



Assessing the impact of toothed whale depredation on socio-ecosystems and fishery management in wide-ranging subantarctic fisheries

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Abstract Marine predators feeding on fisheries catches directly on the fishing gear, a behaviour termed “depredation”, has emerged as a major human-wildlife conflict globally, often resulting in substantial socio-economic and ecological impacts. This study investigated the extent of this conflict in commercial Patagonian toothfish (*Dissostichus eleginoides*) fisheries across subantarctic waters where both killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) feed on toothfish caught on longline hooks. Using long-term datasets from six major fishing areas, from southern Chile to the Indian Ocean sector of the Southern Ocean, statistical models

were developed to quantify the catch removals due to whale depredation interactions. The results indicated that these removals were large, totalling more than 6600 t of toothfish between 2009 and 2016 with an annual mean of 837 t [95% CI 480–1195 t], comprised of 317 t [232–403 t] and 518 t [247–790 t] removed by killer whales and sperm whales, respectively. Catch removals greatly varied between areas, with the largest estimates found at Crozet, where on average 279 t [179–379 t] of toothfish per year, equivalent to 30% [21–37%] of the total catches. Together, these findings provide metrics to assess the impacts of depredation interactions on the fishing industry, whale populations, fish stocks and associated ecosystems. With an estimated \$15 M USD worth of fish depredated every year, this study highlights the large geographic scale and economic significance of the depredation issue and its potential to compromise the viability of some

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toothfish fisheries which are the primary socio-economic activity in subantarctic regions.

Keywords Fisheries interactions · Depredation · Subantarctic · Patagonian toothfish · Killer whales · Sperm whales

Introduction

Increased exploitation of marine living resources over the past 60 years has exacerbated conflicts between fisheries and marine top predators worldwide (Nyhus 2016; Guerra 2018). While indirect conflicts often result from trophic effects associated with reduced fish stocks (Branch et al. 2010; Smith et al. 2011), fisheries can also generate direct interactions between marine predator species and fishing gear (Lewison et al. 2004; Read 2008). Among such interactions, predators feeding on bait and/or on fish caught on fishing gear has recently emerged globally as a major human-wildlife conflict affecting marine social-ecological systems at all levels (Read et al. 2005; Mitchell et al. 2018).

This behaviour, termed depredation, has been reported in large proportions of the world's fisheries (commercial, artisanal and recreational) on most existing types of fishing gear and has multiple impacts on fishing activity, fish resources and marine predator populations (Gilman et al. 2007; Hamer et al. 2012; Trijoulet et al. 2018; Mitchell et al. 2018). For fishermen and fishing companies, depredation-type interactions (hereafter “depredation”) can generate substantial socio-economic costs by decreasing catch rates, increasing fishing effort and/or causing damage to the fishing gear (Brotons et al. 2008; Gilman et al. 2008; Peterson et al. 2014). For affected fisheries, unaccounted fish taken by predators on the gear

represent, if they are surplus consumptions from natural predation, a key concern for stock assessments (Gilman et al. 2013; Peterson and Hanselman 2017; Hanselman et al. 2018). For the depredating species, which primarily include sharks and marine mammals, depredation can provide a new foraging opportunity that takes advantage of resource access facilitated by humans. However, interactions with fishing gear can also have negative effects by increasing the risks of injuries or bycatch and by generating lethal responses from fishermen in some instances (Forney et al. 2011; Cosgrove et al. 2013; Guinet et al. 2014; Werner et al. 2015). In addition, depredation can also alter the natural energy intake balance of individuals and generate artificial food provisioning effects (Tixier et al. 2015; Esteban et al. 2016), which may not only impact predator populations but also entire ecosystems (Oro et al. 2013).

Accurately estimating catch removals due to depredation is therefore critical in assessing the various impacts of depredation and in predicting the sustainability of the social-ecological systems experiencing this conflict (Trijoulet et al. 2018). However, such estimations are often challenging because species may remove whole fish when depredating, leaving no obvious or measurable evidence of depredated fish, and because depredation may occur at depth and/or when fishermen are not in the vicinity of their gear (Gilman et al. 2013; Richard et al. 2020). While in some cases partially eaten fish landed on vessels or damaged fishing gear have been used to estimate fish losses (Dalla Rosa and Secchi 2007; Rafferty et al. 2012; Passadore et al. 2015), most fisheries have to apply indirect methods based on Catch Per Unit Effort (CPUE) models incorporating depredation effects and requiring extensive datasets to be reliable (Roche et al. 2007; MacNeil et al. 2009; Hanselman et al. 2018).

Commercial demersal longline fisheries operating in subantarctic waters targeting Patagonian toothfish (*Dissostichus eleginoides*) are among the fisheries most impacted by depredation, with two odontocete (toothed whales) species removing toothfish catches from hooks: killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) (Hamer et al. 2012). These fisheries, which operate primarily on shelf edges (500–2000 m deep) within Exclusive Economic Zones (EEZs) of southern Chile, southern Argentina, the Falkland Islands (hereafter “Falklands”), South Georgia, Prince Edward and Marion Islands (hereafter

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“PEMI”), Crozet Islands, Kerguelen Islands, and Heard Island and McDonald Islands (hereafter “HIMI”) have all experienced depredation by either one or both of these species (Kock et al. 2006; Tixier et al. 2019a). In some areas, depredation has been reported occurring during > 75% of fishing days and in > 65% of the fishing areas (Tixier et al. 2019a). In response to such high levels, some fisheries have switched from traditional longline fishing systems such as the *autoline* and the *Spanish* systems, to the *trotline* system equipped with “umbrellas”, a fish protection device developed to reduce odontocete depredation (Moreno et al. 2008; Brown et al. 2010). Traditional systems are a series of regularly spaced hooks individually attached to the mainline through individual snoods, with the mainline being auto weighted for the *autoline* system, and manually weighed at intervals for the *Spanish* system. The *trotline* system is a series of regularly spaced clusters of hooks attached together to the mainline through a shared snood. However, whether fisheries use the *autoline* or *Spanish* systems, or *trotline* equipped with umbrellas (hereafter “*trotline/umbrellas*”) or not (hereafter “*trotline*”), killer and sperm whales are still observed depredating fish and to date, the actual effectiveness of fish protection devices in preventing whales from accessing the catch and, therefore, in minimizing the amount of depredated fish, is still unclear (Tixier et al. 2019a).

Legal toothfish fisheries have developed over the last 30 years and have now become the primary economic activity within subantarctic waters being worth > \$500 M USD in 2019 and generating over 1600 jobs within fishing companies and management bodies alone (Coalition for Legal Toothfish Operators, COLTO, pers. comm.). Toothfish stocks experienced substantial Illegal Unreported and Unregulated (IUU) over-exploitation during the 1990s and early 2000s (Agnew 2000; Österblom and Sumaila 2011). Monitoring and enforcement programs have considerably reduced IUU fishing after 2003, and toothfish stocks are now highly regulated and monitored by a combination of national and international governance bodies such as the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Agnew et al. 2009; Collins et al. 2010; Österblom and Bodin 2012). However, despite these efforts, some stocks are likely to still be recovering from exploitation levels during the IUU period (Christensen 2016).

Likewise, odontocete populations depredating on toothfish fisheries may be recovering from past periods of decline. Sperm whales were commercially exploited in subantarctic waters until the early 1980s (Trathan and Reid 2009), and killer whale populations were negatively impacted by lethal retaliation from IUU fishing vessels using explosives and firearms to repel depredating individuals (Poncelet et al. 2010; Tixier et al. 2017).

Together, changes undergone by toothfish stocks and killer and sperm whale populations are likely to have profoundly disrupted subantarctic ecosystems. Strong measures for the recovery of these species, such as the creation of the Southern Ocean Sanctuary by the International Whaling Commission in 1994, the reduction of IUU fishing, the increase of observer coverage and the precautionary approach of legal exploitation of toothfish through the CCAMLR regulatory framework, have been implemented (Constable et al. 2000; Zacharias et al. 2006; Österblom and Bodin 2012). However, while Ecosystem-Based-Management (EBM) approaches are developing in fisheries management strategies (Constable 2011), the amount of depredated fish and, therefore, the extent to which depredation affects populations and ecosystems, are still poorly known. Unaccounted depredation may generate large uncertainty in the fishing mortality estimates of the target species and leads to biased stock assessments (Hanselman et al. 2018). Reducing such bias is especially important for historically overfished populations such as toothfish stocks (Christensen 2016). In addition, the amount of fish lost to depredation is a determinant factor in assessing the costs of depredation for fishing companies. For instance, the amount of depredated toothfish at Crozet was preliminarily estimated to be worth \$5.4 M USD in 2003–2008 and is likely to have induced substantial indirect costs for fishing companies as fishers attempted to fulfil their quota limits, potentially jeopardizing the profitability and the viability of the fishery (Tixier et al. 2010).

In the context of both ecological and socio-economic pressures, accurately estimating the amount of fish depredated by marine predators in toothfish fisheries is critical for assessing the sustainability of this commercial activity in subantarctic waters. Therefore, through a global approach and using datasets from major commercial toothfish fisheries, spanning 15 years (2004–2018), the aim of the present

study was to assess the annual and overall catch removals due to killer whale and sperm whale depredation in subantarctic waters.

Methods

Data collection

Data on fishing operations, toothfish catch and occurrence of whale depredation on fishing gear were collected by fishery observers and crew from all licensed commercial longliners that operated in the EEZs of Chile, Falklands, PEMI, Crozet, Kerguelen and HIMI (Fig. 1). Data from South Georgia was not available. The base unit of these data was a longline set, a mainline of variable length bearing individually baited hooks. Longlines either sit on (weighted *autoline*) or float near the seafloor (*Spanish* longline and *trotline*) with anchors at either end and at intervals in between sitting on the seafloor. In all fisheries, date, time, position and depth were recorded for each of the two ends of longlines at setting (gear deployment) and at hauling (gear retrieval). For each longline set, the total number of hooks set and hauled was recorded, as well as the catch of toothfish landed on-board (hereafter “the observed landed catch”). In Chile and Falklands, data were available for the 2006–2016 and 2009–2016 periods, respectively, with commercial

vessels (12 in Chile, 4 in Falklands) that predominantly used the *trotline/umbrella* system (93% and 98% of all sets in the two areas, respectively), and to a lesser extent the *autoline* system (7% and 0.2% of all sets for the two areas, respectively). In Falklands, the remaining sets (1.8% of all sets) were *trotlines* not equipped with umbrellas. Data at PEMI were available for the 2006–2016 period and included 3 vessels that used a combination of *trotlines* (44% of all sets), *trotlines/umbrellas* (31% of all sets), and *Spanish* fishing systems (25% of all sets). At Crozet and Kerguelen, data were available for the 2004–2018 period (PECHEKER database, Pruvost et al. 2012) and were collected from 10 different vessels (same fleet operating in both EEZs and limited to 7 vessels per year) that all used the *autoline* system only. At HIMI, data were available for the 2009–2018 period and were collected by fishery observers and crew from 6 vessels that all used the *autoline* system.

As killer whales and sperm whales often remove entire fish from hooks leaving no remains on longlines, an indirect approach is necessary to assess catch removals due to depredation. This assessment relied on the modelling of CPUE in the absence and in the presence of depredating whales during hauling of longline sets. The occurrence of whale depredation on longline sets was monitored by fishery observers and crews through surface observations conducted during hauling operations. When depredating fish from hooks

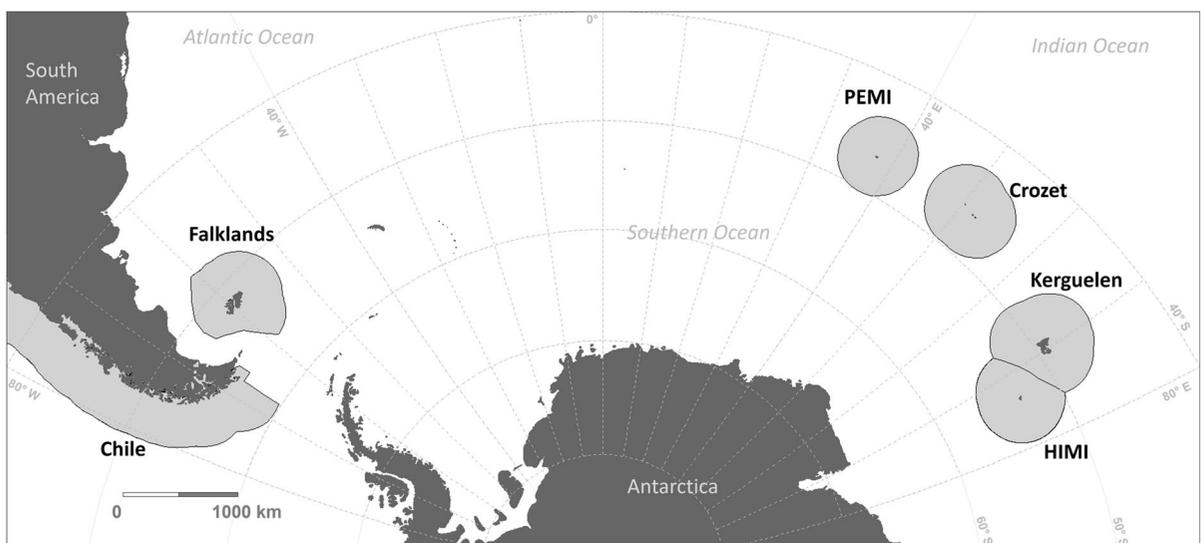


Fig. 1 Location of the study areas (grey EEZs) where the six Patagonian toothfish fisheries operate and experience whale depredation interactions

during hauling, killer whales and sperm whales are typically observed repeatedly surfacing in the vicinity of the vessel, performing long dives towards the longline, being surrounded by seabirds and leaving slicks of fish oil at the surface (Gasco et al. 2016). In all fisheries, these cues were used to assign confirmed occurrences of killer whale and/or sperm whale depredation to longline sets in the data, and for each occurrence provided an estimated range (1 minimum and 1 maximum value) of the number of depredating individuals present for each species. While true depredation occurrences were assumed to be standardized across observers, the accuracy of non-occurrence records varied between fisheries. At Crozet and Kerguelen, observers differentiated between true absences (surface observation effort provided, whales confirmed absent) from uncertain occurrences (no surface observation effort provided) of depredation. In the other areas, true absences and uncertain occurrences were all recorded as an absence state.

Modelling approach

Estimates of depredated fish removed by killer whales and sperm whales in the six study areas were modelled by comparing toothfish CPUE with and without whales present, using a series of Generalised Additive Models (GAM, Wood 2017) following a similar methodology to Peterson and Hanselman (2017). For each study area, a series of models were fitted to the toothfish CPUE and covariates commonly associated with variability in CPUE. CPUE was calculated as the amount of toothfish landed (kg) per 1000 hooks hauled, assuming a normal distribution and a log link function. In all models, discrete predictors included the vessel identity and year, and continuous predictors included the position, depth and month at which longline sets were hauled and soak time of hooks as spline smooth terms with four knots. Four knots were chosen for all spline terms in all areas because preliminary analysis showed it provided an appropriate level of smoothing and to permit direct comparisons among areas. A single position and depth value per longline set, calculated as mid-values of the two latitudes, longitudes and depths (m) of the two ends of sets, were used and incorporated in the model as a smooth interaction predictor between latitude and longitude of sets. The soak time was the time (h) between the time the last hook of a set was

deployed and the time the first hook of that set was retrieved. Month was modelled using a cyclic cubic regression spline to prevent a discontinuity between December and January. In all area-specific models, the effect of whale depredation was incorporated as the number of depredating killer whales and the number of depredating sperm whales (mean of the minimum and maximum estimates) as two distinct additive smooth predictors.

The analysis was conducted on *autolines* as the only fishing system at Crozet, Kerguelen and HIMI, and on *trotlines/umbrellas* as the only fishing system in Chile and Falklands after excluding the negligible number of *autolines* and *trotlines* used in these two areas. For these areas, the saturated model was of the form:

$$\log(\text{CPUE}_{\text{area}} \sim \beta_0 + \text{Year} + \text{cc}(\text{Month}) + \text{Vessel} \\ + s(\text{Depth}) + s(\text{Lat}, \text{Lon}) + s(\text{Soak Time}) \\ + s(\text{Killer Whales}) + s(\text{Sperm Whales})$$

where s represents predictors with spline smoothers, cc represents the cyclic cubic regression spline used for month.

For PEMI, the model included the fishing system as a discrete predictor with 3 levels (*Spanish*, *trotline* and *trotline/umbrellas*) and an interaction (*system*) with the number of killer whales and sperm whales, as follows:

$$\log(\text{CPUE}_{\text{PEMI}} \sim \beta_0 + \text{Year} + \text{cc}(\text{Month}) + \text{Vessel} \\ + s(\text{Depth}) + s(\text{Lat}, \text{Lon}) + s(\text{Soak Time}) \\ + \text{Fishing System} + s(\text{Killer Whales}_{\text{system}}) \\ + s(\text{Sperm Whales}_{\text{system}})$$

Initial data exploration was undertaken prior model fitting to identify the most appropriate covariates structure. This involved plotting each covariate, histograms and an examination of residual plots from preliminary models. Records with missing covariates were excluded along those records with unusually high or low values which indicated likely errors in reporting or transcribing the data or failed sets. This included records with soak times < 1 h and > 100 h, sets of < 1000 hooks and sets with > 20 whales observed. The models best fitting CPUE were selected using a stepwise backward process, starting with the saturated model and removing each predictor in turn and selecting the model with the lowest Akaike

Information Criterion (AIC; Burnham and Anderson 2003). When there were two or more models within two AIC units of the model with the lowest AIC, the most parsimonious model was selected as the optimal model.

Catch removal estimates from model predictions

From the models best fitting the CPUE, catch removals due to whale depredation on longline sets were estimated as the difference between the amount of toothfish expected to have been landed on vessels if whale depredation had not occurred (predicted catch in absence of whales) and the amount of toothfish expected to have been landed if whale depredation had occurred (predicted catch in presence of whales). As such, model predictions were performed on depredated longline sets only by setting the number of whales to 0, and the predicted CPUE and associated 95% Confidence Intervals (CI) were converted into a predicted catch [95% CI] in metric ton (t) by multiplying by the observed number of hooks hauled for each of these sets. These predictions were made separately for killer whales and sperm whales to estimate the respective amounts of toothfish each species removed from longlines they interacted with, including longlines hauled with simultaneous depredation by the two species. This was done by running two sets of calculations: (1) for sets depredated by killer whales, the difference between the CPUE assuming no killer whale depredation (setting the number of killer whales to 0, leaving the observed number of sperm whales unchanged) and the CPUE with killer whale depredation (leaving the observed number of both killer and sperm whales unchanged), and (2) for sets depredated by sperm whales, the difference between the CPUE assuming no sperm whale depredation (setting the number of sperm whales to 0, leaving the observed number of killer whales unchanged) and the CPUE with sperm whale depredation (leaving the observed number of both killer and sperm whales unchanged). Catch removal estimates and 95% CIs for depredated sets were then summed to produce overall estimates per area and per year using area-specific models only. These summed estimates were also used to calculate two depredation rate values: the proportion of catch removals due to whale depredation out of (1) the observed landed catch (noted $Dep(landings)$) and (2) the total catch

(observed landed catch + estimated depredated catch, noted $Dep(total_catch)$). These two metrics were used to allow for direct comparisons with other studies, in which both depredation rates were applied (e.g. Roche et al. 2007; MacNeil et al. 2009; Passadore et al. 2015; Gasco et al. 2015).

Results

Data from 82,682 longline sets from 2004 to 2018 were available from the studied fisheries. In total, 75,241 (91%) of these longline sets were used in the analyses after excluding records with missing/incorrect data for predictors in models, partially hauled sets, sets for which the occurrence of depredation was recorded as an uncertain state (Crozet and Kerguelen) and sets where more than 20 depredating individuals had been reported. Subsample size varied from 81% at Crozet to 99% of all longline sets in Falklands (Table 1). Longline sets used for the analysis included 55,442 longline sets using the *autoline* system, 1085 using the *Spanish* system, 1880 using the *trotline* system and 16,834 using the *trotline/umbrella* system (Table 1). Whale depredation occurred during hauling of 30,860 sets (41% of all sets). Killer whale and sperm whale depredation interactions were recorded occurring on 7647 (10.1% of all sets) and 27,694 (36.8% of all sets) longline sets, respectively (Table 1). Both killer whale and sperm whale depredation was recorded in all study fisheries except in HIMI where only sperm whale depredation was reported. The greatest proportions of longline sets depredated by killer whales occurred in Chile and at Crozet, with a total of 19% and 38.4% of all sets, respectively (Table 1). The occurrence of sperm whale depredation was the highest at Crozet with 54.1% of all sets and the lowest at HIMI with 2.2% of all sets (Table 1).

Effect of the number of depredating whales on catch rates

Saturated models were the optimal area-specific models in Chile, Falklands, Crozet, Kerguelen and HIMI (Online Resource 1). In PEMI, the model with all single predictors including fishing system, but no interaction terms, was the optimal model (Online Resource 1). The percentage of deviance explained by

Table 1 Data summary per study area. Study periods, number and percentage of longline sets for which data on whale depredation were used in models fitted to the toothfish CPUE

Area	Time period	Longline sets used in analysis					
		% of all sets	Fishing system	n total	Killer whales only n (%)	Sperm whales only n (%)	Killer and sperm whales n (%)
Chile	2006–2016	90	<i>Trotline/umbrella</i>	11,528	750 (6.5)	3394 (29.4)	1440 (12.5)
Falklands	2009–2016	99	<i>Trotline/umbrella</i>	3898	73 (1.9)	1907 (48.9)	69 (1.8)
PEMI	2006–2016	98	All	4373	505 (11.5)	289 (6.6)	179 (4.1)
			<i>Spanish</i>	1085	150 (13.8)	50 (4.6)	57 (5.2)
			<i>Trotline</i>	1880	216 (11.5)	105 (5.6)	85 (4.5)
			<i>Trotline/umbrella</i>	1408	139 (9.9)	134 (9.5)	37 (2.6)
Crozet	2004–2018	81	<i>Autoline</i>	11,845	1803 (15.2)	3658 (30.9)	2757 (23.2)
Kerguelen	2004–2018	85	<i>Autoline</i>	34,556	35 (0.1)	13,770 (39.8)	36 (0.1)
HIMI	2009–2018	94	<i>Autoline</i>	9041	0	195 (2.2)	0

the optimal area-specific models ranged from 18.6% at Kerguelen to 34.2% in PEMI (Table 2).

In Chile and Crozet, the two areas most affected by killer whale depredation, models predicted mean catch

removals of 72 kg [49–95 kg] and 81 kg [53–109 kg] of toothfish every 1000 hooks when 1 to 5 individuals interacted with the same sets, respectively. These removals increased with the number of depredating

Table 2 Goodness of fit (% of the deviance explained) of final area-specific GAMs and annual mean estimates of toothfish catch removals due to killer and sperm whale in the study areas

Area	% dev. exp.	Model	Annual catch removals			
			t of toothfish [95% CI]			
			n years	Killer whales	Sperm whales	Total
Chile	29.0		11	100 [71–128]	65 [12–117]	165 [84–245]
Falklands	25.1		8	4.9 [1.4–8.5]	48 [1.9–96]	53 [3.3–105]
PEMI	34.2		11	15 [5.6–24]	0.3 [0–4.1]	15 [1.2–28]
Crozet	28.3		15	179 [134–224]	100 [45–156]	279 [179–379]
Kerguelen	18.6		15	2.1 [1.6–2.5]	247 [144–350]	250 [146–353]
HIMI	30.9		10	0	4.8 [0.8–8.8]	4.8 [0.8–8.8]

killer whales in both areas ranging from 146 kg [117–175 kg] in Chile to 190 kg [150–230 kg] at Crozet when 11–15 individuals were depredating. Among areas where sperm whale depredation frequently occurred (Crozet, Falklands, Chile and Kerguelen), 1–5 individuals were predicted to be removing from 28 kg [14–41 kg] of toothfish every 1000 hooks in Kerguelen to 54 kg [7–101 kg] every 1000 hooks in Falklands. Catch removals increased when 6–10 sperm whales simultaneously depredated the same sets and ranged from 79 kg [29–129 kg] of toothfish every 1000 hooks in Falklands to 97 kg [66–127 kg] every 1000 hooks at Crozet.

Overall catch removals due to whale depredation

Killer whale depredation resulted in mean catch removals ranging from 2.1 t [95% CI 1.6–2.5 t] of toothfish per year at Kerguelen to 179 t [134–224 t] of toothfish per year at Crozet (Table 2). Catch removals due to sperm whale depredation were the lowest in PEMI and HIMI with 0.3 t [0–4.1 t] and 4.8 t [0.8–8.8 t] of toothfish per year, respectively, and the highest at Kerguelen with 247 t [144–350 t] of toothfish per year. In areas where both killer and sperm whales depredated toothfish on longlines, the two species removed between 15 t [1.2–28 t] (PEMI) and 279 t [179–379 t] (Crozet) of toothfish from longline sets per year. Catch removals translated in mean $Dep(landings)$ and $Dep(total_catch)$ rates being the lowest in HIMI with

Fig. 3 Annual toothfish catch removals (t, black line and 95% CI grey area) and $Dep(total_catch)$ (proportions of the total catch—%, red line) due to depredation by killer whales, sperm whales, and any of the two species (total) per area as calculated from final area-specific GAMs fitted to the toothfish CPUE

0.2% [0–0.4%] of the landings and the total catch per year and the highest at Crozet with 43.6% [27.2–60%] of the landings and 30.1% [21.2–37.1%] of the total catch per year (Fig. 2; Online Resource 2). Toothfish catch removals due to whale depredation increased significantly over time for killer whales at Crozet (linear regression, $P < 0.001$) but no trends were detected in the other areas (Fig. 3; Online Resource 2). No temporal trends in depredation rates, neither $Dep(landings)$ nor $Dep(total_catch)$, were detected in any of the study areas (Fig. 3; Online Resource 2).

Between 2009 and 2016, the total toothfish catch removals due to whale depredation over all fisheries were 6699 t [3839–9559 t], which included 2539 t [1853–3225 t] due to killer whales and 4147 t [1976–6318 t] due to sperm whales. Mean catch removals were 837 t [480–1195 t] per year, and were the largest in 2012 with 968 t [579–1357 t] (Fig. 4). Sperm whales removed larger amounts of toothfish than killer whales, on average 518 t [247–790 t] and 317 t [232–403 t] per year, respectively. Out of the total toothfish catches, overall removals due to depredation by the two species represented a mean $Dep(total_catch)$ of 10.2% [6–13.9%] per year, ranging

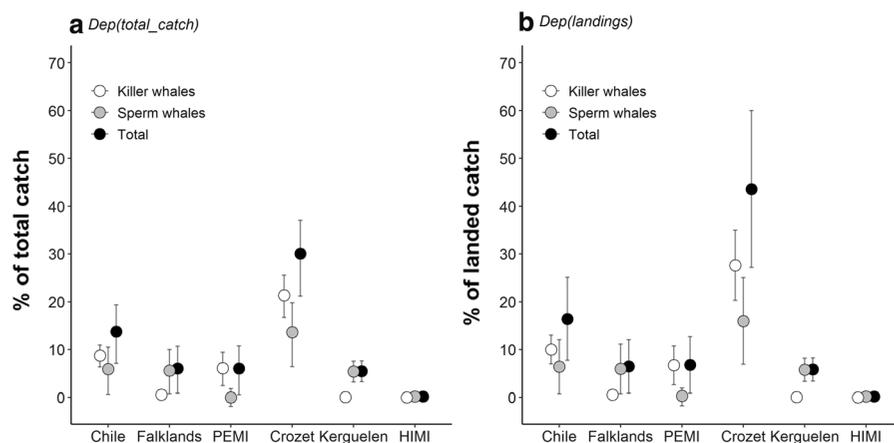
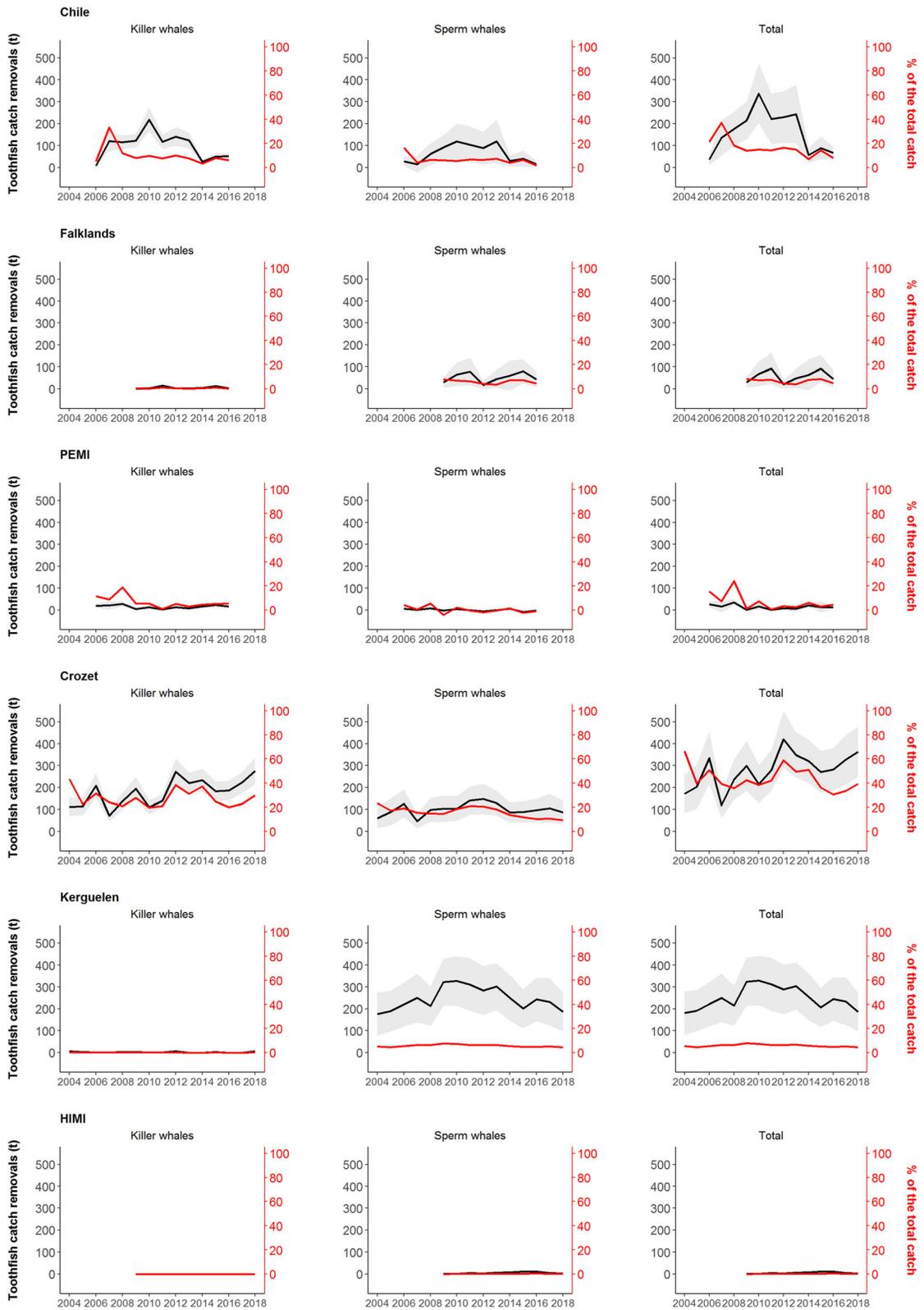


Fig. 2 Mean depredation rates calculated as the proportion of catch removals due to whale interactions as estimated from area-specific GAMs fitted to the toothfish CPUE out of **a** the total catch (observed landed catch + estimated depredated catch,

Dep(total_catch)) and **b** the observed landed catch ($Dep(landings)$) across years (Chile: 2006–2016; Falklands: 2009–2016; PEMI: 2006–2016; Crozet and Kerguelen: 2004–2018; HIMI: 2009–2018). Error bars are mean 95% CI



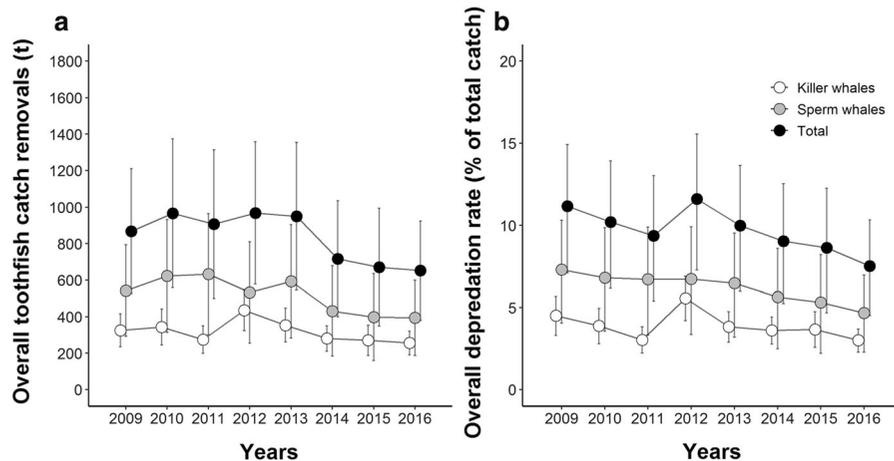


Fig. 4 a Total annual toothfish removals due to whale depredation and **b** overall depredation rate $Dep(total_catch)$: proportion of the catch removals out of the total catch (observed landed fish catch + estimated depredated fish) across the six

from 8.2% [5–11.1%] in 2016 to 12.4% [7.7–16.7%] in 2012 (Fig. 4b). No trends in these overall catch removals or $Dep(total_catch)$ were detected over the 2009–2016 period (Fig. 4a, b).

Discussion

The present study used a modelling approach standardized across the six studied toothfish fisheries to provide estimates of catch removals due to killer and sperm whale depredation in subantarctic waters. The overall amount of toothfish removed and consumed by whales from fishing gear was large, extending over 900 t of toothfish in some years. While variation in the intensity of depredation was detected across areas, the findings highlight the large scale significance of feeding opportunities that fisheries may provide to top marine predators and provide metrics to assess the socio-economic and ecological implications of depredation.

Depredation estimates

Overall catch removals and whale depredation rates reported in the present study were consistent with previous assessments available for some of the study areas. For instance, depredation rates reported for Crozet (30% of the total catch) were close to the 27–29% estimated using a different method for that

study areas between 2009 and 2016. Total catch removals due to whale depredation and depredation rates were calculated as the sum of estimates retrieved from final area-specific GAMs fitted to the toothfish CPUE, and error bars are 95% CI

area over the 2003–2013 period (Gasco et al. 2015). Similarly, the 2649 t of toothfish estimated to have been removed from longlines by sperm whales at Kerguelen between 2008 and 2015 from Generalized Linear Mixed Models (Janc et al. 2018) is within the range of our estimates for that area during the same period (Online Resource 2). While such consistencies support the use of GAMs as a standardized approach to assess depredation and also used in other fisheries (Peterson and Hanselman 2017), uncertainty remained around estimates and was especially large in the Chile, Falklands, PEMI and Crozet fisheries. This uncertainty may be attributed to low amounts and/or low accuracy of data available, such as in areas where observers collected presence-only data for whale interactions, with remaining sets including both true and false absences. Furthermore, all study fisheries have been monitoring whale depredation only during hauling phases, whereas recent studies have shown that depredation may also occur at depth when longline sets are still soaking away from vessels and may, therefore, be missed by observers and not accounted for if the whales are not present when the line is hauled (Towers et al. 2018; Richard et al. 2020). For instance, data from accelerometers deployed on longline sets at Crozet and Kerguelen confirmed the occurrence of interactions between sperm whales and three longline sets on the seafloor during soaking, including one set for which observers did not visually detect sperm whales during hauling (Richard et al.

2020). While more data from alternative monitoring methods are needed to assess the extent to which depredation events may be missed by surface observations, these studies indicate that depredation estimates provided here are likely underestimates and should, therefore, be considered as minimum estimates.

The extent of catch removals and depredation rates greatly varied between areas, with the largest values found in Chile, at Crozet and Kerguelen. This variation can be explained by a combination of factors inherent to the areas, to the size of the fisheries and the patterns of fishing operations and to the abundance, distribution and ecology of local whale populations. For instance, fisheries operated by large fleets over small areas were shown to be more likely to experience whale depredation (Tixier et al. 2019a). A large fleet operating in a small area are specificities found at Crozet and, in addition to likely high densities of killer and sperm whales (Tixier et al. 2014a, b; Labadie et al. 2018), may contribute to the high depredation rates reported for this area. Interestingly, at Crozet, an increasing trend over the 2004–2018 period was detected in catch removals due to killer whale depredation but not in depredation rates. As catch limits and total catches have increased in this area since 2012 (CCAMLR 2018a, Online Resource 3), this result suggests that killer whales are not more frequently or severely depredating, but, rather, that an expansion of the fishery is providing individuals with more opportunities to depredate. The seasonal concentration of the fishing effort is another key factor, especially for sperm whales, which densities and overlaps with toothfish fisheries increase in spring and summer months (Robineau and Duhamel 2006; Janc et al. 2018). As such, fishing occurring during most of spring and summer months (no fishing in February and first 2 weeks of March) at Kerguelen, paired with the fishing area likely to overlap with important feeding areas for sperm whales, were suggested to explain the high frequencies of depredation occurrences and may contribute to the large catch removals reported for this area (Tixier et al. 2019a, c; this study). In addition to these factors, it cannot be excluded that part of the variation in catch removals across areas is due to some fisheries using fish protection devices. The effect of this factor could not be detected in the area (PEMI) that used both *Spanish* and *trotlines* equipped with *umbrellas* but the analysis

may have been hampered by the limited amount of data available for that area. Areas with similar frequencies of whale depredation events but that used different fishing systems, such as Chile (*trotlines* with *umbrellas*) and Kerguelen (*autoline*) for sperm whales, had similar depredation rates. However, catch removals, for a given number of killer whales, were found to be lower in fisheries using fish protection devices than in fisheries not using them. Together, these preliminary observations highlight the need for further finer scale investigations on the effectiveness of fish protection devices in the future, in particular to assess if whales can have access to the soaking line before these devices can cover the catch depending of the setting depth.

Socio-economic implications

The present study indicates that catch removals due to whale depredation are likely to generate substantial socio-economic costs for fishermen and the toothfish fishing industry, both locally and globally. The value of the depredated toothfish, based on the average of 837 t (equivalent to 558 t in net weight) of toothfish removed by killer and sperm whales every year across Chile, Falklands, PEMI, Crozet, Kerguelen and HIMI, represents \$15 M USD worth of fish (calculated from a 2019 average toothfish market price of \$26.50 USD per kg at landing). This value may or may not be recouped by the fishers depending on whether or not that biomass of fish is caught by season-end for quota purposes. However, if fishers aim to fish up to quota limits, as it is likely the case in all toothfish fisheries used in this study with quota limits being vessel-based, catch removals due to whale depredation will induce indirect costs including all extra expenses and labour associated with additional fishing effort (Gilman et al. 2007). As evidenced in other fisheries, additional fishing effort due to depredation translates to longer time spent at sea, more longline sets baited, deployed and retrieved by crews and extra fuel consumption for vessels (Peterson et al. 2014). If it is assumed that such extra fishing effort was undertaken in response to whale depredation, then, for example, the depredation rates reported here for Crozet and Chile, for example, would force vessels to increase their fishing effort respectively by 30 and 14%, respectively, to fill their quotas. However, these approximations, which do not include all other sources of indirect costs of

depredation, such as costs of implementing strategies of avoidance (Tixier et al. 2014c; Richard et al. 2017), could be further examined and accurately quantified through a comprehensive socio-economic costs/benefits analysis.

Implications for depredating whale populations

For depredating whales, fish taken from fishing gear may represent a highly calorific resource with low capture effort requirements (Guinet et al. 2007). Large intakes of this human-induced food source may, therefore, result in substantial changes in the natural energy cost/benefit ratios of foraging for these whales. For instance, from photo-identification of individuals, approximately 90 killer whales were estimated to be interacting annually with the Crozet fishery (Tixier et al. 2014a, 2016). Assuming prey energy requirements of $150,000 \text{ kJ day}^{-1}$ for killer whales (Osborne 1999; Noren 2011) and 7700 kJ kg^{-1} as the energetic value of Patagonian toothfish, the mean depredated fish intake estimated in the present study (179 t year^{-1}) would represent 28% of the annual energy requirements of killer whales at Crozet. Similarly, assuming prey energy requirements of $875,000 \text{ kJ day}^{-1}$ for sperm whales (Spitz et al. 2018), the depredated fish intake of 247 t year^{-1} of toothfish at Kerguelen would represent 5% of the annual energy requirements of the 110 identified depredating sperm whales at Kerguelen (Labadie et al. 2018). As shown in long-lived terrestrial predators feeding on anthropogenic food subsidies, the energetically beneficial prey intake provided by fisheries is likely to result in positive effects on the demographic performances of depredating whales (Newsome et al. 2015). Indeed, it has already been shown that the reproductive output of killer whale populations depredating toothfish at Crozet has increased (Tixier et al. 2015), and similar effects have been observed in populations interacting with tuna fisheries in temperate waters (Esteban et al. 2016). With lower proportions of energy requirements filled by depredated toothfish, these effects are likely to be smaller and have yet to be evidenced for sperm whales. Furthermore, as only adult male sperm whales are present in subantarctic regions, food provisioning from fisheries may essentially influence the condition of these individuals with limited indirect influence on the full populations they belong to.

Implications for fish stocks and ecosystems

As a human induced provision of resource, the biomass of fish that killer and sperm whales take from fisheries may greatly alter the role of these two apex predators in the functioning of ecosystems (Oro et al. 2013). These changes may occur through long-term indirect effects associated with predator populations being numerically enhanced by food subsidies and subsequent alteration of their foraging distribution (Newsome et al. 2015). Depredation may also modify the foraging distribution of whales on the short-term, resulting in the displacement of predation pressures on various functional groups including the exploited fish and/or natural prey species. However, the extent of these modifications depend highly on two key factors. Firstly, is the depredated resource fully artificial for the whales or was it already part of their natural diet? In the case of toothfish fisheries, both sperm whales and killer whales are known to naturally feed on toothfish, indicating that whales interact with fisheries as a facilitated way to access that prey of their diet (Yukhov 1972; Tixier et al. 2019b). Secondly, if toothfish is a natural prey, how much of the natural intake is replaced by intake from fisheries? This aspect is still unclear yet critical to assessing the changes in energy flows, predation pressures caused by depredation interactions as well as toothfish stock management.

Indeed, determining these natural vs artificial intake ratios is essential to increasing the accuracy of the fishery mortality rates used for fish stock assessment models. While depredated catch has not previously been estimated and is not yet incorporated into assessments at PEMI and HIMI (CCAMLR 2018b, c), other toothfish fisheries account for depredation in stock assessment models as additional fishing mortality to apply a precautionary approach (CCAMLR 2018a, d). Uncertainty associated with this mortality makes the precautionary approach especially relevant since the extra fishing effort needed to compensate the catch removals due to depredation indirectly increases the fishing pressure on stocks. Beyond the target species, extra fishing effort due to depredation may also increase the risk and the levels of bycatch. Bycatch of species of conservation concern such as seabirds have been greatly reduced by strong measures in toothfish fisheries (Nilsson et al. 2016), but risks remain for

some vulnerable species of sharks and skates despite regulations in place (Nowara et al. 2017; Jones 2018, Chazeau et al. 2019). While this study has provided standardized estimates of catch removals due to whale depredation that can help fish scientists and managers to improve stock assessments (Hanselman et al. 2018), further research is needed to elucidate the combined effects of fisheries and depredation on target fish and ecosystems.

In summary, the present study provides further evidence of how fisheries may profoundly alter resource biomasses in ecosystems through exploitation and the generation of new feeding opportunities for marine predator species. The findings reveal that these opportunities occur at large scales for two apex predators in remote subantarctic offshore environments. Killer whales and sperm whales have responded to fisheries by developing depredation as a new foraging behaviour and taking large amounts of fish directly from fishing gear. Furthermore, an increasing trend in catch removals due to killer whale depredation over the past 15 years was detected at Crozet where long-term data were available. While additional years of data are needed to assess these trends in other areas, there is concern that the whale-fisheries conflict is currently intensifying in subantarctic waters as some whale populations are potentially recovering from historical whaling and/or new individuals within populations may be switching to depredation, as evidenced in the northeast Pacific Ocean (Schakner et al. 2014). Fisheries have commonly responded to this concern by implementing technological ways of mitigating the conflict. However, as illustrated in the present study with fisheries using fish protection devices being still subject to high depredation, further research is needed to develop effective ways of minimizing depredation and its subsequent social-ecological impacts.

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