range; whiskers: total range of data

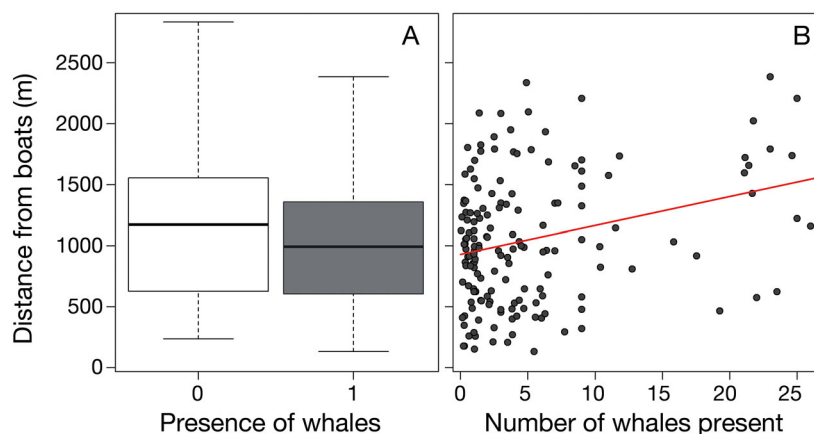


Fig. 3. Average distance from vessel when attending them (<3 km) as a function of depreducer (A) presence (1) or absence (0) or (B) number when present. The red line indicates the significant average predicted effect from a linear mixed model (see 'Results'). Only periods where depreducer presence/absence was assessed were retained to establish average distance during an encounter. Boxplots—midline: median; box: interquartile range; whiskers: total range of data

Depredator presence induced birds to stay longer around vessels, and larger numbers of killer and/or sperm whales induced birds from further distances to attend vessels. However birds often started to attend vessels before depredator presence (nearly 50% of attendance cases where whale presence/absence had been reliably assessed), and conversely, many vessel encounters where depredators were present were not followed by bird attendance (whale presence in nearly 50% of reliable ‘missed opportunities’).

The data used here (concurrent bird tracking, depredator’s presence, absence and numbers, and fishing vessel records of activity) is rarely available. Onboard observations are both challenging to conduct and not well adapted to assess the larger-scale seabird approach phase (Collet et al. 2015). The coarse frequency of our GPS data (both on birds and vessels) warrants some care to interpret the fine-scale behaviour of birds close to vessels. Nevertheless, the low speeds of both birds and vessels during hauling operations and the large number of bird locations recorded within 5 min of recorded (non-interpolated) vessel locations (see the Supplement) provide support to the robustness of our estimations of bird–vessel distances. These caveats in mind, we discuss how our results may be generalized for other seabird species or fishing fleets.

Cetacean presence/absence was not a necessary criteria for albatrosses to decide to attend vessels or not. In the studied fleet, implemented mitigation measures supposedly reduced the availability of food during hauling operations for wandering albatrosses. Facilitation of food access by cetacean depredation was therefore a good candidate to explain variations in bird motivation to initially approach vessels of this fleet (Collet et al. 2017b), but we found no evidence for it. Cetacean presence might be difficult to detect at long distances when bird decisions are made. We showed previously that operating vessels were very attractive to birds (Collet et al. 2017b), and they are much more visible at a distance than whales. Our results are consistent with the view that attraction to vessels in albatrosses is mainly influenced by sight (Collet et al. 2015). In fisheries where mitigation measures are not yet implemented (i.e. illegal fishing within the EEZ and fisheries in unregulated international waters), more food should be available to seabirds, and depredation activities are thus unlikely to have more impact on the initial attraction of wandering albatrosses to vessels. Any measures reducing depredation activities should therefore minimally affect the initial attraction of wandering albatrosses to fishing vessels.

An important question is whether wandering albatrosses likely reflect other seabird species attraction responses. In a previous study, we compared the response to vessels of the same fleet between wandering and black-browed albatrosses *Thalassarche melanophrys* (Collet et al. 2017a). Attraction distances were the same between the 2 species and similar to recent estimates for northern fulmars *Fulmarus glacialis* in the North Sea (Pirodda et al. 2018). We might expect similar maximum attraction distances in other albatross species, in sulids (Thiebault et al. 2014), and maybe most diurnal, large seabird species, as it seems to coincide with the horizon distance (Thiebault et al. 2014, Collet et al. 2015). It is thus likely that detection of vessels by diurnal seabirds will be largely independent of cetacean presence, and most variations should be due to effects on motivation.

In Kerguelen waters, where depredation occurs only by sperm whales and in a lower proportion of fishing events compared to Crozet (Janc et al. 2018, Richard et al. 2018), the probability to attend a vessel within attraction distance was larger in black-browed than in wandering albatrosses (Collet et al. 2017a). Wandering albatrosses are the largest seabird species, generally dominating agonistic interactions with all other seabird species (Weimerskirch et al. 1986, Ashford et al. 1995, Cherel et al. 1996). At Kerguelen, the same mitigation measures reducing food availability apply as in Crozet waters. Hence smaller and less dominant species like black-browed albatrosses can be strongly attracted to vessels in areas where depredators are more rarely present and even though these birds likely experience higher competition costs (Collet et al. 2017a). There might thus be more essential factors of seabird attraction than cetacean presence around vessels (Bodey et al. 2014, Collet et al. 2017a).

Although we found that the initial attraction to vessels appeared to be mostly independent of depredator presence, after being attracted birds attending vessels behaved differently in the presence of cetaceans. When depredators were present, albatrosses spent comparatively more time sitting within 3 km of vessels than in the area between 3 and 30 km from vessels. This suggests a more active attendance of vessels in the presence of depredators. This increased time spent close to vessels is unlikely to have an effect on bycatch risk, even in unregulated fishing fleets. Indeed, during hauling wandering albatrosses and most seabird species do not interact with hooks (Cherel et al. 1996), and most depredation on longlines occurs during haul-

ing. This increased time spent close to vessels is likely to reflect fine-scale associations of birds with depredators and probably food access facilitation by cetaceans (Ridoux 1987, Sakamoto et al. 2009, Thiebot & Weimerskirch 2013). In a previous study, we examined the change of mass before and after a foraging trip in relation with the time spent attending boats, to see whether attendance was beneficial for birds in terms of mass gains. We found no such relationship (Collet et al. 2017b). It was not possible in the present study to examine whether variations in mass gains are related to depredator presence at attended boats because wandering albatrosses can encounter and attend different vessels several times during a single foraging trip (Collet et al. 2017b, Weimerskirch et al. 2018), and depredators are not always present at these encounters. Behavioural data at a finer scale would be required to confirm food access facilitation by cetaceans.

The size of food items that could be generated by cetacean depredation activities is unclear. Onboard observations suggest sperm whales may generate less food at the surface than killer whales (G. Richard, A. Janc, N. Gasco pers. obs.); but we did not find evidence that the 2 cetaceans caused different bird behaviour. Wandering albatrosses are large seabirds and can swallow large food items (often whole fish), whereas giant petrels, smaller albatrosses and petrels are restricted to much smaller pieces (Ashford et al. 1995, Cherel et al. 1996, G. Richard & A. Janc pers. obs.). Wandering albatrosses are dominant over all other species (Weimerskirch et al. 1986) but tend to be less active than black-browed albatrosses or giant petrels when attending fishing boats (Ashford et al. 1995, Cherel et al. 1996, Collet et al. 2017a). Often large prey items are difficult to handle and ingest for black-browed albatrosses and giant petrels, which leaves more time for wandering albatrosses to access and swallow these large prey (G. Richard & A. Janc pers. obs. and unpubl. videos). If cetaceans generate smaller size items than those usually available otherwise, we might expect smaller species than wandering albatrosses to benefit more from cetacean presence. However, this remains to be tested.

We found that birds within 3 km of vessels stayed further from vessels with an increasing number of depredators, but no effects of depredator presence/absence per se were detected. Onboard observations suggest that birds can form rafts around depredators emerging at the surface, which thus keeps from being close to the line being hauled and/or the vessel's deck (G. Richard & A. Janc pers. obs.). This effect occurs, however, at very fine spatial scale, so

that it is unlikely to be picked up by our coarse GPS frequency. However, large numbers of cetaceans may be associated with several social units, which tend to segregate spatially (Tixier 2012), and may indeed increase the spatial spread of these rafts around depredators. Other hypotheses include an increased number of birds (increased spatial competition) and/or increased bird activity with an increased number of depredators. It might also reflect an anti-predator behaviour by birds. Remains of wandering albatrosses have been found in one stranded killer whale in South Africa (Best et al. 2010). However such predation events on albatrosses seem to be very rare (Best et al. 2010, Reisinger et al. 2011) and may concern mainly 'play' or 'practice' behaviour by young or subadult individuals (Ford et al. 1998, Best et al. 2010). We are thus not convinced that our observations could be due to seabird anti-predator behaviour, but again, finer-scale behavioural studies would be needed to confirm this.

In conclusion, we found that depredator presence indeed influenced wandering albatross behaviour at vessels, but that it was not the primary determinant of their initial attraction. Birds were largely attracted during hauling operations, even in the absence of depredators. This is surprising, knowing that mitigation measures implemented in the studied fleet limits the food available to birds during hauling operations. When no such measures are implemented, it is unlikely that cetaceans have a greater influence on bird behaviour. Therefore, while management measures aimed at reducing depredation may perhaps reduce feeding opportunities for seabirds in fleets implementing seabird bycatch mitigation measures, they are unlikely to significantly affect the number of seabirds attracted to fishing vessels. Further fine-scale behavioural studies are required to better understand which seabird species really benefit from food access facilitation by depredators.

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