



Mitigating killer whale depredation on demersal longline fisheries by changing fishing practices

Paul Tixier^{1*}, Jade Vacquie Garcia¹, Nicolas Gasco², Guy Duhamel², and Christophe Guinet¹

¹Centre d'Etudes Biologiques de Chizé (CEBC), CNRS and Université de La Rochelle, Villiers en Bois UMR7372, France

²Département des Milieux et Peuplements Aquatiques, Muséum national d'histoire naturelle, CP 26, 43 rue Cuvier, Paris 75005, France

*Corresponding author: tel: +33 05 49 09 96 04; fax: +33 05 49 09 65 26; e-mail: tixier@cebc.cnrs.fr

Tixier, P., Vacquie Garcia, J., Gasco, N., Duhamel, G., and Guinet, C. Mitigating killer whale depredation on demersal longline fisheries by changing fishing practices. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsu137.

Received 21 March 2014; revised 14 July 2014; accepted 22 July 2014.

Odontocete depredation on longlines involves socioeconomic and conservation issues with significant losses for fisheries and potential impacts on wild populations of depredating species. As technical solutions to this conflict are limited and difficult to implement, this study aimed to identify fishing practices that could reduce odontocete depredation, with a focus on killer whales (*Orcinus orca*) interacting with Patagonian toothfish (*Dissostichus eleginoides*) longliners off the Crozet islands. Data collected by fishery observers from 6013 longline sets between 2003 and 2013 allowed us to statistically detect the significant influence of five operational variables using GLMMs. The probability of interactions between vessels and killer whales was decreased by (i) the number of vessels operating simultaneously in the area: the limited number of depredating killer whales may induce a dilution effect with increased fleet size, and (ii) depth of longline sets: vessels operating in shallow waters may be more accessible to whales that are initially distributed on peri-insular shelves. The cpue was negatively influenced by (iii) length of longlines: longer sets may provide killer whales access to a greater proportion of hooked fish per set, and positively influenced by (iv) hauling speed: increased speed may shorten the time during which toothfish are accessible to whales during hauling. The time it takes for killer whales to reach vessels was positively correlated to (v) the distance travelled between longline sets with an estimated threshold of 100 km beyond which whales seem to temporarily lose track of vessels. These findings provide insightful guidelines about what fishing strategy to adopt given these variables to reduce killer whale depredation here and in similar situations elsewhere. To a greater extent, this study is illustrative of how collaborative work with fishermen in a fully controlled fishery framework may lead to the definition of cost-limited and easy-to-implement mitigation solutions when facing such human-wildlife conflict.

Keywords: demersal longline, depredation, fishing practice, killer whale, mitigation.

Introduction

Depredation of marine predators on fisheries, i.e. the direct removal of captured fish from fishing gear, represents a major human-wildlife conflict as it involves significant socioeconomic and conservation issues (Northridge, 1991; Treves and Karanth, 2003; Woodroffe *et al.*, 2005; Read, 2008). Human responses to such conflict have changed tremendously over the past 50 years. Responses switched from mass killings of individuals or populations involved in depredation on fisheries, to protection and conservation acts regarding these species (Northridge, 1991; Ford *et al.*, 2000). Conservation has become a new factor in the management of depredation to preserve the protected species while maintaining

strong economic returns and ensuring the ecological sustainability of fisheries involved (Brotons *et al.*, 2008; Read, 2008).

Longline fisheries were reported as the most exposed to interactions with marine predators of all fisheries and experience depredation worldwide. For instance, pelagic longlines targeting tuna (*Tuna* spp.) and swordfish (*Xiphias gladius*) are depredated by sharks and marine mammals such as short finned pilot whales (*Globicephalus melas*) and false killer whales (*Pseudorca crassidens*) in tropical and subtropical waters (Baird and Gorgone, 2005; Mooney *et al.*, 2009; Rabearisoa *et al.*, 2012). In the Straits of Gibraltar, killer whales (*Orcinus orca*) depredate drop lines targeting bluefin tuna

(*Thunnus thynnus*) (Guinet *et al.*, 2007). In higher latitudes, killer whales and sperm whales (*Physeter macrocephalus*) deplete local demersal longline fisheries targeting sablefish (*Anoplopoma fimbria*) in North Pacific (Dahleim, 1988; Hill *et al.*, 1999; Matkin *et al.*, 2007; Sigler *et al.*, 2008) and Patagonian toothfish (*Dissostichus eleginoides*) in the Southern hemisphere (Hucke-Gaete *et al.*, 2004; Purves *et al.*, 2004; Roche *et al.*, 2007). In addition to the heavy economic losses such depredation can cause to fishermen and fishing companies, it may also negatively impact the marine mammal population involved, with lethal retaliation from fishermen (use of explosives or firearms to repel the animals), and incidental death of or serious injuries to animals caught on fishing gear (Lewison *et al.*, 2004). However, depredation, which may also provide highly energetic and easy to catch resource to predators (Botsford *et al.*, 1997), may encourage marine mammals to adopt this feeding strategy despite the associated risks.

Various mitigation techniques have been proposed by fishers, fishery managers and researchers, which can be broadly categorized as behavioural, spatial, acoustic, or physical. For instance, technological approaches such as acoustic harassment device (Jefferson and Curry, 1996) or the switch to pot fishing (Pilling *et al.*, 2001; Sigler *et al.*, 2004) have been tested to reduce depredation on Patagonian toothfish fisheries but they brought non-promising results (Gasco *et al.*, 2010). Behavioural mitigation techniques involving changes to fishing behaviour have been poorly investigated as they remain difficult to implement in fisheries if the economic benefits are not immediately apparent (Hamer *et al.*, 2012). Indeed, the few studies available emphasize the difficulty in suppressing or significantly reducing depredation while maintaining economically sustainable profits for fishermen, and recommend increased research effort on those operational variables (i.e. fishing behaviour of skippers) of longline fisheries that could influence depredation levels. However, such research often requires a combination of collaborative work with fishing companies, access to fishing data, full control of activity within fishing areas with strict regulations and fishery observers, and ideally the parallel monitoring of the marine mammal populations involved. The global objective of such approaches addresses optimal foraging theory (MacArthur and Pianka, 1966) such that increasing the foraging cost for the predator decreases its foraging profitability and decreases the net energy intake per unit time that an animal can expect from depredating fishing gears.

The longline fishery for Patagonian toothfish operating off the Crozet Islands (French EEZ—Southern Indian Ocean S 46°25'; E 51°59') meets most of these criteria through a long-term collaboration between fishing companies, governmental fishery managers, and scientists studying both fish stocks and the local killer whale and sperm whale populations. The fishery started in 1996 with both authorized (licensed) and unauthorized (IUU or Illegal, Unreported, Unregulated) fishing vessels. Illegal fishing was significant until 2002 and had major negative impacts on both fish stocks and the Crozet killer whale population. The latter underwent a 50% decline during the 1990s mostly due to additional mortality caused by poachers using firearms and explosives to repel whales depredating their longlines (Poncelet *et al.*, 2010). Since 2003 and the establishment of high-level surveillance efforts from the French Navy within the Crozet EEZ, illegal fishing has become negligible and there are only seven national longliners authorized to operate in the area. Each vessel has a fishery observer aboard for every fishing trip and is subject to strict regulations on catch (one quota per

vessel), fish size, fishing depths, geographical distribution of the fishing effort, and bycatch. For instance, longlines must be set at depths >500 m to avoid catching juvenile Patagonian toothfish and vessels usually operate on the edges of the peri-insular shelf and surrounding banks. The fishing fleet operates alternately between the two main French fishing grounds in the Indian sector of the Southern Ocean: the Kerguelen and Crozet EEZ. The total allowed catch differs between the two locations as the Kerguelen EEZ is significantly larger. The Crozet annual catch (see CCAMLR statistical bulletins) is ~one-fifth of the Kerguelen annual catch. The Kerguelen EEZ is closed to fishing for 40 days per year (February–March), and so the fishing effort of the fleet is mainly focused within the Crozet EEZ during this period. Both killer whales and sperm whales were reported to deplete longline sets when the first vessels arrived in 1996 (Roche *et al.*, 2007) and interaction rates with killer whales (mean = $42 \pm 14\%$ between 2003 and 2008—Tixier *et al.*, 2010) are significantly higher than interaction rates reported in other locations such as Chile and South Georgia (Hucke-Gaete *et al.*, 2004; Purves *et al.*, 2004) where depredation also occurs on Patagonian toothfish. Killer whale depredation in the Crozet waters was found to greatly reduce catch per unit effort (cpue) and the overall biomass of depredated toothfish taken by killer whales was estimated at 116 t yr^{-1} between 2003 and 2010 (Tixier, 2012).

The way killer whales detect vessels and deplete longlines remains poorly understood. Thode *et al.* (2005) showed for instance that sperm whales detect vessels acoustically. Both vessel acoustic signature and acoustic behaviour can vary depending on whether vessels are setting/hauling longlines or travelling, which in turn influences their probability of being detected (Thode *et al.*, 2007). Although killer whales are likely to also detect vessels acoustically, their detection range and their initial position before a vessel arrives on a fishing ground are unknown. The Crozet killer whales feed on a wide range of natural prey items such as seals, penguins, large whales, and fish (Guinet, 1992). Great variations in the level of interaction with fisheries were detected between the matriline (i.e. social units composed of on average 3–4 constantly associated individuals) composing the population (Tixier *et al.*, 2010). Foraging areas of most matriline are known to be inshore waters of the islands during specific periods of the year such as the southern elephant seal breeding period (October–December; Guinet, 1991; Guinet and Bouvier, 1995), but little is known about their foraging areas for the rest of the year. As it is common to observe killer whales reaching a vessel only a few hours after it started to operate on a given fishing ground, it is likely that their initial position was on the oceanic shelf within 30–50 km range (C. Guinet, personal communication). Another unanswered question is whether or not killer whales forage naturally on Patagonian toothfish in areas where they are at depths that are accessible to killer whales. Unlike sperm whales that can dive up to 3000 m and have toothfish as a natural component of their diet (Yukhov, 1982), killer whales are limited to 400–600 m maximum dive depths (Similä and Ugarte, 1993; R. Pitman, personal communication) and can therefore only access fish on hooks during hauling between the surface and a few hundred meters depths. Photo-identification data collected by fishery observers aboard longliners (Gasco *et al.*, 2013) allowed for the identification of all depredating individuals ($n = 78$ in 2012) and also showed that some matriline are able to actively follow vessels travelling from one fishing ground to another, sometimes over great distances (>300 km; Tixier *et al.*, 2010). Killer and

sperm whales are often co-occurring when depredating longlines (Roche *et al.*, 2007; Tixier *et al.*, 2010).

This study focused on operational variables that could significantly reduce interactions with killer whales through a change of fishing behaviours by vessel skippers. Access to fishing data collected by fishery observers aboard longliners from 2003 to 2013 paired with extensive photo-identification data on depredating killer whales provided a unique opportunity to model both killer whale interactions with fisheries and cpue to determine which operational variables may influence depredation levels the most. The final aim was to provide recommendations then guidelines to vessels to reduce interactions with killer whales and losses caused by depredation.

Material and methods

Selection of operational variables

Preliminary analyses showed significant between-vessels differences of interaction rates with killer whales suggesting the influence of intrinsic factors (e.g. variations of detectability correlated to the acoustic signature and amplitude of vessels) and/or the influence of between-vessels variations of fishing behaviours. Among the latter, there are variables that can be controlled by skippers that can influence cpue (here expressed in g of toothfish per hook) in the absence or presence of killer and sperm whales depredating longlines (Tixier *et al.*, 2010). These variables were selected according to existing knowledge, combining technical specificities of demersal longlining, biology of killer whales involved, and behavioural data on the way they interact with vessels. Under specific assumptions, we thus examined (i) *length of longlines*: theoretically, the amount of depredated fish increases with fishing effort (i.e. number of set hooks) and therefore with total length of longline set. In addition, the more hooks per longline, the more time it takes for fishermen to haul a set, and thus the more time will be available for killer whales to locate then interact with that set. (ii) *Hauling speed* of longline sets: one may assume that an increased hauling speed will limit time available for the whales to remove and consume depredated toothfish from hooks. (iii) *Distance travelled by a vessel* to leave an area where it was confronted by depredation to start fishing in another area and the time it takes for killer whales to find the vessel again. Given the travelling speed of vessels, the travelling speed of killer whales and their vessel detection range, one may expect a distance threshold beyond which the likelihood of being depredated again in the new fishing area is reduced. (iv) *Depth*: as fishing grounds are ranging from 500 to 2000 m deep from the slope of the peri-insular shelf to the deep-sea, one may expect a negative effect of depth of longline set on probability of interaction with killer whales if their initial position before detecting the vessel is on the slope closer to the islands and at depths which are within normal diving depths of killer whales. (v) *Number of vessels* operating simultaneously within the Crozet EEZ: one may expect a decreased probability of interaction with killer whales when the number of simultaneous vessels increases through a dilution effect given the limited number of depredating individuals. (vi) *Seasonality*: the probability of Crozet killer whale interaction with fisheries may be lower during specific periods of the year according to their ecology. These variables were investigated using both fishing data and killer whale photo-identification data.

Fishing data and photo-identification

The fishing data used in analyses were retrieved from the "PECHEKER" database host at the Muséum National d'Histoire

Naturelle (Martin and Pruvost, 2007). The data were collected between September 7 2003 and February 6 2013. In all, 7467 longlines were set and hauled during that period within the Crozet EEZ by the seven licensed vessels. For each longline set coordinates of first and last hooks were recorded. We used single location data for longline sets in the analyses that were the mid position between the two end extremities of a longline set. Date and time of hauling of the first hook of longline sets were used for time variables. For each longline set, fishery observers recorded fishing effort (number of hauled hooks) and the Patagonian toothfish biomass (weight of all fish hauled aboard in g), which allowed us to calculate cpue (g of toothfish hook⁻¹). Depth (m) was recorded for both ends of a longline set and we used a single mean depth value for each set. Length of longline sets (m) was calculated with the total number of hooks and spacing between hooks (either 1.2 or 1.5 m depending on vessels). Mean hauling speed (hook min⁻¹) was calculated with the total number of hooks on a longline set and the total time spent hauling these hooks (min).

Killer whale depredation events on longlines were recorded during hauling through three distinct states: presence (1), absence (0), and non-observed (2). The combined effort of observers and skippers provided observation data on 100% of all longline hauling process. The presence data were entered in the database (1) when killer whales had typical depredation behaviour towards longlines: i.e. they repeated dives within a 500 m range of the vessel and came up to the surface usually surrounded by birds, which is indicative that they were feeding on depredated toothfish. Both observers and skippers were trained to distinguish between a true depredation event and a sighting of killer whales that were travelling near the vessel without interacting with the longline set that was being hauled out. In that case, or if killer whales were not observed and weather and light conditions allowed us to confirm the absence of depredation, they entered (0) data in the database. Non-observed data were entered (2) when weather (e.g. fog), sea, and/or light conditions brought uncertainty to either the presence or the absence of killer whales depredating a longline set. We removed all sets for which a (2) was entered as they could not be included in analyses. Consequently, the dataset was filtered down to 6013 longline sets (i.e. 80.5% of the total number of longline sets). The (0) and (1) data were later used to model the killer whale interaction with longlines.

Fishery observers were all equipped with DSLR cameras and minimum 300 mm lenses on every fishing trip during the study period. They collected photo-identification data on killer whales interacting with longline sets according to established protocols (Bigg *et al.*, 1990; Gasco *et al.*, 2013). Photo-identification effort was possible on only a sample of all depredated longline sets because observers were also in charge of many other tasks aboard such as fish stock assessment. Killer whales were identified through natural markings on dorsal fin and saddle patch, and individual representations on photographs were analysed and entered into a database.

Modelling killer whale interaction with longline sets

The presence/absence of killer whales interacting with longline sets [$P(inter)$] was investigated in relation to the number of vessels operating simultaneously on the Crozet fishing grounds ($nbvessels$), the month ($month$), and the depth ($depth$) at which longlines were set. The $nbvessels$ variable ranged from 1, when vessels were operating alone, to 7, when the whole fleet was present. The $month$ variable ranged from 1 for January to 12 for December and the $depth$ variable

ranged from 500 to 2500 m. When killer whales find a vessel, they usually depredate series of longline sets that are hauled successively in the same fishing spot by this vessel. Such time- and space-autocorrelation may lead to biased results. We added the fishing trip of vessels (*trip*) as a random intercept term and we used an autoregressive variance–covariance matrix (*corAR1*) within each fishing trip of each vessel. The number of longline sets per trip per vessel ranged from 4 to 137 and longline sets were numbered chronologically according to date and time of hauling, which allowed us to include the *corAR1* term in models. We thus used a generalized linear mixed model (GLMM) (function *glmmPQL* in MASS package in R 2.10.1—R Development Core Team, 2010). Before modelling, all the explanatory variables were standardized (centred and scaled) to facilitate the convergence of the model (Zuur et al., 2009). The model was fitted with a binomial distribution. The complete GLMM was built as such:

$$\text{Model 1 : } P(\text{inter}) \sim \text{month} + \text{depth} + \text{nbvessels}, \text{ random} \\ = \sim 1|\text{trip}, \text{ correlation} = \text{corAR1}()$$

with the *month*, *depth*, and *nbvessels* variables as fixed effects and the *trip* variable as random effect.

Modelling cpue

Raw cpue data were beta distributed and were first log transformed to allow for testing of fixed effects with the random term and autocorrelation included. The effect of two operational variables (*length* and *haulspeed*) a temporal variable *month*, and the presence of depredation by killer whales during hauling (*presoo*) was tested on the log-transformed raw cpue (*logcpue*). Because the effects of the two operational variables could be different in the presence or absence of depredation by killer whales during hauling, the interactions of *length* and *haulspeed* with *presoo* were also tested in the model. cpue is greatly dependent upon Patagonian toothfish resource distribution regardless of depredation by killer whales. We thus expect series of longline sets that were hauled successively within a short timeframe in the same fishing spot by a given vessel to provide correlated cpues. Similarly to model (1), such time- and space-autocorrelation was also accounted in the analysis using the fishing trip of vessels (*trip*) as a random intercept term and an autoregressive variance–covariance matrix (*corAR1*) within each fishing trip of each vessel. We also used a GLMM (function *glmmPQL* in MASS package in R 2.10.1—R Development Core Team, 2010) to model *logcpue*. The model was fitted with a Gaussian distribution. Before modelling, all the explanatory variables were standardized (centred and scaled) to facilitate the convergence of the model. The complete GLMM was built as such:

$$\text{Model (2) : } \log\text{cpue} \sim \text{length} + \text{haulspeed} + \text{presoo} \\ + \text{length} * \text{presoo} + \text{haulspeed} * \text{presoo}, \text{ random} \\ = \sim 1|\text{trip} + \text{correlation} = \text{corAR1}()$$

with *length*, *haulspeed*, *presoo* and the interactions terms *length*presoo* and *haulspeed*presoo* as fixed effects and the *trip* variable as random effect.

Distance travelled by vessel to avoid killer whales

Photo-identification data paired with fishing data were used to model the time it takes for a killer whale matriline to reach a vessel when the latter moved from one longline set to another and

when this matriline depredated both sets (*timelag*). The dataset was filtered down to pairs of longline sets that met specific criteria: (i) both longline sets were hauled by the same vessel during the same trip, (ii) photo-identification effort was performed during hauling of both sets, and (iii) data confirmed that the same matriline depredated both sets. It often happens that several matriline depredate simultaneously the same longline sets. In this case, data were replicated for each matriline. At the end, there were 637 pairs of longlines that met all criteria and that were used in the analysis. Time between hauls of longline sets was calculated using date and time of the last hauled hook of the longline set, and date and time of the first hauled hook of the next longline set that is depredated by killer whales and by the same matriline. The R function “*rdist.earth2*” was used to calculate distance between these two longlines in kilometres.

Raw *timelag* data was beta distributed and was first log transformed (*logTimelag*). Then, *logtimelag* was investigated in relation to the distance travelled by vessels between longline sets (*dist*). It is likely that whether or not killer whales decide to follow vessels moving from one longline set to another may differ between matriline. Significant between-matriline variations of depredation level have been detected in previous studies and preliminary results suggested that some matriline actively seek vessels in a broad area while others depredate longlines in a more opportunistic way within smaller areas (Tixier et al., 2010). The matriline (*matriline*) was thus included in the model as a random intercept term to account for such variations and to improve model performance. In the same way, the number of vessels operating simultaneously on the Crozet fishing grounds may theoretically influence the decision made by killer whales to follow one vessel or to switch to another. For this reason, the number of vessels (*nbvessels*) was also added in the model as a random intercept term. The full model was thus a GLMM (function *lme* in nlme package in R 2.10.1). The model was fitted with a Gaussian distribution. The complete GLMM was built as such:

$$\text{Model (3) : } \log\text{timelag} \sim \text{dist}, \text{ random} \\ = \text{list}(\sim 1|\text{matriline}, \sim 1|\text{nbvessels})$$

with the *dist* variable as a fixed effect and the *matriline* and the *nbvessels* variables as random effects.

Results

Between 2003 and 2013, killer whales depredated 2424 longlines of the 6013 sets, which represented an interaction rate of 40.3% over the whole period within the Crozet EEZ (Figure 1). Fishery observers collected killer whale photo-identification data during hauling of 762 longline sets. The analysis of 53 813 individual representations on photographs allowed us to identify 125 killer whales that interacted with at least one longline set between 2003 and 2013 and that belong to 33 different matriline (see catalogue—Tixier et al., 2014).

Modelling killer whale interaction with longlines

The frequency of interactions of killer whales with longline sets was negatively influenced by the number of vessels and by the depth (Table 1). The more vessels operating simultaneously, and the deeper the longline sets, the lower the probability that killer whales would interact with longline sets of a given vessel. For instance, from Model 1 output estimates, the probability of whale

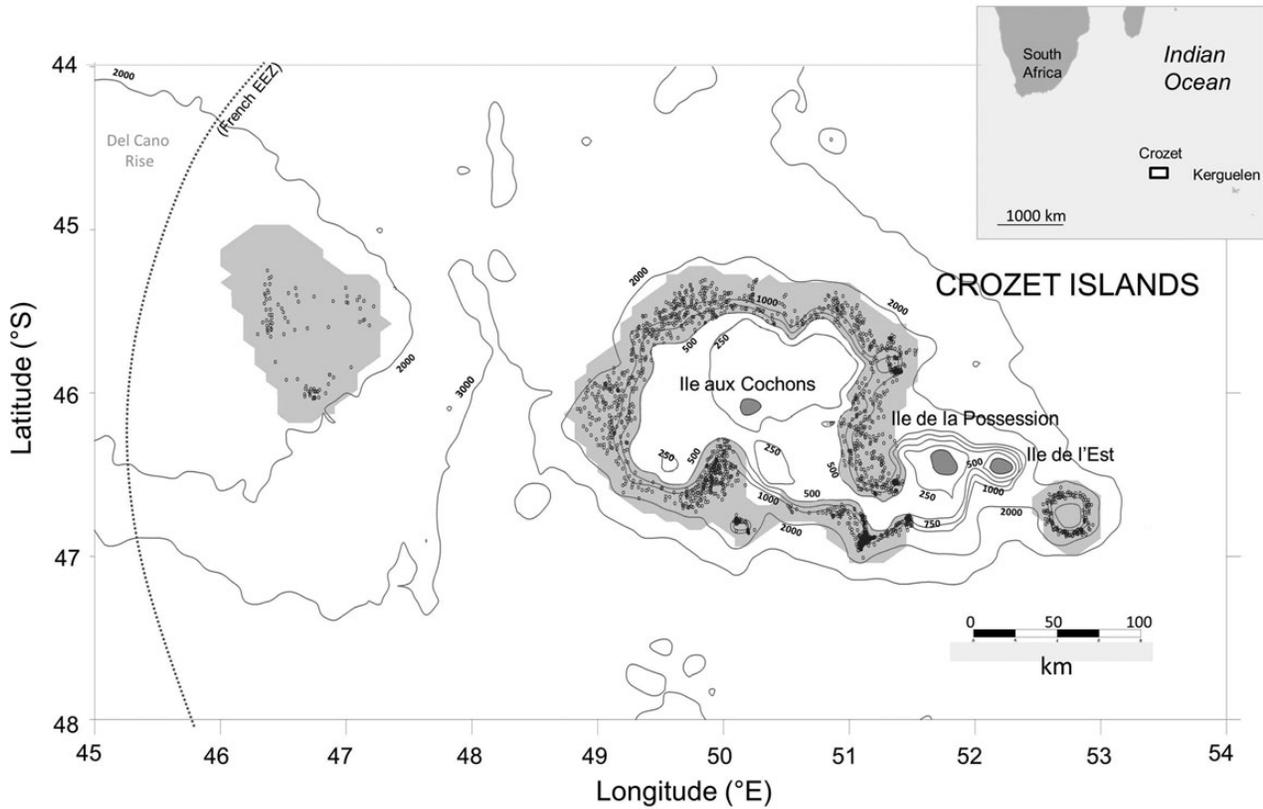


Figure 1. Study area: the Crozet islands and longlines that were depredated by killer whales between 2003 and 2013 (black dots). Patagonian toothfish longline fishing grounds around the islands are drawn (grey background) as well as the Crozet EEZ western limit (dashed line). 250, 500, 750, 1000, 2000, and 3000 m isobaths are represented. NB: the area surrounding the Possession and Est islands is a closed area for fisheries.

Table 1. Parameter estimates of the complete GLMM of killer whale interaction with longline $P(inter)$ (Model 1)

Parameter	Value	SE	d.f.	t-value	p-value
intercept	-0.34	0.083	5852	-4.05	< 0.001
month	0.089	0.073	5852	1.22	0.22
nbvessels	-0.21	0.058	5852	-3.71	< 0.001
depth	-0.34	0.036	5852	-9.35	< 0.001

Fixed effects were the month (*month*), the number of simultaneously operating vessels (*nbvessels*), and the depth of longline sets (*depth*). Vessels' fishing trips (*trip*) were included as random intercept term and autocorrelation was tested as nested effect in *trip* through an autoregressive variance-covariance matrix (*corAR1*).

interaction on sets of a single vessel operating in the EEZ increased by 67% compared with the scenario of six other additional vessels operating simultaneously with that vessel (Figure 2). Similarly, estimated probability of interactions between longlines set in shallow waters (between 500 and 700 m) and killer whales from Model 1 increased by 83% compared with interactions between longlines set in deep waters (> 1700 m—Figure 3) and killer whales. No seasonal variations on the killer whale interaction probability were detected as the month effect was not significant in the Model 1.

Modelling cpue

cpue was found to be negatively influenced by killer whale depredation and by the length of longline sets, both as additive effects

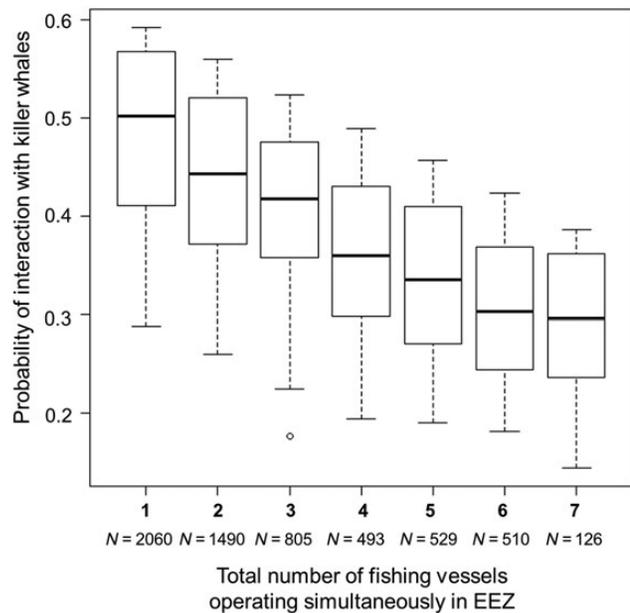


Figure 2. Influence of the number of vessels operating simultaneously on the Crozet EEZ fishing grounds on the probability of interaction with killer whales predicted by the Model 1 and represented as boxplots. The number of longlines (N) hauled between 2003 and 2013 when vessels were operating alone (1) or simultaneously with others (2 : 7) is indicated.

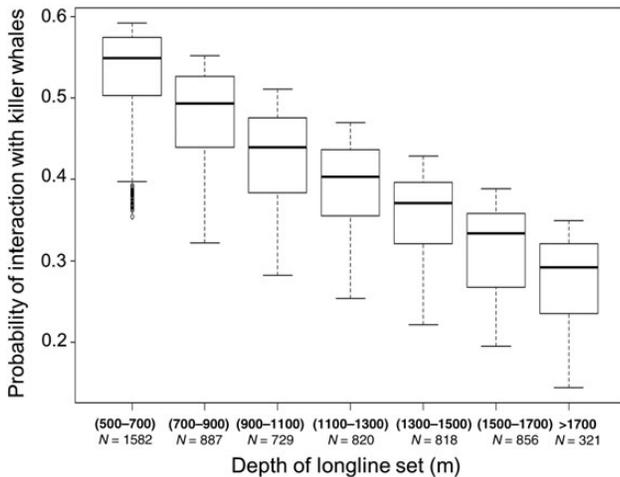


Figure 3. Influence of depth of longline sets on the probability of interaction with killer whales predicted by the Model 1 and represented as boxplots of 200 m depth breaks. The number of longlines (N) hauled between 2003 and 2013 in each depth break is indicated.

Table 2. Parameter estimates of the complete GLMM of cpue (*logcpue*) (Model 2)

Parameter	Value	SE	d.f.	t-value	p-value
intercept	4.60	0.058	5849	79.03	<0.001
month	0.039	0.043	5849	0.80	0.43
length	-0.089	0.025	5849	-3.60	<0.001
haulspeed	-0.039	0.021	5849	-1.82	0.070
presoo	-0.77	0.035	5849	-22.38	<0.001
length*presoo	-0.068	0.032	5849	-2.13	0.033
haulspeed*presoo	0.093	0.028	5849	3.29	0.001

Fixed effects were the month (*month*), the length of longline sets (*length*), hauling speed of longlines (*haulspeed*), and the presence of killer whales depredating longline during hauling (*presoo*), either as additive (+) or interaction (*) variables. Vessels' fishing trips (*trip*) were included as random intercept term and autocorrelation was tested as nested effect in *trip* through an autoregressive variance-covariance matrix (*corAR1*).

and interaction terms (Table 2). In the absence of killer whales, fitted values from Model 2 suggested that short longline sets, such as sets ranging from 2 to 5 km in length, had greater cpue (>100 g hook $^{-1}$) than sets that were >20 km (cpue <70 g hook $^{-1}$) (Figure 4a). The presence of killer whales significantly reduced cpue independently from the other variables but its interaction with longline length was also significant in Model 2. Figure 4a indeed suggests that cpue in the presence of killer whales is higher for short longline sets (e.g. cpue >60 g hook $^{-1}$ for sets <5 km vs. cpue <30 g hook $^{-1}$ for sets >20 km from fitted model estimates). Although no overall effect of hauling speed was detected as an additive effect, its interaction with the presence of killer whales was significant and positive on cpue (Table 2). Figure 4b and fitted estimates from Model 2 suggested that in the presence of killer whales, longline sets that were slowly hauled had lower cpue (e.g. cpue <50 g hook $^{-1}$ for hauling speed of 20 hooks min $^{-1}$) than longline sets that were hauled at high speed (e.g. cpue >60 g hook $^{-1}$ for hauling speed of 70 hooks min $^{-1}$). No seasonality in cpue was detected as the month effect was not significant in Model 2 (Table 2).

Distance travelled by vessel to avoid killer whales

The amount of time it takes for a given killer whale matriline to reach a vessel after it travelled from one longline set to another was positively influenced by the distance between the two sets (value = 0.025; SE = 0.001; DF = 540; t -value = 19.5; p -value < 0.001). Estimates from fitted Model 3 and associated CIs suggested that killer whales quasi-systematically reach vessels within a 1 day lag when longline sets are spaced by <50 km, whereas it takes them on average 2.4 ± 0.2 days to reach vessels when they travelled from two sets spaced apart by 100 km (Figure 5). However, raw data also showed that in some cases, killer whales reach vessels faster, despite travelling greater distances between longline sets. For instance, it took 1 day for a matriline to start depredating again after a vessel moved 180 km to another area.

Discussion

This study indicated that five fishing variables could affect killer whale depredation levels on Patagonian toothfish longlines set in the Crozet EEZ. Three variables had an influence on the probability of killer whales interacting with a fishing vessel: (i) number of vessels operating simultaneously, (ii) depth of longline sets, and (iii) distance travelled between a depredated set and a new one. Two variables influenced the amount of fish loss caused by depredation: (i) length of longline sets and (ii) hauling speed. Based on this study, by acting on these parameters the Crozet fishery should be able to reduce the level of depredation. However, some of these operational decisions may be efficient only under certain conditions and need to be discussed to optimize and propose a fishing strategy aimed at avoiding and reducing depredation levels. Each of the five factors identified will be discussed in further details.

Length of longline sets

Short sets (<5 km) were found to limit losses caused by depredation, which is supported by previous results (Tixier et al., 2010). This may reflect cases when killer whales are not present when hauling starts, but reach longlines later during hauling, leaving parts of the set undepredated. It is indeed likely that this effect might only be significant in cases when killer whales are not present at the beginning of hauling. If whales are already present, depredation will remain high all along the hauled longline independent of its length. However, when killer whales arrive after hauling had started (depending on the time it takes them to reach a vessel once they have detected it) longline cpue was significantly lower for sets >5 km. As killer whales are likely to detect vessels acoustically, the time it takes them to reach a vessel will depend on both their initial distance to the vessel and their swimming speed. For instance, if killer whales are 50 km away from a vessel when they detect it and we assume that they are able to maintain swimming speeds of 15 km h $^{-1}$ for hours (Guinet et al., 2007), it will take them 2 h to reach that vessel. Given that a 3 km longline set bearing 3600 hooks may be hauled in 2 h at a mean hauling speed of 30 hooks min $^{-1}$, killer whales would theoretically not have access to any hook in this example. One limitation of this assumption is the length of the longline set section that links the anchor at the bottom to the buoys at the surface, which does not bear any hook, and the time it takes to haul that section depending on depth. This time may range from 15 to 45 min for depths of 500 and 1500 m respectively (N. Gasco, personal communication). If we assume that killer whales detect vessels as soon as hauling of buoys starts, then we need to account for the depth of longline

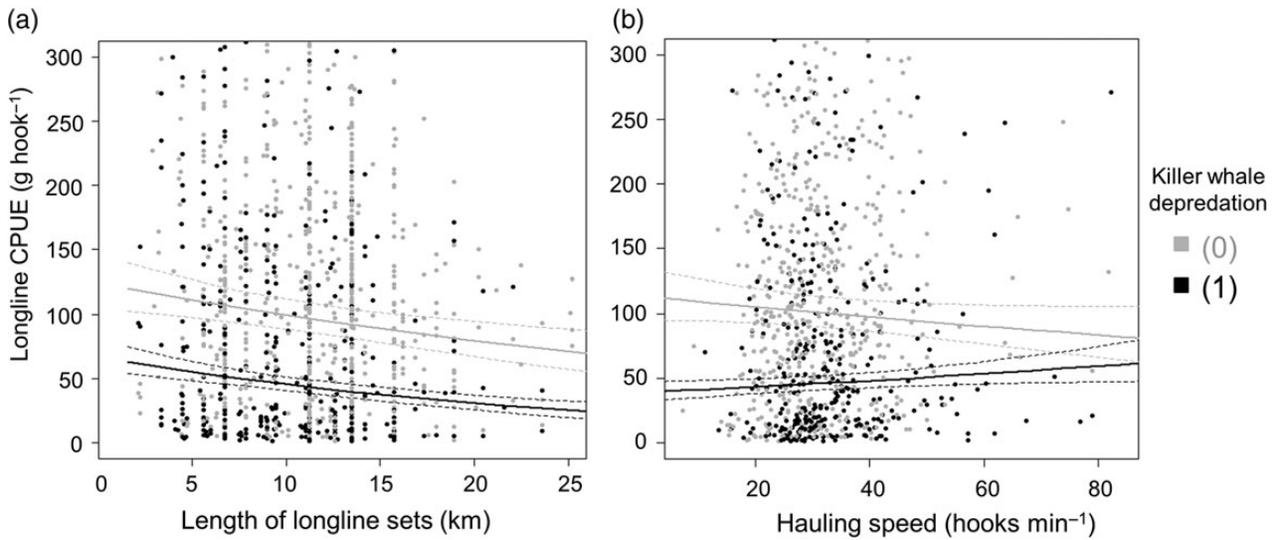


Figure 4. Effects of longline length (“length”—a) and longline hauling speed (“haulspeed”—b) on Patagonian toothfish cpue when longlines were depredated by killer whales (black) or not (grey), i.e. hauling in the absence of cetaceans. For both graphs, raw data visualization were filtered down to a 20% range from mean of the other tested operational variable. Fitted cpue estimates from Model 3 (solid curve) are represented along with the CI (dashed lines) calculated from the variance–covariance matrix of the random effect and autocorrelation of fitted model.

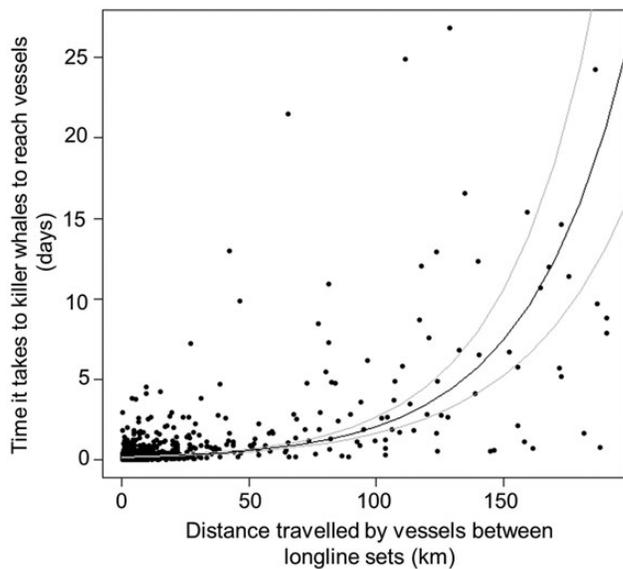


Figure 5. Influence of distance travelled by vessels between longline sets on the time it takes to a given killer whale matriline to reach vessels again. Raw data (black dots) and fitted Timelag estimates from Model 3 (solid curve) are represented along with the CI (dashed lines) of the model calculated from variance–covariance matrix of random parameters of fitted model.

sets in future estimates. Interestingly, short longline sets also had higher cpue in the absence of killer whales. This is likely because short sets may better target highly productive areas in cases of great resource patchiness at the bottom. Such an effect was detected in both the presence and the absence of killer whales, and we therefore advise fishing vessels to favour the use of short sets when they begin operating in an area if killer whales are not present. However, such recommendations may not be practically

implemented as fishermen, when arriving in a new fishing area, tend to use longer lines to find fish aggregations then use shorter lines to fish within those aggregations.

Hauling speed

Results suggest hauling speed of longline sets had a negative effect on toothfish losses when killer whales were depredating on gear. Theoretically, we expect this effect to be especially significant on highly productive fishing grounds. If we assume that killer whales have access to hooks between a depth range of 0–400 m, and that a longline set being hauled has a vertical and straight shape below the vessel, a toothfish caught on a hook may be exposed to killer whale depredation for up to 11 min if hauled at 30 hooks min⁻¹ speed (using a 1.2 m spacing between hooks), but only exposed for 6 min at 50 hooks min⁻¹ speed (calculated for 1.2 m spacing between hooks). Although these are minima estimates—as longline sets are usually curve-shaped during hauling-increased hauling speed significantly reduces the time available for killer whales to remove and handle a large amount of toothfish from hooks. Furthermore, the faster the hooked fish is moving, the more difficult it might be for the whales to remove it from the hook given the small size of toothfish compared with the generally large size of killer whales and because manoeuvrability is inversely proportional to size (Dominici, 2001). However, such mitigation techniques may have consequences on both resource management and fishermen’s work rate. First, depredation behaviour is not avoided but this approach aims to reduce the amount of fish losses. In addition, increased hauling speed is known to cause greater fish losses due to the increased drag effect and increased difficulty of securing them with a gaff when they reach the surface. Increased hauling speed requires fishermen to significantly increase their work rate aboard, with increased fish cutting and gutting rates and also faster preparation of longlines ready for the next setting (i.e. disentangling of lines and fixing hooks) which raises safety issues.

The “move on” technique

Field observation and photo-identification data suggest that when killer whales find a vessel, they remain with it and deplete all hauled longline sets in the area for days following their arrival until the vessel decides to leave. This study suggests that vessels leaving a fishing ground may have to travel sufficient distance to limit probabilities of being depredated again by the same killer whales. Similar to other reported marine mammal–fishery interaction cases (e.g. *Tilzey et al., 2006*), killer whales were found to actively follow vessels when they travel from one fishing ground to another. From the results, there is evidence that killer whales will lose contact with the vessel beyond a certain distance threshold. We may recommend vessels to move distances > 100 km as killer whales were estimated to find vessels at such distances only after at least 3 days. If vessels move shorter distances, killer whales are usually able to locate and deplete that vessel again on the new fishing ground within a day. However, the results also suggested that in some cases, matriline are able to follow vessels great distances and start depredating longline sets in the new fishing ground as soon as the first hook is hauled. It should be noted that large variations in interaction level and depredation behaviours have been reported between matriline (*Tixier et al., 2010*) with some matriline exhibiting broader depredation areas, encompassing all fishing grounds in the EEZ. It is perhaps killer whales actively search for vessels rather than opportunistically detecting them. As their usual 7 km h^{-1} swimming speed (*Guinet et al., 2007*) is lower than the travelling speed of vessels (20 km h^{-1} on average), we can hypothesize that killer whales follow the bearing of a vessel leaving a fishing location. In addition, fishing grounds are highly localized areas on the slope of the shelves and killer whales may have learnt over years to seek vessels in those areas. Cases of killer whales switching from one vessel to another vessel operating nearby are often reported. We thus recommend that vessels move to fishing grounds that are distant from other vessels that are being depredated by killer whales.

Number of simultaneous vessels

The number of vessels operating simultaneously in the Crozet EEZ significantly influenced the probability of vessel interaction with killer whales. This is likely due to the limited number of depredating killer whales present in the Crozet area. Photo-identification data suggested that all killer whales from the population have been identified (P. Tixier, unpublished). In 2012, 78 killer whales were known to be alive and to have interacted at least once with the fisheries over the 2003–2012 period. We estimated that among those 78 individuals, 14 whales belonging to four different matriline were in fact involved in nearly 70% of the depredation events. Therefore, the greater the number of vessels fishing in Crozet waters decreased the probability of killer whale interacting with a given vessel. Such probabilities may also be area-dependent according to the distribution of matriline interactions. As previously mentioned, killer whales tend to remain with a vessel once they have reached it. An increased number of vessels in the area are likely to create a “dilution” effect on a vessels’ probability of interacting with killer whales, by reducing the number of available killer whale individuals for depredation. However, recommending the fleet to operate simultaneously may be a source of concern as it may increase the probability of whales finding a fishing vessel to interact with. It is also necessary to assess—in terms of fish stock management—the consequences of a shorter but more intensive fishing season, with

potential risks of local fish depletion versus a longer and less intensive one.

Depth of longline sets

The relationship between longline set depth and the probability of killer whale interactions was negative. This supports the assumption that killer whales are initially present on the oceanic shelf before detecting vessels. Fishing at 500–600 m depths may position vessels closer to the natural distribution range of killer whales, which may make them easier to detect. Little is known about the natural distribution of Crozet killer whales except during the southern elephant seal breeding period when matriline appear to aggregate around inshore waters of islands to forage on newly weaned pups—a major component of their feeding ecology (*Guinet, 1992*). During the rest of the year, killer whales may forage on elephant seals in offshore waters as seals are distributed either on the peri-insular shelves or further offshore depending on age and sex (*McConnell et al., 2002; Bailleul et al., 2007*). Killer whales may also forage on large whales and penguins that are present offshore from islands (*Guinet, 1991; Bost et al., 1997; Gambell, 1999*). In addition, depredation behaviour was adopted by Crozet killer whales when the first fishing vessels began to operate in the area in 1996. We therefore cannot discount that Patagonian toothfish is also a natural prey item of the killer whale diet. In this instance, one may assume that depredating killer whales forage on toothfish on the peri-insular shelf where it is theoretically present at specific stages of its life cycle (*Arkhipkin et al., 2003; Laptikhovskiy et al., 2006*) when it would be accessible to killer whales. Whether killer whales are initially present in areas of high toothfish abundance—which could be identified through fishing data (i.e. longline cpue without any interaction with odontocetes)—could be examined further using spatial analysis to test the time it takes for killer whales to reach vessels in areas of varying productivity.

Costs and benefits of changing fishing behaviour

Some of the recommendations emanating from these findings and previous studies are already implemented on a voluntarily basis by some of the masters (vessel skippers). There is still a need to implement a global fishing strategy aimed at discouraging killer whales depredating fishing lines by increasing the foraging cost and decreasing the foraging benefit to killer whales interacting with the fishery. The most effective fishing strategies may require a combination of several variables or operational changes to be effective. Previous findings suggest that killer whales were less likely to interact with the fishery during the elephant seal breeding season (November–mid-December), as this is when they concentrate their foraging activity on seal pups along the Crozet Archipelago coastlines (*Tixier, 2012*). Killer whales decide either to interact with the fishing vessels or resume natural foraging habits as it becomes energetically costly for killer whales to do both due to the distance between the coastal areas and offshore fishing grounds. This finding was implemented as a recommendation in recent years when a number of fishing vessels operating within the Crozet fishing grounds began to favour the November–mid-December period. However, usually vessels operated alone in the Crozet area, which is likely to have increased their probability of interacting with killer whales as shown in this study. This may explain the undetected seasonality in probabilities of killer whale interactions using a dataset including these recent years.

This study indicates that using shorter lines may allow retrieval of the complete line before the arrival of killer whales on site. Such

practices are sometimes difficult to implement. Indeed, when arriving at a new fishing location fishermen generally search for the fish by using longer lines. They then use shorter lines to target areas with higher fish densities. As previously mentioned, hauling duration (which is likely to increase the chances that the fishing vessels will be located by killer whales) does not only depend on fishing line length but also on fishing depth. Also, when using shorter lines fishermen tend to set more lines within a given area. While shorter lines may improve the yield by targeting more precise locations, it may be difficult to manage the depredation issue based solely on altering fishing line length.

When killer whale depredation is detected it is highly beneficial to increase hauling speed. Faster hauling speed can be sustained by the crew for a limited duration if using shorter fishing lines. The “move on” strategy, when exposed to depredation can be an efficient technique but only if the vessel is moving a great enough distance (at least 100 km) from the area of a depredation event. This strategy was found to be effective in reducing the number of days a vessel is exposed to depredation. However, this practice can substantially increase the operational cost of the fishery due to fuel consumption and may not be cost-effective for the fishermen. This point requires special evaluation using specific methodology such as the one presented by Peterson *et al.* (2014). This strategy may also only be efficient when a limited number of vessels are occurring together within the Crozet zone. Otherwise, vessels leaving the grounds could inadvertently attract whales to the remaining fishing vessels still operating. Under these conditions, this fishing strategy might be beneficial at the vessel level but not at the fishery level. Although we found the level of whale–vessel interactions per vessel decreased with the number of fishing vessels, the overall whale–vessel interaction rate tended to increase with increasing number of vessels. This indicates that more matriline are interacting with vessels when more vessels are occurring within the fishing zone, which is confirmed by photo-identification data (P. Tixier, unpublished). Increasing the number of fishing vessels operating simultaneously may be beneficial at the fishing vessel level but is not beneficial at the fishery level. A clear negative relationship was found between the fishing depth and the level of interaction. However, fishing in deeper water would have direct consequences on fish stock management as fish size is known to increase with depth.

According to our current understanding of the depredation issue, the best fishing practice for reducing depredation levels is to recommend fishermen use short lines to reduce haul time when confronted to depredation. It is also recommended that fishermen retrieve all the lines in a fishing area at high hauling speed and move to a new fishing location at least 100 km away from the previous one. Such recommendations have been made to fishermen, and although initial feedback from their experience were positive, we not only need to statistically assess the benefits of changing fishing behaviour (in terms of reduction of depredation) but also assess fishing costs associated with limiting or avoiding depredation (e.g. Peterson and Carothers, 2013). A future study should also implement a modelling exercise to assess a range of fishing strategy scenarios to identify the most effective fishing strategy. This exercise could be used to maximize operational financial margins between losses from depredation and increased operational costs (i.e. additional fuel consumed and time spent without fishing) (Peterson and Carothers, 2013; Peterson *et al.*, 2014) based on strategy implementation.

Other operational variables have yet to be tested, especially regarding factors influencing detectability of vessels by killer

whales. For instance, Thode *et al.* (2007) emphasized that frequency and amplitude changes due to engine speed during hauling are acoustically attracting cues for sperm whales. Preliminary observations suggest that captains of the Crozet Patagonian toothfish longline fleet have different ways of using engine speed, which may contribute to the observed between-vessel interaction rate differences with killer whales.

Cases of killer whale depredation at high latitude are often associated with high levels of sperm whale depredation, the two species either co-occurring or depredating in different areas (Purves *et al.*, 2004; Hucke-Gaete *et al.*, 2004; Straley *et al.*, 2005; Sigler *et al.*, 2008; Tixier *et al.*, 2010). Although depredation behaviour differs between the two species (primarily because of physiological and ecological differences), these recommendations should also be tested for sperm whales in Crozet and in other locations. Although fish losses caused by sperm whale depredation off the Crozet and Kerguelen islands are less significant than losses caused by killer whales (Tixier *et al.*, 2010), sperm whales were reported to interact with >60% of longlines set in these locations (Roche *et al.*, 2007). Analyses are currently under way to test the influence of these operational variables on sperm whale depredation.

Implications for other depredation cases

Killer whale depredation is a global issue, and these findings are relevant to longline fisheries operating in regions within and beyond the Crozet EEZ. Operational fishing techniques used by Patagonian toothfish longliners in the Crozet EEZ are the same techniques that are used by their counterparts off South Georgia (Ashford *et al.*, 1996; Purves *et al.*, 2004; Clark and Agnew, 2011), Prince Edward islands (Tilney and Purves, 1999), Falklands (Nolan *et al.*, 2006), and Chile (Hucke-Gaete *et al.*, 2004), and very similar to the sablefish demersal longlining used in Alaskan waters (Yano and Dahlheim, 1995). Because experimental trials are often impossible to implement due to time and economic constraints, communicating recommendations can encourage fishermen to change fishing behaviour under a voluntary scheme (Hamer *et al.*, 2012). Full access to fishing data may *a posteriori* allow the benefits of adopting new mitigation techniques to be assessed. For instance, length of longline sets, hauling speed, longline set depth, and the “move on” technique may be easy for fishermen to implement as part of a voluntary scheme in demersal longline fisheries to reduce killer whale depredation. However, local features of fishing gear, fishing grounds, and killer whale populations involved in depredation may influence the expected results of such trials. For instance, the depredating killer whale populations of Alaska, South Georgia, and Crozet have different ecologies (Guinet, 1992; Saulitis *et al.*, 2000; Purves *et al.*, 2004; Herman *et al.*, 2005; Matkin *et al.*, 2007). In South Georgia, depredating killer whales are Antarctic type-B killer whales that otherwise forage exclusively on marine mammal (Pitman and Ensor, 2003) and only interact with fisheries for a short period of the year (Clark and Agnew, 2011). The Alaskan depredating killer whales naturally forage on fish and interact with vessels year-round (Peterson *et al.*, 2013). Furthermore, while hauling speed may specifically influence depredation on demersal longlining, the length of longline sets, “move on” distance thresholds and number of simultaneous vessels are variables that could be also tested in pelagic longlining. Odontocetes species involved in depredation on tuna and swordfish are closely related to killer whales (Hamer *et al.*, 2012) and although fishing techniques differ, the underlying assumptions made here for these variable could fit such cases.

In addition to providing insights on potential behavioural mitigation solutions to limit odontocete depredation on longline fisheries, this study emphasized the determinants needed to combine collaborative work between scientists, fishing companies, vessel captains and fishery managers. We also highlight the importance of full access to fishing data in a controlled and regulated framework (fishery observers) with extensive long-term monitoring of depredating animal populations. The latter specifically enhances killer whale identification and our understanding of what factors may influence depredation. This will allow better interpretation of fishing data analysis and future implementation of mitigation solutions.

Acknowledgements

We thank all the field workers, the masters and crew of the longliners for their valuable help and specially fishery observers for their on-board work, and for providing the photographs used for these analyses. We are grateful to the Muséum National d'Histoire Naturelle, Paris and especially P. Pruvost and A. Martin, for providing some of the data from the "PECHEKER" database. Support was provided by the Terres Australes et Antarctiques Françaises and the Réunion Island fishing companies. The long-term monitoring of killer whales was supported by program 109 (resp. H. Weimerskirch) of the French Polar Institute. We also thank Malcolm O'Toole for proofreading the manuscript. We are especially thankful to the persons who reviewed this study for their insightful comments. The first author was financially supported by the French fishing association (SARPC), the TAAF administration (Contract N° 782095), and the Secrétariat d'état chargé de l'Outre Mer (Contract N° 782135).

References

- Arkipkin, A., Brickley, P., and Laptikhovskiy, V. 2003. Variation in the diet of the Patagonian toothfish with size, depth and season around the Falkland Islands. *Journal of Fish Biology*, 63: 428–441.
- Ashford, J., Rubilar, P., and Martin, A. 1996. Interactions between cetaceans and longline fishery operations around South Georgia. *Marine Mammal Science*, 12: 452–457.
- Bailleul, F., Charrassin, J. B., Monestiez, P., Roquet, F., Biuw, M., and Guinet, C. 2007. Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical Transactions of the Royal Society B Biological Sciences*, 362: 2169–2181.
- Baird, R. W., and Gorgone, A. M. 2005. False killer whale dorsal fin disfigurements as a possible indicator of long-line fishery interactions in Hawaiian waters. *Pacific Science*, 59: 593–601.
- Bigg, M. A., Olesiuk, P. K., Ellis, G. M., Ford, J. K. B., and Balcomb, K. C. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission (special issue), 12.
- Bost, C. A., Georges, J. Y., Guinet, C., Cherel, Y., Pütz, K., Charrassin, J. B., Handrich, Y., et al. 1997. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Marine Ecology Progress Series*, 150: 21–33.
- Botsford, L. W., Castilla, J. C., and Peterson, C. H. 1997. The management of fisheries and marine ecosystems. *Science*, 277: 509–515.
- Brotans, J. M., Grau, A. M., and Rendell, L. 2008. Estimating the impact of interactions between bottlenose dolphins and artisanal fisheries around the Balearic Islands. *Marine Mammal Science*, 24: 112–127.
- Clark, J. M., and Agnew, D. 2011. 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.
- Dahlheim, M. E. 1988. Killer whale (*Orcinus orca*) depredation on long-line catches of sablefish (*Anoplopoma fimbria*) in Alaskan waters. NWAFC Processed Report, 88-14, Northwest and Alaska Fisheries Center, Seattle, Washington. 31 pp.
- Domenici, P. 2001. The scaling of locomotor performance in predator prey encounters: from fish to killer whales. *Comparative and Biochemistry and Physiology, Part A*, 131: 169–182.
- Ford, J. K. B., Ellis, G. M., and Balcomb, K. C. 2000. Killer Whales: the Natural History and Genealogy of *Orcinus Orca* in British Columbia and Washington. UBC Press, Vancouver. 104 pp.
- Gambell, R. 1999. The International Whaling Commission and the contemporary whaling debate. In *Conservation and Management of Marine Mammals*, pp. 179–198. Ed. by J. Twiss, and R. Reeves. Smithsonian Institution Press, Washington and London. 471 pp.
- Gasco, N., Tixier, P., and Guinet, C. 2010. Results of trials undertaken around Crozet Island using pots to target Patagonian toothfish. Document WG-FSA-10/10. CCAMLR, Hobart, Australia. 20 pp.
- Gasco, N., Tixier, P., and Guinet, C. 2013. Guidelines to whale photo-identification from fishing boats derived from experience in Kerguelen (ASD 58.5.1) and Crozet (ASD 58.6) Document WG-FSA-13/08. CCAMLR, Hobart, Australia. 16 pp.
- Guinet, C. 1991. Intentional stranding apprenticeship and social play in killer whales *Orcinus orca*. *Canadian Journal of Zoology*, 69: 2712–2716.
- Guinet, C. 1992. Predation behaviour of killer whales *Orcinus orca* around Crozet Islands. *Canadian Journal of Zoology*, 70: 1656–1667.
- Guinet, C., and Bouvier, J. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, 73: 27–33.
- 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.
- Hamer, D. J., Childerhouse, S., and Gales, N. J. 2012. Odontocete bycatch and depredation in longline fisheries: a review of available literature and of potential solutions. *Marine Mammal Science*, 28: 345–374.
- Herman, D. P., Burrows, D. G., Wade, P. R., Durban, J. W., Matkin, C. O., LeDuc, R. G., Barrett-Lennard, L. G., et al. 2005. Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. *Marine Ecology Progress Series*, 302: 275–291.
- Hill, P. S., Laake, J. L., and Mitchell, E. A. 1999. Results of a pilot program to document interactions between sperm whales and longline vessels in Alaska waters. U.S. Dept. of Commerce, NOAA Technical Memorandum, NMFS-AFSC-108, 42 pp.
- Hucke-Gaete, R., Moreno, C., 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.
- Jefferson, T. A., and Curry, B. E. 1996. Acoustic methods of reducing or eliminating marine mammal-fishery interactions: do they work? *Ocean and Coastal Management*, 31: 41–70.
- Laptikhovskiy, V., Arkipkin, A., and Brickley, P. 2006. Distribution and reproduction of the Patagonian toothfish *Dissostichus eleginoides* around the Falkland Islands. *Journal of Fish Biology*, 68: 849–861.
- Lewis, R. L., Crowder, L. B., Read, A. J., and Freeman, S. A. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution*, 19: 598–604.
- Martin, A., and Pruvost, P. 2007. Pecheker, relational database for analysis and management of fisheries and related biological data from the French Southern Ocean fisheries monitoring scientific programs. Muséum National d'Histoire Naturelle.
- Matkin, D., Straley, J., and Gabriele, C. 2007. Killer whale feeding ecology and non-predatory interactions with other marine mammals. In *Proceedings of the Fourth Glacier Bay Science*

- Symposium, 2004, pp. 147–150. Ed. by J. F. Piatt, and S. M. Gende. U.S. Geological Survey, Juneau, AK.
- MacArthur, R. H., and Pianka, E. R. 1966. On the optimal use of a patchy environment. *American Naturalist*, 100: 603–609.
- McConnell, B. J., Fedak, M. A., Burton, H. R., Englehard, G. H., and Reijnders, P. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. *Journal of Animal Ecology*, 71: 65–78.
- Mooney, T. A., Pacini, A. F., and Nachtigall, P. E. 2009. False killer whale (*Pseudorca crassidens*) echolocation and acoustic disruption: implications for longline bycatch and depredation. *Canadian Journal of Zoology*, 87: 726–733.
- Nolan, C., Liddle, G., and Elliot, J. 2006. Interactions between killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) with a longline fishing vessel. *Marine Mammal Science*, 16: 658–664.
- Northridge, S. P. 1991. An updated world review of interactions between marine mammals and fisheries. *FAO Fisheries Technical Paper*, 251.
- Peterson, M. J., and Carothers, C. 2013. Whale interactions with Alaskan sablefish and Pacific halibut fisheries: surveying fishermen perception, changing fishing practices and mitigation. *Marine Policy*, 42: 315–324.
- 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.
- Peterson, M., Mueter, F., Hanselman, D., Lunsford, C., Matkin, C., and Fearnbach, H. 2013. Killer whale (*Orcinus orca*) depredation effects on catch rates of six groundfish species: implications for commercial longline fisheries in Alaska. *ICES Journal of Marine Science*, 70: 1220–1232.
- Pilling, G., Purves, M., Daw, T., Agnew, D., and Xavier, J. 2001. The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). *Journal of Fish Biology*, 59: 1370–1384.
- Pitman, R. L., and Ensor, P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management*, 5: 131–140.
- Poncet, E., Barbraud, C., and Guinet, C. 2010. Population dynamics of killer whales in Crozet Archipelago, southern Indian Ocean: exploiting opportunistic and protocol-based photographs in a mark-recapture study. *Journal of Cetacean Research and Management*, 11: 41–48.
- Purves, M. G., Agnew, D. J., Balguerias, 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 Development Core Team. 2010. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org> (last accessed 13 August 2014).
- Rabearisoa, N., Bach, P., Tixier, P., and Guinet, C. 2012. Pelagic longline fishing trials to shape a mitigation device of the depredation by toothed whales. *Journal of Experimental Marine Biology and Ecology*, 432–433: 55–63.
- Read, A. J. 2008. The looming crisis: interactions between marine mammals and fisheries. *Journal of Mammalogy*, 89: 541–548.
- Roche, C., Guinet, C., Gasco, N., and Duhamel, G. 2007. Marine mammals and demersal longlines fishery interactions in Crozet and Kerguelen Exclusive Economic Zones: an assessment of the depredation level. *CCAMLR Science*, 14: 67–82.
- Saulitis, E., Matkin, C., Barrett-Lennard, L., Heise, K., and Ellis, G. 2000. Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science*, 16: 94–109.
- Sigler, M. F., Lunsford, C. R., Fujioka, J. T., and Lowe, S. A. 2004. Alaska sablefish assessment for 2005. NPFMC Bering Sea and Aleutian Islands and Gulf of Alaska SAFE. Alaska Fisheries Science Center, Seattle, WA.
- 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.
- Similä, T., and Ugarte, F. 1993. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71: 1494–1499.
- Straley, J. M., O’Connell, T., Mesnick, S., Behnken, L., and Liddle, J. 2005. Sperm Whale and Longline Fisheries Interactions in the Gulf of Alaska. North Pacific Research Board R0309 Final Report, 15 pp.
- Thode, A., Straley, J. M., Tiemann, C. O., Folkert, K., and O’Connell, V. 2007. Observations of potential acoustic cues that attract sperm whales to longline fishing in the Gulf of Alaska. *The Journal of the Acoustical Society of America*, 122: 1265–1277.
- Thode, A., Straley, J. M., Tiemann, C., Teloni, V., Folkert, K., O’Connell, T., and Behnken, L. 2005. Sperm whale and longline fisheries interactions in the Gulf of Alaska—passive acoustic component. North Pacific Research Board Final Report F, 412, 57 pp.
- Tilney, R., and Purves, M. G. 1999. The status of integrated fisheries monitoring in South Africa. *In Proceedings of the International Conference on Integrated Fisheries Monitoring*, pp. 343–356. Ed. by C.P. Nolan. FAO Rome, Sydney, Australia.
- Tilzey, R., Goldsworthy, S. D., Cawthorn, M., Calvert, N., Hamer, D. J., Russel, S., et al. 2006. Assessment of seal-fishery interactions in the winter blue grenadier fishery off west Tasmania and the development of fishing practices and seal exclusion devices to mitigate seal by-catch by factory trawlers. Report, Fisheries Research and Development Corporation (FRDC) Project no. 2001/008. Bureau of Rural Sciences (BRS). 69 pp. http://data.daff.gov.au/brs/brsShop/data/frdc_final_reportv2.pdf (last accessed 13 August 2014).
- Tixier, P. 2012. Déprédation par les orques (*Orcinus Orca*) et les cachalots (*Physeter Macrocephalus*) sur les palangriers à la legine australe dans la ZEE de l’archipel de Crozet. PhD dissertation, Université d’Aix Marseille II. 367 pp. <http://www.cebc.cnrs.fr/Fthese/PUBLI/Tixier.pdf> (last accessed 13 August 2014).
- Tixier, P., Gasco, N., Duhamel, G., Viviant, M., Authier, M., and Guinet, C. 2010. Interactions 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.
- Tixier, P., Gasco, N., and Guinet, C. 2014. Killer whales of the Crozet islands, photo-identification catalogue 2014. doi: 10.6084/m9.fig-share.1060247.
- Treves, A., and Karanth, K. U. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17: 1491–1499.
- Woodroffe, R., Thirgood, S. J., and Rabinowitz, A. 2005. People and Wildlife: Conflict or Co-Existence?. Cambridge University Press, Cambridge, UK.
- Yano, K., and Dahlheim, M. 1995. Killer whale, *Orcinus orca*, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters. *Fishery Bulletin*, 93: 355–372.
- Yukhov, V. L. 1982. Antarkticheskij Klyklash. Nauka, Moscow (in Russian).
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.