



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 demersal 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 odontocetes 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

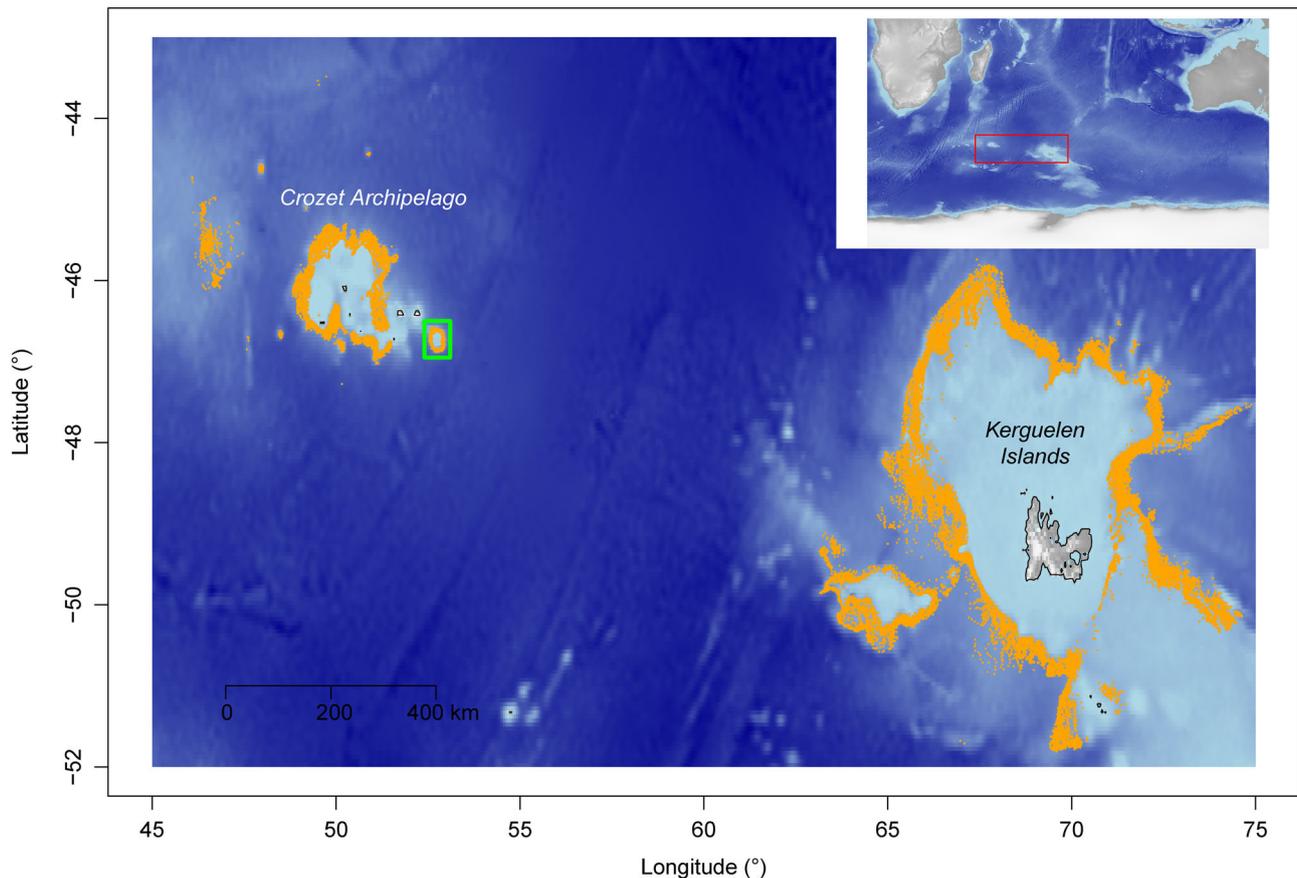


Fig. 1 Map of the study area with the locations of the fishing activity (orange dots) around Crozet and Kerguelen. The green rectangle indicates the seamount where the deployment of instruments on killer whales occurred

unsuitable and/or no observation undertaken). Data were available through the PECHER 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: ≥ 1 500 m; (iii) class 1: 500–1500 m; (iv) class 2: 250–500 m; and (v) class 3: ≤ 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:

$$\text{Norm} = \sqrt{ax^2 + ay^2 + az^2} \quad (1)$$

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 Zealand). 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

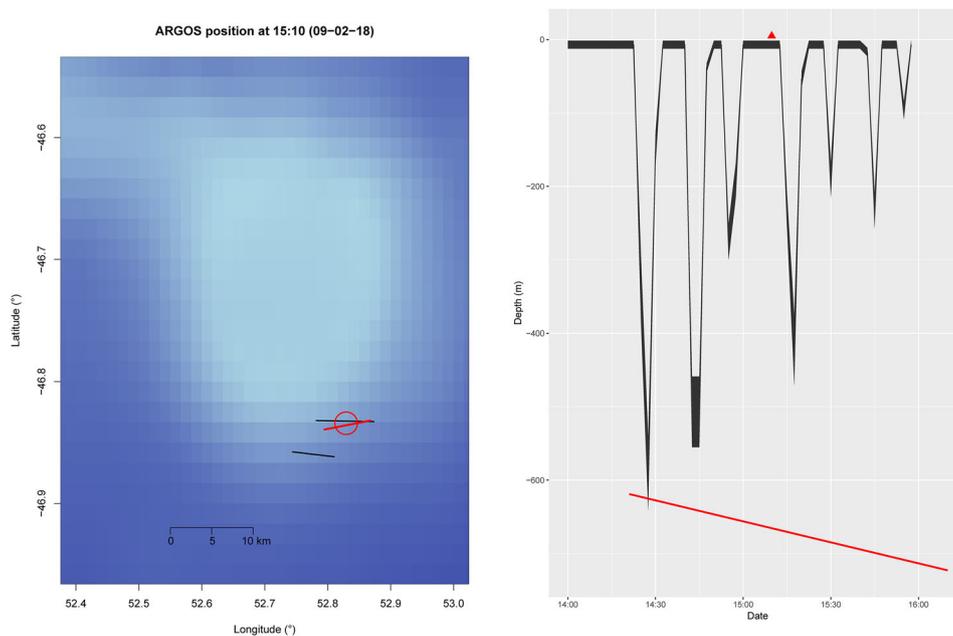


Fig. 2 ARGOS position (left panel) of an ‘interaction during hauling’ with its associate dive profile (right panel). The ARGOS position is indicated on the map by the red circle with the diameter representing the location estimate error buffer (*cf.* CLS classes). The colour shade depicted the bathymetry. 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)

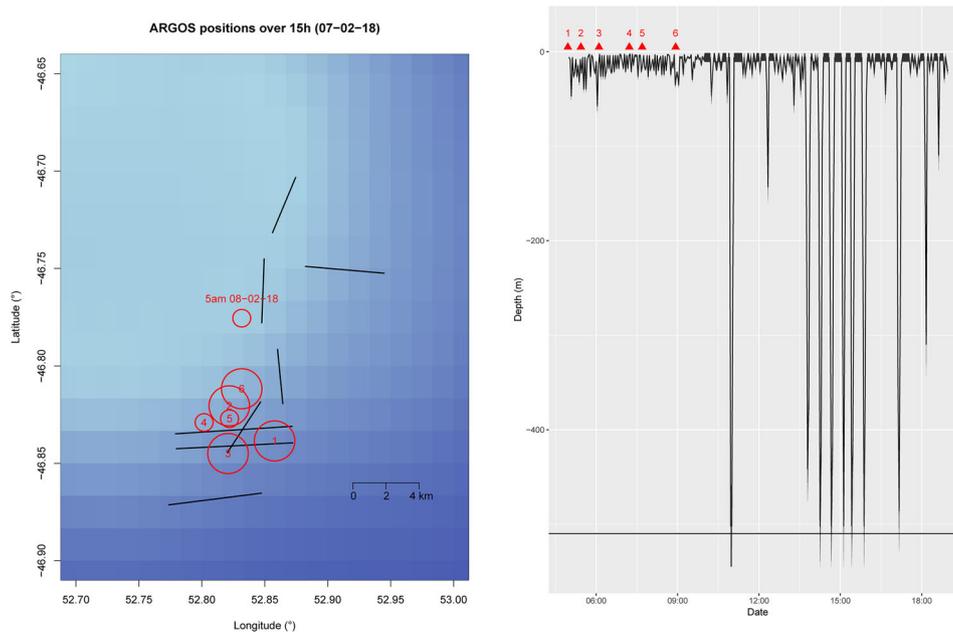


Fig. 3 ARGOS positions (left panel) of an ‘interaction before hauling’ with their associate dive profile (right panel) within a 15-h window. The ARGOS positions are indicated on the map by the red circles (numbered chronologically along track) with the diameter representing the location estimate error 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)

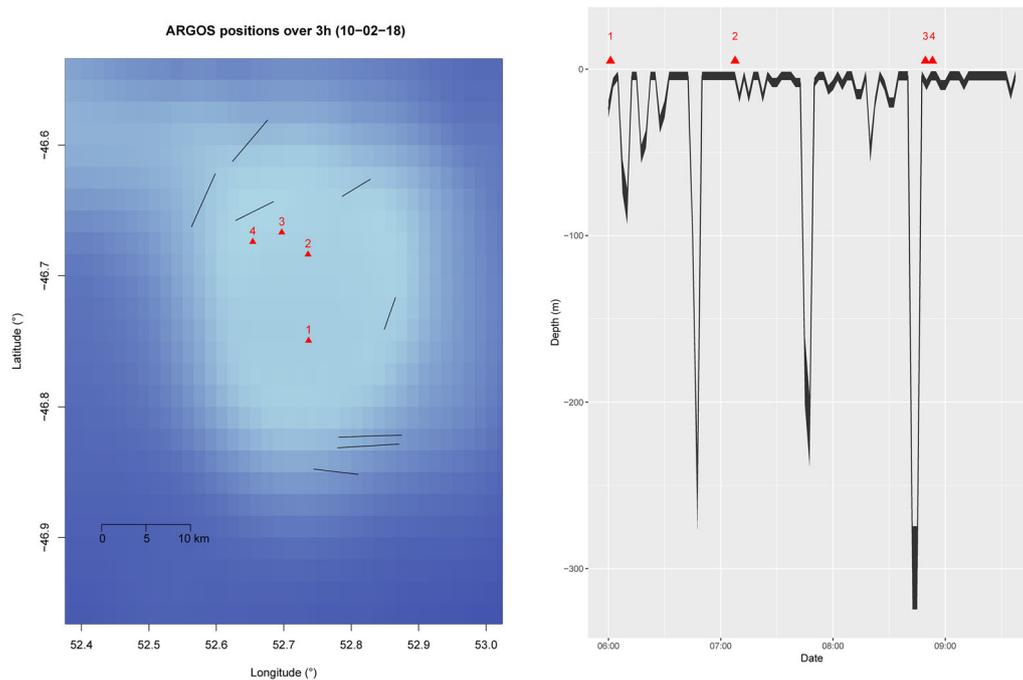


Fig. 4 ARGOS positions (left panel) within a 3-h window of ‘no interaction’ with the associate dive profile (right panel). The ARGOS positions are represented on the map by the red buffers with the diameter standing for the estimate error (cf. CLS classes) and the numbers assessed the chronology of the 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.

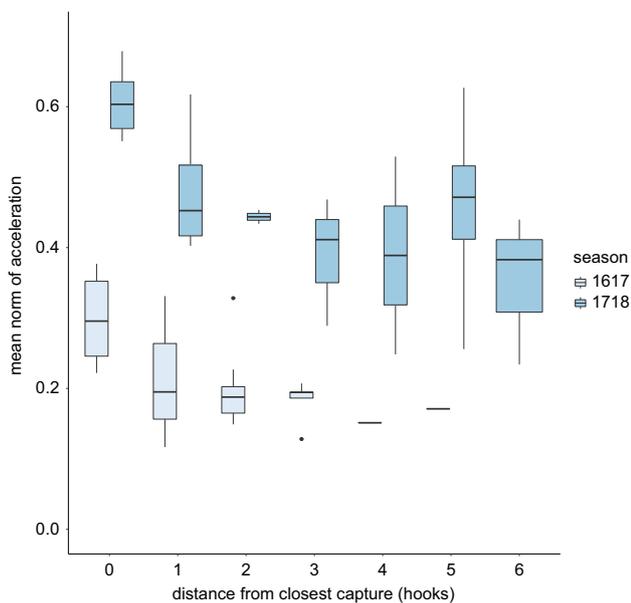


Fig. 5 Boxplots of the mean acceleration norm recorded during the bottom phase on accelerometers with the closest distance and for the two different seasons

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

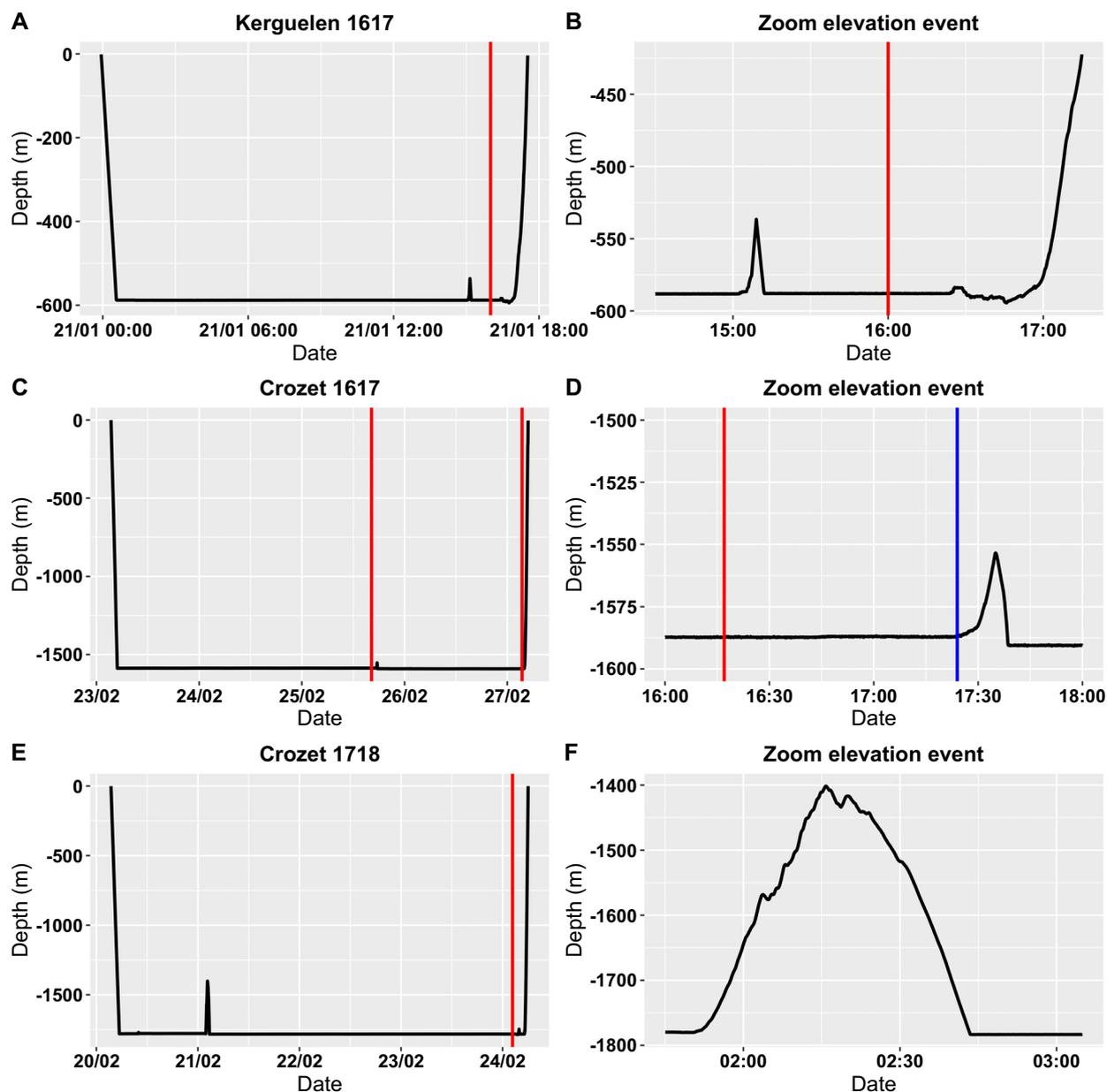


Fig. 6 Dive profiles (a, c, e) of three accelerometers hauled without any fish and showing some depth anomalies, zoomed on the right column (b, d, f). Each row represent a different logger monitoring a precise event: the first line represents the event which occurred at Kerguelen during the first field 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

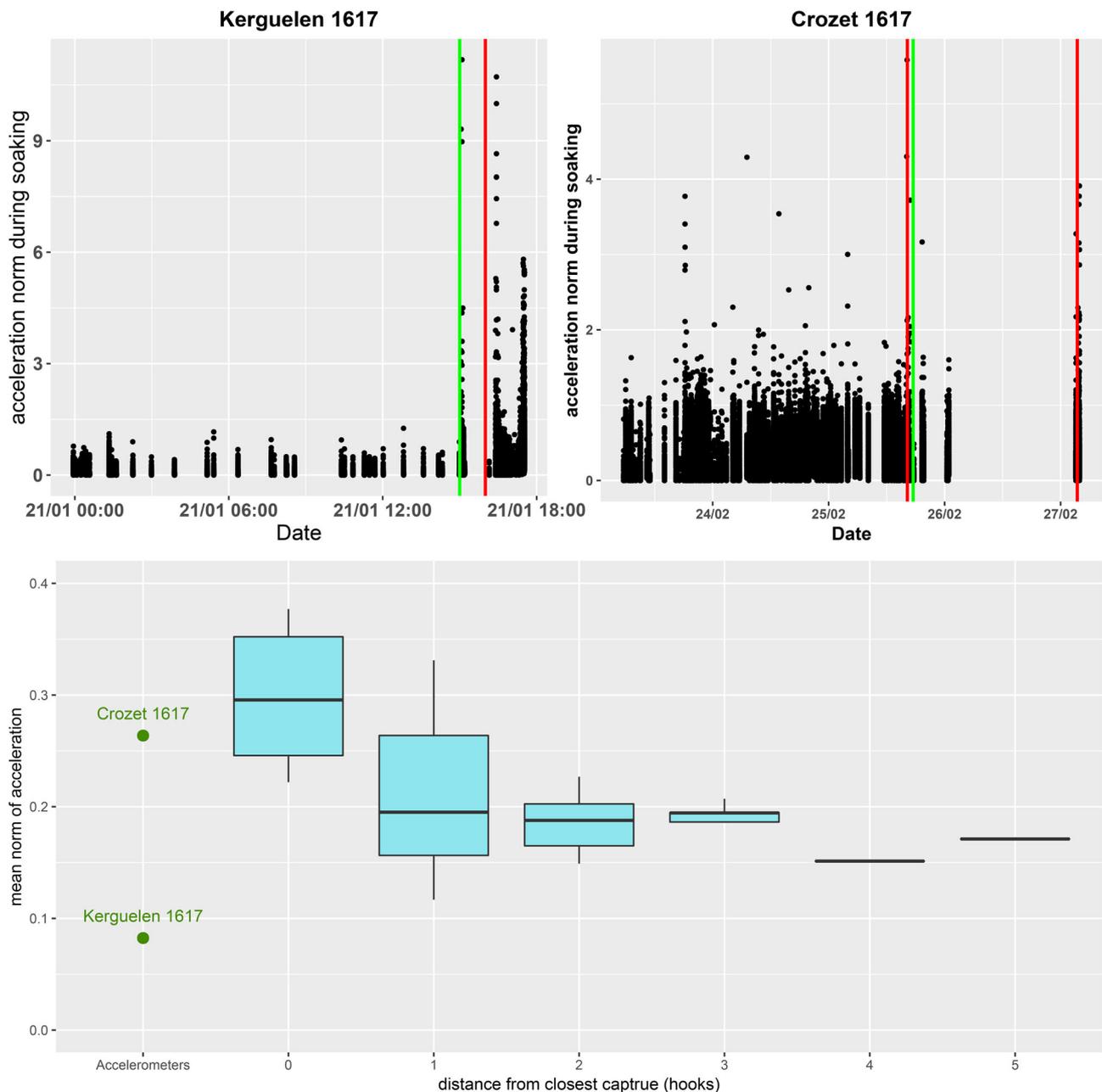


Fig. 7 The first row depicts acceleration norm over the dive of the two equipped hooks showing activity before the elevation event (green line). The mean acceleration norm before the elevation event (green line) was compared for each accelerometer with mean acceleration norm estimated with the distance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