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

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Abstract

Within the Crozet Islands Exclusive Economic Zone (EEZ), the Patagonian toothfish (*Dissostichus eleginoides*) longline fishery is exposed to high levels of depredation by killer (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*). From 2003 to 2008, sperm whales alone, killer whales alone, and the two species co-occurring were observed on 32.6%, 18.6% and 23.4% respectively of the 4 289 hauled lines. It was estimated that a total of 571 tonnes (€4.8 million) of Patagonian toothfish were lost due to depredation by killer whales and both killer and sperm whales. Killer whales were found to be responsible for the largest part of this loss (>75%), while sperm whales had a lower impact (>25%). Photo-identification data revealed 35 killer whales belonging to four different pods were involved in 81.3% of the interactions.

Significant variations of interaction rates with killer whales were detected between vessels suggesting the influence of operational factors on depredation. When killer whales were absent at the beginning of the line hauling process, short lines (<5 000 m) provided higher yield and were significantly less impacted by depredation than longer lines. Also, when facing depredation, it is recommended that vessels leave their fishing area and travel distances >40 n miles to prevent killer whales from finding them within a few hours. Although more data are still needed to better understand the way killer whales search and detect vessels, this study gives preliminary insights into possible mitigation solutions to the widespread depredation issue.

Résumé

Dans la zone économique exclusive (ZEE) de l'archipel de Crozet, la pêcherie palangrière à la légine australe (*Dissostichus eleginoides*) est exposée à des niveaux élevés de déprédation exercée par les orques (*Orcinus orca*) et les cachalots (*Physeter macrocephalus*). De 2003 à 2008, sur les 4 289 palangres virées, 32,6% étaient touchées par des cachalots, 18,6%, par des orques et 23,4% par les deux espèces ensemble. Nous estimons que la perte de légine australe due à la déprédation des orques ou des orques et des cachalots combinés s'élève à un total de 571 tonnes (4,8 millions €). Les orques sont responsables de la plus grande part de cette perte (>75%), et les cachalots, dans une moindre mesure (>25%). Des données de photo-identification ont révélé que 81,3% des interactions concernaient 35 orques appartenant à quatre troupeaux différents.

De fortes variations des taux d'interaction avec les orques ont été détectées entre les navires, ce qui montre l'influence de facteurs opérationnels sur la déprédation. Lorsque les orques étaient absentes au début du processus de virage, les palangres courtes (<5 000 m) produisaient un meilleur rendement et étaient nettement moins touchées par la déprédation que les palangres plus longues. Par ailleurs, en cas de déprédation, il est recommandé aux navires de quitter leur zone de pêche et de s'en éloigner de >40 miles nautiques pour empêcher les orques de les retrouver en quelques heures. Bien que davantage de données soient encore nécessaires pour mieux appréhender la manière dont les orques cherchent et détectent les navires, cette étude donne un premier aperçu des solutions possibles pour atténuer le problème généralisé de la déprédation.

Резюме

При ярусном промысле патагонского клыкача (*Dissostichus eleginoides*) в пределах Исключительной экономической зоны (ИЭЗ)о-вов Крозе отмечаются высокие уровни хищничества косаток (*Orcinus orca*) и кашалотов (*Physeter macrocephalus*). С 2003 по 2008 гг. только кашалоты, только косатки и оба этих вида вместе наблюдались соответственно при подъеме 32.6%, 18.6% и 23.4% ярусов из 4 289. По нашей оценке, потери составили в общей сложности 571 т (EUR 4.8 млн) патагонского клыкача в результате хищничества косаток, а также косаток и кашалотов вместе. Было обнаружено, что наибольшая часть этих потерь происходит из-за косаток (>75%), тогда как кашалоты оказывают меньшее воздействие (>25%). Данные фотоидентификации показали, что в 81.3% взаимодействий участвовало 35 косаток, принадлежащих к четырем различным стадам.

Было обнаружено, что коэффициенты взаимодействия с косатками значительно колебались от судна к судну, что говорит о воздействии на хищничество эксплуатационных факторов. Когда косатки отсутствовали в начале процесса выборки яруса, короткие ярусы (<5 000 м) давали более высокий улов и значительно меньше подвергались хищничеству, чем более длинные ярусы. Кроме того, если судно сталкивается с хищничеством, ему рекомендуется покинуть свой район промысла и перейти на расстояние >40 мор. миль, чтобы помешать косаткам вновь найти судно в течение нескольких часов. Хотя по-прежнему требуется больше данных для лучшего понимания способов поиска и обнаружения судов косатками, настоящее исследование дает предварительную информацию о возможных решениях, смягчающих воздействие широко распространенной проблемы хищничества.

Resumen

Dentro de la zona de exclusividad económica de las Islas Crozet (ZEE), la pesquería de palangre de austromerluza negra (*Dissostichus eleginoides*) está expuesta a altos niveles de depredación por orcas (*Orcinus orca*) y cachalotes (*Physeter macrocephalus*). Se observaron sólo cachalotes en un 32.6% de los 4 289 palangres calados de 2003 a 2008, sólo orcas en un 18.6% y las dos especies combinadas en un 23.4% de los mismos. Estimamos una pérdida total de 571 toneladas (€4.8 millones) de austromerluza negra por la depredación de orcas y una combinación de orcas y cachalotes. Se encontró que las orcas fueron responsables de la mayor parte de esta pérdida (>75%), mientras que el impacto de los cachalotes fue menor (>25%). Los datos de la identificación fotográfica revelaron que 35 orcas, de cuatro manadas diferentes, participaron en un 81.3% de las interacciones.

Se detectaron grandes variaciones en las tasas de interacción de los barcos con las orcas, lo que sugiere que factores operacionales influyen en la depredación. Cuando no hubo presencia de orcas al inicio del virado de la línea, se obtuvo un mayor rendimiento con las líneas cortas (<5 000 m) que fueron afectadas mucho menos por la depredación que las líneas más largas. Además, es aconsejable que los barcos se trasladen distancias >40 millas náuticas cuando se observan problemas de depredación, para prevenir que las orcas los encuentren en unas pocas horas. Si bien se necesitan más datos para entender mejor la forma como las orcas buscan y detectan los barcos, este estudio entrega reflexiones preliminares sobre las posibles soluciones para mitigar el problema generalizado de la depredación.

Keywords: Patagonian toothfish, fisheries, depredation, Crozet Islands, killer whales, sperm whales, CCAMLR

Introduction

Interactions between marine mammals and fisheries have been reported worldwide as a case of use conflict (Northridge and Hofman, 1999). Among such conflicts, depredation, which is defined as an operational interaction and concerns the removal of fish from lines or from nets by marine mammals (Donoghue et al., 2002), represents a major issue. The implications of the latter can be economic, with significant losses for fishers, on the management of fish resources (losses due to depredation are generally not accounted for in fish stock assessments and quota allocation processes) (Read, 2008), as well as on marine mammal species (risks of mortality by entanglement, modification of energy balance by giving access to new prey sources) (Northridge and Hofman, 1999 ; Fertl; 2002, Goldsworthy et al., 2003; Secchi et al., 2005).

Longline fisheries are the most impacted by depredation. In tropical and sub-tropical zones, pelagic longlines targeting tuna (Thunnus spp.) and swordfish (Xiphiius gladius) are generally depredated by false killer whales (Pseudorca crassidens) and short-finned pilot whales (Globicephala macrorhynchus) (Secchi et al., 2005; Dalla Rosa and Secchi, 2007; Hernandez-Milian et al., 2008). In higher latitudes, it is primarily killer (Orcinus orca) and sperm whales (Physeter macrocephalus) that interact with demersal longlines. In the northern hemisphere, they remove sable fish (Anoplopoma fimbria) and Greenland halibut (*Reinhardtius hippoglossoides*) from hooks in Alaskan and Icelandic waters (Yano and Dalheim, 1995; Dyb, 2006; Sigler et al., 2008). In the southern hemisphere, they are reported to interact with the Patagonian toothfish (Dissostichus eleginoides) fisheries off southern Chile (Hucke-Gaete et al., 2004), South Georgia (Ashford et al., 1996; Purves et al., 2004), Falkland Islands (Nolan et al., 2000), Prince Edward Islands (Tilney and Purves, 1999) and Crozet and Kerguelen Islands (Capdeville, 1997; Roche et al., 2007).

The Patagonian toothfish fishery is primarily operated by longline-type fishing techniques. Most vessels use the same autoline-system longlines set in series of 1 km long sections fitted with approximately 1 000 hooks each. Previous studies showed differences in the level of interaction with killer and sperm whales between fishing vessels (Hucke-Gaete et al., 2004) suggesting the existence of factors that vary between vessels which could influence depredation rate. Longlines are set at depths ranging from 500 to 2 000 m. Unlike sperm whales, killer whales are unable to dive to such depths (Papastavrou et al., 1989; Baird et al., 2005), and consequently can only retrieve the fish from the line when they arrive close to the surface.

This study provides a detailed update of the depredation situation in the Crozet Islands Exclusive Economic Zone (EEZ) (Figure 1a) where seven licensed longliners fish for Patagonian toothfish under strict governmental regulations and with the systematic presence of on-board observers (CCAMLR, 2006). From the data collected between 2003 and 2005, Roche et al. (2007) estimated that 333 tonnes of Patagonian toothfish were depredated during this period (i.e. a financial loss of €3.3 million) by killer and sperm whales. Killer whales were responsible for a higher loss than sperm whales, a trend that was already reported in other locations (Kock et al., 2006). Killer whales operate in groups (i.e. pods) that seem to actively follow the fishing vessels and, when present, remove most of the catch from the lines. The current strategy used by vessels when facing killer whale depredation is to stop fishing in that area and move to another, which incurs significant costs in time and fuel.

The aims of the current study are (i) to provide detailed annual estimates of Patagonian toothfish losses due to depredation by killer and sperm whales between 2003 and 2008; (ii) to identify killer whale individuals interacting with fishing vessels and possible differences in interaction levels between pods; (iii) to assess the operational factors which may impact depredation by killer whales and could help explain the reported difference in interaction levels between vessels; and (iv) to provide advice to optimise the current strategy of leaving a fishing area when faced with depredation by killer whales.

Material and methods

From 1 September 2003 to 31 August 2008, 4 289 lines were hauled by the seven legal longliners operating in the Crozet Islands EEZ. The vessels operated all year round with higher activity in February when the fishery is closed in the Kerguelen EEZ because of seabird conservation measures. A fishing season runs from 1 September to 31 August.

Observer protocol

The data were collected by fishery observers who were required (i) to collect data for fishery management purposes (e.g. species targeted, catch size, fishing location); (ii) to assess the resource (e.g. sampling of fish length and weight); (iii) to record by-catch of non-target species; and (iv) to record interactions between the fishery and protected seabirds and marine mammals present in the vicinity of the longlines as well as incidental seabird mortality.

The dataset used in this study provided, for every hauled line, information on the vessel identity, date, time, location, number of hooks set and the total weight of toothfish caught.

The number of hooks hauled per line was used as the unit of fishing effort. The catch-per-unit-effort (CPUE) was calculated for each line by dividing the total toothfish weight (in grams) by the number of hooks hauled. The number of hooks hauled can vary from the number of hooks set, as hooks can be lost while underwater, because of entanglement during setting, or entanglement or drag on the bottom during hauling.



Figure 1: Map of the Crozet Islands with (a) positions of the lines set by the seven legal longliners between 1 September 2003 and 31 August 2008 (the dashed line represents the French EEZ boundary) and (b) positions of lines that were depredated by killer whales between 1 September 2003 and 31 August 2008.

Interaction with the fishery was considered to occur when cetaceans were present in the vicinity (maximum 500 m) of a line being hauled for at least five minutes (Roche et al., 2007). When visibility conditions permitted, fishery observers recorded species identity, estimates of the number of individuals present and a brief description of their behaviour. Lines that were hauled at night or in conditions of very poor visibility (less than 50 m) were not included in the analysis. When possible, the time of arrival (which was considered as the time of the first sighting), was also noted. Co-occurrence of killer and sperm whales was recorded as an event during which both species were reported at least once during the hauling process.

When photo equipment was provided, killer whale photo-identification was also conducted. Photo-identification is widely used in research on cetaceans and has proved to be a reliable technique for the identification of individual killer and sperm whales (Bigg, 1982; Whitehead, 2001). Identification of individuals relies on the shape and natural markings such as scars, nicks or notches visible on the dorsal fin and the saddle patch for killer whales, and nicks or notches present on the fluke (tail) and the back of sperm whales. Most pictures were taken so as to represent the whole dorsal fin and saddle patch of a killer whale or back of a sperm whale surfacing or the fluke (tail) of a diving sperm whale with an angle from the photographer as perpendicular as possible. Relevant information, such as individual identity, sex and life stage, as well as type and quality of individual representation were entered in an Access database. Photo-identification catalogues were produced for killer and sperm whales. For the killer whales catalogue, identified individuals were organised into pods. A pod is defined as a group of individuals that were seen together on at least 50% of sightings, which means that each pair of individuals share an association index higher than 0.5 (Bigg et al., 1990). Killer whale identification is more straightforward than sperm whale identification because the natural markings are easier to photograph and distinguish. This study considers that all killer whales interacting with fishing vessels were identified. However, capture-mark-recapture methods had to be used to estimate the total number of sperm whales (Cormack, 2001). Classical sequential models for closed populations were used (Otis et al., 1978). The best-fitted model was selected through the CAPTURE program, taking into account the conditions of observations and the ecology of sperm whales, as recommended by Pollock et al. (1990). Model selection was also performed through examination of the sample coverage and the coefficient of variation of capture probabilities (Chao et al., 1992). Only very distinctive animals were used in the analysis in order to reduce identification errors. As a consequence, the proportion of distinctive individuals among all identified sperm whales was used as a correction factor to provide a final estimate. In this study, the sperm whale abundance estimations were performed for 2008 only.

Interaction and depredation level estimates

The rate of interaction with killer or sperm whales was expressed as the ratio of the number of longlines hauled in the presence of cetaceans divided by the total number of longlines set by a given fishing vessel. This rate was calculated for each vessel for each fishing season.

Depredation levels cannot be reliably assessed by recording the number of fish damaged or partly eaten by killer and sperm whales. Indeed, when depredating longlines, both species entirely remove most fish from the hooks. Therefore, taking into account only damaged fish would lead to serious underestimation of depredation levels. Depredation rates were first estimated through CPUE comparison between lines hauled in the absence and in the presence of cetaceans over the whole Crozet Islands EEZ. This allowed an assessment of CPUE reduction in the presence of cetaceans. To provide an estimate of the amount of toothfish lost to depredation, the same method was used, taking into account the spatial variation of the CPUE of Patagonian toothfish in the Crozet Islands EEZ. The whole fishing area was divided in $0.1^{\circ} \times 0.1^{\circ}$ cells. For each cell and fishing season the difference of CPUE between all combinations of lines hauled in the absence (CPUE_{abs}) and in the presence of cetaceans (CPUE_{pres}) was estimated. This provided a mean loss of CPUE ($CPUE_{loss}$) for each cell *c* in which lines were hauled both in the presence and absence of cetaceans:

$$CPUE_{loss}c = \frac{\sum_{i=1}^{I} \sum_{j=1}^{J} (CPUE_{abs}(i) - CPUE_{pres}(j))}{IJ} \quad (1)$$

in which *I* is the number of lines hauled in the presence of cetaceans, *J* is the number of lines in the presence of cetaceans, and *IJ* is the number of combinations of lines used to calculate the mean loss of CPUE in each cell *c*.

To obtain the amount of toothfish lost to depredation in each cell (B_{loss} c), the mean loss of CPUE, and its associated standard error, were multiplied by the number of hooks on lines that were hauled in the presence of cetaceans (E_{pres}) in that cell: Tixier et al.

$$B_{loss}c = CPUE_{loss}c \cdot E_{tot}c.$$
⁽²⁾

The initial estimation of the total amount of toothfish lost to depredation for each fishing season was calculated as the sum of toothfish losses estimated in cells for which there were lines hauled both in the presence and absence of cetaceans. The uncertainty ($se_{losstot}$) was calculated from the standard error of the loss in each cell ($se_{loss}c$) according to:

$$se_{losstot} = \sqrt{\sum_{c=1}^{C} \left(\frac{se_{loss}c^2}{IJ}\right)}$$
(3)

in which *C* is the number of cells *c* in which lines were hauled both in the presence and absence of cetaceans.

It was not possible to estimate depredation for cells in which cetaceans were present at each line hauled. Therefore, to obtain a final estimate of losses due to depredation over the whole Crozet Islands EEZ, the total number of hooks hauled in the presence of cetaceans in all cells of the Crozet fishing area was multiplied by the mean CPUE loss calculated for the cells *c* in which depredation could be estimated. The same method was used to calculate the uncertainty in the final estimates from the uncertainty calculated in the cells *c*.

Depredation rates (*Dep*) were derived from the final estimates as followed:

$$Dep = \frac{B_{loss}}{(B_{loss} + B_{landed})}$$
(4)

in which B_{landed} is the amount of toothfish declared by fishing vessels.

For all depredation estimations, three categories of cetacean occurrence were distinguished: killer whales only, sperm whales only and both killer and sperm whales present simultaneously.

Effect of fishing practice to reduce depredation

Previous work conducted in the Crozet Islands EEZ had shown that killer whales were responsible for most depredation (Roche et al., 2007). Furthermore, killer whales are unable to reach the fish naturally at fishing depth (500–2 000 m) which is not the case for sperm whales. For these two reasons, the focus here is on killer whale depredation and the effect of two operational factors that could influence the killer whale depredation rate: the length of the fishing lines and the depths at which

they were set. Both factors are known to affect the duration of line hauling and consequently the chances that killer whales could locate the fishing vessel before the end of this process. The effect of these two factors on CPUE was tested in the absence or presence of killer whales through generalised linear mixed models (GLMM) with vessel position considered as a random factor. Vessel identity was included as a fixed effect and tested for its effect alone or in interaction with the other two variables.

Effect of ship movement to reduce depredation

To optimise the vessel's displacement strategy in response to killer whale depredation, the effect of the distance travelled by the vessel was compared to the time necessary for killer whales to find it again once it had left the fishing zone. This time lag was calculated as the time between the last observation and the next observation of killer whales. Two scenarios were considered: (i) the time lag necessary for the same pod of killer whales to find the same fishing vessel again and (ii) the time lag for any other killer whale pod to find the vessel leaving the fishing zone. The distance covered by the fishing vessel was calculated using its position data when it left the first fishing zone and arrived at the next, assuming that it cruised in a straight direction between the two positions. In the current study, VMS data were not accessible to calculate the exact distance travelled and to take into account possible changes in vessel direction.

Analyses were conducted using the R software (R Development Core Team, 2009) and results are expressed as mean ±SEM.

Results

Interaction rate

Between 2003 and 2008, sperm whales alone, killer whales alone, and the two species cooccurring, were observed on 32.6%, 18.6% and 23.4% respectively of the 4 289 lines hauled during this period. Only 25.4% of the 4 289 lines were hauled in the absence of cetaceans.

Killer whales interacted with 1 801 lines (Figure 1b) and sperm whales interacted with 2 359 hauled lines. No trend in interaction rate was detected between 2003 and 2008; sperm whale and killer whale interaction rates remained relatively constant over time (Figure 2) with mean rates of $53 \pm 7.5\%$ and $39 \pm 5.4\%$ respectively.



Figure 2: Mean interaction rates of killer and sperm whales with longlines between 2003 and 2008.



Figure 3: Interaction rates of killer and sperm whales with longlines calculated for each of the seven legal fishing vessels (named A to G), between 2003 and 2008.

However, over the same period, the interaction rate with killer whales varied significantly between fishing vessels (range $27 \pm 14\%$ to $45 \pm 16\%$; z = 23.4; p < 0.005) but not for sperm whales (p > 0.05; Figure 3).

Losses due to depredation

CPUE was significantly and negatively impacted by the presence of any category of cetaceans (GLMM: sperm whales alone: z = -12.3, p < 0.001; killer whales alone: z = -255, p < 0.001; killer whales and sperm whales together z = -287.3, p < 0.001; Figure 4).

Overall, by comparing CPUE in the absence and presence of cetaceans, it was estimated that killer whales alone, sperm whales alone and the combined presence of killer whales and sperm whales resulted in a mean loss of fish of $27 \pm 25\%$, $9 \pm 13\%$ and $37 \pm 31\%$ respectively.

Estimates of losses due to depredation, taking into account the spatial variation of CPUE, could on average be estimated in $58 \pm 9\%$ of cells for killer whales alone, $51 \pm 9\%$ for sperm whales alone, and $68 \pm 13\%$ for both killer and sperm whales which represented $64 \pm 11\%$, $69 \pm 9\%$ and $62 \pm 12\%$ of hauled hooks respectively. After extrapolating the estimates made in these cells to the total number of hooks in the presence of cetaceans, killer whales alone, and the combined presence of killer and sperm whales, resulted in a total estimated loss of approximately 256 and 315 tonnes of toothfish respectively between 2003 and 2008 (Figure 5).

The losses due to depredation on lines hauled in the presence of sperm whales only are not presented as they appeared to be significantly biased. This is because higher CPUE in the presence of sperm whales than in the absence of cetaceans was observed on a proportion of combinations ($52 \pm 4\%$ versus $31 \pm 6\%$ for killer whales alone and $33 \pm 3\%$ for killer whales and sperm whales together) suggesting the potential for a significant underestimate in losses due to sperm whale depredation.

From 2003 to 2008, the seven fishing vessels declared a total catch of 2 933 tonnes. Therefore, the minimum estimated amount of toothfish caught was 3 504 tonnes if the losses due to depredation by killer whales alone and by both killer and sperm whales (2 933 + 571) are taken into account. For these two cases of cetacean occurrence, the total depredation rate was estimated to be 17.7% (killer whales alone 8.0%, and killer and sperm whales 9.7%).

When calculated for each fishing season, depredation rates were found to vary significantly between years (Figure 6), with a minimum in 2004/05 (2.8 ± 9.6%), and a maximum in 2007/08 (13.8 ± 5.4%).

Photo-identification

Total number of killer whales involved in depredation

Between 2003 and 2008, a total of 24 025 pictures of cetaceans were taken from longliners by fishery observers, which represented 32 914 fins to be analysed. This allowed the identification of 97 different killer whales interacting with the fisheries. These 97 individuals belonged to 11 distinct pods in which the killer whales shared association indices higher than 0.5. However, amongst these 11 pods, four were observed in 81.3% of the total number of interactions. In 2008, these four pods involved 35 different individuals which represented a mean number of 9 ± 4 killer whales per pod. The number of individuals interacting with a given line did not vary significantly over the study period. However, it had a significant positive effect on fish losses due to depredation (r = 0.65; p < 0.001) on lines that were depredated by killer whales only.

Total number of sperm whales interacting with the fishery

In 2008, 2 844 photographs were taken which allowed identification of 25 distinctive sperm whales that were used in capture/mark/recapture (CMR) abundance estimation. The M_{th} (Otis et al., 1978) model (CV(pi) = 0.47; SC = 84%), which takes into account both time and inter-individual heterogeneity in capture probability variations, was selected. After correction by the proportion of distinctive individuals (c = 2.068), the model provided a final estimate of 64 (95% CI 42–209) sperm whales interacting with vessels in 2008. The number of individuals interacting with a given line did not vary significantly over the study period and it was not found to have an effect on fish losses due to depredation (r = 0.13; p > 0.05).

Effects of operational factors on depredation by killer whales

The depth at which the lines were set had no significant effect on the CPUE both in the absence and presence of killer whales (p > 0.05). In the absence of killer whales, short lines (2 000–5 000 m) tended to have a higher mean CPUE (283 ± 104 g/hook) than longer lines (>5 000 m) for which average



Figure 4: Mean CPUE per fishing season in the absence of cetaceans (grey bars), in the presence of killer whales alone (white bars), sperm whales alone (black bars) and both species together (hatched bars).



■ Vessels ■ Killer whales ■ Killer and sperm whales

Figure 5: Biomass of Patagonian toothfish landed each fishing season (positive values) and the estimated losses due to depredation (negative values) by killer whales alone (white) and both killer and sperm whales (hatched). Calculation of the error bars is described under 'Methods'.



Figure 6: Depredation rates by killer whales alone and both killer and sperm whales between 2003 and 2008. Error bars were calculated using the ratio of the variance of the toothfish losses and the mean squared amount of toothfish landed.



Figure 7: Mean CPUE of Patagonian toothfish calculated for different classes of line length both in the absence (grey bars) and presence (black bars) of killer whales.

CPUE was 164 ± 92 g/hook. The effect of the length of the lines was only detected in the presence of killer whales when the latter started to interact with the lines at least 10 minutes after the haul started (z = -85.3; p = 0.004). In this situation, short lines (2 000–5 000 m) had a higher mean CPUE (261 ±

72 g/hook) than longer lines (>5 000 m) for which CPUE significantly dropped to 89 ± 61 g/hook) (Figure 7).

When vessel identity was included in the model, it had a significant effect on CPUE in the presence

of killer whales (z = 42.3; p < 0.001), but no interaction effect between the vessel identity and the other two variables was found.

Distance covered by fishing vessels on killer whale depredation

When a fishing vessel was being depredated by a pod of killer whales and left the area to set its lines in another area, the time necessary for the same pod to be detected near the vessel was not correlated to the distance travelled by the vessel. However, when calculating the mean time lag for different 20 n mile distance classes, killer whales needed significantly more time to find the same vessels travelling more than 40 n miles compared to shorter distances. On average, 0.9 ± 0.3 days was necessary for a given pod of killer whales to reach the same vessel when the distance travelled was less than 40 n miles, while it took on average 4.7 ± 2.8 days for the same pod to find the same vessel moving more than 40 n miles away.

When considering all pods of killer whales in the analysis, a fishing vessel travelling more than 40 n miles away could fish on average 3.1 ± 3.0 days before being located by any of these pods.

Discussion

Losses due to depredation

Between 2003 and 2008, the interaction between killer whales alone and both killer and sperm whales with lines hauled within the Crozet Islands EEZ resulted in an estimated total loss of 571 tonnes of Patagonian toothfish to depredation. According to the current market price of Patagonian toothfish, which is approximately €8.40 per kilo (T. Clot, pers. comm.), this represents a financial loss of €4 800 000. Beyond the heavy economic consequences of such an estimation, it has great implications on conservation and should be incorporated into fish stock assessments for resource management purposes. However, this should be considered as a minimum, as the depredation due to sperm whales alone could not be accounted for in the total loss estimates. The CPUE comparison method between lines hauled in the absence and in the presence of sperm whales only in $0.1 \times 0.1^{\circ}$ cells could not detect any effect on depredation. Indeed, CPUE was greater in the presence of sperm whales for a large proportion of cells which would induce a significant bias in estimations. One likely reason for such a bias is the co-occurrence between sperm whales, which are known to feed naturally on toothfish (Abe and Iwani, 1989), and fishing vessels in areas with the highest density of Patagonian toothfish, as already suggested in previous studies (Roche et al., 2007; Purves et al., 2004).

When testing the covariates that influence CPUE variations, this study shows a significant effect of the presence of sperm whales over the whole 2003-2008 period, with a mean loss of about 9%. Furthermore, the co-occurrence of both killer whales and sperm whales during depredation events resulted in a greater loss in percentage (about 10%) of fish compared to killer whales only, also suggesting an additive effect of the presence of sperm whales. The presence of killer whales only resulted in a CPUE reduction of 27 %. When compared to CPUE reduction of sperm whales only (9%), depredation by killer whales was estimated to account for the largest part (75%) of the total depredation with sperm whales accounting for 25% only.

With an estimate of 64 sperm whales interacting with the fisheries off the Crozet Islands in 2008, this study emphasises a critical need to further investigate sperm whale depredation and to reliably assess the amount of toothfish loss. The CPUE comparison method should be made at a finer spatiotemporal scale, although it would be constrained by the very high rate of interaction observed with sperm whales (i.e. a low number of lines without cetacean interactions).

Variations in depredation rates

No significant trend was detected over the study period. However, it was observed that in 2004/05, the depredation level was very low, before increasing and reaching a maximum in 2007/08. These variations are not related to the interaction rate (i.e. the number of lines where whales were observed) which remained relatively constant over the study period for both killer and sperm whales. Although losses due to depredation were positively correlated to the number of killer whales interacting with a given line, the mean number of killer and sperm whales interacting per line remained unchanged. However, in 2004/05 estimates were obtained from the lowest proportion of cells (i.e. a low number of cells for which there was both no depredated and depredated lines) with which to estimate depredation rates; it was not possible to estimate the depredation rate for cells in which lines were always exposed to depredation and the proportion of such cells was highest in this period. Furthermore, the lowest proportion of the total number of hooks set that could be used to estimate killer whale (48%) and sperm whale (49%) depredation had occurred in that year. These two factors could account for the lower estimated depredation rate for that year, which could be an artefact related to the method used to estimate depredation (Figures 5 and 6). One limit to this method is that the estimate of losses due to depredation could only be derived from a fraction of the total number of hooks, and the total amount of losses was calculated through a simple proportional relation using all hooks. Years of high depredation rates could also be explained by a greater efficiency (i.e. an increase in the amount of fish removed from the hooks) of cetaceans interacting with a vessel. In 2007/08, losses increased to 192 tonnes of Patagonian toothfish, which represent 19% of the amount of fish harvested that year for the Crozet Islands EEZ. Future years will be critical in determining a depredation trend.

Significance of killer whale depredation

The killer whale population of the Crozet Islands is composed of pods that interact with the fisheries and others that do not (Roche et al., 2007). Amongst the 97 killer whales interacting with longlines between 2003 and 2008, photo-identification revealed that four pods were responsible for more than 80% of the interactions. These four pods, representing 35 individuals, seem to specialise in longline depredation. According to the energy requirement of killer whales (Guinet et al., 2007), it was estimated that the amount of fish they depredated represented about 30% of the energy budget of these 35 individuals.

In the recent past, killer whales at the Crozet Islands have undergone a marked decline in both their abundance and survival rate (Tixier, 2008; Poncelet et al., 2009). As cases of killer whales being accidentally caught on hooks while depredating a longline are rare (Dalla Rosa and Secchi, 2007), further investigations are needed to assess the ecological consequences, and in particular the demographic consequences, of depredation to these killer whales.

Operational measures to reduce depredation

In the absence of killer whales, short lines (<5 000 m) had a greater CPUE than longer ones, suggesting that they were more effective in fishing. Many factors can contribute to such a trend, one of them being that a shorter line may allow the vessel to target areas of high fish density more precisely. When killer whales were not present when hauling commenced but arrived during the hauling process, CPUE was reduced to a much greater extent for longer lines. This can be interpreted as the consequence of the time necessary for killer whales to reach the vessel during the process of hauling the

line. Killer whales are likely to detect fishing vessels acoustically (Kock et al., 2006; Thode et al., 2006) and appear to be able to rapidly relocate a vessel when the latter changed its fishing area within less than 40 n miles from its previous location. Killer whales are able to sustain a swimming speed of 7–8 m s⁻¹ (Guinet et al., 2007). Therefore, assuming the limit of the detection range to be 30 n miles, they will require only about two hours to reach a vessel that has moved this distance. The further away killer whales are, the longer it will take them to reach a vessel during the hauling process. As short lines require less time to be hauled, there will be fewer fish on the line remaining in the water when they reach the vessel. Given these results, when a fishing vessel is operating in an area without any interaction with killer whales, the use of short lines is recommended, e.g. shorter than 5 000 m.

When pods of killer whales have found a fishing vessel, they tend to stay in the area and begin interacting with the lines as soon as the haul starts. In this case, there was no effect of the length of the line on CPUE. Indeed, the latter remained low for all classes of line length. In such a situation, according to the results of this study, it is recommended that the vessel leaves the area and travels a minimum distance of 40 n miles. Indeed, below 40 n miles, the fishing vessel is likely to be confronted with killer whales again in less than a day; the low variance observed suggests this to be systematic. When travelling a distance greater than 40 n miles, it will take the same pod of killer whales between four and five days to reach the vessel again, however, following such a movement this vessel is likely to be confronted with a different pod of killer whales within three days. This result is particularly important as it means that fishing vessels can operate without any killer whale depredation for several days and therefore increase their CPUE. There were no additional benefits to vessels of travelling distances greater than 40-60 n miles.

The data presented here indicate that in some cases, a given pod of killer whales can actively follow a fishing vessel over great distances (>40 n miles) and be seen in the vicinity as the first lines are deployed in the new fishing zone. Photoidentification revealed that killer whales are able to travel long distances within the archipelago, but also, for some of them, between the Crozet and Kerguelen Islands. Currently, their searching behaviour for vessels remains unknown. However, it is likely that killer whales are able to detect the bearing taken by a fishing vessel leaving the zone and use that information to find it over great distances. Furthermore, the fishing zone is restricted to an area along the edge of the Crozet plateau and killer whales may use that information to search actively for fishing vessels. Additionally, photoidentification revealed that pods switch easily from one vessel to another if the two are operating in close proximity. Thus, while recommending that vessels travel long distances if confronted with killer whales, it may not be advisable to choose a new fishing zone in the vicinity of another fishing vessel facing depredation.

Conclusion

This study has allowed the development of guidelines for longliners to follow in order to reduce depredation by killer whales, which are responsible for a large part of the losses. However, while these mitigation measures are intended to reduce depredation they will not remove it. Depredation is a behaviour that has been fully integrated by a significant number of killer whale pods. A number of systems, whether they were fish-protective systems or acoustic systems, have been tested in different places of the world to repel marine mammals from longlines and most of them provided unsuccessful results (Jefferson and Curry, 1996; Reeves et al., 1996; Donoghue et al., 2002). In 2010, an experimental campaign tested fish traps especially designed for Patagonian toothfish within the Crozet Islands EEZ. It reduced both cetacean depredation and by-catch of seabirds but CPUE remained significantly lower than the longline CPUE (C. Guinet, pers. comm.). Future efforts should focus on systems adapted to longlines. Recent insights into longline gear modification, such as hook sleeves to protect the fish, have been proposed (Kock et al., 2008) and similar systems should be tested within the French EEZ in future years.

In the Kerguelen Islands EEZ, killer whales interacted with only 34 lines between 2003 and 2008: their impact remained negligible. However, photo-identification data indicated that they were new individuals as well as individuals belonging to one of the four specialist pods of the Crozet Islands EEZ. This raises a major concern about a possible displacement of the killer whale depredation issue to the Kerguelen Islands EEZ. If it reaches similar levels as in the Crozet Islands EEZ, it would have critical consequences, as most of the Patagonian toothfish catches within the French EEZs are from the Kerguelen Islands EEZ (90%). To reduce the risk of spreading the depredation behaviour, it is strongly recommended that vessels stop hauling, buoy off their lines and sink them to the bottom out of reach of killer whales (i.e. deeper than 400 m) in order not to reward them and hence reinforce this depredation behaviour. Finally, this study highlights the critical need of a better (i) assessment of sperm whale depredation which requires a finer method taking into account their co-occurrence with highly productive zones, and (ii) understanding of the spatial behaviour of both killer and sperm whales in relation to the fishing activity in the EEZ. While photo-identification provides reliable data, it is fully dependent on observations conducted from fishing vessels. Data on the behaviour of these species when they are not associated with fishing vessels are currently lacking. Satellite tracking, by Argos tag deployment on certain individuals from different pods, would lead to a better knowledge of the ecology, distribution and inter-island movements of Crozet Island killer whales (Andrews et al., 2008). Satellite tracking would bring critical insights into the way killer whales search or detect fishing vessels, and would consequently help to establish better guidelines to avoid or reduce depredation, if the operation of fish traps is unsuccessful.

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