Comparison of two methods to assess fish losses due to depredation by killer whales and sperm whales on demersal longlines

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Abstract

Depredation is a human–wildlife interaction over access to resources, which often includes a combination of socio-economic, ecological and conservation issues. However, estimating the amount of resource depredated can be especially challenging when depredation occurs on fish in the marine environment. This is the case for killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) depredation on the demersal Patagonian toothfish (*Dissostichus eleginoides*) longline fishery operating within the Crozet Islands EEZ (southern Indian Ocean). This study aimed at providing two indirect methods of assessment of depredated biomass over an 11-year period (2003 to 2013), accounting for spatial variations of depredation levels. In the first method, fishing data from 6 525 longline sets were used to calculate the difference between catch-per-unit-effort (CPUE) of non-depredated and depredated lines. When killer whales and sperm whales occurred separately, 575 ± 35 tonnes and 739 ± 87 tonnes of Patagonian toothfish respectively were estimated to be depredated by the two species. When the two species co-occurred around vessels, 1 679 ± 74 tonnes were depredated. The second method used the differences in the proportion of grenadiers (*Macrourus* spp.) between non-depredated and depredated longline sets to estimate the number of depredated Patagonian toothfish. This approach, which can only be implemented when a sufficient level of by-catch species occurs, provides comparable results and thus strong support for the CPUE method. From these two methods, depredation rates were estimated to range from 27.3% to 29.1% of the total catch (landed and depredated), which is one of the highest among all similar situations where depredation is reported elsewhere in the world. In addition to providing a methodology that could be used in other areas with depredation issues, these findings emphasise the critical importance for fishery managers and researchers to account for depredation when assessing fish stocks, fishery economics and/or conservation of odontocetes.

Introduction

Depredation is a human–wildlife interaction over resources, which often includes a combination of socio-economic (financial losses for humans), ecological (negative and/or positive effects on depredating species) and conservation issues (impacts on depredated resources). Historically, socio-economics has been the primary focus when assessing depredation levels, such as estimating the amount of biomass loss caused by predators. While these losses can be directly assessed in terrestrial cases (e.g. O'Connell-Rodwell et al., 2000; Breck and Meier, 2004), they are considerably harder to estimate in the marine environment where the initial state of the depredated resource is often unknown. Depredation can rarely be assessed directly by witnessing the event. Depredation of tuna and swordfish pelagic longlines by false killer whales and pilot whales are among the few cases for which losses are assessed by counting remains of heads and lips coming up on the lines (Ramos-Cartelle and Mejuto, 2008).

In the context of declining world fisheries (Pauly et al., 2005), depredation of longlines may also have major implications on fishery management and fish stock assessment. The amount of depredated fish is part of the total catch and is often disregarded when defining quotas (Roche et al., 2007). Like in most other fisheries, fish stocks targeted by longlining (and associated by-catch) have suffered from over-fishing caused by illegal activity (Agnew et al., 2009) over the past 50 years. This is the case for many demersal longline fisheries at high latitudes on both hemispheres. These fisheries are often subject to depredation by two odontocete species: the killer whale (*Orcinus orca*) and the sperm whale (*Physeter macrocephalus*) (Yano and Dalheim, 1995; Sigler et al., 2008; Hucke-Gaete et al., 2004; Ashford et al., 1996; Purves et al., 2004; Nolan et al., 2000; Tilney and Purves, 1999; Capdeville, 1997; Roche et al., 2007; Söffker et al., 2015). Both species often remove the whole fish from longlines, making depredation particularly difficult to assess. Depredation losses are generally estimated through indirect methods, such as comparisons of catch-per-unit-effort (CPUE) in the presence and the absence of odontocetes (Hucke-Gaete et al., 2004; Thode et al., 2005; Purves et al., 2004; Roche et al., 2007).

In the Crozet Islands Exclusive Economic Zone (French EEZ), seven fishing vessels, using bottom longline, target Patagonian toothfish (*Dissostichus eleginoides*). In the southern hemisphere, killer and sperm whale depredation on those longliners is among the highest in the region (Hucke-Gaete et al., 2004; Ashford et al., 1996; Purves et al., 2004; Nolan et al., 2000; Tilney and Purves, 1999), with more than 75% of longlines set subjected to interactions (Tixier et al., 2010). Furthermore, the stock of Patagonian toothfish around the Crozet Islands underwent a significant decline due to illegal, unreported and unregulated (IUU) fishing in the late 1990s. IUU fishing was ended in 2003 following the establishment of strict regulations and increased patrolling effort enforced by the French government and fishery managers. Since then, only seven authorised vessels operate in the EEZ and each vessel has a fishery observer on board observing 100% of the fishing operations. The acquired dataset from fishery observations, as well as collaboration with fishery managers and fishing companies, led to the first preliminary estimates of depredation levels by killer and sperm whales around Crozet and Kerguelen Islands (Roche et al., 2007; Tixier et al., 2010). As odontocetes leave almost no heads or lips of depredated fish that could be used to assess losses, the authors used an indirect method: they compared CPUE between depredated and non-depredated longline sets, taking into account spatial heterogeneity of both the fish resource and the interactions with odontocetes. They estimated that 571 tonnes were removed from the lines by odontocetes in the Crozet Islands between 2003 and 2008, which corresponds to US$ 6.7 million of fish value (Tixier et al., 2010). Financial loss for the fishing company is related to extra days at sea to achieve quotas and avoid odontocetes. However, such biomass losses are likely to be underestimated, considering the complex spatial distribution of data and the complete depredation of all longlines in some areas, which leaves no information to compare catch rates in the absence of odontocetes.

In order to support those results, the use of another indirect method was developed to estimate losses caused by depredation: the use of by-catch rates of two particular species of grenadiers, *Macrourus carinatus* and *M. holotrachys*. Observations from vessels, as well as underwater footage (B. Loyer, pers. comm.), suggested that killer and sperm whales are highly selective when depredating longlines. They only remove Patagonian toothfish, which is likely to be the fish prey

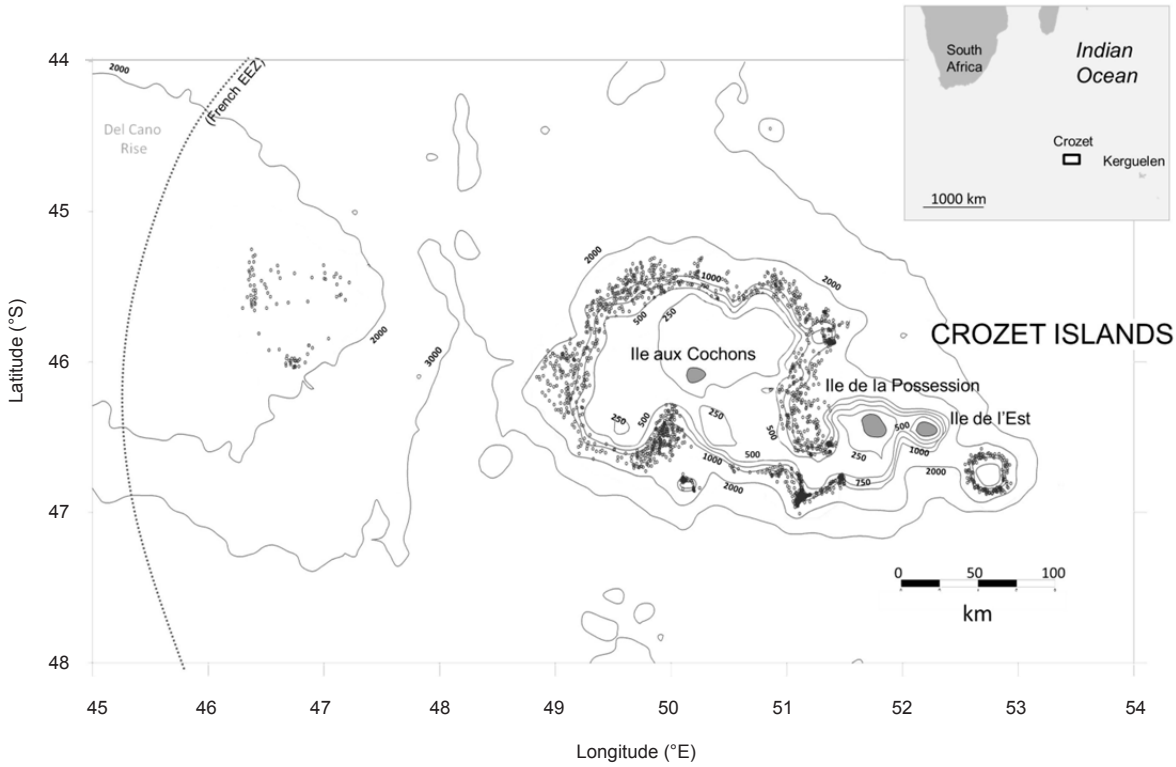

Figure 1: Study area: the Crozet Islands and Patagonian toothfish fishing grounds (depth ranging from 500 m to 2 000 m). Dots represent the positions of longline sets that were depredated by killer whales and/or sperm whales between 2003 and 2013. The 200 n miles boundary of the Crozet Islands EEZ is depicted (dashed line) as well as isobaths (grey lines) and location of the Crozet Islands in the southern part of the Indian Ocean (upper right).

species providing the highest energetic income, and leave most by-catch species on the hooks. This has been recorded by scientific observers who noted that grenadier catch rates remain unchanged on a longline after odontocetes begin to depredate, while Patagonian toothfish catch rates noticeably drop. Grenadiers are the most abundant and widespread species of by-catch around the Crozet Islands, representing 60.5% of the number of fish by-caught on lines in this area (Gasco, 2010). If this proves true, it is reasonable to assume that changes in the ratio of grenadiers to Patagonian toothfish for a given fishing location in the presence or the absence of odontocetes are likely to be related to depredation and, therefore, could be used as an indicator of depredation loss.

This study therefore aims to: (i) update the previous estimation of the level of depredation around the Crozet Islands using a similar method of CPUE comparison (Tixier et al., 2010), (ii) investigate an alternative method of assessment of losses caused by depredation using grenadier by-catch rates, and (iii) assess the reliability of the by-catch method through comparison to the established CPUE-derived method.

Material and methods

Data collection

The study area is situated in the southern Indian Ocean around the Crozet Islands, located just north of the Polar Front and south of the sub-Antarctic Front (Figure 1). The Patagonian toothfish fishery operates year-round, but within the Crozet Islands EEZ, 35% of fishing activity occurs in February.

Fishery observers are deployed on every vessel for the entire operational duration to collect data which feed into the management of the fishery. As part of the data collection process, the observers record depredation events for each longline set. The exact number and weight of target and by-catch species are also reported for each line along with date and time, hook count, position and depth. In cases of low visibility or night hauling,

the observers report the line as 'not observed' for odontocetes and those lines were not included in this study.

Calculating CPUE and assessing influence of area

In a preliminary analysis prior to estimating the biomass losses caused by depredation, the relevance of accounting for spatial variations of the CPUE was tested by analysing the influence of the CPUE in the absence of odontocetes on the CPUE loss caused by killer and/or sperm whales. Recent studies have indeed suggested that killer and sperm whales may be found in greater numbers and may interact with fisheries at higher levels on the richest fishing grounds, which are likely to be traditional feeding grounds for these two species (Sigler et al., 2008; Tixier et al., 2015a). Similarly to Tixier et al. (2010), a 0.2 × 0.2° grid was created over the fishing ground area. CPUE comparisons were made using all possible combinations of longline sets in the absence and the presence of odontocete depredation and estimated a mean CPUE loss per cell (c). CPUE reductions were expected to be greater in rich areas. This assumption was tested through a correlation between the $\mathrm{CPUE}_i(c_d)$ and the estimated CPUE loss caused by odontocetes in the same 0.2 × 0.2° cell (i.e. $\mathrm{CPUE}_{loss_{j,k,l}}(c_d)$) using linear regression.

In previous studies, losses caused by killer and sperm whale depredation were assessed using CPUE (in g of toothfish per hook, noted g hook^{-1}) comparisons between longline sets that were hauled in the presence and the absence of odontocetes (Hucke-Gaete et al., 2004; Roche et al., 2007; Tixier et al., 2010). However, such an approach may induce non-negligible bias to final estimates as (i) the fishing effort (number of hooks) can greatly vary between longline sets (from 2003 to 2013 it ranged from 500 to 22 050 hooks per set), and (ii) the number of longline sets can greatly vary between cells (from 2003 to 2013 it ranged from 1 to 518 sets per cell). To reduce such bias, the decision was made not to use the longline set as the primary unit of calculations but instead to sum the total amount of fish landed and the total number of hooks hauled in each 0.2 × 0.2° cell and for each depredation case: (i) absence of odontocetes (i), (ii) presence of killer whales only (j), (iii) presence of sperm whales only (k), and (iv) presence of both species depredating simultaneously (l). This allowed us to provide a single CPUE estimate per cell with depredation (c_d). CPUE was calculated as follows:

$$\mathrm{CPUE}_{i,j,k,l}(c_d) = \frac{\sum B_{i,j,k,l}(c_d)}{\sum E_{i,j,k,l}(c_d)} \quad (1)$$

where $B_{i,j,k,l}(c_d)$ is the amount of fish biomass captured and landed in cell c_d and $E_{i,j,k,l}(c_d)$ the number of hooks hauled in cell c_d in which both data in the absence (i) and in the presence (j, k or l) were available.

The CPUE loss caused by depredation (CPUE_{loss}) was then estimated in each cell c_d as follow:

$$\begin{aligned}&\mathrm{CPUE}_{loss_{j,k,l}}(c_d)\\&= \mathrm{CPUE}_i(c_d) - \mathrm{CPUE}_{j,k,l}(c_d)\end{aligned} \quad (2)$$

where $\mathrm{CPUE}_{loss_{j,k,l}}(c_d)$ is the CPUE loss in cell c_d for each depredation case j, k and l, $\mathrm{CPUE}_i(c_d)$ is the CPUE in the absence of depredation in cell c_d and $\mathrm{CPUE}_{j,k,l}(c_d)$ is the CPUE in the presence of odontocetes in cell c_d for each depredation case: j, k or l.

Method 1: estimating the depredated biomass using CPUE

The amount of Patagonian toothfish biomass lost to depredation between 2003 and 2013 was estimated from the CPUE loss (difference of CPUE in the absence and in the presence for each cell) and the total number of hooks in the presence of odontocetes for each case j, k and l in each cell c_d as follows:

$$\begin{aligned}&B_{loss_{j,k,l}}(c_d)\\&= \mathrm{CPUE}_{loss_{j,k,l}}(c_d) \bullet \sum E_{j,k,l}(c_d)\end{aligned} \quad (3)$$

where $B_{loss_{j,k,l}}(c_d)$ equals the fish biomass lost to depredation in each cell c_d, for each depredation case j, k and l.

However, fishing effort and landed fish biomass data both in the absence and the presence of odontocetes were not available in all cells in which fishing occurred during the study period. In some cells odontocetes were present during 100% of hauls,

which prevented a CPUE comparison. In such cases, equation (1) was used to estimate the global CPUE loss from all cells with available data (C_d) and the sum of all hooks hauled in cells with 100% presence of odontocetes (cells c_u) to estimate fish biomass loss (B_{loss}) in all cells of the ensemble of cells (C_u) as follows:

$$B_{loss_{j,k,l}}(C_u) = \mathrm{CPUE}_{loss_{j,k,l}}(C_d) \bullet \sum E_{j,k,l}(C_u) \quad (4)$$

where $B_{loss_{j,k,l}}(C_u)$ the total fish biomass lost to depredation in all cells c_u, $\mathrm{CPUE}_{loss_{j,k,l}}(C_d)$ the global CPUE loss in all cells c_d and $E_{j,k,l}(C_u)$ the total number of hooks hauled in the presence of odontocetes in cells c_u for each case of depredation j, k and l.

The final estimates of fish biomass lost to depredation were then calculated by summing the results of equation 3 and 4.

The calculations were run using all longline sets of the 2003–2013 period, which provided three estimates of Patagonian toothfish biomass loss due to depredation by killer whales only, sperm whales only and both species co-occurring. For each case, uncertainty of the final biomass loss estimates were estimated through a non-parametric stratified bootstrap procedure (Davison and Hinkley, 1997). A total of 10 000 replicates were performed on randomly sampled differences of mean CPUEs between longline sets hauled in the absence and in the presence of odontocetes over all cells. The standard errors of the mean loss of CPUE in the presence of odontocetes were multiplied by the total number of hooks hauled in the presence of killer whales alone, sperm whales alone and both species co-occurring to provide estimates of the uncertainty of the amount of Patagonian toothfish biomass lost to depredation. To be able to provide an error estimate to the global depredation losses, the calculations and the bootstrap procedure were also run considering depredation to occur regardless of the species involved, that is when any of the two species were present during hauling. The notation *j,k,l* was used to indicate that all three cases were pooled to run this parallel analysis.

Method 2: estimating the number of depredated fish using by-catch rates

A second and new method was developed here to estimate depredation. Unlike the CPUE-based method, this new method relies on estimating the proportion of a commonly encountered by-catch species, the grenadier, on lines in the absence and the presence of odontocete depredation. As grenadier by-catch levels vary geographically, analyses were performed according to the fishing location and the relative proportion of grenadier on the lines in the absence (*i*) or the presence (*j, k, l*) of killer whale and/or sperm whale depredation, with the prediction that grenadier occurrence relative to Patagonian toothfish should increase on depredated longline sets.

It is then possible to estimate the amount of Patagonian toothfish removed using the difference of grenadier proportion in the presence and the absence of odontocetes. In order to avoid a possible bias due to average weight variation of fish in the proportion, the number of individuals instead of the weight has been used to estimate losses with the grenadier method.

To account for spatial variations of catch rates of grenadiers, the estimation of losses was carried out on the same 0.2° cells, including only cells with at least four longlines and a proportion of grenadiers ranging from 35% to 65% (by number) in the absence of odontocetes to be able to estimate a change in grenadier proportion. The ideal case would be an exact 50% proportion for both species to best detect effect of depredation but no data would have been available for comparison so the arbitrary choice was made to use data 15% away from this ideal case to obtain sufficient sample size. These cells were referred to as c_g individually and C_g as a whole. The implementation of a new and more rigorous by-catch monitoring protocol in 2007 led to the restriction of the dataset to test this method on data for 2007–2013 only. For each grid cell c_g and for each case the number of Patagonian toothfish lost to depredation ($N_{loss_{j,k,l}}(c_g)$) was estimated as follows:

$$N_{loss_{j,k,l}}(c_g) = \left(\frac{N_{g_i}}{\%_{g_i}}\right)(c_g) - N_{g_{j,k,l}}(c_g) - N_{j,k,l}(c_g) \quad (5)$$

Table 1: Mean CPUE loss (estimated from a non-parametric stratified bootstrap procedure) and total amount of Patagonian toothfish biomass loss caused by depredation of killer whales and sperm whales between 2003 and 2013 within the Crozet EEZ. Calculations were run using method 1 on (a) all hooks (E) exposed to depredation by any of the two odontocete species (j,k) and (b) hooks (E) that were exposed to depredation by killer whales only (j), sperm whales only (k) and both species co-occurring (l). The number of cells used for calculations is provided as C_d: cells c_d with available data in both absence and presence of odontocetes (equations 1, 2, 3, 4 and 6) and C_u: cells c_u with lacking data in absence of odontocetes (equations 4). The amount of Patagonian toothfish landed on board fishing vessels both in absence and in presence of depredating odontocetes is provided ($B_{landed_{i,j,k,l}}$). Error estimates (SE) were obtained using a non-parametric bootstrap procedure with 10 000 replicates.

Depredation case	Mean CPUE loss ± SE (g hook^{-1})	C_d	C_u	E (hooks)	B_{loss} (tonnes)	$B_{landed_{i,j,k,l}}$ (tonnes)
j	55.5 ± 7.0	83	13	4 977 066	575 ± 35	6 530
k	19.6 ± 6.2	101	9	14 138 056	739 ± 87	
l	57.2 ± 6.4	79	16	11 568 511	1 679 ± 74	
j,k,l	39.2 ± 2.7	105	26	30 683 633	2 568 ± 82	

where $N_{loss_{j,k,l}}(c_g)$ is the number of Patagonian toothfish lost in the cell c_g, N_{g_i} is the total number of grenadier in the absence of odontocetes, $\%_{g_i}$ is the proportion of grenadier in the absence of odontocetes, $N_{g_{j,k,l}}$ is the total number of grenadier in the presence of odontocetes and $N_{j,k,l}$ is the total number of Patagonian toothfish in the presence of odontocetes.

Comparison of the depredation rates provided by the two methods

Depredation rate is defined here as the amount of fish depredated divided by the amount of fish that were actually caught on the line. In order to compare the results of the two methods, the number of depredated Patagonian toothfish was first calculated using method 1 on the 2007–2013 study period and in cells c_d that matched the cells c_g used in method 2. To do so, the CPUE term of equation (1) was here calculated in Excel® as follows:

$$\mathrm{CPUE}_{i,j,k,l}(c_d) = \frac{\sum N_{i,j,k,l}(c_d)}{\sum E_{i,j,k,l}(c_d)} \qquad (6)$$

where $N_{i,j,k,l}(c_d)$ is the number of Patagonian toothfish captured and landed in cell c_d in the absence of odontocetes (i) and in the presence of killer whales alone (j), sperm whales alone (k) and both species co-occurring (l). The CPUE was thus expressed as the number of Patagonian toothfish per-unit-effort (n hook^{-1}) and equations (2) and (3) were used replacing the fish biomass (B) by the number of fish (N) to provide final estimates of the number of depredated fish $N_{loss_{j,k,l}}(C_d)$ in cells c_d.

From estimates of both methods, depredation rates were calculated as the proportions of depredated Patagonian toothfish out of the total amount of captured fish in each cell c_g and c_d, that is the total sum of landed fish and estimated depredated fish. The correlation between depredation rate estimates of the two methods was then tested with a simple linear regression.

Results

From 1 September 2003 to 31 August 2013, 7 467 longline sets were hauled by the seven longliners operating in the Crozet Islands EEZ (Figure 1). Only longlines observed for the presence and the absence of odontocetes (6 525) have been incorporated in the analyses. Of these 6 525 sets, 24.9% (n = 1 627 sets) were hauled without any odontocetes present, 12.5% (n = 816 sets) in the presence of killer whales alone, 33.4% (n = 2 178 sets) in the presence of sperm whales alone and 29.2% (n = 1 904 sets) in the presence of both species combined. A total of 41 427 989 hooks were hauled and resulted in 6 530 tonnes of landed Patagonian toothfish. Overall depredation rates due to odontocetes, killer whales only, sperm whales only and killer whales and sperm whales occurring simultaneously, are presented in Table 1.

Differences of CPUE in the absence and in the presence of odontocetes calculated in 0.2° × 0.2° cells c_d were found to be positively and significantly correlated to the CPUE of cells in the absence of odontocetes (Figure 2). For instance, when killer whales alone interacted with longline sets that were hauled in rich cells ($CPUE_i$ > 400 g hook^{-1}), losses of CPUE exceeded 200 g hook^{-1} in that cell whereas such losses were < 50 g hook^{-1} in cells with limited productivity ($CPUE_i$ > 100 g hook^{-1}).

Depredation estimates of biomass using CPUE

The number of cells c_d in which depredated fish biomass could be estimated using differences of CPUE in the absence and in the presence of odontocetes (equation 3) varied from 79 when depredation by both killer whales and sperm whales occurred simultaneously, to 101 when sperm whales were the only species to depredate (Table 1). The number of cells c_u in which the depredated biomass could only be estimated using equation (4) because 100% of lines were depredated, represented less than 20% of all cells ($C_d + C_u$). Out of 145 cells in total, 83 were used for killer whales, 101 for sperm whales and 79 for killer whales and sperm whales combined. Between 2003 and 2013, the depredation of any of the two odontocete species (i.e. regardless of what species was present during depredation events) was estimated to cause a global loss of 2 568 ± 82 tonnes of Patagonian toothfish using equations (3) and (4). When summed to the landed biomass (6 530 tonnes), the total amount of captured Patagonian toothfish may be estimated to 9 098 tonnes, which provides an estimated overall odontocete depredation of 28.2% of the total capture. Killer whales alone removed an estimated biomass of 575 ± 35 tonnes of Patagonian toothfish, killer whales and sperm whales combined removed 1 679 ± 74 tonnes and sperm whales alone removed 739 ± 87 tonnes. When compared to the total amount of Patagonian toothfish caught, these estimates suggest that killer whales removed 6.0% of the total catch when depredating alone, sperm whales removed 7.8% when depredating alone, and both species removed 17.6% when depredating simultaneously.

Depredation estimates using the by-catch method

The proportion of grenadiers to Patagonian toothfish in the absence of killer whales varies spatially around the island (Figure 3), but no seasonal trend could be detected in grenadier catch rate (R^2 = 0.00, P = 0.99) with a mean number of 18.3 ± 3.8 grenadiers/thousand hooks). Among all cells, 14 cells c_g could be used for comparison of the proportion of grenadier relative to Patagonian tooth fish in the presence of killer whales and 19 cells c_g in the presence of killer whales and sperm whales together as both data in the absence and in the presence were available. Not enough data were available to estimate the change in by-catch proportion in the presence of sperm whales only. From this method 40 434 Patagonian toothfish were estimated to be depredated (28 862 due to killer whales and sperm whales, 11 571 due to killer whales alone).

Comparison of the depredation rates provided by the two methods

In the cells c_d that matched the cells c_g used in method 2, method 1, used with numbers instead of weight, provided an estimate of 46 328 depredated Patagonian toothfish (32 991 due to killer whales and sperm whales, 13 338 due to killer whales alone). The linear regressions fitted through the estimated depredation rates derived from methods 1 and 2 showed that the results obtained are statistically consistent between the two methods (Table 2). Some outliers are present but for killer whales and sperm whales combined, the coefficient (a) is 0.97 and 0.89 for killer whale alone, meaning that the two methods provide very consistent results with a very high R^2 (Figure 4, Table 2). However, losses estimated from the by-catch method tended to be lower than those estimated from the CPUE method, but the regression slope was not significantly different from 1 (Figure 4).

This estimate of 46 328 depredated Patagonian toothfish represents an equivalent of US$ 2.5–2.9 million of fish value per year based on the average market price of toothfish.

Discussion

This study presented two distinct methods to assess the losses of Patagonian toothfish biomass caused by depredation by killer and sperm whales in the Crozet Islands EEZ, and both provided

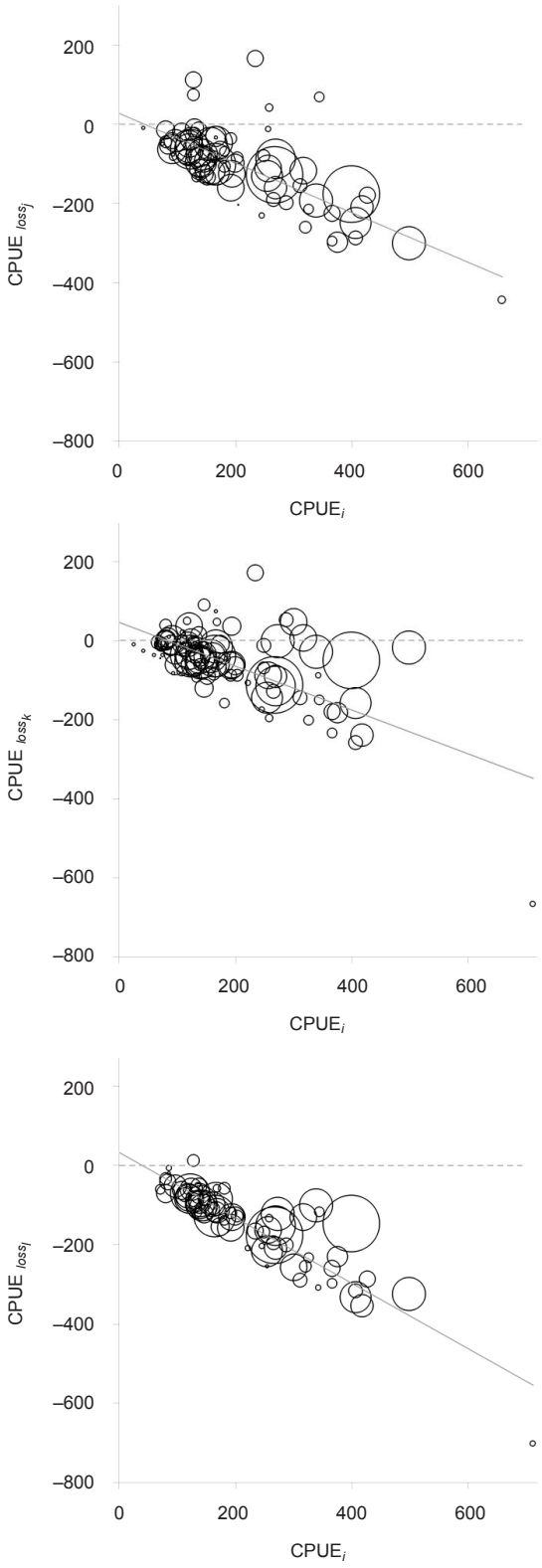

Figure 2: Influence of area richness (Patagonian toothfish CPUE in the absence of odontocete depredation – *i*) on the decrease in CPUE caused by depredation (difference of CPUE between non-depredated and depredated hooks – $CPUE_{loss}$) in cells c_d. $CPUE_{loss}$ was calculated for hooks that were exposed to depredation by killer whales only (*j* – top), sperm whales only (*k* – centre) and both species co-occurring (*l* – bottom). Linear regression curves are depicted (dark line – R^2 = 0.53; 0.44; 0.88 for *j*, *k* and *l* respectively). The size of the circles indicates the amount of toothfish caught on undepredated hooks in each cell c_d, the largest circle represents 108 tonnes.

Table 2: Final estimates of the number of Patagonian toothfish that were depredated (N_{loss}) on hooks exposed to killer whales only (j) and to both killer and sperm whales co-occurring (l) provided by methods 1 and 2. Depredation rates (proportion of depredated fish out of the total number of caught fish) are provided for both methods and both depredation cases j and l, as well as the number of cells used for calculations in method 1 (C_d) and in method 2 (C_g). The coefficient of linear regression between outputs of the two methods, as well as the square multiple (R^2), are provided.

		Method 1	Method 2	Correlation method 1/method 2	
				Coefficient	R^2
j	C_d, C_g	14	14	0.89	0.90
	N_{loss}	13 338	11 571		
	Depredation rate	56%	52%		
l	C_d, C_g	19	19	0.97	0.96
	N_{loss}	32 991	28 862		
	Depredation rate	63%	60%		

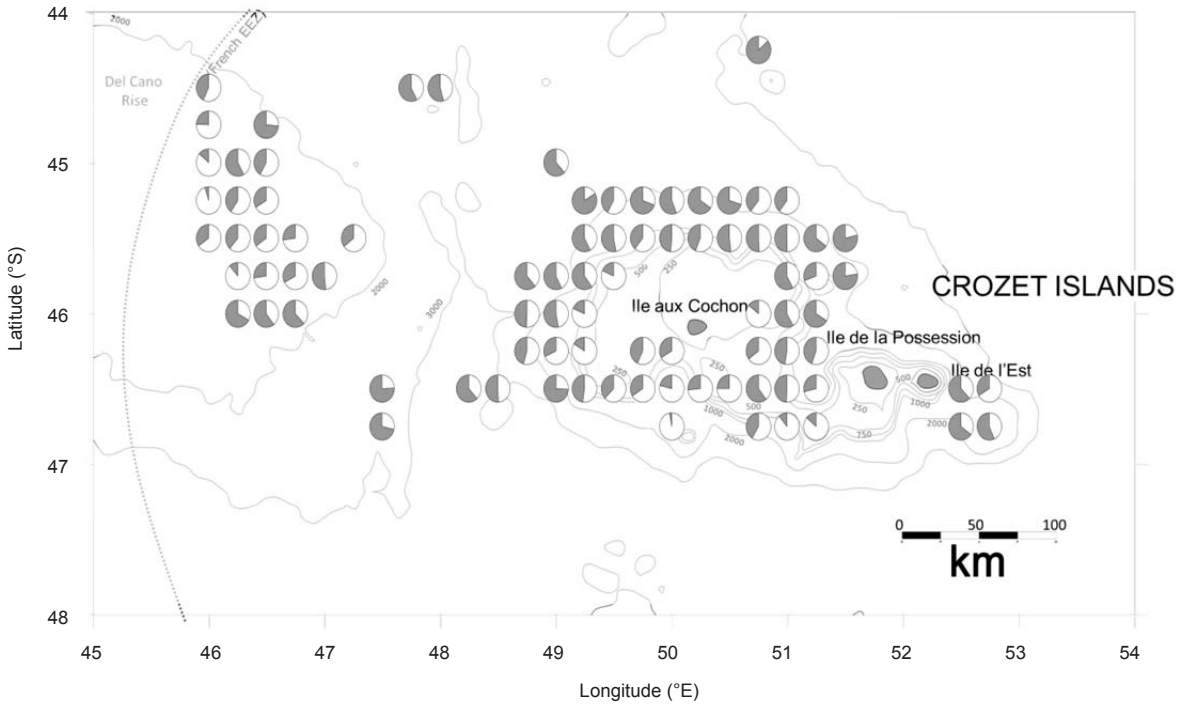

Figure 3: Spatial variations of the proportional amounts (%) of Patagonian toothfish (white in pie charts) and grenadiers (black in pie charts) in 0.2° × 0.2° cells covering the demersal longline fishing grounds of the Crozet Islands EEZ. The 200 n miles boundary of the Crozet Islands EEZ is depicted (dashed line) as well as the 500, 1 000 and 1 500 m isobaths (grey lines).

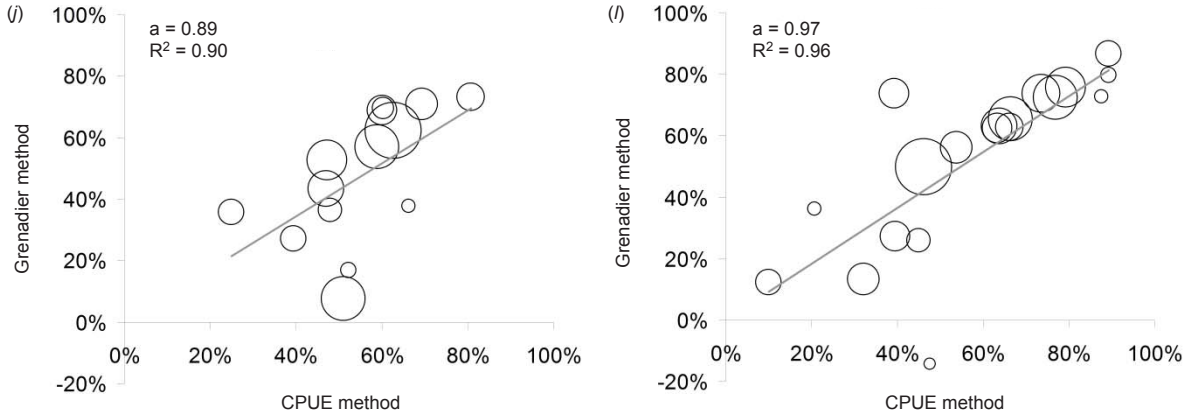

Figure 4: Tests of consistency of the results between the depredation rate estimates provided by method 1 and the depredation rate estimates provided by method 2 in cells c_d and c_g in which data were available for both methods and for killer whales alone (*j*) and killer and sperm whales combined (*l*). The regression coefficient (a) and correlation coefficient (R^2) are provided at the top left. The size of circles indicates the amount of toothfish caught on undepredated hooks in each cell (amount ranges from 724 to 10 538 individuals).

consistent estimates. Spatial CPUE comparisons estimated an overall loss of 2 568 ± 82 tonnes caused by odontocetes over the 2003–2013 period. Grenadier catch rate provided comparable results to the CPUE estimates, restricted to cells where the balance between Patagonian toothfish and grenadier ranges from 35% to 65% and only for the 2007–2013 period.

Application of indirect methods of biomass loss assessment

Both the CPUE method and the by-catch method have their advantages and disadvantages. The CPUE method is limited to areas where odontocetes absence and presence data are available and, therefore, estimations spanning only a short period of time are less robust as fewer data are available for each area. Losses estimated from the by-catch method tended to be lower than those estimated from the CPUE method, this might be explained by underestimated numbers of grenadier reported when odontocetes are absent in equation 5. When toothfish and by-catch are both present on consecutive hooks, the crew will choose to bring on board the most valuable of the two and some of the by-catch may drop out back into the water and consequently will not be incorporated in counts made at the factory. When odontocetes are present, toothfish numbers are very low and the crew has more time to gaff grenadier on board. This leads to under-reported numbers of grenadier when odontocetes are present and more accurate numbers when they are absent. Outliers in Figure 4 might be explained by misreported numbers by the skipper. Also, eliminating high and low grenadier ratio might add some bias to the method. Those differences should be investigated through GAMs or GLMMs in further studies.

This study spans a total of 10 years to estimate losses, which gives a more robust result than evaluating individual seasons. Estimations in this study are higher than those of Tixier et al. (2010). This might be explained by changing behaviour of the fishing fleet in the more recent years of this study: fishing vessels no longer concentrate in the Crozet Islands in February as much as in early years, and thus the number of vessels operating at the same time lowered. This means that the probability of encountering killer whales may have increased for each vessel due to more focused targeting by orcas, which may increase the interaction rate and consequently the higher depredation rate observed in this study. Since 2010 new killer whale groups have been identified from photo-identification, and those additional groups interacting with the fishing vessels are likely to have also contributed to the higher interaction and depredation rate (Tixier et al., 2011). Furthermore, in previous studies (Roche et al., 2007; Tixier et al., 2010) the positive relationship between CPUE and depredation rates was not considered when modelling depredation rates, resulting in an underestimation of the amount of fish lost.

The grenadier by-catch method, on the other hand, relies on the presence of substantial quantities of by-catch available and good quality data for

by-catch counts. The type of longline may also play a role in catching by-catch. For instance, trotline-system hooks do not lay on the bottom.

The method using grenadier by-catch showed that results obtained are extremely consistent to those using the CPUE method with no significant differences between the estimated yield by the two methods.

Furthermore, the two independent methods provided similar results, which suggests limited uncertainty in the depredation estimates provided here. However, as this method is restricted to areas where grenadier concentrations are close to Patagonian toothfish concentrations in terms of number, it cannot be used to estimate losses for the entire area. Results obtained for killer whales alone, and combined with sperm whales, were consistent with the CPUE method but analyses for sperm whales alone were not conclusive due to limited sample size. In addition, when depredating longlines in high latitudes, sperm whales usually occur in significantly smaller groups than killer whales. This was emphasized in other similar depredation cases in high latitudes and involving the same two species (Sigler et al., 2008; Söffker et al., 2015). In the Crozet Islands, previous studies reported a mean number of sperm whales of 1–3 individuals per depredated set. Furthermore, sperm whales are likely to be less efficient than killer whales in removing fish from hooks due to their larger size and lower manoeuvrability (Dominici, 2002). The clear benefit of this by-catch method is that it provides an independent validation of the estimates using the CPUE methods. Macrouridae, or any abundant and widespread by-catch species not targeted by depredating odontocetes, can be used in other locations or fisheries to assess depredation levels when targeted fish species are entirely removed from hooks by depredating odontocetes.

Implication of depredation in resource management

The stock assessment for Patagonian toothfish is based on catch data, length-frequency distribution collected by observers and a mark-recapture program. Catch data, and thus CPUE, are strongly biased as about a third of the Patagonian toothfish (in weight) actually caught are not landed due to odontocetes.

Preliminary results (Gasco, 2013) show that sperm whales and killer whales tend to select large Patagonian toothfish on the line, likely for energetic benefit and manoeuvrability reasons. Length-frequency distributions collected by fishery observers are thus biased by a selective effect of odontocetes.

Patagonian toothfish are known to move short distances (a few miles) in different areas (Williams et al., 2002; Marlow et al., 2003; Agnew et al., 2006). In the Crozet Islands, Patagonian toothfish is tagged at a rate of one fish/tonne. Fishing vessels concentrate their effort in toothfish-rich areas, so tagged fish tend to concentrate in these areas as they do not travel long distances. Killer and sperm whale depredation is positively correlated with the richness of these areas, so depredation impacts may even be greater on the tag-recapture rate of fish caught. Furthermore, sperm whales also have an impact on tagged fish not caught as they feed naturally on toothfish (Abe and Iwani, 1989).

Depredation by odontocetes introduces a significant bias into the data used for management. When compared to other regions like South Georgia, where the depredation rate does not exceed 5% (Söffker et al., 2015), the situation in the Crozet Islands certainly represent the highest depredation rate in the Southern Ocean. Consideration of the depredation rate is likely to change over time, this study emphasised the critical need to account for depredation with the best available data to update stock assessments.

Consequences of depredation activity on the killer whale population

The development of the Antarctic longline fishery has made a highly energetic and easily accessible resource available to killer whales, for which Patagonian toothfish was not known to be a major component of their natural feeding ecology. Such artificial resource provisioning has significant implications in killer whale population dynamics (Tixier, 2012; Tixier et al., 2015b). In 2011, a total of 78 killer whales belonging to 21 social groups (matrilines) were known to have interacted at least once with the fisheries. Significant between-matriline variations of level of interaction have been reported, with a small subset (< 25 individuals) being responsible for over 80% of all depredation events (Tixier et al., 2010, 2011). While

interactions with illegal fishing vessels negatively impacted the depredating killer whales in the early years of the fishery because of lethal responses from fishers, contributing to a 70% decline of the population (Poncelet et al., 2010), nowadays it is likely that such artificial food provisioning may greatly benefit a part of the population. For instance, recent studies showed that the fecundity of mature female killer whales was positively correlated to their level of interaction with fisheries (Tixier et al., 2015a). Given the energetic value of Patagonian toothfish (Collins et al., 2010) and the energetic requirements of killer whales (Williams et al., 2004; Noren, 2011), the 200 tonnes of depredated Patagonian toothfish estimated to be lost annually from depredation may sustain 11 to 14 whales during the average 148 ± 34 days of presence of fishing vessels in the Crozet Islands EEZ per year. Although access to Patagonian toothfish on longlines is limited in time (the maximum number of days of interaction per matriline is 37 days per year) (Tixier et al., 2015a), such artificial income may contribute to the recovery of the Crozet Islands killer whale population in decades to come if fishing activity is maintained (Tixier et al., 2015a).

Killer and sperm whales interact with more than 75% of all longline sets that are hauled off the Crozet Islands. With an estimated 30% depredation rate over the total capture of Patagonian toothfish, this study reports levels of depredation that are amongst the highest of all other reported similar depredation situations elsewhere in the world. For instance, killer and sperm whales were reported to interact with less than 10% of all longline sets of the Patagonian toothfish fisheries occurring off South Georgia and Southern Chile (Hucke-Gaete et al., 2004; Purves et al., 2004; Clark and Agnew, 2010; Söffker et al., 2015). The situation in the Crozet Islands is unique because the fleet size is limited, fishing grounds are small and fishing activities are regulated thanks to great collaboration amongst fishing companies, fishery managers and scientists. Long-term monitoring of depredation in this context is illustrative of the importance of implementing similar research frameworks when investigating the range of consequences of human–wildlife interactions such as depredation.

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