Fisheries interaction data suggest variations in the distribution of sperm whales on the Kerguelen Plateau

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Abstract

The emergence of longline fishing for Patagonian toothfish (Dissostichus eleginoides) on the Kerguelen Plateau over the past two decades is concomitant with the development of depredation-type interactions by sperm whales (Physeter macrocephalus). Through a unique collaboration between the French and the Australian fisheries operating respectively around Kerguelen, and Heard Island and McDonald Islands (HIMI), this study preliminarily investigated the spatio–temporal variations of the rate of occurrence of sperm whale depredation on the Kerguelen Plateau. Between 2011 and 2016, sperm whales depredated toothfish on 29.1% of all longline sets and over 49.4% of the fished area. The probability of vessels to experience depredation decreased with the latitude and decreased in winter. Vessels operating in Kerguelen experienced significantly higher rates of occurrence of sperm whale depredation (33.2 ± 4.5% of sets; 48.2 ± 7.2% of the area) than vessels operating in HIMI (3.1 ± 1.2% of sets; 5.4 ± 2.0% of the area) over the 2011–2016 period, but also during any season of the year. The results suggested that heterogeneity in the distribution of sperm whales is likely a key driver of depredation. The Kerguelen Plateau fisheries represent a unique opportunity to investigate the spatial factors influencing this distribution, and therefore to predict the occurrence of depredation.

Variations de la répartition des cachalots sur le plateau de Kerguelen suggérée par les données d’interaction avec les pêcheries

Résumé

L’émersion de la pêche palangrière à la légine australe (Dissostichus eleginoides) sur le plateau de Kerguelen ces 20 dernières années coïncide avec l’intensification des interactions de type dépédition avec les cachalots (Physeter macrocephalus). Grâce à une collaboration unique entre les pêcheries françaises et australiennes opérant
Variations in the distribution of sperm whales

The emergence of longline fishing throughout the world’s oceans is concomitant with increasing reports of depredation interactions by marine top-predators, primarily odontocetes (toothed whales), with fishing vessels (Northridge, 1991; Northridge and Hofman, 1999; DeMaster et al., 2001; Read, 2008; Hamer et al., 2012). Depredation occurs when odontocetes feed on fish caught by fishers on longline sets (Read et al., 2005, Hamer et al. 2012, Werner et al. 2015). This depredation often results in socio-economic (financial losses for fishers), ecological (effects on depredating species) and conservation issues (impacts on depredated resources) (Gasco et al., 2015; Tixier et al., 2015, 2017; Werner et al., 2015; Esteban et al., 2016; Peterson and Hanselman, 2017; Hanselman et al., 2018).

The underlying mechanisms of depredation, as a behaviour, may combine both opportunistic and active processes (Karpouzli and Leaper, 2004; Esteban et al., 2016; Peterson and Hanselman, 2017). Odontocetes may interact with fishing gear when fishing operations overlap in space and time with their natural distribution (Hernandez-Milian et al., 2008; Cruz et al., 2016). However, odontocetes may also actively search and/or follow fishing vessels once they have found fishing gear to interact with (Tixier et al., 2010; Janc et al., 2018). As a result, the observed rates of occurrence of odontocete depredation are likely to be primarily driven by both the natural distribution of odontocetes and the spatio–temporal patterns of fishing operations.

On the Kerguelen Plateau, the two commercial Patagonian toothfish (Dissostichus eleginoides) longline fisheries operating respectively around Kerguelen Island (French economic exclusive zone – EEZ) and around Heard Island and McDonald Islands (HIMI) (Australian EEZ) have experienced depredation by two odontocete species: sperm whales (Physeter macrocephalus) and killer whales (Orcinus Orca). While both species have been reported depredating toothfish from longlines in the French EEZ, only sperm whales were documented depredating in the Australian EEZ (Roche et al., 2007; Tixier et al., 2010, 2016; Guinet et al., 2014; Welsford and Arangio, 2015; Janc et al., 2018). The French fishery, for which commercial longlining started in the 1990s, has experienced consistent high rates of occurrence of sperm whale depredation (> 40% of fishing operations) for over two decades (Roche et al., 2007; Tixier et al., 2010; Janc et al., 2018). The seven licensed longliners operate all year round except in February and early March. Commercial longlining in the Australian EEZ started in 2003 although sperm whale depredation was first reported in 2011 and has remained low (<10 % of the fishing operations) over the following years (Welsford and Arangio, 2015). This fishery includes four licensed fishing vessels and operates from April to November. Whether the large differences of the rate of occurrence of sperm whale depredation between the French and the Australian EEZs are explained by differences in fishing patterns or difference in the natural presence of sperm whales, or a combination of both, remains unknown.

Using a dataset including fishing and observation data from both areas over the 2011–2016

Keywords: Fisheries interactions, sperm whale, Patagonian toothfish, Kerguelen, depredation

Introduction

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Using a dataset including fishing and observation data from both areas over the 2011–2016
period, the aim of this study was to investigate the rates of occurrence of sperm whale depredation over an area encompassing both the French and the Australian EEZs.

**Methods**

**Data**

Fishing data and whale interaction data from the French and Australian EEZs, hereafter referred to as the ‘Kerguelen’ fishery and the ‘HIMI’ fishery respectively, were collected by fishery observers and/or crews from 2011 to 2016 (Martin and Pruvost, 2007). The base unit was the longline set, and for each set, the date and time, as well as GPS coordinates, were recorded at hauling (i.e. retrieved and landed on board).

The occurrence of sperm whale depredation with longline sets was recorded during hauling operations by visual cues. An interaction was confirmed when whales were sighted at the surface within 500 m of the vessel with typical depredation behaviour: individuals made repeated dives towards the line being hauled and throughout the hauling process; they were usually surrounded by birds when surfacing after long dives; and slicks of fish oil were visible at the surface. Depredation events (recorded as 1) were, therefore, assumed to be monitored in a standardised way across Kerguelen and HIMI fisheries. Observers distinguished between longline sets with confirmed non-occurrence of depredation (recorded as 0) and sets with lacking information due to insufficient or impossible monitoring effort (recorded as ‘no data available’ – N/A) caused by poor weather (e.g. fog), sea or light conditions.

The rate of occurrence of sperm whale depredation was estimated as: (i) a proportion of depredated longline sets out of all longline sets hauled (Pr(sets)); and (ii) a proportion of $0.1^\circ \times 0.1^\circ$ spatial cells in which at least one set was depredated out of all cells in which fishing occurred (Pr(area)). These two indices were calculated per fishery or per vessel within fisheries, either per year or per month to assess the inter- and intra-annual variations of sperm whale depredation. The spatial variations of sperm whale depredation were explored by calculating and spatialising Pr(sets) over a $0.1^\circ \times 0.1^\circ$ cell grid. Data are presented as Mean ± SE unless otherwise stated.

**Statistical analyses**

Spatial and temporal variations of sperm whale depredation were examined through generalised linear mixed models (GLMM) fitted to the records of presence/absence of sperm whale depredation data per set and per spatial cell with a binomial distribution and a logit link function. The null model fitted at the set level included the interaction between the presence/absence of sperm whale depredation on the set that was previously hauled and the distance between this set and the next as a structural term to account for spatio–temporal autocorrelation as previously reported in depredation data (Tixier et al., 2014; Janc et al., 2018). The null model fitted at the spatial cell level included the fishing effort, calculated as the total number of hooks set per spatial cell per vessel per year and per season, as a structural term to account for increased likelihood of vessels to experience depredation with increased fishing time in cells (Janc et al., 2018). The null model, for models fitted both at the set and at the spatial cell levels, included the vessel identification (ID) as a random term to account for unidentified vessel-dependent variables influencing whale depredation (Tixier et al., 2010, 2014; Richard et al., 2018; Janc et al., 2018). The fishery (Kerguelen or HIMI) and the latitude at which sets were hauled were included as spatial fixed terms. Temporal terms included the year and the season and were, respectively, tested as continuous and categorical fixed terms. The season was a four-level variable, defined as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). Models best fitting the data were selected through a stepwise forward Akaike Information Criterion (AIC) selection process. These models were then fitted to sperm whale depredation data on sets and in spatial cells for each of the three seasons (autumn, winter, spring) during which fishing occurred both in Kerguelen and HIMI to examine differences in the level of sperm whale depredation between the two fisheries during a given season.

**Results**

Data from a total of 20,163 longline sets hauled from January 2011 to December 2016 were available for the study. Sperm whale depredation occurred on Pr(sets) = 29.1% of these longline sets and in Pr(area) = 49.4% of all fished spatial cells ($n = 2,618$). Visual exploration of spatialised
Pr(sets) showed large variations across the full area, but also within the Kerguelen and HIMI fisheries over the study period (Figure 1). Concentrations of 0.1° × 0.1° grid cells with high proportions of depredated sets (> 60%) were visible in the northwestern part of Kerguelen, and these areas were consistent across seasons (Figure 2).

Pr(sets) and Pr(area) per vessel were significantly higher in Kerguelen than in HIMI (GLMM $z = 4.06; P < 0.001$ and $z = 3.48; P < 0.001$ respectively, Table 1). Over the study period, sperm whale depredation occurred on an average of 33.2 ± 4.5% of all sets per vessel in Kerguelen (n = 9 vessels) and 3.1 ± 1.2% of all sets in HIMI (n = 6 vessels). Vessels experienced sperm whale depredation in Pr(area) = 5.4 ± 2.0% of the spatial cells in HIMI and in Pr(area) = 48.2 ± 7.2% of the spatial cells in Kerguelen. Pr(sets) and Pr(area) per vessel linearly and significantly decreased with the latitude (GLMM $z = -10.47; P < 0.001$ and $z = -14.83; P < 0.001$ respectively, Table 1) at which longlines were hauled.

No trend over the study period could be detected in Pr(sets) nor in Pr(area) per vessel as the year term was not selected in the final models. However, significant variations of Pr(sets) and Pr(area) between seasons were detected (Table 1). Pr(set) and Pr(area) per vessel were the highest in summer with respectively 42.0 ± 7.9% of the sets and 52.3 ± 9.8% of the spatial cells, and the lowest in winter with respectively 8.8 ± 2.6% of the sets and 12.9 ± 7.7% of the spatial cells.

Models run by season indicated that Pr(sets) and Pr(area) were consistently significantly lower for vessels operating in HIMI than for vessels operating in Kerguelen during autumn, winter and spring (Table 1 and Figures 3a and 3b). In HIMI, Pr(sets) and Pr(area) per vessel were the highest in autumn with 7.3 ± 3.1% of the sets and 11.6 ± 4.3% of the spatial cells, whereas for that season Pr(sets) and Pr(area) in Kerguelen were 27.5 ± 3.3% of the sets per vessel and 36.3 ± 4.6% of the spatial cells per vessel respectively (Figures 3a and 3b). In Kerguelen, sperm whale interaction rates were the highest in spring for Pr(sets) with 42.3 ± 1.6% of the sets per vessel and for Pr(area) with 53.0 ± 3.1 of the spatial cells per vessel. In HIMI in spring, Pr(sets) was 3.3 ± 3.3% of the sets per vessel and Pr(area) was 4.3 ± 4.3% of the spatial cells per vessel. While no fishing occurred in summer in HIMI, Pr(sets) and Pr(area) for that season in Kerguelen were high and similar to spring values for that area (Figures 3a and 3b).

**Discussion**

This study demonstrated large variations in the level of sperm whale depredation with commercial Patagonian toothfish fishing vessels on the Kerguelen Plateau. While the proportions of both longline sets and fished area with sperm whale depredation varied seasonally and with latitude, the probability of vessels experiencing depredation varied in space and was substantially lower in HIMI than in Kerguelen.

The difference between Kerguelen and HIMI may be due to variations in the way vessels operate when fishing. In previous studies, factors such as the time of year were found to significantly influence the probability of vessels experiencing sperm whale depredation (Tixier et al., 2010; Janc et al., 2018). In the Southern Ocean, this probability has been shown to decrease in winter and increase in summer/spring months in areas such as Chile, South Georgia, Crozet and Kerguelen (Hucke-Gaete et al., 2004; Clark and Agnew, 2010; Janc et al., 2018; Tixier et al., 2019). The present study confirmed this seasonal pattern on the Kerguelen Plateau. However, for any given season, vessels operating in Kerguelen experienced substantially higher rates of occurrence of sperm whale depredation than the vessels operating in HIMI. While the HIMI fishery primarily operates during winter months and is closed to fishing in summer, which could contribute to the low observed rates of occurrence of depredation, the results of the present study suggest other factors are likely to explain the observed differences with Kerguelen. Among other operational factors, differences in the distance travelled between longline sets, variations in the acoustic cues produced by vessels used by sperm whales to locate them, or the decisions made by skippers when confronted by sperm whale depredation between Kerguelen and HIMI should be further examined as these factors have also been shown to influence the probability of sperm whales to depredate on fishing gear (Thode et al., 2007, 2015; Tixier et al., 2010, 2014, 2018, 2019; Richard et al., 2018; Janc et al., 2018; Towers et al., 2019).

The large spatial variations reported in the present study, paired with a strong latitudinal gradient
## Table 1: Summary outputs of the final GLMMs fitted to the occurrence of sperm whale depredation at the longline set level and at the 0.1° × 0.1° spatial cell level.

(−) indicates that the predictor was not tested in models.

<table>
<thead>
<tr>
<th>Level</th>
<th>Predictor</th>
<th>All data</th>
<th>Autumn</th>
<th>Winter</th>
<th>Spring</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Est. ± SE</td>
<td>z</td>
<td>P</td>
<td>Est. ± SE</td>
</tr>
<tr>
<td>Set</td>
<td>Intercept</td>
<td>-3.49 ± 0.25</td>
<td>-13.76 &lt;0.001</td>
<td>-3.12 ± 0.26</td>
<td>-11.85 &lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Presence/absence *</td>
<td>-0.46 ± 0.04</td>
<td>-12.10 &lt;0.001</td>
<td>-0.34 ± 0.08</td>
<td>-11.21 &lt;0.001</td>
</tr>
<tr>
<td></td>
<td>distance (previous set)</td>
<td>1.24 ± 0.30</td>
<td>4.06 0.001</td>
<td>1.13 ± 0.32</td>
<td>3.51 &lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Area: Kerguelen</td>
<td>0.41 ± 0.04</td>
<td>-10.47 &lt;0.001</td>
<td>-0.06 ± 0.09</td>
<td>-0.65 0.516</td>
</tr>
<tr>
<td></td>
<td>Latitude</td>
<td>-0.46 ± 0.04</td>
<td>-12.10 &lt;0.001</td>
<td>-0.34 ± 0.08</td>
<td>-11.21 &lt;0.001</td>
</tr>
<tr>
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<td>Season: winter</td>
<td>-0.69 ± 0.09</td>
<td>-7.79 &lt;0.001</td>
<td>-0.06 ± 0.09</td>
<td>-0.65 0.516</td>
</tr>
<tr>
<td></td>
<td>Season: spring</td>
<td>0.60 ± 0.06</td>
<td>9.76 &lt;0.001</td>
<td>-2.11 ± 0.34</td>
<td>-6.23 &lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Season: summer</td>
<td>-0.40 ± 0.04</td>
<td>-10.47 &lt;0.001</td>
<td>-0.06 ± 0.09</td>
<td>-0.65 0.516</td>
</tr>
<tr>
<td>Spatial cell</td>
<td>Intercept</td>
<td>-2.78 ± 0.37</td>
<td>-7.41 &lt;0.001</td>
<td>-4.81 ± 0.37</td>
<td>-12.00 &lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Fishing effort</td>
<td>0.30 ± 0.03</td>
<td>12.00 &lt;0.001</td>
<td>0.34 ± 0.05</td>
<td>6.49 &lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Area: Kerguelen</td>
<td>-0.61 ± 0.04</td>
<td>-14.83 &lt;0.001</td>
<td>-0.06 ± 0.09</td>
<td>-0.65 0.516</td>
</tr>
<tr>
<td></td>
<td>Latitude</td>
<td>0.60 ± 0.06</td>
<td>9.76 &lt;0.001</td>
<td>-2.11 ± 0.34</td>
<td>-6.23 &lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Season: winter</td>
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<td>-10.47 &lt;0.001</td>
<td>-0.06 ± 0.09</td>
<td>-0.65 0.516</td>
</tr>
<tr>
<td></td>
<td>Season: spring</td>
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<td>9.76 &lt;0.001</td>
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<tr>
<td></td>
<td>Season: summer</td>
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<td>-10.47 &lt;0.001</td>
<td>-0.06 ± 0.09</td>
<td>-0.65 0.516</td>
</tr>
</tbody>
</table>
Figure 1: Map of spatialised rates of occurrence of sperm whale depredation (Pr(sets)) on the Kerguelen Plateau from 2011 to 2016. Grey filled cells indicate cells in which fishing occurred (at least one set was hauled) but sperm whale interaction was never reported. 250, 500, 750, 1 000, 2 000, 3 000 and 4 000 m isobaths are depicted (black lines) as well as the limits of the Exclusive Economic Zones (EEZ – dashed line) of Kerguelen (France) and Heard Island and McDonald Islands (HIMI – Australia).
Figure 2: Map of spatialised rates of occurrence of sperm whale depredation (Pr(sets)) on the Kerguelen Plateau between 2011 and 2016 per season: autumn (March–May), winter (June–August), spring (September–November) and summer (December–February). Grey filled cells indicate cells in which fishing occurred (at least one set was hauled) but sperm whale interaction was never reported. The 500 and 1000 m isobaths are depicted (black lines) as well as the limits of the Exclusive Economic Zones (EEZ) of Kerguelen (France) and Heard Island and McDonald Islands (HIMI – Australia).
Variations in the distribution of sperm whales

Variations in the distribution of sperm whales detected in models fitted to the occurrence of sperm whale depredation, suggests the degree of spatial overlap between fishing operations and the natural distribution of sperm whales may have major influence on the rate of occurrence of depredation. Areas of consistent high probability of sperm whale depredation were identified in the northern reaches of the Kerguelen Plateau, and this probability decreased linearly as vessels operated further south. Previous studies based on whale–vessel depredation data suggested that spatial variables such as local bathymetry may influence the probability of the fishing gear to be depredated (Janc et al., 2018). However, fishing operations in HIMI and Kerguelen are conducted over similar depth frequency distributions (Péron et al., 2016), which suggests that other spatial factors may influence the observed variation in the rate of occurrence of sperm whale depredation.

Sperm whales, as a species, are characterised by age- and sex-dependent temporary segregation patterns, with females and juveniles distributed in tropical and sub-tropical waters, and adult males seasonally using high latitude areas as feeding grounds (Best, 1979; Rice, 1989; Jaquet, 1996; Mellinger et al., 2004; Whitehead, 2009; Wong and Whitehead, 2014). As such, factors influencing their distribution are likely to involve a large extent of oceanographic features driving prey abundance and availability. The natural diet of these adult male sperm whales feeding in the Southern Ocean is poorly know but is believed to be made of a combination of cephalopods and fish (Kawakami, 1980; Rice, 1989). These prey groups have also already been observed in the diet of sperm whales in southern Australian waters (Evans and Hindell, 2004) and in the Gulf of Mexico (Judkins et al., 2015). The distribution of adult male sperm whales in other high-latitude areas was found to be highly driven by static oceanographic features such as the bathymetric slope and dynamic oceanographic variables such as eddies and fronts (Whitehead et al., 1992; Jaquet, 1996; Jaquet and Whitehead, 1996; Jaquet et al., 2000; Straley et al., 2014; Wong and Whitehead, 2014). The high site fidelity of individual sperm whales on small-scale ranges within the Kerguelen area over periods of nearly 10 years (Labadie et al., 2018) further supports that animals seek for specific feeding grounds, and the spatial variables characterising these feeding grounds should be examined in details in the near future.

The Kerguelen longline fishery is older than the HIMI longline fishery and, consequently, it is possible that sperm whales in HIMI are less experienced in depredating toothfish from longlines. This would lead to them being less likely to switch

Figure 3: Seasonal variations of the mean ± SE rates of occurrence of sperm whale depredation with (a) Pr(set) and (b) Pr(area), in Kerguelen (black) and HIMI (grey). N/A indicates season for which fishing did not occur.
from natural feeding to depredation than sperm whales in Kerguelen. Indeed, in other depredating sperm whale populations such behaviour has been shown to progressively spread spatially and, possibly, across individuals over time (Schakner et al., 2014). While sperm whale depredation is believed to have started as soon as longline fishing began in Kerguelen in the early 1990s, the first reports of sperm whale depredation in HIMI occurred in 2011, nine years after longline fishing started in that area. Whether the depredating sperm whales in HIMI are the same individuals as the ones depredating in Kerguelen, or new ones, is still unknown, and should be assessed and accounted for when investigating the spatial drivers of sperm whale interactions with vessels.

The large variations in sperm whale depredation reported in the present study between two adjacent fisheries over a large latitudinal gradient, highlights the Kerguelen Plateau as a unique area to investigate the mechanisms underlying this behaviour. It also illustrates the potential built for collaboration and data sharing between two fisheries extensively managed and controlled by two different countries.

Acknowledgements

The contribution of captains, crews and fishery observers who collected the data is gratefully acknowledged. In particular, we thank the Museum National d’Histoire Naturelle (MNHN) de Paris (Charlotte Chazeau, Patrice Pruvost, Alexis Martin – PECHEKER database), the Australian Antarctic Division (AAD – Tim Lamb), the Australian Fisheries Management Authority (AFMA) for managing, consolidating and sharing the data. We thank the Terres Australes et Antarctiques Françaises (TAAF), the Réserve Naturelle Nationale des TAAF and the French Polar Institute (Program 109 – H. Weimerskirch). Support was provided by the Australian Research Council (Linkage Project 160100329), the Agence National de la Recherche (ANR – project OrcaDepred), the French Ministry of Environment, the Fondation d’Entreprises des Mers Australes, the Syndicat des Armements Réunionnais des Palangriers Congélateurs (SARPC), Australian fishing companies Austral Fisheries Pty. Ltd. and Australian Longline Pty. Ltd. and by the Coalition of Legal Toothfish Operators, Inc. (COLTO).

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