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

Jared R. Towers[1],[*],[‡], Paul Tixier[2], Katherine A. Ross[3],[‡], John Bennett[4], John P. Y. Arnould[2], Robert L. Pitman[5], and John W. Durban[5]

[1]Bay Cetology, Box 554, Alert Bay, BC V0N 1A0, Canada
[2]School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia
[3]Falklands Conservation, Stanley, Falkland Islands
[4]Sanford Seafood, Hall Street, North Mole, Timaru 7910, New Zealand
[5]Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA

*Corresponding author: tel: +1 250 902 1779; e-mail: jrtowers@gmail.com.

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

---

[‡]Former affiliation: Government of South Georgia and South Sandwich Islands, Government House, Stanley, Falkland Islands.

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
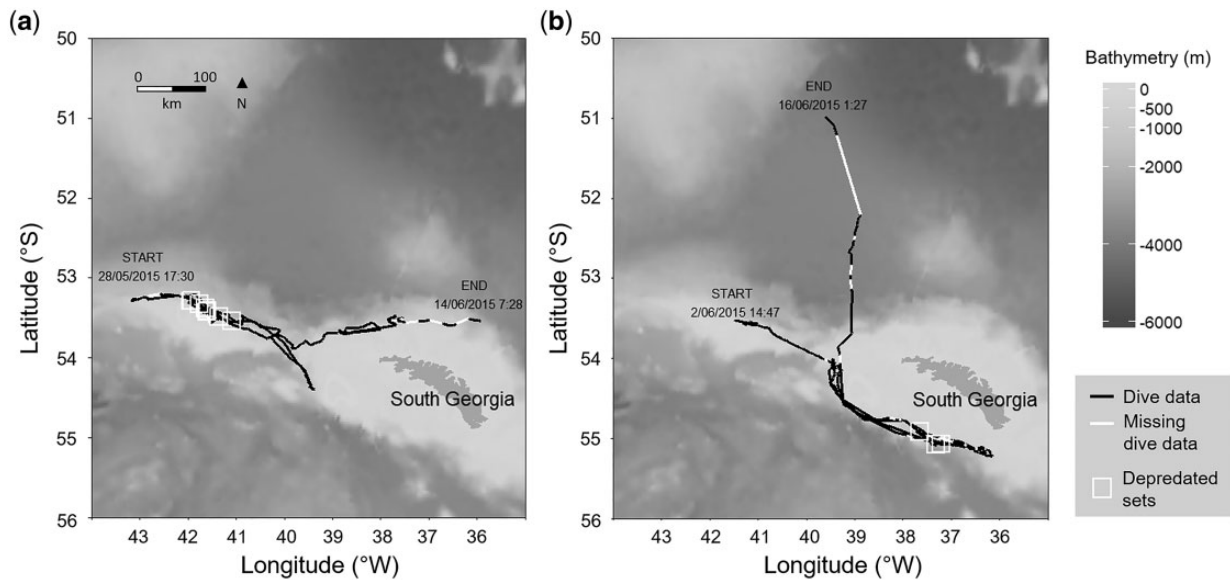
Figure 1. Full filtered and interpolated tracks of (a) the sperm whale from 28 May to 14 June 2015 and (b) the killer whale from 2 to 16 June 2015 with recorded dive data (black) and missing dive data (white). The locations of the longline sets retrieved by the *San Aspiring* that were depredated by 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 ~1.9 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 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 ± 1.9 *SD* 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).
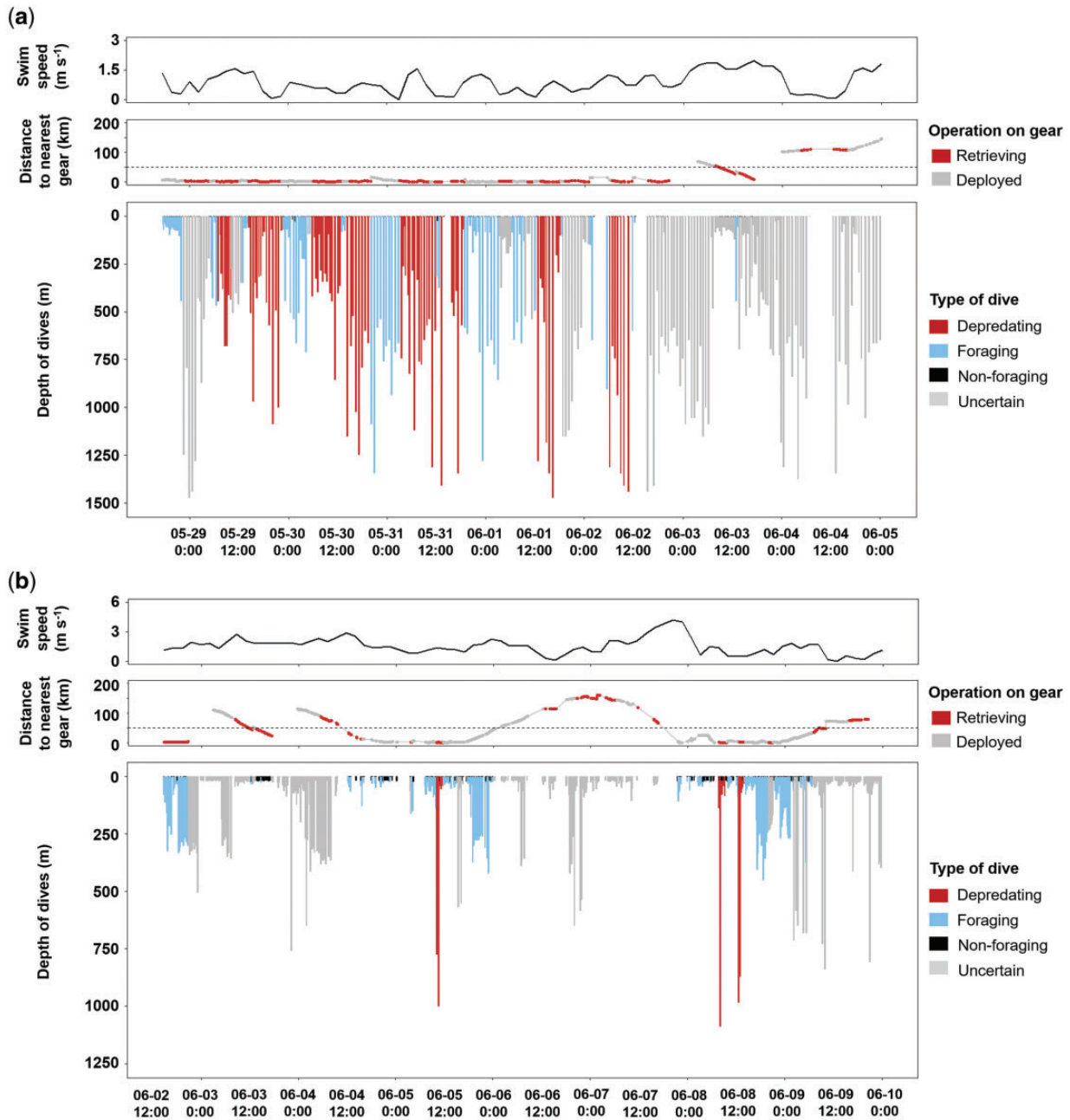
Figure 2. Swim speed, distance to nearest longline set and dive profiles of (a) the sperm whale from 28 May to 4 June 2015 and (b) the killer whale from 2 to 9 June 2015. The swim speed was calculated from successive filtered location data and is depicted as a smooth curve using a "loess" method. The 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 $1122 \pm 327\,SD$ m ($n = 7$ dives), including some of the maximum depths recorded (1407 and 1439 m). While tagged, the killer
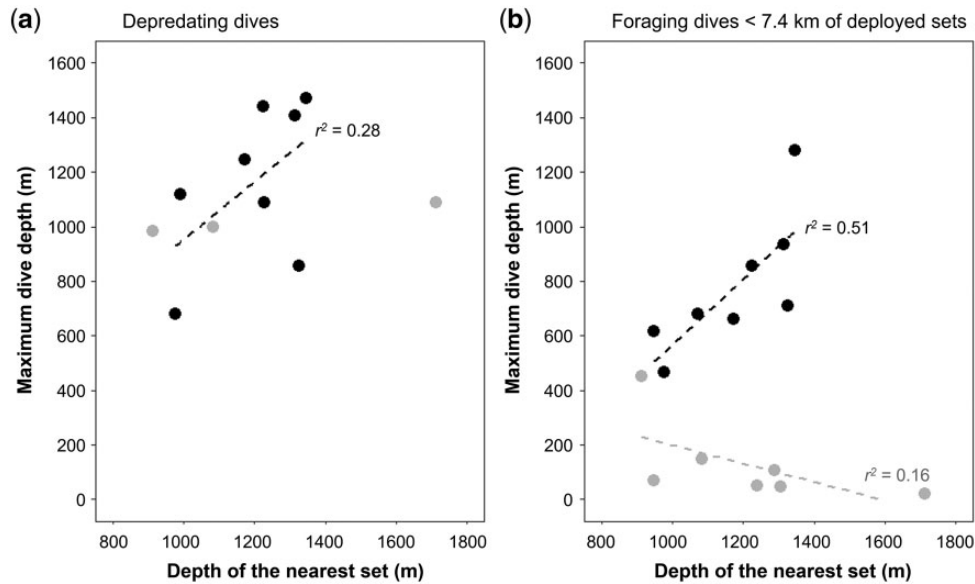
Figure 3. Correlations between the maximum dive depths of the sperm whale (black) and killer whale (grey) and the depths of the nearest longline set during (a) depredating dives, and (b) foraging dives when the animals were <7.4 km from the nearest set deployed on the seafloor. r^2 values from linear 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.

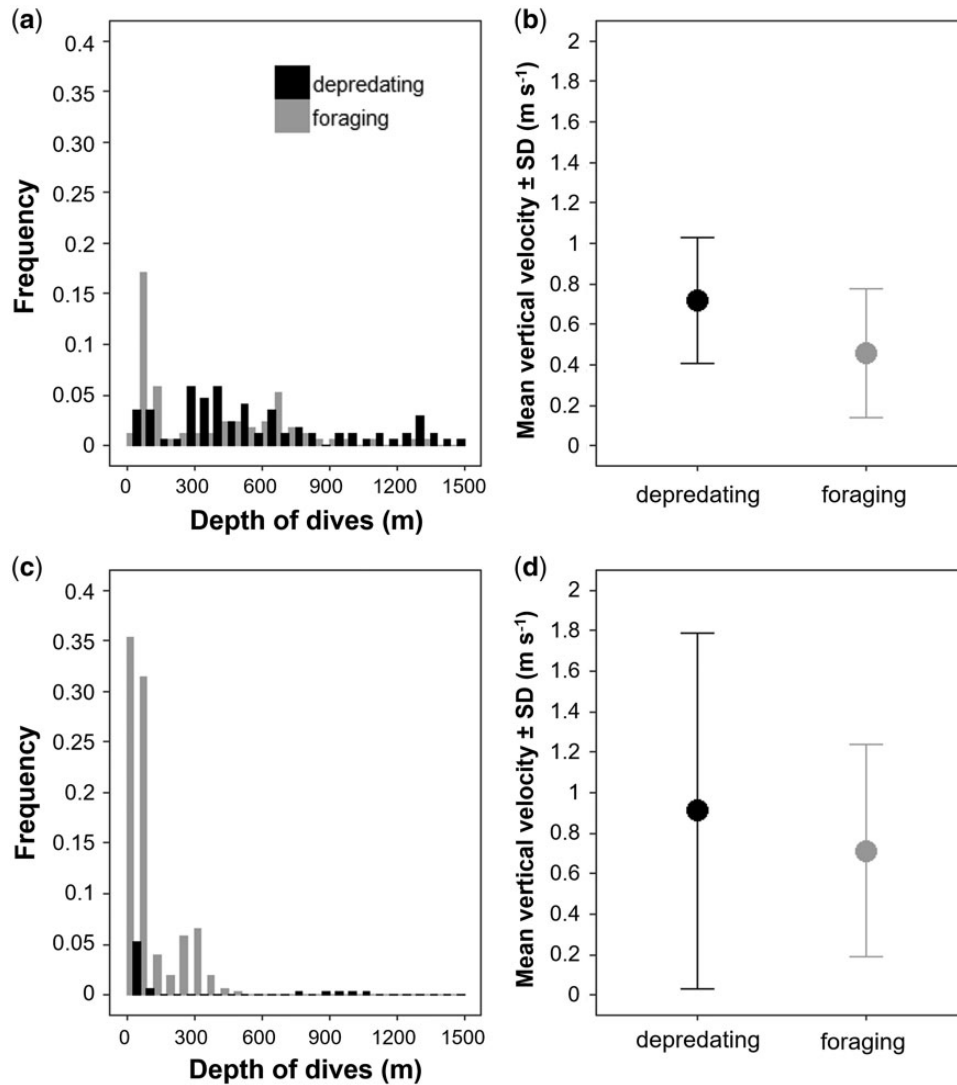|			Dive depth (m)		Dive duration (min)		Vertical velocity (m s^{-1})	
	Behaviour	N	Mean ± SD	Maximum	Mean ± SD	Maximum	Mean ± SD	Maximum
Sperm whale	Foraging	83	345 ± 324	1 343	21.7 ± 10.0	42.1	0.5 ± 0.3	1.3
	Depredating	87	590 ± 398	1 471	25.7 ± 9.0	55.4	0.7 ± 0.3	1.5
Killer whale	Foraging	270	87 ± 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}.
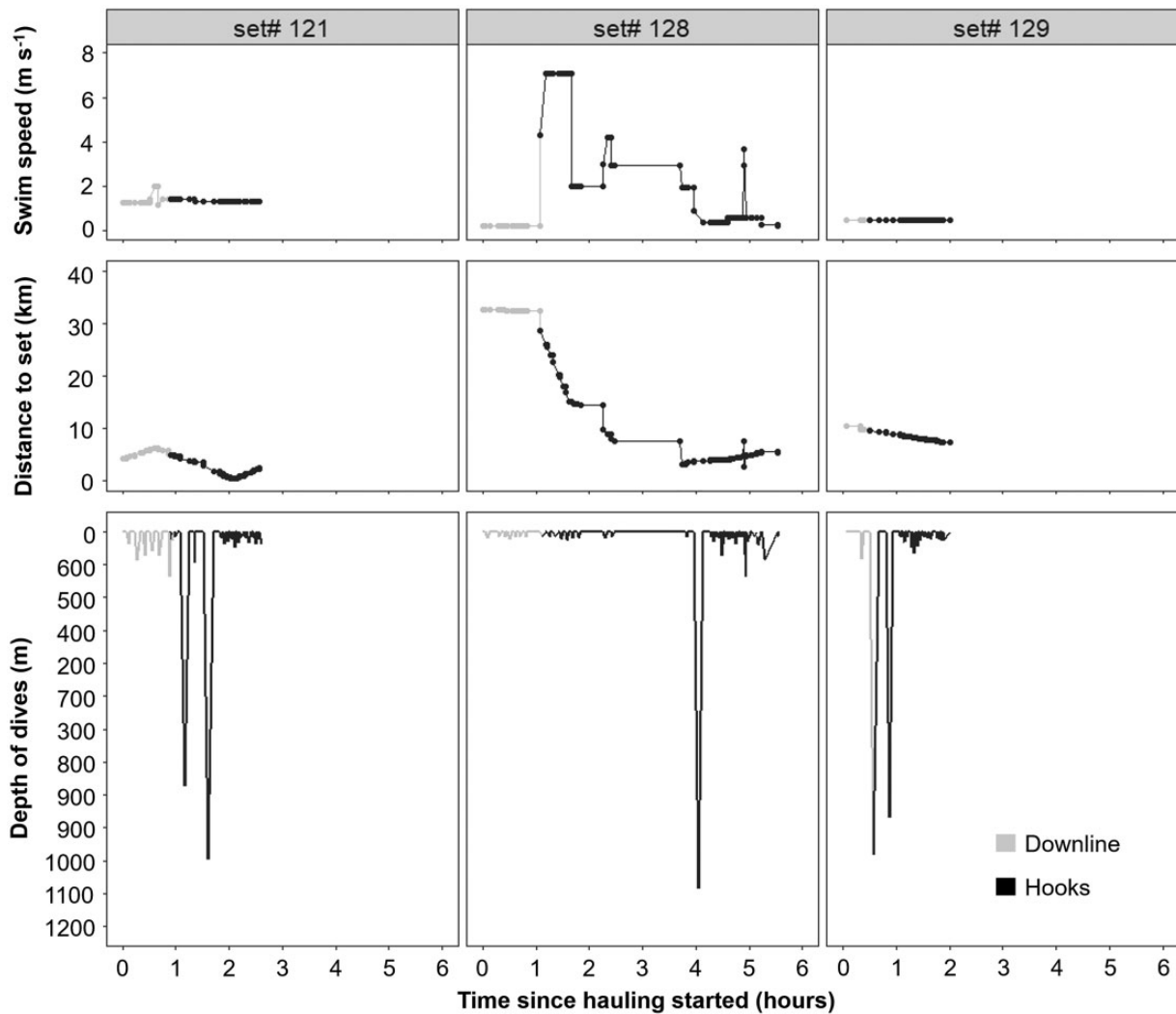
Figure 5. Detailed profiles of the killer whale behaviour when confirmed depredating three longline sets (sets 121, 128, and 129). The distance of the whale to the depredated set, the swim speed, and the dive depth are plotted against the time since retrieval of these sets began. The retrieval process 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 north-bound movements were the beginning of a physiological mainte-nance 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 lati-tudes (Teloni *et al.*, 2008; Fais *et al.*, 2015; Guerra *et al.*, 2017). This indicates that dive behaviour required for successful depre-dation 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 ex-ample, 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 mo-bile. 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 be-tween 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 di-ves when it and associated pod members first arrived in the vicin-ity 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 ob-served 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 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 popula-tions (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 signifi-cantly 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 me-dian 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 depre-dating 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 m for long periods of time (232–277 min) after making one or two consecutive deep di-ves. 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, physi-ological and behavioural adaptations to reduce risk of decom-pression 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.

Acknowledgements

References

Ashford, J. R., Rubilar, P. S., and Martin, A. R. 1996. Interactions between cetaceans and longline fishing operations around South Georgia. Marine Mammal Science, 12: 452–457.

Baird, R. W., Hanson, M. B., and Dill, L. M. 2005. Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. Canadian Journal of Zoology, 83: 257–267.

Berzin, A. A., and Vladimirov, V. L. 1983. A new species of killer whale (Cetacea, Delphinidae) from Antarctic waters. Zoologicheskii Zhurnal, 62: 287–295.

Clark, J. M., and Agnew, D. 2010. Estimating the impact of depredation by killer whales and sperm whales on longline fishing for toothfish (*Dissostichus eleginoides*) around South Georgia. CCAMLR Science, 17: 163–178.

Clarke, M. R. 1976. Observation on sperm whale diving. Journal of the Marine Biological Association of the United Kingdom, 56: 809–810.

Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. Discovery Reports, 37: 1–324.

Collins, M. A., Allcock, A. L., and Belchier, M. 2004. Cephalopods of the South Georgia slope. Journal of the Marine Biological Assocation of the United Kingdom, 84: 415–419.

Collins, M. A., Brickle, P., Brown, J., and Belchier, M. 2010. The Patagonian toothfish: biology, ecology and fishery. Advances in Marine Biology, 58: 227–300.

Cox, T. M., Ragen, A. J., Vos, E., Baird, R. W., Balcomb, K., Barlow, J., and Caldwell, J. 2006. Understanding the impact of anthropogenic sound on beaked whales. Journal of Cetacean Research and Management, 7: 177–187.

Dahlheim, M. E. 1988. Killer whale (Orcinus orca) depredation on longline catches of sablefish (Anoplopoma fimbria) in Alaskan Waters. NWAFC Processed Report, 88-14. Alaska Fish Sci Cent, NMFS, NOAA, Seattle, Washington.

Durban, J. W., and Pitman, R. L. 2012. Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations?. Biology Letters, 8: 274–277.

Durban, J. W., and Pitman, R. L. 2013. Out of Antarctica: dive data support 'physiological maintenance migration' in Antarctic Killer Whales. In 20th Biennial Conference on the Biology of Marine Mammals. Society for Marine Mammalogy (9–13 December 2013, Dunedin, New Zealand).

Durban, J. W., Fearnbach, H., Burrows, D. G., Ylitalo, G. M., and Pitman, R. L. 2017. Morphological and ecological evidence for two sympatric forms of Type B killer whale around the Antarctic Peninsula. Polar Biology, 40: 231–236.

Fais, A., Soto, N. A., Johnson, M., Pérez-González, C., Miller, P. J. O., and Madsen, P. T. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. Behavioural Ecology and Sociobiology, 69: 663–674.

Fearnbach, H., Durban, J. W., Ellifrit, D. K., Waite, J. M., Matkin, C. O., Lunsford, C. R., Peterson, M. J., *et al.* 2014. Spatial and social connectivity of fish-eating "Resident" killer whales (*Orcinus orca*) in the northern North Pacific. Marine Biology, 161: 459–472.

Foote, A. D., Vijay, N., Ávila-Arcos, M. C., Baird, R. W., Durban, J. W., Fumagalli, M., Gibbs, R. A., *et al.* 2016. Genome-culture co-evolution promotes rapid divergence of killer whale ecotypes. Nature Communications, 7: 11693.

Ford, J. K. B. 2009. Killer whale: Orcinus orca. In Encyclopedia of Marine Mammals. 2nd edn, pp. 650–657. Ed. by W. F. Perrin, B. Wursig, and J. G. M. Thewissen. Academic Press, San Diego, California.

Ford, J. K. B. 2014. Marine Mammals of British Columbia. Royal BC Museum, Victoria, British Columbia. 460 pp.

Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S., Balcomb, K. C. III, 1998. Dietary specialization in two sympatric populations of killer whales (Orcinus orca) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology, 76: 1456–1471.

Freitas, C., Lydersen, C., Fedak, M. A., and Kovacs, K. M. 2008. A simple new algorithm to filter marine mammal Argos locations. Marine Mammal Science, 24: 315–325.

Garcia Párraga, D., Moore, M., and Fahlman, A. 2018. Pulmonary ventilation – perfusion mismatch: a novel hypothesis for how diving vertebrates may avoid the bends. Proceedings of the Royal Society B, 285: 20180482.

Gasco, N., Tixier, P., Duhamel, G., and Guinet, C. 2015. Comparison of two methods to assess fish losses due to depredation by killer whales and sperm whales on demersal longlines. CCAMLR Science, 22: 1–14.

Gaskin, D. E., and Cawthorn, M. W. 1967. Diet and feeding habits of the sperm whale (Physeter catadon L.) in the Cook Strait region of New Zealand. New Zealand Journal of Marine and Freshwater Research, 1: 156–179.

Gerlinsky, C. D., Rosen, D. A. S., and Trites, A. W. 2014. Sensitivity to hypercapnia and elimination of CO_2 following diving in Steller sea lions (Eumetopias jubatus). Journal of Comparative Physiology B, 184: 535–544.

Gilman, E., Brothers, N., McPherson, G., and Dalzell, P. 2006. A review of cetacean interactions with longline gear. Journal of Cetacean Research and Management, 8: 215–223.

Goetz, S., Laporta, M., Martínez Portela, J., Santos, M. B., and Pierce, G. J. 2011. Experimental fishing with an "umbrella-and-stones" system to reduce interactions of sperm whales (Physeter macrocephalus) and seabirds with bottom-set longlines for Patagonian toothfish (Dissostichus eleginoides) in the Southwest Atlantic. ICES Journal of Marine Science, 68: 228–238.

Government of South Georgia & South Sandwich Islands. 2017. South Georgia & the South Sandwich Islands Toothfish Fishery (48.3 and 48.4) Management Plan 2018. Government House, Stanley, Falkland Islands.

Guerra, M., Hickmott, L., van der Hoop, J., Rayment, W., Leunissen, E., Slooten, E., and Moore, M. 2017. Diverse foraging strategies by a marine top predator: sperm whales exploit pelagic and demersal habitats in the Kaikōura submarine canyon. Deep Sea Research Part I, 128: 98–108.

Guinet, C., Domenici, P., de Stephanis, R., Barrett-Lennard, L., Ford, J. K. B., and Verborgh, P. 2007. Killer whale predation on bluefin tuna: exploring the hypothesis of the endurance-exhaustion technique. Marine Ecology Progress Series, 347: 111–119.

Guinet, C., Tixier, P., Gasco, N., and Duhamel, G. 2015. Long-term studies of Crozet Island killer whales are fundamental to understanding the economic and demographic consequences of their depredation behaviour on the Patagonian toothfish fishery. ICES Journal of Marine Science, 72: 1587–1597.

Hamer, D. J., Childerhouse, S. J., and Gales, N. J. 2012. Odontocete bycatch and depredation in longline fisheries: a review of available literature and potential solutions. Marine Mammal Science, 28: E345–E374.

Hanson, B., and Walker, W. A. 2014. Trans-Pacific consumption of cephalopods by North Pacific killer whales (Orcinus orca). Aquatic Mammals, 40: 274–284.

Hucke-Gaete, R., Moreno, C. A., and Arata, J. 2004. Operational interactions of sperm whales and killer whales with the Patagonian toothfish industrial fishery off southern Chile. CCAMLR Science, 11: 127–140.

Janc, A., Richard, G., Guinet, C., Arnould, J. P. Y., Villanueva, M. C., Duhamel, G., Gasco, N., et al. 2018. How do fishing practices influence sperm whale (Physeter macrocephalus) depredation on demersal longline fisheries?. Fisheries Research, 206: 14–26.

Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A. P., Castro, P., Baker, J. R., Degollada, E., et al. 2004. Whales, sonar and decompression sickness. Nature, 428: 2–576.

Jonsgård, A., and Lyshoel, P. B. 1970. A contribution to the knowledge of the biology of the killer whale. Norwegian Journal of Zoology, 18: 41–48.

Joyce, T. W., Durban, J. W., Claridge, D. E., Dunn, C. A., Fearnbach, H., Parsons, K. M., Andrews, R. D., et al. 2017. Physiological, morphological, and ecological tradeoffs influence vertical habitat use of deep-diving toothed-whales in the Bahamas. PLoS One, 12: e0185113.

Kock, K. H., Purves, M. G., and Duhamel, G. 2006. Interactions between cetacean and fisheries in the Southern Ocean. Polar Biology, 29: 379–388.

Kooyman, G. L., Schroeder, J. P., Denison, D. M., Hammond, D. D., Wright, J. J., and Bergman, W. P. 1972. Blood nitrogen tensions of seals during simulated deep dives. American Journal of Physiology, 223: 1016–1020.

Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. W., and Sinnett, E. E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. Journal of Comparitive Physiology B, 138: 335–346.

Kvadsheim, P. H., Miller, P. J. O., Tyack, P., Sivle, L. D., Lam, F. P. A., and Fahlman, A. 2012. Estimated tissue and blood N2 levels and risk of decompression sickness in deep intermediate and shallow diving toothed whales during exposure to naval sonar. Frontiers in Aquatic Physiology, 3: 125.

Lopez, R., and Malardé, J-P. 2011. Improving ARGOS Doppler Location Using Kalman Filtering. CLS-DT-MEMO-11-65. Ramonville Saint-Agne, France.

Martin, A. R., and Clarke, M. R. 1986. The diet of sperm whales (Physeter macrocephalus) captured between Iceland and Greenland. Journal of the Marine Biological Association of the United Kingdom, 66: 779–790.

Mathias, D., Thode, A., Straley, J., and Folkert, K. 2009. Relationship between sperm whale (Physeter macrocephalus) click structure and size derived from videocamera images of a depredating whale. Journal of the Acoustical Society of America, 125: 3444–3453.

Mathias, D., Thode, A., Straley, J., Calambokidis, J., Schorr, G., and Folkert, K. 2012. Acoustic and diving behavior of sperm whales (Physeter macrocephalus) during natural and depredation foraging in the Gulf of Alaska. Journal of the Acoustical Society of America, 132: 518–532.

McConnell, B. J., and Fedak, M. A. 1996. Movements of southern elephant seals. Canadian Journal of Zoology, 74: 1485–1496.

Miller, P. J. O., Shapiro, A. D., and Deecke, V. B. 2010. The diving behaviour of mammal-eating killer whales (Orcinus orca): variations with ecological not physiological factors. Canadian Journal of Zoology, 88: 1103–1112.

Moore, J. K., Abbott, M. R., and Richman, J. G. 1999. Location and dynamics of the Antarctic polar front from satellite sea surface temperature data. Journal of Geophysical Research, 104: 3059–3073.

Moreno, C. A., Castro, R., Mujica, L. J., and Reyes, P. 2008. Significant conservation benefits obtained from the use of a new fishing gear in the Chilean Patagonian toothfish fishery. CCAMLR Science, 15: 79–91.

Morin, P. A., Archer, F. I., Foote, A. D., Vilstrup, J., Allen, E. E., Wade, P., Durban, J., et al. 2010. Complete mitochondrial genome phylogeographic analysis of killer whales (Orcinus orca) indicates multiple species. Genome Research, 20: 908–916.

Nishiwaki, M., and Handa, C. 1958. Killer whales caught in the coastal waters off Japan for recent 10 years. Scientific Reports of the Whales Research Institute, 13: 85–96.

Nolan, C. P., Liddle, G. M., and Elliot, J. 2000. Interactions between killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) with a longline fishing vessel. Marine Mammal Science, 16: 658–664.

O'Connell, V., Straley, J., Liddle, J., Wild, L., Behnken, L., Falvey, D., and Thode, A. 2015. Testing a passive deterrent on longlines to reduce sperm whale depredation in the Gulf of Alaska. ICES Journal of Marine Science, 72: 1667–1672.

Pante, E., and Simon-Bouhet, B. 2013. Marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. PLoS One, 8: e73051.

Peterson, M. J., Mueter, F., Criddle, K., and Haynie, A. C. 2014. Killer whale depredation and associated costs to Alaskan sablefish, Pacific halibut and Greenland turbot longliners. PLoS One, 9: e88906.

Pitman, R. L., and Durban, J. W. 2010. Killer whale predation on penguins in Antarctica. Polar Biology, 33: 1589–1594.

Pitman, R. L., and Ensor, P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. Journal of Cetacean Research and Management, 5: 131–139.

Pitman, R. L., Durban, J. W., Greenfelder, M., Guinet, C., Jorgensen, M., Olson, P. A., Plana, J., *et al.* 2010. Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters. Polar Biology, 34: 303–306.

Pitman, R. L., Perryman, W. L., LeRoi, D., and Eilers, E. 2007. A dwarf form of killer whale in Antarctica. Journal of Mammalogy, 88: 43–48.

Purves, M. G., Agnew, D. J., Balguerías, E., Moreno, C. A., and Watkins, B. 2004. Killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) interactions with longline vessels in the Patagonian toothfish fishery at South Georgia, South Atlantic. CCAMLR Science, 11: 111–126.

R Core Team. 2017. R: A Language and Environment for Statistical Computing. https://www.R-project.org/ (last accessed 8 August 2018).

Raverty, S. 2016. Final Report AHC Case: 16-1760. 7 pp.

Read, A. J. 2008. The looming crisis: interactions between marine mammals and fisheries. Journal of Mammalogy, 89: 541–548.

Reisinger, R. R., Gröcke, D. R., Lübcker, N., McClymont, E. L., Hoelzel, A. R., and de Bruyn, P. J. N. 2016. Variation in the diet of killer whales *Orcinus orca* at Marion Island, Southern Ocean. Marine Ecology Progress Series, 549: 263–274.

Reisinger, R. R., Keith, M., Andrews, R. D., and de Bruyn, P. J. N. 2015. Movement and diving of killer whales (*Orcinus orca*) at a Southern Ocean archipelago. Journal of Experimental Marine Biology and Ecology, 473: 90–102.

Reisinger, R. R., Oosthuizen, W. C., Péron, G., Toussaint, D. C., Andrews, R. D., and de Bruyn, P. J. N. 2014. Satellite tagging and biopsy sampling of killer whales at Subantarctic Marion Island: effectiveness, immediate reactions and long-term responses. PLoS One, 9: e111835.

Ridgway, S. H., and Howard, R. 1979. Dolphin lung collapse and intramuscular circulation during free diving: evidence from nitrogen washout. Science, 206: 1182–1183.

Roche, C., Guinet, C., Gasco, N., and Duhamel, G. 2007. Marine mammals and demersal longline fishery interactions in Crozet and Kerguelen Exclusive Economic Zones: an assessment of depredation levels. CCAMLR Science, 14: 67–82.

Rodhouse, P. G., and White, M. G. 1995. Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic polar front zone. Biology Bulletin, 189: 77–80.

Rodhouse, P. G., Arnbom, T. R., Fedak, M. A., Yeatman, J., and Murray, A. W. A. 1992. Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. Canadian Journal of Zoology, 70: 1007–1015.

Santos, R. A., and Haimovici, M. 2001. Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21–34°S). Fisheries Research, 52: 99–112.

Schakner, Z. A., Lunsford, C., Straley, J., Eguchi, T., and Mesnick, S. L. 2014. Using models of social transmission to examine the spread of longline depredation behavior among sperm whales in the Gulf of Alaska. PLoS One, 9: e109079.

Schorr, G. S., Falcone, E. A., Moretti, D. J., and Andrews, R. D. 2014. First long-term behavioural records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. PLoS One, 9: e92633.

Sigler, M. F., Lunsford, C. R., Straley, J. M., and Liddle, J. B. 2008. Sperm whale depredation of sablefish longline gear in the northeast Pacific Ocean. Marine Mammal Science, 24: 16–27.

Sivle, L. D., Kvadsheim, P. H., Fahlman, A., Lam, F. P. A., Tyack, P. L., and Miller, P. J. O. 2012. Changes in dive behaviour during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. Frontiers in Aquatic Physiology, 3: 400.

Söffker, M., Trathan, P., Clark, J., Collins, M. A., Belchier, M., and Scott, R. 2015. The impact of predation by marine mammals on Patagonian Toothfish longline fisheries. PLoS One, 10: e0118113.

Straley, J., O'Connell, V., Liddle, J., Thode, A., Wild, L., Behnken, L., Falvey, D., *et al.* 2015. Southeast Alaska Sperm Whale Avoidance Project (SEASWAP): a successful collaboration among scientists and industry to study depredation in Alaskan waters. ICES Journal of Marine Science, 72: 1598–1609.

Straley, J. M., Schorr, G. S., Thode, A. M., Calambokidis, J., Lunsford, C. R., Chenoweth, E. M., O'Connell, V. M., *et al.* 2014. Depredating sperm whales in the Gulf of Alaska: local habitat use and long distance movements across putative population boundaries. Endangered Species Research, 24: 125–135.

Teloni, V., Johnson, M. P., Miller, P. J. O., and Madsen, P. T. 2008. Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. Journal of Experimental Marine Biology and Ecology, 354: 119–131.

Thode, A., Mathias, D., Straley, J., O'Connell, V., Behnken, L., Falvey, D., Wild, L., *et al.* 2015. Cues, creaks, and decoys: using passive acoustic monitoring as a tool for studying sperm whale depredation. ICES Journal of Marine Science, 72: 1621–1636.

Thode, A., Straley, J., Mathias, D., Wild, L., Falvey, D., O'Connell, T., and Behnken, L. 2012. Reducing sperm whale depredation via decoy deployments and active deterrent testing. North Pacific Research Board Final Report 0918, 235 pp.

Tixier, P. 2012. Depredation par les orques (Orcinus Orca) et les cachalots (*Physeter macrocephalus*) sur les palangriers _a la legine australe dans la ZEE de l'archipel de Crozet [Depredation of killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) on the Patagonian toothfish longline fishery in the Crozet and Kerguelen EEZs]. Ph.D. dissertation, CEBC-CNRS, University of Aix-Marseille II, Marseille, France. 367 pp. Available at: http://www.theses.fr/en/2012AIXM4096.

Tixier, P., Garcia, J. V., Gasco, N., Duhamel, G., and Guinet, C. 2015b. Mitigating killer whale depredation on demersal longline fisheries by changing fishing practices. ICES Journal of Marine Science, 72: 1610–1620.

Tixier, P., Gasco, N., Duhamel, G., and Guinet, C. 2015a. Habituation to an acoustic harassment device (AHD) by killer whales depredating demersal longlines. ICES Journal of Marine Science, 72: 1673–1681.

Tixier, P., Gasco, N., Duhamel, G., and Guinet, C. 2016. Depredation of Patagonian toothfish (*Dissostichus eleginoides*) by two sympatrically occurring killer whale (*Orcinus orca*) ecotypes: insights on the behavior of the rarely observed type D killer whales. Marine Mammal Science, 32: 983–1003.

Tixier, P., Gasco, N., Duhamel, G., Viviant, M., Authier, M., and Guinet, C. 2010. of Patagonian toothfish fisheries with killer and sperm whales in the Crozet Islands Exclusive Economic Zone: an assessment of depredation levels and insights on possible mitigation strategies. CCAMLR Science, 17: 179–195. Interactions

Towers, J. R. 2015. Final Report for Contract as Cetacean Research Technician for the Government of South Georgia and South Sandwich Islands in 2015.

Tyack, P. L., Johnson, M., Aguilar Soto, N., Sturlese, A., and Madsen, P. T. 2006. Extreme diving of beaked whales. Journal of Experimental Biology, 209: 4238–4253.

van den Hoff, J., Kilpatrick, R., and Welsford, D. 2017. Southern elephant seals (*Mirounga leonina* Linn.) depredate toothfish longlines in the midnight zone. PLoS One, 12: e0172396.

Watkins, W. A., Daher, M. A., Dimarzio, N. A., Samuels, A., Wartzok, D., Fristrup, K. M., Howey, P. W., *et al.* 2002. Sperm whale dives tracked by radio tag telemetry. Marine Mammal Science, 18: 55–68.

Watkins, W. A., Moore, K. E., and Tyack, P. L. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. Cetology, 49: 1–15.

Werner, T. B., Northridge, S., Press, K. M., and Young, N. 2015. Mitigating bycatch and depredation of marine mammals in longline fisheries. ICES Journal of Marine Science, 72: 1576–1586.

Whitehead, H. 2003. Sperm Whales: Social Evolution in the Ocean. University of Chicago Press, Chicago. 456 pp.

Whitehead, H. 2009. Sperm whale: *Physeter microcephalus*. *In* Encyclopedia of Marine Mammals. 2nd edn, pp. 1091–1097. Ed.

By W. F. Perrin, B. Wursig, and J. G. M. Thewissen. Academic Press, San Diego, California.

Wong, R. M. 1999. Tarvana revisited: decompression illness after breath-hold diving. SPUMS Journal, 29: 126–131.

Wright, B. M., Ford, J. K. B., Ellis, G. M., Deecke, V. B., Shapiro, A. D., Battaile, B. C., and Trites, A. W. 2017. Fine-scale foraging movements by fish-eating killer whales (*Orcinus orca*) relate to the vertical distributions and escape responses of salmonid prey (*Oncorhynchus* spp.). Movement Ecology, 1: 1181.

Wright, B. M., Stredulinsky, E. H., Ellis, G. M., and Ford, J. K. B. 2016. Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish eating killer whales, *Orcinus orca*. Animal Behaviour, 115: 81–95.

Yamada, T. K., Uni, Y., Amano, M., Brownell, Jr, R. L., , Sato, H., Ishikawa, S., Ezaki, I., *et al.* 2007. Biological indices obtained from a pod of killer whales entrapped by sea ice off northern Japan. Report SC/59/SM12 to the IWC Scientific Committee.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. 2009. Mixed Effects Models and Extensions in Ecology with R Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Handling editor: Simon Northridge