COLTO study on whale depredation
2017-2019

TECHNICAL REPORT
Year 2

CHILE
Industry partners: AOBAC (GLOBAL PESCA SpA., PESCA CHILE, PESCA CISNE)

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Contents

1. Summary of the findings

Using fishing data spanning from 2006 to 2016 and photo-identification data collected in 2017 and 2018, this study aimed to i) assess the extent of whale depredation, ii) examine the variables influencing this extent, and iii) identify potential ways of minimizing this issue in the commercial toothfish fishery operating in Southern Chile.

The main findings can be summarized as follows:

- Sperm whale depredation interactions occurred on 42% of the hauls and killer whale depredation interactions on 19% of the hauls;
- 191 [95% CI 124-257] t of toothfish were estimated being removed every year by whales from longlines, that is a depredation rate of 12.1% [8.6-15] of the total catch (landed + depredated);
- A minimum of 61 killer whales were involved in depredation interactions, including 41 from the "regular" form and 20 from the "Type D" form;
- "Regular" killer whales were found to move over large distances (>600 km) across the fishing area, sometimes over short periods of time to repeatedly interact with fishing vessels. "Type D" killer whale movements were more spatially restricted (limited to the southern part of the area);
- Low probabilities of depredation were detected across the whole fishing area in Autumn for sperm whales, and in Summer and Winter for killer whales;
- Whale depredation hotspots were identified and mapped;
- The use of trotlines equipped with cachaloteras and increased hauling speed significantly reduced the amount of the catch removed by whales when depredating;
- Vessels needed to move on across distances > 100 km to reduce their probability of being followed by whales. For sperm whales, this distance threshold was substantially decreased in Autumn;

The project has also allowed for extensive research and increase of knowledge on other aspects of whale depredation across subantarctic fisheries, with major findings provided here. From this first study, questions for which further research effort is needed were identified and included: i) a fine scale analysis of the combined movements of vessels and whales to better understand the drivers of the detectability of vessels; and ii) development, design and testing of cachaloteras with increased effectiveness and other technological means to reduce depredation.

2. Introduction

Using the Coalition of Legal Toothfish Operators (COLTO) as an opportunity for international collaboration between science, industry, government and NGO groups, a study was initiated in 2017 to investigate whale depredation in Chile, Falkland Islands, South Georgia/South Sandwich Islands (UK) and Marion/Prince Edward Islands (South Africa). This study was designed to develop multi-disciplinary research aimed at identifying the best combination of measures, both technological and behavioural, to reduce depredation both locally and globally, i.e. across the different Patagonian toothfish longline fisheries operating in the Southern Ocean.

An interim report was produced in 2018 and primarily examined the operational and environmental variables influencing the occurrence of depredation interactions with killer whales and sperm whales. Following this first report, this document is the final report of the program for the Chilean industry partners, AOBAC, who have supported the study. Using existing fishing, observation and photo-identification datasets, the report presents the final results on:

- the frequency of depredation interactions,
- the estimated amount of toothfish removed by whales when depredating on longlines,
- the minimum number of whales involved in depredation interactions;
- the potential ways of avoiding depredation interactions and minimizing the amount of toothfish removed by whales when depredating.

Two datasets were received to conduct the analyses, both from IFOP. The first dataset was sent on December 12th 2016 and included data spanning from 2006 to 2013. The second was sent on August 3rd 2017 and included data from 2014 to 2016. Both datasets included details on fishing operations (date/time, GPS coordinates, depth of longline sets at setting and hauling), data on the number of depredating whales during hauling, which was later converted to presence/absence data, as well as data on the fishing effort and catch of Patagonian toothfish.

Data from a total of 12,748 longline sets (hereafter “hauls”) hauled in southern Chile were processed and data from 12,298 hauls were eventually used for analyses over the 2006-2016 period (450 hauls were excluded due to missing information on the variables needed) (Figure 1). These hauls included hauls sets using autoline and 11,470 using trotline equipped with a cachalotera system. Data from 12 different vessels were available, but the majority were collected from 7 vessels. Data were available for all months of the year, but fishing effort was substantially less from June to August.

3. Frequency of depredation interactions

In this section, the frequency of depredation interactions was primarily measured and depicted as an “interaction rate”, which was calculated as the proportion of hauls depredated out of the total number of hauls. Additionally, secondary measures were also calculated and provided: the proportion of fishing days during which at least one haul was depredated out of all fishing days and the proportion of the fishing area (0.1 x 0.1° grids) in which at least one haul was depredated out of all grids.

3.1. Overall

From 2006 to 2016, 2,373 hauls (19.3% of all hauls) occurred in the presence of depredating killer whales, and 5,208 hauls (42.3% of all hauls) occurred in the presence of depredating sperm whales. The two species were recorded simultaneously depredating during 1,095 hauls (8.9% of all hauls) (Figure 1). Sperm whale depredation interactions occurred during 73% of the fishing days and over 75% of the fishing area (Figure 2). Killer whale depredation interactions occurred during 48% of the fishing days and over 52% of the fishing area (Figure 2).

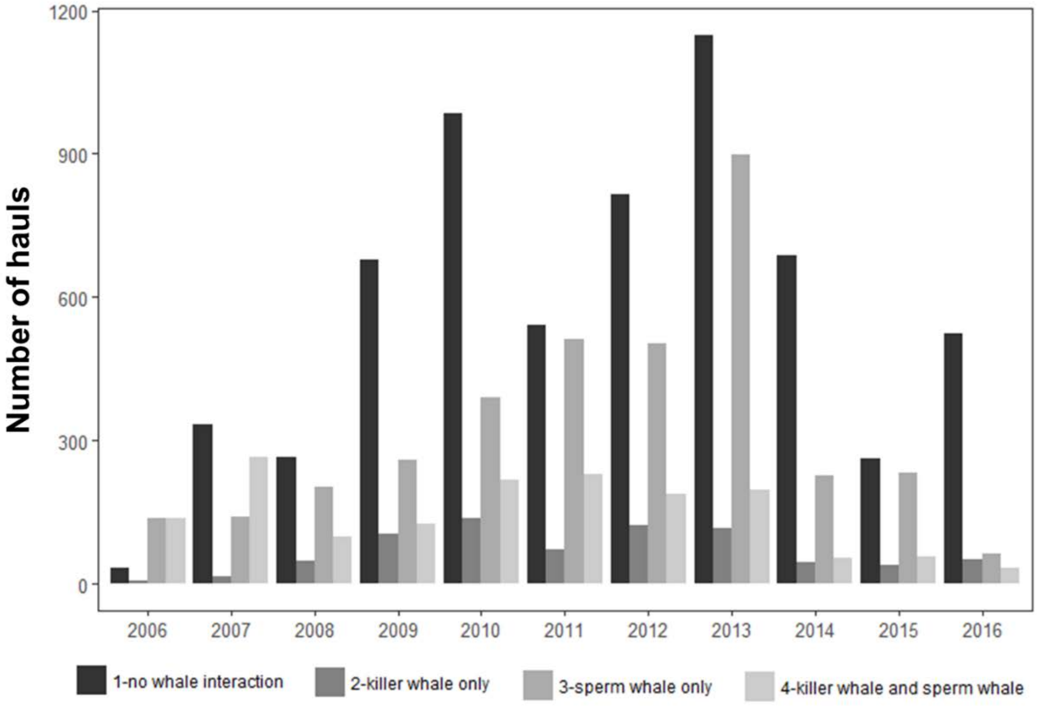

Figure 1. Annual occurrences of whale depredation interactions (number of hauls) for the Patagonian toothfish fishery operating in southern Chile from 2006 to 2016. Distinction was made between hauls with presence of killer whales as the only depredating species (dark grey), with presence of sperm whales as the only depredating species (grey), with both killer and sperm whales depredating simultaneously (light grey) and in absence of any depredating species (black).

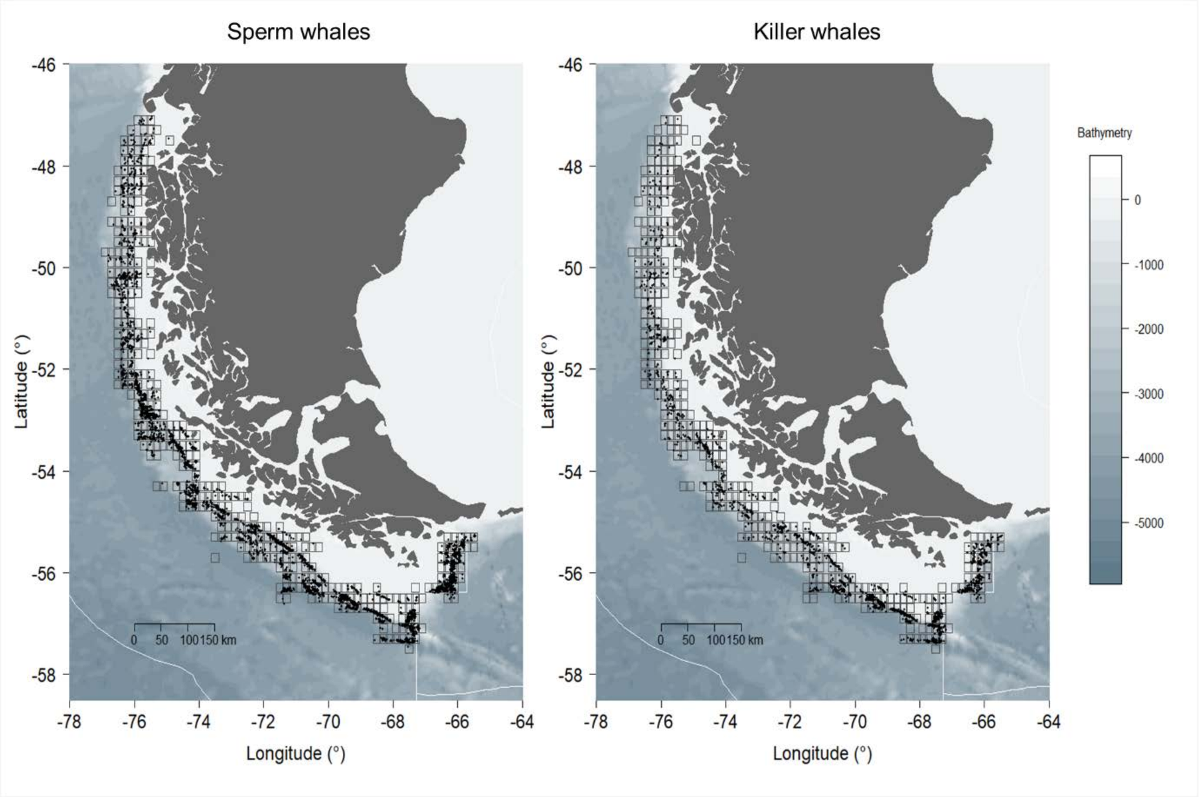

Figure 2. Distribution of fishing effort in southern Chile from 2006 to 2016 (squares) and hauls (black dots) with presence of depredating sperm whales (left) and killer whales (right) by the commercial Patagonian toothfish longline fishery.

3.2. Variation between vessels

Large variation in the frequency of depredation interactions was detected between the 12 vessels of the fleet (Figure 3). While 75% of the vessels experienced sperm whale depredation during >30% of their hauls, low interaction rates were reported for PWI and SPI with 7% and 6% of their hauls, respectively, however, these two vessels only operated for 1 year of the study period. Among vessels that operated over more than 2 years, ABA had the highest interaction rate with sperm whales with 62 ± 12% SE (n = 3 years) of its hauls. For 11 of the 12 vessels, killer whale depredation interactions occurred during between 8 and 22% of the hauls. GPI was the vessel with the highest interaction rate with killer whales with 35 ± 10% SE (n = 9 years) of its hauls.

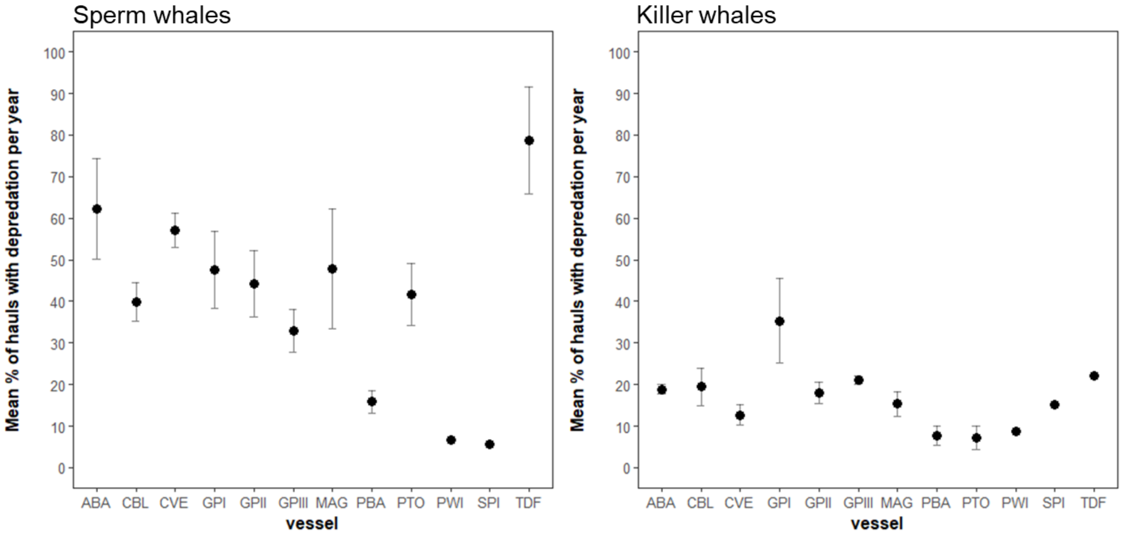

Figure 3. Mean proportions of hauls with presence of depredating sperm whales (left) and killer whales (right) for each of the 12 vessels of the Chilean toothfish commercial fishing fleet. Black dots are mean values across years and error bars are the standard error of the mean.

3.3. Inter- and intra-annual variation

The frequency of sperm whale depredation interactions varied from 89 ± 5% of the hauls per vessel (n = 4) in 2006 to 18 ± 2% per vessel (n = 4) in 2016 (Figure 4). The apparent declining trend is biased by high levels of sperm whale depredation in 2006, for which the available data were limited and collected over the September – December period only. Over the 2006-2016 period, the interaction rate of killer whales varied from 37 ± 17% of the hauls per vessel (n = 4) in 2006 to 15 ± 3% per vessel (n = 4) in 2016 (Figure 4). Years 2006, 2007 and 2008 were characterized by high interaction rates (>30% of the hauls) and large variation across vessels (large SE). From 2009 to 2016, killer whale interaction rates showed less variation across vessels and remained within 11-20% of the hauls for all years.

The frequency of sperm whale depredation interactions varied between months with an apparent decrease from March to May (each month having < 31% of the hauls per vessel) and in July (25 ± 3% of the hauls per vessel, n = 3 vessels) (Figure 5). The months of high sperm whale interaction rate were from September to February, each month with > 48 % of the hauls that occurred during that month. The frequency of killer whale depredation interactions showed less intra-annual variation than that of sperm whales, but was minimal in August (11 ± 5% of the hauls per vessel, n = 3 vessels) and November (12 ± 2% of the hauls per vessel, n = 9 vessels) and maximal in June (26 ± 10% of the hauls per vessel, n = 5 vessels) (Figure 5).

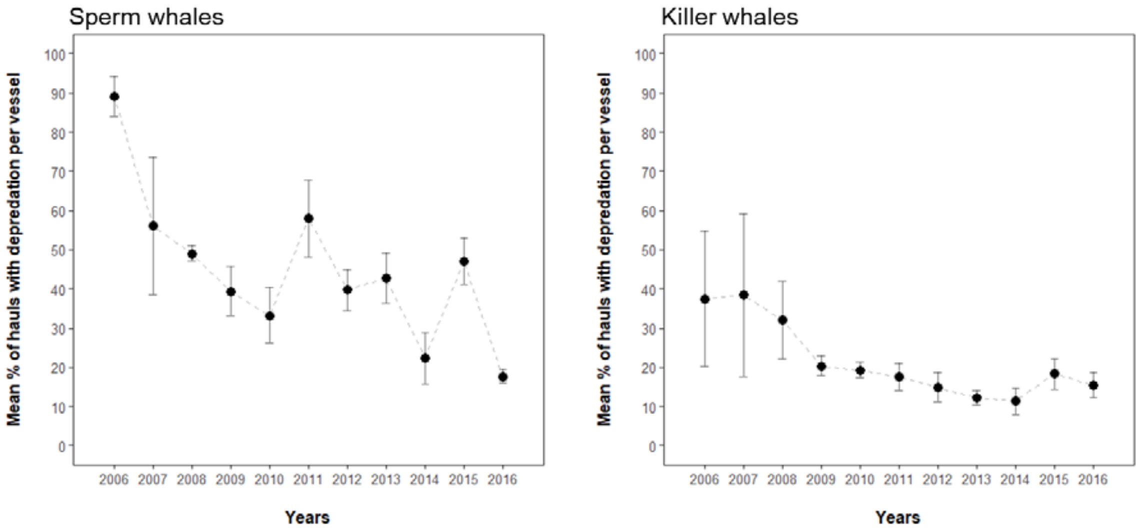

Figure 4. Mean proportions of hauls with presence of depredating sperm whales (left) and killer whales (right) by year over the 2006-2016 period. Black dots are mean values across vessels and error bars are the standard error of the mean.

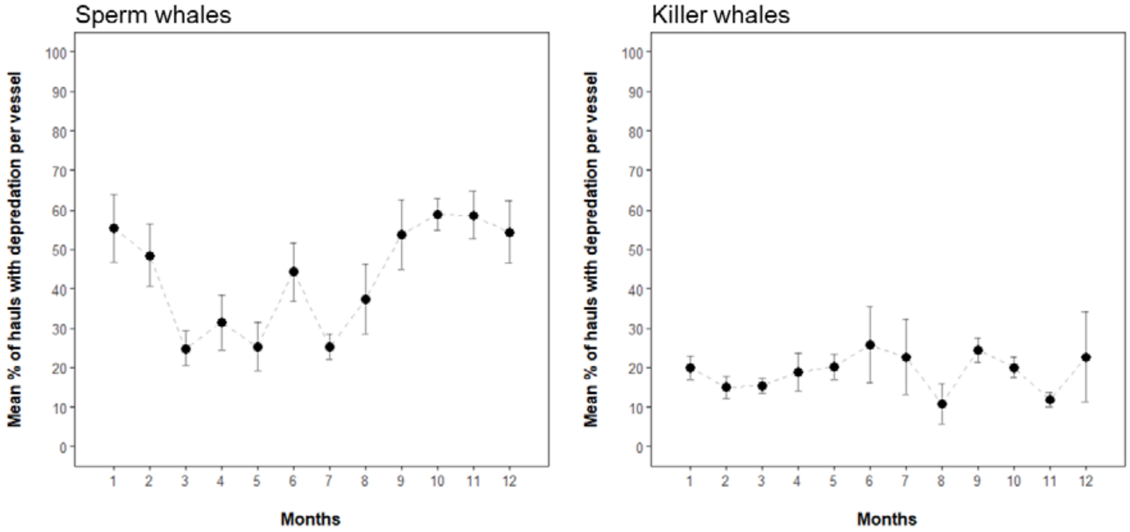

Figure 5. Mean proportions of hauls with presence of depredating sperm whales (left) and killer whales (right) by month over the 2006-2016 period. Black dots are mean values across vessels and error bars are the standard error of the mean.

4. Catch removals due to whale depredation

4.1. Methods

In the studied Patagonian toothfish fisheries, these whales primarily depredate toothfish and disregard other fish species caught on longlines. Whales usually remove the entire fish from a hook, which increases the difficulty to reliably assess the amount of depredated fish biomass. Previous methods to estimate biomass losses were primarily based on comparisons of Catch Per Unit Effort (CPUE) between hauls with absence and hauls with presence of depredating whales, and performed at various spatio-temporal scales. As part of this COLTO study on whale depredation, one of the aims is to develop a standardised methodology leading to more accurate estimates of the amount of depredated fish in fisheries.

A Generalised Additive Model (GAM) was developed and fitted to the Patagonian toothfish CPUE in the partner fisheries. For Chile, the model was built using data from 2008 to 2016 (2006 and 2007 were excluded because of the limited amount of data available for these years). The model was fitted to CPUE values of individual hauls using a Gaussian distribution and a log link function. Covariates included the calendar year and the vessel as factors, and the depth (in m), the longitude (in decimal °), the latitude (in decimal °), the soak time (time elapsed between the time the first hook of a longline is set in the water and the time the last hook is hauled and landed, in hours), the hauling speed (in number of hooks per min) and the month as numeric smooth terms. The number of killer whales and the number of sperm whales recorded depredating during hauls were restricted to < 15 individuals per haul and were both incorporated as smooth terms. Extreme values for the numeric covariates were also excluded. For the soak time, the outlier values of < 1 hour and > 100 hours were excluded. For the depth, the analysis was restricted to sets with depths < 2000m. The analysis was also restricted to the fishing systems “autoline” and “trotline” equipped with “cachaloteras”.

Model selection was performed by using backward stepwise selection based on AIC, and the CPUE was predicted from the best model by setting the number of whales depredating during hauls to 0. The catch that fishermen should have had without whales for hauls during which depredation was observed was calculated by multiplying the predicted CPUE by the number of hooks of these hauls. The catch removal due to whale depredation was then estimated as the difference between the predicted catch and the observed catch. The same procedure was applied to the 95% confidence intervals of the predicted CPUE to calculate uncertainty around the final depredation estimates per year. The total catch removals were calculated as the sum of catch removals for hauls during which whales depredated. To estimate the catch removals due to each whale species, the catch removals for hauls during which either killer whales or sperm whales depredated separately were added to an estimated part of the catch removals due to each species for hauls during which they were both present. These respective parts were calculated from catch removal estimates per whale number obtained for hauls when only one species was present. For instance, if 2 sperm whales are found to remove 60 kg of toothfish every 1,000 hooks during hauls when they are the only depredating species, and 5 killer whales are found to remove 80 kg of toothfish every 1,000 hooks during hauls when they are the only depredating species, sperm whales were assumed to take 60/(60+80) = 43 % of the catch removals for hauls when 2 sperm whales and 5 killer whales simultaneously depredated.

4.2. Results

The model best fitting the data was the saturated model with all covariates and explained 37.6% of the deviance of the data. Both the number of sperm whales and killer whales significantly influenced the toothfish CPUE ($F = 58.2$, $P < 0.001$ and $F = 128.0$, $P < 0.001$ for the two terms, respectively). From the model, depredation by 1-3 sperm whales resulted in a catch removal of 22 [3-42] kg of toothfish every 1,000 hooks, and this increased to 48 [28-69] kg of toothfish every 1,000 hooks when 4-6 sperm whales were simultaneously depredating during the same haul (Figure 6). Catch removals due to killer whale depredation increased from 75 [55-96] kg of toothfish every 1,000 hooks when 1-3 individuals were present to 142 [120-163] kg of toothfish every 1,000 hooks when more than 10 individuals were present (Figure 6).

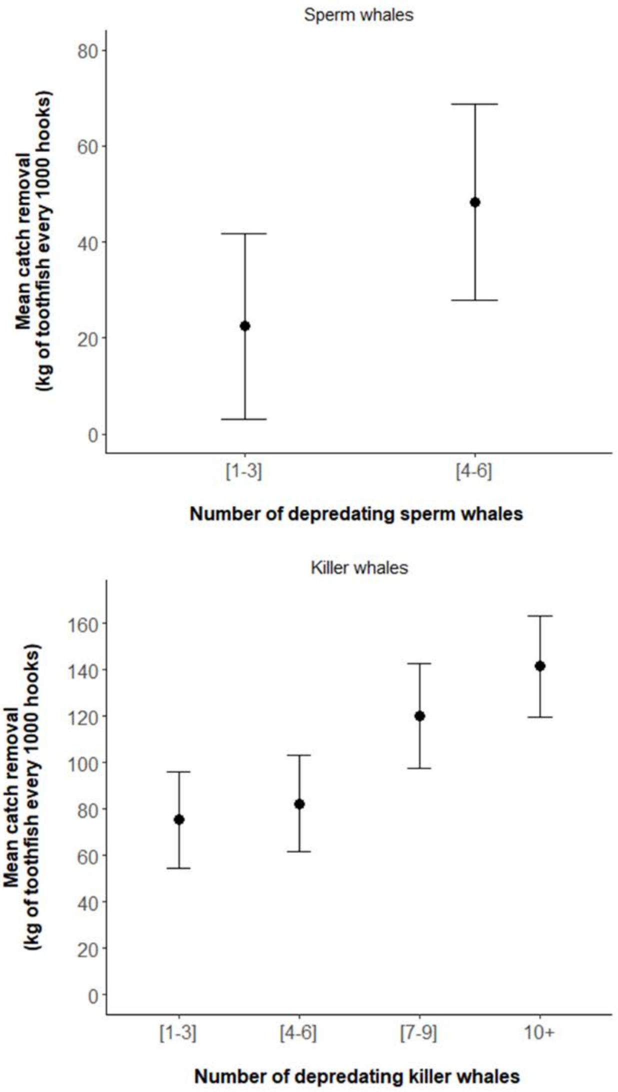

Figure 6. Mean toothfish catch removal (in kg per 1,000 hooks) per number of sperm whales (top) and killer whales (bottom) depredating on longline sets. Black dots are mean estimates across hauls and error bars are 95% Confidence Intervals per cluster of 3 individuals, and were calculated from the full GAM fitted to the toothfish CPUE.

Overall, the total catch removals due to whale depredation for the Chilean commercial toothfish fishery between 2008 and 2016 was 1,716 [95% CI 1,118-2,314] t of toothfish, representing 12.8% [9.3-15.8] of the total catch (landed catch + catch removals due to whale depredation) (Table 1). The mean total catch removal per year due to whale depredation was 191 [124-257] t of toothfish (12.1% [8.6-15] of the total catch, n = 9 years), and annual estimates varied from 48 [17-78] t in 2014 to 422 [322-522] t in 2012 (Table 1 and Figure 7).

Sperm whale depredation resulted in an estimated mean catch removal of 83 [35-130] t of toothfish every year from 2009 to 2016, with a maximum of 181 [121-241] t in 2012 and a minimum of 6.5 [-17-30] t in 2014. Killer whale depredation resulted in an estimated mean catch removal of 117 [93-141] to of toothfish every year from 2008 to 2016 with a maximum of 241 [201-281] t in 2012 and a minimum of 41 [35-48] t in 2014 (Table 1 and Figure 7).

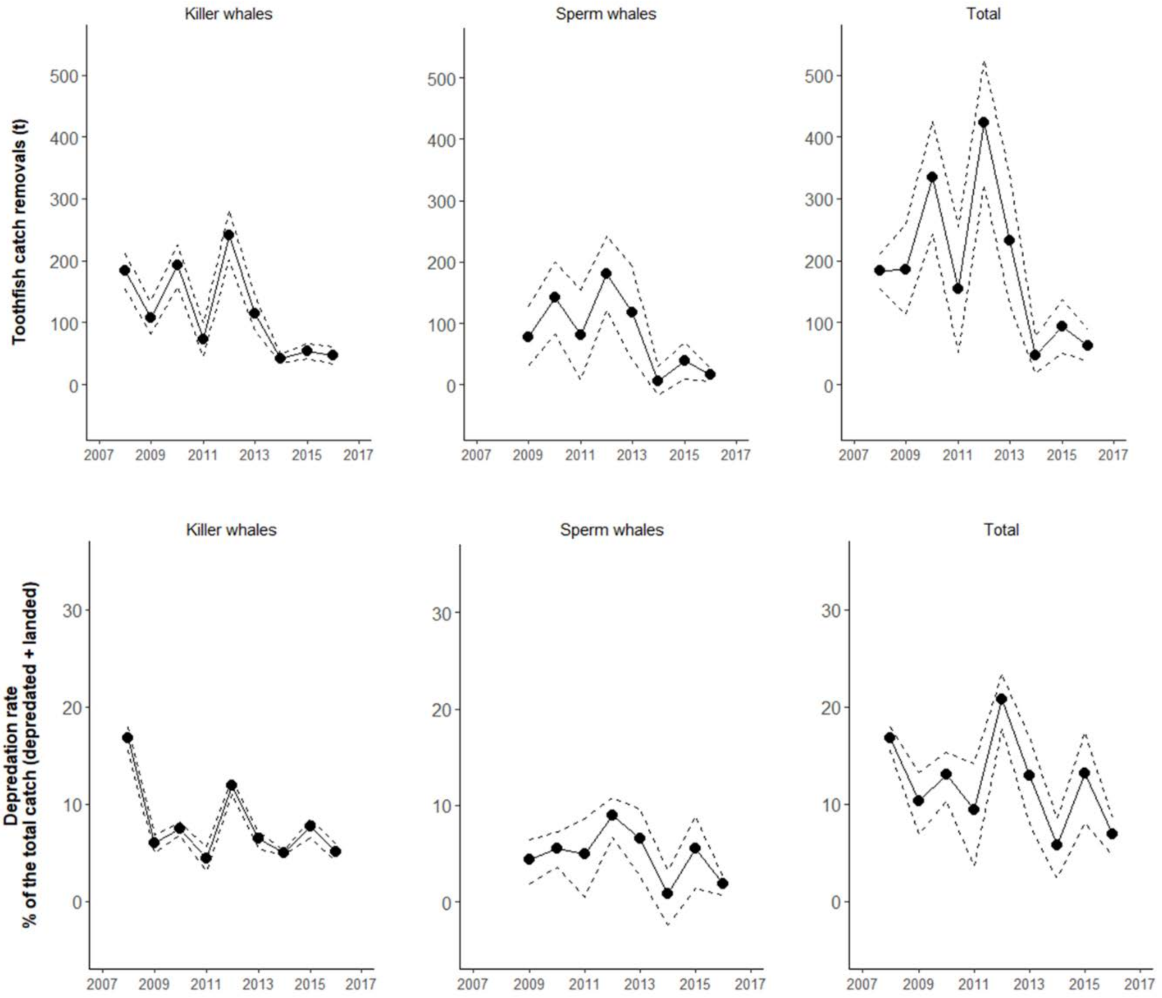

Figure 7. Annual toothfish catch removals (t) due to depredation by killer whales, sperm whales, and both species (total) per in the Chilean commercial toothfish fishery from 2008 to 2016. Estimates (black dots) and 95% Confidence Intervals (dashed lines) were calculated from the full GAM fitted to the toothfish CPUE.

Table 1. Final estimates and 95% confidence intervals of sperm whale and killer whale depredation on Patagonian toothfish (in tonnes, t, of fish taken from longlines) in Chile from 2008 to 2016 for hauls with sperm whale depredation only, killer whale depredation only, and depredation by both species together. Estimates were obtained from the difference between predicted catch values (produced from the best GAMs fitted to the CPUE) without depredation, and the observed catch.

Years	**Catch removals due to whale depredation (t)** [95% CI]			**Depredation rate (% of the total catch)*** [95% CI]		
	Sperm whales	*Killer whales*	*Total*	*Sperm whales*	*Killer whales*	*Total*
2008	**NA**	**183** [154– 212]	**183** [154 – 212]	**NA**	**16.8** [15.5 – 17.9]	**16.8** [15.5 – 17.9]
2009	**78** [31 – 126]	**108** [82 – 133]	**186** [112 – 259]	**4.3** [1.9 – 6.4]	**6.0** [5.0 – 6.8]	**10.3** [6.8 – 13.2]
2010	**142** [84 – 200]	**192** [159 – 226]	**334** [242 – 426]	**5.5** [3.6 – 7.2]	**7.5** [6.8– 8.1]	**13.0** [10.3– 15.3]
2011	**82** [8 – 155]	**72** [45 – 100]	**154** [53 – 255]	**5.0** [0.5 – 8.7]	**4.4** [3.0 – 5.5]	**9.4** [3.5 – 14.2]
2012	**181** [121– 241]	**241** [201 – 281]	**422** [322 – 523]	**8.9** [6.6 – 10.8]	**11.9** [11.0 – 12.6]	**20.8** [17.7 – 23.4]
2013	**117** [42 – 193]	**115** [86-145]	**233** [128 – 337]	**6.5** [2.6 – 9.6]	**6.4** [5.4 – 7.2]	**12.9** [8.0 – 16.9]
2014	**7** [-17 – 30]	**41** [35 – 48]	**48** [17 – 78]	**0.8** [-2.4– 3.3]	**5.0** [4.8 – 5.2]	**5.8** [2.4 – 8.5]
2015	**39** [9 – 70]	**54** [41 – 67]	**93** [50 – 136]	**5.6** [1.4 – 8.9]	**7.6** [6.6 – 8.5]	**13.2** [8.0 – 17.3]
2016	**17** [6 – 28]	**47** [33 – 60]	**63** [39 – 88]	**1.8** [0.7 – 2.7]	**5.0** [4.0 – 5.9]	**6.9** [4.7 – 8.6]

*Total catch = amount of toothfish landed + amount of toothfish depredated

5. Number and movements of depredating whales

5.1. Number of individuals per depredated haul

When depredation was recorded during hauling, the number of whales simultaneously depredating was estimated for both sperm whales and killer whales. Over the 2006-2016 period, the mean number of individuals per depredated haul was 3.5 ± 0.04 for sperm whales and 6.4 ± 0.1 for killer whales. For the latter, the annual means indicated a maximum of 8.4 ± 0.4 in 2016 (Figure 8a). The number of sperm whales showed a sharp decline from 2007 (7.2 ± 0.2) to 2008 (3.0 ± 0.1), and then dropped to less than 3 individuals from 2012 to 2016. At the intra-annual level, the minimum number of sperm whales was recorded in June (2.0 ± 0.2) and the maximum in May (4.4 ± 0.2) – Figure 8b). For killer whales, the lowest mean was in August (4.6 ± 0.4 individuals) and the highest mean was in January (6.9 ± 0.3 individuals).

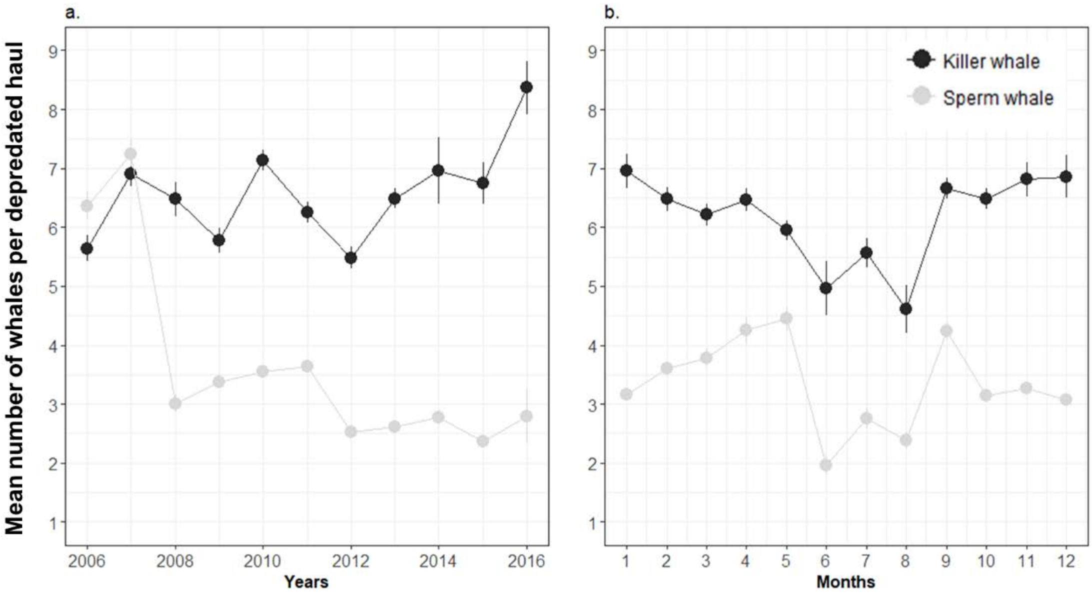

Figure 8. Mean number of sperm whales (grey) and killer whales (black) simultaneously depredating during the same haul, a. per year and b. per month over the 2002-2016 period. Error bars are the Standard Error of the mean.

5.2. Photo-identification data: total number and movements of depredating individuals.

The primary methodology used to estimate the total number of whales depredating in a given area, or the size of local whale populations, is to implement a long-term consistent photo-identification program from fishing vessels. This program was implemented in January 2017 for the commercial Chilean fishery in collaboration with AOBAC and IFOP. IFOP fishery observers were provided with camera equipment and received training on photo-identification protocols used for both killer whales and sperm whales.

A total of 6,662 pictures taken by fishery observers and crews from January 2017 to May 2018 and were received from Eduardo Infante (Global Pesca, AOBAC). These pictures were taken from 3 vessels: GPI (3 trips), GP II (3 trips) and PWI (1 trip). A total of 1,017 pictures of sperm whales and 5,645 pictures of killer whales were taken. While photo-identification of sperm whales could not be conducted as the number of pictures of the tail flukes (the primary body parts used for identification) was too limited, all pictures of killer whales were processed and photo-identification information entered in a data base. These pictures first revealed the occurrence of two ecologically and genetically distinct forms of depredating killer whales, a “regular” form and a Type D form, and results from the photo-identification analysis were therefore produced for each separately.

5.2.1. “Regular” killer whales

“Regular” killer whales are characterized by typical morphological features for the species with standard shape and size of eye patches, dorsal fin and saddle patch (Figure 9). This form occurred on photographs taken during 66 hauls from January 12th 2017 to May 24th 2018, and across a broad spatial range from 51°S to 57.5°S and from 66°W to 76°W (Figure 9).

4,319 photographs were taken during hauls with presence of depredating “regular” killer whales, including 2,199 photographs of quality high enough to be analysed. These photographs were primarily taken over the January-May period for both 2017 and 2018 (Figure 10). Information from a total of 3,159 individual representations on photographs was analysed and resulted in the identification of 41 individuals at the end of the study period (Figure 10). These individuals included 7 adult males and the photographs best showing the identification features of all individuals were selected to develop a photo-identification catalogue (Figure 11).

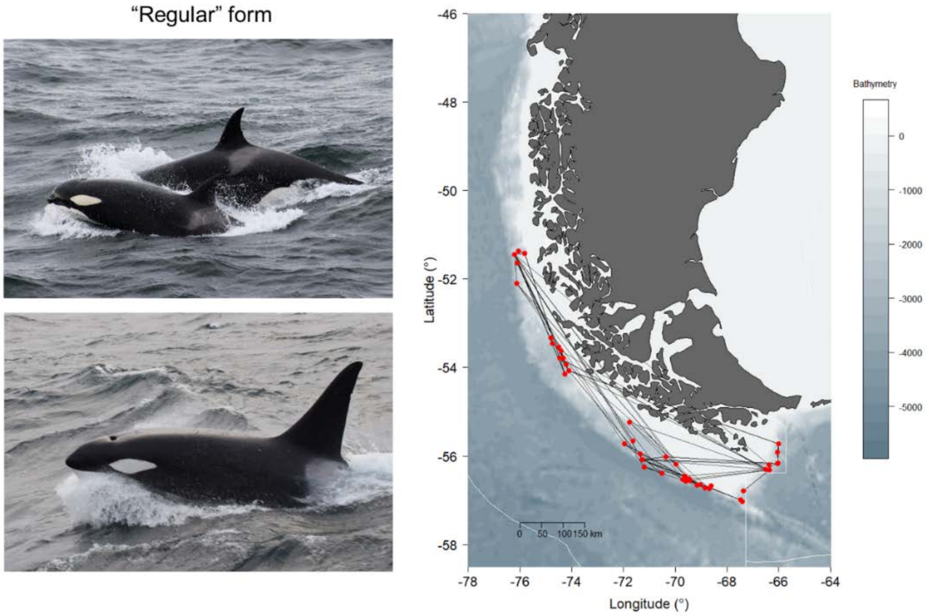

Figure 9. Sample of pictures taken from the Chilean toothfish fishing vessels in 2017 and 2018 depicting the morphological features of the "regular" killer whale form depredating toothfish from longlines (left), distribution (red dots) and movements (black lines) of individuals over the study area from January 2017 to May 2018 (right).

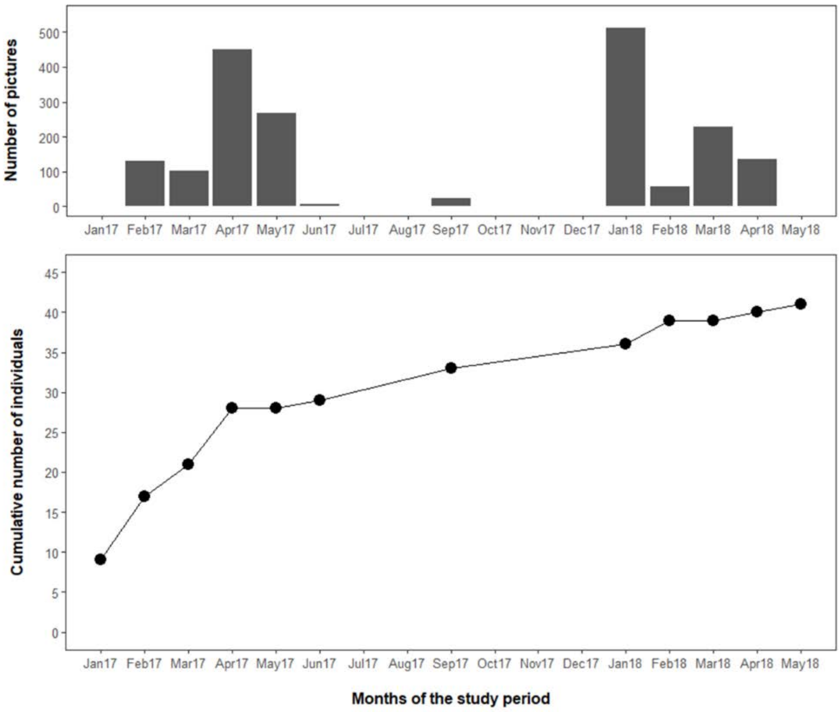

Figure 10. Photo-identification effort (number of pictures taken, top) and cumulative number of killer whale individuals from the "regular" form identified per month from January 2017 to May 2018

CH003 2017

CH004 2017-2018

CH005 2017

CH006 2017-2018

CH008 2017

CH010 2017

CH011 2017-2018

CH012 2017-2018

CH013 2017-2018

CH015 2017

CH016 2017-2018

CH018 2017

CH019 2017-2018

CH024 2017-2018

CH025 2017

CH026 2017

CH029 2018

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CH031 2018

CH032 2018

CH033 2018

CH034 2017-2018

CH037 2017

CH038 2017

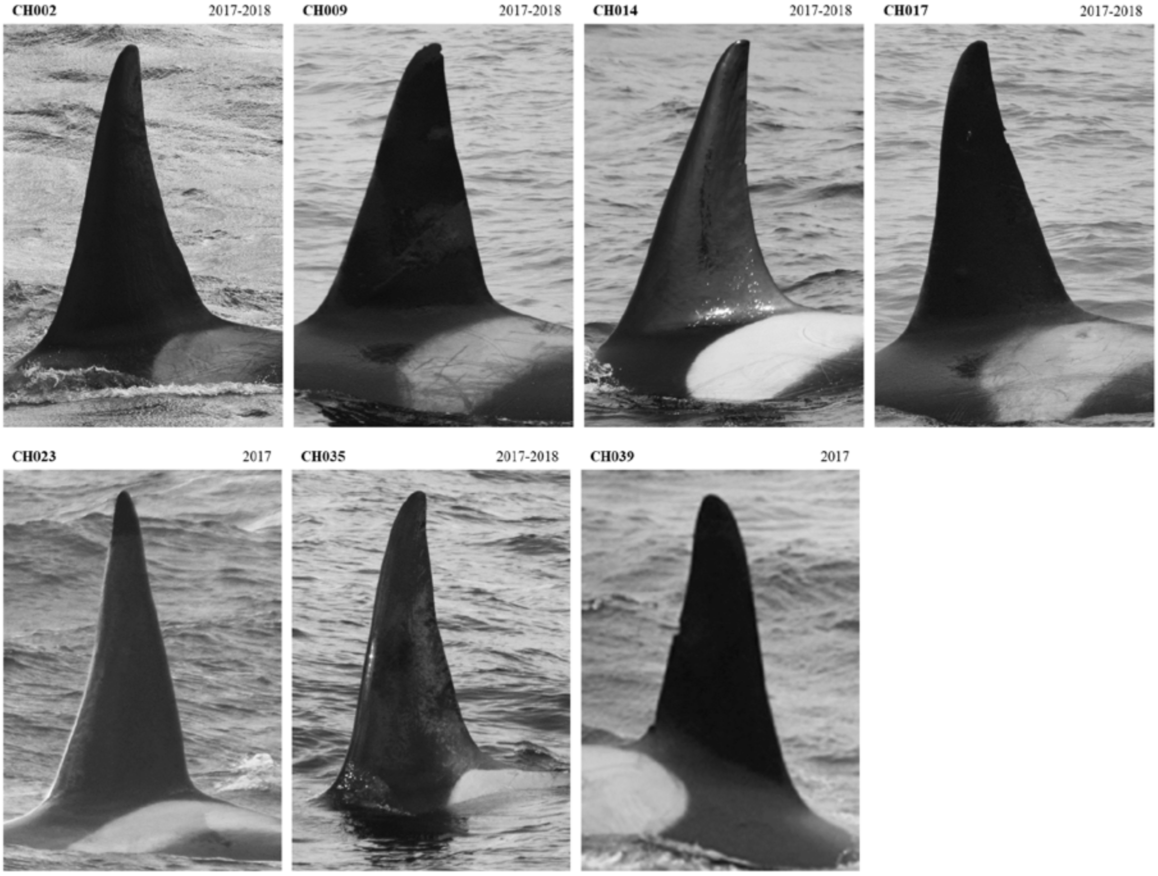

Figure 11. Photo-identification catalogue of the 31 most distinctive killer whale individuals from the “regular” form depredating on toothfish in southern Chile, developed from pictures taken by fishery observers and crews on-board fishing vessels in 2017 and 2018. The individual ID (top left) and years of observations (top right) are depicted.

The “discovery curve” or the cumulative number of newly identified individuals as a function of the cumulative number of observations was best fitted with a polynomial regression of order 2 indicating a decelerating rate of new identifications with increasing effort (Figure 12). This suggested that the 41 killer whales identified as part of this study may represent a large proportion of the full “depredating population” of “regular” killer whales in Southern Chile. However, as new individuals were still identified in the most recent observations and because a number of potentially new individuals were not given any ID due to missing high quality photographs, 41 individuals should be considered as minimum estimate at this stage of the study. Further photo-identification effort provided from fishing vessels over a longer time period will allow to implement more accurate methods such as Capture-Mark-Recapture analyses to reliably estimate the full number of depredating “regular” killer whales.

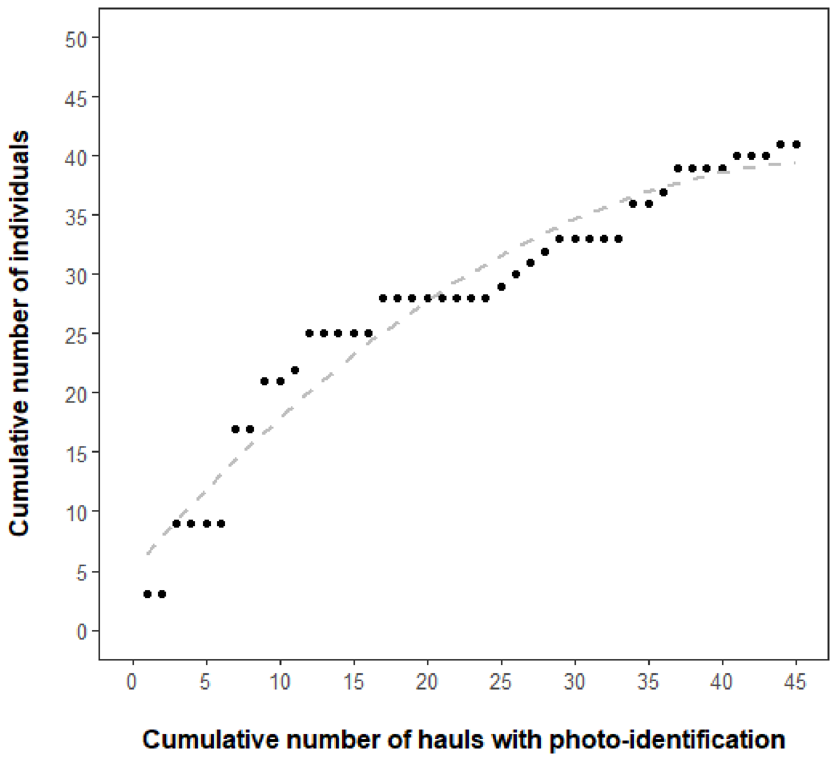

Figure 12. Cumulative number of killer whale individuals from the “regular” form identified in Chile from commercial toothfish fishing vessels from January 2017 to May 2018 over the cumulative number of observations (hauls) with photo-identification effort. The black dots are the observed values and the dashed line is a fitted curve from a polynomial regression of order 2.

In addition to killer whale number estimates, the photo-identification data provided insights on whale movements across the fishing area when individuals were photographed over multiple depredation interactions. These data indicated that “regular” killer whales readily travelled large distances to repeatedly interact with fishing vessels (Figure 13). For instance, individual CH004 moved over 782 km from first interaction on January 22nd 2017 in the South East part of the fishing area to an interaction that occurred on June 18th 2017 in the North West part of the fishing area. This individual also travelled 431 km in 27 days to interact successively with two different fishing vessels (PWI on February 10th and GPI on March 9th 2017). More interestingly, individual CH014 travelled 578 km between two successive interactions with the same vessel (GPI) within 10 days from February 28th to March 10th 2017 (Figure 13).

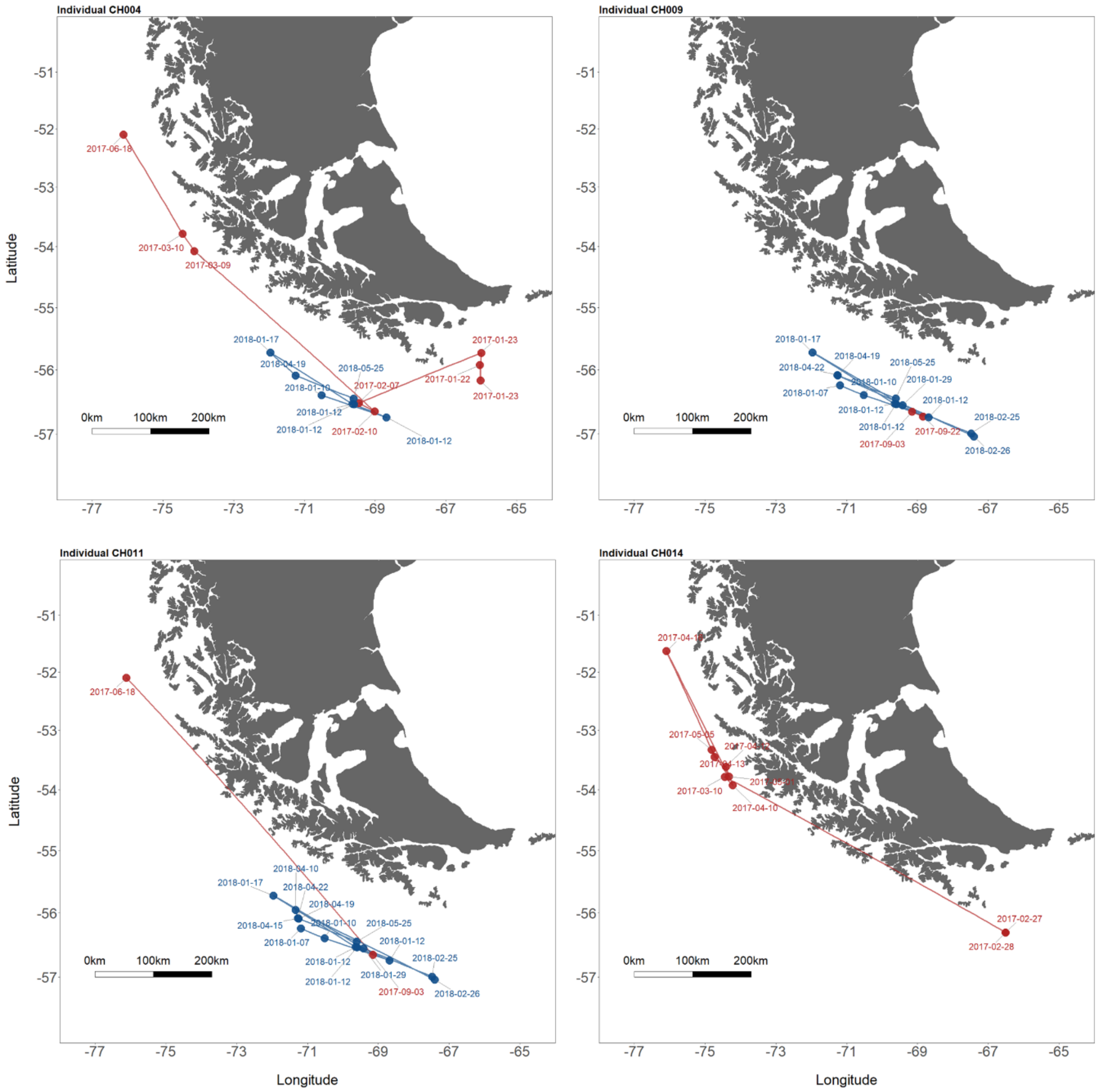

Figure 13. Movements across consecutive observations of 4 killer whale individuals (CH004, CH009, CH011 and CH014) from the "regular" form when interacting with commercial toothfish fishing vessels in 2017 (red) and 2018 (blue). The date of hauls during which the individual was confirmed present through photographs is indicated near the haul location (dots) and lines connect consecutive observations.

5.2.2. "Type D" killer whales

"Type D" killer whales are morphologically characterized by small eye patches, a bulbous head and a backswept dorsal fin with a sharply pointed tip (Figure 14). This form occurred on photographs taken during 25 hauls from February 9th 2017 to April 19th 2018, and across a restricted spatial range from 55.9°S to 57°S and from 67.5°W to 71.5°W (Figure 13).

1,326 photographs were taken during hauls with presence of depredating “Type D” killer whales, including 438 photographs of high enough quality to be analysed. These photographs were primarily taken February 2017 and in January and April 2018 (Figure 15). Information from a total of 525 individual representations on photographs were analysed and resulted in the identification of 20 individuals at the end of the study period (Figure 15). These individuals included 2 adult males and the photographs best showing the identification features of all individuals were selected to develop a photo-identification catalogue (Figure 16).

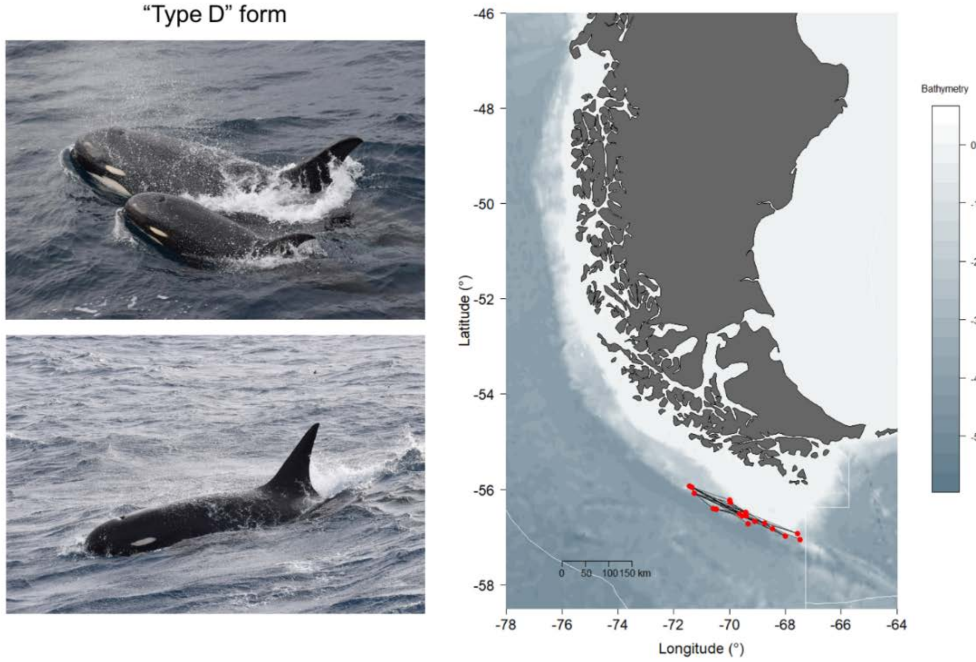

Figure 14. Sample of pictures taken from the Chilean toothfish fishing vessels in 2017 and 2018 depicting the morphological features of the “Type D” killer whale form depredating toothfish from longlines (left), distribution (red dots) and movements (black lines) of individuals over the study area from February 2017 to April 2018 (right).

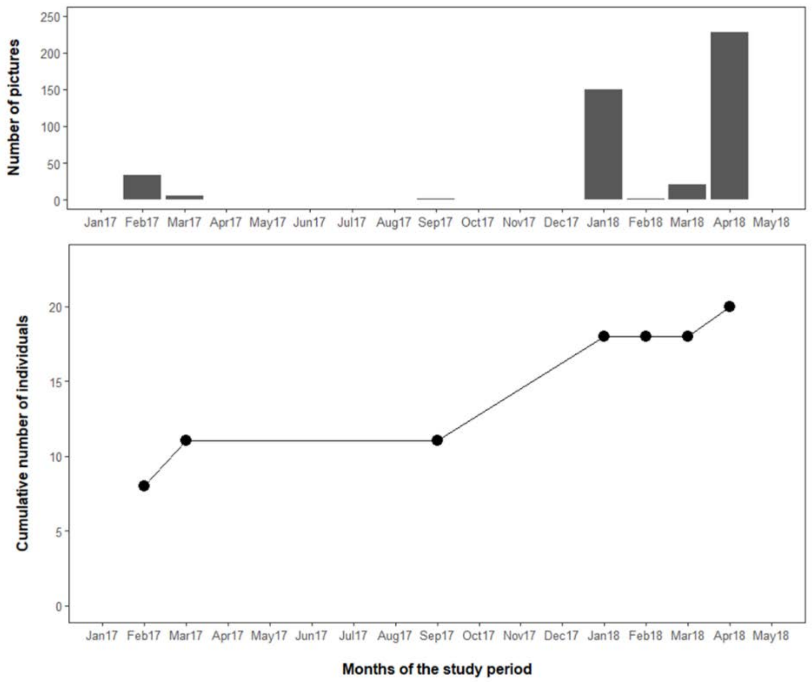

Figure 15. Photo-identification effort (number of pictures taken, top) and cumulative number of killer whale individuals from the "Type D" form identified per month from January 2017 to May 2018.

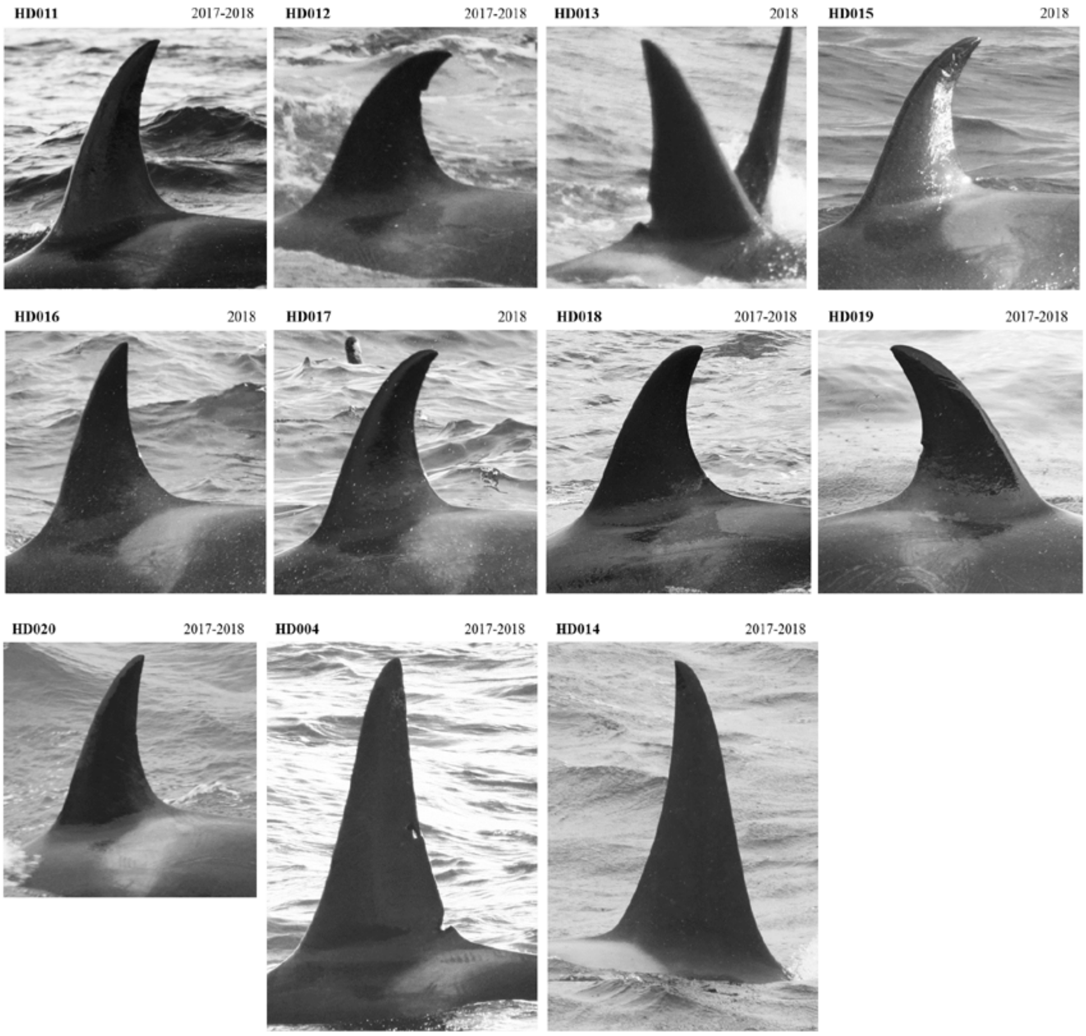

Figure 16. Photo-identification catalogue of the 19 most distinctive killer whale individuals from the “Type D” form depredating on toothfish in southern Chile, developed from pictures taken by fishery observers and crews on-board fishing vessels in 2017 and 2018. The individual ID (top left) and years of observations (top right) are indicated.

The cumulative number of newly identified individuals was best fitted with a polynomial regression of order 2 indicating a decelerating rate of new identifications with increasing effort (Figure 17). This suggested that the 20 killer whales identified as part of this study may represent a large proportion of the full “depredating population” of “Type D” killer whales in Southern Chile. However, as new individuals were still identified in the most recent observations and because a number of potentially new individuals were not given any ID due to missing high quality photographs, 20 individuals should be considered as minimum estimate at this stage of the study. Similarly to “regular” killer whales, further photo-identification effort provided from fishing vessels over a longer time period will allow to implement more accurate methods such as Capture-Mark-Recapture analyses to reliably estimate the full number of depredating “Type D” killer whales.

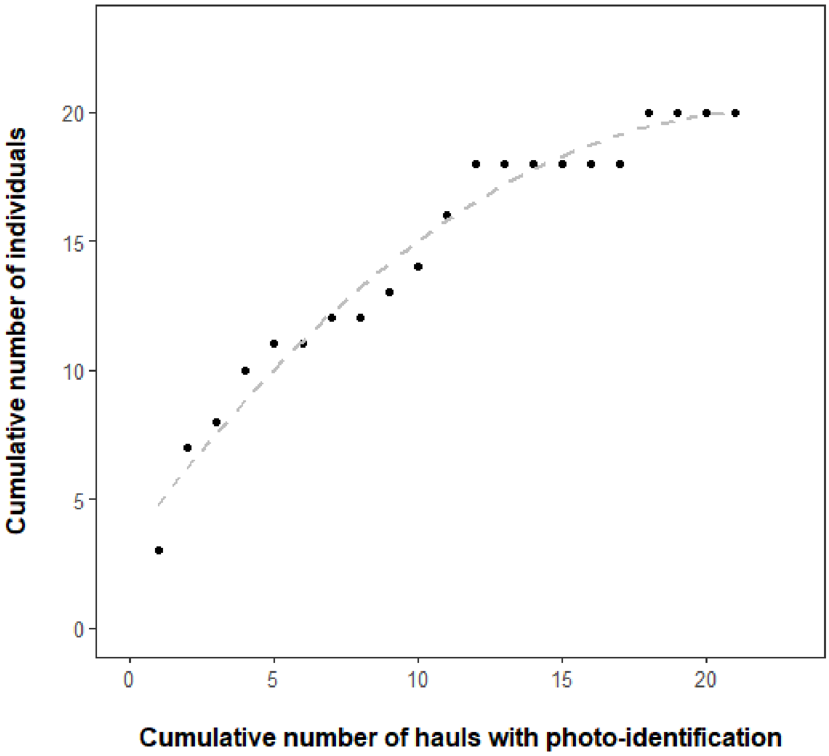

Figure 17. Cumulative number of killer whale individuals from the “Type” form identified in Chile from commercial toothfish fishing vessels from January 2017 to May 2018 over the cumulative number of observations (hauls) with photo-identification effort. The black dots are the observed values and the dashed line is a fitted curve from a polynomial regression of order 2.

No distinct cluster of individuals clearly appeared while processing photographs from multiple observations, suggesting that individuals may form a single social group. This is further supported by movements across the fishing area being similar between individuals over multiple depredation interactions. The distances travelled by “Type D” killer whales were limited, even between interactions that occurred ~ 1 year apart from one another. (Figure 18). For instance, individual HD006 was photographed while depredating on two occasions 346 days apart during hauls located 44 km from one another. However, photo-identification data also suggested that “Type D” individuals may actively travel towards fishing vessels to depredate during hauls. For instance, this happened with individual HD019 that moved from an interaction with vessel GPII on April 8th 2018 to an interaction with vessel GPI on April 10th 2018 130 km away (Figure 18).

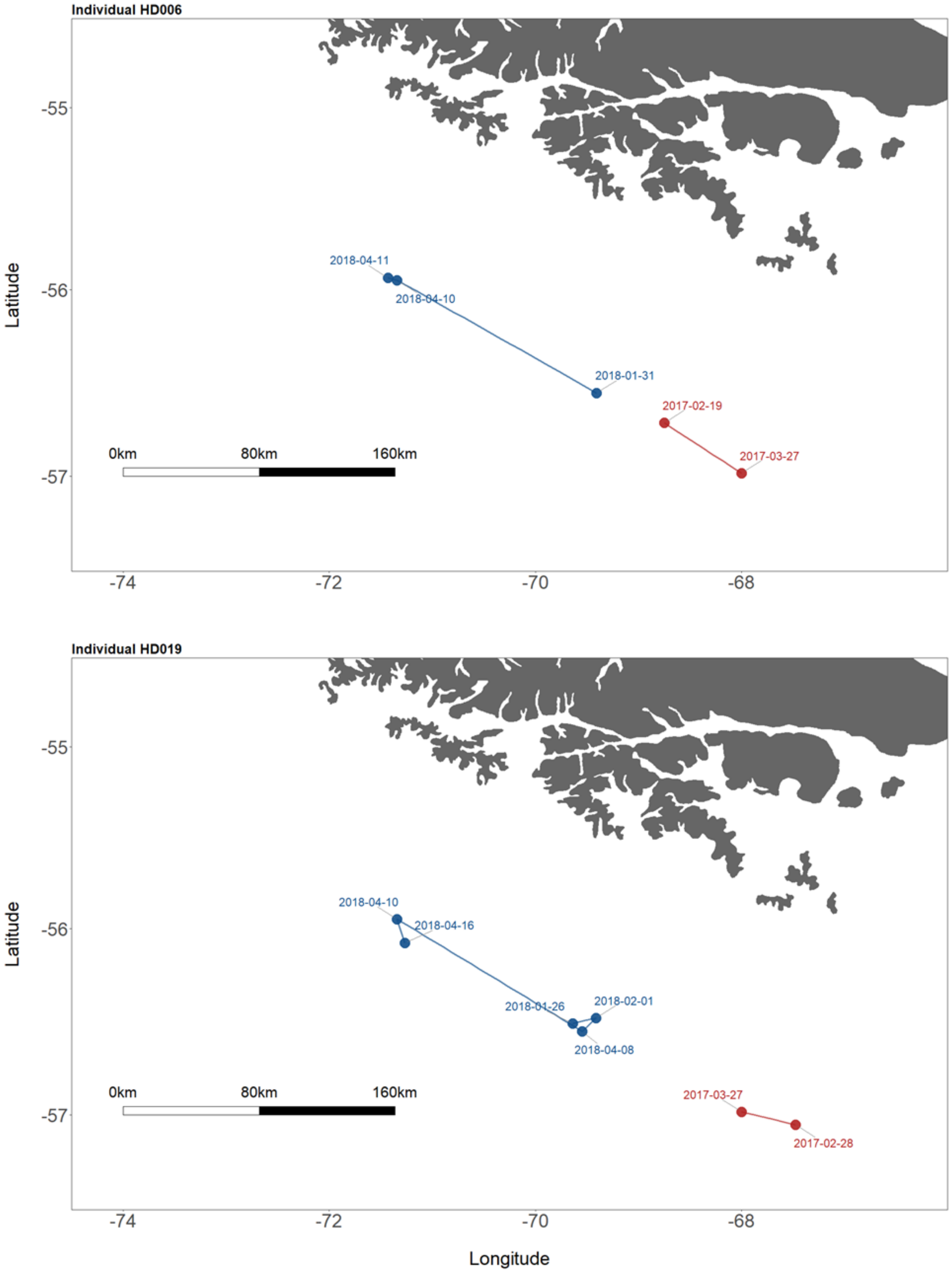

Figure 18. Movements across consecutive observations of 2 killer whale individuals (HD006 and HD019) from the “Type D” form when interacting with commercial toothfish fishing vessels in 2017 (red) and 2018 (blue). The date of hauls during which the individual was

confirmed present through photographs is indicated near the haul location (dots) and lines connect consecutive observations.

6. Minimizing whale depredation

In order to provide captains and fishing companies with guidance on decisions and practices minimizing whale depredation, this section investigated a range of variables either influencing the probability of depredation interactions to occur or minimizing catch removals during depredation interactions. Six variables were investigated including the occurrence of depredation interactions in space and time, the noise produced by fishing vessels, the use of cachaloteras as fish protection devices, the hauling speed of hooks and the distance travelled by vessels when attempting to move away from an area where they had experienced depredation. The results are presented as two distinct sections for two situations: before interactions occur and when depredation occurs.

6.1. Before depredation interactions occur

6.1.1. Avoiding areas and time of the year of high probabilities of whale interaction

This first analysis aimed to identify specific times of year and areas when/where vessels were less likely to experience depredation interactions. GAM models were fitted to the proportions of hauls with sperm whale and killer whale depredation using the 2006-2016 dataset to predict the seasonal and spatial variation of the probability of occurrence of depredation interactions with each of the two species. The model used a binomial distribution and a log link function. The month and the location of hauls (latitude/longitude) were the variables to be tested and were included in the model as numeric smooth terms. Other smooth terms included a range of environmental variables: the bathymetry (in metres) and the slope (in degrees) on which hauls occur and the sea surface temperature (SST, in °C). Average values of these environmental variables were calculated or extracted on a 0.25 x 0.25 ° spatial grid. The bathymetry was extracted from the GEBCO 1-minute resolution database and used to calculate the bathymetric slope. The SST was extracted from the COPERNICUS database providing average values per grid over the 2011-2016 period.

For sperm whales, the best model was the model including all variables. However, the month, the latitude/longitude and the slope were the only variables with a statistically significant effect (*F*= 487.1, *P* < 0.001, *F* = 7.187, *P* = 0.04 and F=16.504, *P* < 0.001, respectively). For killer whales, the best model was also the full model, and like for sperm whales, the month, the latitude/longitude and the slope were the only variables with a statistically significant effect (*F* = 156.63, *P* < 0.001, F = 9.487, P < 0.001 *F* =13.702, *P* = 0.04 respectively).

The probability of sperm whale depredation interactions as estimated by the model decreased to < 0.4 in autumn/winter months, from March to July, and was the highest (>0.7) in October and November (Figure 19). For killer whales, the estimated probabilities of depredation interactions were the lowest in November and December (< 0.2), and the highest from March to July (> 0.3 – Figure 19).

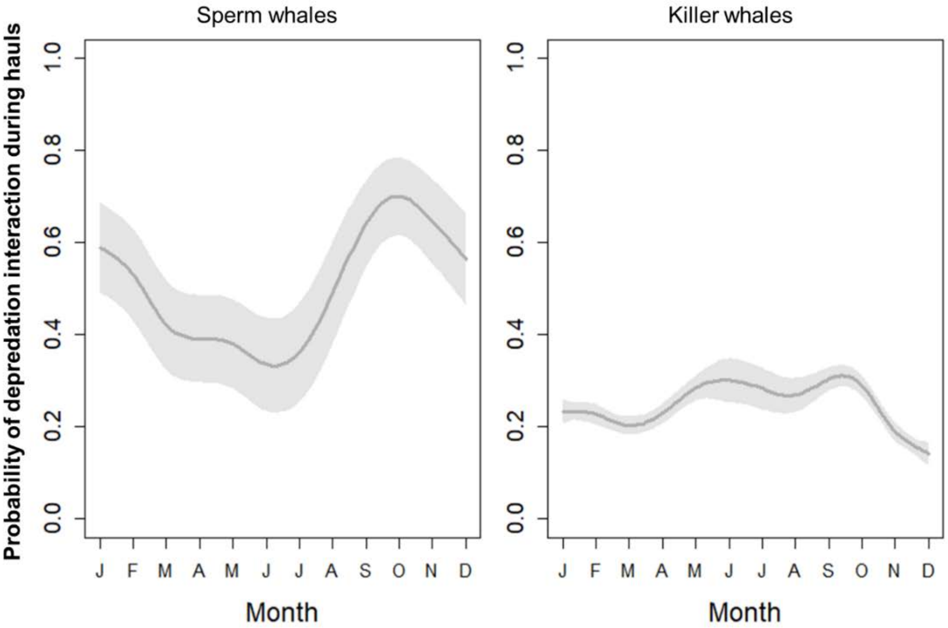

Figure 19. Probability of sperm whale (left) and killer whale (right) depredation interactions during hauls as a function of the month as estimated by the best GAMs fitted to the presence/absence records of whales during hauls (dark grey line) and 95% confidence intervals (grey shade).

The probability of both sperm whale and killer whale depredation interactions increased on steeper bathymetric slopes, with estimates > 0.8 for slopes > 2° and slopes > 3° for the two species, respectively (Figure 20)

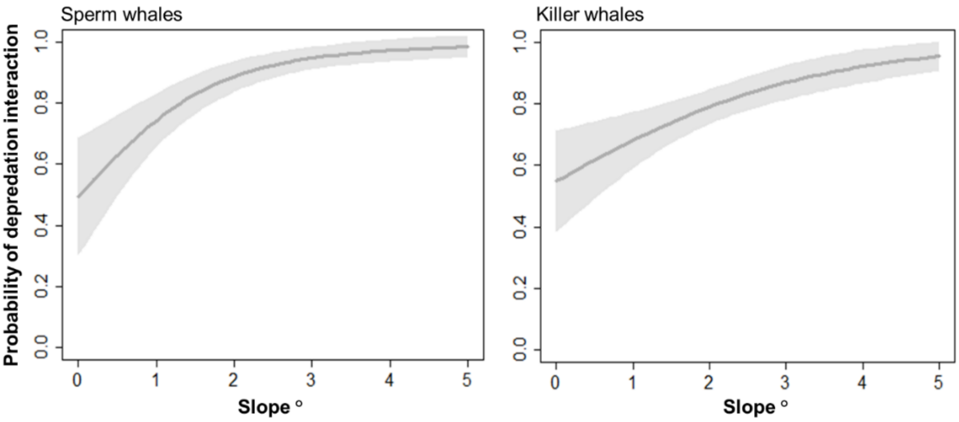

Figure 20. Effect of the bathymetric slope on the probability of the occurrence of sperm whale (left) and killer whale (right) depredation interactions as estimated from the best GAMs fitted to the proportion of depredated hauls (dark grey line) and 95% confidence intervals (grey shade).

Over the study period, five spots of high probability (> 0.5) of sperm whale depredation interactions were identified: at latitudes 48°S and between latitudes 53 and 54.5°S on the West coast of Chile, between latitudes 55 and 55.6°S at longitude 72°W, at latitude 57.5°S and at latitude 56°S and longitude 66°W (Figure 21). For killer whales, depredation interactions were the most likely to occur (probability > 0.2) in between latitudes 55°S and 57.5°S and between longitudes 67°W and 73°W (Figure 21).

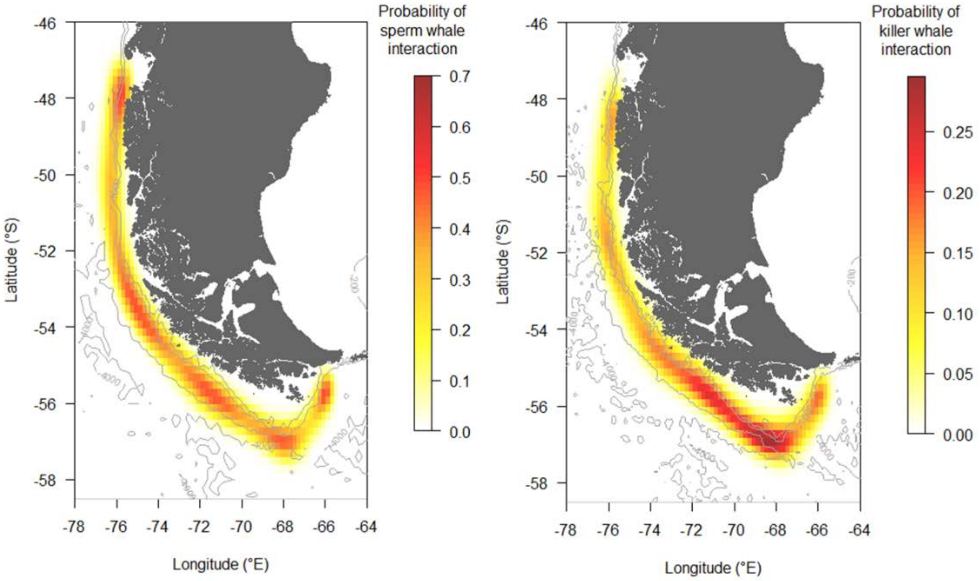

Figure 21. Spatial variation of the probability of sperm whale (top) and killer whale (middle) depredation interactions over the 2006-2016 period as estimated from the best GAMs fitted to the proportion of depredated hauls.

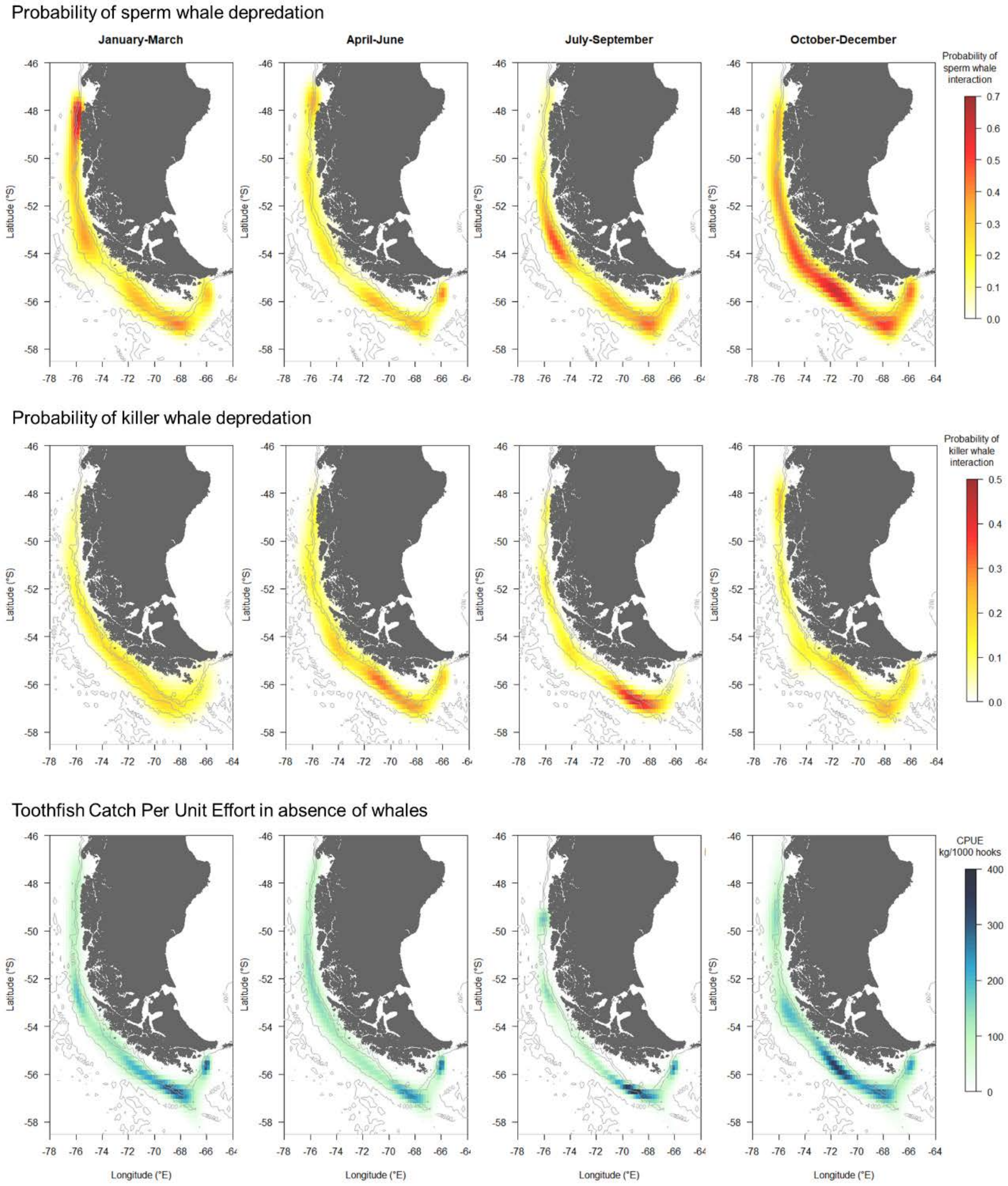

Figure 22. Spatial variation of the probability of sperm whale (top) and killer whale (middle) depredation interactions per season (summer: January-March, Autumn: April-June, winter: July-September and spring: October-December) as estimated from the best GAMs fitted to the proportion of depredated hauls, and spatial variation of the toothfish CPUE (bottom, in kg per 1,000 hooks) per season as estimated from a GAM fitted to the CPUE of non-depredated hauls.

To account for intra-annual heterogeneity detected in the model, whale depredation interactions were also spatially predicted per season, and these predictions were compared with spatial predictions of the toothfish CPUE in absence of whales (predictions made from a simple GAM fitted to the toothfish CPUE using non-depredated hauls only, a normal distribution and a log link function) (Figure 22). From October to December, while high probabilities (> 0.5) of sperm whale depredation interactions covered the majority of the fishing area with areas of high CPUE, the probabilities of killer whale interactions were low (< 0.1) in areas where CPUE was average (200 kg/1000 hooks). From July to September, areas of high CPUE (> 300 kg/1000 hooks) fully overlapped with areas of high probabilities of sperm whale and killer whale depredation interactions, especially in the southernmost part of the fishing area. From April to June, the probabilities of sperm whale depredation interactions dropped to < 0.2 over the majority of the fishing area but probabilities of killer whale depredation were high (>0.3) in areas of high CPUE in the southernmost part of the fishing area. From January to March, the probabilities of killer whale depredation interactions were homogeneously low across the fishing area, and probabilities of sperm whale depredation were low (<0.2) or average (0.3-0.4) everywhere except in the Northernmost part of the fishing area. During that period, hotspots of toothfish CPUE were detected in the Southernmost and Easternmost parts of the fishing area (Figure 22).

6.1.2. Reducing the probability of vessels to be acoustically detected by whales

While investigating acoustics around the whale depredation issue was not part of this project, collaboration with concomitant research projects has allowed for new insights on the influence of the noise level and types of sound signals produced by fishing vessels on the likelihood of being detected by whales underwater from the distance. The work conducted by Gaetan Richard as part of his PhD thesis and by the ENSTA in Brest (France) has suggested that:

- Each fishing vessel has a unique acoustic signature;
- Fishing vessels produce typical signals at setting that may play an important informative role for whales on fishing activity detection;
- For a given sound frequency, the signals produced by vessels when manoeuvring backward may propagate 5 times further than the signals produced by vessels when moving forward (at 250 Hz, 30-40 km when moving forward, 120 – 270 km when moving backward).

These preliminary insights will be further investigated during the coming year. However, they support the assumption that in addition to the sounds intrinsically produced by vessels, the way captains (or the person in command) use the engine and the propeller speed and direction during fishing operations is likely to be determinant in their probability of being detected by whales. Typically, brutal changes of direction from forward to backward, in contrast to continuous and smooth forward movements, may substantially increase the detectability of vessels on fishing grounds and, therefore, avoided.

6.2. When depredation interactions occur

6.2.1. Using cachaloteras as fish protection devices

As part of this study, an attempt was made to assess the effectiveness of cachaloteras as fish protection devices deployed on the trotline fishing system by the Chilean commercial fishing vessels. However, the limited amount of data available for trotlines not equipped with cachaloteras and for the autoline system in this fishery prevented reliable comparisons to be reliably made between these systems in terms of their respective effect on the extent of whale depredation. This question was, therefore, addressed at a larger scale by incorporating data from other commercial toothfish fisheries such as fisheries operating at Prince Edward/Marion, Crozet and Kerguelen. Analyses are still ongoing but preliminary results from a GAM model fitted to the toothfish CPUE and incorporating the number of depredating whales and the fishing system as interaction terms suggested larger catch removals due to killer whale depredation for the autoline system than for the trotline with cachalotera system (Figure 23). Predictions made from the model indicated that 77 [48-99] and 37 [13-60] kg of toothfish every 1,000 hooks would be removed by 1-2 killer whales whether interacting with autolines or trotlines with cachaloteras, respectively. These estimates increased to 106 [72-132] and 77 [56-99] kg of toothfish every 1,000 hooks removed by 9-10 killer whales whether interacting with autolines or trotlines with cachaloteras, respectively (Figure 23).

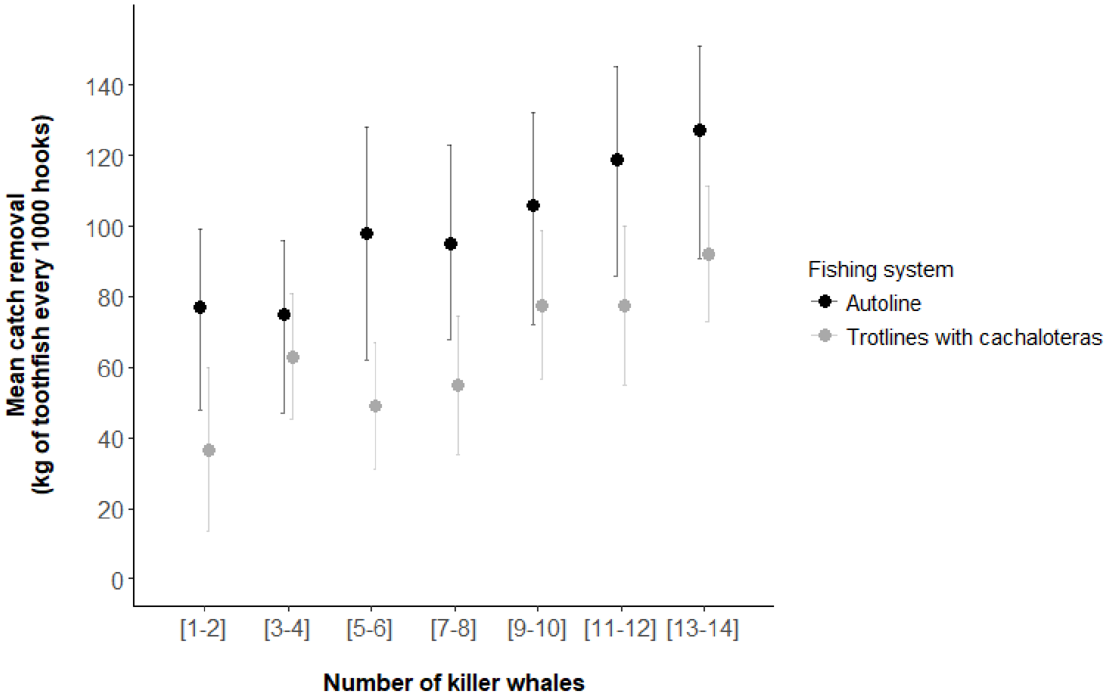

Figure 23. Preliminary result on the effect of the fishing system (Autoline or Trotlines equipped with cachaloteras) on the toothfish catch removals due to killer whale depredation per cluster of number of individuals simultaneously present during the same haul. These estimates were retrieved from a GAM model fitted to the toothfish CPUE across multiple toothfish fisheries in subantartic waters as part of a scientific publication in preparation.

6.2.2. Increasing the hauling speed

Previous studies have shown that increasing the speed at which hooks may be hauled when retrieving longline sets from the bottom in the presence of depredating whales may reduce the amount of fish whales may remove from hooks. Therefore, this effect was examined as part of the study as a numeric covariate incorporated in the GAM fitted to the toothfish CPUE to estimate catch removals due to whale depredation in Chile (see section 4.). The hauling speed (in number of hooks hauled per min) was found to significantly influence the toothfish CPUE ($F = 622.9$, $P < 0.001$). When predicting catch removals due to whale depredation (any species), estimates decreased from 72 [45-98] kg of toothfish removed every 1,000 hooks for hauling speeds of 1-10 hooks per min, to 28 [14-41] kg of toothfish removed every 1,000 hooks for hauling speeds of 21-30 hooks per min (Figure 24).

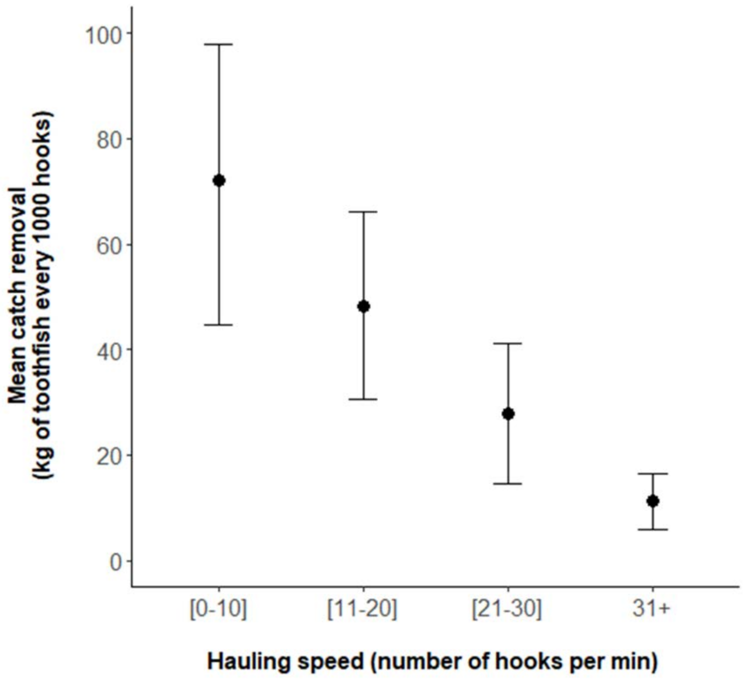

Figure 24. Effect of the hauling speed on the toothfish catch removals due to whale depredation. Catch removals were estimated from the best GAM fitted to the toothfish CPUE and averaged per hauling speed clusters of 10 hooks per min across all hauls with whale depredation (all whale species and numbers). Error bars are the mean 95% CI.

6.2.3. Implementing "move-on" practices

The probability of both sperm whales and killer whales to repeatedly and successively interact with hauls from the same vessels was shown to decrease with the distance vessels may travel between hauls. This effect was assumed to result from the fact that whales cannot sustain the travel speeds of vessels over great distances and may, therefore, lose track of vessels past a certain distance threshold. As such, leaving a fishing area where depredation interactions are occurring to go fishing in a new area located far enough so the vessel decreases its chances to experience depredation again was proposed as the "move-on" strategy in many fisheries.

The effect of the distance travelled by vessels between consecutive hauls on the probability of the next haul to occur with depredation by sperm whales or killer whales was examined for Chile through Generalized Linear Models (GLMs). From the full 2006-2016 dataset, data were restricted to distance values between a depredated haul and the next, and the model was fitted to the occurrence (0 or 1) of depredation during the next haul with the distance as a quadratic covariate and using a binomial distribution. Distance between hauls were calculated from the mean GPS coordinates of hauls. Other predictors included the year (factor), the vessel (factor), the latitude and longitude (numeric), and the depth of sets (numeric). Model selection was performed by using backward stepwise selection based on AIC. The best model was further developed by adding one segmented (i.e., piece-wise linear) relationship to identify a distance breakpoint beyond which this predictor had no effect on the proportion of sets next hauled depredated.

For sperm whales, the best model was the full model including all predictors. This model indicated a significant effect of the distance travelled to the next haul ($z = -6.424$, $P < 0.001$) with a breakpoint of 173.9 ± 19.1 km. When a vessel experienced sperm whale depredation on a given haul, the probability of the next haul to be also depredated by sperm whales was > 0.7 if these two hauls were located less than 100 km from each other (Figure 22).

For killer whales, the best model was the full model excluding the depth as a predictor. The effect of the distance travelled to the next haul on the probability of this next haul to be depredated again was significant ($z = -3.105$, $P = 0.002$) with a breakpoint of 108.1 ± 11.6 km. When a vessel faced killer whale depredation on a given haul, the probability of the next haul to be also depredated by killer whales was > 0.7 if these two hauls were located less than 10 km from each other (Figure 22). When this distance was greater than 108.3 km, the probability of killer whale depredation on the next haul dropped to < 0.5.

Because large seasonal variations in the probability of depredation by sperm whales were detected, the distance travelled by vessels between sets was also modelled as a function of the time of year. Results indicated that for sperm whales, the correlation between this distance and the probability of depredation was stronger in autumn than during other seasons, decreasing from 0.7 for distances < 10 km to 0.45 for distances > 100 km (Figure 23).

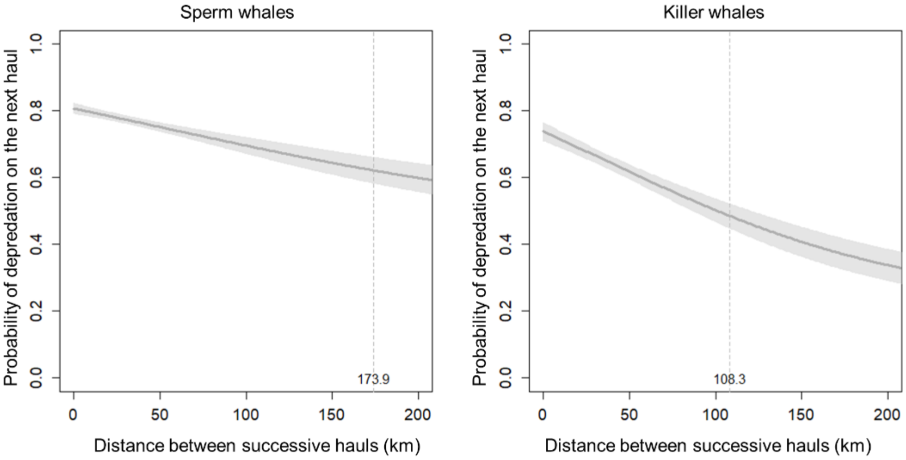

Figure 22. Probability of a. sperm whale and b. killer whale depredation on a set that was successively hauled after a depredated set as a function of the distance travelled between these two sets as estimated by the best GLMs fitted on the proportion of longline sets next hauled depredated (dark grey line) and 95% confidence intervals (grey shade). The vertical dashed line indicates the breakpoint in the relationship.

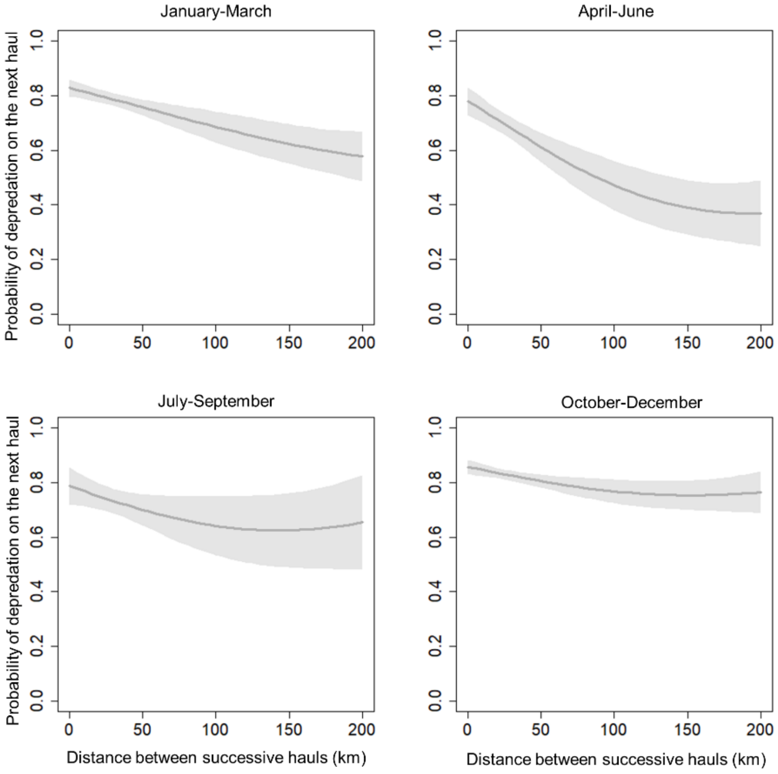

Figure 23. Probability of sperm whale depredation on a set that was successively hauled after a depredated set as a function of the distance travelled between these two sets as estimated by the best GLMs fitted on the proportion of longline sets next hauled, for each season of the year.

7. Conclusion

Following an interim document produced in 2018, this report presented the final results from the various analyses aimed at better understanding the extent and patterns of whale depredation in the commercial Patagonian toothfish longline fishery operating off Chile as part of the COLTO project. Using long term datasets spanning from 2006 to 2016, this report assessed the spatio-temporal frequency of depredation interactions, the catch removals due to these interactions and the number of depredating whales in the area. Together, these results have multiple implications in the socio-economic and ecological management of the whale depredation conflict in Southern Chile. In addition, this report identified multiple variables influencing the extent of depredation interactions and used these results to list potential practices captains/crews/companies may implement to minimize these interactions.

Before starting the analyses, this study had identified issues with the way data on whale depredation interactions have been collected by fishery observers / crews from fishing vessels. The data set only included one data field with estimates of the number of killer whales and or sperm whales observed from the vessel and these estimates were assigned to hauls. For this study, it was assumed that estimates > 0 were occurrences of depredation interactions, but there was uncertainty about records of 0's or empty cells in the data set. Specifically, whether 0's and missing records referred to the same information or whether they meant true 0's or uncertain presence of whales, was unknown. To avoid this confusion and record the occurrence of depredation interactions more accurately with a methodology standardized across other toothfish fisheries in years to come, it is recommended that for each haul for each whale species, data should be collected as follows:

- Absence: weather/light/visibility conditions are good, observation effort is provided by the observer/crew, and the absence of depredating whales around the vessel is confirmed;
- Presence: weather/light/visibility conditions are good, observation effort is provided by the observer/crew, and the presence of whales around the vessel depredating on the line (repeated dives towards the line, seabird activity around the whales at the surface, fish oil slick visible on the water, etc.) is confirmed;
- Unknown: Weather and/or light and/or visibility conditions are poor and/or observation effort could not be performed by the observer/crew, and therefore

whether whales were present and depredating or absent during hauling of this set is not known.

In addition, because of the difficulty in knowing exactly how many whales are around the vessel during a depredation interaction, it is recommended that observers/crews provide two whale number estimates per haul: a minimum and a maximum.

The frequency of sperm whale and killer whale depredation interactions in Chilean waters (42% and 19% of hauls for the two species, respectively) is high in comparison with other subantarctic areas where toothfish fisheries operate. However, large variation in this frequency was observed across vessels, years, months and in space across the fishing area. When modelled, this frequency allowed for probabilities of vessels to experience depredation interactions to be predicted.

For sperm whales, the probability of depredation interactions:

- decreased from 2006 to 2016;
- decreased in spring and summer months, and was the highest in winter;
- was highly localised in the North in summer, and at mid and low latitudes in winter;
- was homogeneously low across the fishing area in autumn, and homogeneously high across the fishing area in spring.

For killer whales, the probability of depredation interactions:

- decreased from 2006 to 2016;
- decreased in autumn and winter months, and was the highest in spring;
- was highly localised in the southernmost part of the fishing area in winter;
- was homogeneously low across the fishing area in summer.

This variation therefore suggests that by targeting specific areas and time of the year, the Chilean toothfish vessels may reduce their probabilities of experiencing depredation interactions. Furthermore, this report provided spatio-temporal predictions of the toothfish CPUE that may be used by fishermen/companies to better target these areas/time of the year for their operations. For instance, operating primarily from January to March in the South part of the area may be one strategy combining increased CPUE with low probabilities of depredation interactions with both killer and sperm whales.

This report provided estimates of the catch removals due to whale depredation interactions in Chile using an advanced modelling approach standardized with other fisheries/areas. A mean of 191 [124-257] t of toothfish were estimated being removed every year by whales from longlines, which represented a depredation rate of 12.1% [8.6-15] of the total catch (landed + depredated). This depredation rate has remained relatively stable over the 2008-2016 period, meaning that the reported decrease of catch removals from 2014 is likely to be explained by a reduction of the fishing effort from that year.

As catch removals due to whale depredation were found to greatly vary with the number of whales, the hauling speed and the fishing system, this study reported potential ways of minimizing these removals when vessels are confronted to depredation. The results indicated that:

- Increased hauling speed during depredation interactions may substantially decrease the amount of toothfish removed by whales from hooks;
- For a given number of whales, the use of trotlines equipped with cachaloteras reduced the amount of toothfish removed by whales when compared to the autoline system without fish protection devices.

As part of this study, photo-identification data from 2017 and 2018 were analysed and results provided first estimates of the number of depredating killer whales fishermen are dealing with across the Chilean fishing area. Results indicated that:

- A minimum of 61 killer whales are involved in depredation interactions, including 41 from the “regular” form and 20 from the “Type D” form;
- The cumulative numbers of newly identified individuals have levelled off as the cumulative photo-identification effort increased, suggesting that 61 individuals may represent a large part of the total number of depredating whales in the area.

Unfortunately, these numbers could not be assessed for sperm whales due to insufficient data. For both killer whale and sperm whales, the continuation of the photo-identification effort from fishing vessels by fishery observers and/or crew members is therefore strongly encouraged to produce accurate estimates of numbers for both species, and increasing the number of years of monitoring will also allow to determine trends in these numbers.

Additionally, further photo-identification effort should allow for a more accurate assessment of the movements of depredating whales in response to movements of fishing vessels. More specifically, killer whales of the “regular” form were found to move over large distances

(>600 km), sometimes over short periods of time, to repeatedly interact with vessels within the fishing area. However, the analysis of distance between hauls indicated that vessels are less likely to be followed by the depredating killer whales if leaving an area with depredation and travelling >100 km to a new fishing area. Combining consistent photo-identification data over multiple hauls with fine scale movements of fishing vessels will allow for a better understanding of how whales follow vessels, and therefore how vessels can outrun the whales during fishing operations and avoid being repeatedly depredated by the same individuals. In the meantime, and given that fishermen are dealing with a limited number of whales as highlighted by this study, it is still strongly encouraged to implement “move-on” strategies in Chilean waters. These strategies involve buoying off the fishing gear at the bottom as soon as the killer whales show up around the vessel, and leaving the fishing area by travelling a distance >100 km. The gear remaining in the water can be picked up several days later. Similarly, when experiencing depredation interactions with sperm whales, vessels are less likely to be followed by the depredating sperm whales if leaving the area and travelling >170 km to a new fishing area. However, this distance threshold is high, higher than in other fisheries (67 km for the Falkland Islands for example). This is likely due to a combination of features of the Chilean fishing area: narrow profile / small size of the fishing area (steep slope on the shelf edge) and higher densities of sperm whales, resulting in a high probability for vessels to encounter new sperm whales in the new fishing area. However, this distance threshold was lower in Autumn months, likely because sperm whales are present in lower densities during this time of year.

Lastly, while this report was focused on the Chilean commercial toothfish fishery and the Southern Chile fishing area, funding received as part of the COLTO project on whale depredation has allowed for research and knowledge to be substantially enhanced on various aspects of the depredation issue. Major findings have been produced from this research in scientific publications that are likely to be useful for all partners. These findings include:

- Depredating killer whales and sperm whales in subantarctic waters were found to naturally feed on toothfish in absence of fishing vessels (Appendix 1). This is likely to generate large spatio-temporal overlaps between fishermen and whales in fishing areas and may explain the development of depredation as a new feeding behaviour in response to a facilitated access to a prey that whales search for in natural conditions.

- Killer whales are able to dive to great depths (>1,000m) when depredating toothfish during hauls, and make decisions to swim towards a fishing vessels from > 100 km away from this vessel (Appendix 2);
- Sperm whales perform deep dives both when depredating toothfish during hauls and when present in the vicinity of fishing gear while hooks are still at the bottom (Appendix 2);
- Sperm whales do interact with longline sets at the bottom before hauling starts (Appendix 3);
- Variation in the way vessels operate in space and time across different subantarctic areas was found to partly explain differences in the extent of whale depredation between the major Patagonian toothfish fisheries (Appendix 4);
- Fishermen acting on specific fishing variables such as the hauling speed, the soak time, the time of the year and the distance travelled between fishing areas were found to reduce both their probability of experiencing sperm whale depredation and the amount of toothfish removed by sperm whales from hooks (Appendix 5).

8. Further research

While this study has extensively assessed of the extent of whale depredation, catch removals, drivers of interactions and whale numbers, it has also allowed for areas of research and questions for which information is still missing to be identified.

Firstly, a fine scale analysis of the behaviour of fishing vessels, the decisions made by skippers and the movements of whales in response to the movements and fishing operations of vessels, is still needed. Specifically, by combining fishing data set at the haul level (or the even more accurate Vessel Monitoring System data) with a photo-identification effort being consistently performed during multiple and repeated depredation interactions, this analysis would allow for:

- The level of detectability of vessels (distance at which vessels are detected by whales) to be examined;
- The operational drivers of this detectability (type of engine propulsion, type of fishing operation and use of the engine/propeller by skippers) to be identified;
- The variables influencing the decisions made by the whales to follow or to not follow fishing vessels (number and distance of other vessels around, distance

travelled by vessels, spatial factors such as the productivity of areas) to be investigated.

Together, this information would be crucial in guiding skippers in the decisions to be made to further minimize the chances of being detected and/or followed by whales when operating in Southern Chile.

Secondly, as the Chilean commercial toothfish fishing vessels have been extensively using trotlines equipped with cachaloteras as fish protection devices, this fishery offers a unique opportunity to:

- Assess the specific factors and features of the system maximizing the effectiveness of this system in reducing the catch removals due to whale depredation;
- Work on the development of improved designs and versions of the cachalotera system to further reduce the amount of toothfish removed by whales while remaining manageable and easy to implement for fishing crews.

Other systems have been tried to either keep the whales away from the fishing gear (e.g. acoustic repulsive) or make the fishing gear harder to detect for the whales. Again, the Chilean fishery and the collaborations already established offer a good opportunity to develop protocols and testing procedures of these possible technological means to reduce depredation.

Additionally, while this study has suggested a number of practices to either avoid or minimize depredation, a full costs and benefits analysis should be conducted over these practices. Typically, while increasing the fishing success, implementing strategies of avoidance of depredation interactions by targeting areas/time of the year of low probability of interaction, or by moving over large distances to outrun the whales may generate additional costs for fishermen and fishing companies. As such, assessing the ratio between these costs and the benefits gained from implementing these strategies would be one additional information further guiding fishermen in their decisions.

Lastly, this analysis was conducted over a 11-year period (with limited data in 2006 and 2007) and overtime trends in depredation levels, whale numbers, catches and catch removals could not be assessed. With additional years of data, including consistent photo-identification data on both sperm whales and killer whales, further research would allow to determine how the different components of the Chilean system (fishery, toothfish and whale populations) are evolving and to predict how they would do so in the future.

9. Appendices

Appendix 1

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Importance of toothfish in the diet of generalist subantarctic killer whales: implications for fisheries interactions

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ABSTRACT: Fisheries may generate new feeding opportunities for marine predators, which switch foraging behaviour to depredation when they feed on fish directly from fishing gear. However, the role of diet in the propensity of individuals to depredate and whether the depredated resource is artificial or part of the natural diet of individuals is often unclear. Using stable isotopes, this study investigated the importance of the commercially exploited Patagonian toothfish *Dissostichus eleginoides* in the diet of generalist subantarctic killer whales *Orcinus orca* depredating this fish at Crozet (45°S, 50°E). The isotopic niche of these killer whales was large and overlapped with that of sperm whales *Physeter macrocephalus* from the same region, which feed on toothfish both naturally and through depredation. There was no isotopic difference between killer whales that depredated toothfish and those that did not. Isotopic mixing models indicated that prey groups including large/medium sized toothfish and elephant seal *Mirounga leonina* pups represented ~60% of the diet relative to prey groups including penguins, baleen whales and coastal fish. These results indicate that toothfish are an important natural prey item of Crozet killer whales and that switching to depredation primarily occurs when fisheries facilitate access to that resource. This study suggests that toothfish, as a commercial species, may also have a key role as prey for top predators in subantarctic ecosystems. Therefore, assessing the extent to which predators use that resource naturally or from fisheries is now needed to improve both fish stock management and species conservation strategies.

KEY WORDS: Diet · Fisheries · Southern Ocean · Killer whale · Stable isotopes · Fishery interactions

1. INTRODUCTION

Anthropogenic activities may influence the dietary niche width of wild populations by modifying the availability of resources (Van Valen 1965, Newsome et al. 2015). While human activities often result in resource scarcity, sometimes they generate new feeding opportunities for species (Votier et al. 2004, Woodroffe et al. 2005, Jennings et al. 2009). This is the case when predators feed on a resource that is either produced, raised or captured by humans (Woodroffe et al. 2005). This behaviour, defined as

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'depredation', has been increasingly reported both in terrestrial (e.g. predators feeding on livestock; Sillero-Zubiri et al. 2007) and marine environments (e.g. predators feeding on fish raised in farms or caught in fishing gears; Northridge & Hofman 1999, Gilman et al. 2007, 2008, Read 2008).

The depredated resource may already be part of the natural diet of predators, with access facilitated by humans, or it may be an entirely artificial resource which would not otherwise have been used by predators in natural conditions. This distinction is critical in understanding the underlying behavioural mechanisms of predators switching from a natural to a depredated resource (Boitani & Powell 2012). Generalist predators may be more likely to depredate artificial new resources opportunistically while highly specialised predators may depredate a resource only if it is already part of their natural diet (Stoddart et al. 2001, Sidorovich et al. 2003). Knowing the importance of the depredated resource in the natural diet of predators is also needed to assess the effects of depredation and fisheries on wild populations, fish stocks and ecosystems as a whole. Depredation may substantially modify the energy balance of the predator and its role in ecosystem food web dynamics (Woodroffe et al. 2005). For instance, if the depredated resource is fully artificial for the predator, depredation may lead to decreased availability of that resource for other functional groups in the ecosystem, subsequently affecting these groups through trophic effects (Woodroffe et al. 2005). Also, by feeding on fish caught in fishing gear, marine predators may cause increased and difficult-to-quantify mortality for fish stocks, thereby increasing the catches needed for fisheries to reach their quotas (Gilman et al. 2013, Gasco et al. 2015, Mitchell et al. 2018).

In subantarctic waters, extensive commercial longline fisheries target economically highly valuable Patagonian toothfish *Dissostichus eleginoides* (hereafter 'toothfish'). These fisheries provide artificial feeding opportunities for a range of large marine predators through discards (primarily for albatrosses and petrels) and depredation (for odontocetes) (Tasker et al. 2000, Kock 2001, Kock et al. 2006). Toothfish are large (0.5–2 m) fish that dominate the biomass of the bathypelagic zone, but may also be found in the meso- and epi-pelagic zones (Collins et al. 2010). However, the role of toothfish in subantarctic ecosystems and their importance as a natural prey for predators is unclear (Cherel et al. 2000, 2017, Constable et al. 2000). Specifically, determining the extent to which predators naturally feed and rely on toothfish is critical to assess the impacts of exploitation of that resource by fisheries on the conservation of subantarctic predators, many of which are threatened or endangered (Croxall et al. 2012).

Killer whales *Orcinus orca* are one of the main species depredating toothfish from subantarctic longline fisheries (Kock et al. 2006). Unlike some other regions, where killer whales have highly specialised prey preferences (Similä et al. 1996, Ford et al. 1998, Foote et al. 2009), subantarctic populations have relatively broad dietary niches that include mammals, birds, fish and sometimes cephalopods (Guinet & Jouventin 1990, Guinet 1992, Guinet et al. 2000, de Bruyn et al. 2013, Capella et al. 2014, Reisinger et al. 2016, Travers et al. 2018). This generalist diet may be driven by the subantarctic ecosystem's spatio-temporal heterogeneity in the availability of high-quality resources, such as seals, penguins and whales (Laws 1977, Knox 2006, Reisinger et al. 2018). This heterogeneity may force killer whales to supplement their primary diet with other prey such as fish and cephalopods. While toothfish are a confirmed depredated resource, there is no direct evidence of natural predation by killer whales on this fish species.

The killer whale population of the Crozet Islands (subantarctic islands located at 45° S, 50° E), hereafter 'Crozet killer whales', is among the populations that have most extensively depredated toothfish from fisheries since the mid-1990s (Roche et al. 2007, Tixier et al. 2010, 2016, Guinet et al. 2015). Crozet killer whales prey on seals, penguins, baleen whales and small notothenioids in inshore waters (Guinet 1992, Guinet et al. 2000); not all individuals have switched to depredation on toothfish from fisheries (Tixier et al. 2015, 2017). Elucidating the extent to which these killer whales naturally rely on toothfish as a resource whose availability is modified by fisheries would therefore provide insights into the ecological mechanisms of prey switching to depredation. Critically, this information would clarify the role of these prey and predator species in subantarctic ecosystem food web dynamics and the impacts of fisheries on the conservation of predator populations and fish stocks. Therefore, using stable isotope and diet reconstruction analyses for Crozet killer whales, the aims of this study were to (1) assess the importance of toothfish relative to other prey items for Crozet killer whales, and compared with other Southern Ocean killer whale populations and odontocete species, and (2) examine variation in the dietary importance of toothfish across individuals of the same population, with respect to whether or not they depredated from fisheries.

2. MATERIALS AND METHODS

2.1. Species and sample collection

Killer whale skin samples were collected at Crozet from biopsies performed remotely on free-ranging individuals, using a Barnett Rhino 150 lb compound crossbow and custom-built darts (Ceta-Dart) equipped with sterilized stainless steel tips (35 mm length, 7 mm diameter). Sampling was conducted opportunistically and passively (i.e. animals were not actively approached or followed using motorized means) from land on Possession Island and from a toothfish fishing vessel operating in the Crozet Exclusive Economic Zone (EEZ), from February 2011 to December 2012. Samples were collected from the mid-lateral region of the body, below the dorsal fin. Sub-samples containing skin tissue were stored in 70% ethanol. Only weaned individuals (>2 yr old) were sampled. Sampling occurred only when a single individual surfaced within 15 m of the sampler, and only when this individual was positively identified by eye during surfacing events directly preceding sampling. The sequence made of multiple surfacing events and the sampling event was monitored by photographs and/or video. Photographs of the dorsal fin of the sampled individual were systematically taken using a DSLR camera with 400 mm telephoto lens, and were used to confirm the identity of that individual after sampling, using an existing photo-identification database (Tixier et al. 2014). An additional skin sample was obtained from an individual found stranded and dead on Possession Island on 17 August 2006. The individual was an apparently healthy sub-adult male (total length [TL]: 6.90 m) which was known to be part of the Crozet killer whale population based on photo-identification records. However, because this sample was collected 5 yr before the biopsy samples, at a different time of year (winter) and lacked information about the behaviour of the individual over the pre-sampling period, isotopic information for this sample was not included in the analyses.

Isotopic information from skin samples collected from the Crozet killer whales was first examined through large-scale comparisons with other isotopic information available for other killer whale populations and other large odontocete species with different feeding ecologies and/or different habitats in the Southern Ocean (south of the Subtropical Front, ~40° S). Published isotopic values for weaned killer whales (>2 yr old) were obtained for one other subantarctic (Marion Island, 1000 km west of Crozet at a similar latitude) and 3 Antarctic populations (Types B1 and B2 around the Antarctic Peninsula [Durban et al. 2017] and Type C in the Ross Sea [Pitman & Ensor 2003]). The isotopic niche of the Crozet killer whales was expected to be similar to that of killer whales at Marion, as the 2 populations share similar habitats and appear to have a generalist feeding strategy based on consumption of the same prey species (Reisinger et al. 2016). In contrast, Antarctic killer whales, which use a different habitat and specialise on either fish (Type C; Pitman & Ensor 2003, Krahn et al. 2008), krill consumers (e.g. pygoscelid penguins) (Type B2; Pitman & Durban 2010) or predators of krill consumers, such as Weddell seals *Leptonychotes weddellii* (Type B1; Pitman & Durban 2012, Durban et al. 2017), were expected to have limited isotopic overlap with the Crozet killer whales. Isotopic information was also compared with that of sperm whales *Physeter macrocephalus*, which also depredate toothfish on longline fisheries, and southern long-finned pilot whales *Globicephala melas edwardii* from populations using similar habitats to that of the Crozet killer whales at Crozet and/or adjacent waters. Sperm whale skin samples were collected from fishing vessels operating in the Crozet and Kerguelen EEZs in January and February 2011, using the same equipment and protocols, and were treated using the same process as for the Crozet killer whale samples. For southern long-finned pilot whales, whose pelagic habitat overlaps with areas where toothfish fisheries operate but were never observed depredating toothfish on longlines, published skin isotopic values from weaned individuals (>3 m in length) at Kerguelen were used (Fontaine et al. 2015).

Species were considered confirmed prey for the Crozet killer whales if predation was directly observed and/or remains were found in the stomach contents of the individual found dead in 2006 (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m613p197_supp.pdf). From these data, species confirmed as prey items and for which spring/summer isotopic values were available for the study at Crozet included southern elephant seals *Mirounga leonina* (adult females and pups, confirmed as prey from observations and stomach contents); Antarctic and subantarctic fur seals *Arctocephalus gazella* and *A. tropicalis* (pups, from stomach contents); king penguins *Aptenodytes patagonicus*, gentoo penguins *Pygoscelis papua*, macaroni penguins *Eudyptes chrysolophus*, rockhopper penguins *E. chrysocome filholi* (all adults, from observations and stomach contents); and Patagonian toothfish (TL 81–174 cm, from observations) (Table 1).

Table 1. Mean ± SD δ^{13}C and δ^{15}N values for prey species and prey groups of the Crozet killer whale used in the MixSIAR models. Prey groups were determined via Ward's hierarchical clustering based on isotopic similarities. Prey species were differentiated based on age class (adults vs. juveniles; here, 'pups' for seal species), sex, season in which sampling occurred or size (total length [TL] for fish species) when relevant, and an abbreviation code is assigned to each. Sampling sites included Crozet Islands (CR), Kerguelen Islands (KE) and New Zealand (NZ). Isotopic values are provided for the type of tissue sampled: red blood cells (RBC), whole blood (WB), skin or muscle. These values were adjusted to represent muscle values for all prey species

Species	Code	Site	n	Tissue	δ^{13}C (‰)	δ^{15}N (‰)	δ^{13}C (‰) (adjusted)	δ^{15}N (‰) (adjusted)	Source
Group A							**−19.5 ± 0.6**	**8.2 ± 0.5**	
Gentoo penguin (spring) *Pygoscelis papua*	GP_sp	CR	11	RBC	−18.6 ± 0.3	8.2 ± 0.6	−18.2 ± 0.3	8.3 ± 0.6	This study
Macaroni penguin (spring) *Eudyptes chrysolophus*	MP_sp	CR	10	RBC	−19.4 ± 1.0	7.0 ± 0.2	−19.0 ± 1.0	7.1 ± 0.2	This study
Macaroni penguin (summer) *Eudyptes chrysolophus*	MP_su	CR	20	RBC	−20.0 ± 0.7	8.6 ± 0.4	−19.6 ± 0.7	8.7 ± 0.4	This study
Rockhopper penguin (spring) *Eudyptes chrysocome filholi*	RP_sp	CR	10	RBC	−20.2 ± 0.4	8.1 ± 0.5	−19.8 ± 0.4	8.2 ± 0.5	This study
Rockhopper penguin (summer) *Eudyptes chrysocome filholi*	RP_su	CR	10	RBC	−20.8 ± 0.3	8.6 ± 0.4	−20.4 ± 0.3	8.7 ± 0.4	This study
Southern right whale *Eubalaena australis*	SRW	NZ	18	Skin	−19.8 ± 0.6	8.1 ± 0.7	−19.8 ± 0.6	8.2 ± 0.7	Torres et al. (2017)
Group B							**−21.4 ± 0.4**	**10.4 ± 0.3**	
Southern elephant seal (adult females) *Mirounga leonina*	SES_fem	CR	70	WB	−21.9 ± 0.7	10.2 ± 0.2	−22.3 ± 0.7	10.9 ± 0.17	This study
King penguin (spring) *Aptenodytes patagonicus*	KP_sp	CR	11	RBC	−21.8 ± 0.4	10.1 ± 0.2	−21.4 ± 0.4	10.2 ± 0.2	This study
King penguin (summer) *Aptenodytes patagonicus*	KP_su	CR	10	RBC	−22.2 ± 0.2	10.3 ± 0.2	−21.8 ± 0.2	10.4 ± 0.2	This study
Patagonian toothfish (TL 43 cm) *Dissostichus eleginoides*	TOP_43	KE	6	Muscle	−20.3 ± 0.4	10.0 ± 0.8	−20.3 ± 0.4	10.0 ± 0.8	This study
Group C							**−20.5 ± 0.5**	**12.7 ± 0.4**	
Southern elephant seal (pups) *Mirounga leonina*	SES_pup	CR	70	WB	−21.6 ± 0.7	11.6 ± 0.4	−22.0 ± 0.7	12.3 ± 0.4	This study
Antarctic fur seals (pups) *Arctocephalus gazella*	AFS_pup	CR	10	WB	−20.7 ± 0.5	12.4 ± 0.2	−21.1 ± 0.6	13.1 ± 0.2	Cherel et al. (2015)
Subantarctic fur seals (pups) *Arctocephalus tropicalis*	SAFS_pup	CR	10	WB	−19.4 ± 0.2	12.0 ± 0.3	−19.8 ± 0.2	12.7 ± 0.3	Cherel et al. (2015)
Patagonian toothfish (TL 63 cm) *Dissostichus eleginoides*	TOP_63	KE	17	Muscle	−19.2 ± 0.6	12.6 ± 0.9	−19.2 ± 0.6	12.6 ± 0.9	This study
Group D							**−18.9 ± 0.6**	**14.4 ± 0.6**	
Patagonian toothfish (TL 95 cm) *Dissostichus eleginoides*	TOP_95	CR	14	Muscle	−18.3 ± 0.5	14.2 ± 0.7	−18.3 ± 0.5	14.2 ± 0.7	This study
Patagonian toothfish (TL 107 cm) *Dissostichus eleginoides*	TOP_107	CR	10	Muscle	−19.1 ± 0.5	14.3 ± 0.4	−19.1 ± 0.5	14.3 ± 0.4	This study
Patagonian toothfish (TL 160 cm) *Dissostichus eleginoides*	TOP_160	CR	22	Muscle	−19.3 ± 0.8	14.9 ± 0.7	−19.3 ± 0.8	14.9 ± 0.7	This study

Additional Patagonian toothfish samples for small and medium size individuals (TL 38–71 cm) were collected at Kerguelen (Table 1). For southern right whales *Eubalaena australis* (confirmed as prey from observations), isotopic values were from individuals sampled near subantarctic Campbell Island (Torres et al. 2017) (Table 1).

2.2. Stable isotope analyses

Killer whale skin samples were first oven-dried at 50°C for 48 h to allow ethanol evaporation, then ground and freeze-dried. As stable isotope values may be influenced by the lipid content of the tissue (Lesage et al. 2010, Giménez et al. 2017), 2 successive and identical lipid extractions were conducted using cyclohexane, each through 1 h sonication and subsequent centrifugation at 3000 rpm (i.e. 1613 × *g*). The lipid-extracted samples were then oven-dried again at 50°C for 48 h before being sub-sampled down to 0.3–0.4 mg. These sub-samples were processed at LIttoral ENvironnement et Sociétés (LIENSs; University of La Rochelle, France) through a continuous-flow isotope-ratio mass spectrometer (Micromass Isoprime) paired with an elemental analyser (Euro Vector EA 3024) for carbon and nitrogen isotope relative abundance ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively). The isotopic compositions are reported in the conventional δ notation as the per mil (‰) deviation relative to the standards Vienna Peedee Belemnite (for carbon) and air (for nitrogen), expressed in parts per thousand (‰). Within-run (n = 10) replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors <0.15‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Samples with a C:N mass ratio <3.6 were considered lipid-free (Yurkowski et al. 2015, Giménez et al. 2017) and included in subsequent analyses. Prey samples for which the analysed tissue was muscle (toothfish) were processed using the same protocol as for killer whale skin, including cyclohexane lipid extraction. For the other prey (elephant seals, fur seals and penguins), where isotopic values were measured for whole blood or red blood cells, values were adjusted to represent muscle using adjustment values presented in Reisinger et al. (2016). The isotopic method was validated in the southern Indian Ocean (encompassing the killer whale feeding areas), with $\delta^{13}C$ values of consumers indicating their foraging habitats (Cherel & Hobson 2007) and their $\delta^{15}N$ values increasing with trophic level (Cherel et al. 2010).

The isotopic niche width of the Crozet killer whale population was estimated and compared to other populations of killer whales, sperm whales and southern pilot whales within the Southern Ocean in a Bayesian framework using multivariate ellipse-based metrics (Jackson et al. 2011). Standard ellipse areas corrected for sample size (SEA_c) and Bayesian Standard Ellipse Areas (SEA_B) were calculated for each group. SEA_B was estimated using 10^5 posterior draws and used to statistically compare niche metrics, which included niche width and niche overlap between groups. The niche overlap for 2 given groups was calculated as an isotopic area of overlap from the maximum likelihood fitted ellipses of the 2 groups (Jackson et al. 2011). All niche metric calculations and comparisons were conducted with the package 'SIBER' (Jackson et al. 2011) in R v.3.4.1 (R Development Core Team 2017).

The effect of toothfish depredation on the isotopic values of Crozet killer whales was examined through a 2-state index assigned to each sample. Samples were categorised as 'depredating' or 'non-depredating' depending on whether the biopsied individuals were observed interacting with fisheries in the 24 or 48 d preceding the sampling date. These 2 periods were defined based on isotopic half-time turnover rates estimated for bottlenose dolphin *Tursiops truncatus* skin: 24 ± 8 d for carbon and 48 ± 19 d for nitrogen (Giménez et al. 2016). Thus, depredating samples were samples from individuals that were photographed at least once while depredating toothfish caught by fishing vessels during the 24 d before sampling for $\delta^{13}C$ analyses, and 48 d before sampling for $\delta^{15}N$ analyses. Photographs were taken from fishing vessels by fishery observers, who are present onboard licenced toothfish longliners for all fishing trips. They monitor 100% of the fishing operations and provide a quasi-systematic (on average >95% of fishing days with killer whale presence around vessels covered) photo-identification effort during killer whale–fishing gear interaction events using DSLR cameras with 400 mm telephoto lenses. Non-depredating samples were samples from individuals for which the biopsy was performed when no fishing occurred in the Crozet EEZ 24 or 48 d before sampling, based on the PECHEKER database (Martin & Pruvost 2007), or from individuals that were not photographed from fishing vessels 24 or 48 d before sampling. The absence of fishing vessels operating illegally inside and/or in the vicinity of the Crozet EEZ during the 48 d preceding biopsies was checked through satellite and ship-based surveillance data requested from the French administration. This ruled out the possibility that killer whales had depredated toothfish from vessels other than the ones from which we received data. Additionally, recent satellite/dive recorder data from a killer whale depredating toothfish at South Georgia indicated that depredation events only occurred in the vicinity of the vessel during gear retrieval phases, which is when observers provide photo-identification effort (Towers et al. 2019).

Niche metric comparisons and statistical tests performed on $\delta^{13}C$ and $\delta^{15}N$ values were used to assess dietary variations between depredating and non-depredating samples. SEA_c and SEA_B were calculated separately for depredating and non-depredating samples; here, this assignment was made using information on the occurrence of depredation in the 48 d preceding sampling. After the normality of the $\delta^{13}C$ and $\delta^{15}N$ values was tested (Shapiro-Wilk test), differences between depredating and non-depredating groups were tested using either parametric (*t*-test) or non-parametric (Mann-Whitney *U*-test) tests.

2.3. Diet reconstruction

The relative contribution of various prey items to the diet of the Crozet killer whales, and the influence of fishery interactions on this contribution, were assessed through Bayesian stable isotope mixing models fitted in the 'MixSIAR' package (Stock & Semmens 2013, Stock et al. 2018) in R v.3.4.1 (R Development Core Team 2017). This analysis was conducted using prey data only for confirmed prey items, as described above. The mean stable isotope values of these species were used to *a priori* identify statistically different clusters through a Ward's hierarchical cluster analysis ('hclust' function in R package 'stats') and ANOVAs. MixSIAR models were fitted using the individual isotopic values of the Crozet killer whales (consumer), the mean ± SD isotopic values of prey clusters (sources) and the diet-to-tissue discrimination factors (DTDF) estimated by Giménez et al. (2016) for bottlenose dolphin skin (DTDF for δ^{13}C = 1.01 ± 0.37‰; δ^{15}N = 1.57 ± 0.52‰). Fishery interaction was incorporated in the MixSIAR models as a fixed effect using samples categorised as depredating or non-depredating based on the 48 d preceding sampling. The effect of depredating or non-depredating on the relative contribution of prey groups to killer whale diet was tested through model selection based on the leave-one-out information criterion (LOO_{ic}) (Vehtari et al. 2017, Stock et al. 2018). Models were run with a generalist type prior, 3 Markov chain Monte Carlo (MCMC) chains of 300 000 draws and a burn-in of 200 000 draws. The convergence of models was checked using both Gelman-Rubin and Geweke diagnostics. Model evaluation and validation were conducted by determining the likelihood of prey groups being included in the mixing polygon of the Crozet killer whales, based on simulations developed by Smith et al. (2013). Unless otherwise stated, data are presented as mean ± SD.

3. RESULTS

Biopsy samples were obtained from 18 individuals from the Crozet killer whale population (Table S2 in Supplement 1). Values of δ^{13}C of lipid-extracted skin ranged from −19.6 to −18.0‰ and values of δ^{15}N from 12.5 to 14.3‰ (Table 2). Tests for potential age- and sex-effects on δ^{13}C and δ^{15}N values indicated no significant differences between males (n = 3) and females (n = 15), nor between adults (n = 14) and subadults (n = 4) (*t*-tests, all with $p > 0.5$). Similarly, there were no significant differences between months of sampling (n = 9 in February, n = 6 in November and n = 3 in December). The isotopic values of the skin sample collected from the individual found dead in 2006 were δ^{13}C = −18.8‰ and δ^{15}N = 13.4‰ (Table S2).

3.1. Stable isotope analyses

The isotopic niche area of the Crozet killer whales, which was estimated at SEA_c = 0.64‰^{2} and SEA_B =

Table 2. Mean ± SD δ^{13}C and δ^{15}N values of lipid-extracted skin and isotopic niche metrics for killer whales *Orcinus orca*, sperm whales *Physeter macrocephalus* and southern pilot whales *Globicephala melas erwardii* within the Southern Ocean. Niche metrics include the standard ellipse areas corrected for sample size (SEA_c) and the Bayesian SEA (SEA_B). SEA_B was used to estimate the probability (Pr) of the Crozet killer whale isotopic niche being smaller than that of other groups (Pr <SEA_B), as well as the degree of overlap of isotopic niches (% SEA_B overlap)

	n	δ^{13}C (‰)	δ^{15}N (‰)	SEA_c (‰^{2})	SEA_B (‰^{2})	Pr <SEA_B	% SEA_B overlap	Source
Orcinus orca								
Crozet Islands	18	−19.0 ± 0.5	13.6 ± 0.4	0.64	0.57	–	–	This study
Marion Island	32	−18.6 ± 0.4	12.3 ± 0.6	0.94	0.87	0.90	3	Reisinger et al. (2016)
Ross Sea (Type C)	27	−23.8 ± 0.4	13.2 ± 0.4	0.21	0.2	0.00	0	Krahn et al. (2008)
Antarctic Peninsula (Type B1)	11	−22.4 ± 0.4	12.2 ± 0.4	0.45	0.38	0.17	0	Durban et al. (2017)
Antarctic Peninsula (Type B2)	8	−22.8 ± 0.3	11.3 ± 0.2	0.20	0.16	0.01	0	Durban et al. (2017)
Physeter macrocephalus								
Crozet Islands/Kerguelen Islands	6	−18.6 ± 0.4	14.0 ± 0.4	0.70	0.51	0.49	24	This study
Globicephala melas edwardii								
Kerguelen Islands	65	−18.4 ± 0.5	12.2 ± 0.3	0.36	0.40	0.07	0	Fontaine et al. (2015)

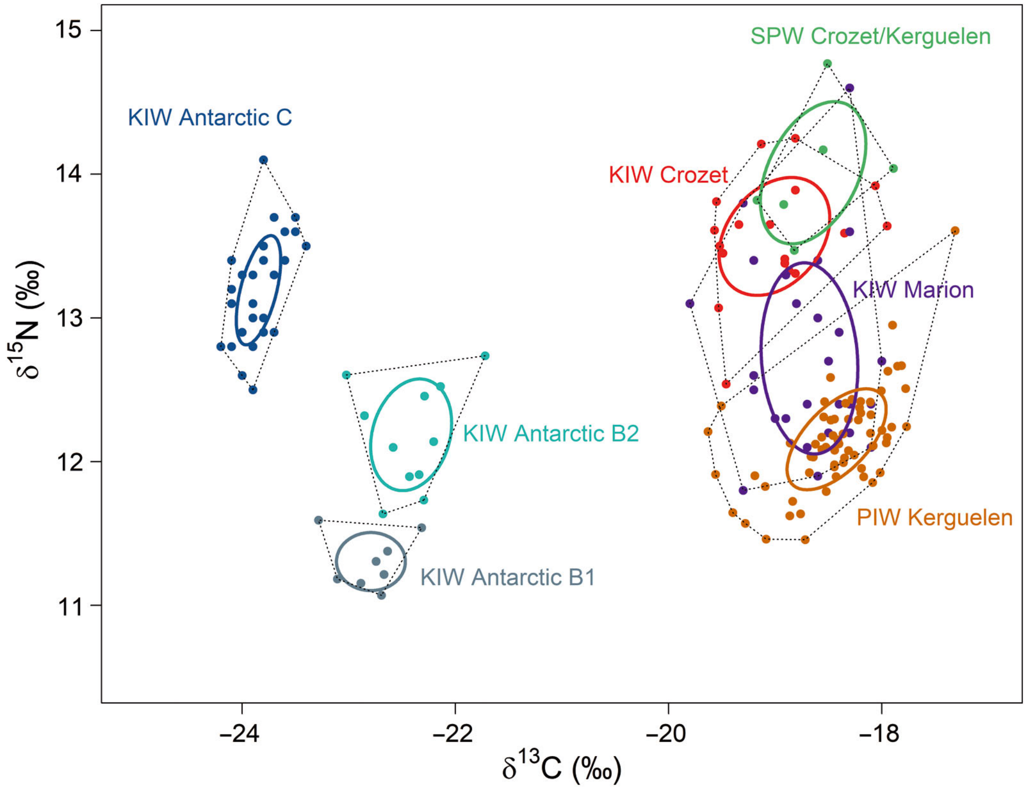

Fig. 1. Sample-size corrected standard ellipse areas (SEA$_c$; solid lines) and convex hull areas (dotted lines) for killer whales (KIW), sperm whales (SPW) and southern pilot whales (PIW) in Antarctic and subantarctic waters. Individual values of δ^{13}C and δ^{15}N of skin samples (points) for Crozet (this study), Marion (Reisinger et al. 2016), Antarctic Type C (Krahn et al. 2008), Antarctic Type B1 and B2 (Durban et al. 2017) killer whales, sperm whales from Crozet/Kerguelen (this study) and southern pilot whales from Kerguelen (Fontaine et al. 2015) are shown

0.57 ‰^{2}, had a high probability of being smaller than that of the Marion killer whales (SEA$_c$ = 0.94 ‰^{2} and SEA$_B$ = 0.87 ‰^{2}), but was likely larger than those of Type B1, B2 and C killer whales sampled in Antarctica, and southern pilot whales from Kerguelen waters (Table 2, Fig. 1). However, with a probability of 0.49, the isotopic niche width of the Crozet killer whales was statistically similar to that of sperm whales sampled in Crozet and Kerguelen waters. Niche overlap of the Crozet killer whales was zero with Antarctic killer whales and Kerguelen southern pilot whales, low with the Marion killer whales (3 %) and highest with the Crozet and Kerguelen sperm whales (24 %).

In total, 9 of the sampled killer whales were sighted depredating toothfish from fisheries during the 24 d preceding sampling, and these samples were thus considered as depredating for δ^{13}C comparisons (Tables S2 & S4 in Supplement 1). Values of δ^{13}C of these samples (δ^{13}C = −19.0 ± 0.7 ‰, n = 9) were not significantly different (Mann-Whitney *U*-test, p = 0.57) from those of non-depredating samples (δ^{13}C = −19.0 ± 0.3 ‰, n = 9). Values of δ^{15}N of samples from 11 individuals sighted depredating from fisheries in the 48 d preceding sampling (δ^{15}N = 13.4 ± 0.4 ‰, n = 11) were not statistically different from those of samples from individuals that did not depredate from fisheries over that period (δ^{15}N = 13.8 ± 0.4 ‰, n = 7; *t*-test, p = 0.09). The isotopic niche area of non-depredating samples (SEA$_c$ = 0.27 and SEA$_B$ = 0.16 ‰^{2}) was likely smaller than that of depredating samples (SEA$_c$ = 0.77 and SEA$_B$ = 0.71 ‰^{2}) (Fig. S1 in Supplement 1).

3.2. Diet reconstruction

In total, 4 statistically different prey groups were identified from the Ward's hierarchical clustering of δ^{13}C and δ^{15}N values (Figs. 2, 3a & Fig. S2, Table S5 in Supplement 1). Group A included species with the lowest δ^{15}N values (8.2 ± 0.5 ‰): 3 species of penguins (*Eudyptes* spp. and gentoo penguins) and southern right whales (Table 1). Group B had a higher mean δ^{15}N value (δ^{15}N = 10.4 ± 0.4 ‰) and

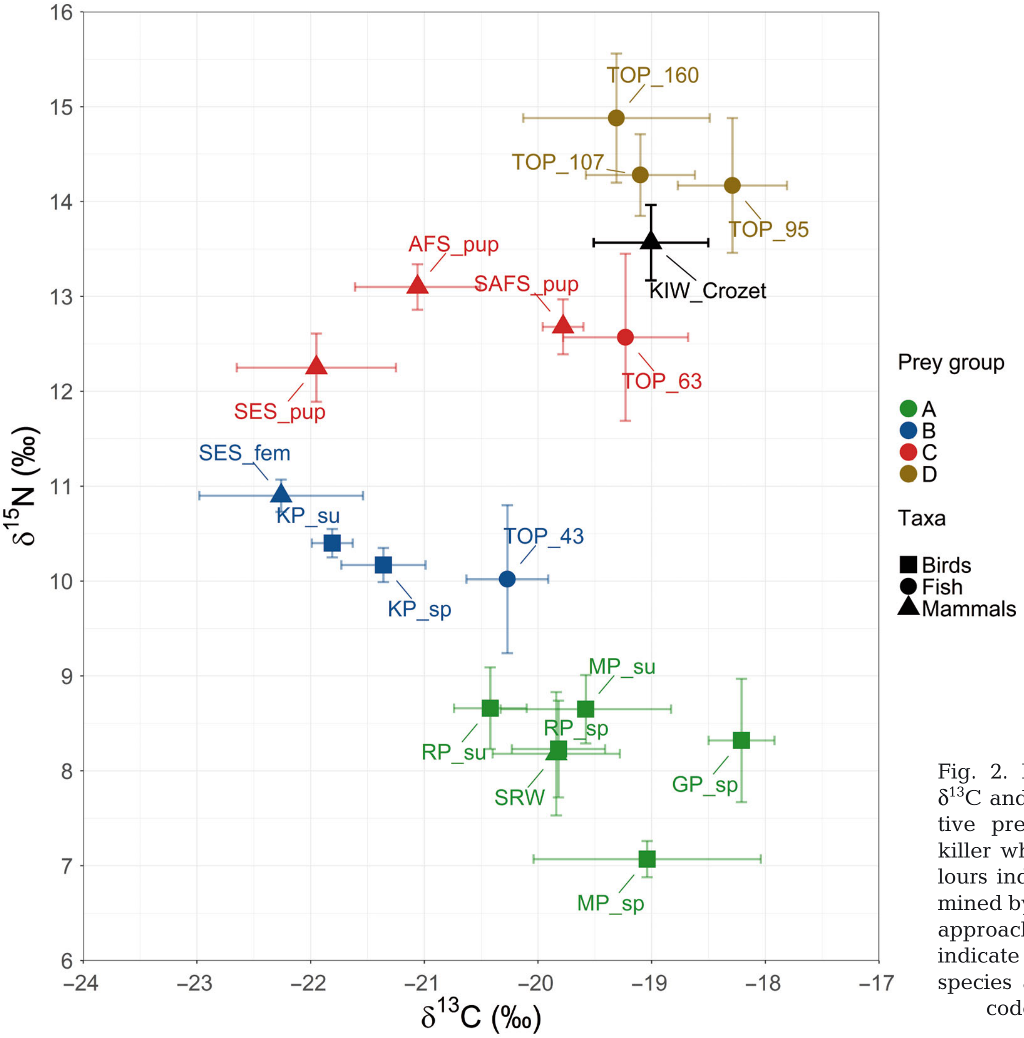

Fig. 2. Isospace of mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of the putative prey items for the Crozet killer whales ('KIW_Crozet'). Colours indicate prey groups determined by a hierarchical clustering approach, and the shape of points indicate prey taxa. See Table 2 for species associated with the prey codes used for the figure

included king penguins, small sized Patagonian toothfish (TL 43 cm) and the prey item with the lowest $\delta^{13}C$ value, adult female southern elephant seals ($\delta^{13}C = -21.9 \pm 0.7$‰, n = 70). Group C ($\delta^{15}N = 12.7 \pm 0.4$‰) contained medium sized toothfish (TL 63 cm), elephant seal pups, Antarctic fur seals and subantarctic fur seals. Group D had the highest $\delta^{15}N$ (14.4 ± 0.6‰) and $\delta^{13}C$ (–18.9 ± 0.6‰) values and included only large (TL 95, 107 and 160 cm) Patagonian toothfish. Toothfish of TL 160 cm was the prey item with the highest $\delta^{15}N$ value of all prey items ($\delta^{15}N = 14.9 \pm 0.7$‰).

All killer whale isotopic values were inside the 95% mixing region of the mixing polygon delimited by the isotopic values of the 4 prey groups adjusted to DTDFs, thus validating the MixSIAR models fitted with these prey groups (Fig. 3b). The best MixSIAR model (Model 1) included whether or not killer whales interacted with fisheries before sampling (LOO_{ic} = 24.2; Table 3). However, this model and the null model were differentiated by LOO_{ic} = 0.1, and the 2 models had close weights (0.51 and 0.49, respectively), indicating that the depredation factor had low explanatory power. According to the null model, prey Group C was most important in the diet of Crozet killer whales with a mean contribution of 33 ± 19% (Fig. 4a). Group D was the second most important prey group with 28 ± 11% mean contribution. Group A and Group B were the least contributing prey groups with 17 ± 7 and 22 ± 13%, respectively. According to Model 1, Group C contributed 35 ± 21% for depredating samples, and 33 ± 20% for non-depredating samples (Fig. 4b). The contribution of Group D to the diet of depredating samples was higher than for non-depredating samples (32 ± 13 and 28 ± 11%, respectively). The diet of non-depredating samples included Group A and B in larger proportions (17 ± 7 and 22 ± 13%, respectively) than for depredating samples (12 ± 7 and 21 ± 13%, respectively).

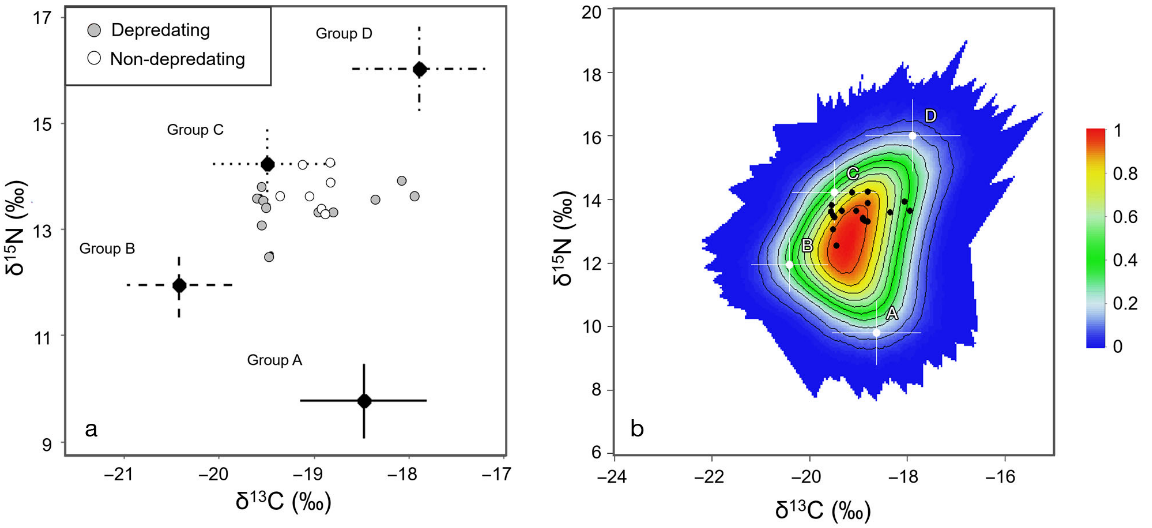

Fig. 3. (a) $\delta^{13}C$ and $\delta^{15}N$ values of the skin samples of Crozet killer whales that depredated or did not depredate toothfish from fisheries before sampling, and mean with 95% confidence intervals of the putative prey groups (black dots and error bars) estimated from the source isotopic values and the diet-to-tissue discrimination factors. (b) Mixing polygon including the Crozet killer whale isotopic values (black dots) and prey groups (mean ± SD isotopic value: white dots and error bars); background shows the probability of prey groups being included in the diet, with probability contours drawn every 10%. Details on species included in prey groups are provided in Table 2

4. DISCUSSION

The present study provides key insights into the role of toothfish as a prey resource for a generalist subantarctic predator, the killer whale. The findings of different stable isotope analysis approaches, which combined inter- and intra-specific comparisons and dietary reconstruction, suggest that killer whales do rely on toothfish as well as marine mammals and penguins as natural prey items. While fisheries may facilitate access to toothfish for killer whales depredating on the fishing gear, fisheries also exploit toothfish stocks that are likely used by killer whales as a natural resource. This study therefore highlights the trophic interactions between fisheries and killer whales through depredation and competition for the same resource in subantarctic waters.

Table 3. MixSIAR model selection outputs based on leave-one-out cross validation information criterion (LOO_{ic}). Models were fitted with the occurrence of depredation on toothfish from fisheries over the 48 d preceding sampling as a fixed effect ('Depredation'), or without any covariate ('Null'). The LOO_{ic} differences between each model and the model with lowest LOO_{ic} (ΔLOO_{ic}), standard errors (SE) for both LOO_{ic} and ΔLOO_{ic} values, as well as the relative weight of models are provided

Model #	Model	LOO_{ic}	SE LOO_{ic}	ΔLOO_{ic}	SE ΔLOO_{ic}	Weight
1	Depredation	24.2	8.6	–	–	0.51
2	Null	24.3	9.0	0.1	2.6	0.49

Results of the stable isotope analyses confirmed previous visual observations suggesting that Crozet killer whales have a generalist feeding strategy. Their niche width was larger than that of specialised killer whale populations (Antarctic Type C, B1 and B2; Pitman & Ensor 2003, Krahn et al. 2008, Pitman & Durban 2010, 2012, Durban et al. 2017) but similar to that of Marion killer whales, another subantarctic population with a generalist feeding strategy (Reisinger et al. 2016). The Crozet killer whales were sampled in spring/summer and, during this time of year, the contribution of elephant seal pups to their diet was higher than that of prey groups including adult elephant seals, penguins and baleen whales. Recently weaned elephant seal pups are a concentrated and abundant high-quality food resource in inshore waters from October to January. While killer whales may favour elephant seal pups over other prey during that period, which is consistent with an increase in killer whale abundance in inshore waters in spring and summer (Guinet 1992), the importance of seals as prey throughout the year remains unknown. The fact that the stomach contents of the individual found dead on Possession Island in winter included elephant seal remains suggests that this resource may still be consumed during that time of year. While this suggestion is supported by skin isotopic values of that dead individual being similar to values from biopsy sam-

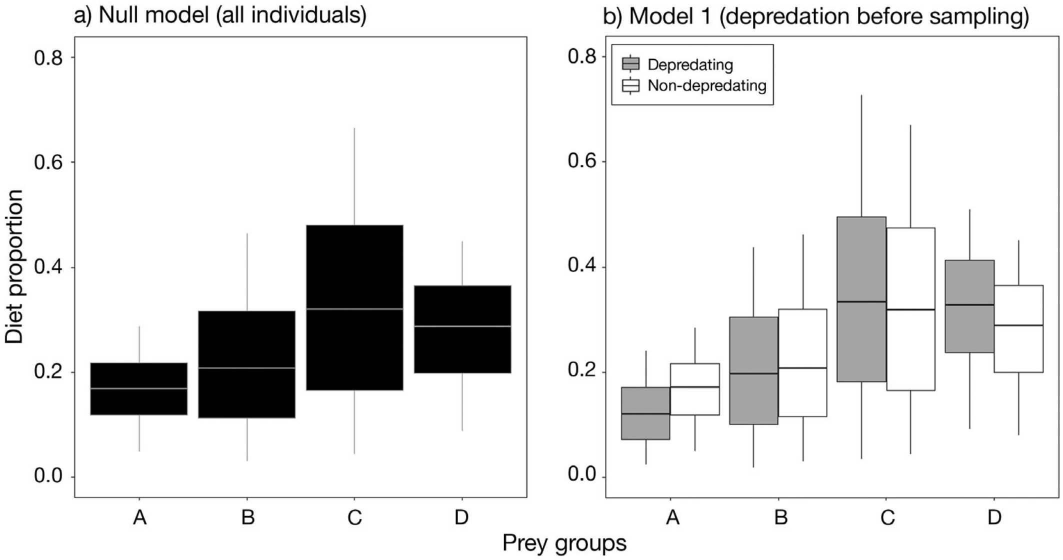

Fig. 4. Relative proportions of prey groups in the diet of (a) all Crozet killer whale samples and (b) samples from individuals that depredated toothfish from fisheries (depredating) or did not (non-depredating) 48 d before sampling. Diet proportions were estimated from the MixSIAR models (null model and Model 1) and are depicted as boxplots with the median (middle line), 25th and 75th percentiles (box hinges) and 95% confidence intervals (whiskers). Prey groups included the following items: Group A: gentoo, macaroni and rockhopper penguins and southern right whales; Group B: king penguins, elephant seals (adult females) and small Patagonian toothfish (TL 43 cm); Group C: southern elephant seals (pups), Antarctic/subantarctic fur seals (pups) and medium Patagonian toothfish (TL 63 cm); Group D: large Patagonian toothfish (TL > 95 cm)

ples collected in spring/summer, also suggesting low seasonal variation in diet, additional samples collected in winter would be needed to further examine that aspect.

The 2 prey groups (C and D) including medium and large-sized Patagonian toothfish dominated the diet of Crozet killer whales (over 60% by mass when pooled, including nearly half from the group exclusively made of large toothfish). In addition, there was no difference in the contribution of these prey groups between depredating and non-depredating samples. The use of isotopic mixing models paired with the fact that none of the prey species included in our analysis also prey on toothfish ruled out the possibility of a secondary contamination effect. Instead, this result suggests that toothfish may be an important natural prey item for Crozet killer whales. This conclusion is supported by other lines of evidence. Firstly, subantarctic killer whales are able to dive to great depths (>1000 m at South Georgia; Towers et al. 2019) and they do so when foraging naturally (>750 m at Marion, >300 m at Crozet; Reisinger et al. 2015, G. Richard et al. unpubl. data). This depth range largely overlaps with the bathypelagic depth distribution of Patagonian toothfish, making them potentially naturally accessible to killer whales (Arkhipkin et al. 2003, Collins et al. 2010, Péron et al. 2016). Secondly, $\delta^{15}N$ values of the Crozet killer whales, as a proxy of trophic position, were similar to that of Antarctic Type C killer whales, which are known to feed preferentially on Antarctic toothfish *Dissostichus mawsoni* (Krahn et al. 2008), a species closely related to the Patagonian toothfish (Collins et al. 2010, Hanchet et al. 2015). Lastly, the isotopic niche of Crozet killer whales partly overlapped with that of sperm whales from Crozet and Kerguelen, which feed on both Patagonian and Antarctic toothfish both naturally (Yukhov 1972) and through depredation (Janc et al. 2018, Labadie et al. 2018) in Crozet and Kerguelen waters.

This study therefore suggests that depredation at Crozet is a facilitated behaviour in response to fisheries making toothfish an aggregated and easily accessible resource that killer whales would otherwise naturally forage on, but at higher energetic costs. By setting their gear at great depths, fisheries may provide killer whales with facilitated access to large toothfish (>80 cm), which are primarily found in waters >800 m (Collins et al. 2010). This may explain the greater contribution of that prey group to the diet of depredating individuals. These findings are consistent with dietary studies on other depredating killer whale populations, such as in Gibraltar Strait, where facilitated access to bluefin tuna through depredation on fishing lines was found to be substantially less energetically costly than if this prey species was naturally and actively hunted (Guinet et al. 2007, Esteban et al. 2016).

More broadly, this study presents further evidence that toothfish have a key role as prey in subantarctic food web dynamics. While fisheries may facilitate access to toothfish for some predators, they may also impact populations that naturally depend on that resource through direct fish biomass removal. Toothfish has been confirmed as natural prey of sperm whales and sleeper sharks *Somniosus antarcticus* (Yukhov 1972, Cherel & Duhamel 2004) and suggested as natural prey for meso- and epi-pelagic predators such as albatrosses (Cherel et al. 2000, 2017). While the commercial exploitation of toothfish stocks is now highly regulated, stocks underwent substantial illegal over-exploitation across the Southern Ocean in the 1990s that likely affected these apex predator species through direct trophic effects (Kock et al. 2007). The Crozet killer whales underwent a sharp decline in the 1990s and this was partly attributed to illegal fishers using lethal means to repel whales depredating toothfish (Poncelet et al. 2010, Tixier et al. 2015, 2017). However, from our results, it is likely that the illegal over-exploitation of toothfish stocks, paired with substantial decreases of southern elephant seals, king penguins and large whales (Guinet et al. 1992, Clapham et al. 1999, Weimerskirch et al. 2003, 2018, Pruvost et al. 2015), has also contributed to the decline of this population. Decreased toothfish availability may also have caused dietary shifts for killer whales in areas where stocks were depleted. For instance, killer whales at Marion Island were expected, from observations, to have large isotopic overlap with killer whales at Crozet (Reisinger et al. 2011), but this was not the case. The Marion killer whales are at a lower trophic level than the Crozet whales, and this difference may be explained by lower toothfish intake because toothfish stocks have been more impacted by illegal fishing at Marion than at Crozet (Boonzaier et al. 2012) (see Supplement 2 for further discussion).

In summary, this study has provided a preliminary assessment of the diet of killer whales that consume a wide range of subantarctic resources. However, determining the diet of a generalist predator is often hampered by temporal variations in prey consumption and limited information on prey. This is the case for cephalopods — their contribution to the diet could not be assessed in the present study (see Supplement 3 for further discussion). Therefore, further studies using higher resolution dietary methods, such as compound-specific stable isotope or fatty acid analyses (e.g. Herman et al. 2005, Matthews & Ferguson 2014), are needed. Despite these limitations, the present study provided new insights on the role of natural prey preferences in the propensity of killer whales to switch prey in response to environmental changes. Specifically, our results support the assumption that killer whales are more likely to develop depredation on fisheries as a new foraging tactic if fish is already part of their natural diet. This assumption was proposed as explaining why not all killer whale populations, which greatly differ in prey preferences, switch from natural feeding to depredation despite large overlaps with fishing activity (e.g. Fearnbach et al. 2014, Peterson et al. 2014). The role of variation in prey preferences at the intra-population level, as reported in other killer whale populations (e.g. Samarra et al. 2017), should therefore be further examined with a larger sample size to understand the heterogeneity observed across groups/individuals at Crozet in regards to depredation (Tixier et al. 2017). More importantly, our findings have emphasised the importance of toothfish, a species of high commercial value, in the natural diet of killer whales. However, the amount of toothfish that killer whales eat naturally compared to the toothfish biomass they remove from longlines when depredating is still unknown. This information is required for (1) assessing the minimum amount of toothfish biomass required to sustain killer whale populations, and (2) estimating the extent to which the depredated part of that amount (estimated at several hundred t yr^{-1}) should be considered as natural or artificial mortality in fish stock assessments.

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Movements and dive behaviour of a toothfish-depredating killer and sperm whale

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Depredation of demersal longlines by killer and sperm whales is a widespread behaviour that impacts fisheries and whale populations. To better understand how depredating whales behave in response to fishing activity, we deployed satellite-linked location and dive-profile tags on a sperm and killer whale that were depredating Patagonian toothfish from commercial longlines off South Georgia. The sperm and killer whale followed one fishing vessel for >180 km and >300 km and repeatedly depredated when longlines were being retrieved over periods of 6 and 7 d, respectively. Their behaviours were also sometimes correlated with the depths and locations of deployed gear. They both dove significantly deeper and faster when depredating compared with when foraging naturally. The killer whale dove >750 m on five occasions while depredating (maximum: 1087 m), but these deep dives were always followed by long periods (3.9–4.6 h) of shallow (<100 m) diving. We hypothesize that energetically and physiologically costly dive behaviour while depredating is driven by intra- and inter-specific competition due to the limited availability of this abundant resource.

Keywords: competition, depredation, diving, foraging, killer whales, movements, Patagonian toothfish, South Georgia, sperm whales

Introduction

Killer (*Orcinus orca*) and male sperm whales (*Physeter macrocephalus*) are among the top predators in high latitude food webs. They normally occupy different ecosystem niches, but in some regions both will take advantage of opportunities to remove fish from commercial longlines (Kock *et al.*, 2006). This behaviour, referred to as depredation, is a deviation from natural foraging behaviour (Gilman *et al.*, 2006) and reflects the behavioural plasticity and adaptive capabilities of each species. However, physically harmful interactions with fishing gear and fishers can negatively impact the health of cetaceans that engage in this behaviour. Furthermore, depredation can reduce the accuracy of stock assessments and have a major financial impact on fisheries economies (Gilman *et al.*, 2006; Read, 2008; Hamer *et al.*, 2012; Peterson *et al.*, 2014). The severity of these impacts have been increasing worldwide since depredation of commercial longlines was first reported in the 1960s (Hamer *et al.*, 2012). This has

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resulted in an increased need to understand and mitigate this behaviour.

A number of operational and technological mitigation techniques have been used to minimize the impacts of depredation by killer and sperm whales (Gilman *et al.*, 2006; Tixier *et al.*, 2010; Goetz *et al.*, 2011; Thode *et al.*, 2012; Straley *et al.*, 2014; O'Connell *et al.*, 2015; Tixier *et al.*, 2015a; Towers, 2015; Werner *et al.*, 2015; Janc *et al.*, 2018). Some, such as modifying gear (Moreno *et al.*, 2008) or ceasing gear retrieval, buoying off the line, and leaving the area to return several h after whales have left (Tixier *et al.*, 2015b) have proved to be successful at times. However, none has come without an economic cost or been completely effective at eliminating depredation. Effective mitigation is complicated further because killer and sperm whales often depredate repeatedly and concurrently (Purves *et al.*, 2004; Roche *et al.*, 2007; Tixier *et al.*, 2010; Straley *et al.*, 2015; Tixier *et al.*, 2016), spread knowledge of this behaviour to other whales via social transmission (Tixier, 2012; Fearnbach *et al.*, 2014; Schakner *et al.*, 2014), appear to have unique depredation strategies (Hucke-Gaete *et al.*, 2004; Tixier *et al.*, 2015b) and may compete for opportunities to depredate (Nolan *et al.*, 2000).

The limited efficacy of depredation mitigation strategies and the escalating impacts of this behaviour indicate that a better understanding of killer and sperm whale depredation is necessary to reduce and discourage this behaviour. Studies using photo-identification (Tixier *et al.*, 2010; Straley *et al.*, 2015), hydrophones (Mathias *et al.*, 2009, 2012; Thode *et al.*, 2015), and underwater video (Mathias *et al.*, 2009; Guinet *et al.*, 2015) have all provided insight, but the fine-scale horizontal and vertical movements of depredating whales have rarely been investigated. In fact, only two studies have used telemetry to assess and compare the movements and dive patterns of depredating whales to their natural behaviour. Straley *et al.* (2014) found that some tagged depredating male sperm whales followed a fishing vessel for several hundred km while others engaged in natural migratory movements, and Mathias *et al.* (2012) discovered that some tagged male sperm whales repeatedly dove under 200 m while depredating, but that most dove between 400 and 700 m both while depredating and naturally foraging. Male sperm whales typically descend to depths up to 1900 m for as long as 60 min when foraging (Watkins *et al.*, 2002; Teloni *et al.*, 2008; Fais *et al.*, 2015; Guerra *et al.*, 2017), but the species may be capable of diving much deeper and longer (Clarke, 1976; Watkins *et al.*, 1985). Although no depredating killer whales have been tagged, this species typically dives <300 m for under 4 min (Baird *et al.*, 2005; Miller *et al.*, 2010; Wright *et al.*, 2017), but can descend to at least 767 m and remain submerged for nearly 16 min (Reisinger *et al.*, 2015).

The dive capacity of both species, but especially of sperm whales, indicates that they can access the depths at which some longlines are set (700–2250 m; Government of South Georgia & South Sandwich Islands, 2017). However, depredation by killer and sperm whales has only been observed to take place during gear retrieval (Dahlheim, 1988; Sigler *et al.*, 2008; Goetz *et al.*, 2011; Gasco *et al.*, 2015), and the depth range at which this behaviour occurs remains largely unknown. Under natural circumstances, both species dive to depths that correspond to where their prey are found or chased to (Fais *et al.*, 2015; Wright *et al.*, 2017). For sperm whales, these prey include several species of cephalopods (Clarke, 1980; Whitehead, 2009) and large teleost fishes (Gaskin and Cawthorn, 1967; Martin and Clarke, 1986) that they catch in epipelagic, mesopelagic, bathypelagic and benthic zones (Teloni *et al.*, 2008; Guerra *et al.*, 2017). Killer whales also prey on several cephalopod and high lipid content fish species that they catch in different bathymetric zones (Guinet *et al.*, 2007; Hanson and Walker, 2014; Wright *et al.*, 2017), but some distinct killer whale ecotypes specialize on these, and/or other prey, such as mammals, birds, and reptiles (Ford *et al.* 1998; Pitman and Ensor, 2003; Ford, 2009; Morin *et al.*, 2010; Foote *et al.*, 2016; Durban *et al.*, 2017). Patagonian toothfish (*Dissostichus eleginoides*) are a large bottom-dwelling teleost fish with high lipid contents that typically occur at depths ranging from 500 to 2500 m throughout the sub-Antarctic (Collins *et al.*, 2010). Longlining for this species can therefore create an abundant and easily accessed source of preferred prey for some populations of killer and sperm whales.

In the South Atlantic Ocean around the island of South Georgia, six commercial longlining vessels remove up to 2200 t of toothfish from shelf edge waters each year in a sustainably managed fishery (Government of South Georgia & South Sandwich Islands, 2017). Killer whales and male sperm whales have been depredating from this fishery since the 1990s (Ashford *et al.*, 1996; Kock *et al.*, 2006) and impact 3–5% and 13–40% of lines retrieved each year, respectively (Purves *et al.*, 2004; Clark and Agnew, 2010; Söffker *et al.*, 2015). It is estimated that these species are responsible for reducing the total toothfish catch at South Georgia by up to 8% in some years (Clark and Agnew, 2010). Although, the extent to which sperm and killer whales in this region depredate as compared with feeding on naturally obtained prey is not known, depredation rates are generally reported to be increasing at South Georgia (Towers, 2015).

To better understand the horizontal and vertical movements of depredating killer and sperm whales and how depredation differs from natural foraging behaviours, daily observations of depredation were recorded from a toothfish longliner at South Georgia and depth-recording satellite transmitter tags were applied to one individual of each species while they were depredating in the area. Here, we use data obtained from the tags to determine how often the whales depredated when opportunities to do so were available, compare how their dive behaviours differed between depredating and natural foraging, test whether they depredated longlines that were not being retrieved, and describe their natural foraging behaviour. The results provide new insights into the natural and depredatory foraging ecology of killer and sperm whales that can be used to help develop depredation mitigation strategies and improve fisheries management practices.

Material and methods

Field effort

Field effort around South Georgia was undertaken from the Patagonian toothfish longliner *San Aspiring* in May and June 2015. Longline sets made by this vessel consisted of a main line ranging in length from 4 to 12 km. Each line was equipped with ~1000 baited hooks km^{-1} that were tethered to the main line by snoods (short lines) <1 m in length. Lines were secured on the seafloor by anchors positioned at each end, at depths ranging from 700 to 1700 m. Each anchor was attached to a vertical downline equipped with a buoy at the surface. Longlines were always set at night and were left deployed on the seafloor for periods of 5–44 h. They were typically retrieved during the day at a rate of 2 km of line h^{-1}.

Observations of depredating whales were conducted with naked eye and monopod mounted Swarovski 8X42 binoculars from a height of ~7 m above sea level from the bridge of *San Aspiring* during 39 d between 7 May and 15 June, 2015. The number and species of depredating whales and the number of intact and partially eaten toothfish recovered on the line were recorded. Individual depredating whales were photo-identified at every opportunity with Nikon D800 and D300 SLR cameras outfitted with a 300 mm F2.8 lens.

SPLASH10 transmitter tags (see Schorr *et al.*, 2014) developed by Wildlife Computers (Wildlife Computers, Redmond, WA, USA) were used to collect location and dive data from depredating killer and sperm whales. These 54 g tags were outfitted with two titanium posts, each with six barbs designed to penetrate and anchor up to 6.5 cm into the dorsal fin or ridge of the whale. They were also outfitted with a wet/dry sensor to activate transmissions through the Argos satellite system via an antenna when the whale surfaced. Tags were programmed to provide up to 600 locations d^{-1} between 00:00 and 04:00, 07:00 and 12:00, 15:00 and 20:00, and 23:00 and 00:00 UTC every d until 20 June and at 5 d intervals thereafter. Tags were also pre-programmed to only record dives deeper than 15 m and longer than 30 s. Surface time therefore included all activities that occurred between the end and beginning of these dives. Tags were mounted on the end of a crossbow bolt and deployed from a 150 lb draw Excalibur Vixen crossbow onto the dorsal fin of a killer whale and the dorsal hump of a sperm whale (e.g. Reisinger *et al.*, 2014). After contact, the floating bolt bounced off the whale, leaving the tag attached. Deployment effort was undertaken from the 4 m tender of the *San Aspiring* at ranges <10 m whenever whale activity, weather, and fishing activity were conducive.

Data analysis

Tag data analyses were conducted in the R Statistical Environment 3.4.1 (R Core Team, 2017). Location data calculated with the Argos Kalman filter (Lopez and Malardé, 2011) were then further filtered using the Speed-Distance-Angle (SDA) algorithm and the *SDAfilter* function in R package "Argosfilter" (Freitas *et al.*, 2008). Maximum swim speeds used as a threshold in this algorithm were 2.5 m s^{-1} for sperm whales (Whitehead, 2003) and 7 m s^{-1} for killer whales (Durban and Pitman, 2012). Filtered tag locations were used to assign an estimated location to each dive record through a linear interpolation (function *interp1* in the "pracma" package). This interpolation was performed using the dates and times of dive records as the dates and times at which locations were estimated.

Data collected on the fishing operations of the *San Aspiring* included the GPS coordinates and depths of both ends of each longline at setting, as well as the date and time of the beginning of setting and the end of retrieval. Since longlines were set in a straight line over the seafloor, we calculated the coordinates of the middle point (the mean position of the two ends) to provide a single location per longline. The distance between the tagged animals and the nearest longline set was calculated as the least distance between the location of each dive record and the three locations (two ends and middle point) of all longline sets.

Dive records were assigned to one of the following behaviour states: depredating, natural foraging, non-foraging or uncertain. Taking into account that tag settings prevented dives <15 m from being recorded, dives were first classified as non-foraging dives if shallower than 25 m for the sperm whale (based on threshold estimated by Fais *et al.*, 2015) and 20 m for the killer whale (based on threshold estimated by Wright *et al.*, 2017). Deeper dives were then classified as depredating if they completely or partially occurred during gear retrieval when the tagged animal was photo-identified near the *San Aspiring* and there was evidence that toothfish were being removed from the longline (catch was lower than expected and/or some hooks were recovered with only partially intact toothfish on them). The gear retrieval process was defined for depredating dives as the period of time between the first and last hook reaching the surface. Foraging dives were non-depredating dives that met two conditions. First, these dives were confirmed as occurring within a 50 km range from the nearest fishing gear deployed by the *San Aspiring*. This threshold was chosen because although data on operations of other toothfish longliners were not available for this study, information on their positions received regularly by the *San Aspiring* indicated that none was within 50 km during the times that data were transmitted from the tagged whales. This range therefore allowed us to exclude dives that could have been made by the whales while interacting with other vessels. Secondly, foraging dives were identified if they occurred in between phases of gear retrieval and during phases of gear retrieval for which there was no visual evidence that tagged whales were depredating. Dives were classified as uncertain if they occurred: (i) during gear retrieval phases at times that photo-identification and visual effort could not be conducted due to darkness or snow, (ii) during times that the location and depth of the nearest longline set had been modified by buoying off the line, or (iii) when the tagged whales were >50 km from the nearest gear set by *San Aspiring*.

Depredating dives were first compared with the depth at which the longlines were set on the seafloor. For each depredated set, the correlation between the maximum recorded dive depth of tagged whales and the depth of the longline set was tested using standard least-squares regressions. As two depth records both recorded by the sounder of the vessel were available per set (one for each end), three tests were separately conducted using the depth of each end and their mean depth. The same tests were then performed on dives that were classified as foraging dives when they occurred near a longline set deployed on the seafloor. Foraging dives were only selected for this analysis if they occurred within the same range to deployed gear as gear that was being depredated from while being retrieved. The depths of all remaining foraging dives (not in proximity to gear) were examined in relation to the local bathymetry. The bathymetry was retrieved from the ETOPO1 database at a 1 min resolution using the *marmap* package in R (Pante and Simon-Bouhet, 2013), and assigned to individual dive records based on the nearest interpolated location at the start of the dive.

Differences in depths, durations and vertical velocities between available depredating and foraging dives were statistically tested using Generalized Least Squares models (GLS) using the function *gls* in R package "nlme". Data on dive depth and duration are provided as maximum values from tags. For each dive, the vertical velocity was calculated as twice the depth divided by the total duration of the dive, and expressed in m s^{-1}. Velocities presented do not account for any non-vertical movements and are therefore estimated values. A square root transformation was applied to dive depths and durations, and a log transformation was applied to vertical velocities to meet the normality assumptions. GLS models included an autoregressive (AR1) correlation structure to

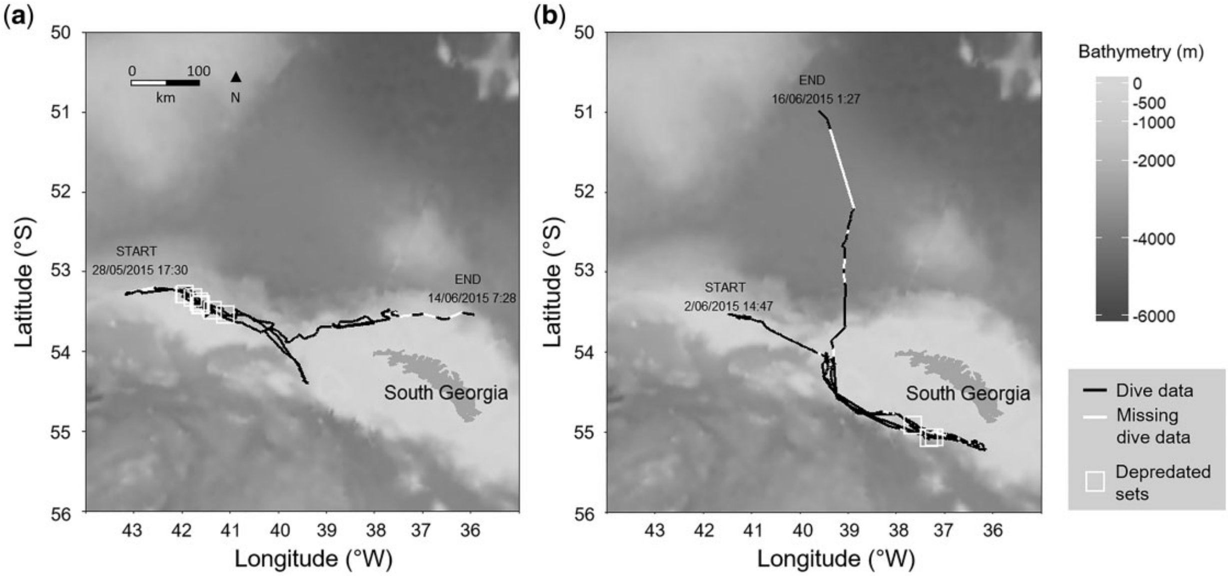

Figure 1. Full filtered and interpolated tracks of (a) the sperm whale from 28 May to 14 June 2015 and (b) the killer whale from 2 to 16 June 2015 with recorded dive data (black) and missing dive data (white). The locations of the longline sets retrieved by the *San Aspiring* that were depredated by the whales while tagged are depicted with white squares (*n* = 8 sets for the sperm whale, *n* = 3 sets for the killer whale).

account for temporal autocorrelation between successive dives (Zuur *et al.*, 2009).

Results

Horizontal movements

Tags were deployed on one adult male sperm whale and one adult female killer whale near Shag Rocks to the west of South Georgia on 28 May 2015 and 2 June 2015, respectively (Figure 1a and b). The sperm whale tag provided 260 Argos locations for 17 d and 23 h, with an average of 14.4 ± 0.7 SE locations d^{-1}. The killer whale tag transmitted 348 locations for 14 d and 16 h, with an average of 23.2 ± 1.3 SE locations d^{-1}. The SDA filtering resulted in the removal of 37 (14%) and 20 (5.7%) Argos records for the sperm and killer whale, respectively.

The sperm and killer whale spent 156 and 79 h within 50 km of the nearest longline set by the *San Aspiring*, respectively. Over these time periods, 90 SDA filtered Argos locations were recorded from the sperm whale and 87 were recorded from the killer whale. The sperm whale remained within 25 km of the nearest set gear for 5 consecutive d after being tagged (Figure 2a). After the killer whale was tagged on 2 June the *San Aspiring* moved 75 km away to begin fishing further to the east in an effort to avoid depredation, but both tagged whales and the 20 associated pod members of the killer whale (see Towers, 2015) followed. The swim speed of the sperm whale increased to $\sim 1.9\,\mathrm{m\,s^{-1}}$ and it and the killer whale came within 20 km and 30 km, respectively, of gear retrieved by *San Aspiring* on 3 June before the vessel moved 200 km further to the east to find a more productive fishing area (Figure 2a and b). Only the tagged killer whale and associated pod members continued to follow and on 4 and 5 June were documented near *San Aspiring* (Figure 2b). On 5 June, a set being depredated was buoyed off and then the *San Aspiring* left the area. The killer whale remained near the set gear for the next 5 h and then moved off. On 7 June, the swim speed of the killer whale increased to $4.2\,\mathrm{m\,s^{-1}}$ and then slowed as it and associated pod members located *San Aspiring* and then spent 8 June in its vicinity (Figure 2b). The last set the tagged whale depredated from this day was buoyed off while the vessel transited away and then returned the next morning to retrieve it. After retrieving the set, the *San Aspiring* traveled 385 km west to avoid depredation by fishing in a different area before returning to port.

Overall, the tagged sperm whale followed the *San Aspiring* over a distance of 182 km and the tagged killer whale and associated pod members interacted with the vessel over a range of 302 km. After the last time the tagged killer whale was verified in the vicinity of *San Aspiring* on 9 June, it traveled west along the shelf edge, and then from 13 to 16 June swam directly north away from the fishing grounds at $2.6 \pm 1.9\,SD\,\mathrm{m\,s^{-1}}$ ($n = 74$ locations) before the tag stopped transmitting (Figure 1b). By comparison, after 3 June the sperm whale travelled back to Shag Rocks and then reversed course and travelled east along the shelf edge to the north side of South Georgia, where tag transmissions ceased on 14 June (Figure 1a).

Vertical movements

Dive types and totals

For the sperm whale, dive and surface data were available for 88% of the deployment time (Figure 1a). Of the available data, 24% were surface time and 76% were dives >15 m and longer than 30 s. Information on a total of 611 dives was recorded, including 239 dives performed within a 50 km range of the nearest longline set (Figure 2a). Among the 239 dives, four (2%) were considered non-foraging dives based on the 25 m depth threshold. The tagged sperm whale was visually confirmed depredating from eight sets resulting in 87 dives being categorized as depredating dives. Among the remaining dives, 65 were classified as uncertain because they occurred near a set that was being retrieved at night, and 83 were classified as natural foraging dives because they occurred when no gear was being retrieved (Figure 2a).

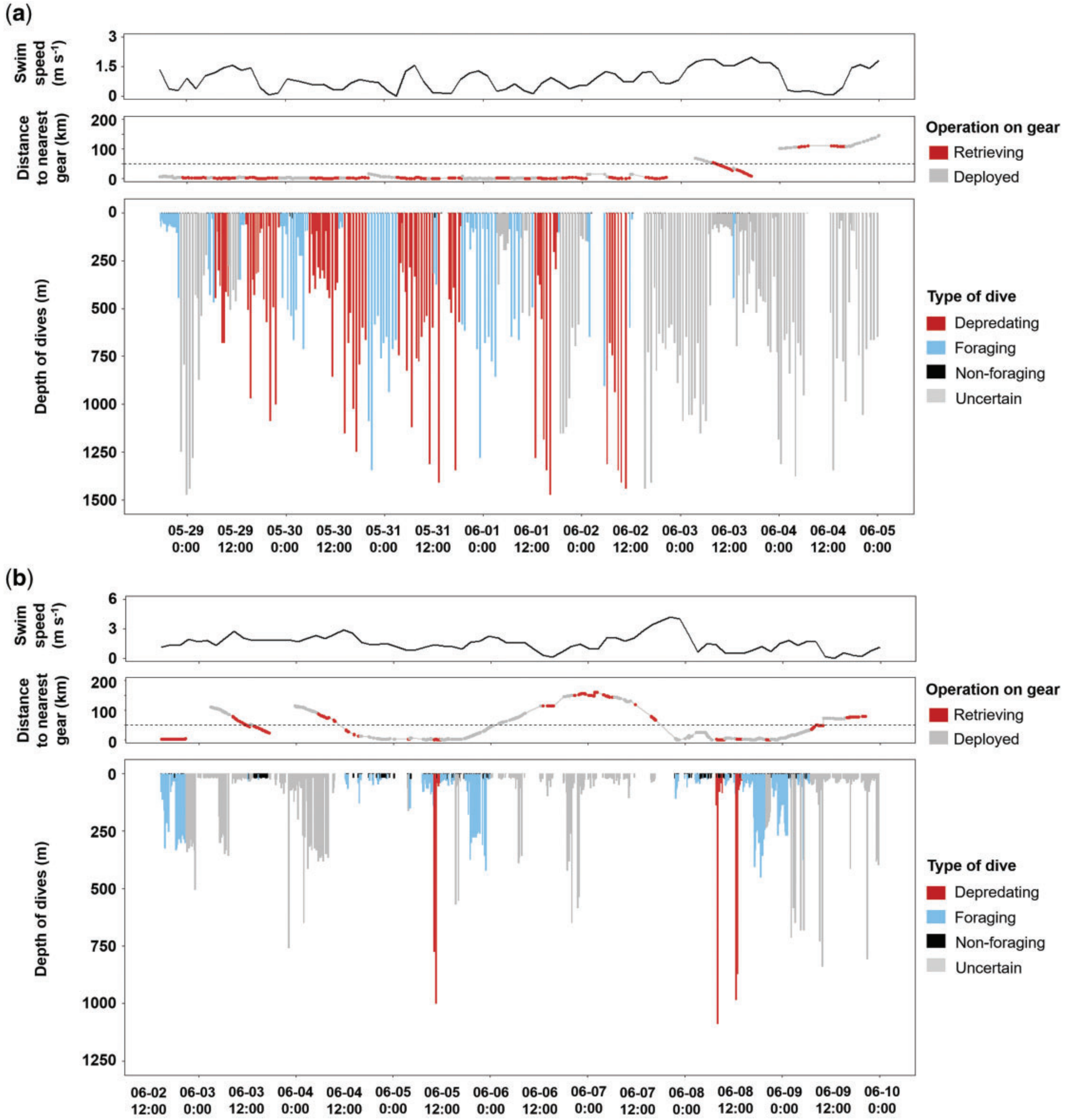

Figure 2. Swim speed, distance to nearest longline set and dive profiles of (a) the sperm whale from 28 May to 4 June 2015 and (b) the killer whale from 2 to 9 June 2015. The swim speed was calculated from successive filtered location data and is depicted as a smooth curve using a "loess" method. The distance to nearest gear is presented as the least distance between the location of each dive record and the three locations (two ends and middle point) of all longline sets. Whether the nearest set was deployed on the seafloor or being retrieved is depicted. Dive types were classified as depredating (red), foraging (blue), non-foraging (black), and uncertain (grey) depending on the distance of the animal to the nearest set, depth thresholds and behavioural observations as described in the Material and methods.

For the killer whale, dive and surface data were recorded during 86% of the tag transmission period (Figure 1b). Of the available data, 71% were surface time and 29% were dives >15 m and longer than 30 s. A total of 489 dives (33% of all dives recorded) were performed within 50 km of the nearest longline set (Figure 2b). Among them, 133 (28%) were considered non-foraging dives based on the 20 m depth threshold. The tagged killer whale was visually confirmed depredating during the retrieval of three sets (Figure 2b), resulting in 37 dives being classified as depredating dives. Among the remaining dives, 270 were classified as natural foraging and 49 as uncertain.

While tagged, the sperm whale was visually confirmed depredating simultaneously with killer whales during only one set. On this set, the mean dive depth of the tagged sperm whale was 1122 ± 327 *SD* m ($n = 7$ dives), including some of the maximum depths recorded (1407 and 1439 m). While tagged, the killer

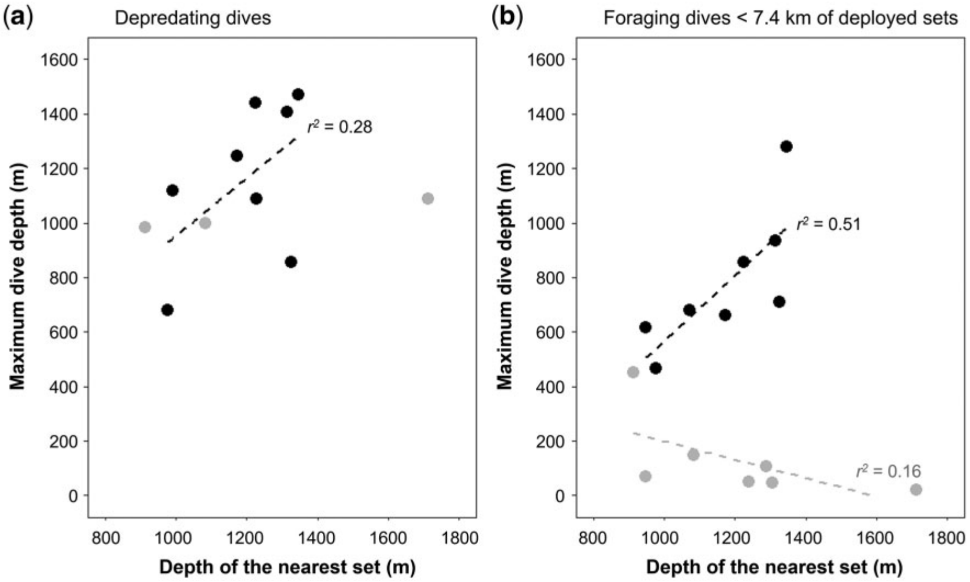

Figure 3. Correlations between the maximum dive depths of the sperm whale (black) and killer whale (grey) and the depths of the nearest longline set during (a) depredating dives, and (b) foraging dives when the animals were <7.4 km from the nearest set deployed on the seafloor. r^2 values from linear regression lines (dashed lines) are depicted.

whale was not observed depredating sets also depredated by sperm whales.

Dive depths compared with depth of set longlines

When confirmed depredating, the maximum dive depth of the sperm whale was not significantly correlated to the depth at which the retrieved longline was set, whether the shallowest end, the deepest end, or the mean depth of sets were tested ($F_{1,6} = 3.21$, $r^2 = 0.24$, $p = 0.12$; $F_{1,6} = 0.66$, $r^2 = 0.10$, $p = 0.45$ and $F_{1,6} = 2.37$, $r^2 = 0.28$, $p = 0.17$ respectively, $n = 8$ sets) (Figure 3a). With only three sets depredated during retrieval, this correlation could not be tested for the killer whale (Figure 3a).

During the confirmed depredation events, the maximum distances of the sperm and killer whale to the depredated longline set were 7.4 km (mean 2.6 ± 0.1 SE, $n = 87$ locations) and 4.1 km (mean 2.0 ± 0.2 SE, $n = 37$ locations), respectively. The correlation between dive depths of the two whales and the depths at which longline sets were deployed was therefore examined using foraging dives that occurred within 7.4 km of the nearest set. The tagged sperm and killer whale were both recorded within 7.4 km of eight sets deployed on the seafloor. During these phases, the maximum depths of foraging dives of the sperm whale were positively correlated to the shallowest of the two ends of set longlines ($F_{1,6} = 31.25$, $r^2 = 0.74$, $p = 0.003$, $n = 8$ sets), to the mean depth at which longlines were set ($F_{1,6} = 8.42$, $r^2 = 0.51$, $p = 0.027$, $n = 8$ sets), but not to the depth of the deepest end of the longline ($F_{1,6} = 1.83$, $r^2 = 0.11$, $p = 0.225$, $n = 8$ sets) (Figure 3b). No correlations were found for the killer whale when using the shallow ($F_{1,5} = 1.12$, $r^2 = 0.16$, $p = 0.330$) or deep ($F_{1,6} = 0.98$, $r^2 = 0.14$, $p = 0.361$, $n = 8$ sets) or mean depths of sets ($F_{1,6} = 1.66$, $r^2 = 0.16$, $p = 0.322$, $n = 8$ sets) (Figure 3b). However, while in the vicinity of a line that was buoyed off on 5 June the tagged killer whale made two dives >550 m within 1 h and then moved away from the gear (Figure 2b). These dives were classified as uncertain, however, when this line was retrieved again the next morning there were no toothfish on the first 500 m or so of the line, but several further along.

The correlation between dive depth and bathymetry was also tested for foraging dives that occurred when the animals were between 7.4 and 50 km from the nearest longline set. There was no correlation for the sperm whale ($F_{1,22} = 5.18$, $r^2 = 0.19$, $p = 0.33$, $n = 24$ dives) or the killer whale ($F_{1,88} = 29.76$, $r^2 = 0.24$, $p = 0.052$, $n = 90$ dives).

Comparisons of depredating and foraging dives

The sperm whale dove significantly deeper, for longer durations and at greater vertical velocities when depredating during the retrieval of gear, as compared with when foraging naturally (GLS $t = 3.697$, $p < 0.001$ for dive depth; $t = 2.029$, $p = 0.04$ for dive duration; $t = 4.622$, $p < 0.001$ for vertical velocity). Depredating dive depths averaged 590 ± 398 *SD* m and the maximum dive depth during depredation (1471 m) was 128 m deeper than the maximum recorded depth of a foraging dive (1343 m) (Table 1; Figure 4a and b). The maximum duration of a depredating dive (55.4 min) was 13.3 min longer than the maximum duration of a foraging dive (42.1 min).

The killer whale also dove significantly deeper and at greater vertical velocities when depredating than when foraging (GLS $t = 4.322$, $p = 0.002$ for dive depth; $t = 3.385$, $p < 0.001$ for vertical velocity), but no difference was detected for dive duration (Table 1; Figure 4c and d). The foraging dives showed a bimodal distribution with 76% ($n = 206$) of the depths <100 m, and 17% ($n = 47$) of the depths >200 m (Figure 4c). A total of 41 foraging dives >200 m were performed successively on three occasions (2, 5, 8 June) during foraging bouts 2.2–3.7 h. During these continuous natural foraging events, the between-dive variance in maximum depths was low, respectively averaging 17.5 m (6% of the mean 292 ± 6 SE m, $n = 11$ dives), 39.6 m (15% of the mean 263 ± 21 SE m, $n = 13$) and 57.5 m (21% of the mean 272 ± 18 SE m, $n = 17$) for each of the three bouts. The depredating dives of the killer whale also showed a bimodal distribution, but

Table 1. Sample size and descriptive statistics (mean, standard deviation and maximum) of depth, duration and estimated vertical velocity of depredating and foraging dives performed by the tagged sperm and killer whale.

			Dive depth (m)		Dive duration (min)		Vertical velocity (m s^{-1})	
	Behaviour	***N***	**Mean ± *SD***	**Maximum**	**Mean ± *SD***	**Maximum**	**Mean ± *SD***	**Maximum**
Sperm whale	Foraging	83	345 ± 324	1 343	21.7 ± 10.0	42.1	0.5 ± 0.3	1.3
	Depredating	87	590 ± 398	1 471	25.7 ± 9.0	55.4	0.7 ± 0.3	1.5
Killer whale	Foraging	270	87 ± 100	451	3.7 ± 1.6	7.8	0.7 ± 0.6	3.0
	Depredating	37	163 ± 316	1 087	3.6 ± 2.8	11.5	0.9 ± 0.9	3.5

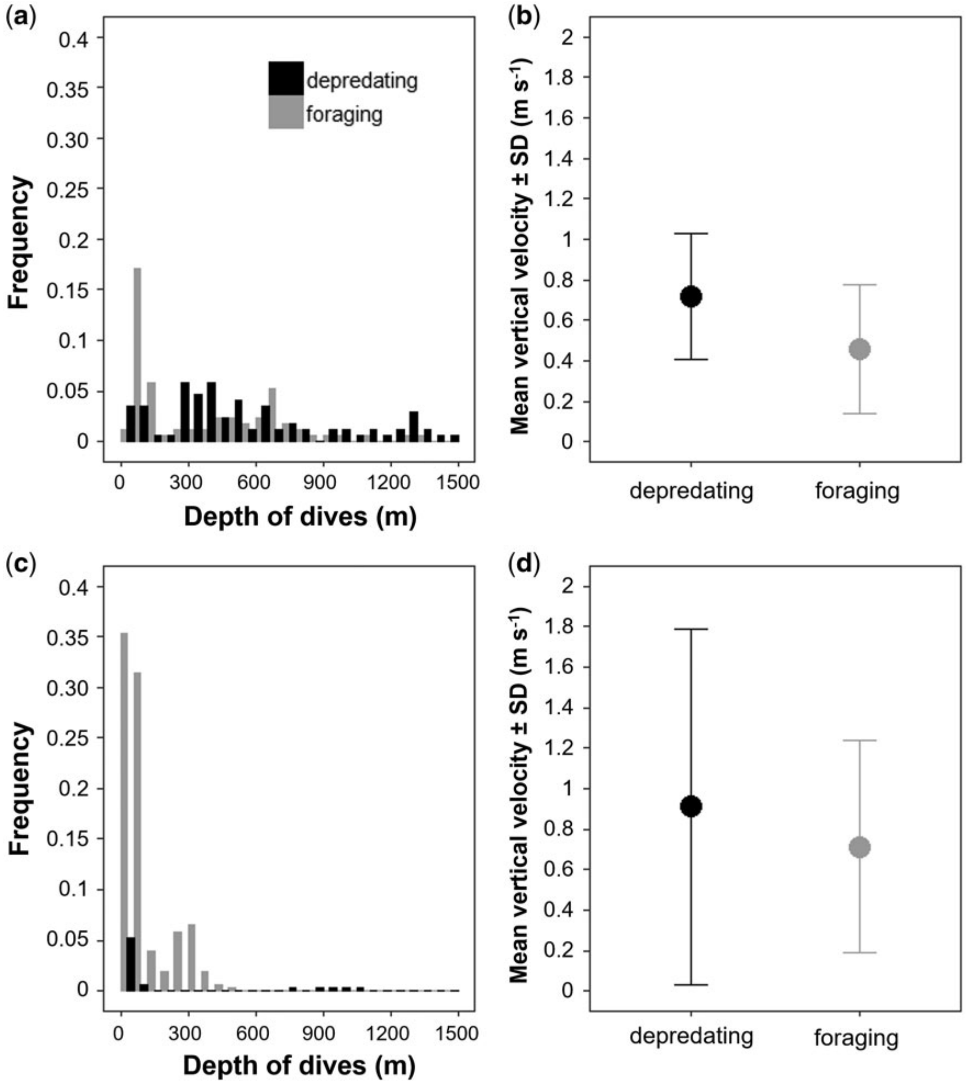

Figure 4. Frequency histograms of the dive depths (left) and mean vertical velocities (right) of (a, b) the sperm whale, and (c, d) the killer whale, for depredating dives (black, $n = 87$ dives for the sperm whale, 37 dives for the killer whale) and foraging dives (grey, $n = 83$ dives for the sperm whale, 270 for the killer whale). Error bars are the Standard Deviation of the mean vertical velocity in m s^{-1}.

consisted of one or two deep dives >750 m ($n = 5$ for the three depredated sets representing 13% of all depredating dives) followed by repeated shallow dives ($n = 31$ dives <100 m representing 84% of all depredating dives) over periods of 3.9–4.6 h (Figure 2b). The whale dove to a maximum depth of 1087 m when depredating set 128 on 8 June 2015 (Figures 2b and 5). The duration of this dive was 11.4 min with a subsequent estimated vertical velocity of 3.2 m s^{-1}. When combined with the other depredating dives >750 m ($n = 5$), the average duration was 10.1 ± 1.4 *SD* min and the average vertical velocity was 3.1 ± 0.3 *SD* m s^{-1}. Contrastingly, depredating dives <100 m ($n = 31$) were performed at a mean vertical velocity of 0.5 ± 0.4 *SD* m s^{-1}.

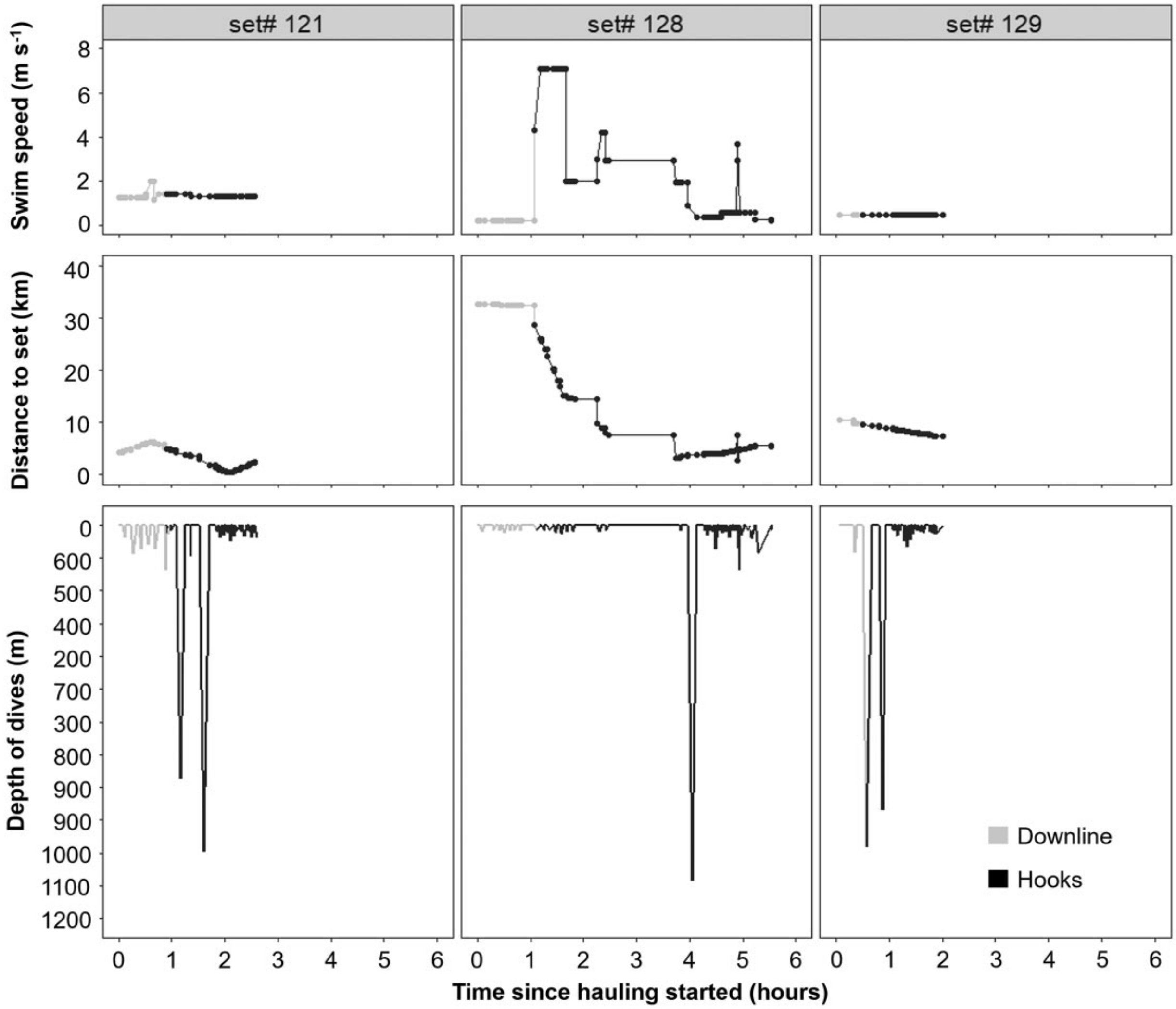

Figure 5. Detailed profiles of the killer whale behaviour when confirmed depredating three longline sets (sets 121, 128, and 129). The distance of the whale to the depredated set, the swim speed, and the dive depth are plotted against the time since retrieval of these sets began. The retrieval process is depicted by the period in which the downline was being hauled (grey) and the period after which the first hooks reached the surface (black).

For two of the depredated sets, the killer whale was within a 10 km range of the set before retrieval started. In both cases, the deep dives coincided with the end of retrieval of the downline, when the first hooks reached the surface (sets 121 and 129—Figure 5). These sets were eventually buoyed off to deter further depredation by the killer whales. When retrieval of set 128 began, the tagged killer whale was estimated to be >30 km distant. It started to move towards the set when the first hooks reached the surface, as indicated by an increase of the swim speed and a decrease in the distance to the set (Figure 5). As retrieval of most of this set was complete by the time the killer whales arrived, the remainder of the line was retrieved while they were depredating.

Discussion

The horizontal and vertical movements of depredating killer and sperm whales were correlated with fishing activity, indicating that both species are extremely motivated by opportunities to depredate Patagonian toothfish from demersal longlines at South Georgia. The tagged killer and sperm whale undertook direct movements to relocate the ship after it moved away to fish in a new area and each species dove deeper, faster and longer while depredating. Even when depredation could not be confirmed, the movements and dive behaviour of the sperm whale were often correlated with the locations and depths of set longlines, respectively. The killer whale travelled along the shelf edge while not depredating, but some of its horizontal and vertical movements were correlated with the location of gear that was buoyed off, while other behaviours were indicative of natural foraging.

Horizontal movements of tagged whales

Associated with fishing gear

Tag data, supported by identification photos acquired from *San Aspiring* (see Towers, 2015), indicate that the horizontal movements of both species were often directly correlated with fishing activity. The sperm whale mostly depredated in the same general area over several consecutive d but in total, followed *San Aspiring* for >180 km, while the killer whale travelled >300 km in <50 h to depredate even though two out of three depredated sets were buoyed off soon after it arrived. This exploitation of even small windows of opportunity to depredate toothfish suggests that this prey provides energetic benefits outweighing the cost of some long-distance travel. It also indicates that depredation is favoured over natural foraging because toothfish may not be easily accessible to killer whales under natural circumstances due to the great depths and benthic habitat in which they live (Collins *et al.*, 2010).

Not associated with fishing gear

Both tagged whales eventually disassociated from *San Aspiring*, but while the sperm whale travelled along the shelf edge, the killer whale headed north away from the fishing grounds. Given the previous behaviour of the sperm whale and the fact that toothfish longliners operate in the areas it went to (Purves *et al.*, 2004), it is possible that these movements were motivated by depredation opportunities. In contrast, given the speed at which the killer whale travelled and that waters around South Georgia lie within the polar front (Moore *et al.*, 1999), we believe its final northbound movements were the beginning of a physiological maintenance migration to warmer waters, as described by Durban and Pitman (2012) and reported by Reisinger *et al.* (2015).

Dive behaviour of tagged whales

While depredating during gear retrieval

The two tagged individuals modified their diving behaviour to depredate. Both species dove significantly deeper and faster when depredating than when naturally foraging. The sperm whale also dove significantly longer when depredating. However, its dive depths and durations while depredating were similar to natural dive behaviour of other male sperm whales tagged at high latitudes (Teloni *et al.*, 2008; Fais *et al.*, 2015; Guerra *et al.*, 2017). This indicates that dive behaviour required for successful depredation are well within the physiological limits of this species. However, we believe that the motivation for this whale to access prey more quickly and at greater depths while depredating was driven by intra- and possibly, inter-specific competition. For example, between 3 and 13 other sperm whales were present on all sets that the sperm whale depredated from during the time it was tagged (Towers, 2015) and some of the deepest dives this whale made were performed when killer whales were also depredating. Confirming competition between cetaceans is difficult, given that their prey are often heterogeneous, widespread, and highly mobile. Toothfish provided by longliners on the other hand, are not only energy-dense (Collins *et al.*, 2010) and highly desired, but their availability is temporally limited, static, and localized. The characteristics of this resource may set the stage for inter-specific interference competition and help explain why killer and sperm whales have been observed acting aggressively towards each other while depredating (Nolan *et al.*, 2000; Hucke-Gaete *et al.*, 2004).

Compared with the sperm whale, the dives of the killer whale showed substantially greater variation in maximum depth between the naturally foraging and depredating states. In particular, the deep dives made by the killer whale while depredating were over 300 and 700 m deeper than any dives previously reported for this species in the southern (Durban and Pitman, 2013; Reisinger *et al.*, 2015) and northern hemispheres (Baird *et al.*, 2005; Miller *et al.*, 2010; Wright *et al.*, 2017), respectively. As related killer whales are known to share prey as an inclusive fitness benefit (Wright *et al.*, 2016), and no sperm whales were documented depredating at the same time as the tagged killer whale, its deep dives were likely not due to resource competition with other whales. Instead, the fact that the killer whale only made deep dives when it and associated pod members first arrived in the vicinity of a line being retrieved suggests that it has learned that this may be the only opportunity to depredate, because longlines in this fishery are often buoyed off as soon as killer whales are observed during gear retrieval (Clark and Agnew, 2010). However, the relative infrequency of these deep dives, even in situations when the retrieval of gear continued, suggests not only that deep diving behaviour is energetically costly for killer whales and is only conducted when a positive net gain is likely, but also, that these dives may represent the physiological limits of this species.

The durations of two deep depredating dives $>750\,\mathrm{m}$ (11.4 and 11.5 min) slightly exceeded the aerobic dive limit (cADL) for adult female killer whales (10.2 min) calculated by Miller *et al.* (2010) [This value was calculated from mean mass estimates of captive adult female killer whales and considering there is much variation in the size of adult females from different wild populations (Pitman *et al.*, 2007; Ford, 2014; Durban *et al.*, 2017), this limit should be considered approximate.]. Tagged adult and juvenile killer whales sometimes exceed cADL during natural diving behaviour (Miller *et al.*, 2010; Reisinger *et al.*, 2015). Furthermore, most small beaked whale species regularly exceed cADL to pursue and obtain prey at depth (Tyack *et al.*, 2006; Joyce *et al.*, 2017). For the tagged killer whale, acquisition of prey from a previously undepredated set is highly likely, so significantly exceeding cADL may not be necessary despite the depths to which deep depredating dives were occurring. However, as time at depth was likely necessary to find and remove prey from the longline, this indicates that vertical commutes during deep depredating dives were conducted at relatively high velocities. Killer whales have been known to chase fish at speeds up to $6.7\,\mathrm{m\,s^{-1}}$ in the North Pacific (Wright *et al.*, 2017), but the median vertical descent and ascent velocities of these killer whales while on foraging dives (0.7 and $0.6\,\mathrm{m\,s^{-1}}$ respectively) and their mean velocity while chasing fish ($2.7\,\mathrm{m\,s^{-1}}$) are lower than the mean vertical velocity of the tagged killer whale during all depredating dives ($0.9 \pm 0.9\,\mathrm{m\,s^{-1}}$) and it's estimated average vertical velocity during only deep depredating dives ($3.1 \pm 0.3\,SD\,\mathrm{m\,s^{-1}}$).

The tagged killer whale made dives $<100\,\mathrm{m}$ for long periods of time (232–277 min) after making one or two consecutive deep dives. It is hypothesized that other marine mammals that spend long periods of time engaged in shallow dive behaviour following a deep dive do so to offload carbon dioxide (Gerlinsky *et al.*, 2014) and repay oxygen debt associated with the accumulation of lactic acid due to exceeding cADL (Kooyman *et al.*, 1980; Tyack *et al.*, 2006; Joyce *et al.*, 2017). The deep dives made by this killer whale were all near cADL, but deep diving behaviour alone may lead to supersaturation of nitrogen in body tissue that could make individuals vulnerable to diving related pathologies (Cox *et al.*, 2006). Additionally, the short intervals between some deep dives recorded for this killer whale and rarely in some species of beaked whales (Joyce *et al.*, 2017) have been associated with higher risk of decompression sickness (Wong, 1999). Although marine mammals are thought to have evolved anatomical, physiological and behavioural adaptations to reduce risk of decompression sickness associated with nitrogen supersaturation, how these features function is poorly understood (Kooyman *et al.*, 1972; Ridgway and Howard, 1979; Cox *et al.*, 2006; Garcia

Párraga *et al.*, 2018). Durations of some of the deep dives recorded for this killer whale are some of the shortest known for any cetacean diving to such depths. It is possible that the limited duration of these deep dives combined with following long periods of shallow diving help to mitigate any potential negative physiological effects.

In the vicinity of deployed gear

A positive correlation existed between the maximum dive depths of the sperm whale and the depths of the nearest longline not being retrieved. This indicates that by remaining in close proximity to a fishing vessel over the course of several days, the sperm whale may have learned the locations of deployed gear and, as documented in southern elephant seals (*Mirounga leonina*) (van den Hoff *et al.*, 2017), took advantage of opportunities to depredate before gear retrieval began. However, as these dives were not always to the same depths as deployed longlines and depredation took place when the gear was being retrieved, it is likely that they also included natural foraging behaviour.

The lack of correlation between the killer whale's dives and the depths of gear deployed nearby verifies that there was no depredation from longlines before they were retrieved. This is not surprising, because while toothfish caught on lines are likely easy to locate and capture due to their inability to flee, those near the seafloor are less likely to be taken due to the limited amount of time killer whales can spend at these depths. However, the depths of two deep dives made by this whale in the vicinity of a line several h after it was buoyed off were correlated with the depth to which the longline had been stripped of toothfish, suggesting that it depredated from gear that had only been partially retrieved.

When foraging naturally

Characteristics of several of the dives made by the tagged killer and sperm whales while not depredating are indicative of natural foraging behaviour. For example, on several occasions while not depredating, the tagged killer whale successively dove to depths >200 m with little variance for periods up to 3.7 h. Similarly, the tagged sperm whale engaged in repeated diving, but to a variety of depths, when not depredating. The resolution of bathymetric data for interpolated locations of the tagged whales was too low to verify the exact depths of the seafloor where they dove. Around South Georgia, toothfish occur in the benthic zone at a variety of depths (Collins *et al.*, 2010), however, cephalopods replace the role of fish as mesopredators in the epipelagic zone (Rodhouse and White, 1995) and are also abundant in the mesopelagic and bathypelagic zones (Collins *et al.*, 2004) where few, if any, large fish species occur. Cephalopods have been documented in the diets of several species around South Georgia, including sperm whales and southern elephant seals (Clarke, 1980; Rodhouse *et al.*, 1992). Interestingly, the dive depths of southern elephant seals over the shelf edge in this region (mean maximum—350 m; McConnell and Fedak, 1996) are similar to the foraging dive depths of the tagged killer whale. Many killer whale populations feed at least in part on cephalopods (Nishiwaki and Handa, 1958; Jonsgård and Lyshoel, 1970; Ford *et al.*, 1998; Yamada *et al.*, 2007; Hanson and Walker, 2014) and they have been documented in the diet of killer whales in nearby Antarctica (Berzin and Vladimirov, 1983) and the South Atlantic (Santos and Haimovici, 2001). Cephalopods are also predicted to constitute significant portions of the diets of killer whales known to feed on mammals and birds, as well as depredate toothfish from demersal longlines off the Prince Edward Islands (Reisinger *et al.*, 2015, 2016). However, several killer whale populations specialize on different types of prey (Ford *et al.*, 1998; Pitman and Ensor, 2003) and at South Georgia, at least three distinct types are sympatric (Pitman *et al.*, 2010; Towers, 2015). Among them, only a population of individuals hypothesized to be B2s based on morphology and behaviour depredates in the region (Söffker *et al.*, 2015; Towers, 2015). Nitrogen isotope values indicate that B2s do not feed on marine mammals (Durban *et al.*, 2017), but aside from depredated toothfish, only penguins have been documented in their diet (Pitman and Durban, 2010).

Implications and recommendations

This study provides key findings on the movements and dive behaviour of depredating killer and sperm whales that have implications for the toothfish longline fishery and its management. The results also enhance our understanding of the behaviour and ecology of killer and sperm whales off South Georgia. However, as only one individual of each species was tagged, caution should be taken when applying these results to larger populations due to the potential for individual variations in behaviour.

Nevertheless, the deep dives made by the killer whale while depredating were to depths this species was not previously thought capable of attaining (Purves *et al.*, 2004; Kock *et al.*, 2006; Clark and Agnew, 2010; Collins *et al.*, 2010; Tixier *et al.*, 2010, 2015b). However, the long recovery periods following these dives may represent times that whales are physiologically constrained in their depredation capabilities. Additionally, whales may be prone to lethal effects of acoustic disturbance during these times. For instance, it is hypothesized that decompression sickness documented in beaked whales occurs due to behavioural responses to naval sonar when the whales are physiologically limited during their recovery periods following deep dives (Jepson *et al.*, 2004; Tyack *et al.*, 2006). Both killer and sperm whales change their dive behaviour in response to high intensity sound (Sivle *et al.*, 2012), thereby altering nitrogen levels in their bodies and increasing risk of decompression sickness (Kvadsheim *et al.*, 2012). Therefore, the use of acoustic disturbance devices to deter depredation, although seemingly ineffective (Tixier *et al.*, 2015a; Towers, 2015), may have implications for the health of deep diving depredating whale populations at South Georgia.

Another key finding of this study is that the dive behaviour of both species when not depredating is suggestive of a natural diet that may include cephalopods. This indicates that depredating killer and sperm whales at South Georgia only supplement their natural diet with toothfish obtained from commercial longlines. However, it remains unclear if longlining has only benefited whale populations by providing easy access to toothfish that was not historically present, or if the effect that longlining has had on the toothfish stock in this region has reduced the natural availability of this prey resource for local whale populations. In any case, since dietary preferences and associated foraging strategies can evolve as different prey species become more or less available in the environment, effective mitigation is therefore paramount not only for protecting catch but also to ensure that whale populations do not become more reliant on depredated resources.

Data collected in this study indicate that some mitigation techniques caused whales to disassociate from the fishing vessel. For instance, the horizontal movements of the killer and sperm whale were not always correlated with fishing activity after gear was buoyed off or when the *San Aspiring* left the area in which depredation was occurring. This is consistent with previous findings by Tixier *et al.* (2015b). Other studies have also shown that both species exhibited a westward trend in occurrence throughout the South Georgia fishing season that was not correlated with fishing effort (Clark and Agnew, 2010; Söffker *et al.*, 2015). This is supported by the photo-identification data of Towers (2015) showing that eight sperm whales moved ≤463 km west through the fishing grounds in ≤22 d. However, Towers (2015) and this study also show that killer whales moved >300 km east through the fishing grounds in <50 h. Given the high mobility of these species and the size of the fishing grounds, further study into the large-scale movements of depredating whales in relation to fishing vessels may help inform how, when, and where depredation can be avoided.

Further studies into the fine-scale movements of whales while gear is deployed are also necessary because some evidence from this study indicates that sperm and killer whales may remove toothfish from longlines that are not being actively retrieved. For instance, on one occasion the vertical and horizontal movements of the tagged killer whale were correlated with the location of fishing gear that was buoyed off and the depth to which toothfish had been removed from it. This suggests that keeping hooked fish at greater depths by attaching extra line before buoying off would result in greater retention of catch. On the other hand, the behaviour of the tagged sperm whale was on several occasions correlated with the depths and locations of deployed gear, indicating that it may have been depredating at the seafloor. However, this practice cannot be too common or widespread or there would not be much incentive for so many whales to depredate while gear was being retrieved. Nevertheless, if depredation from deployed gear were to become an effective means for sperm whales to acquire prey, this practice could result in greater reduction of catch, increased uncertainty in stock assessments and further difficulty utilizing efficient mitigation techniques.

This study demonstrates the value of fine-scale movement and dive data to study depredation. However, considering that tags are not without some risk to whale health and survival (Raverty, 2016), this technology should be used with caution whenever conservation of the study population is of concern. Nevertheless, continued research on the ecology and behaviour of depredating whales at South Georgia will be important to help direct fisheries management practices and depredation mitigation procedures and technology. To this end, we recommend that fishing and patrol vessels continue to be utilized at South Georgia to conduct depredation studies in the region.

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Appendix 3

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RESEARCH ARTICLE

Evidence of deep-sea interactions between toothed whales and longlines

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Abstract Toothed whales (odontocetes) feeding on fish caught on hooks in longline fisheries is a growing issue worldwide. The substantial impacts that this behaviour, called depredation, can have on the fishing economy, fish stocks and odontocetes populations, raise a critical need for mitigation solutions to be developed. However, information on when, where and how odontocete depredation occurs underwater is still limited, especially in demersal longline fisheries (fishing gear set on the seafloor). In the present study, we investigated depredation by killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) on demersal longlines in the French Patagonian toothfish fishery (Southern Ocean). Using a combination of animal-borne behavioural and longline-attached data loggers, we demonstrated that both species are able to depredate longlines on the seafloor. This study, therefore, suggests that odontocetes whales–longline interaction events at depth may be unrecorded when assessing depredation rates from surface observations during hauling phases only. This result has implications for the management of fisheries facing similar depredation issues as underestimated depredation rates may result in unaccounted fish mortality in fish-stock assessments. Therefore, while further research should be conducted to assess the extent of deep-sea whale–longline interaction events during soaking, the evidence that depredation can occur at any time during the whole fishing process as brought out by this study should be considered in future developments of mitigation solutions to the issue.

Keywords Bio-logging · Demersal longlines · Depredation · Killer whales · Patagonian toothfish · Sperm whales

INTRODUCTION

The intensification of fishing activity over the last few decades has been associated with an increase in direct interactions between fisheries and marine top predators worldwide (Northridge 1991; Northridge and Hofman 1999; Read et al. 2006; Read 2008). Depredation, which occurs when marine predators remove or damage fish from fishing gear, is a type of interaction often resulting in substantial impacts on fishing activity, depredating species and fish stocks (Donoghue et al. 2002; Gilman et al. 2006; Read 2008). Longlines are fishing systems composed of a main line with baited hooks. The main line is either deployed in the water column, *i.e.* pelagic longlines, or on the seafloor, *i.e.* demersal longlines. Therefore, longlining is a fishing technique that makes caught fish easily accessible for depredating animals. It has been reported to be the fishing technique most impacted by depredation, especially by toothed whales, *i.e.* odontocetes (Northridge and Hofman 1999; Donoghue et al. 2002; Gilman et al. 2006; Hamer et al. 2012). Indeed, at least 31 species of odontocetes have been reported to interact (either through depredation or bycatch) with longline fisheries worldwide (Werner et al. 2015).

Depredation on fisheries leads to greater costs for fisheries. This is due to the cost of damaged fishing gear, damaged fish losing economical value, and increased effort to both avoid competition and reach quota limits (Peterson and Carothers 2013; Peterson et al. 2014; Tixier et al. 2015c; Werner et al. 2015). For odontocetes, interactions

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with longlines may increase risks of mortality, either by entanglement in fishing gear, *i.e.* bycatch (Northridge 1991; Trites et al. 1997; Read et al. 2006; Hamer et al. 2012), or by the use of lethal methods by illegal fisheries to eliminate competitors (Poncelet et al. 2009; Guinet et al. 2015). Also, depredation often involves access to new and easy-to-catch prey resource for predators, which may modify both the energy balance of odontocetes and the natural predator–prey dynamics of local ecosystems (Trites et al. 1997; Northridge and Hofman 1999; Boyd 2002; Guénette et al. 2006; Morissette et al. 2012; Tixier et al. 2017). For fish stocks, depredation may result in biased assessments and over-exploitation if the amount of depredated fish is not precisely estimated (Roche et al. 2007; Read 2008). Together, these multiple impacts of depredation may jeopardize the sustainability of local fishing activity, urging the need for mitigation solutions.

Depredation has been described to occur during both soaking and hauling phases for pelagic longlines (Dalla Rosa and Secchi 2007; Forney et al. 2011; Rabearisoa et al. 2012; Passadore et al. 2015; Thode et al. 2016), whereas this behaviour has only been assumed to occur during hauling phases for demersal longlines (*e.g.* Mathias et al. 2012, Tixier 2012, Werner et al. 2015). In dermersal longline fisheries, depredation rates are mostly assessed from the difference in fishing efficiency in the absence and in the presence of odontocetes. Importantly, the presence/absence of odontocete is visually evaluated, while animals are at the surface, and this evaluation is performed from fishing boats during hauling (Hucke-Gaete et al. 2004; Purves et al. 2004; Roche et al. 2007; Rabearisoa et al. 2012; Gasco et al. 2015; Passadore et al. 2015; Söffker et al. 2015; Straley et al. 2015; Tixier et al. 2019a). However, there are still large knowledge gaps on the underwater depredation behaviour of odontocetes. Specifically, it is not known if the odotoncetes depredate on demersal longlines soaking on the seafloor, while the fishing vessel is potentially hundreds of kilometres away. This unknown factor introduces serious uncertainties in the depredation rate evaluation.

In the present study, we approached this problem using fine-scale bio-logging technology deployed on both depredating odontocetes (ARGOS satellite tracking loggers equipped with depth sensors) and longline sets (accelerometers paired with depth sensors) from commercial demersal longline fisheries. By combining these two approaches, our primary aim was to investigate the occurrence of odontocetes depredation events on demersal longlines in the underwater dimension during both soaking and hauling phases of the fishing process. The initial objective was to use the two methods to study both killer whales and sperm whales. Unfortunately, this turns out to be impossible. In the following, we will see that accelerometers deployed on longlines have been useful to study sperm whales ("Longline accelerometry" section), while tags deployed on animals were useful to study killer whales only ("Odontocetes tracking data loggers" section).

MATERIALS AND METHODS

Research context

The study focused on a depredation conflict involving the French Patagonian toothfish fishery with killer whales and sperm whales. The Patagonian toothfish is a long-lived (> 50 years) and a large (> 200 cm in length and > 200 kg in weight) species (Collins et al. 2010), with high-quality flesh making the species economically highly valuable (Collins et al. 2010; Grilly et al. 2015). The French longline fishery is of particular scientific interest since it holds the largest Patagonian toothfish quota in the Southern Ocean (COLTO 2016) allocated between the subantarctic islands of the Crozet Archipelago (46°25′S, 51°59′E) and Kerguelen Islands (49°20′S, 70°20′E, see Fig. 1). In addition, this fishery also experiences the highest depredation levels of all toothfish fisheries, with more than 30% and 9% of the total annual catch taken at Crozet and Kerguelen, respectively, by killer and sperm whales (Roche et al. 2007; Tixier et al. 2010; Gasco et al. 2015; Janc et al. 2018). Interaction levels are fundamentally different between the two EEZs with sperm whales being present around both islands but at different densities (Labadie et al. 2018) and killer whales being almost exclusively found at Crozet (Tixier et al. 2010; Guinet et al. 2015).

Fishing seasons last a year, starting in September and ending in August. A fishing season consists of three or four trips of approximately 3 months each. During a trip, vessels fish continuously through a diel pattern. Longlines are set at night and primarily hauled during the day, since fishing regulations prohibit setting at daylight to avoid seabird bycatch (Weimerskirch et al. 2000). During trips, all longline positions (latitude and longitude), bathymetry at deployments (500–2000 m), and setting and hauling times are recorded. Fishing in waters shallower than 500 m is prohibited to avoid the capture of juvenile toothfish (Collins et al. 2010; Gasco 2011). Vessels use auto-weighted longlines set between two anchors and linked to buoys at the surface for retrieval. The lines are composed of sections of 750 hooks, with 1.2 m between hooks. The length of the longlines varies from 1 to 40 km, with an average of approximately 8 km. For each longline hauled, the presence of cetaceans (killer whales and/or sperm whales) is monitored according three classes: (i) whales absent (condition suitable for a confident observation); (ii) whales present; and (iii) uncertain observation (conditions

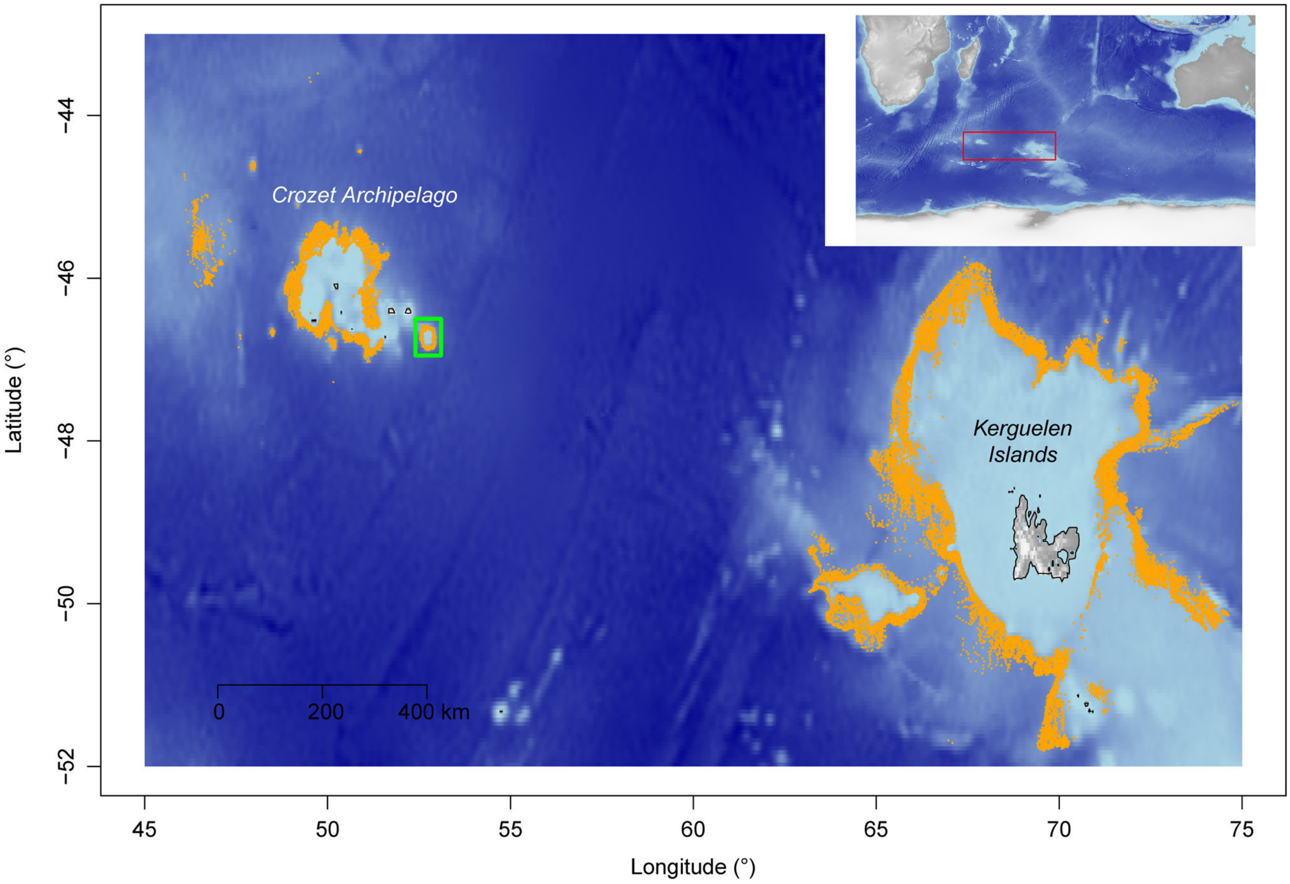

Fig. 1 Map of the study area with the locations of the fishing activity (orange dots) around Crozet and Kerguelen. The green rectangle indicates the seamount where the deployment of instruments on killer whales occurred

unsuitable and/or no observation undertaken). Data were available through the PECHEKER database (Museum National d'Histoire Naturelle de Paris; Martin and Pruvost 2007).

Data collection for this study was conducted from two commercial demersal longline fishing vessels during two summer trips (December–March) in 2016–2017 and in 2017–2018.

Odontocetes tracking data loggers

We deployed six ARGOS satellite tracking tags equipped with depth sensors (2 SPLASH10-292A units and 4 SCOUT-DSA units, Wildlife Computers, Redmond, Washington, USA) on three killer whales and three sperm whales. The six loggers were deployed from the fishing boat during longline hauling operations using modified crossbow arrows (Wildlife Computers) and fired from a 68-kg draw weight crossbow (Barnett Rhino, Barnett Outdoors Inc., Tarpon Springs, Florida, USA). The devices recorded diving depths using a pressure sensor every 2.5 min, with an associated error band. Between dives, the instruments were set to transmit geographical positions and depth data every 2 h through the ARGOS system (Collecte Localisation Satellites, Toulouse, France).

Position estimates were categorized into five estimated accuracies: (i) class with no estimate; (ii) class 0: $\geq$ 1 500 m; (iii) class 1: 500–1500 m; (iv) class 2: 250–500 m; and (v) class 3: $\leq$ 250 m (Collecte Localisation Satellites, Toulouse, France). These accuracies were used to determine a confidence area around the ARGOS positions. Position without uncertainty estimates (class i) were removed from the dataset. ARGOS positions were processed using the software R (version 3.4.4, R Development Core Team 2015). We mapped every position using a buffer function (*create.buffer*, package *marmap* version 1.0.2) to account for potential location accuracy errors. Bathymetric data were obtained from the ETOPO1 dataset (NOAA) and plotted using a custom R code. For a given ARGOS position and associated date/time, all longlines at sea and their statuses (soaking, hauling) were also plotted on the map. We then estimated the distance from the instrumented animal to the closest longline using the ARGOS positions and the longline coordinates.

From there, we defined interactions between an individual and the fishing gear based on the geographical proximities of both entities. We used a method that defines odontocete interactions with fishing vessels at hauling in other studies (Roche et al. 2007; Tixier et al. 2010; Mathias et al. 2012). Animals were considered to be interacting with a longline if they were within a 1.5 km proximity, independent of the fishing activity. Thus, we determined two behavioural states for every individual's ARGOS position: (i) 'interaction' with a longline; and (ii) 'no interaction' with any longline. Simultaneously, we monitored the individual's depth profile of every ARGOS position. We also added the depths of the closest longlines to the diving profile when the individual was in 'interaction'. Moreover, if the closest longline was being hauled, we also monitored bathymetry under the boat during the hauling. As the equipped individual was in interaction with the boat at this time, we considered it to be in waters with the same bathymetry rather than the fishing vessel.

All instrument deployments followed the ethics policies of the Terres Australes et Antarctiques Françaises (TAAF) and were authorized by the Réserve Naturelle Nationale (RNN des TAAF) through approval A-2017-154.

Longline accelerometry

We deployed 3-axis accelerometer/pressure sensor data loggers (Sextant Technology, New Zealand) on longlines to detect activity events at the hooks (fish catch and/or depredation events) and the depth at which they occurred during soaking and hauling. Accelerometer/depth data loggers were deployed singularly on snoods (*i.e.* short lines connecting individual hooks to the main longline; Fig. S1). In the 2016/2017 field season, the data loggers were attached to snoods by a snap connector fixed on the mainline (Fig. S1), while in 2017/2018 they were attached with a thick rope to the swivel between the snood and the main line (Fig. S1), allowing the data loggers to roll around the mainline as normal snoods do. We used two different versions of data logger: 2016/2017 recorded acceleration at 10 Hz with a precision of 10 bits; 2017/2018 recorded acceleration at 12.5 Hz with a precision of 12 bits. In both versions, the acceleration range was set at ± 16 g per axis and, to conserve battery life and memory capacity, an acceleration threshold (2016/2017 0.03 g, 2017/2018 0.01 g) was set to start recording when a movement occurred on the hook. The pressure sensor recorded continuously at 0.2 Hz.

Sets of accelerometers were deployed along a longline on every hook (*i.e.* every 1.2 m), or separated by 3, 5, or 10 unequipped hooks. When the equipped longline was retrieved on the vessel, the presence of a captured fish (and its species) on an equipped snood was recorded. For equipped hooks without any capture, we recorded whether the bait was still present and the condition of hook (undamaged, twisted or ripped off the snood).

To assess the potential for detecting events on non-equipped snoods, the distance from equipped hooks to the nearest capture along the longline was recorded, counting 0 when a catch occurred on the equipped hook. Simultaneously, we monitored the amplitude of the movement received on the loggers nearby. Thus, we estimated the norm of the acceleration vector using the equation:

$$\text{Norm} = \sqrt{ax^2 + ay^2 + az^2} \tag{1}$$

with ax, ay and az, being the three components of the acceleration vector. Acceleration data were extracted using the software Hermes DeepG (Sextant Industry, New Zeland). Accelerometer data and pressure profiles were processed using custom-built routines in Matlab (version R2015, The MathWorks, Natick, MA, USA).

We then examined how the acceleration norm (Eq. 1) varied with respect to the distance (in number of hooks) of the closest capture. To do so, we produced boxplots depicting the median with the 25th and 75th percentiles (McGill et al. 1978). Also a 95% of confidence interval was represented (the two whiskers) with the outlying points shown individually (McGill et al. 1978). The dataset did not allow for linear regressions to be assessed because of a violation of independence when a same catch was monitored on several accelerometers nearby. The low number of accelerometers recording signals from a same catch did not allow for nested linear models to be used to correct the violation of independence. Boxplots were developed per season because of the difference in the sampling schedule of the loggers and their method of attachment to the longlines between the two field seasons.

Finally, we assessed the depth profile of each accelerometer and mean norm acceleration. We manually looked for any depth anomalies and assessed the distance of closest capture to equipped hooks. Our aim was to determine if the acceleration/depth data could reveal depredation events for hooks that were hauled without fish.

RESULTS

Odontocetes tracking data loggers

Only two loggers of the six deployed transmitted correctly. The other four loggers failed to transmit, most likely because of an on-board software issue. The two operational loggers were deployed on two adult female killer whales in February 2018 near the seamount located 40 km south-east from East Island, Crozet Archipelago (Fig. 1). The two instruments provided 28 and 65 ARGOS locations during 3 and 7 days, respectively, before they stopped transmitting (*i.e.* fell off the animal or battery expired). Of these locations, 20 and 31, respectively, had an accuracy estimates and, thus, were included in further analyses.

Out of the 20 useful locations from the first logger, nine locations were identified as "interactions" with five different longlines. For the second logger, 14 points were identified as "interactions" with 11 different longlines. Among the 'interactions' positions of the first individual, three were recorded during the hauling of three different longlines, and six were recorded as overlapping with two different longlines during soaking. For the second individual, six positions were recorded during the hauling of five different longlines and eight positions overlapped with six different soaking longlines.

The dive data corresponding to the nine 'interaction' positions on longlines being hauled indicated that killer whales started diving at the beginning of hauling activities and stopped diving once all hooks were landed onboard the vessel (Fig. 2 and Figs. S3–S7). Interestingly, during the hauling operations, the diving depths of the killer whales ranged throughout the entire water column (from the surface to the sea-floor).

The dive data corresponding to the 14 "interaction" positions on soaking longlines indicated that the killer whales mostly performed shallow dives (< 50 m). An exception to this behaviour occurred for one "interaction" position, where a killer whale performed a dive to 502 ± 22 m only 1:30 h after the "interaction" position time (Fig. 3). This "interaction" position was the last of a series of six consecutive positions recorded within a 4.5-h window and all overlapping with the same cluster of longlines soaking within a 6 km radius (Fig. 3). The next position was recorded 20 h later and at 4 km from the last position of previous series. During this 20-h time window, the killer whale conducted eight dives deeper than 450 m in < 6 h, with five of these being consecutive dives to the same estimated depth (502 ± 22 m) within 2 h (Fig. 3). These dive depths correspond to the bathymetry at the extremity of the closest longline (set at 515; Fig. 3). All these events occurred around the soaking longlines (*i.e.* the ARGOS positions and the recorded dives within the 15-h window; Fig. 3) while no vessel was in the area. Indeed, after setting the longlines, the fishing vessel left the area and travelled a distance of 140 km away. It then returned to haul the considered longline, 3 h after the last deep dive (502 ± 22 m) was recorded. In addition, no other fishing vessel was active in this sector.

We observed with the two loggers that 68% of the ARGOS positions with 'no interaction' were associated with shallow dives (< 50 m) and occurred between two positions with 'interaction'. However, for one of the two instrumented individuals, nine "no interaction" positions coincided with seven relatively deep dives. The maximum depths were between 200 and 325 m, and three of these dives were performed within a 3-h period (Figs. 4, S8). This specific event occurred on a seamount. The area is characterized by steep slopes reaching a plateau at depths of approximately 200–300 m, with two peaks rising to depths of up to 100 m. As fishermen are not allowed to set longlines on the seafloor shallower than 500 m, these deep dives could not be associated to longline depredation.

Longline accelerometry

Accelerometer/depth data loggers were deployed on 556 hooks across 126 sections for 115 longline sets. Equipped hooks captured 38 fish, including 19 Patagonian toothfish. Other captures included grenadier (*Macrourus* spp.), antimora (*Antimora rostrata*) and skate species (*Bathyraja* spp.). The catch rate of Patagonian toothfish on the equipped hooks (3.42%) was similar to the catch rate of all longlines for the whole fleet for the same period (3.85%). However, due to device malfunctions, accelerometer data were obtained for only 13 toothfish captures.

Acceleration norms recorded during the second season were higher than those recorded during the first season (Fig. 5). This is likely due to modifications in the newer generation of accelerometers that were used on the second year of the study, and to modifications in the way accelerometers were attached to longlines. In the second year, a smoother attachment was used, allowing a complete rotation of the snood around the mainline. However, for both field seasons, the accelerometer data showed the same feature: the accelerometer norm globally decreases when the distance of the closest capture increases (Fig. 5).

Over the total 126 sections of data logger deployments, we observed three events of significant depth variation during three separate longline soaking phases, one at Kerguelen in January 2017, one at Crozet in February 2017 and one at Crozet in February 2018 (Fig. 6). These events occurred at depths of 600, 1600 and 1800 m, respectively, while the lines were soaking on the seafloor. The elevation events lasted 6, 9 and 52 min, respectively (Fig. 6). The first event in Kerguelen occurred 1 h before the arrival of the fishing vessel at the longline (Fig. 6a, b). The second event happened just after fishermen stopped hauling the longline half way through and let it fall back to the seafloor (Fig. 6c, d). The third event occurred 1 day after the longline was set and 3 days before the hauling (Fig. 6e, f). During these events, longlines were elevated by 30, 40 and

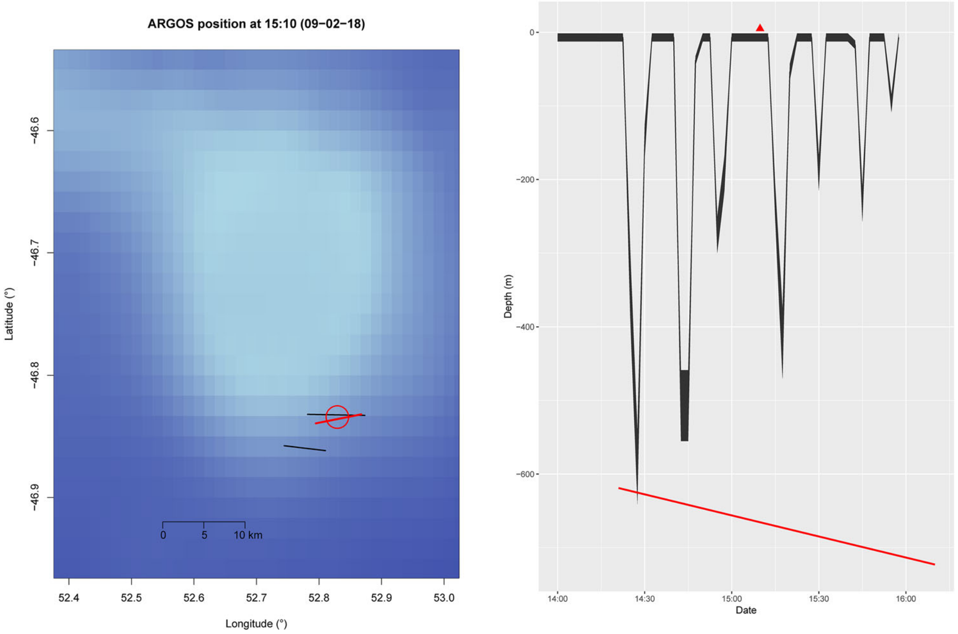

Fig. 2 ARGOS position (left panel) of an 'interaction during hauling' with its associate dive profile (right panel). The ARGOS position is indicated on the map by the red circle with the diameter representing the location estimate error buffer (*cf.* CLS classes). The colour shade depicted the bathymetry. The soaking longlines are shown in black, and the longline being hauled is shown in red at the given transmission time of the ARGOS position (left panel). The dive profile assessed the depth range estimated by the tag through the thickness of the drawing (right panel). On the dive profile, the transmission time of the ARGOS position is represented by the red triangle, and the bathymetry recorded by the boat during the hauling session is indicated by the red line, as the killer whale was interacting with the boat, the red line represented then the bathymetry below the individual for a given time (right panel)

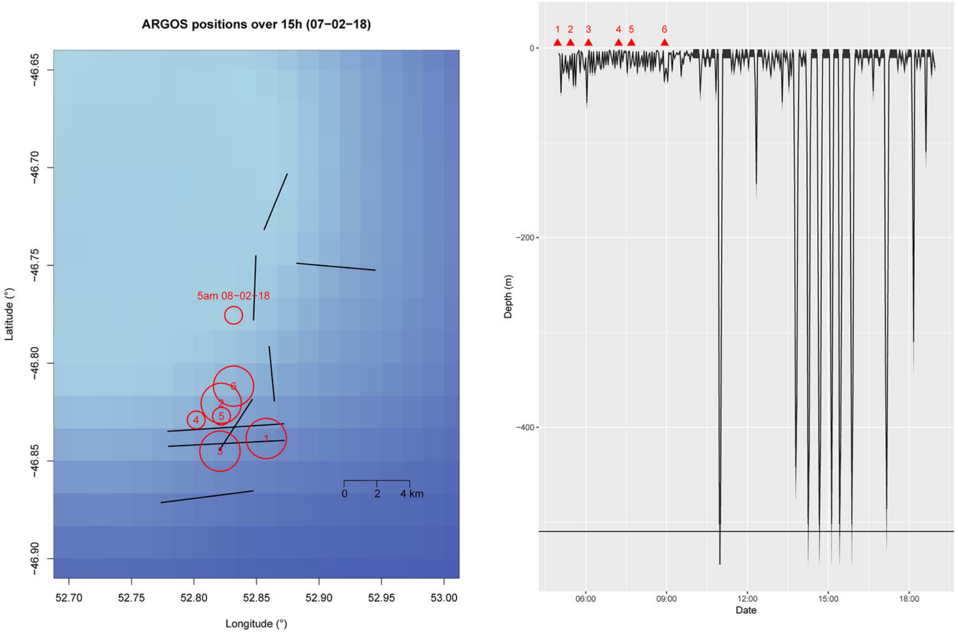

Fig. 3 ARGOS positions (left panel) of an 'interaction before hauling' with their associate dive profile (right panel) within a 15-h window. The ARGOS positions are indicated on the map by the red circles (numbered chronologically along track) with the diameter representing the location estimate error buffer (*cf.* CLS classes). The soaking longlines are indicated by the black lines on the map, and the closest soaking longlines to the most recent transmitted positions are in green (left panel). The dive profile assessed the depth range estimated by the tag through the thickness of the drawing (right panel). On the dive profile, the transmission times of the ARGOS positions are represented by the red triangles and the bathymetry of the closest longlines (at their extremities) at the time of the most recent ARGOS determined positions are outlined in green (right panel)

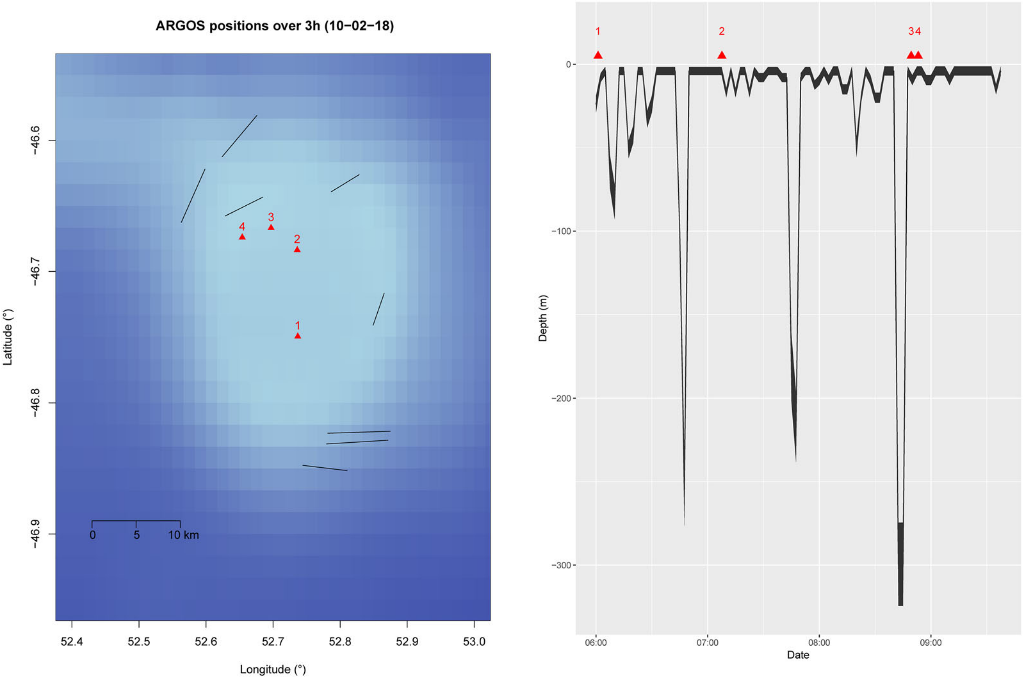

Fig. 4 ARGOS positions (left panel) within a 3-h window of ‘no interaction’ with the associate dive profile (right panel). The ARGOS positions are represented on the map by the red buffers with the diameter standing for the estimate error (*cf.* CLS classes) and the numbers assessed the chronology of the track. The longlines at sea during these 3 h are plotted in black on the map (left panel). The dive profile assessed the depth range estimated by the tag through the thickness of the drawing. On the dive profile the four transmission times of the ARGOS positions are represented by the red triangles (right panel)

300 m, respectively, above the seafloor (Fig. 6). Sperm whale presence was confirmed on the first event (Fig. 6a, b) by visual observations and passive acoustic recordings (obtained as part of concurrent studies). No such cues of sperm whale presence were detected near the set during the second event, though no passive acoustic monitoring occurred in the area at that time (Crozet 2016–2017, Fig. 6c, d). However, a sperm whale was found entangled and dead (Fig. S2) on the longline of the third event (Fig. 6e, f). The logger was located 1 km from the dead sperm whale. During the three events, all equipped hooks were hauled without caught fish and one of the equipped hooks was hauled in a row of ten hooks twisted or ripped off the snood.

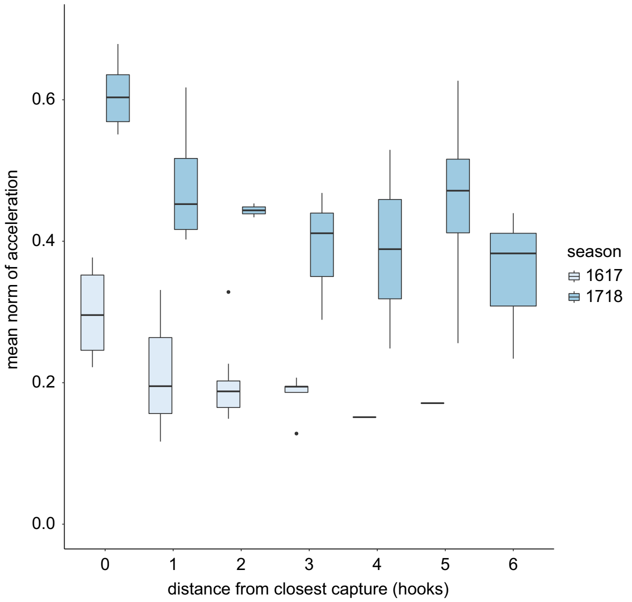

Fig. 5 Boxplots of the mean acceleration norm recorded during the bottom phase on accelerometers with the closest distance and for the two different seasons

The accelerometer of the third elevation event (*i.e.* with the dead sperm whale) did not reveal any acceleration activity while the longline was on the sea floor. This suggests that no fish were captured on any of the hooks located near the logger. However, the loggers monitoring the two other events revealed acceleration occurring before each elevation event and then stopped recording any activity until the hauling process began. This indicates the occurrence of a fish capture and then depredation. We then compared the mean acceleration norm of the equipped hook during the soaking phase until these elevation events with the boxplot of mean acceleration norm per closest capture (Fig. 7). These comparisons allowed for the distances of the activities recorded on the accelerometers to be roughly estimated before the elevation events occurred. We observed that the mean acceleration norm before the second elevation event (Crozet 1617) was higher than the

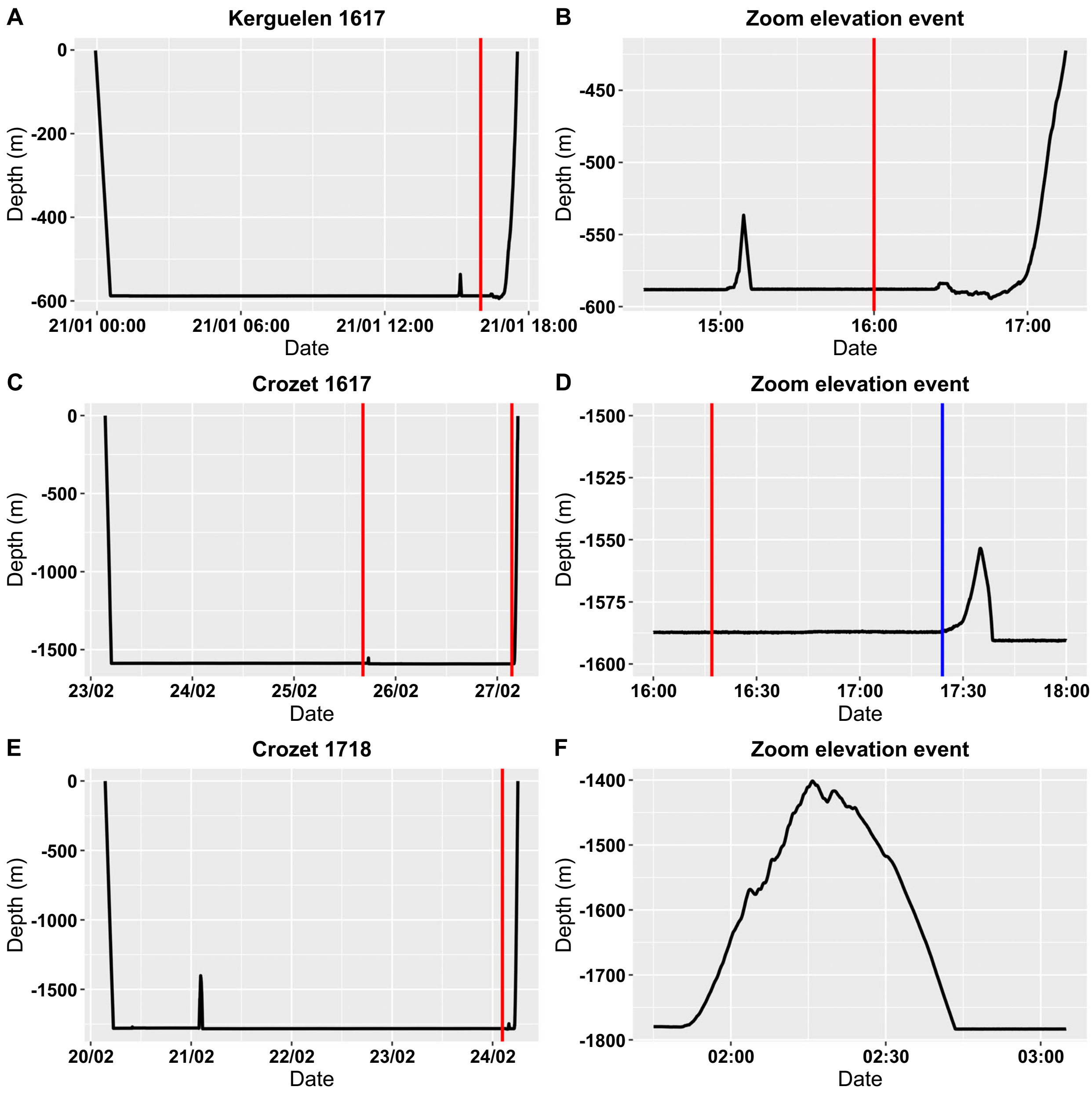

Fig. 6 Dive profiles (**a**, **c**, **e**) of three accelerometers hauled without any fish and showing some depth anomalies, zoomed on the right column (**b**, **d**, **f**). Each row represent a different logger monitoring a precise event: the first line represents the event which occurred at Kerguelen during the first field season (2016–2017); the second line represents the event which occurred at Crozet the same field season (2016–2017); and the third line represents the event with the dead sperm whale hauled at Crozet in February 2018. We assessed on the depth profiles and elevation zooms the arrival time of the fishing boat on the longline (red line), and for the second event (**d**) we also monitored the time at which fishermen stopped the fishing activity and cut the longline (blue line) before leaving

lower quartile of the boxplot at a distance of 0, *i.e.* fish hauled on the equipped hook (Fig. 7). This revealed that the equipped hook, hauled undamaged and with no fish, probably caught a fish during the soaking and before the elevation event. In contrast, the mean acceleration norm before the elevation first event (Kerguelen 1617) was too low to indicate a capture on the equipped hook, suggesting some activity further away (Fig. 7).

DISCUSSION

Insights into depredation behaviour during hauling and soaking phases of longlines

The diving behaviour of instrumented killer whales showed that individuals actively and repeatedly dived to depths matching those of longlines while they were being hauled

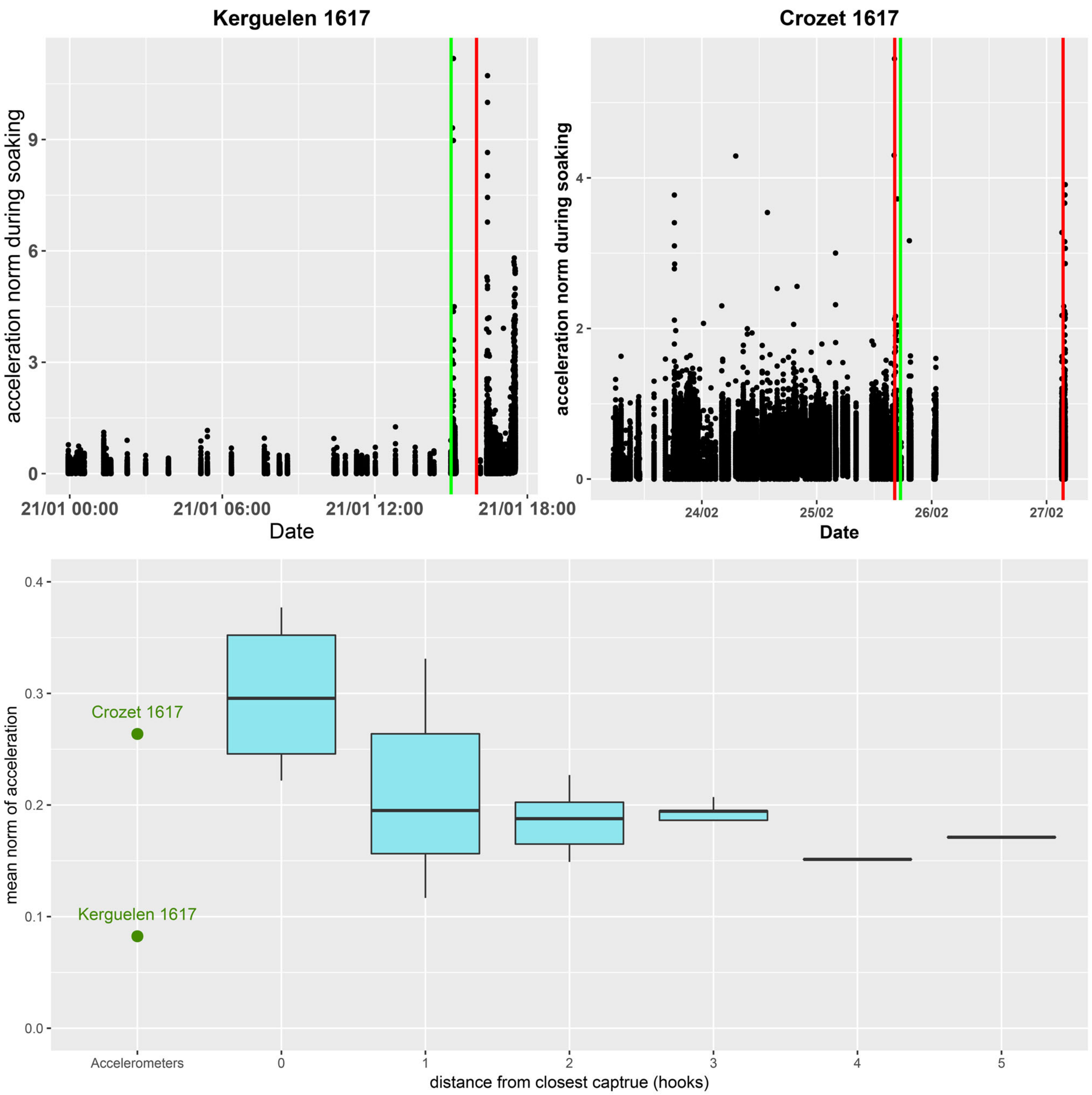

Fig. 7 The first row depicts acceleration norm over the dive of the two equipped hooks showing activity before the elevation event (green line). The mean acceleration norm before the elevation event (green line) was compared for each accelerometer with mean acceleration norm estimated with the distance of the closest toothfish capture

onto vessels. Interestingly, these dives were performed as soon as hauling was initiated by fishermen, with the first dives being the deepest (on occasions > 600 m) and matching the seafloor depth. Together, these findings suggest that depredating killer whales readily spend high amounts of energy in deep, short-spaced successive dives and that these costs are likely outweighed by the benefits gained from feeding on toothfish caught on hooks. These benefits may be maximized if individuals are the first to access the resource offered on the hooks, potentially with a choice of bigger fish. It may therefore be hypothesized that deep dives performed at the beginning of hauling is a response to both intra- and inter-specific competition. Competition is likely generated by a highly localized, short-term availability of easy-to-catch resource, such as toothfish caught on longlines. The large concentrations of both killer whales and sperm whales (sometimes co-occurring) around fishing vessels suggests such competition (Roche et al. 2007; Tixier et al. 2010). Deep diving behaviour while depredating on longlines being hauled has also been reported for killer whales off South Georgia (Towers et al. 2019) and for sperm whales in Alaska (Mathias et al. 2012), suggesting competition for the hauled resource in both cases.

In the present study, the diving/tracking data for the killer whales and the longline accelerometry/depth data for the sperm whales suggest that these species also interact with longlines during soaking. For killer whales, interactions with longline sets on the seafloor during soaking phases are suggested by the matched maximum dive depths and bathymetry when positions of individuals overlapped with those of longlines. In addition, the repeated deep dives within a short duration (5 dives in 2 h) to the same depth, strongly suggests a foraging activity on a highly localized resource remaining available at the same depth for extended periods of time, strengthening the idea that the killer whale was foraging on the soaking longlines. While more data are required to fully address these interactions, our dataset demonstrates that killer whales can forage on soaking longlines and suggests that they do.

The unfortunate by-catch of a sperm whale entangled in a longline equipped with a logger confirms the species does depredate on soaking longline. The event also helps the interpretation of the other longline logger data. The elevation signals detected on loggers were identified as interaction events and confirmed by additional cues such as toothfish capture events on the same portion of sets, wrested and twisted hooks, and the presence of sperm whales in the vicinity of sets. While such cues were undetected for one of the nominally identified events, the depth of the event (1600 m) makes it unlikely to be the result of killer whales as they are not known to dive deeper than 1100 m (Reisinger et al. 2015; Towers et al. 2019). In contrast, sperm whales are known to be able to reach depths of 1500–2000 m (Teloni et al. 2008; Fais et al. 2015; Guerra et al. 2017).

In addition, the variation in depth data obtained during longline soaking suggests how depredation events may occur. The two elevations of longlines up to 30 and 40 m off the seafloor indicate a significant pull must have been exerted directly on the line, and not on a hooked toothfish. Pulling on a hook or a fish may only support an elevation of 1 or 2 m, as observed in video data obtained by Van den Hoff et al. (2017) showing an elephant seal pulling a toothfish to unhook it. Furthermore, sperm whales depredating hauled lines near Alaska appear to bite and scrape sections of lines in order to remove fish instead of directly targeting hooked fish (Mathias et al. 2009, 2012). In the present study, the observation of twisted and wrested hooks in a row, even if no fish captures were recorded in the accelerometry record, suggests that sperm whales rake the mainline while lifting it from the seafloor. Such a hypothesis may also explain why the dead sperm whale hauled on a longline with equipped hooks had the mainline wrapped around its jaw. It is also known from subsurface video data that killer whales are more likely to pull fish to remove them from lines (Guinet et al. 2015) such that it is unlikely this species was involved in elevation events of soaking longlines.

Fisheries management and odontocetes conservation implications

This study has major implications for the way depredation is estimated and incorporated into fish-stock assessment as well for the conservation of depredating odontocete populations. Our results demonstrate that visual observations from fishing vessels are not enough to correctly quantify depredation rates. Indeed, depredation rates are estimated by the difference between catch per unit effort on longlines in absence of cetacean and longlines in presence of cetaceans (*e.g.* Hucke-Gaete et al. 2004; Purves et al. 2004; Roche et al. 2007; Gasco et al. 2015). Within cases that seafloor depredation occurs on longlines hauled in the absence of cetaceans, depredation rates will be underestimated. This insight has significant implications for fish-stock management, since even with the recent efforts to consider depredation in quota management (Roche et al. 2007; Gasco et al. 2015), our study shows that the fishing stock might be more impacted than previously assumed. Furthermore, to clearly estimate the impact of depredation on the fish stock, it is essential to know whether the targeted fish belong to the natural diet of the depredating odontocetes.

In the present study, we observed killer whales diving to the seafloor of a seamount, where no longlines were set. As Patagonian toothfish was recently confirmed as a natural prey of Crozet killer whales (Tixier et al. 2019b), these bottom dives may be associated with foraging events on this fish species. In addition, similar behaviour has been observed with killer whales at Marion Island while foraging on the seafloor of a seamount at 800 m depth, where they were considered as preying upon squids or Patagonian toothfish (Reisinger et al. 2015). Under this assumption, depredation may therefore have a limited impact on the toothfish stocks but it nonetheless suggests that fishermen and odontocetes are clearly in competition for the same resource.

The dead sperm whale found entangled in the gear and reported here highlights the potential risk of bycatch. This incident is the fifth of its kind reported at Crozet between 2007 and 2018, which represents a bycatch rate of 0.04%

individual per longline over that period. Among these five bycatch events, three resulted in the death of a sperm whale, which represents 2.6% of the 114 known individuals of the Crozet population (Labadie et al. 2018). While this proportion is low, it still may significantly impacts this low fecundity, long-lived marine mammal (Whitehead 2009). In addition, the increase of sperm whale bycatch rate in recent years (4 of the 5 reported events occurred in the past 3 years) raises concern about a potentially increased competition between the fishing activity and the local whale populations, which may be due to a greater dependency to depredation and/or a depletion of the toothfish stock. Although the easy-to-get food provided by longlines may complement an individual's energy intake and improve reproduction (Tixier et al. 2015b, 2017), seafloor depredation may pose serious threats to odontocete populations by an increase in entanglement risk.

Previous efforts to minimize odontocetes depredation on demersal longline fisheries have primarily relied on the assumption that fish were removed from hooks only during hauling of longlines (Gilman et al. 2006; Werner et al. 2015). However, if both killer and sperm whales depredate fish on the seafloor as suggested by the present study, efforts to develop new mitigation techniques should be reorientated to the development of deterrence/protection systems of the longline/hooks throughout the whole soaking and hauling periods. Until now, solutions have mostly been targeted at hauling operations where it might be easier to apply systems to protect the caught fish, such as acoustic deterrent devices to switch on while hauling longline, *e.g.* the 'OrcaSaver' system (Tixier et al. 2015a), or floating net sleeves sliding down over individual caught fish when the longline is hauled to protect it from depredating whales, *e.g.* the 'Cachalotera' (Moreno et al. 2008). Another example is the SAGO, a catching pod going down the longline to collect the fish during hauling (Arangio 2012). However, these mitigation solutions may be costly and difficult to implement if they require changing fishing gear, or they may be efficient only for a while before odontocetes understand how to bypass these devices (Tixier et al. 2015a). Rather, our results suggest changing the fishing system with a global protection of the targeted fish, such as fishing pots, may be needed. However, new fishing methods may not be as efficient as the conventional fishery. For instance, in Alaska, pot fisheries have been approved and seem to be effective in preventing sperm whale depredation, but they are more expensive compared to conventional longlines (Sullivan 2015; Peterson and Hanselman 2017). The same conclusion has been drawn after a preliminary trial performed as part of the ORCASAV program in 2010 around Crozet Archipelago (captains' communications, personal observations and see Bavouzet et al. 2011; Gasco 2013).

Further investigations should examine whether the occurrence of sea-floor depredation is negligible compared to depredation during hauling. Such quantification would allow for the extent to which depredation rates are underestimated to be assessed and this information would help in determining whether efforts should be put to develop mitigation devices that protect the hooks during hauling only or during the whole fishing process to reduce the economic losses caused by depredation. This study provided preliminary insights to this aspect by suggesting that seafloor depredation might occur more sporadically for killer whales than for sperm whales. With three interaction events recorded for sperm whales over a low coverage of the fishing effort by accelerometers ($\sim$ 0.02% of hooks set by fishermen), we might assume that depredation on longlines on the seafloor during soaking may be relatively frequent for that species. Increasing the bio-logging effort on individuals with longer logger deployment might bring more cues on the occurrence of this behaviour. Alternatively, the use of passive acoustic monitoring may help quantifying depredation at seafloor, since killer whales and sperm whales are vocal animals and use echolocation to forage (Norris 1968; Barrett-Lennard et al. 1996; Madsen et al. 2002; Miller et al. 2004; Watwood et al. 2006; Zimmer 2011). Thus, the clicks can be used as an acoustic proxy of the depredation behaviour, which can help to assess the depredation rates during interactions between soaking and hauling (Thode et al. 2014).

CONCLUSION

Using bio-logging technology on both odontocetes and demersal longlines, this study brought new behavioural insights into sperm whale and killer whale depredation behaviour on demersal longlines. Depredation was confirmed during hauling phases from the observations of killer whales diving behaviour around the fishing gear in the water column during that phase as described at South Georgia (Towers et al. 2019). More importantly, although the capabilities of sperm whales to interact with the longline on the seafloor has been previously suggested (Janc et al. 2018) our results confirm that sperm whales do, and that killer whales very likely also, depredate on longlines while they are soaking on the seafloor. Although seafloor depredation still needs to be accurately quantified, we have demonstrated the occurrence of this behaviour which has major implications both for past depredation assessment and management, and for future mitigation developments.

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Appendix 4

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SCIENTIFIC REPORTS

OPEN

Commercial fishing patterns influence odontocete whale-longline interactions in the Southern Ocean

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The emergence of longline fishing around the world has been concomitant with an increase in depredation-interactions by odontocete whales (removal of fish caught on hooks), resulting in substantial socio-economic and ecological impacts. The extent, trends and underlying mechanisms driving these interactions remain poorly known. Using long-term (2003–2017) datasets from seven major Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries, this study assessed the levels and inter-annual trends of sperm whale (*Physeter macrocephalus*) and/or killer whale (*Orcinus orca*) interactions as proportions of fishing time (days) and fishing area (spatial cells). The role of fishing patterns in explaining between-fisheries variations of probabilities of odontocete interactions was investigated. While interaction levels remained globally stable since the early 2000s, they varied greatly between fisheries from 0 to >50% of the fishing days and area. Interaction probabilities were influenced by the seasonal concentration of fishing effort, size of fishing areas, density of vessels, their mobility and the depth at which they operated. The results suggest that between-fisheries variations of interaction probabilities are largely explained by the extent to which vessels provide whales with opportunities for interactions. Determining the natural distribution of whales will, therefore, allow fishers to implement better strategies of spatio-temporal avoidance of depredation.

Over the last 60 years, the world's commercial fisheries have undergone substantial changes in distribution, intensity, regulations and technology[1]. Fishing techniques have evolved towards greater efficiency but declines in catch per unit effort, paired with environmental impacts, have led some fisheries to increase target selectivity in their technological development. A number of trawling and gillnetting fisheries have progressively switched to longlining as a more selective fishing technique[2–4]. However, the emergence of longline fishing throughout the world oceans is concomitant with increasing reports of depredation interactions by marine top-predators, primarily odontocete (toothed) whales[5–10], with fishing vessels.

Depredation interactions, hereafter termed interactions, are a form of human-wildlife conflict that occurs when wild species consume a resource caught or raised/grown by humans. Here, odontocetes directly remove

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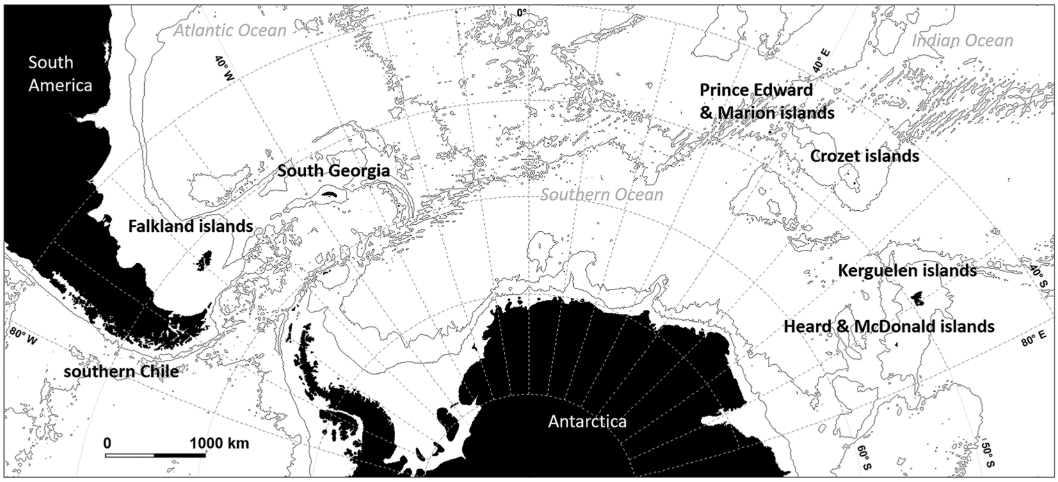

Figure 1. Location of areas where the seven commercial Patagonian toothfish demersal fisheries used in the study operate in the Southern Ocean.

fish from hooks on longlines, which results in a combination of socio-economic and conservation impacts. Socio-economic impacts include financial losses and increased fishing time for humans. Conservation impacts for the depredated fish include inaccurate stock assessments due to difficulties in estimating the amount of fish taken by odontocetes. For the depredating species, conservation impacts include negative effects due to increased risks of injury caused by fishing gear or lethal responses from fishers, increased dependency to depredation and alteration of natural energy intake balances, and positive effects from artificial food provisioning[8,10–20].

While odontocete interactions have been increasingly reported over the past decade, it is unclear whether the issue is actually increasing in frequency and intensity[10]. In addition, the mechanisms leading whales to change from natural foraging behaviours to depredation are poorly understood. This change may be driven by two processes, occurring either separately or together. Firstly, depredation may be a purely opportunistic behaviour simply resulting from the spatio-temporal overlap of fishing operations with the natural distribution of whales and their normal prey. Secondly, depredation may be an active behaviour occurring when whales modify their natural distribution by actively searching for fishing vessels or by following them over great distances[21].

Whether interactions result from opportunistic or active behaviour, their occurrence may be highly dependent upon the extent to which fishing vessels provide odontocetes with opportunities to depredate, and therefore the spatio-temporal patterns of fishing operations. The present study used this hypothesis to investigate the influence of fishing patterns of different commercial fisheries in the Southern Ocean on the levels of interaction between fishing vessels and two odontocete species: killer whales (*Orcinus orca*); and sperm whales (*Physeter macrocephalus*). These commercial fisheries operating in the waters of southern Chile, and around the Falklands, South Georgia, Prince Edward and Marion islands (hereafter "PEMI"), Crozet islands, Kerguelen islands, and Heard and MacDonald islands (hereafter "HIMI") all use demersal longlines to catch Patagonian toothfish (*Dissostichus eleginoides*). Patagonian toothfish longline fisheries emerged as commercial fisheries in the 1980s-2000s, replacing existing bottom-trawling fisheries, and have all been subject to killer and/or sperm whale depredation interactions since the first years following their commencement[22–29]. These fisheries have now become the primary economic activity of Southern Ocean[30,31] but greatly vary in size of fleets and fishing area, length of fishing seasons, quotas and longline fishing system. For instance, fisheries operating in Chile, the Falklands and PEMI predominantly use the trotline system (longlines with clusters of hooks) equipped with "cachalotera", a fish protection device developed to reduce odontocete depredation and seabird mortality[32], whereas the other fisheries use the autoline system (weighted longlines with individual hooks to reduce seabird mortality). Most fisheries also experienced substantial Illegal Unreported and Unregulated (IUU) fishing in the 1980s and 1990s, resulting in an over-harvest of local fish stocks and impacts on seabird and whale populations interacting with illegal vessels[30,33–39].

Depredation by killer whales and sperm whales represent a major challenge for the economic viability of the toothfish fisheries, for the assessment of fish stocks and their management, and for the conservation of whale populations in the Southern Ocean[29]. Determining the role of fishing patterns in explaining variations in the level of whale interaction with vessels would bring important insights for fisheries to minimize depredation by adjusting their spacio-temporal fishing patterns. Therefore, the aims of this study were to: i) assess the level and annual trends of whale-fishing vessel interaction, both locally and globally in the Southern Ocean; and ii) examine the effect of variations in spatio-temporal fishing patterns on observed interaction levels.

Results

Spatial and temporal variations in interaction levels.

Data from a total of 97,688 longline sets hauled in the seven study areas/fisheries (southern Chile, the Falklands, South Georgia, PEMI, Crozet, Kerguelen, HIMI, Fig. 1), were available for this study. Confirmed depredation interactions by killer whales occurred during hauling of 8,271 sets (8.5%) and 30,875 sets (31.6%) for sperm whales. The mean level of interactions per vessel per year varied between the seven fisheries for both sperm whales and killer whales. *Pr(days)* and *Pr(area)* were the highest

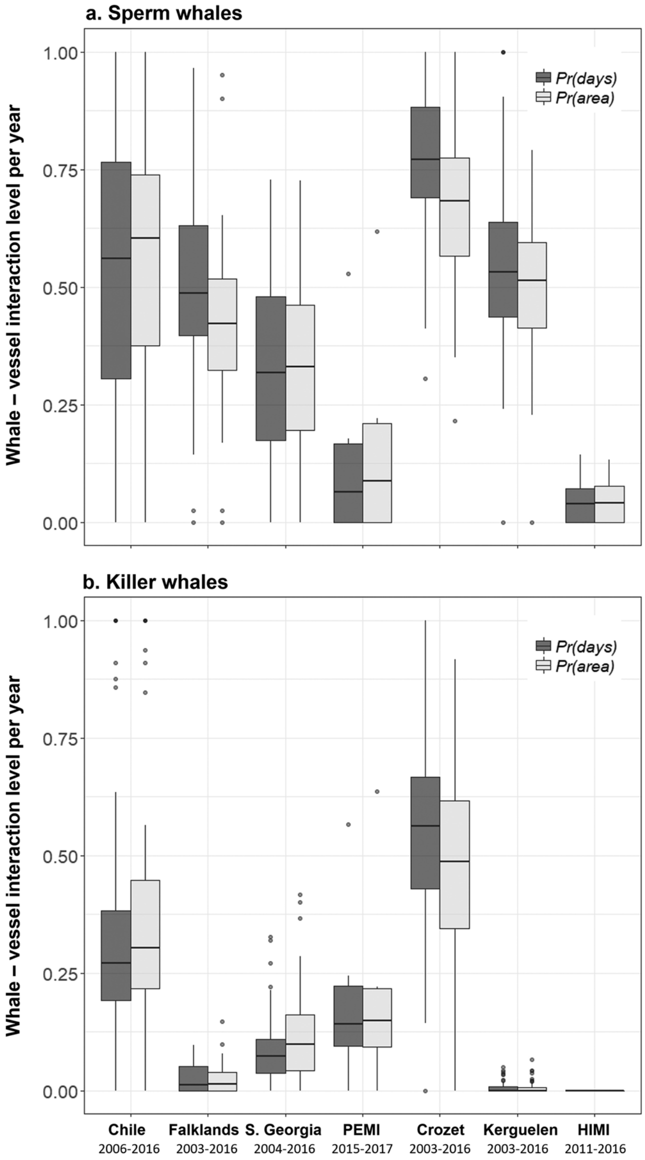

Figure 2. Between-fisheries variations of whale-vessel interaction levels in the Southern Ocean. Boxplots were calculated from *Pr(days)* and *Pr(area)* observed values per vessel per year in fisheries for (**a**) sperm whales and (**b**) killer whales.

for vessels that operated in Crozet, for both sperm whales (0.77 ± 0.02 of fishing days, 0.68 ± 0.02 of the fishing area with depredation, n = 96 vessels per year, Fig. 2a) and killer whales (0.55 ± 0.02 of fishing days, 0.49 ± 0.02 of the fishing area with interactions per vessel per year, n = 96 vessels per year, Fig. 2b). HIMI was the only fishery where killer whale interactions were never recorded. Vessels that operated in HIMI also had the lowest mean *Pr(days)* and *Pr(area)* for sperm whales (0.04 ± 0.01 of fishing days, 0.05 ± 0.01 of the fishing area, n = 20 vessels per year, Fig. 2).

At the vessel level, significant decreases of *Pr(days)* over time were detected in Chile, Crozet and Kerguelen for sperm whales ($t = -3.51$, $P < 0.01$; $t = -2.07$, $P = 0.04$; $t = -2.79$, $P < 0.01$ for the three fisheries, respectively, Table S1a; Fig. 3a). However, *Pr(days)* for sperm whales significantly increased in the Falklands ($t = 2.70$, $P = 0.01$), with 0.43 ± 0.12 of the fishing days per vessel in 2003 ($n = 6$ vessels) to 0.59 ($n = 1$ vessel) in 2016 (Fig. 3a). *Pr(days)* for killer whales decreased significantly in Chile ($t = -2.31$, $P = 0.02$) but increased in South Georgia ($t = 2.88$, $P < 0.01$, Table S1b; Fig. 3b). In Chile, *Pr(days)* varied from 0.98 ± 0.02 of the fishing days per vessel with sperm whale interactions in 2006 ($n = 4$ vessels) to 0.22 ± 0.06 ($n = 5$ vessels) in 2016 (Fig. 3a), and from 0.60 ± 0.19 in 2006 ($n = 4$ vessels) to 0.20 ± 0.06 in 2016 ($n = 5$ vessels) for killer whales (Fig. 3b). At the fleet level, *Pr(days)* decreased in South Georgia ($t = -3.23$, $P < 0.05$) and increased in HIMI ($t = 2.88$, $P = 0.04$) for sperm whales (Table S1a; Fig. 3a). In HIMI, *Pr(days)* varied from 0.05 of the fishing days in 2011 to 0.17 in 2016 (Fig. 3a). No trend in *Pr(days)* was detected at the fleet level for killer whales. No general trends were detected at either the vessel or the fleet level when using data from all fisheries combined (Table S1a,b).

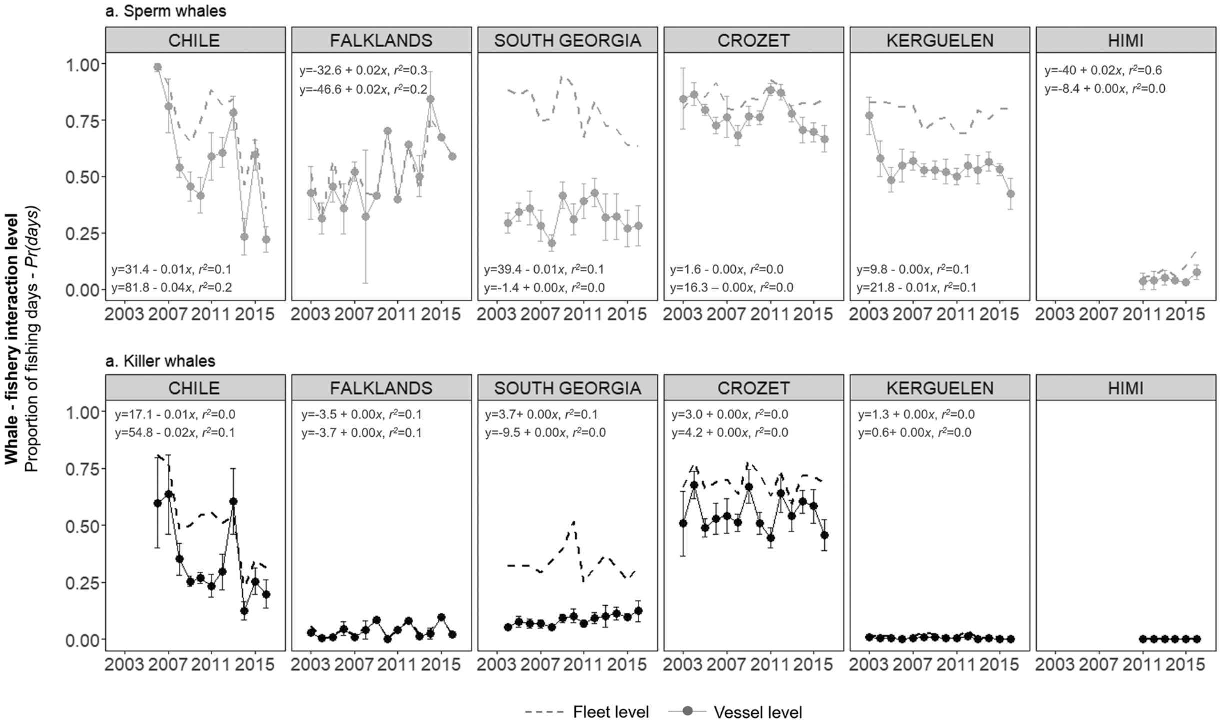

Figure 3. Observed annual variations of (**a**) sperm whale and (**b**) killer whale interaction levels with fisheries. Interaction levels (*Pr(days)*) were calculated as a proportion of fishing days during which at least one interaction was recorded out or all fishing days in a year, at the vessel level (mean ± SE per vessel per year, points and solid lines) and a the fleet level (dashed lines). Equations and r^2 values of the linear regressions conducted at the fleet level (upper line) and at the vessel level (lower line) are also provided for each plot.

Fisheries could be categorized into two groups based on the slope ($\hat{\beta}_1$) of the linear correlation between the spatial spread of fishing operations and the cumulative proportion of the full fishing area where interactions occurred during the study (Fig. 4). The spatial spread of sperm whale interactions increased at a rate of $\hat{\beta}_1 > 0.5$ with the spatial spread of fishing operation in all fisheries but HIMI ($\hat{\beta}_1 = 0.1$). For killer whales, the spatial spread of interactions correlated with that of fishing operations at a rate of $\hat{\beta}_1 > 0.5$ in Chile, South Georgia and Crozet and at a rate $\hat{\beta}_1 < 0.5$ in the Falklands and Kerguelen (Fig. 4).

Influence of fishing patterns on interaction probabilities. Models best fitting the level of sperm whale interactions, at both the vessel and the fleet levels, included all predictors including the interaction between fishery and mobility (Data S1, Table 1, Table S2.1 & S2.2). These models indicated that *Pr(days)* of sperm whales decreased with increasing size of the fishing area, proportion of effort in winter and depth of sets, and decreasing mobility of vessels and proportion of sets using trotlines equipped with cachalotera (Table 1). The density of vessels in fisheries decreased *Pr(days)* at the vessel level (GLM P = 0.04) but increased *Pr(days)* at the fleet level (GLM P < 0.01, Table 1).

For killer whales at the vessel level, *Pr(days)* was best explained by the model including the fishery, the size of fishing areas, the density of vessels, their mobility, the depth of sets and an interaction between fishery and mobility (Data S2, Table 2, Table S2.3). The model without the interaction term was within 2 AIC of the optimal model (Table S2.3), however, trends in the common covariates were identical to the optimal model so it is not further discussed. At the vessel level, *Pr(days)* decreased with increasing size of fishing areas (GLM P < 0.01), increasing mobility of vessels (GLM P < 0.01) and increasing density of vessels (GLM P < 0.01, Table 2). At the fleet level for *Pr(days)* six models were within 2 AIC of the optimal model (Data S2, Table S2.4) which included the fishery, the density of vessels and the depth of sets and mobility (Data S2, Table 2, Table S2.4). All models within 2 AIC of the optimal model included fishery and the depth of sets, while the density of vessels was significant in five of the six models. Mobility of vessels was included in one model other than the optimal model, while the size of the fishing area, proportion of effort in winter and proportion of cachalotera errors were significant in one model each. For all models at the vessel level within 2 AIC of the optimal model, *Pr(days)* increased with the density and mobility of vessels and decreased with the depth of sets (Data S2, Table 2, Table S2.4).

Discussion

The present study demonstrated large variations in the level of killer whale and sperm whale interactions with Patagonian toothfish fishing vessels between commercial fisheries in the Southern Ocean, and indicated that some of this variation can be explained by the fishing patterns of vessels. These findings suggest that the level of whale-fisheries interactions may primarily depend upon the extent to which fisheries provide whales with

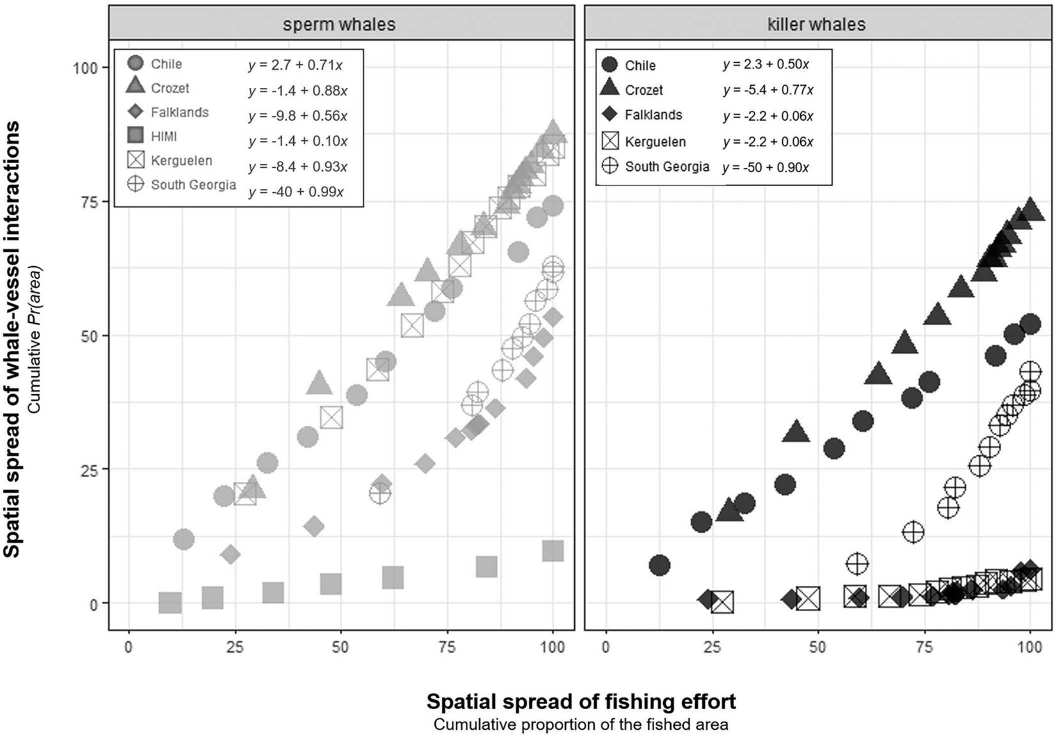

Figure 4. Relationship between the spatial spread of fishing effort and the spatial spread of whale-vessel interactions in fisheries (*Pr(area)*). The spatial spread of fishing effort and whale vessel interactions were calculated as the cumulative proportion of 0.1° × 0.1° cells over the full fished area in which fishing occurred and interactions were recorded, respectively, per year per fishery for sperm whales (grey) and killer whales (black). Linear regression equations are shown for each species and fishery.

opportunities to depredate in space and time. However, the present study also demonstrated that some of the variability around whale-vessel interaction levels was attributed to as yet unknown area-specific factors that are further discussed here as potential directions for future research on odontocete depredation in the Southern Ocean.

Over the last 14 years, Patagonian toothfish fisheries operating in Chile, the Falklands, South Georgia, PEMI, Crozet, Kerguelen and HIMI all experienced sperm whale interactions, and six of them experienced killer whale interactions. In most fisheries, the level of interaction has remained stable. Interactions, which were reported as soon as demersal longlining started in the Southern Ocean in the 1980s and 1990s, are now an established behaviour for the majority of local whale populations. The exception is sperm whale interactions at HIMI which were first reported in 2010 despite longlining for Patagonian toothfish commencing in 2003[40].

Increased fishing effort by vessels in winter coincided with decreased sperm whale interaction levels. This decrease is likely explained by seasonal shifts in the local abundance of mature male sperm whales, possibly driven by ecological and/or reproduction factors, with smaller numbers of individuals found at high latitudes in winter months[41–45]. As a result, lower densities of sperm whales in winter months may contribute to interaction levels being the lowest with vessels at HIMI and South Georgia, which are both primarily winter fisheries. As the fishing season at HIMI has extended in recent years, vessels concentrating increasing proportions of their effort in spring may also explain the emergence of sperm whale interactions in this fishery since 2010[40].

Larger fishing areas were associated with decreased levels of both killer and sperm whales interaction with vessels. A larger fishing area is likely to decrease the probability of vessels being detected by whales[46–48], to decrease the predictability of the fishing activity[29,49] and to increase the effectiveness of move-on strategies which have been implemented to avoid/escape depredation[27,49,50]. However, these effects may be also driven by the density of vessels operating simultaneously in fishing areas. At the fleet level, greater densities of vessels were associated with higher interaction levels (present study). Increased number of vessels combined with a small fishing area may increase the detectability of fleets as a whole. This combination is, therefore, likely to contribute to the high interaction levels observed at Crozet, which, with 7 vessels operating in an area of 17,900 km^2, hosts one of the largest fleets and one of the smallest fishing areas of the Southern Ocean.

Interestingly, increased density of vessels in fishing areas was associated with decreased sperm whale and killer whale interactions at the individual vessel level. This effect may result from a limited number of depredating specialist individuals which, once they have found a vessel, may keep interacting with its fishing gear until this vessel leaves and travels over distances sufficiently large to outrun the whales. Consequently, increased numbers of vessels operating simultaneously in the same region may generate a "dilution" effect decreasing the level of whale interaction per vessel[50].

Predictors	*Vessel level*			*Fleet level*		
	Est. [95% CI]	**z**	**P**	**Est. [95% CI]**	**z**	**P**
Fishery						
Chile	0.59 [0.55–0.63]	3.99	<0.01	0.99 [0.98–0.99]	12.57	<0.01
Crozet	0.66 [0.61–0.71]	2.56	0.01	0.78 [0.61–0.89]	−7.74	<0.01
Falklands	0.39 [0.35–0.43]	−9.35	<0.01	0.76 [0.59–0.87]	−8.85	<0.01
HIMI	0.06 [0.05–0.08]	−19.77	<0.01	0.12 [0.06–0.24]	−16.30	<0.01
Kerguelen	0.67 [0.61–0.71]	2.75	0.01	0.82 [0.71–0.90]	−8.85	<0.01
PEMI	0.04 [0.03–0.07]	−13.36	<0.01	0.14 [0–0.85]	−3.54	<0.01
South Georgia	0.36 [0.31–0.42]	−7.79	<0.01	0.63 [0.41–0.80]	−9.11	<0.01
Total size of fishing area	0.48 [0.46–0.50]	−11.50	<0.01	0.99 [0.98–0.99]	−2.65	0.01
Density of vessels	0.57 [0.56–0.59]	−2.09	0.04	0.99 [0.99–0.99]	3.75	<0.01
Mobility of vessels	0.70 [0.67–0.72]	8.19	<0.01	1.00 [1.00–1.00]	9.85	<0.01
Depth	0.58 [0.57–0.59]	−2.13	0.03	0.99 [0.99–0.99]	−5.29	<0.01
Proportion of effort in winter	0.56 [0.54–0.57]	−5.34	<0.01	0.99[0.99–0.99]	−3.30	<0.01
Proportion of effort using trotlines and cachalotera	0.62 [0.61–0.62]	5.52	0.00	0.99 [0.99–0.99]	1.95	0.05
Fishery* Mobility of vessels						
Crozet	0.49 [0.45–0.53]	−5.08	<0.01	0.74 [0.55–0.81]	−8.18	<0.01
Falklands	0.50 [0.46–0.55]	−4.08	<0.01	0.89 [0.79–0.94]	−6.38	<0.01
HIMI	0.57 [0.46–0.66]	−0.48	0.63	0.82 [0.70–0.90]	−8.38	<0.01
Kerguelen	0.49 [0.46–0.52]	−6.10	<0.01	0.75 [0.60–0.86]	−9.57	<0.01
PEMI	0.30 [0.20–0.42]	−4.36	<0.01	0.77 [0.14–0.99]	−2.16	0.03
South Georgia	0.49 [0.45–0.53]	−5.16	<0.01	0.84 [0.71–0.92]	−7.13	<0.01

Table 1. Parameter estimates for the optimal GLMs fitted to yearly sperm whale interaction levels with fishing vessels in fisheries through index *Pr(days)* at both the vessel and fleet level. Parameter estimates are presented as probabilities relative to the Chilean fishery which was the default fishery in all models. Covariates with interaction probabilities higher than the Chilean fishery are associated with an increase in whale interactions while those with lower with interaction probabilities are associated with a reduction in whale interactions.

Greater vessel mobility was associated with decreased interaction levels for killer whales. Increased vessel mobility may reduce interaction levels either by limiting the detectability/predictability of vessels prior to interactions and/or by working as an effective strategy to outrun depredating whales in response to the occurrence of interaction events[50–52]. However, for sperm whales, greater mobility of vessels was associated with higher interaction levels. Firstly, this result may be due to an ineffectiveness of vessels of avoiding interactions by being mobile because of naturally large densities of sperm whales overlapping with areas of fishing operations. Varying densities of sperm whales across areas used by different fisheries may also explain the significance of the fishery-mobility interaction terms in models. For instance, vessels were more mobile at Crozet and Kerguelen than in any of the other fisheries, but these two areas were recently described as hosting densities of depredating sperm whales substantially larger than densities of killer whales[17,53]. In such areas, the probabilities of interaction with any sperm whale may be high across large proportions of fishing areas and vessels may, therefore, experience high levels of interaction regardless of their mobility. Secondly, this result may also be explained by sperm whales actively following vessels, and vessels not moving on distance great enough to outrun these whales. In a recent study, Janc *et al.*[51] showed a drop in the probability of sperm whale interaction when vessels travelled over a range of 40 to 60 km between sets. While this distance is lower than the distance estimated for killer whale (100 km[50]), it is likely that vessels are less incline to implement costly strategies of avoidance of sperm whales given the lower impact of that species on catch rates compared to that of killer whales[15,27].

Interestingly, the use of trotline equipped with cachalotera, a fishing system designed to prevent whales from accessing fish caught on longlines[32], did not significantly influence the level of killer whale-vessel interactions, and was associated with higher levels of sperm whale-vessel interactions. Therefore, it is unlikely that the significant decrease in both sperm and killer whale interaction levels observed in Chile since 2006, when vessels switched from the autoline to the trotline and the cachalotera system[23,32], may be attributed to that change in fishing system. While cachaloteras may increase the difficulty for whales to remove fish from hooks[54,55], this study suggests that whales still gain benefit from feeding off longlines equipped with such a system. In addition, if cachaloteras are effective means to lower depredation and maintain high catch rates, vessels may be more likely to stay and keep fishing despite the presence of depredating sperm whales, further increasing interactions with this species. Further research is therefore needed to identify the causes of the decrease in killer and sperm whale interactions in the Chilean fishery. As this fishery has undergone substantial decreases in both quotas and fleet size[56], it is possible that lower numbers of vessels paired with the implementation of fishing strategies being more effective in avoiding depredation have contributed to this decrease.

Part of the variability in interaction rates across fisheries was due to unexplained area-specific factors. The importance of such local factors was further emphasized by different levels of correlation between the spatial spread of interactions and the spatial spread of fishing operations between fisheries. Spatial variations in the

	Vessel level			*Fleet level*		
Predictors	**Est. [95% CI]**	**z**	**P**	**Est. [95% CI]**	**z**	**P**
Fishery						
Chile	0.31 [0.28–0.35]	−9.37	<0.01	0.66 [0.61–0.70]	6.37	<0.01
Crozet	0.37 [0.32–0.42]	2.15	0.03	0.63 [0.56–0.70]	−0.78	0.44
Falklands	0.02 [0.01–0.02]	−23.25	<0.01	0.05 [0.04–0.06]	−25.23	<0.01
HIMI	0.00 [0.00–1.00]	−0.04	0.97	0.00 [0.00–1.00]	−0.02	0.98
Kerguelen	0.01 [0.01–0.02]	−16.46	<0.01	0.01 [0.01–0.02]	−24.98	<0.01
PEMI	0.09 [0.07–0.12]	−8.54	<0.01	0.23 [0.18–0.29]	−12.03	<0.01
South Georgia	0.08 [0.07–0.10]	−14.19	<0.01	0.28 [0.23–0.33]	−11.51	<0.01
Total size of fishing area	0.17 [0.15–0.19]	−11.43	<0.01	NS		
Density of vessels	0.26 [0.24–0.27]	−6.78	<0.01	0.68 [0.66–0.70]	2.51	0.01
Mobility of vessels	0.28 [0.26–0.30]	−2.70	0.01	NS		
Depth	0.26 [0.25–0.27]	−8.51	<0.01	0.58 [0.56–0.61]	−5.79	<0.01
Proportion of effort in winter						
Proportion of effort using trotlines and cachalotera	NS			NS		
Fishery * Mobility of vessels						
Crozet	0.33 [0.29–0.36]	0.72	0.47	NS		
Falklands	0.42 [0.35–0.49]	2.90	<0.01			
HIMI	0.36 [0.00–1.00]	0.00	1.00			
Kerguelen	0.40 [0.31–0.51]	1.79	0.07			
PEMI	0.36 [0.27–0.45]	0.94	0.35			
South Georgia	0.36 [0.32–0.41]	2.18	0.03			

Table 2. Parameter estimates for the optimal GLMs fitted to yearly killer whale interaction levels with fishing vessels in fisheries through index *Pr(days)* at both the vessel and fleet level. Parameter estimates are presented as probabilities relative to the Chilean fishery which was the default fishery in all models. Covariates with interaction probabilities higher than the Chilean fishery are associated with an increase in whale interactions while those with lower with interaction probabilities are associated with a reduction in whale interactions.

natural presence and density of whales in the Southern Ocean are likely to contribute to these differences. The depth at which longlines were set on the seafloor had a negative influence on the levels of both killer and sperm whale interactions with vessels, suggesting that depredating individuals in the Southern Ocean may be generally naturally distributed on the shallowest part of the bathymetric range used by fishing vessels. However, the natural distribution of the depredating whales is likely to be influenced by a number of other habitat drivers that have characteristics which may differ between areas where fisheries operate. For instance, the distribution of mature male sperm whales at high latitudes was found to be highly correlated with oceanographic variables, such as frontal zones, bathymetric slope and primary productivity likely to drive the abundance and availability of their natural prey items[42,44,45]. These prey items may include Patagonian toothfish but also cephalopods, a resource with a distribution and abundance that is highly influenced by oceanographic processes. The variability of these processes across the Southern Ocean[57] may, therefore, greatly influence the degree of overlap between sperm whales and fishing operations.

Among other unexplained area-specific factors, local ecological specializations may also influence the natural distribution patterns and movements and, therefore, the degree of overlap of whales with fishing operations. Such specializations have been extensively described across killer whale populations, including among those involved in interactions in the Southern Ocean[58,59]. For instance, killer whales interacting with fisheries are all fish specialists or generalist foragers whereas individuals feeding exclusively on marine mammals have never been observed undertaking this behaviour[14,60–62].

In addition, the probability of whales to switch from natural foraging to depredation may also depend upon the level of experience to this behaviour and, therefore, on the history of the fisheries and the number of years whales have been exposed to fishing operations[63]. Depredation is assumed to be a learnt artificial behaviour and likely transmitted across individuals of populations through social pathways[63]. As such, and paired with natural individual heterogeneity in foraging behaviours, the experience of depredating whales, their propensity to find/follow vessels and to efficiently remove fish from longlines may vary between fisheries.

Finally, the influence of the fishing vessel itself on the occurrence of depredation interactions was not examined in this study and would require a dedicated investigation. From previous studies, odontocetes were found to detect fishing vessels through specific acoustic cues produced by the engine, such as cavitation noise generated during the hauling phase of longlines[46,47]. While Patagonian toothfish commercial fishing vessels operating in the Southern Ocean are similar in size and design to those in previous studies, there may be variation in the type and the level of acoustic signals vessels produce during fishing operations. As these signals may be intrinsic to the vessel itself (type of engine and propulsion, features of the hull), and/or determined by the way fishers operate the engine, further studies should examine whether variation in the acoustic detectability of vessels for whales may also contribute to differences of depredation levels reported between fishing areas of the Southern Ocean.

In summary, sperm whale and killer whale interaction with Patagonian toothfish fishing vessels is a widespread and established issue in the Southern Ocean. The drivers of these interactions include the spatio-temporal patterns of fishing operations and the extent to which these operations give opportunities for whales to feed on fish caught on fishing gear. Changing the simple operational aspects of fishing could, therefore, mitigate the issue. However, further research is needed to identify the factors driving whale habitat selection, distribution, movements and the mechanisms leading these whales to switch from natural foraging to depredation interactions. These drivers, which depend upon the ecology of local whale populations, could be used to better predict the occurrence of interactions and may, therefore, be used to implement effective strategies of avoidance in the future.

Methods

Data collection and standardisation. Fishing and whale interaction data from the seven study fisheries were collected by fishery observers and/or crews over periods ranging from 3 to 14 years. These fisheries are all fully controlled by local and/or international (Commission for the Conservation of Antarctic Marine Living Resources – "CCAMLR") management authorities and all fishing operations are monitored. Data from Chile and the Falklands, regions which are not part of the CCAMLR Convention Area, were collected by fishery observers following protocols based on those used by CCAMLR observers in the other fisheries of the study. Data from all vessels legally operating in these fisheries and all fishing trips of these vessels were therefore accessed for the study. In all fisheries, the base unit was the longline set *i.e.* a mainline bearing series of hooks (autoline) or clusters of hooks (trotline) with, at each end, one anchor at the bottom connected to a buoy at the surface by a downline. For each longline set, fishery observers and/or crews collected the same data on the date and time, as well as GPS coordinates, at setting (*i.e.* deployed at sea) and at hauling (*i.e.* retrieved and landed on-board), in the same way in all seven fisheries.

The occurrence of whale depredation interactions with longline sets was recorded during hauling operations by visual cues. An interaction was confirmed when one of these two species, or the two species co-occurring with a typical depredation behaviour were sighted within a 500 m range from the vessel. During depredation, individuals made repeated dives towards the line being hauled and throughout the hauling process, they were usually surrounded by birds when surfacing after long dives, and slicks of fish oil were visible at the surface. When all these cues were observed, true depredation interaction events (recorded as 1) were monitored in a standardised way across all fisheries. However, only the Crozet, Kerguelen and South Georgia fishery observers distinguished between longline sets with confirmed non-occurrence of depredation (recorded as 0) and sets with lacking information due to insufficient or impossible monitoring effort (recorded as "N/A") caused by poor weather (e.g. fog), sea or light conditions. As Chile, Falklands and HIMI recorded zeros for sets with either a true non-occurrence of depredation and/or a set for which the occurrence of depredation was unknown, we consider all the Crozet, Kerguelen and South Georgia sets with N/A's as zeros for the sake of between-fisheries standardisation needed for this study. As a result, the estimates of depredation should to be considered as minimum estimates.

Differences in spatial and temporal frequencies of killer whale and sperm whale interactions were estimated using two indices, which were both calculated annually for each fishery per vessel (one value for each vessel that operated in a given fishery during a given year), and per fleet (one value for all data collected in a given fishery during a given year regardless of the vessel identity). Firstly, we calculated the proportion of fishing days (days of hauling operations only) with a minimum of one depredated longline set during the day out of all fishing days per year (*Pr(days)*). Secondly, we calculated a proportion of the fishing area for which depredation interactions occurred as the number of 0.1° latitude × 0.1° longitude cells in which a minimum of one longline set was depredated out of the total number of cells in which fishing occurred (*Pr(area)*).

Statistical analyses. Annual trends of whale-fishery interaction levels over the study periods were examined using linear regressions. PEMI was excluded from this analysis due to the limited time series ($n = 3$ years of data) available for that fishery. Trends were tested on *Pr(days)* calculated per vessel (several values per year depending on the number of vessels) or per fleet (a single value per year), separately for killer whales and sperm whales, in each fishery and across all fisheries. In addition, a regression analysis was conducted to investigate the inter-annual changes in *Pr(area)* in relation to inter-annual changes in the spatial spread of the fishing effort. For this analysis *Pr(area)* was calculated annually as a cumulative number of new 0.1° × 0.1° cells in which interactions occurred every year, out of the total number of 0.1° × 0.1° cells fished during the respective study periods in the respective fisheries. The spatial spread of fishing effort was calculated annually as the cumulative number of new 0.1° × 0.1° cells in which fishing occurred every year, out of the total number of 0.1° × 0.1° cells fished during the respective study periods in the respective fisheries.

The influence of fishing operations on *Pr(days)* was investigated using Generalised Linear Models (GLMs). GLMs were developed for each species at both the vessel (using individual *Pr(days)* values per vessel per year per fishery) and the fleet (using individual *Pr(days)* values per year per fishery) levels. As fisheries differed in fleet size and study periods, the number of *Pr(days)* values per vessel per year varied between fisheries and ranged from 1.5 ± 0.3 vessels per year ($n = 5$ values) in PEMI to 8.4 ± 0.8 ($n = 109$ values at South Georgia, Table 3).

A series of binomial GLMs with logit link functions were fitted using the function glm in R 3.3.0[59] to the proportion of total fishing days for each vessel, in each year (Table 3) where depredation was observed. To account for variability in the number of days each vessel/fleet fished the total number of days fished each year was used as the model weights (i.e. equivalent to using the *weights* argument in the *glm* function in R) for each vessel/fleet. The fishery was included in models as a categorical variable with seven levels for each of the studied fisheries, with Chile being the fishery compared to each one of the others. The other predictors included were all continuous and were calculated as annual values, either at the vessel or at the fleet level, as follows i) the spatial spread of fishing effort calculated as the total number of 0.1° × 0.1° spatial cells in which at least one set was hauled by vessels; ii) the mean density of vessels per fishing day, calculated as the mean number of different vessels operating

Term	Unit	Chile	Falklands	South Georgia	PEMI	Crozet	Kerguelen	HIMI
	vessels per year	**N_{total} = 60**	**29**	**109**	**5**	**96**	**102**	**20**
		mean = 5.5 ± 0.5	**2.1 ± 0.4**	**8.4 ± 0.8**	**1.5 ± 0.3**	**6.9 ± 0.2**	**7.3 ± 0.2**	**3.3 ± 0.6**
		range = [3–8]	**[1–6]**	**[6–16]**	**[1–2]**	**[5–8]**	**[7–9]**	**[2–6]**
Fishing effort	n days	116 ± 9	101 ± 11	75 ± 2	83 ± 19	38 ± 2	131 ± 3	128 ± 8
Spatial spread of effort	n 0.1 × 0.1° cells	308 ± 12	248 ± 15	303 ± 3	127 ± 19	205 ± 4	750 ± 10	450 ± 37
Density of vessels	n vessels/100 cells	1.04 ± 0.05	0.59 ± 0.05	2.00 ± 0.04	1.04 ± 0.2	1.19 ± 0.05	0.06 ± 0.02	0.06 ± 0.02
Seasonal spread of effort	proportion of days in winter	0.03 ± 0.02	0.24 ± 0.04	0.63 ± 0.02	0.31 ± 0.09	0.16 ± 0.02	0.10 ± 0.01	0.47 ± 0.05
Mobility of vessels	n cells/day	0.87 ± 0.03	1.2 ± 0.05	0.85 ± 0.02	1.07 ± 0.12	1.55 ± 0.03	1.43 ± 0.03	1.02 ± 0.04
Depth of sets	meters	1580 ± 20	1341 ± 25	1248 ± 14	1339 ± 43	1099 ± 19	1186 ± 14	1311 ± 51
Fishing technique	proportion of sets with trotline & cachalotera	0.88 ± 0.04	0.48 ± 0.09	0 ± 0	0.52 ± 0.17	0 ± 0	0 ± 0	0 ± 0

Table 3. Summary of terms used as fishing patterns variables and considered in GLMs fitted on the level of whale-vessels interaction levels. Mean ± SE per vessel per year are here presented for each of the seven studied Patagonian toothfish fisheries of the Southern Ocean. N_{total} (total number of vessel per year values), the mean and the range of the number of vessels operating in fisheries per year are provided.

during the same day in the same fishery out of the spatial spread of fishing effort previously calculated; iii) the seasonal spread of fishing effort, measured as the proportion of fishing days during winter months (from 1 June to 31 Aug) out of all fishing days during a given year; iv) the mobility of vessels, calculated as the ratio between the spatial spread of fishing effort and the total number of fishing days during a given year; v) the mean depth at which longlines were set; and vi) the fishing system, calculated as the proportion of sets using trotlines equipped with cachalotera out of all sets (Table 3). In addition to the single predictors described above, we also tested an interaction between fishery and mobility, when both were present in the optimal model. Collinearity between continuous predictors was checked using Pearson tests and predictors were retained if $r < 0.8$ (Table S3). All continuous predictors were centred then scaled using the *scale* function in R and variable selection was conducted using stepwise forward selection of models with the lowest Akaike Information Criterion (AIC)[64]. When multiple models were within 2 AIC of the model with the lowest AIC (i.e. the optimal model) we considered all of them. The proportion of the total variance explained was quantified for each model using the pseudo r^2 statistic[65]. Model estimates are presented as probabilities with 95% confidence intervals by applying an inverse logit transformation.

Guidelines and regulations. All methods were carried out in accordance with relevant ethical guidelines and regulations of Deakin University, Australia. Data used in this manuscript were collected by national and international fishery observers under the authority of CCAMLR, Instituto de Fomento Pesquero (IFOP) and the Fisheries Department of the Falkland Islands Government.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author Contributions

P.T., P.B., G.R., K.O., M.S. and J.A. conceived the study. P.T. performed the primary analysis. P.T., P.B., G.R., K.O., D.W., MA.L., M.H., C.G., A.J., N.G., G.D., M.C.V., L.S., R.A., M.S. and J.A. were involved in developing the manuscript and P.T. took a lead role in writing.

Additional Information

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Appendix 5

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How do fishing practices influence sperm whale (*Physeter macrocephalus*) depredation on demersal longline fisheries?

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ABSTRACT

Marine mammal depredation on fisheries (animals removing fish caught on fishing gear) is a worldwide issue involving socio-economic and ecological consequences. Longline fisheries are the most impacted by odontocete (toothed whales) depredation. While technological means have provided limited efficacy in reducing depredation, this study examined the fishing practices influencing both the proportion of depredated longline sets and the amount of fish removed by whales. We used an 8-year dataset from the Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries operating in Crozet and Kerguelen Economic Exclusive Zones (EEZs) (South Indian Ocean) and GLMMs to investigate sperm whale (*Physeter macrocephalus*) depredation. Sperm whale depredation occurred on 61% of 5260 sets in Crozet and 41% of 16,902 sets in Kerguelen, and resulted in minimum estimated toothfish losses of 702 tons and 2649 tons, respectively, in the two areas. The probability of depredation decreased in winter months, increased with depth fished and decreased when vessels travelled over distances of > 60 km from fishing grounds with encountering depredation. These findings suggest the natural spatio-temporal distribution of sperm whales and their ability to follow vessels over limited ranges influence the number of captured fish removals. The amount of depredated toothfish decreased with the speed at which longline sets were hauled and increased with the soaking time of sets suggesting that whales may depredate sets during both hauling and soaking operations. Together, these observations indicate that rates of depredation may be influenced by the conditions of fishing operations and could therefore be employed to implement strategies of avoidance in all fisheries facing similar depredation impacts.

1. Introduction

Human-wildlife conflicts, which often result from competition between animals and humans over the same resources, are as old as humankind (Anand and Radhakrishna, 2017; Treves et al., 2006; Woodroffe et al., 2005). In the marine environment, the global expansion of fisheries over the last fifty years has led to the over-exploitation of many fish stocks and major changes in fishing techniques. It also has resulted to changes in food-search behavior of some predators such as marine mammals that has resulted in the emergence of direct marine predators–fisheries interactions, including depredation on fishing gears (Augé et al., 2012; Fertl, 2008; Kaschner and Pauly, 2004; Plagányi and Butterworth, 2002; Read, 2008). Depredation on fisheries is defined as the partial or total removal of captured fish from fishing equipment by marine predators (Donogue et al., 2002; Fertl, 2008; Read, 2005) and has received growing attention over the past five decades (Northridge, 1991). Marine mammals were reported as the taxa with the broadest range of depredating species. These species have been documented to depredate on a wide variety of fishing gears such as purse seines, trawls, gill nets, pots and baited longlines (Bearzi, 2002; Donogue et al., 2002; Fertl, 2008; Gales, 2003; Gilman et al., 2007; Hamer et al., 2012; Read, 2005; Werner et al., 2015).

Marine mammal depredation on fisheries often results in major socio-economic and ecological issues (Gilman et al., 2007). Economic

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issues for fisheries include both direct costs (*i.e.*, catch losses) and indirect costs (*i.e.*, additional fishing time, fuel consumption and payroll needed to complete fishing quotas, the implementation of strategies of marine mammals avoidance) (Maccarrone et al., 2014; Peterson et al., 2014). Ecological and conservation issues may include the over-exploitation of the targeted fish resources (*i.e.*, the amount of depredated fish are often not accounted for in fish stock assessments and quota allocation processes) and effects on the survival of marine mammal populations (*e.g.*, increased risks of by-catch on fishing gear; lethal responses from illegal, unreported and unregulated fishers who may perceive these animals as competitors; habituation to an artificial foraging behavior; modification of energy balance; etc.) (Baird et al., 2002; Gasco et al., 2015; Gilman et al., 2007). For instance, artificial food provisioning from fisheries may increase prey availability for depredating predators, and was shown to positively influence the survival and reproduction of individuals in various populations (Oro et al., 2004; Tixier et al., 2015a, 2017; Ward et al., 2009). Together, these ecological consequences of marine mammal depredation were recently suggested as important to consider when managing fisheries, fish stocks and marine mammal populations through ecosystem-based approaches (Boyd, 2002; Guénette et al., 2006; Morissette et al., 2012; Trites et al., 1999; Williams et al., 2011).

Longline gear is a fishing device which is made up of a horizontal line, to which are attached droppers ending in baited hooks and takes fish by hooking (Brock, 1962). Longlining progressively emerged as the most selective fishing technique for large fish species during the 1980s and 1990s (Løkkeborg and Bjordal, 1992). Unlike other techniques, this fully exposes the hooked fish in the water column, making this catch easily accessible for depredating marine mammals (Fertl, 2008). Both pelagic and demersal longlining are subject to depredation worldwide (Forney et al., 2011; Mesnick et al., 2006; Muñoz-Lechuga et al., 2016; Passadore et al., 2015; Rabearisoa et al., 2012; Roche et al., 2007; Straley et al., 2006; Visser, 2000). While the issue on depredation remains sporadic in some fisheries, it has spread and substantially increased in others, jeopardizing their sustainability (Powell and Wells, 2011; Schakner et al., 2014) and raising a critical need for solutions to minimize or suppress it (Hamer et al., 2012).

Extensive efforts have been made by fishers and ship-owners to develop technological solutions to either deter marine mammals from fishing gear or to protect the fish caught on hooks. However, most trials of such devices have showed limited efficacy (Dyb, 2006a; Hamer et al., 2012; Mooney et al., 2009; O'Connell et al., 2015; Tixier et al., 2015b). The development of fishing strategies for avoiding interactions has provided more promising insights into ways to reduce depredation levels. For instance, increased knowledge of local marine mammal populations ecology has allowed some fisheries to target the timing or areas of low marine mammal presence and, thus, lower the probability of depredation (Guinet et al., 2015; Straley et al., 2015; Tixier, 2012; Tixier et al., 2016). Other studies have focused on the behavior of fishing vessels and operational factors that can be controlled. For instance, Tixier et al. (2015b) showed that the depth at which longlines are set, longline length, the hauling speed and the distance travelled by vessels between fishing grounds can significantly influence the proportion of fishing gear depredated by killer whales (*Orcinus orca*) and the impact of this depredation on the Catch Per Unit Effort (CPUE) of the target species.

The influence of such operational factors on sperm whale (*Physeter macrocephalus*) depredation, however, has remained poorly investigated despite several reports on significant depredation in the majority of longline fisheries operated in high latitudes (Mesnick et al., 2006; Taylor et al., 2008). In both hemispheres, demersal longline fisheries are primarily depredated by adult male sperm whales whose natural foraging grounds often overlap with fishing areas (Ashford et al., 1996; Best, 1979; Mesnick et al., 2006; Whitehead, 2003). Sperm whale depredation has been reported in the North Pacific on fisheries targeting Pacific halibut (*Hippoglossus stenolepis*) and sablefish (*Anoplopoma fimbria*) (Hill et al., 1999; Peterson and Carothers, 2013; Schakner et al., 2014; Sigler et al., 2008; Straley et al., 2006), in the North Atlantic on fisheries targeting Greenland halibut (*Reinhardtius hippoglossoides*) (Dyb, 2006b) and in the Southern Ocean on fisheries targeting Patagonian toothfish (*Dissostichus eleginoides*) (Duhamel, 2003). For the latter, sperm whale depredation occurs off Chile (Hucke-Gaete et al., 2004; Moreno et al., 2008), the Falklands/Malvinas (Goetz et al., 2011; Nolan et al., 2000), South Georgia (Ashford et al., 1996; Moir Clark and Agnew, 2010; Purves et al., 2004; Söffker et al., 2015), Prince Edward Island (Kock et al., 2006; Tilney and Purves, 1999), Heard and McDonald Islands (Arangio, 2012) and Crozet and Kerguelen Islands (Ashford et al., 1996; Capdeville, 1997; Gasco et al., 2015; Roche et al., 2007; Tixier et al., 2010).

The Patagonian toothfish longline fishery operating off the Crozet and Kerguelen Islands has been reported as one of the most impacted by sperm whale depredation, with an estimated reduction of 8–12% in the toothfish CPUE between 2003 and 2013 (Gasco et al., 2015; Roche et al., 2007; Tixier et al., 2010). These estimates were recently incorporated in the Crozet and Kerguelen fish stock assessments and used to increase accuracy of quota allocation processes. This fishery, with a fleet comprised of seven commercial vessels, is highly regulated, closely monitored by onboard fishery observers at all times, and benefits from a long-term fishing dataset covering 100% of fishing operations. This fully controlled environment has proved to be particularly suitable for studies on operational factors influencing depredation by killer whales, the other major depredating species of demersal longline fisheries in high latitudes (Gasco et al., 2014; Guinet et al., 2015; Tixier et al., 2010, 2016).

Therefore, the long-term datasets from the Crozet and Kerguelen Patagonian toothfish fisheries were here used as a unique opportunity to investigate the spatio-temporal and operational factors of fishing practices influencing the level of sperm whale depredation on demersal longlining. The aims of this study were to test for the effects of these factors on (i) the proportion of fishing gear depredated by sperm whales, and (ii) the CPUE during sperm whale depredation events.

2. Material and methods

2.1. Study areas and data collection

During the study period (1 January, 2008–25 July, 2015), seven commercial fishing vessels were authorized to operate in the Crozet (between 44° and 48°S–46° and 54°W) and Kerguelen (between 45° and 52°S–63° and 75°W) Exclusive Economic Zones (EEZs). These vessels all used auto-weighted longlines that were set between two anchors at each end of the mainline, on which 375–47,250 hooks were positioned with an individual hook every 1.2 m. These hooks were automatically baited and dropped to the bottom at depths ranging from 500 to 2300 m (*i.e.*, legal depth range to avoid the capture of juvenile toothfish (Collins et al., 2010)). Fishing regulations also imposed fishers to set their lines at night to avoid seabird bycatch (Cherel et al., 1996; Weimerskirch et al., 2000). Hauling, which was allowed at any time of the day, took between 00:30–9:58 to be completed depending on the number of hooks on the longline and the hauling speed. The fishing fleet was allowed to operate all year round in the Crozet, but is closed for a 45-day period from the 1st February to mid-March in the Kerguelen EEZ to comply with seabird conservation measures (CCAMLR, 2015a, 2015b).

All data used in the study were collected by fishery observers and were provided by the Muséum d'Histoire Naturelle de Paris (MNHN – PECHEKER database (Martin and Pruvost, 2007)). The unit of this dataset was the longline set. Each set was affiliated with one captain, one vessel and one fishing trip. A fishing trip (lasting 2–3 months) was defined as the time between the departure of a vessel with a given captain from Reunion Island and its return to the port. The date, time, number of hooks set and hauled, spatial coordinates and depth of downlines at the beginning and the end of both setting and hauling processes were recorded for each longline set. The total number and the biomass of fish caught and landed for Patagonian toothfish was assessed as well as for three bycatch species groups (bigeye grenadier, *Macrourus carinatus*; blue antimora, *Antimora rostrata* and skate species grouped into a single group, *Bathyraja eatonii*, *Bathyraja irrasa*, *Bathyraja murrayi* for Kerguelen and *Amblyraja taaf* for Crozet). From these data, the CPUE was calculated as the biomass of entire caught fish in grams divided by the number of hauled hooks ($g.hook^{-1}$) for each hauled longline, for Patagonian toothfish and for each of the three bycatch species groups:

$$CPUE_i\,(g.hook^{-1}) = \Sigma Biomass\ of\ entire\ caught\ fish_i / \Sigma hauled\ hooks_i$$

$CPUE_i$ is the obtained CPUE on longline *i*

Concurrently, fishery observers visually monitored odontocetes (*i.e.*, sperm whales and killer whales) depredating on longlines during hauling. Depredation was classified according to three states for each of the two depredating species: (i) “Depredation” – depredation of whales on the fishing gear was confirmed by whales repeating long dives (> 15 min) within a 500 m radius from the vessel and surrounded by seabirds when surfacing, slicks of fish oil visible at the surface of the water and/or chunks of fish observed in the mouth of whales; (ii) “No depredation” – no whales sighted from the vessel or if sighted, whales were in transit with no indicators of depredation (see above) observed; (iii) “not observed” – observations were not possible due to weather, sea state and/or visibility conditions (*e.g.*, night). For sets for which depredation was recorded during hauling, fishery observers provided minimum and maximum estimates of the number of whales present around the vessel. For the purposes of this study, and to limit bias due to overestimated numbers, only the minimum estimate was used to test the number of depredating sperm whales as an explanatory variable in the models presented below.

2.2. Models on the proportion of fishing gear depredated by sperm whales

Generalized Linear Mixed Models (GLMM) (Zuur et al., 2009, 2013) were used to explore the relationship between the proportion of hauled sets depredated by sperm whales out of all hauled sets (noted “*Pr(set)*”) and three spatio-temporal predictors. Temporal predictors included a year (“*Year*” – continuous) and a month (“*Month*” – discrete) effects to respectively test for annual trends and intra-annual variations of the proportion of sets depredated by sperm whales. The depth at which sets were hauled was considered here as the vertical spatial predictor (“*Depth*” – continuous and expressed in meters). As observers recorded one depth value for each of the two ends of a set, we used the mean of these two values in the model. The continuous explanatory predictors were centered at their mean and scaled by their standard deviation (*i.e.*, standardized). Data were restricted to longline sets with confirmed presence (“Depredation”) or absence (“No depredation”) of depredating sperm whales during hauling and fitted with a binomial distribution and a logit link function, which was defined as follows:

$$\text{logit}(\pi_{ij}) = \eta_{ij} \Leftrightarrow \pi_{ij} = \exp(\eta_{ij})/(1 + \exp(\eta_{ij}))$$

in which π_{ij} represented the expected value of Pr(set) for each longline *j* in trip *i* (*i.e.*, the mean of $Pr(set)_{ij}$) and $Pr(set)_{ij}$ took values of 0 or 1 for each longline *j* in trip *i*.

The fishing trip (“*Trip*”) was used as a random intercept to impose a correlation structure on the presence of depredating sperm whales because of multiple observations recorded for each trip (Zuur et al., 2013). The model was extended with a temporal auto-correlation structure to account for the fact that the interaction of sperm whales with a given longline set could depend upon their interaction with the previously hauled longline (Tixier, 2012). The full model (*Model 1*) was separately fitted on data from Crozet and Kerguelen using the function *glmmPQL* in packages *MASS* (Venables and Ripley, 2002) and *nlme* (Pinheiro et al., 2016) in R (R Core Team, 2015) as follows:

$$Model\ 1\colon \eta_{ij} = Intercept + \beta_1\, Year + \beta_2\, Month_{ij} + \beta_3\, Depth_{ij} + a_i + \varepsilon_{ij}$$

in which a_i and ε_{ij} were the residuals: $a_i \sim N(0, \sigma^2_{Trip})$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$, and $\beta_{1,2,3}$ were the coefficients of the explanatory variables.

Cleveland dot plots were used as an alternative to bar charts to inspect the outliers of variables. Collinearity between continuous variables was assessed using pair plots and variance inflation factor (VIF) values calculated as the ratio of variance in a model with multiple terms, divided by the variance of a model with one term alone (Zuur et al., 2009, 2010; Zuur, 2012). Model selection was performed by using backward stepwise selection, dropping the least significant interaction term from the model and refitting the model until terms were significant at 5% level (Zuur et al., 2013).

Using the same modeling approach, a second GLMM was developed to investigate the effect of the distance travelled by fishing vessels from one hauled set depredated by sperm whales to the set hauled next in time. Previous studies have shown depredating odontocetes follow fishing vessels between fishing operations, sometimes over great distances (Tixier et al., 2015c). Preliminary analyses of photo-identification data collected in Crozet and Kerguelen suggested that sperm whales also follow vessels from one haul to the next, likely because vessels remain within the acoustical detection range of the whales (Thode et al., 2015). Fishing vessels travel at speeds ranging from 8 to 12 knots, which exceed the average swimming speed of sperm whales during travelling (1.5–3 knots; Aoki et al., 2007; Whitehead, 2003). Hence, increased distances between sets may result in vessels being able to outrun the depredating sperm whales which may eventually lose the acoustical detection of vessels. To test this assumption, *Pr(set)* was here fitted with data restricted to pairs of sets that were hauled successively in time (by the same fishing vessel during the same fishing trip) after the first set was hauled in presence of depredating sperm whales. Longlines hauled with in presence of killer whales, whether depredating alone or simultaneously with sperm whales, were not included in the analysis to limit the bias due to the effect of killer whale depredation on the distance travelled by fishing vessels. Assuming that there is a straight trajectory of the vessel between the two sets, the distance between pairs of sets (“*Distance*” – continuous and expressed in kilometers) was calculated from the GPS coordinates of the mid-point between the two ends of the first set and the mid-point of the second set. The number of sperm whales recorded depredating on the previous set (“$Nb.ind.set_{-1}$” – continuous) was also entered in the model and tested both as a single term and in interaction with *Distance*. We assumed that the greater $Nb.ind.set_{-1}$, the more likely that at least one individual would be depredating again on the next set. As 99% of the values by $Nb.set_{-1}$ were comprised between 1 and 8 individuals, the dataset was restricted to 8 sperm whales recorded on the previous set to avoid bias due to extreme values while maintaining statistical power. The full model (*Model 2*) was also separately fitted on data from Crozet and Kerguelen with a binomial distribution and a logit link function as follows:

$$Model\ 2\colon \eta_{ij} = Intercept + \beta_1\, Distance_{ij} + \beta_2\, Nb.ind.set_{-1ij} + \beta_3\, Distance_{ij} \times Nb.ind.set_{-1ij} + a_i + \varepsilon_{ij}$$

in which a_i and ε_{ij} were residuals: $a_i \sim N(0, \sigma^2_{Trip})$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$, *and* $\beta_{1,2,3}$ were the coefficients of the explanatory terms.

2.3. Modelling the CPUE of longline sets

As an exploratory analysis, and prior to modelling the CPUE, the fishing data on Patagonian toothfish and on bycatch were initially used to statistically identify which fish species were primarily removed by sperm whales from longline sets when depredating. Several *t*-test comparisons were performed on mean CPUEs of 4 groups of species caught on longlines (Patagonian toothfish and 3 bycatch groups: blue antimora, bigeye grenadier and skate species) between sets hauled without (absence of any odontocete species) and sets hauled in the presence of depredating sperm whales over the 2008–2015 period.

Longlines hauled with in presence of killer whales were not included in the analysis to limit the bias due to the effect of killer whale depredation on the CPUE.

GLMMs were then developed to examine the relationship between the CPUE of the depredated fish species and 4 operational predictors depending on the number of sperm whales simultaneously depredating during hauling of a given set. This number ("*Nb.ind*") ranged from 0 for sets hauled in absence to 16 for Crozet and 15 individuals for Kerguelen. However, as 93% of the values taken by this variable were comprised between 0 and 5 for Crozet and 94% were comprised between 0 and 4 for Kerguelen; the data used in models on the CPUE were restricted to a maximum number of 5 individuals for Crozet and 4 for Kerguelen to avoid bias due to extreme values while maintaining statistical power. *Nb.ind* was tested both as a single term because it was hypothesized that increasing *Nb.ind* negatively influenced on the CPUE of the depredated fish species. *Nb.ind* was also tested in interaction with the following operational predictors. First, we tested for the effect of the length of longline sets ("*Length*" – continuous and expressed in kilometers). Here, it was hypothesized that shorter sets, for which hauling time is reduced, may decrease the amount of depredated fish by sperm whales, usually approaching the longline after the hauling has started (Tixier et al., 2015c). Second, we tested for the effect of the hauling speed of sets ("*HaulingSpeed*" – continuous and expressed in number of hauled hooks per minute (hooks.min^{-1})), which was calculated as the total number of hooks hauled on a given set divided by the total hauling time of that set. If sperm whales depredate on the catch only during hauling, we assumed that while reducing the time available for whales to access the catch, a simultaneous increase in hauling speed may also make the removal of captured fish from the sets more difficult for them (Tixier et al., 2015c). Third, we tested for the effect of the soaking time of sets ("*SoakingTime*" – continuous and expressed in hours), which was the time elapsed between the end of setting and the start of hauling. This variable was used to specifically investigate the possibility that sperm whales may also depredate on sets before hauling while the line is still at the bottom of the sea. If it is the case, shorter soaking time can also reduce the time available for whales

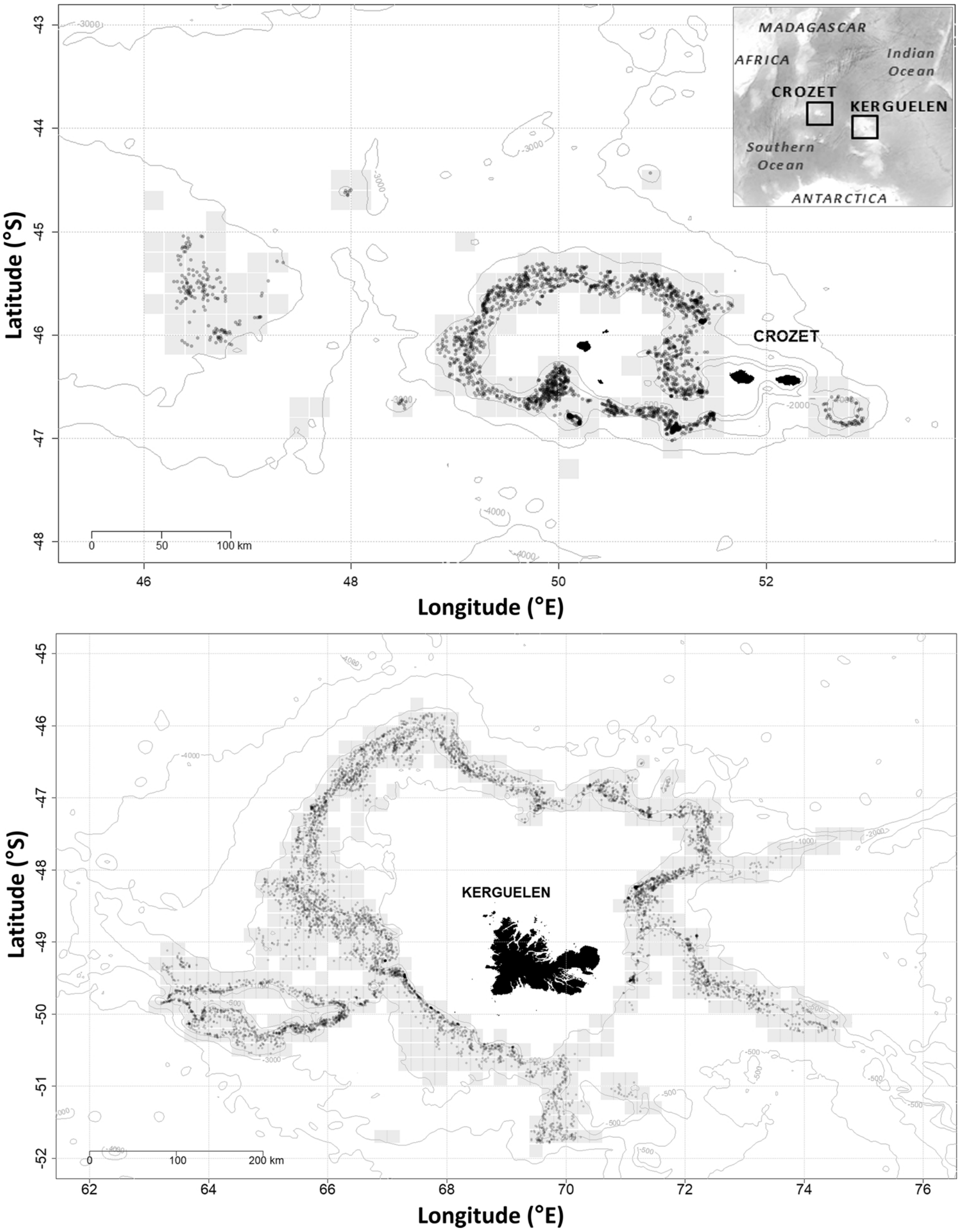

Fig. 1. Distribution of longline sets hauled in presence of depredating sperm whales (black dots) and fishing grounds (0.2° × 0.2° squares in which at least one set was hauled over the 2008–2015 period – grey squares) in Crozet (top) and in Kerguelen (bottom). Thin grey lines are the 500, 1000, 2000 and 4000 m isobaths.

to access the catch and, therefore, reduce the amount of depredated fish. Lastly, the effect of the depth at which sets were hauled ("*Depth*" – continuous and expressed in meters) was also entered in the models to account for bathymetric variations of fish abundance. The continuous predictors were centered at their mean and scaled by their standard deviation. The fishing trip (*Trip)* was then used as a random intercept. Using the function *glmer* in package *lme4* (Bates et al., 2015) in R (R Core Team, 2015), models were fitted with a Gamma distribution and the logarithmic link function, which was defined as follows:

$$\log(\mu_{ij}) = \eta_{ij} \leftrightarrow \mu_{ij} = \exp(\eta_{ij})$$

in which μ_{ij} represented the expected value of CPUE of longline j in trip i (*i.e.*, the mean of $CPUE_{ij}$).

The full model (*Model 3*) was separately fitted on data from Crozet and from Kerguelen as follows:

$$\begin{aligned} &\textit{Model 3}: \eta_{ij} = \textit{Intercept} + \beta_1\,\textit{Nb.ind}_{ij} + \beta_2\,\textit{Length}_{ij} + \beta_3\,\textit{Depth}_{ij} \\ &+ \beta_4\,\textit{Soaking Time}_{ij} + \beta_5\,\textit{Hauling Speed}_{ij} + \beta_6\,\textit{Length}_{ij} \times \textit{Nb.ind}_{ij} \\ &+ \beta_7\,\textit{Depth} \times \textit{Nb.ind}_{ij} + \beta_8\,\textit{Soaking Time}_{ij} \times \textit{Nb.ind}_{ij} \\ &+ \beta_9\,\textit{Hauling Speed}_{ij} \times \textit{Nb.ind}_{ij} + a_i + \varepsilon_{ij} \end{aligned}$$

in which a_i and ε_{ij} were residuals: $a_i \sim N(0, \sigma^2_{\mathrm{Trip}})$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$, and $\beta_{1,2,3,4,5,6,7,8,9}$ were the coefficients of the explanatory terms.

Cleveland dot plots were also used to inspect the outliers of variables and collinearity between continuous variables was assessed using pair plots and VIF values (Zuur et al., 2009, 2010; Zuur, 2012). Model selection was performed using backward stepwise selection by dropping the least significant term interaction from the model and refitting the model until terms were significant at 5% level (Zuur et al., 2013).

3. Results

3.1. Data summary

During the study, a total of 25,715 longlines were set and hauled in both study areas: 6343 (25%) in Crozet and 19,372 (75%) in Kerguelen. A total of 42,688 tons of Patagonian toothfish were landed during the study with 5622 tons (13%) in Crozet and 37,066 (87%) in Kerguelen. The absence or presence of depredating odontocetes was confirmed for 83% and 87% of all longline sets hauled in Crozet and Kerguelen, respectively. Sperm whales depredated on 60.5% and 40.7% of these sets in Crozet and Kerguelen, respectively (Fig. 1).

In Crozet, 34.7% ± 2.1% SE of the sets were hauled in the presence of sperm whales as the only depredating species and 25.8% ± 1.4% SE (n = 8 years) with sperm whales and killer whales depredating simultaneously. In Kerguelen, sets were primarily depredated by sperm whales alone at 40.6% ± 1.1% SE while 0.1% ± 0.05% SE (n = 8 years) in presence of both sperm whales and killer whales. When depredation occurred, the average number of depredating sperm whales per set was significantly different between Crozet and Kerguelen (Student *t*-test: $t = -16.87$, $df = 10038$, $P < 0.001$) and was estimated at 3.5 ± 2.9 SD individuals per set in Crozet (n = 3188 sets) and 2.6 ± 1.9 SD individuals per set in Kerguelen (n = 6852 sets). The average number of depredating sperm whales per set varied between months in both areas. In Crozet, it was the highest in December (5.31 ± 4.02 SD) and the lowest in September (1.89 ± 1.15 SD, Fig. 2a). In Kerguelen, it was the highest in April (3.17 ± 2.40 SD) and the lowest in July (2.00 ± 1.01 SD, Fig. 2a).

3.2. Models on the proportion of fishing gear depredated by sperm whales

Results from *Model* 1 indicated in Table 1 showed that no significant annual trend in the proportions of sets depredated by sperm whales from 2008 to 2015 was observed in either area. However, significant inter-month variations were detected. Predicted probabilities of sperm whale depredation from the model were the highest between November (0.75 [95% CI: 0.65–0.83]) and January (0.85 [95% CI: 0.78–0.90]) in Crozet and between November (0.62 [95% CI: 0.55–0.69]) and December (0.65 [95% CI: 0.59–0.71]) in Kerguelen (Fig. 2b). These probabilities were the lowest between July (0.48 [95% CI: 0.34–0.63]) and October (0.44 [95% CI: 0.35–0.54]) in Crozet and between April (0.27 [95% CI: 0.22–0.33]) and July (0.06 [95% CI: 0.03–0.11]) in Kerguelen (Fig. 2b).

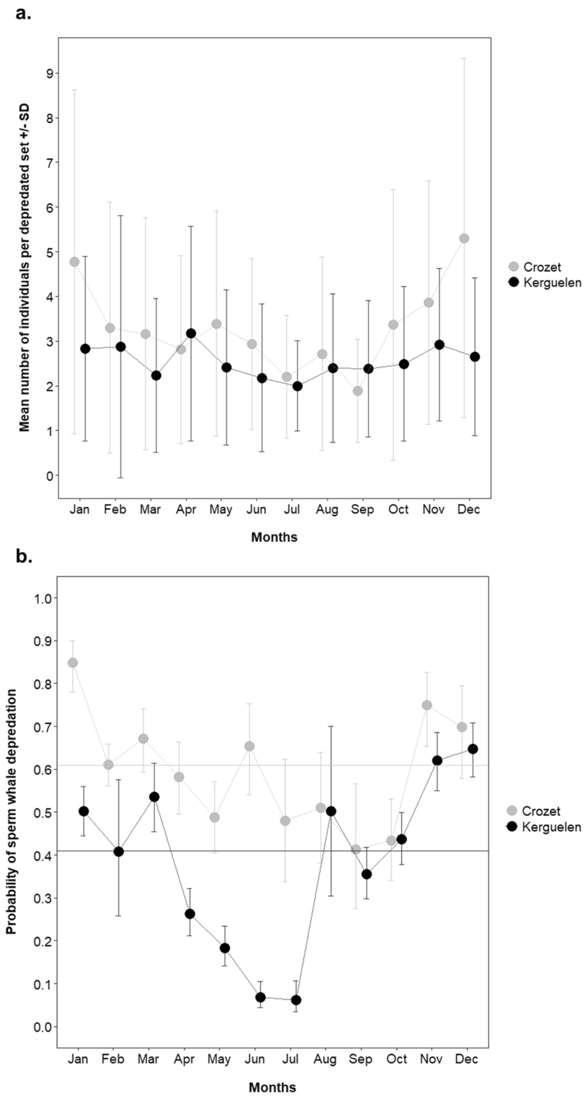

Fig. 2. Intra-annual variations of a. the number of sperm whale individuals depredating the same set (mean ± SD calculated from observed values) and b. the probability and confidence interval at 95% (error bars) of sperm whale depredation to occur during hauling of sets as predicted by *Model 1* outputs of the month as a discrete predictor in Crozet (grey) and in Kerguelen (black). The mean proportions of sets depredated by sperm whales per year over the study period (horizontal lines) are also depicted.

The depth at which longlines were set had no effect on the proportion of depredated sets in Crozet (Table 1). However, the depth effect was significant and positive in Kerguelen ($t = 7.94$, $df = 16559$, $P = 0.00$). For a typical trip in Kerguelen, the probability of sperm whale depredation increased from 0.30 [95% CI: 0.09–0.50] for sets hauled 506 m deep to 0.48 [95% CI: 0.27–0.70] for sets hauled 2140 m deep.

Results from *Model* 2 indicated in Table 2 showed that the number of depredating sperm whales recorded during the hauling of the first longline had a significant and positive effect on the proportion of subsequent sets hauled with depredation, both in Crozet ($z = 4.04$, $P < 0.001$) and in Kerguelen ($z = 12.18$, $P < 0.001$). In the same case, the distance travelled by vessels between the two sets had a

Table 1
Numerical outputs from *Model 1* testing the effects of the year (*Year*) and the depth (*Depth*) at which longline sets were hauled as continuous standardized predictors, as well as the effect of the month (*Month*) as discrete predictor on the proportion of sets depredated by sperm whales out of all sets hauled in Crozet and in Kerguelen. The baseline is represented by the month having the lowest probability of interaction and is the level with which the estimated probabilities of sets to be depredated of the other months are compared. The fishing trip (*Trip*) was added as a random term in *Model 1* along with an autocorrelation structure AR1 within each *Trip*.

	CROZET (N = 5217 sets)					KERGUELEN (N = 16738 sets)				
	Value	*SE*	*df*	*t*	*P*	*Value*	*SE*	*df*	*t*	*P*
Intercept	−0.35	0.32	5094	−1.11	0.27	−2.74	0.31	16559	−8.86	0.00
Year	–	–	–	–	NS	–	–	–	–	NS
January	2.09	0.39	5094	5.30	0.00	2.76	0.33	16559	8.37	0.00
February	0.81	0.33	5094	2.45	0.01	2.28	0.46	16559	4.91	0.00
March	1.07	0.36	5094	2.99	0.003	2.89	0.35	16559	8.38	0.00
April	0.69	0.36	5094	1.91	0.06	1.74	0.33	16559	5.24	0.00
May	0.33	0.36	5094	0.92	0.36	1.24	0.32	16559	3.86	< 0.001
June	1.00	0.40	5094	2.51	0.01	0.10	0.32	16559	0.30	0.76
July	0.28	0.44	5094	0.65	0.51	Baseline	Baseline	Baseline	Baseline	Baseline
August	0.39	0.41	5094	0.95	0.34	2.79	0.47	16559	5.91	0.00
September	Baseline	Baseline	Baseline	Baseline	Baseline	2.11	0.34	16559	6.28	0.00
October	0.10	0.37	5094	0.28	0.78	2.48	0.33	16559	7.41	0.00
November	1.44	0.39	5094	3.71	< 0.001	3.23	0.34	16559	9.41	0.00
December	1.19	0.41	5094	2.88	0.004	3.36	0.34	16559	9.90	0.00
Depth	–	–	–	–	NS	0.18	0.02	16559	7.94	0.00
	Random intercept: 0.51 Residual variance: 0.98 Auto-correlation parameter estimate: 0.36					Random intercept: 0.77 Residual variance: 0.96 Auto-correlation parameter estimate: 0.51				

Table 2
Numerical outputs from *Model 2* testing the effects of the distance travelled by fishing vessels between two successively hauled sets (*Distance*) and the number of sperm whales recorded depredating during the hauling of the first of these two sets ($Nb.ind.set_{-1}$) as continuous standardized predictors on the proportion of next sets depredated by sperm whales. The fishing trip (*Trip*) was entered in *Model 2* as a random term.

	CROZET (N = 1180 sets)				KERGUELEN (N = 4223 sets)			
	Estimate	*SE*	*z*	*P*	*Estimate*	*SE*	*z*	*P*
Intercept	1.65	0.11	14.70	< 0.001	1.91	0.10	19.74	< 0.001
$Nb.ind.set_{-1}$	0.42	0.10	4.04	< 0.001	0.90	0.07	12.18	< 0.001
Distance	−0.76	0.08	−9.62	< 0.001	−0.66	0.04	−14.74	< 0.001
$Distance{:}Nb.ind.set_{-1}$	−0.19	0.08	−2.40	0.02	−0.24	0.04	−5.26	< 0.001
	Random intercept: 0.28				Random intercept: 0.77			

significant and negative effect on the proportion of the next sets depredated by sperm whales, both in Crozet ($z = -9.62$, $P < 0.001$) and in Kerguelen ($z = -14.74$, $P < 0.001$). The interaction term between the variables *Distance* and $Nb.ind.set_{-1}$ was significant and negative both in Crozet ($z = -2.40$, $P = 0.02$) and in Kerguelen ($z = -5.26$, $P < 0.001$). From the model outputs, the effect of the number of depredating sperm whales during hauling of the first set on the proportion of next sets depredated became negligible if vessels travelled more than 55.8 km in Crozet and 48.6 km in Kerguelen (Fig. 3). Based on an average number of sperm whales depredating on the first set, the estimated probabilities of the next sets to be depredated in Crozet was decreased by 10.7% when vessels travelled 20 km from the previous set, and by 39.8% when vessels travelled 50 km. This rate was greater in Kerguelen. The probability of the next sets to be depredated was decreased by 15.9% when vessels travelled 20 km from the previous set and by 65.2% when vessels travelled 50 km (Fig. 3).

3.3. Modelling the CPUE of longline sets

A significant decrease of CPUE of Patagonian toothfish between non-depredated and depredated longline sets by sperm whales was detected both at Crozet (Student *t*-test: $t = -3.07$, $df = 402$, $P = 0.002$) and at Kerguelen (Student *t*-test: $t = -4.58$, $df = 1194$, $P < 0.001$) while no effect could be detected on monitored bycatch species (Fig. 4).

Results from *Model 3*, which was therefore run on Patagonian toothfish CPUE, indicated in Table 3 showed that the number of depredating sperm whales per set had a significant and negative effect on toothfish CPUE for both study areas ($t = -8.56$, $P < 0.001$ for Crozet and $t = -14.09$, $P < 0.001$ for Kerguelen). From the model output, the CPUE loss was estimated at 24.72 $g.hook^{-1}$ in Crozet and 17.65 $g.hook^{-1}$ in Kerguelen per sperm whale individual (see Supplementary Data for details on calculations). For both areas, the interaction term between the number of sperm whales interacting *Nb.ind* and the variable *Length* or the variable *Depth* had no significant effect on toothfish CPUE.

The soaking time had no effect on toothfish CPUE in absence of cetaceans in Crozet ($t = 0.91$, $P = 0.36$) whereas it had a significantly positive effect in Kerguelen ($t = 9.83$, $P < 0.001$). The interaction term between the number of sperm whales and the variable *SoakingTime* had no significant effect on toothfish CPUE in Kerguelen. However, this interaction term was significant and had a negative effect on toothfish CPUE in Crozet ($t = -1.97$, $P = 0.05$). For instance, soaking times of 10 and 60 h, respectively, resulted in toothfish CPUEs of 169.68 and 168.27 $g.hook^{-1}$ (*e.g.,* CPUE reduction of 0.8%) when two sperm whales simultaneously depredated on a given set. CPUEs further decreased to values of 134.94 and 105.45 $g.hook^{-1}$ (*e.g.,* CPUE reduction of 21.9%) when five sperm whales simultaneously depredated on a given set (Fig. 5).

The hauling speed had a significant negative effect on toothfish CPUE in the absence of cetaceans both at Crozet ($t = -3.74$, $P < 0.001$) and at Kerguelen ($t = -16.16$, $P < 0.001$). In interaction

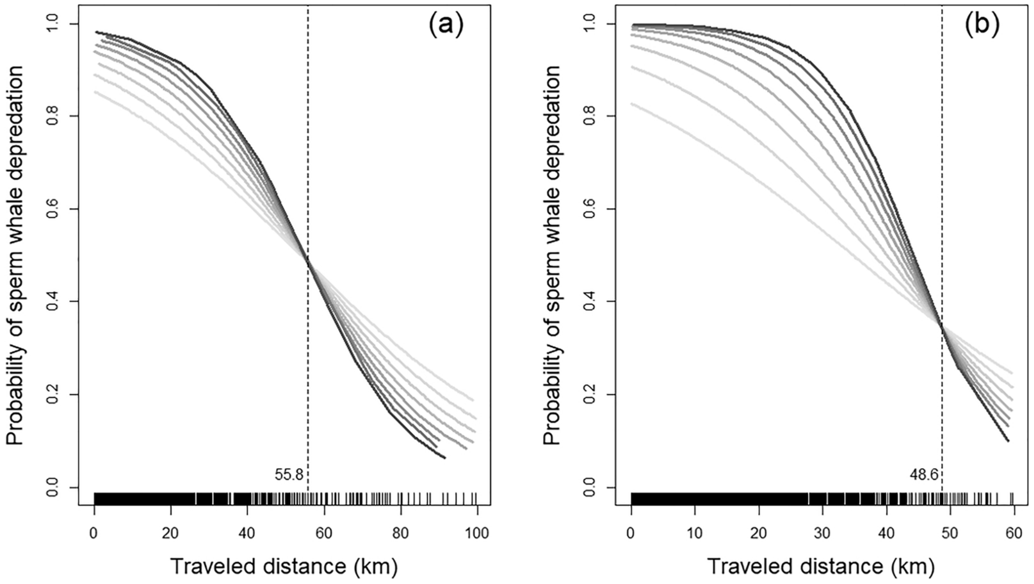

Fig. 3. Predicted probabilities from *Model 2* outputs of sperm whale depredation to occur during hauling of the second of two successively hauled sets against the interaction effect between the distance travelled by vessels between these two sets and the number of sperm whales depredating on the first set in Crozet (a) and in Kerguelen (b). Each curve corresponds to a given number of sperm whales simultaneously depredating the first set, ranging from 0 (light grey) to 8 (dark grey).

with the number of sperm whales, the hauling speed had no significant effect on the toothfish CPUE in Crozet, but the effect was significant and positive in Kerguelen ($t = 3.54$, $P < 0.001$). For instance, the presence of 1 and 4 depredating whales on a given set resulted in toothfish CPUEs of 288.50 and 229.69 g.hook^{-1} (*e.g.*, CPUE reduction of 20.4%), respectively, when using a hauling speed of 20 hooks.min^{-1}. A further decrease was observed at 199.48 and 185.07 g.hook^{-1} (*e.g.*, CPUE reduction of 7.2%) when a hauling speed of 50 hooks.min^{-1} was used (Fig. 6). The model also estimated that the effect of the number of sperm whales on the amount of depredated toothfish became negligible for speeds greater than 60 hooks.min^{-1} (Fig. 6).

4. Discussion

This study provided evidence that sperm whales specifically remove Patagonian toothfish from longlines when depredating on fisheries of the Crozet and Kerguelen EEZs. This depredation varied in space and time and was influenced by a number of operational variables. The proportion of depredated sets depended upon the season and the depth at which longlines were set and was influenced by the distance travelled by vessels when switching from one fishing ground to another while trying to avoid depredation. This study also demonstrated that the amount of Patagonian toothfish depredated by sperm whales varied with (1) the number of individuals co-occurring around the vessels, (2) the speed at which longline sets were hauled, and (3) the soaking time of sets. These findings provide interesting insights to the understanding of factors that may influence and mitigate sperm whale depredation on the studied fisheries, as well as for other longline fisheries facing similar sperm whale interactions.

4.1. Sperm whale depredation levels

The proportions of longline sets hauled in presence of depredating sperm whales in Crozet (61%) and Kerguelen (41%) are among the highest ever recorded in the Southern Ocean region and in other demersal longline fisheries experiencing depredation. For example, sperm whales have been reported depredating on 18–25% of Patagonian toothfish longline sets in South Georgia (Moir Clark and Agnew, 2010; Purves et al., 2004; Söffker et al., 2015) and 35% of the sets in the Falklands (Goetz et al., 2011; Yates and Brickle, 2007). In Alaska, 10–35% of all longline sets were depredated by sperm whales on the sablefish fisheries (Hill et al., 1999; O'Connell et al., 2015; Peterson and Carothers, 2013; Straley et al., 2006, 2015; Thode et al., 2015).

The proportions of sets depredated by sperm whale reported here, which were calculated over the 2008–2015 period, are consistent with estimates from other studies including years preceding the study period considered in this work (Gasco et al., 2015; Roche et al., 2007; Tixier et al., 2010). In addition, no annual trend in the proportion of depredated sets was detected in this study. Together, these results suggest that the proportion of fishing gear depredated by sperm whales in Crozet and Kerguelen remains relatively constant over a period of nearly 13 years.

While sperm whales may naturally forage on other prey items such as large cephalopods that are not caught on longlines (Clarke and MacLeod, 1974; Kawakami, 1980), Patagonian toothfish has been observed as being part of their natural diet (Abe and Iwami, 1989; Duhamel et al., 2005; Gon and Heemstra, 1990; Yukhov, 1972, 1982). During depredation events, sperm whales primarily removed Patagonian toothfish from longlines despite the presence of other species caught as by-catch. Greater numbers of toothfish on longline sets and its larger size compared to bycatch species may respectively increase the probability of sperm whales to encounter toothfish and facilitate its detection during depredation events, which may therefore contribute to this selectivity. However, the latter is more likely to be explained by the optimal energetic intake sperm whales may gain when feeding on this fish species, which energetic richness is higher than that of other fish species caught on longlines (Capdeville, 1997; Collins et al., 2010; Duhamel, 2003; Fertl, 2008; Péron et al., 2016). As selective depredation towards Patagonian toothfish was also reported for killer whales in Crozet (Tixier et al., 2016), interspecific competition for the same resource can also likely occur when two odontocete species simultaneously depredate on the same longline sets.

Decreases in Patagonian toothfish CPUE caused by sperm whale depredation were detected both in Crozet and Kerguelen (*i.e.*, 24.72 g.hook^{-1} and 17.65 g.hook^{-1} per sperm whale individual, respectively). If multiplied by the number of hooks hauled and the number of individuals for each of the longline sets hauled in presence of sperm whales as the only depredating species, such declines in toothfish CPUE resulted in estimated total losses of 702 tons in Crozet and 2649 tons in Kerguelen for the period of 2008–2015. However, the extent of this CPUE decrease is likely to be underestimated. First, as the distribution of sperm whales is often correlated with highly productive fishing grounds (Gasco et al., 2015; Goetz et al., 2011; Hucke-Gaete et al., 2004; Purves et al., 2004; Tixier, 2012), simple comparisons between the CPUE of all sets hauled in the absence and in the presence of depredating sperm whales are likely to be biased upward. Second,

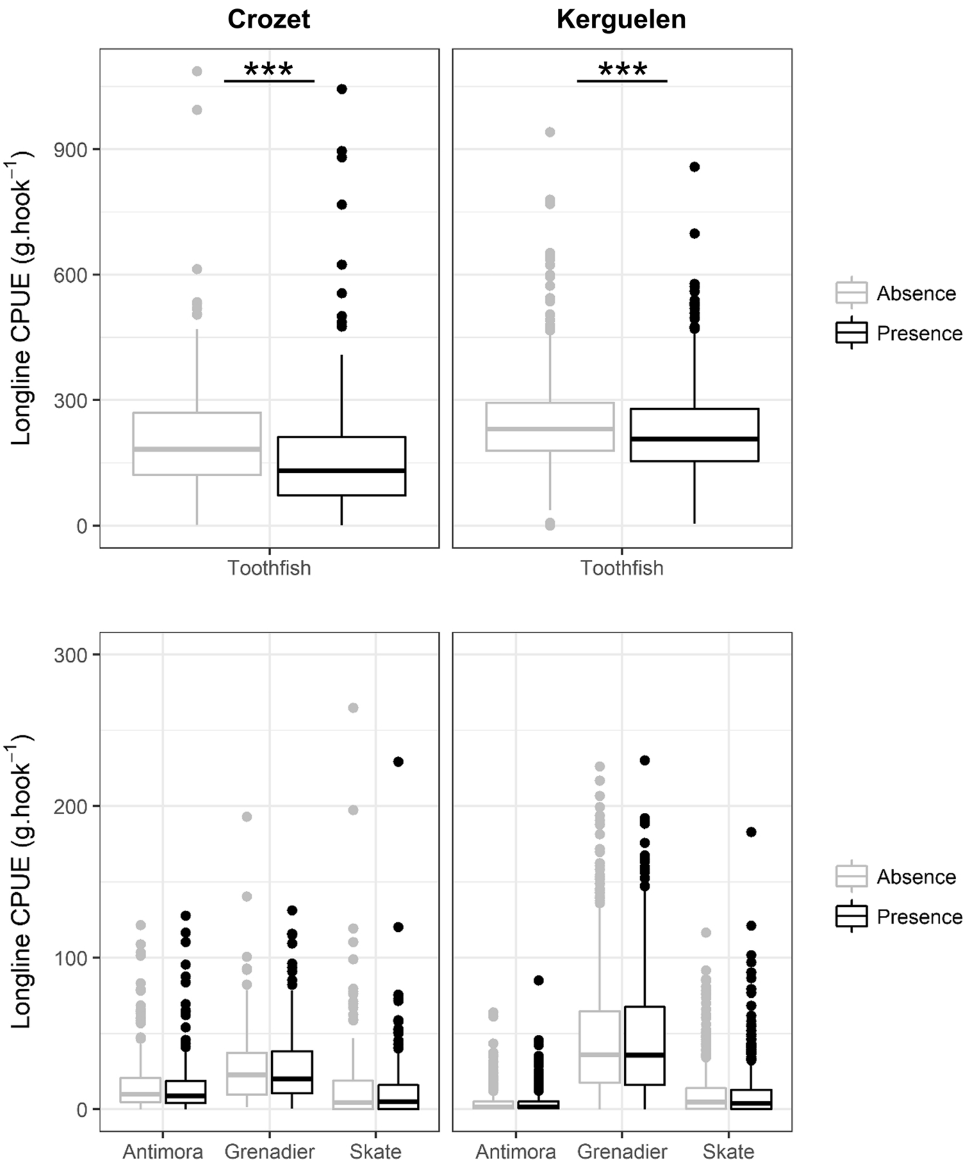

Fig. 4. Boxplots of observed CPUE values per longline set for Patagonian toothfish (top) and for the bycatch species groups (Antimora, Grenadier and Skate, bottom) when sets were hauled without depredation (absence of any odontocete species confirmed – light grey) and with confirmed depredation by sperm whales as the only depredating species (black) in Crozet (left) and in Kerguelen (right). Points are the outliers of the boxplots. *** indicate a significant difference ($P < 0.001$) in CPUE values between sets hauled in absence and in presence of sperm whales (Student *t*-test comparisons).

Table 3

Numerical outputs from *Model 3* testing the effects of the number of sperm whales simultaneously depredating the same set (*Nb.ind*), the length of longline sets (*Length*), the soaking time (*SoakingTime*), the speed (*HaulingSpeed*) and the depth (*Depth*) at which sets were hauled as continuous standardized predictors on the Patagonian toothfish CPUE. The fishing trip (*Trip*) was entered in *Model 3* as a random term.

	CROZET (N = 2695 sets)				KERGUELEN (N = 15080 sets)			
	Estimate	*SE*	*t*	*P*	*Estimate*	*SE*	*t*	*P*
Intercept	5.20	0.05	97.39	< 0.001	5.49	0.02	305.25	< 0.001
Nb.ind	−0.15	0.02	−8.56	< 0.001	−0.07	0.005	−14.09	< 0.001
Length	−0.14	0.02	−6.30	< 0.001	−0.08	0.005	−16.63	< 0.001
Depth	−0.06	0.02	−2.78	0.005	–	–	–	NS
SoakingTime	0.02	0.02	0.91	0.36	0.05	0.005	9.83	< 0.001
HaulingSpeed	−0.09	0.02	−3.74	< 0.001	−0.10	0.006	−16.16	< 0.001
Length:Nb.ind	–	–	–	NS	–	–	–	NS
Depth:Nb.ind	–	–	–	NS	–	–	–	NS
SoakingTime:Nb.ind	−0.03	0.02	−1.97	0.05	–	–	–	NS
HaulingSpeed:Nb.ind	–	–	–	NS	0.02	0.004	3.54	< 0.001
	Random intercept: 0.15 Residual variance: 0.56				Random intercept: 0.02 Residual variance: 0.25			

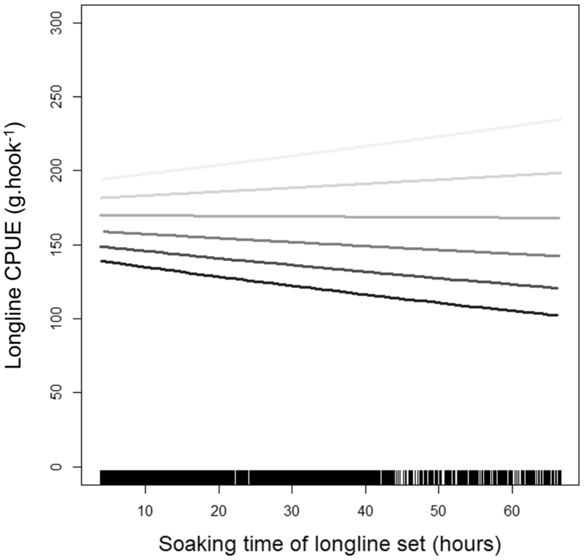

Fig. 5. Predicted estimates from *Model 3* outputs of the interaction effect between the soaking time of longline sets and the number of sperm whales depredating the same set on the Patagonian toothfish CPUE in Crozet. Each curve corresponds to a given number of sperm whales depredating the same set, ranging from 0 (light grey) to 5 (dark grey).

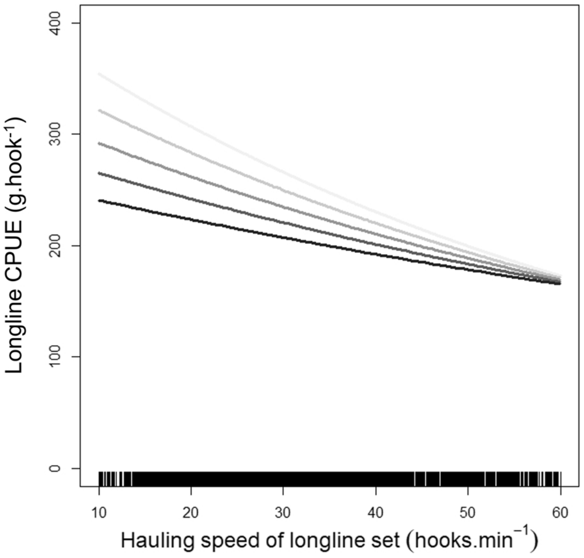

Fig. 6. Predicted estimates from *Model 3* outputs of the interaction effect between the hauling speed of longline sets and the number of sperm whales depredating the same set on the Patagonian toothfish CPUE in Kerguelen. Each curve corresponds to a given number of sperm whales depredating the same set, ranging from 0 (light grey) to 4 (dark grey).

visual monitoring may lead to some depredation events being missed and unrecorded. The diving behaviour and capabilities of sperm whales (Jaquet, 1996; Watkins et al., 1985) which allow them to interact with longline sets at greater depths, may result in individuals remaining at great distances from the vessels and for longer period of time underwater.

4.2. Spatio-temporal variations in the proportion of sets depredated

For both Crozet and Kerguelen, the models developed on the proportion of depredated sets indicated that sperm whales were significantly less likely to depredate on fishing gear in winter months. This result was also reported in previous studies (Labadie et al., 2018; Tixier, 2012), and was attributed to the male sperm whale migration patterns of moving between feeding grounds in cold waters and reproduction grounds in tropical and sub-tropical waters (Jaquet et al., 2000; Madsen et al., 2002; Mellinger et al., 2004; Teloni et al., 2008).

The amplitude in the likelihood of sperm whale-fishery interaction between winter and summer months was lower in Crozet than in Kerguelen. However, variations in the mean number of sperm whales simultaneously depredating the same set were greater in Crozet than in Kerguelen, with increased numbers in summer months in Crozet. These differences may be explained by the size of the fishing area being smaller and the density of depredating sperm whales being greater in Crozet than in Kerguelen. The size of the Crozet fishing area is 20,512 km^2, a third of the Kerguelen fishing area (63,200 km^2). From Labadie et al. (2018), the annual number of depredating sperm whales was estimated to 82 in Crozet and 106 in Kerguelen, which, if divided by the size of the fishing areas, resulted in 0.0040 sperm whale per km^{-2} in Crozet, and 0.0017 sperm whale per km^{-2} in Kerguelen. As a result, the likelihood of vessels to be detected and depredated may remain higher in Crozet than in Kerguelen.

Restricting the fishing activity to winter months is likely to minimize the rate of interaction of sperm whales with vessels, and therefore the amount of depredated toothfish. A possible evidence of such application is the extremely low proportion of sets depredated by sperm whales in the Australian Patagonian toothfish longline fishery operating around Heard and MacDonald Island (HIMI), at the Southern border of the Kerguelen EEZ. Unlike the Kerguelen longlining, which operates all year round, HIMI demersal longlining has been restricted to the April–November period. In the latter, the rate of depredation by sperm whales has remained lower than 5% ever since (CCAMLR, 2015c). However, this low depredation rate may also be explained by sperm whale densities being naturally low at the latitudes of HIMI fishing grounds and/or by the fact that trawling has been the primary fishing technique used in this area until longlining emerged in recent years.

Different sizes in fishing areas may also explain the fact that the depth at which longlines were set influenced the proportion of sets depredated in Kerguelen but not in Crozet. Paired with higher densities of depredating individuals and steeper bathymetric slopes, vessels are more likely to be detected and reached more quickly by sperm whales in the small fishing areas of Crozet than in Kerguelen. As such, the spatial variations in the proportion of sets depredated may better reflect the natural distribution of sperm whales in Kerguelen. Increased probability of depredation on sets hauled at greater depths may indicate that sperm whales are naturally distributed at the outer edge of the Kerguelen oceanic shelf, which corresponds to the type of feeding ground preferentially used by other males in other high latitude areas (Whitehead, 2003).

4.3. Operational means to mitigate sperm whale depredation

When leaving a given fishing ground where sperm whale depredation occurred, vessels were significantly less likely to have their next longline sets depredated if they travelled over large distances, on average greater than 60 km (*i.e.*, 32 nautical miles) because sperm whales may lose acoustical detection of vessels (G. Richard, pers. comm.). While further analysis would be required at the individual level using photo-identification, this result indicate that sperm whales do not follow fishing vessels over large distances and could be used as a mitigation measure to reduce depredation. From previous studies, implementing a “move-on” technique may be an effective strategy to avoid odontocete depredation (Peterson and Carothers, 2013; Tixier et al., 2015c). However, as indicated by a lower distance effect on sperm whale depredation in Crozet than in Kerguelen, this strategy may be highly dependent upon the size of the fishing areas and the densities of sperm whales as we explained in the previous section.

In Crozet, the hauling speed had no effect on sperm whale depredation but increased soaking time of longline sets at the bottom combined with increased number of depredating sperm whales present around the vessel resulted in lower toothfish CPUE. Together, these results suggest that sperm whales may also depredate toothfish caught on longline sets before hauling. While this assumption remains poorly investigated, preliminary acceleration/acoustic data indicated that sperm whales were already present in the vicinity of the fishing gear prior to hauling and may interact with longlines at the bottom (A. Janc and G. Richard, pers. comm.). Sperm whales are deep diving animals and their diving range does overlap with the depths at which longlines are set (Fiscus, 1982; Jaquet et al., 2000; Jaquet and Gendron, 2002). As depredation can also occur when sets are soaked, depredation events can be missed, and therefore underestimated, if this process is only monitored visually from vessels during hauling operations.

In Kerguelen, the soaking time of sets had no effect on sperm whale depredation but the increased hauling speed was found to decrease sperm whale depredation. The extent of this correlation increased with increasing number of sperm whales simultaneously depredating on longline sets during hauling. Leaving toothfish caught on hooks in the water column for a shorter amount of time may prevent the whales from removing large proportions of toothfish. As a large body size reduces its maneuverability (Dial et al., 2008), a faster moving line may also make depredation more difficult for sperm whales. This assumption is supported by a lower hauling speed threshold above which CPUE remained unchanged for sperm whales (60 hooks.min^{-1} – this study) than for killer whales (80 hooks.min^{-1} – Tixier et al., 2015c).

Hauling speed and soaking time had different effects on sperm whale depredation depending on whether vessels operated in Crozet or Kerguelen. The influence of the soaking time detected in Crozet only suggests that sperm whales are more likely to depredate during soaking in this area than in Kerguelen. This difference can be interpreted by higher densities of sperm whales paired with high depredation by killer whales in Crozet (Gasco et al., 2015; Guinet et al., 2015; Tixier, 2012; Tixier et al., 2010, 2016), which are likely to increase both inter- and intra-specific competition for toothfish caught on longlines. Depredation on sets on the seafloor, which may be more energetically costly than depredation at shallow depths during hauling, may be a response of sperm whales to competition when the number of depredating odontocetes increases around vessels.

4.4. Conclusions

Together, the findings of this study could be used to develop operational fishing strategies that minimize odontocete depredation on longline fisheries of the Southern Ocean region. Targeting fishing periods of low depredating sperm whales presence, paired with other factors such as an increase in distance travelled between fishing grounds, an optimal depth at which longlines are set, a shorter soaking time at the bottom and a faster speed at which hooks are hauled may work as easy-to-implement mitigation measures to avoid or mitigate response to depredation. However, as these strategies may induce additional constraints for fishers (Maccarrone et al., 2014; Peterson et al., 2014), full bio-socio-economic assessments of the costs and benefits of changing fishing practices would be needed. For instance, the “move-on” technique may involve increased non-fishing time and motor-fuel consumption that can render this fishing strategy less advantageous to fishers or sustainable to the fishery itself. To increase profitability, these additional costs should not exceed the benefits gained by minimizing depredation (Trijoulet, 2016; Trijoulet et al., 2018). Further assessments are also be needed to ensure that these operational adaptive measures are in agreement with fisheries regulations and resource management strategies, which is currently one of the key challenges for various stakeholders (Doyen et al., 2017, 2012; Gourguet et al., 2013; Nielsen et al., 2018). This study has also emphasized the various gaps of knowledge on odontocete depredation. For instance, sperm whales interaction with the fishing gear, and more importantly, the possible occurrence of depredation when lines are still fishing before hauling. These may have direct implications on various aspects of the issue, including toothfish stock management, whale population conservation, and the ecosystem stability. Such information can also provide knowledge on other possible technical means and opportunities that can reduce depredation, such as the use of toothfish protecting devices which are currently receiving a growing attention and may be further developed in the future.

Author contributions

Study conception and design: AJ, CG, PT.
Acquisition of data: AJ, CG, PT.
Analysis and interpretation of data: AJ, GR, PT.
Drafting of manuscript: AJ, GR, CG, JA, MCV, GD, NG, PT.
Critical revision: AJ, GR, PT.

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Conflicts of interest

None.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fishres.2018.04.019.

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