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Tracking data reveal both indirect and direct interactions between killer whales and fisheries in subantarctic waters

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ABSTRACT

Conflicts between large marine predators and fisheries often involve both indirect (competition for fish stocks) and direct negative interactions (bycatch or depredation). However, the extent and the mechanisms of these conflicts are hampered by lack of data on the behavior of predators in natural situations (absence of fishing vessels) and in response to fishing activities. For killer whales *Orcinus orca* in the remote subantarctic waters of the southern South Atlantic and Indian Oceans, this lack of understanding is particularly problematic since negative interactions with industrial fisheries targeting toothfish affect the conservation of populations. In this study, we combined data from 36 satellite tags deployed on killer whales in these regions between 2011 and 2024 with tracking (AIS) data of toothfish fishing vessels to i) assess the overlap between killer whale offshore foraging areas and fishing areas, and ii) examine the factors influencing the decision of individuals to engage in depredation. Through kernel utilization distributions and statistical models we show that killer whales foraged in offshore areas used by fishing vessels to catch toothfish, but this overlap varied greatly across individuals within populations. We found that killer whales changed their trajectories and headed toward fishing vessels as far as > 100 km from them, possibly to engage in depredation. However, this behavior was not systematic and differed across individuals and areas. The behavior was detected only 55% of the times killer whales entered a 60 km range from a vessel. By highlighting areas of co-occurrence of killer whales and fisheries and the extent to which killer whales are able to change their behavior in response to fishing activities, our findings provide information that can be used to mitigate the negative impacts of interactions.

1. Introduction

Competition for resources and space can lead to both indirect and direct negative interactions between humans and wildlife, called human-wildlife conflicts (Nyhus, 2016). In the marine environment, conflicts between fisheries and large marine predators involve indirect interactions in the form of competition for the same fish stocks (Branch et al., 2010), and direct interactions in the form of predators feeding on fish caught by fishers on fishing gear (Nyhus, 2016; Guerra, 2019; Tixier et al., 2021a). The latter is a behavior termed "depredation". Depredation has been developed by many large marine predator species, especially sharks and marine mammals, and has been increasingly documented in fisheries from all sectors (industrial, artisanal, recreational) over the past 50 years (Tixier et al., 2021a; Mitchell et al., 2018).

Depredation incurs costs for the fishers in the form of reduced catch, additional efforts to recoup fish losses and damage to fishing gear, and for marine predators through injury or death caused by incidental bycatch or retaliatory killing from the fishers (Tixier et al., 2021a). While measures have been tested to mitigate shark and marine mammal depredation, including fish protection devices, acoustic deterrents or changes in fishing practices, their effectiveness varies (Guerra, 2019; Mitchell et al., 2018; Luck et al., 2025). Poor effectiveness of these

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measures is often caused by a lack of understanding of the mechanisms of depredation (Tixier et al., 2021a; Luck et al., 2025). These mechanisms include the extent to which foraging areas of marine predators overlap with fishing areas, and the determinants of the decision made by these predators to engage in depredation when they co-occur with fishing vessels (Nyhus, 2016; Tixier et al., 2021a).

Fisheries that operate in subantarctic waters and target Patagonian toothfish (*Dissostichus eleginoides*) using demersal longlines (lines bearing a series of baited hooks set on the seafloor) are subject to depredation by killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) (Tixier et al., 2019a, 2020). These industrial fisheries started in the 1990s and have now become a major socio-economic activity in the subantarctic (Tixier et al., 2020; Grilly et al., 2015). Fishing vessels generally operate at the edge of shelves and deploy longlines that sink to depths between 500 and 2000 m (setting phase), which they leave for hours (soaking phase) before retrieving (hauling phase). Killer whales and sperm whales depredate an estimated 837 tons of toothfish (worth USD 15M) every year across the main toothfish fisheries spanning from southern Chile to the Indian Ocean sector of the Southern Ocean (Tixier et al., 2020).

Particularly high killer whale depredation on toothfish catches was documented around the Crozet Islands (38.4% of longlines, removing around 20% of the total catch), around Prince Edward and Marion Islands (hereafter "PEI" – 15.6% of longlines, 6% of the total catch) and around South Georgia (4.7% of longlines, 3.7% of the total catch) (Tixier et al., 2020). In these areas, three genetically, morphologically and ecologically distinct forms of killer whales were confirmed to depredate: Type B at South Georgia (Clark and Agnew, 2010), Type D and Type A-like (hereafter "Crozet/Marion killer whales") in Crozet and PEI (de Bruyn et al., 2013; Reisinger et al., 2015; Tixier et al., 2016). However, knowledge about the feeding ecology, distribution and movements of these killer whales is limited, hampering our understanding of the drivers of their interactions with fishing vessels. For instance, the natural diet (i.e., when not depredating on fishing lines) of Type D killer whales is unknown. Around the Antarctic Peninsula, type B1 killer whales are reported feeding on seals and whales - type B2 killer whales on pygoscelid penguins and probably fish (Pitman and Durban, 2010; Durban et al., 2017), but aside from depredated toothfish (Towers et al., 2019), their natural diet and population identity around South Georgia is poorly understood. Toothfish was only indirectly confirmed as a natural prey of the Crozet/Marion killer whales, which also feed on seals, penguins and whales (Reisinger et al., 2016; Tixier et al., 2019b). Observations and photo-identification data have shown that killer whales actively follow fishing vessels to repeatedly depredate toothfish on their longlines (Guinet et al., 2015), mainly during hauling but potentially also during soaking (Towers et al., 2019; Richard et al., 2020). Yet, the extent to which they compete and co-occur with toothfish fishing vessels and the distance at which they detect these vessels remains unknown.

Observational data of killer whales are limited to those from fishing vessels or from the shore of the remote subantarctic islands (Tixier et al., 2016; Pitman et al., 2011). In these harsh sea conditions, satellite tracking data are useful to assess the unobservable foraging behavior and movements of killer whales (Towers et al., 2019; Reisinger et al., 2014; Durban and Pitman, 2012). The few studies that have used satellite tag data to supplement photographic data have shown that killer whale foraging activities in the region were driven by both environmental variables and the presence of fishing vessels (Reisinger et al., 2015; Towers et al., 2019). However, potential overlap between killer whale foraging areas and toothfish fishing areas, as well as the fine scale behavioural response of killer whales to depredation opportunities at fishing lines, have yet to be assessed. Such information is essential to quantify the magnitude of the conflict between fisheries and killer whales and to assess the ecological drivers and consequences of the conflict (competition for toothfish stocks, changes in killer whale diet and behavior, etc.) to develop effective mitigation solutions (e.g. (Oksanen et al., 2015)).

This study examined both direct and indirect interactions between tagged killer whales and Patagonian toothfish fisheries by integrating tracking data from tags and fishing vessels around South Georgia, PEI and Crozet collected between 2011 and 2024. Specifically, our aims were: i) to assess the extent to which killer whale natural offshore foraging areas overlap with toothfish fishing areas; and ii) to characterize direct interactions between killer whales and fishing gear by examining the movements of both killer whales and fishing vessels before, during and after depredation occurred.

2. Methods

2.1. Killer whale and fishing vessel activity data

We used satellite tracking data from 36 Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) type tags (17 SPOT5, 8 Mk10-A, 5 SPLASH10) from Wildlife Computers (Redmond, WA, USA), and 6 Kiwisat 202 from Sirtrack (Havelock North, New Zealand) deployed on 25 different individuals between 2011 and 2023 in three areas: South Georgia (1 tag on a Type B killer whale), PEI (30 tags on Crozet/Marion killer whales) and Crozet Islands (5 tags on Crozet/Marion killer whales). At PEI, the 30 tags were deployed from shore on 19 different individuals (13 individuals were tagged once, 3 individuals were tagged twice, 1 individual was tagged 3 times and 2 individuals were tagged 4 times). At the time of tagging, 17 tags were deployed on adults (10 males, 7 females), 6 on subadults (6 males), 2 on juveniles and 5 on individuals from unknown age/sex class. At Crozet, 2 tags were deployed from shore and 3 from fishing vessels, on 4 adults (1 male and 3 females) and on one subadult male. At South Georgia, the tag was deployed from a fishing vessel on an adult female. All tags were deployed on the dorsal fin of killer whales using a 68 kg draw weight recurve crossbow (Reisinger et al., 2015; Towers et al., 2019; Richard et al., 2020) or a CO_2 rifle (Dan Inject Dart Gun JM25). Twenty-two of the 25 tagged individuals were identified and known from existing photo-identification monitoring programs (Reisinger and de Bruyn, 2014; Tixier et al., 2021b). These monitoring programs were used to assess preliminary survival of tagging on the individuals equipped and showed no apparent negative effect in the initial years following deployment (Reisinger et al., 2014). To extend tag longevity while capturing biologically sensible data (Clark and Agnew, 2010; Reisinger et al., 2015), three types of setup were used for the tags: i) transmission 01:00–22:00 UTC for 30 days, thereafter 1:00–22:00 UTC on every second day, ii) transmission 01:00–22:00 UTC for 25 days, thereafter 01:00–22:00 UTC on every fourth day, and iii) transmission 00:00–04:00, 07:00–12:00, 15:00–20:00, and 23:00–00:00 UTC for 30 days and thereafter every fifth day. All tags were programmed not to provide more than 600 locations per day (this threshold was never reached).

For fishing vessels, we used both Automatic Identification System (AIS) data and fishing effort (FE) data available from Global Fishing Watch (Kroodsma et al., 2018). The AIS data included the type of activity of vessels, either transiting or fishing, which was determined from trajectories using a convolutional neural network (Kroodsma et al., 2018). This database does not include fishing activities when AIS was disabled by vessels, which can obscure up to 6% of vessel activity (Welch et al., 2022). The FE was calculated from the AIS data as the cumulative time (in hours) fishing vessels spent fishing in $0.1^\circ \times 0.1^\circ$ grid cells during the 2012-2023 period. In our dataset, vessels transmitted a mean of 115 locations.vessel^{-1}.day^{-1} (sd = 88 locations.vessel^{-1}.day^{-1}).

2.2. Tracking data preparation

We reconstructed killer whale tracks from raw Argos location data and fishing vessel tracks from AIS location data. For each killer whale track, we used either the random walk (RW) or the correlated random

walk (CRW) method based on the Akaike Information Criterion (AIC (Akaike et al., 1973);) to estimate positions at a 1-h interval. We assumed a straight track between consecutive reconstructed positions. Only reconstructed positions estimated between raw positions consecutively transmitted by the tag with a time interval of less than 12 h were used for all subsequent statistical analyses using reconstructed tracking data. We selected the CRW if its AIC was lower than the AIC of RW by more than 2 units, since the RW is more parsimonious than the CRW, unless model validation conditions were not met for one or the other method. For fishing vessels, we only used the RW to estimate positions at a 1-h interval. We also applied a routing function to adjust the tracks off land.

We estimated the foraging activity of killer whales through move persistence (MP). MP is a value ranging from 0 (high likely foraging activity) to 1 (low likely foraging activity), which is calculated as an index of similarity between consecutive points in regards to the turning angle and the speed of the movement of the animal (Jonsen et al., 2023). The lower the MP the less similar the turning angle and speed and the more likely the animal is in an area of restricted search of prey (foraging) (Jonsen et al., 2023; Vogel et al., 2021). High values of MP likely indicate transiting behavior. We chose the MP to assess killer whale foraging activity as this metric provides a continuous scale of movement behavior, instead of discrete and arbitrary behavioral states (Vogel et al., 2021). We assigned an estimated value of the MP to each killer whale position on the reconstructed tracks.

2.3. Overlap between killer whale offshore foraging areas and fisheries: kernel approach

We first assessed the extent to which killer whale foraging areas overlap with fishing areas using a kernel approach, with a bandwidth for kernel density estimation selected using a plug-in bandwidth selector (Wand and Jones, 1994). We restricted the killer whale tracking data to positions that occurred in waters deeper than 500 m, to focus the analysis on offshore foraging activities and co-occurrence with fisheries activities. Boundaries were defined by latitude and longitude extrema of killer whale tracks for each of the three zones of tag deployment: Crozet, PEI and South Georgia. Utilization distributions (UD) at thresholds 25, 50, 75 and 90% probabilities of spatial occurrence densities of the tagged killer whales were estimated for killer whale positions weighted by the MP (hereafter the "foraging UD") and for grid cells of fishing activity weighted by the FE (hereafter the "fishing UD"), as well as the percentage of overlap between the two UDs. Calculating UD, a probabilistic model that describes the relative frequency of an animal's locations across space (Fieberg and Kochanny, 2005), here with different thresholds, allowed us to determine what was the level of importance of killer wales foraging areas overlapping with fishing activities.

2.4. Overlap between killer whale offshore foraging areas and fisheries: modelling approach

We used Generalized Linear Mixed Models (GLMM) to assess the relationship between fishing activities and killer whale foraging. We fitted the GLMM to the MP using a beta distribution and a probit function with an auto-regressive process of order 1 to account for temporal autocorrelation. We examined the influence of fishing activity on the MP by testing the effect of the FE.

In addition to the FE, we included environmental covariates in the model: bathymetry (B, retrieved from the GEBCO dataset at a spatial resolution of 15 arc seconds (GEBCO Compilation Group, 2025),), distance to shore (DSh, derived from coastline retrieved from natural earth fine scale data (Massicotte et al),), distance to seamount (DSe, derived from (Yesson et al., 2011)), sea surface temperature (SST, retrieved from Copernicus Marine Services, using Global Ocean Physics Reanalysis GLORYS12V1 product at a 1-month temporal resolution and 1/12° spatial resolution), sea surface height (SSH, retrieved from Copernicus Marine Services using the same product as SST at a 1-month resolution) and area (A, Crozet Islands, PEI, South Georgia). The 1-month resolution of SST allowed us to investigate the influence of large-scale oceanic structures (Goh et al., 2024). We tested distance to shore and distance to seamount as alternatives to bathymetry and thus did not include them with bathymetry in the same model as they were highly correlated (Pearson correlation: −0.74 between bathymetry and distance to shore, −0.55 between bathymetry and distance to seamount).

In the GLMMs we specified a random effect (RE) of killer whale track id (each tag deployment corresponds to one killer whale track id) on the intercept and on bathymetry and fishing effort slopes, to account for inter-individual variability. We also specified a predictive relation for variance as preliminary models presented clear residual deviation. The full model was:

$$probit(MP_{ij}) = \alpha + (\beta_B + \beta_{B,i}) \times B_{ij} + \beta_{SST} \times SST_{ij} + \beta_{SSH} \times SSH_{ij} + (\beta_{FE} + \beta_{FE,i}) \times FE_{ij} + \beta_A \times A_{ij} + \beta_{FE.A} \times FE_{ij} \times A_{ij} + \alpha_i + \varepsilon_{ij}$$

$$log(\Phi_{ij}) = \lambda + \delta_B \times B_{ij} + \delta_{SST} \times SST_{ij} + \delta_{SSH} \times SSH_{ij} + \lambda_i$$

$$\alpha_i \sim N(0, \sigma_\alpha^2)$$
$$\lambda_i \sim N(0, \sigma_\lambda^2)$$
$$\beta_{x,i} \sim N\left(0, \sigma_{\beta_x}^2\right)$$

where MP_{ij} is the move persistence measure for track i at time j and Φ is the beta variance parameter. α and λ represent fixed intercept of MP and Φ respectively. α_i and λ_i represent random intercept for track i of MP and Φ and are drawn in a centered gaussian distribution of variance σ_α^2 and σ_λ^2 respectively. β_x and δ_x are fixed coefficients for variable x. $\beta_{x,i}$ is the random coefficient for variable x and track i and is drawn in a centered gaussian of variance $\sigma_{\beta x}^2$. ε is the residual error.

We fitted this model using only tracks with a model that converged for MP estimation and longer than 5 days, and only positions where bathymetry was >500 m. This limited the bias associated with short-lived tags that sampled only positions near the tagging site (mostly coastal zones) and focused the analysis on the behavior of killer whales in offshore waters where their natural foraging areas are unknown. The final dataset used in the models included 21 tracks from 17 individuals and 3799 positions.

We fitted competing models in a Bayesian framework. We used weakly informative priors (default priors) on all parameters except the autocorrelation parameter, on which we imposed a strong prior (mean = 0.95, sd = 0.03) chosen based on visual examination of autocorrelation functions for each track to facilitate model convergence. We ran the fitting procedure with 4 chains of 2000 iteration steps and 1000 warm up steps. We then selected the models using leave-one-out cross validation expected log pointwise density (loo-elpd (Doll and Jacquemin, 2019);). When two models had overlapping loo-elpd, we selected the simplest one. We performed the selection stepwise by i) selecting the random effect structure (all fixed terms were included in this phase) and ii) selecting the fixed terms with a stepwise backward selection. We did not consider models in which: i) there was an interaction between two terms but one of these two terms was absent as an additive effect, ii) there was a RE on the slope of the response to a variable that was missing as fixed term. We checked model conditions for validation and in particular, we checked if correlation between fixed terms influenced our model using Variance Inflation Factor (VIF), assuming that VIF <10 was acceptable to validate the model (Hair, 1995).

2.5. Characterizing direct interactions with fishing vessels

We synchronized killer whale tracking data and the AIS data of fishing vessels using a 300 km buffer around killer whale tracks to examine the occurrence of direct interactions in the form of depredation on fishing longlines. As killer whale tracks and vessel tracks were both

reconstructed with a 1h time step, we obtained for each killer whale and each vessel a unique pair of positions between which the time difference was at most 30 min. We described killer whale movement through three metrics: killer whale speed, distance from vessel and relative heading. Distances were calculated as straight-line distances between the killer whale and a given vessel. Speed was derived from distance and elapsed time between two positions (1h). Speeds and actual distances were probably underestimated as we considered a straight-line distance. Relative heading was determined from the angle of the killer whale movement based on 3 positions: the position of the vessel at time t, the position of the killer whale at time t and the position of the killer whale at time t+1 (Fig. S2). To avoid the 0-360° discontinuity, we calculated relative heading cosinus, a 1 value meaning the killer whale was heading exactly towards the vessel and −1 meaning the killer whale was going the opposite way.

We defined the beginning of a potential direct interaction with a fishing vessel when the distance between the killer whale and the fishing vessel at time t was <20 km while it was not the case at time t-1. We chose this threshold to take into account the possible time lag of up to 30 min between the times positions of the killer whale and positions of the vessel were transmitted, as well as the uncertainty of these positions (mainly for the positions of the killer whale as Argos data are more error-prone than AIS GPS data). Assuming the fishing vessel moving in one direction at a speed of 20 km/h and the killer whale moving at a speed of 13.4 km/h (based on the maximum killer whales can sustain over extended periods of time - (Guinet et al., 2007)) in the opposite direction, the 20 km threshold corresponds coarsely to the distance at which a killer whale that was at 0 m from the vessel could be from it when the next position is transmitted 30 min later. Similarly, we defined the end of a potential interaction when the distance between the killer whale and the vessel at time t was >20 km while it was not the case at time t-1. Consecutive interactions with the same vessel that were temporally separated by < 12 h were considered as one interaction because these events could not be considered as independent.

We considered three conditions to confirm direct interactions between tagged killer whales and fishing vessels: i) the tagged killer whale moved actively towards the fishing vessel (cos(relative heading) > 0.75 with the vessel) for > 4h; ii) killer whale depredation was recorded by fishery observers present on the vessel from which the tagged whale was within a 20 km range (data from the PECHEKER database at Crozet - (Martin et al., 2021)) and the tagged whale was identified while depredating around the fishing vessel from photo-identification data; iii) the tagged killer whale maintained high swimming speed and its absolute heading varied more than its relative heading, meaning the whale was adjusting its trajectory to the trajectory of the vessel. Direct interactions were considered as confirmed if conditions i) or ii) were met. Condition iii) was a used as an additional confirmation for i).

We excluded from the analyses any unconfirmed interactions and interactions during which a killer whale was tagged. For each confirmed interaction, we estimated the distance at which the killer whale had likely detected the vessel before the interaction started. A detection event was determined as the time when the relative azimuth of the killer whale with the fishing vessel it interacted with had reached a plateau. When the interaction started, we computed its total duration until it ended. When the interaction ended, we calculated the time until the next interaction began for that killer whale. We examined the effect of two factors in explaining the end of an interaction: i) the presence of another fishing vessel nearby with which the killer whale could have interacted, and ii) the vessel speed. We performed a bootstrap ($n_{resampling} = 10{,}000$) with percentile method (Puth et al., 2015) to assess the statistical significance of the two factors: i) by comparing the distribution of distances at which the killer whale was from the second closest vessel when the whale exited the 20 km range of a direct interaction with the distribution of this distance at any time, and ii) by comparing the distribution of speeds at which the vessel traveled when the whale exited the 20 km range with the distribution speeds at which the vessel traveled at any time.

All analyses were performed using R v4.3.3 software (R Core Team, 2024). Additional details on the R packages used are available in supplementary material.

3. Results

The 36 tags deployed between 2011 and 2023 had a mean longevity of 16.7 days (range: 0.33 – 79 days) during which killer whales traveled a mean distance of 1320 km (range: 19.6 – 5022.7 km) (Table 1). Tags transmitted a mean of 19.5 positions.day^{-1} (n = 582 days with positions; range: 1 – 33 positions.day^{-1}) and a total of 11,355 raw locations. After removing the gaps of more than 12 h between 2 consecutive positions, we obtained 11,337 hourly positions. Killer whale movements overlapped with fishing zones (Fig. 1), with 33% of all positions associated with non-zero FE and 58% of tracks including at least one position associated with non-zero FE. Seven of the 36 tracks (19%) and 7 of the 17 tracks from tags that transmitted for more than 2 weeks (41%) went outside of Exclusive Economic Zones (EEZ). These proportions were 17% and 39% at PEI, 20% and 33% at Crozet and 100% and 100% at South Georgia. Three killer whale tracks were long northward travels, up to 36°N. Thirty tracks went to positions where depth was >500 m and positions with depth >500 m represented 40.9% of all positions. Restricted behavior (MP < 0.5) was located at 70% around islands or above seamounts (distance from shore or from seamount centroid <5 km; Fig. 2). Three restricted behavior events occurred without any prominent bathymetric feature, for instance during long northward movements from PEI (Figs. 1 and 2).

3.1. Overlap between killer whale offshore foraging areas and fisheries: kernel approach

The proportion of the killer whale foraging UD in zones were bathymetry exceeded 500 m overlapping with the fishing UD ranged between 0 and 1 at Crozet, 0 and 0.86 at PEI and 0.46 and 1 at South Georgia (Fig. 3a and b). This proportion increased as fishing UD increased (since only overlap increased) and tended to decrease as killer whale foraging UD increased.

3.2. Overlap between killer whale offshore foraging areas and fisheries: modelling approach

The model best fitted to the MP of killer whale positions included the FE, SST, SSH and bathymetry as covariates, with track random effects on intercept and bathymetry slope. The other models all had lower loo-elpd or were not converging (Table 2). Replacing bathymetry by distance to seamount and distance to shore did not improve the model. Killer whale foraging activity increased with the FE (i.e. negative effect of FE on MP in the model), with the bathymetry and the SSH (i.e. negative effect of bathymetry and SSH on MP), and decreased with the SST (i.e. positive effect of SST on MP; Table 3). Variance increased with SST and SSH but decreased with bathymetry (Table 3). No divergent transition was detected and chains mixed well ($\hat{r} \leq 1.02$). Variance inflation factors were all inferior to 4 evidencing low collinearity between variables.

3.3. Direct interactions with fishing vessels

Five killer whales entered 22 times in a 60 km radius from a fishing vessel. Four of these killer whales were involved in 12 direct interactions with toothfish fishing vessels that we detected, of which 2 were confirmed by photo-identification data and 7 by killer whale movement. The 12 interactions involved 6 fishing vessels. Their mean duration was 21.3 h (range: 1 – 87) (Table 5). These interactions included 256 h (2.3% of all time; 54.2% of the time spent within a 60 km range from a fishing vessel). These proportions were respectively 0.02% and 15.4% at PEI, 13.3% and 47.0% at Crozet and 42.0% and 65.4% at South Georgia

Table 1
Details of the 36 killer whales equipped with a satellite tag, tagging and tracking data included in the study.

Track			Tagging						Tracking data				
Individual iD	**Sex**	**Age Class**	**Area**	**Tag**	**Platform**	**Longitude** (°E)	**Latitude** (°S)	**Date**	**Last position date**	**Tag longevity** (days)	**Nb positions**	**Cumulative distance** (km)	**Method of track reconstruction**
CR068_1	M	adult	Crozet	SPOT5	shore	51.8	46.4	December 02, 2011	December 24, 2011	21.4	400	1457.5	rw
CR140_1	F	adult	Crozet	SPLASH10	fishing vessel	52.8	46.8	February 06, 2018	February 14, 2018	8.1	62	337.3	rw
CR004_1	F	adult	Crozet	SPLASH10	fishing vessel	52.8	46.8	February 09, 2018	February 12, 2018	3.1	32	69.8	rw
CR184_1	F	adult	Crozet	SPLASH10	fishing vessel	51.4	46.9	February 21, 2018	March 08, 2018	15.1	49	1462.9	crw
CR161_1	M	subadult	Crozet	SPLASH10	shore	51.9	46.4	December 06, 2023	February 23, 2024	79	698	4472.7	crw
NI_1			PEI	Kiwisat 202	shore	37.9	46.9	June 04, 2011	June 05, 2011	0.8	15	5518.9	rw
M030_1	M	subadult	PEI	Kiwisat 202	shore	37.9	46.9	November 15, 2011	November 18, 2011	2.8	36	130.1	rw
M007_1	M	adult	PEI	Kiwisat 202	shore	37.9	46.9	November 17, 2011	November 18, 2011	0.7	14	425	crw
NI_2			PEI	Kiwisat 202	shore	37.9	46.9	November 19, 2011	November 20, 2011	0.9	19	105.9	rw
M037_1	F	adult	PEI	Kiwisat 202	shore	37.9	46.9	November 24, 2011	November 28, 2011	3.9	37	1080.8	rw
M001_1	M	subadult	PEI	Kiwisat 202	shore	37.9	46.9	December 02, 2011	December 04, 2011	1.8	37	146.9	rw
M007_2	M	adult	PEI	SPOT5	shore	37.9	46.9	April 25, 2012	April 25, 2012	0.3	10	119.3	crw
M001_2	M	subadult	PEI	SPOT5	shore	37.9	46.9	April 28, 2012	May 09, 2012	10.8	179	2576.8	rw
M007_3	M	adult	PEI	SPOT5	shore	37.9	46.9	May 01, 2012	June 23, 2012	53.2	1107	5031.2	crw
M030_2	M	subadult	PEI	SPOT5	shore	37.9	46.9	November 08, 2012	November 27, 2012	18.8	341	1466.6	rw
M026_1			PEI	SPOT5	shore	37.9	46.9	November 29, 2012	December 29, 2012	29.7	532	3554.8	rw
NI_3			PEI	SPOT5	shore	37.9	46.9	December 04, 2012	January 12, 2013	39.4	693	3393.2	crw
M005_1	M	adult	PEI	SPOT5	shore	37.9	46.9	December 14, 2012	December 30, 2012	16	367	1280.9	rw
M035_1	F	adult	PEI	SPOT5	shore	37.9	46.9	December 31, 2012	January 16, 2013	16	341	1542.5	crw
M017_1	F	adult	PEI	SPOT5	shore	37.9	46.9	January 12, 2013	February 21, 2013	40	851	2817.8	rw
M049_1		juvenile	PEI	Mk-10A	shore	37.9	46.9	April 27, 2013	May 10, 2013	12.5	272	946.9	rw
M001_3	M	subadult	PEI	Mk-10A	shore	37.9	46.9	April 28, 2013	May 21, 2013	23	597	1635.5	rw
M030_3	M	subadult	PEI	SPOT5	shore	37.9	46.9	December 02, 2013	December 08, 2013	5.6	99	487.6	rw
M012_1	F	adult	PEI	Mk-10A	shore	37.9	46.9	December 11, 2013	December 12, 2013	1.2	35	755.4	rw
M002_1	F	adult	PEI	Mk-10A	shore	37.9	46.9	April 09, 2014	April 16, 2014	7.2	100	550.8	rw
M004_1	F	adult	PEI	SPOT5	shore	37.9	46.9	November 11, 2014	November 16, 2014	4.7	85	432.8	rw
M015_1	F	adult	PEI	SPOT5	shore	37.9	46.9	December 22, 2014	December 29, 2014	7.2	124	316.2	rw
M008_1	M	adult	PEI	SPOT5	shore	40	46.7	June 01, 2015	July 21, 2015	50.4	826	4556.3	crw
M005_2	M	adult	PEI	SPOT5	shore	37.9	46.9	April 03, 2016	April 22, 2016	18.6	455	1664	rw
M007_4	M	adult	PEI	SPOT5	shore	39.1	44.6	May 01, 2017	May 02, 2017	1.3	42	430.8	crw

(*continued on next page*)

Table 1 (*continued*)

Track			Tagging					Tracking data				
Individual iD	**Sex**	**Age Class**	**Area**	**Tag**	**Platform**	**Longitude (°E)**	**Latitude (°S)**	**Date**	**Last position date**	**Tag longevity (days)**	**Nb positions**	**Cumulative distance (km)**	**Method of track reconstruction**
M053_1		juvenile	PEI	SPOT5	shore	37.9	46.9	July 01, 2017	July 30, 2017	28.8	392	1564.1	rw
M026_2			PEI	Mk-10A	shore	37.9	46.9	December 27, 2017	January 06, 2018	9.7	148	1985.7	rw
M016_1	M	adult	PEI	Mk-10A	shore	37.9	46.9	January 01, 2018	January 23, 2018	22.2	521	2912.2	crw
M016_2	M	adult	PEI	Mk-10A	shore	37.8	46.8	January 01, 2019	January 03, 2019	2.5	57	1282.4	rw
M001_4	M	adult	PEI	Mk-10A	shore	37.9	46.9	February 22, 2019	March 26, 2019	31.9	663	2155.4	rw
SGB031_1	F	adult	S. Georgia	SPLASH10	fishing vessel	−41.1	53.3	June 02, 2015	June 16, 2015	14	257	7723.1	crw

(Table 4).

Before two direct interactions, both at South Georgia, we found changes in the killer whale (SGB031) trajectory relative to movements of fishing vessels at particularly long distances from them. The first of these events was on June 5th, 2015 when the tagged killer whale headed towards v-SG2 from a 130 km distance. The second occurred on June 7th, 2015 when the killer whale headed towards v-SG1 from a 90-100 km distance. For this event, the killer whale headed towards v-SG1 from a 150 km distance at high speed (range: 10.2 - 14.4 km/h), and with an absolute azimuth varying less than the relative azimuth but was also heading towards v-SG2 at the beginning of this movement. Despite not approaching to within 20 km of the vessel, we found a third event on June 3rd, 2015, with the trajectory of the killer whale tagged at South Georgia heading towards v-SG1 from a 110 km distance before turning and heading towards v-SG2, which was at 40 km from the whale when this turn occurred (Fig. 4).

Killer whale CR140_1 interacted for 115 h with the fishing vessel v-CR1 but did not travel towards it. Interaction #1 ended when the vessel left the area and interaction #2 began when it came back to the area where CR140 remained. Interactions #1 and #2 were confirmed thanks to photo-identification data but no clear depredation-linked movement from the killer whale was detected with the resolution we had. Interaction #3 was not confirmed.

Killer whales M049_1 and CR161_1 entered the 20 km radius from a fishing vessels v-M1 and v-CR2 but we were not able to confirm these interactions through photo-identification nor killer whale movements.

At the end of an interaction, the speed of the fishing vessel was significantly higher (on average by 6.66 km/h; 95% CI: [3.47; 9.47]) than at any other time. Fishing vessels traveled a median distance of 81.9 km (range: 3.1 km – 149.3 km) between the last set of an interaction and the next set. We found no significant difference in the distance of a killer whale to the second closest vessel when an interaction ended compared to that distance at any other time.

4. Discussion

Using killer whale tracking data from when the tagged killer whales were in waters deeper than 500 m, we found a positive correlation between the demersal longline fishing effort and killer whale offshore foraging activity. This suggests an overlap between killer whale offshore foraging areas and areas used by longliners to target toothfish in the offshore waters of around PEI, Crozet and South Georgia. In the latter, the only tagged individual actively and repeatedly interacted with fishing vessels to depredate during the tracking period, thus limiting inference on the natural foraging behavior. However, the spatial overlap we detected around Crozet and PEI was confirmed as occurring when killer whales were foraging in absence of fishing vessels and supported by both the kernel and modeling approaches. Together, these results suggest that off Crozet and PEI, killer whales from the Crozet/Marion form and fishing vessels independently use the same areas and may compete for Patagonian toothfish in these areas. Consistent with previous studies using indirect approaches such as trophic markers (Reisinger et al., 2016; Tixier et al., 2019b) or inferences from killer whale dive data (Reisinger et al., 2015; Richard et al., 2020), these results support the assertion that toothfish is an important prey for killer whales in the region. We also found that when offshore beyond the 500 m isobath, killer whale foraging activity decreased when the water depth increased. Although killer whales are able to dive to depths >1000 m, such deep dives remain occasional and are likely to be energetically costly (Reisinger et al., 2015; Towers et al., 2019). As toothfish is a demersal fish occupying depths from 10 m – to 2500 m, killer whales may therefore favor catching this prey within the lower bathymetric range of the species (e.g. (Richard et al., 2020)) and target small to medium-sized individuals as large toothfish are usually found >1200 m (Péron et al., 2016).

We found that when moving to waters >500 m deep, killer whale

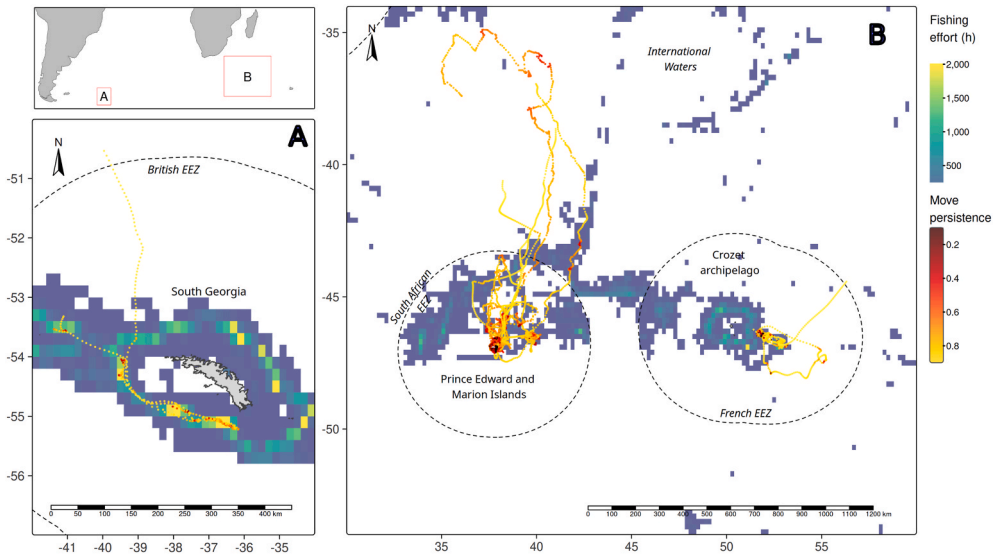

Fig. 1. Killer whale tracks and fishing effort: A. for the tag deployed around South Georgia, and B. for tags deployed around PEI and Crozet islands. Fishing effort was quantified as the total number of hours fishing vessels spent fishing in 0.1° × 0.1° grid cells over the 2012-2023 period. Killer whale tracks are colored as per the foraging activity estimated by the move persistence (the lower the move persistence the higher the foraging activity).

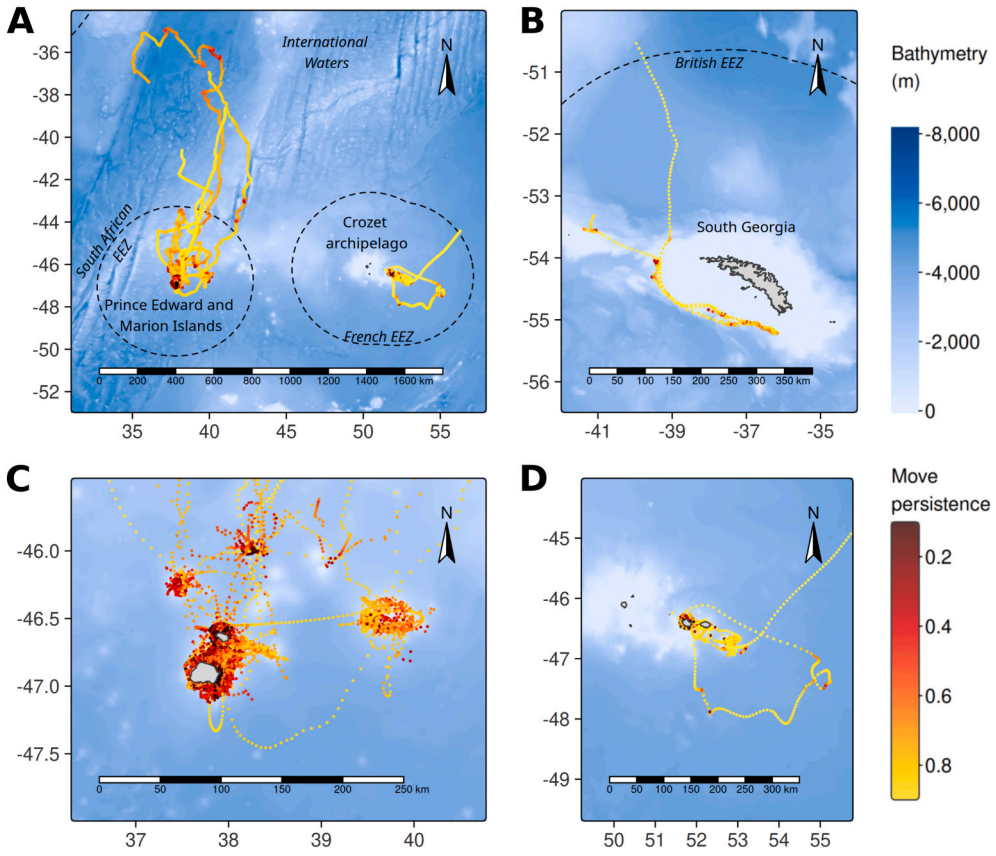

Fig. 2. Killer whale tracks and bathymetry A. for tags deployed around PEI and Crozet islands, and B. for the tag deployed around South Georgia, with C. and D. a zoom in on track sections close to the PEI and Crozet islands, respectively. Killer whale tracks are colored as per the foraging activity estimated by the move persistence (the lower the move persistence the higher the foraging activity).

foraging activity was also associated with oceanographic factors that are unlikely to influence toothfish distribution, suggesting that killer whales may feed on other offshore prey. In particular, killer whale foraging activity increased when sea surface height increased, a feature often associated with anticyclonic eddies regarded as pelagic prey aggregation zones for marine predators (Bestley et al., 2020). Anticyclonic eddies have been shown to attract squids (Xing et al., 2024), king penguins (*Aptenodytes patagonicus*) (Cotté et al., 2007), and southern elephant seals (Bailleul et al., 2007). The former has been suggested as part of killer whale diet at PEI (Reisinger et al., 2016) while the two latter

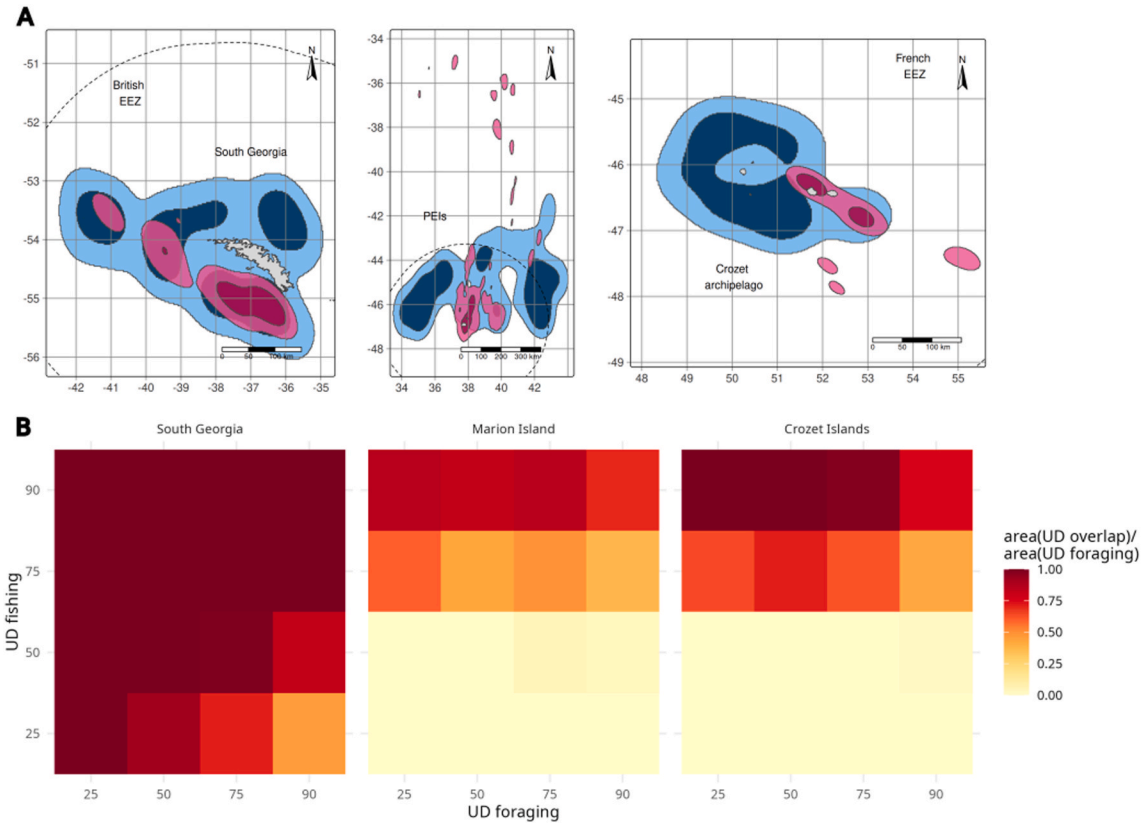

Fig. 3. Overlap between killer whale foraging areas and fishing areas, with A. Maps of the killer whale foraging UD (pink) and fishing UD (blue) with both the 90% UD (light) and 50% UD (dark); and B. the percentage of killer whale foraging UD overlapping with the fishing UD. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Selected models fitted to the move persistence γ. Δelpd: difference in leave-one-out expected log pointwise density relative to reference model. se_elpd: elpd difference standard error. If uncertainty overlapped with elpd difference, the simplest model was considered as the best model.

Model		Δelpd	se elpd
1	probit(MP) ~ B + FE + A + SST + SSH + (1+B + FE|Track)	0	0
Null	probit(MP) ~ (1|Track) log(φ) ~ (1|Track)	−3063478	356675

Table 3
Best model (model 1) parameters estimates. SE: standard errors; CI: confidence interval.

Parameter	Estimate	Estimate Error	Lower 95% CI	Upper 95% CI
B	−0.31	0.07	−0.45	−0.17
FE	−0.19	0.08	−0.34	−0.04
SSH	−0.20	0.02	−0.25	−0.16
SST	0.37	0.02	0.33	0.42
Area PEI	−0.47	0.57	−1.58	0.67
Area SG	0.33	0.74	−1.16	1.81
PEI:FE	0.22	0.08	0.07	0.37
SG:FE	−0.09	0.09	−0.26	0.09
phi_B	−0.08	0.04	−0.17	−0.02
phi_SST	1.93	0.07	0.87	1.14
phi_SSH	−1.35	0.07	−0.37	−0.16

species have been confirmed as prey for killer whales of the Crozet/Marion form when foraging in inshore waters around the Crozet and Marion islands (Tixier et al., 2019b; Guinet, 1992; Reisinger et al., 2011). While inshore foraging activities on elephant seals appear concentrated on newly weaned pups during the breeding period of the species on the islands in austral spring (Martin et al., 2021; Reisinger et al., 2011), killer whales may also find this prey in offshore waters where juveniles and adult females are during periods outside breeding (Martin et al., 2021; Reisinger et al., 2011). Among the other resources Crozet/Marion killer whales may find in offshore waters are baleen whales, which have also been confirmed as prey in inshore waters in summer (Guinet et al., 2000). In particular, predation on southern right whales *Eubalaena australis*, using the waters around subantarctic islands as foraging grounds (Shabangu et al., 2024), has been observed from a toothfish longliner in offshore waters around Crozet in 2013 (Tixier et al., 2019b; Vermeulen et al., 2024).

By combining tracking data from killer whales with tracking data from fishing vessels (AIS data), we detected sharp changes in the heading of some of the tagged killer whales followed by high-speed movements towards fishing vessels, in some cases over distances >100 km, suggesting decision-making events of killer whales to engage in depredation on fisheries catches. The clear change in the trajectory directed towards the nearest fishing vessel paired with an increased traveling speed (range: 10.2 - 14.4 km/h) were two behavioral features only observed when fishing vessels were present, independently from the spatialized fishing effort (used as a proxy of spatial variation in toothfish abundance), and systematically ending in the tagged killer whale being within the 20 km range of a fishing vessel. Together, these findings support the assumption that although killer whales and fishing vessels can indirectly use the same areas, the changes in killer whale behavior we detected in situations when they spatio-temporally co-occurred may not be driven by the search of natural foraging areas but instead by a response to opportunities to depredate. About the mechanisms of such response, we can suggest two possible explanations: i) the killer whales searched for fishing vessels in areas where they knew

Table 4
Time (in hours) killer whales spent likely engaging in direct interactions with fishing vessels relative to the total time tags transmitted positions, and relative to the time killer whales spent within 100 km and 60 km ranges of the nearest fishing vessel. Percentages of the time likely spent engaging in direct interactions relatively to the total tagging time, the time spent within a 100 km range, and the time spent within a 60 km range are shown in brackets.

	Time likely spent in direct interaction with fishing vessels	Number of hourly reconstructed positions	Time spent within a 100 km range of fishing vessels	Time spent within a 60 km range of fishing vessels
All areas	256	11337 (2.3%)	836 (30.6%)	472 (54.2%)
PEI	2	10126 (0.02%)	166 (1.2%)	13 (15.4%)
Crozet	118	887 (13.3 %)	446 (26.5%)	251 (47.0%)
South Georgia	136	324 (42.0%)	224 (60.7%)	208 (65.4%)

Table 5
Details of direct interactions between tagged killer whales and fishing vessels. The interaction # refers to one interaction event between a killer whale and a given fishing vessel and increases chronologically in case of multiple interaction events of the same killer whale with the same fishing vessel.

Killer whale iD	Vessel	Interaction #	Date interaction started	Date interaction ended	Duration (h)	Closest position (km)	Detection range (km)	Time to next interaction (h)	Confirmed
M049_1	v-M1	1	May 03, 2013	May 04, 2013	2	15.2	NA	NA	0
SGB031_1	v-SG1	1	June 02, 2015	June 03, 2015	7	0.7	NA	28	1
SGB031_1	v-SG2	1	June 04, 2015	June 04, 2015	13	12.6	40	2	1
SGB031_1	v-SG1	2	June 04, 2015	June 05, 2015	21	0.7	60	20	1
SGB031_1	v-SG2	2	June 06, 2015	June 06, 2015	3	4.4	130	18	1
SGB031_1	v-SG2	3	June 07, 2015	June 07, 2015	12	6.8	40	3	1
SGB031_1	v-SG1	3	June 07, 2015	June 09, 2015	26	1.7	100	7	1
SGB031_1	v-SG3	1	June 09, 2015	June 11, 2015	56	0.7	50	NA	1
CR140_1	v-CR1	1	February 06, 2018	February 07, 2018	7	2	NA	14	1
CR140_1	v-CR1	2	February 07, 2018	February 14, 2018	87	1	NA	47	1
CR140_1	v-CR1	3	February 13, 2018	February 14, 2018	21	3.5	NA	NA	0
CR161_1	v-CR2	1	February 11, 2024	February 11, 2024	3	19.9	NA	NA	0

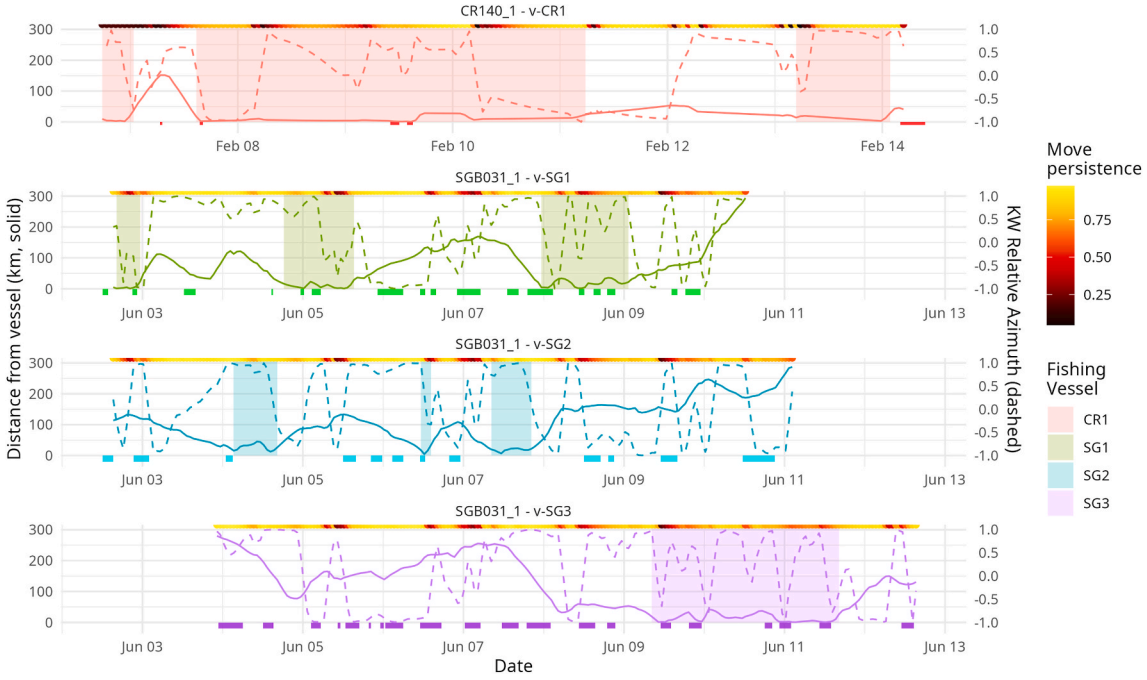

Fig. 4. Killer whale movement and foraging activity in relation to vessel fishing activity. Solid line represents the distance from the killer whale to the vessel and dotted line represents the killer whale relative azimuth to the vessel. Background color represents an interaction with a specific vessel. Segments below the graph indicate phases when the vessel was fishing (either setting or hauling longlines). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

fishing effort was high until they detected the fishing vessel, and ii) the killer whales initiated the movements because they detected a fishing vessel from the distance, likely acoustically. For the latter, the detection range we suggest here (>100 km) from the changes in heading and speed of the tagged killer whales is consistent with the range at which high intensity low frequency cavitation noises generated by fishing

vessels, especially when maneuvering during hauling., may propagate and be heard by killer whales. These noises have been shown, for instance, to act as potential attractive cues for depredating sperm whales in Alaska (Thode et al., 2007). Unlike for hauling, the detection range of traveling fishing vessels or vessels setting their lines should be in the orders of 10-20 km (Richard et al., 2021). These results suggest that both Type B and Crozet/Marion killer whales, which have developed depredation as a new feeding strategy over the past three decades, likely know that the benefits they can gain from depredation outweigh the costs of traveling long distances, and maximize these benefits through prolonged interactions. As shown for other species, both marine and terrestrial, individuals are more likely to engage in feeding on anthropogenic food subsidies when these are highly predictable (Oro et al., 2013). This is the case of toothfish fisheries, which operate on spatially-restricted fishing areas over extended periods of time (toothfish longliners usually remain at sea for months) (Tixier et al., 2020). In addition, toothfish fisheries offer opportunities to feed at low foraging cost on a highly calorific prey (9 kJ g^{-1} for toothfish (Schaafsma et al., 2018; Faure et al., 2021);) especially by bringing large toothfish to the surface. These opportunities are further increased by the fact that longliners often operate simultaneously, and we showed here that killer whales can switch from one vessel to another operating nearby to repeatedly depredate on longlines. While predictability of opportunities to feed at low foraging effort can drive the start of an interaction, the determinants of the end of an interaction are more difficult to interpret. We found that most direct interactions ended when fishing vessels left a fishing area and traveled at a speed greater than mean speed by 6.66 km/h to begin fishing again in an area located at a mean distance of 82 km away from the previous one. Following these vessels can presumably be energetically costly because killer whales are not able to sustain fishing vessels speed over large distances (Guinet et al., 2007). On multiple occasions killer whales stopped depredating despite other fishing vessels operating nearby. This suggests that other factors likely influence the occurrence of direct interactions between killer whales and fishing vessels, and the low number of events we detected here precludes general patterns from being identified. Among these factors, killer whales may stop following a vessel to depredate on soaking sets if these are at reachable depths ((Towers et al., 2019; Richard et al., 2020); Figs. S1 and S6).

We found that the occurrence of direct and indirect interactions between killer whales and fishing vessels varied across individuals, both between and within populations. Although limited to only one tagged individual, the extent of the overlap between foraging activities of the Type B killer whale with fishing activities at South Georgia was greater than that of the Crozet/Marion killer whales from different populations do not equally overlap with fishing activities. While this may reflect a greater contribution of Patagonian toothfish to the diet of Type B (Pitman and Durban, 2010; Durban et al., 2017)killer whales at South Georgia, which appear to be less generalist in their feeding preferences than the Crozet/Marion killer whales (Pitman and Durban, 2010; Reisinger et al., 2016; Tixier et al., 2019b), this has yet to be confirmed and the lack of dietary information for this type of killer whales in this region precludes any conclusion at this stage. Within populations, among the factors influencing the occurrence of direct and indirect interactions between killer whales and fishing vessels is individual heterogeneity. We provided evidence of such heterogeneity across the tagged killer whales both when foraging naturally and when depredating on longlines. We found that killer whales from different populations do not equally overlap with fishing activities.These results are not surprising since these killer whales, which are considered as generalist in their feeding preferences as populations (Reisinger et al., 2016; Tixier et al., 2019b), show wide variation in their foraging behaviours. There is likely also variability in contribution of prey types to their diet, seasonally, but also between social groups within populations (Reisinger et al., 2016; Guinet, 1991; Auguin et al., 2025). As such, one may assume that individuals whose foraging areas overlapped the most with fishing areas belong to social groups that are more specialized for feeding on toothfish than others. Individual heterogeneity was associated with direct interactions with fishing vessels. For instance, depredation by individual CR140, which belongs to a social unit (CR027/CR139) frequently depredating on fishing lines (Auguin et al., 2024), occurred opportunistically. The killer whale did not move toward or follow a fishing vessel, but depredated when the vessel came fishing in the area it already was, while individual SGB031_1 at South Georgia repeatedly and actively searched for fishing vessels. Similarly, the extent to which killer whales exploited opportunities to depredate when vessels were nearby differed between individuals tagged at PEI (15% of killer whale positions within a 60 km range from a fishing vessel were part of a direct interaction) and those tagged at Crozet (47%). This is in line with the heterogeneity demonstrated through tracking data in other killer whale populations, for example where killer whales engaged differently with herring fisheries in Norway (Mul et al., 2020). It is also supported by large variation across killer whale social groups in the frequency and spatial range at/over which they engaged in depredation at Crozet (Auguin et al., 2024). Most of the tags were deployed over the same time of the year (between November and April), and sample size greatly varied between areas, being low at Crozet and South Georgia. These prevented from potential factors influencing the observed heterogeneity, including seasonal variation in the propensity of individuals to engage in depredation, from being further investigated. In particular, investigating killer whale behavior at times of the year outside the periods over which whales were tagged here, including during periods when fishing vessels may be less active, would be essential to complete our understanding of the feeding ecology of killer whales from these subantarctic populations.

The indirect and direct interactions between killer whales and fishing activities presented in this study suggest that toothfish fisheries may have a combination of both negative and positive impacts on killer whales. First, the overlap between killer whale offshore foraging areas and fishing areas supports the assumption that fisheries may negatively impact killer whales through the exploitation of toothfish and competition for that resource. The extent of this competition has yet to be quantified, but is likely to have been detrimental given local depletions of toothfish stocks by the combination of legal and illegal, unreported, unregulated (IUU) or poorly regulated fishing activities (Österblom and Sumaila, 2011), especially in international waters where we confirmed killer whale foraging activity in this study. Second, the engagement of killer whales in direct depredation interactions with fisheries catches, sometimes over extended periods of time, may positively impact individual fitness of killer whales through provisioning effects (Tixier et al., 2015, 2017; Esteban et al., 2016; Podofillini et al., 2019). This was demonstrated at Crozet where the depredating subset of the population had a higher growth rate than the non-depredating set when interacting with legal fisheries (Tixier et al., 2017). However, these positive effects may be overshadowed by the negative effects of interacting with IUU or poorly regulated fishing vessels that use lethal means to repel depredating killer whales. High levels of IUU fishing occurred within EEZs in the early years of toothfish fisheries and had detrimental effects on the survival of depredating whales (Guinet et al., 2015; Busson et al., 2019). IUU fishing is likely to persist near the EEZ boundaries as recently evidenced in the PEI/Crozet region (Weimerskirch et al., 2020). Our results confirm that killer whales tagged in this region frequently leave EEZs: 19.4% of all tracks were partly outside EEZs and 38.5% of the tracks from Marion Island that transmitted data for over two weeks went outside the PEI EEZ. Since up to 6% of the world fishing activities may be obscured by vessels disabling AIS (Welch et al., 2022), we cannot exclude that some of the killer whale foraging activity we detected in international waters was associated with interactions with fishing vessels for which AIS data were unavailable. Last, long-range decisions made to engage in depredation, paired with active following of fishing vessels and repeated interactions over periods of days suggest that fisheries may modify the natural foraging behavior, of killer whales to a non-negligible extent. Whether a prey-switching or only a

technique-switching to catch the same prey is occurring is still unclear. While such changes in behavior were not systematic (<60% of the time spent within a 60 km range of a fishing vessels resulted in a direct interaction), technique-switching could result in dependency of killer whales on fisheries. Alternatively, potential prey-switching to depredation would likely alter killer whale predation pressures on other prey, and thus trophic interactions within local ecosystems (Clavareau et al., 2020).

In this study, we used Argos data from tags deployed on killer whales from different populations around multiple subantarctic islands. Although this dataset is, to our knowledge, the largest dataset of killer whale tracking data in the subantarctic, the sample size remained limited, and this may constrain the strength or generalizability of the conclusions drawn from the results. Firstly, the uneven repartition of tags across the different areas and populations, with only one tag deployed on a type B killer whale at South Georgia, made difficult of the interpretation of our findings in regards to the likely variation in the feeding ecology and propensity to depredate on fisheries catches ecotypes (de Bruyn et al., 2013). Secondly, while the resolution of Argos data allowed us to infer large scale tendencies about preferred foraging areas and to detect long distance movements likely associated with fishing activities, it was not possible to assess fine scale behavioral variation between individuals, especially when directly interacting with fishing vessels. In the absence of otherwise obtained cues, like photographs taken from the fishing vessels the tagged killer whales interacted with, the low sample size and data resolution prevented us from confirming direct interactions with fishing vessels. Lastly, the low temporal resolution of the killer whale Argos data and the lack of detailed information about the fishing phases vessels were in when operating (i.e., setting or hauling the gear) prevented us from i) assessing how the phases influenced the propensity of killer whales to engage in depredation, and ii) the extent to which killer whales may depredate on longlines during the soaking phase between setting and hauling. Although the observation data suggests that killer whales predominantly engage in depredation during hauling, likely because the energetic costs of accessing the fish caught on hooks, without diving deep, are the lowest, the diving abilities of killer whales would allow them to access longlines set on the seafloor at depths >500 m and we cannot exclude that they may engage in depredation during the soaking phase too (Richard et al., 2020). The latter was indeed suggested by the dive behavior recorded for the killer whale tagged at South Georgia, with dives to the bottom in areas where longlines were set and soaking on the seafloor (see Fig. S6).

5. Conclusion

In this study, we provide evidence for both direct and indirect interactions between killer whales and toothfish longline fisheries in subantarctic waters of the southern Atlantic and Indian Oceans. Despite a number of limitations associated with a low sample size and the low temporal resolution of the Argos data, the findings bring insights to our understanding of the ecology and behaviour of killer whales both in natural situations (in absence of fishing vessels) and in response to fishing vessels that can be used to improve the management of their conflict with fisheries, in this region but also in other regions where the species depredates on fisheries catches. Strategies fishers could use to mitigate depredation may include avoiding areas identified as important killer whale offshore foraging areas, as well as leaving an area where depredation is occurring and moving at high speed to go fishing in a new area being sufficiently distant from the previous one to decrease the chances of killer whales following the vessel. While these recommendations are in line with those made in previous studies (Guinet et al., 2015), our study highlights that the decision killer whales make to engage in depredation is not systematic when fishing vessels are around. Other factors, which have yet to be elucidated, likely influence this decision and may include factors associated with prey availability, prey predictability and individual heterogeneity. Despite these limitations, the findings demonstrate that combining satellite tracking data of wild species with tracking data of human activities can bring key insights on the mechanisms of human-wildlife conflicts involving large marine predators and fisheries in remote marine regions. Specifically, this approach, by increasing our understanding of the behavior of predators beyond observational capacity, can help improve ecosystem-based management of fisheries, as well as conservation measures for predators' populations exposed to competition with fishers and lethal retaliation practices from illegal or poorly regulated fisheries.

CRediT authorship contribution statement

Vinicius Robert: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Anaïs Laurioux:** Writing – review & editing, Formal analysis, Data curation. **Ryan R. Reisinger:** Writing – review & editing, Resources, Investigation. **Jared R. Towers:** Writing – review & editing, Resources, Investigation. **Erwan Auguin:** Writing – review & editing. **Margaux Mollier:** Writing – review & editing. **Gaëtan Richard:** Writing – review & editing, Investigation. **P.J. Nico de Bruyn:** Writing – review & editing, Resources, Investigation. **Christophe Guinet:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Paul Tixier:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.107938.

Data availability

The authors do not have permission to share data.

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