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BEHAVIOURAL ECOLOGY OF FISHERMEN AND ODONTOCETES IN A DEPREDATION CONTEXT



Gaëtan RICHARD

M.Sc. BioSciences Ecole Normale Supérieure-Université Claude Bernard, Lyon

Submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy

Deakin University

&

Université de La Rochelle

Ecole Doctorale EUCLIDE

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ABSTRACT

Behavioural ecology of fishermen and odontocetes in a depredation context on the Patagonian toothfish longliners around Crozet and Kerguelen islands

Many marine predator species feed on fish caught by fishers directly from the fishing gear. Known as depredation this interaction issue has substantial socio-economic consequences for fishermen and conservation implications for the wildlife. Costs for fishers include damages to the fishing gear and increased fishing effort to complete quotas. For marine predators, depredation increases risks of mortality (lethal retaliation from fishers or bycatch on the gear). Longline fisheries are the most impacted worldwide, primarily by odontocetes (toothed whales) depredation, urging the need for mitigation solutions to be developed. Most of studies assessing depredation have primarily relied on surface observation data, thus the way odontocetes interact with longlines underwater remains unclear. Besides, the way fishermen respond to depredation during fishing operations, or can influence their detectability to odontocetes, have been poorly investigated. This thesis therefore aimed at investigating these aspects through a passive acoustic monitoring, bio-logging and human ecology approaches, focusing on the French Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries impacted by killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*). Firstly, this thesis reveals that captains behave as optimal foragers but with different personal perception of competition and fishing fulfilment. Some captains would thus be more likely to stay within a patch or to haul closest longline even in presence of competition, suggesting these captains would show higher interaction rates. Additionally, the propagation of vessels' acoustics varied depending on the type of manoeuvre (*e.g.* going backward vs. forward). The way captains use their vessels to navigate may therefore influence their detectability and so their depredation level. Secondly, loggers deployed on both the longlines (accelerometers) and odontocetes (GPS-TDR) revealed that killer whales and sperm whales are able to depredate on longlines while soaking on the seafloor. These observations suggest, therefore, that odontocetes can localise fishing activity before the hauling, which could be partially explained by specific acoustic signatures recorded during the setting process. Altogether, the results of the thesis suggest that depredation rates on demersal longlines are most likely underestimated. The thesis also brings some important insights for mitigation measures, suggesting that countermeasures should start from setting to hauling.

Keywords: depredation, demersal longline, killer whale, sperm whale, bio-logging, human behavioural ecology passive acoustic monitoring

RESUME

Écologie comportementale des pêcheurs et odontocètes dans un contexte de déprédation sur les palangriers à la légine australe autour des îles Crozet et Kerguelen

De nombreux prédateurs marins se nourrissent directement des prises des pêcheurs. Ces interactions, définies comme de la déprédation, engendrent des conséquences socio-économiques considérables pour les pêcheurs ainsi que des implications de conservation pour la faune sauvage. D'un côté, la déprédation endommage le matériel et augmente l'effort de pêche pour atteindre les quotas. D'un autre côté, la déprédation augmente le risque de mortalité des prédateurs marins (prise accidentelle ou rétorsion létale par les pêcheurs). La pêcherie à la palangre est la plus impactée par la déprédation, principalement par les odontocètes, ce qui incite à trouver des solutions. La majorité des études se concentrant sur la déprédation s'est principalement basée sur des observations en surface, de ce fait la manière dont les prédateurs retirent les poissons sur les lignes reste confuse. Par ailleurs, l'impact de la déprédation sur le comportement des pêcheurs ainsi que les facteurs expliquant leur détectabilité n'ont reçu que peu d'intérêt. L'objectif de cette thèse est donc d'étudier ces problématiques par un suivi acoustique, une utilisation de balises et une approche en écologie comportementale humaine, en se concentrant sur la pêcherie palangrière française ciblant la légine australe (*Dissostichus eleginoides*) impactée par la déprédation des orques (*Orcinus orca*) et des cachalots (*Physeter macrocephalus*). Les capitaines ont été décrits comme recherchant leur ressource selon la théorie de « l'optimal foraging », mais avec des perceptions de la compétition et du succès de pêche qui divergent. Certains capitaines seraient ainsi plus enclins à remonter les palangres au plus proche et à rester sur une zone, même en présence de compétition, augmentant alors le risque d'interaction. L'acoustique des navires a révélé que certaines manœuvres (marche arrière par exemple) propagent différemment sous l'eau. La manière dont les capitaines manœuvrent leur palangrier influencerait ainsi leur détectabilité et donc leur risque d'interaction avec les prédateurs. D'autre part, l'utilisation de capteurs sur les palangres et les animaux a révélé que les orques et les cachalots sont capables de déprédater sur les palangres posées sur le fond marin. Ces observations laissent à penser que les odontocètes sont en mesure de localiser l'activité de pêche bien avant la remontée de la ligne, ce qui pourrait être expliqué par une signature acoustique spécifique du déploiement de la ligne. L'ensemble des résultats de cette thèse suggère que la déprédation sur les palangres démersales est très probablement sous-estimée. Cette thèse apporte également des éléments importants pour la lutte contre la déprédation, en montrant la nécessité de protéger les palangres dans l'intégralité du processus de pêche.

Mots clés : déprédation, palangre démersale, orques, cachalots, bio-logging, écologie comportementale humaine, acoustique passive

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*To my grandfather,
à mon papy Milo...*

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1) Peer review articles:

Articles drafted as the first author during this PhD and constituting the core of the thesis:

- **Richard, G.**, C. Guinet, J. Bonnel, N. Gasco and P. Tixier. **2017**. Do commercial fisheries display optimal foraging? The case of longline fishers in competition with odontocetes. *Canadian Journal of Fisheries and Aquatic Sciences*. doi:10.1139/cjfas-2016-0498. (Chapter 2)
- **Richard, G.**, C. Guinet, J. Bonnel, N. Gasco and P. Tixier. Evidence of deep-sea interactions between toothed whales and longlines bring new insights to fisheries management. **under review** *Ambio* (Chapter 4)

Articles drafted as a co- author, contributing to the thesis:

- Janc, A., **G. Richard**, C. Guinet, J. P. Y. Arnould, M. C. Villanueva, G. Duhamel, N. Gasco and P. Tixier. **2018**. How do fishing practices influence sperm whale (*Physeter macrocephalus*) depredation on demersal longline fisheries? *Fisheries Research* 206: 14–26. doi:10.1016/j.fishres.2018.04.019. (Appendix 4)

this article was realized as part of a collaborative work with my colleague Anaïs Janc, I have contributed to the analyses process and I have helped to the manuscript's drafting.

- Tixier, P., D. Welsford, M-A. Lea, M. A. Hindell, C. Guinet, A. Janc, **G. Richard**, N. Gasco, G. Duhamel, R. Arangio, M. C. Villanueva, L. Suberg and J. P. Y. Arnould. Fisheries interaction data suggest variations in the distribution of sperm whales on the Kerguelen Plateau. **accepted** *CCAMLR Science* (Appendix 5)

this article was realized in a collaborative study led by Dr. Paul Tixier, I have been involved in developing the manuscript

- Tixier, P., P. Burch, **G. Richard**, K. Olson, D. Welsford, M-A. Lea, M. A. Hindell, C. Guinet, A. Janc, N. Gasco, G. Duhamel and J. P. Y. Arnould. Commercial fishing patterns influence odontocete whale-longline interactions in the Southern Ocean. **accepted** *Scientific Reports* (Appendix 6)

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- Lennert, A. E. and **G. Richard**. 2017. At the cutting edge of the future: Unravelling depredation, behaviour and movement of killer whales in the act of flexible management regimes in Arctic Greenland. *Ocean & Coastal Management* 148: 272–281. doi:10.1016/j.ocecoaman.2017.08.016. ([Appendix 7](#))

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2) Oral communication:

Scientific conferences:

- **Poster** at the French workshop SERENADE organized in the context of the Sea Tech Week in Brest from the 11th to the 13th of October 2016.
- **Poster** at the 6th Bio-logging Science Symposium in Konstanz (Germany), September 2017: “how to assess depredation from longlines with accelerometers?”
- **Talk** at the French workshop SERENADE organized at the ENSTA Bretagne, Brest from the 15th to the 18th of October 2018.

Science popularization:

- **Tutoring** Master’s students of Poitiers university (2 weeks, French and English), September 2016
- **Talk** at the Festival International du Film Ornithologique, in Ménégoûte, October 2016
- **Stand** at the Fête de la science, Museum of La Rochelle, October 2017
- **Webinar** for primary school students during the Polar week with APECS-France, October 2017
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1. GENERAL INTRODUCTION

1.1. CONSERVATION CONFLICTS

1.1.1. CONTEXT OF CONSERVATION CONFLICTS: THE ANTHROPOCENE

Humans are exceptional ecosystem engineers. As all species, we have attempted to enhance our environment to survive, but we distinguished ourselves by the use of tools and technologies that we transmitted through culture over generations (Smith 2007, Ellis and Ramankutty 2008). The shift that we created with the nature occurred with the learning process to ignite and master fire during the Palaeolithic (Marlowe 2005, Smith 2007, Ellis and Ramankutty 2008, Glikson 2013). Fire allowed an increase of the hunting pressure and the first landscape modification through controlled burning of vegetation (Marlowe 2005, Smith 2007, Archibald et al. 2012, Glikson 2013). Another profound impact of humans on fauna was the domestication of animals. First domestication occurred with the dog between 32 000 and 15 000 years ago (*e.g.* Freedman et al. 2014, Germonpré et al. 2015, 2017, Frantz et al. 2016), and was followed by the domestication of other animals but also plants, 12 000 - 10 000 years ago (Pluciennik 1996, Leach 2003, Steffen et al. 2007). These domestications led to the Neolithic Revolution with a settlement of the human population and the development of early agriculture. This transition started to shape permanently ecosystems, by clearing forest and irrigating fields, and might have led to the first small increases in atmospheric carbon dioxide and methane concentrations between 8000 and 5000 years ago (Ruddiman 2003, Steffen et al. 2007). Preindustrial human societies have, thus, influenced their local environment with these new artificial habitats, but it was with the Industrial Revolution in Europe (end 18th -beginning 19th centuries) that human activity started to impact heavily on ecosystems (Steffen et al. 2007, 2011, Ellis 2011, Lewis and Maslin 2015). The industrial revolution was first and foremost an energy revolution and constitutes the starting point of a new drastic shift between human and nature. Human societies used to rely on energy captured from ongoing flows (wind, water, animals, plants and trees) and changed in the 1800's to fossil fuels (coal, oil and gas), increasing the carbon dioxide and methane emissions. However, the transition to these high-energy fuels

brought new technologies improving then the mobility and revolutionizing the agriculture. These innovations have been constantly improving human health condition and, thus, resulting to an important growth of the human population, with a demographic explosion in the second half of the 20th century (Steffen et al. 2007, 2011, 2015). It is now considered that no ecosystem on Earth remains free of human influence (Vitousek et al. 1997, Ellis and Ramankutty 2008). Overexploitation of resources and pollution due to Human activity is now altering the atmosphere, the hydrosphere, the lithosphere and the biosphere (Vitousek et al. 1997, VöRöSmarty and Sahagian 2000, Crutzen 2002, Foley 2005, Ellis and Ramankutty 2008, Rockström et al. 2009, Ellis 2011). These rapid and significant shifts of the global environment due to human activity have led to the definition of a new geological era: the Anthropocene (Crutzen 2002, Steffen et al. 2007, Zalasiewicz et al. 2011, Lewis and Maslin 2015). This human domination over the ecosystems questions also the definition of “biomes” in ecology commonly considered as “natural ecosystems with humans disturbing them”, and some specialists suggest rather talking about “anthromes” defined as “human systems, with natural ecosystems embedded within them” (Ellis and Ramankutty 2008). Within this context, conflicts with wildlife are unavoidable.

1.1.2. DEFINITION OF THE CONSERVATION CONFLICTS

Human-wildlife conflict has been defined as an action by humans or wildlife with an adverse effect on the other (Conover 2002). Their causes have been attributed mostly to the loss and fragmentation of existing habitats and to the increase of the competition for resources between human and wildlife. The first conflicts occurred during the Palaeolithic while first hominids were both hunted and hunters (Lee-Thorp et al. 2000, Dickman and Hazzah 2016). Although humans are not systematically hunted anymore, attacks still occurred and can be considered the most direct damage for humans, even though they remain rare (Löe and Röskaft 2004, Dickman and Hazzah 2016). With the advent of the agriculture and human settlements, thus depredation developed as another major human-wildlife conflict (Sillero-Zubiri and Laurenson 2001, Woodroffe et al. 2005, McManus et al. 2015, Dickman and Hazzah 2016). Depredation is the feeding behaviour adopted by wild animals upon food either produced, farmed or captured by humans. The loss of crops or livestock to wildlife has significant consequences on people’s livelihoods and agricultural security (Barua et al. 2013, Dickman and

Hazzah 2016). Historically, humans primarily responded to these conflict by lethal retaliation towards the depredating species (Treves et al. 2006). With the growth of human populations, their spreading around the world and the increase of their activity, impacts of lethal retaliation on the wildlife have become increasingly severe. These responses, paired with growing anthropic pressure upon ecosystems, have caused a massive loss of biodiversity, leading some specialists to talk about “defaunation” as an analogy of “deforestation” (Dirzo et al. 2014). We may be assisting the Earth’s sixth mass extinction (Chapin III et al. 2000, Barnosky et al. 2011, Dirzo et al. 2014).

The mass extinction of biodiversity combined with an increase resource depletion led to a rise of awareness within human societies in the 70s with the club of Rome and their report “The Limits to Growth” (1972). Indeed, biodiversity is an essential provider of ecosystem goods but also services, contributing to societies’ economy (Millennium Ecosystem Assessment 2005). With this trigger alarm, a new field of research arose: the conservation biology, defined as the “application of science to conservation problems that addresses the biology of species, communities, and ecosystems that are perturbed, either directly or indirectly, by human activities or other agents” (Soulé 1985). One purpose of this new field was to address the issues of human-wildlife conflicts in order to mitigate the anthropic pressure upon the biodiversity. Thus, biologists in conservation mostly urge decision toward the preservation of wildlife. However, within a conflict context, these decisions might be at the expense of human activities and therefore tend to generate a “human-human” conflicts rather than “human-wildlife” conflict. Two types of conflicts are then distinguished: (i) “human-wildlife conflicts defined as the direct damages between humans and other species) and (ii) “conservation conflicts” referring to “situations that occur when two or more parties with strongly held opinions clash over conservation objectives and when one party is perceived to assert its interests at the expense of another” (Woodroffe et al. 2005, White et al. 2009, Young et al. 2010, Redpath et al. 2013, 2015).

1.1.3. HOW TO SOLVE CONSERVATION CONFLICTS?

A solved “conflict” is a situation where both parties can coexist, and within a conservation context it also includes a decrease of the human-wildlife impact (Treves et al. 2006, Redpath et al. 2013, Sarrazin and Lecomte 2016). A clear identification of the actors

involved in a conflict along with their respective interests is therefore necessary to achieve right management and to tend toward a win-win situation (Treves et al. 2006, Young et al. 2010, Colyvan et al. 2011, Redpath et al. 2013, 2015). As such, a third party is often requested to plan a sustainable management of the conflict as long as they maintain transparency in their assumptions and inferences to be trusted by the actors involved in the conflict (Treves et al. 2006, Redpath et al. 2013). The role of scientists is first to measure the perceptions of conflicts as well as the behaviours of the involved actors either humans or animals (Treves et al. 2006, Redpath et al. 2013, Blackwell et al. 2016). As part of this process, behavioural ecology is a field of importance as it allows for a better understanding of the human impacts on wildlife. This field of ecology aims indeed at investigating the evolutionary basis for animal behaviour in response to ecological pressures. When environments are shaped by human activity, this approach can target how human activity influences the behaviours of wild animals and the consequences on the adaptability and survival of the wildlife populations. Besides, a good understanding of animal behaviour, both in presence and absence of human activity, may help to develop possible trade-offs involving alternative options for the actors to be used as techniques avoiding lethal retaliation (Treves et al. 2006, Sarrazin and Lecomte 2016, Blackwell et al. 2016). The implementation of solutions must always be followed by monitoring to judge the effectiveness of interventions. Scientists have to evaluate whether the shared objectives between the wildlife conservation and human welfare have been reached (Treves et al. 2006).

The steps for a good management of a conservation conflict seem in theory quite achievable. However, these conflicts are in practice very complex as they require balance of the interests between all actors and might be in some case unreachable (Treves et al. 2006, Redpath et al. 2013, Dickman and Hazzah 2016). In addition, the complexities of ecosystems where conflicts occur paired with the lack of knowledge on animals' behaviour often result in a poor understanding of the conservation priority. This may be especially true for ecosystems which are not directly shaped by humans, such as in agriculture where land modification allows the control and understanding of most ecosystem parameters. This is the case for marine environments, a complex ecosystem hardly accessible to humans (Lewison et al. 2018). However, although humans cannot settle and thus shape directly the marine environments, they nevertheless succeeded to exploit aquatic ecosystems all over human evolution.

1.2. MARINE DEPREDATION

1.2.1. CONTEXT OF MARINE DEPREDATION: FISHING ACTIVITY

The Earth's surface is 71 % covered by water and 96.5% of this water is held within the oceans. Marine ecosystems are predominant on our planet and all of them have been impacted by anthropic activities, either indirectly through human pollution or directly through resources exploitation (Halpern et al. 2008). The exploitation of the oceans started as early as the Palaeolithic with the hunter-gatherer foraging on fish and molluscs along the coast (Erlandson 2001, Erlandson and Moss 2001, Jackson 2001). Through human evolution and techniques developments, humans have then been able to go further away from the coast and to exploit offshore ecosystems, increasing their fishing pressure on target species and on their supporting ecosystems (Jackson 2001). Nowadays, all humans fisheries capture more than 90 million of tonnes of fish per year, including fish not targeted but kept on board (bycatch), with more than 30% considered as overfished (FAO 2016). These estimations do not account for discards, *i.e.* fish and other marine life that are thrown overboard, estimated around 10% of the global total catches, which represents a hidden impact not marginal (Kelleher 2005, Zeller et al. 2018). However, even by assessing these discards, the total catch is still underestimated since Illegal, Unregulated and Unreported (IUU) fishing is not accounted. With an estimated 18% of the global catch in the early 21st century, IUU fishing is likely to greatly contribute to the current overexploitation of fish stocks (Agnew et al. 2009). Thus, through human evolution, fisheries have led to important depletion of species, questioning the sustainability of this activity (Jackson 2001, Pauly et al. 2002). However, despite the collapse of some fishing stocks during the last decades, most of fishing efforts have kept growing (Pauly et al. 2002, FAO 2016).

Fisheries affect marine wildlife and ecosystems in various ways. The first direct impact of fishing is the reduction of the target species' abundance, threatening the stocks with extinction through overexploitation (Casey 1998, Pauly et al. 2002). Removing species, or at least part of a population, modifies the natural balance of ecosystems through a reduction of the number and length of pathways within food webs (Pauly 1998, Pauly et al. 2002). Fisheries can generate both top-down and bottom up effects. On the one hand, top-down effects occur when fisheries primarily target large individuals from upper trophic levels, this reduces predatory pressure on prey, which therefore leads to overloaded populations in lower trophic levels of the ecosystem, subsequently causing deleterious effects (Jackson 2001, Daskalov 2002, Pauly et

al. 2002, Lynam et al. 2017). On the other hand, bottom-up effects occur when fisheries exploit a resource used by marine predators. The marine top predators may either change their diet and thus introduce a new predatory pressure on other species disrupting the ecosystem balance (Jackson 2001, Lynam et al. 2017), or enter in direct competition with fisheries (Trites et al. 1997, DeMaster et al. 2001, Matthiopoulos et al. 2008). Competitive interaction between top marine predators and fisheries could result in a negative impact on marine predators populations due to marine resources depletion (Trites et al. 1997, Yodzis 2001, DeMaster et al. 2001, Matthiopoulos et al. 2008). However, competition also leads to operational interactions defined when marine predators come into physical contact with fishing gear to withdraw the catch (Northridge 1991, Donoghue et al. 2002, Gilman et al. 2006, Read et al. 2006, Read 2008). These interactions happen when there is co-occurrence of foraging activity or when marine predators are attracted by fishing activity. This latter behaviour has been defined as depredation, since the predators feed upon a resource captured by humans (Donoghue et al. 2002, Gilman et al. 2006, Read 2008). With the extension of fishing activity over the last decades, direct interactions between human fisheries and marine top predators have been increasing, raising new conservation conflicts (Northridge 1991, Northridge and Hofman 1999, Read et al. 2006, Read 2008).

1.2.2. DEFINITION OF THE MARINE DEPREDATION CONFLICTS

Depredation on fisheries by marine predator is a type of situation where human activity and wildlife behaviour have both an adverse effect on the other, defining thus a “human-wildlife conflict” (Conover 2002). On the one hand, depredation has substantial socio-economic consequences for fishermen. Indeed, this behaviour by marine predators is characterised by the removal of the whole capture or the partial consumption of the fish, decreasing the fish economic value and damaging the fishing gear at the same time (Donoghue et al. 2002, Gilman et al. 2006, 2008, Read 2008). Additionally to these induced costs, fishermen increase their fishing effort to complete their quota or to avoid depredation, increasing expenses due to fuel consumption, extra food and crew salaries (Gilman et al. 2006, Peterson and Carothers 2013, Peterson et al. 2014, Tixier et al. 2015c, Werner et al. 2015). On the other hand, depredation for marine predators increases risks of mortality by the use of lethal retaliation by fishermen (Yano and Dahlheim 1995, Woodroffe et al. 2005, Treves et al. 2006, Read 2008), or by a

greater risk of bycatch, especially in gillnets (Northridge 1991, Gilman et al. 2006, Read et al. 2006, Read 2008, Hamer et al. 2012, Reeves et al. 2013). For instance, it has been observed that at least 75% of odontocetes, 64% of mysticetes, 66% of pinnipeds, and all sirenians and marine mustelids species have been recorded as gillnet bycatch since the 1990's (Reeves et al. 2013).

Depredation has been observed on all fisheries and by a broad range of large marine vertebrates (Northridge and Hofman 1999, Donoghue et al. 2002, Gilman et al. 2006, 2008, Read 2008, Hamer et al. 2012, Werner et al. 2015). However, most of these conflicts involved the longline fisheries, with a growing cases since the 1950s (Northridge and Hofman 1999, Donoghue et al. 2002, Gilman et al. 2006, Read 2008, Hamer et al. 2012), and have involved mainly odontocetes species (Northridge 1991, Northridge and Hofman 1999, Gilman et al. 2006, Read 2008, Reeves et al. 2013, Werner et al. 2015). Indeed, at least 31 species of odontocetes have been reported to interact (either depredation or bycatch) with longline fisheries against 15 species of pinnipeds, 6 species of mysticetes, and 2 species of sirenians (Werner et al. 2015). Increasing longline depredation may be firstly explained by the large expansion of this fishing gear worldwide in the last 70 years. Indeed, longlines are more selective in catching targeted fish species than most of the other fishing gears and have thus been favoured in many fisheries (Gilman et al. 2006, Read 2008). Secondly, longline is an easy target for marine predators as baits and fish are freely accessible. Indeed, longlines consist of snoods connecting unprotected hooks at intervals along a mainline. The longline fishing process is composed of three steps (Figure 1-1): (i) the setting, which is the phase when hooks are baited and longlines are deployed at sea, and which generally lasts from less than an hour to a few hours; (ii) the soaking, which is the phase when fish is caught as the longline is left at sea with no boat activity, and which lasts from a few hours to a few days depending on fisheries; (iii) the hauling, which is the phase when longlines with the catch are retrieved aboard boats, and which, for a given longline, generally lasts longer than the setting phase. Longlines can either be deployed within the water column close to the surface, *i.e.* pelagic longlines, or on the seafloor, *i.e.* demersal longlines. Depredation has been mostly described to occur during hauling of the longlines for both types (Hucke-Gaete et al. 2004, Gilman et al. 2006, Read 2008, Mathias et al. 2012, Rabearisoa et al. 2012, Söffker et al. 2015, Guinet et al. 2015, Passadore et al. 2015, Tixier et al. 2015c, Werner et al. 2015) and also during the soaking time for pelagic longlines (Gilman et al. 2006, Dalla Rosa and Secchi 2007, Read 2008, Forney et al. 2011,

Rabearisoa et al. 2012, Passadore et al. 2015, Werner et al. 2015, Thode et al. 2016). As longlines may increase the availability of food for top marine predators, the development of this fishing technique has caused substantial ecological chain reactions. For marine predators, foraging on fish already caught requires very low capture effort and therefore increases energetic intake. This may result in a positive influence on the survival and reproduction of individuals in some populations, even though the risk of mortality by entanglement on longlines remains high (Donoghue et al. 2002, Gilman et al. 2006, Read 2008, Tixier et al. 2017). As a result marine predators are likely to favour this behaviour over natural foraging, subsequently increasing the risk of a habituation to fisheries and/or a switch of their natural diet and so their foraging strategies, and also their natural spatial distribution (Gilman et al. 2006). In turn, these behavioural modifications longline depredation may threaten the prey-predatory balance established in the ecosystem by increasing the predatory pressure on the targeted fish, threatening the fish stocks of depletion.

All these ecological impacts paired with bycatch on longlines of emblematic species have created a negative public perception of longline fishing and raised conservation programs to protect either marine predators and fish stocks (Gilman et al. 2006). As most of these actions are more likely to reduce fishing activity, the “human-wildlife conflicts” should be better considered as a “human-human conflicts” (Treves et al. 2006, Redpath et al. 2013, 2015). This conservation conflicts requires solution to reach a situation where marine wildlife is not threaten and fisheries are sustainable (Treves et al. 2006).

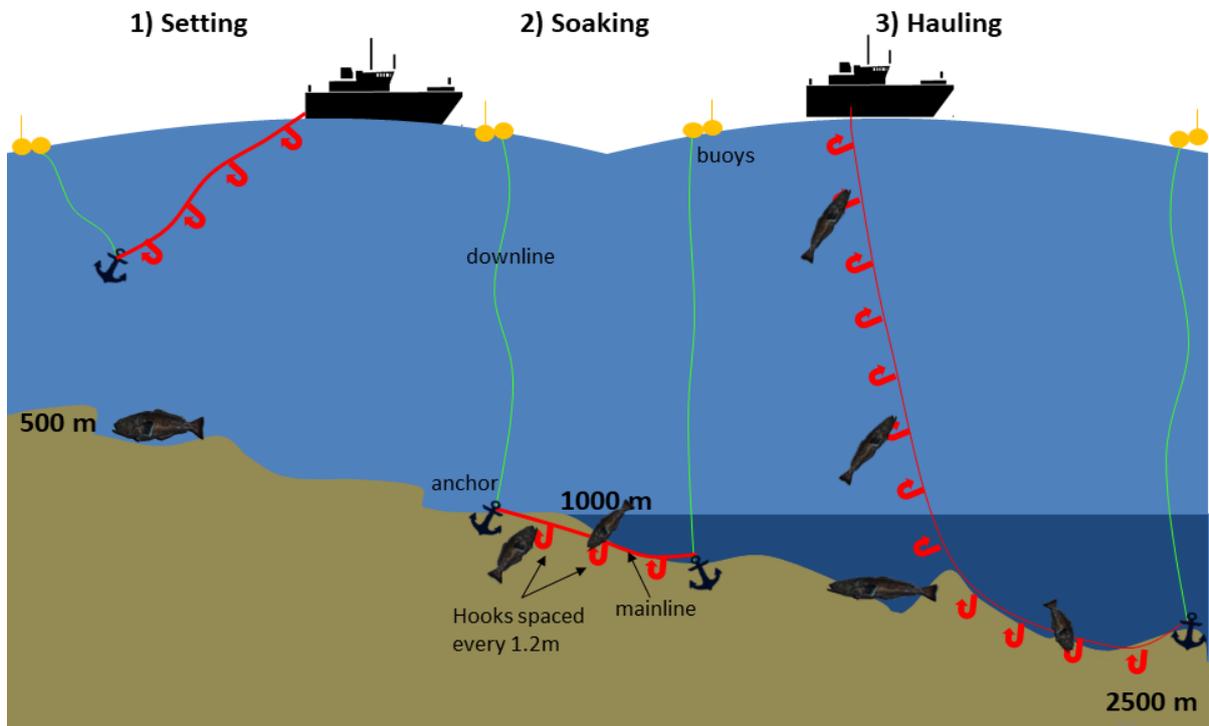


Figure 1-1 – Fishing phases of a demersal longline.

1.2.3. HOW TO SOLVE THE MARINE DEPREDATION CONFLICTS?

Identifying solutions to marine depredation involves developing mitigation measures with limited costs for all parties of the conflict. On one hand, preventing marine predators from interacting with fisheries would suppress/decrease the mortality risk of these animals as well as all the ecological consequences of depredation on the ecosystem. Besides, it would allow reducing the fishing effort to catch the same amount of fish, and thus decrease fishing pressure on the environment as well as improving fisheries sustainability. However, to find the appropriate mitigation is challenging since preventing marine predators from interacting with fishing gear should not decrease the fishing efficiency. Solutions are then mostly dependant on the fish targeted, the fishing gear used and the depredating species. The first step toward a resolution of the conflict is then a good understanding of these three components. Thus, as previously discussed, scientists have an important role to play as they can study interaction between marine predators and fisheries, by assessing behaviour of both actors, and then implement experimental solutions and monitor their efficiency.

Depredation is a conflict that can theoretically be mitigated using two non-lethal approaches either operational or technological. Firstly, a better understanding of fishing practice and strategy with their causes or consequences on depredation rates may lead to relatively easy mitigation solution to implement with limited cost for fisheries. Indeed, through this operational approach scientists can make recommendation for fishermen on the use of their fishing gears and propose more efficient strategies to limit marine predators' access to catch and bait (Gilman et al. 2006, Hamer et al. 2012, Werner et al. 2015). For instance, the hauling speed or the setting length or deployment depth of longlines may gain time and reduce the probability of interaction (Gilman et al. 2006, Tixier et al. 2010, 2015c, Werner et al. 2015). Another improvement of fishing strategy involves a better spatio-temporal use of the fishing area by targeting grounds where and when the probability of encounter with marine predators is the lowest (Dunn et al. 2014, Tixier et al. 2015c, Werner et al. 2015, Janc et al. 2018). This approach requires assessing the marine predators' ecology to know if the predators have some preferential foraging areas/seasons within the fishing zone, or whether they have diel feeding variations or also if they might be migratory species. However, it is likely to have strong spatio-temporal overlaps between the fishing activity and the predators' foraging, as both wildlife and humans may be attracted by high fish densities grounds. Thus, changes of fishing strategies may sometimes decrease fishing success as well as increase cost for fisheries. For instance, alternative fishing practices might have a human impact when requiring fishermen to work either faster or longer or in worst condition. As a result, these changes in fishing strategies could reduce depredation levels but they rarely solve completely the conflict.

Additional approaches are then needed, such as methods to protect the catch either by repelling the predators or by avoiding detection of the fishing activity or by using a physical protection of the gear to avoid access to the fish. These technological approaches seem in theory the best ways to avoid depredation. Nevertheless, it is in practice hard to implement since it faces a lot of constraints to meet a trade-off between being economically viable for fishermen and harmless for marine predators. Behavioural ecology has an important role to play as it is essential to know how fishing activity is detected by the predators and how the depredation occurs to target the most appropriate solution. For the first purpose, it is essential to assess how marine predators perceive their environment and localise they prey. For instance, using a sensory ecological approach, some studies have found that shark are sensitive to chemical, magnetic, electropositive rare earth metal and electrical repellents (Gilman et al. 2008). As for

odontocetes some studies have focused on developing the use of acoustic deterrence, since they primarily rely on acoustic to forage. Although it seems impossible to deter cetaceans by acoustics, using pingers on gillnets to signal their presence to dolphins and porpoises have shown promising results in decreasing odontocete bycatch (Reeves et al. 2013, Maccarrone et al. 2014). However, for fishing gears where fish is freely accessible, the interest is not to increase fishing gear detection with pingers but to repel the animals with acoustic harassment (Arangio 2012, Tixier et al. 2015b, Werner et al. 2015). Trials of acoustic harassment have yet not been conclusive in the literature (Götz and Janik 2015, Tixier et al. 2015b, Werner et al. 2015). Another approach to repel odontocetes from the fishing gears using acoustic is to attract them toward a decoy producing fishing vessels playbacks (Thode et al. 2015, Wild et al. 2017). These playbacks require to assess the vessels acoustic signatures and determine any acoustic clues which may attract odontocetes (Gilman et al. 2006, Thode et al. 2007, 2015). Furthermore, the identification of the sounds that attract the odontocetes could also lead to improvement of fishing vessel to decrease their detection range (Gilman et al. 2006, Thode et al. 2007, Hamer et al. 2012, Werner et al. 2015). When it seems inefficient to avoid the attraction of odontocetes of the fishing gear, then the last option seems to be the use of physical protections. Although a physical protection is the most complicated method to implement, since it requires changing the fishing gear and so the setting system of the fishing boat, it may offer the most efficient solution. Thus, this approach may be considerably expensive for fisheries but the benefits gained from suppressing depredation may cover the costs engaged. This approach was first developed by Chilean fishermen to mitigate sperm whale depredation from demersal longlines, using a floating net sleeves sliding down to protect the fish during hauling, called the 'Cachalotera' (Hucke-Gaete et al. 2004, Moreno et al. 2008, Arangio 2012). In contrast, pelagic longlines may be exposed to depredation during the entire fishing process, *i.e.* both during soaking and hauling, thus using a triggered device that could encapsulate the fish caught may avoid depredation (Hamer et al. 2012, 2015, Rabearisoa et al. 2012, Werner et al. 2015). This approach has nevertheless not received a lot of attention yet (Hamer et al. 2012, 2015, Rabearisoa et al. 2012, Werner et al. 2015). This may be partially explained by the complexity to test experimental devices on commercial fishing boats not adapted to scientific trials, and to logistical constraint to equip all fishing gear with numerous hooks deployed by commercial longliners. Fishing gear modification can require a period to optimise the new practice, whereas other fishing methods might be already optimised and useful to reduce depredation, such as the fishing pots. For instance in Alaska pot fisheries have been approved and seem to be effective

in preventing sperm whale depredation, but are more expensive to use compared to conventional longlines (Sullivan 2015, Peterson and Hanselman 2017). The same conclusion has been drawn after a preliminary trial performed as part of the ORCASAV program in 2010 around Crozet Archipelago (captains and Guinet personal communications, and see (Bavouzet et al. 2011, Gasco 2013). Furthermore, with the recent expansion of longline fisheries some depredation cases are relatively new and still require some assessments.

As all conservation conflict, depredation requires a good understanding of the issue and then a good monitoring of solutions. Although mitigation is on its way many studies are still at the understanding stage and scientist start to monitor solutions. The complexity of the issue comes from the ecological, socioeconomic and cultural dimension of the conflict. Indeed this interaction involves in one side one of the most important human activity (*i.e.* fishery); and in the other side some emblematic species which are still poorly known as they evolve in an ecosystem hardly accessible. The knowledge of these mysterious animals has yet substantially increased with the improvement of technologies, such as in acoustics, bio-logging, or molecular biology. With these progresses researcher have recently described unobserved populations or even new species of marine mammals (Robineau et al. 2007, Pitman et al. 2011, Morin et al. 2016) or assessed new insights of diving behaviour by some odontocetes (Schorr et al. 2014, Reisinger et al. 2015). These studies revealed how much we still have to learn about marine mammals and especially about their underwater behaviours. As previously discussed, the understanding of marine mammal behaviours is crucial to assess the conservation conflicts. This thesis falls in this purpose to better understand interactions between marine mammals and longline fisheries for a better lead to mitigation solutions.

1.3. CONTEXT AND PURPOSE OF THE THESIS

1.3.1. CONTEXT OF THE THESIS: A GAP IN FINE SCALE

UNDERSTANDING OF LONGLINES DEPREDATION

Research effort on interaction between odontocetes and longlines has substantially increased over the last 15 years (Northridge and Hofman 1999, Donoghue et al. 2002, Gilman et al. 2006, Straley et al. 2015, Guinet et al. 2015, Thode et al. 2015, Tixier et al. 2015c, Werner et al. 2015, 2015). These studies have considerably improved our understanding of these

conflicts by identifying the species involved and estimating impacts on fisheries at the fleet level (*e.g.* Hucke-Gaete et al. 2004, Dyb 2006, Tixier et al. 2010, Rabearisoa et al. 2012, Peterson et al. 2014, Straley et al. 2015, Söffker et al. 2015, Passadore et al. 2015) and on wildlife populations, both depredating species and fish stocks (*e.g.* Gilman et al. 2008, Read 2008, Forney et al. 2011, Hamer et al. 2012, Gasco et al. 2015, Guinet et al. 2015, Tixier et al. 2017). However, most of these studies have relied on large spatio-temporal scales and have been limited to visual surface data, such as direct surface observations of depredating animals around fishing boats (especially for demersal longlines, *e.g.* Hucke-Gaete et al. 2004, Purves et al. 2004, Kock et al. 2006, Roche et al. 2007, Gasco et al. 2015, Söffker et al. 2015, Janc et al. 2018) or through the presence of damaged fish on hauled longlines (especially for pelagic longlines, *e.g.* Dalla Rosa and Secchi 2007, Rabearisoa et al. 2012, Straley et al. 2015, Passadore et al. 2015). The underwater dimension of depredation has remained poorly investigated. First studies using alternative types of data, such as underwater videos, acoustics and bio-logging revealed that odontocetes may depredate baits and remove the whole fish (Mathias et al. 2009, Thode et al. 2014, 2015, 2016, Guinet et al. 2015). These investigations question the accuracies of interaction estimations, and suggest that depredation rates may be underestimated, which could have critical consequences on fishing management and stocks assessments. It is therefore essential to increase research effort on this underwater dimension, and to question our vision of interactions between fishermen and marine predators.

Depredation conflicts have been mainly described as “fishery-odontocetes” interactions, therefore considering the fishing gear and fishermen as a unique entity. Indeed, for demersal longline fisheries, “interactions” have been assumed to primarily occur during hauling phases when animals are seen in the vicinity of fishing boats (Mathias et al. 2012, Tixier 2012, Werner et al. 2015). However, during soaking, the fishing gear is independent from fishermen activity and studies on pelagic longlines revealed that depredation could occur during this phase (Dalla Rosa and Secchi 2007, Forney et al. 2011, Rabearisoa et al. 2012, Passadore et al. 2015, Thode et al. 2016). Thus, a finer approach may be to assess “fishing gear-odontocetes” interactions separately from the “fishermen-odontocetes” interactions. By dissociating fishermen from their fishing gear, we may consider three “actors” involved in the depredation conflict (fishermen, fishing gears and odontocetes). This categorisation of entities adds the possibility to describe the relationships/interactions between them at different scales. We can therefore assess the “fishing gear-fishermen” interaction which relates to fishermen behaviour in regards to their

setting and hauling strategies. Fishing behaviours and strategies include the way fishers use the fishing gear (*i.e.* longlines' length, the hauling speed, etc.) or the fishing vessels (*i.e.* manoeuvres, mobility) and make decisions during fishing operations to exploit the fish stock. Fishermen behaviours and strategies have been poorly assessed at individual scale. As an analogy to other predators, it is of interest to better understand fishermen foraging behaviours within a context of competition with odontocetes (McCay 1978, Begossi 1992, Orians et al. 2003, Nettle et al. 2013). Individual foraging behaviours may indeed imply different risks of detectability by the odontocetes. This behavioural ecology approach may highlight mechanisms of the conflict at a “fishermen-odontocetes” dimension. Finally, we may wonder how odontocetes depredate on the fishing gear once the competition starts. Similarly to fishermen behaviour, an individual scale of marine predators behaviour would then tackled gaps in the knowledge of “fishing gear-odontocetes” interactions. This approach requires monitoring odontocetes' behaviours underwater. This PhD aimed therefore at assessing a depredation conflict case from the three interactions dimensions described here before and using individuals' behaviours of both fishermen and odontocetes.

1.3.2. STUDY CASE

This thesis focused on an example of the depredation conflict involving the commercial Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries with killer whales and sperm whales in the Southern Ocean.

The Patagonian toothfish belongs to the Nototheniidae family and the *Dissostichus* spp. genus, which includes two species that are both endemic to the southern hemisphere and bathypelagic. While the other species, the Antarctic toothfish, *Dissostichus mawsoni*, is found at high latitudes around Antarctica, the Patagonian toothfish is primarily found in sub-Antarctic waters (Collins et al. 2010). These are long-lived (>50 years) and large size (> 200 cm in length and > 200 kg in weight) species (Collins et al. 2010). A high-quality flesh makes the two species economically highly valuable (Collins et al. 2010, Grilly et al. 2015) and toothfish fisheries have developed as a primary economic activity of Antarctic and sub-Antarctic waters (Figure 1-2, Croxall and Nicol 2004, Collins et al. 2010, Grilly et al. 2015). The average prices of imports for toothfish have recently increased by 62.24% (between 2007-2012 - Grilly et al. 2015), with an estimated current value of 30-35 US\$/kg. The Antarctic toothfish fisheries

started in the 2000s, and are primarily operated in areas regulated by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The Patagonian toothfish was first caught as a bycatch species by the trawl fisheries operating in the Exclusive Economic Zones (EEZ) of Chile in the 1950s and of Kerguelen and South Georgia in the early 1980s. The species later became a target species between the mid-1980s and the 2000s, initially caught by trawl fisheries until the emergence of demersal longlining, which progressively replaced trawling in the 1990s (Collins et al. 2010). Patagonian toothfish fisheries now primarily operate in areas under CCAMLR jurisdiction, which includes international waters and EEZs around French, Australian, British and South African sub-Antarctic islands, as well as in non-CCAMLR areas such as the EEZs of Argentina, Chile and the Falklands/Malvinas (Croxford and Nicol 2004, Collins et al. 2010, Grilly et al. 2015).

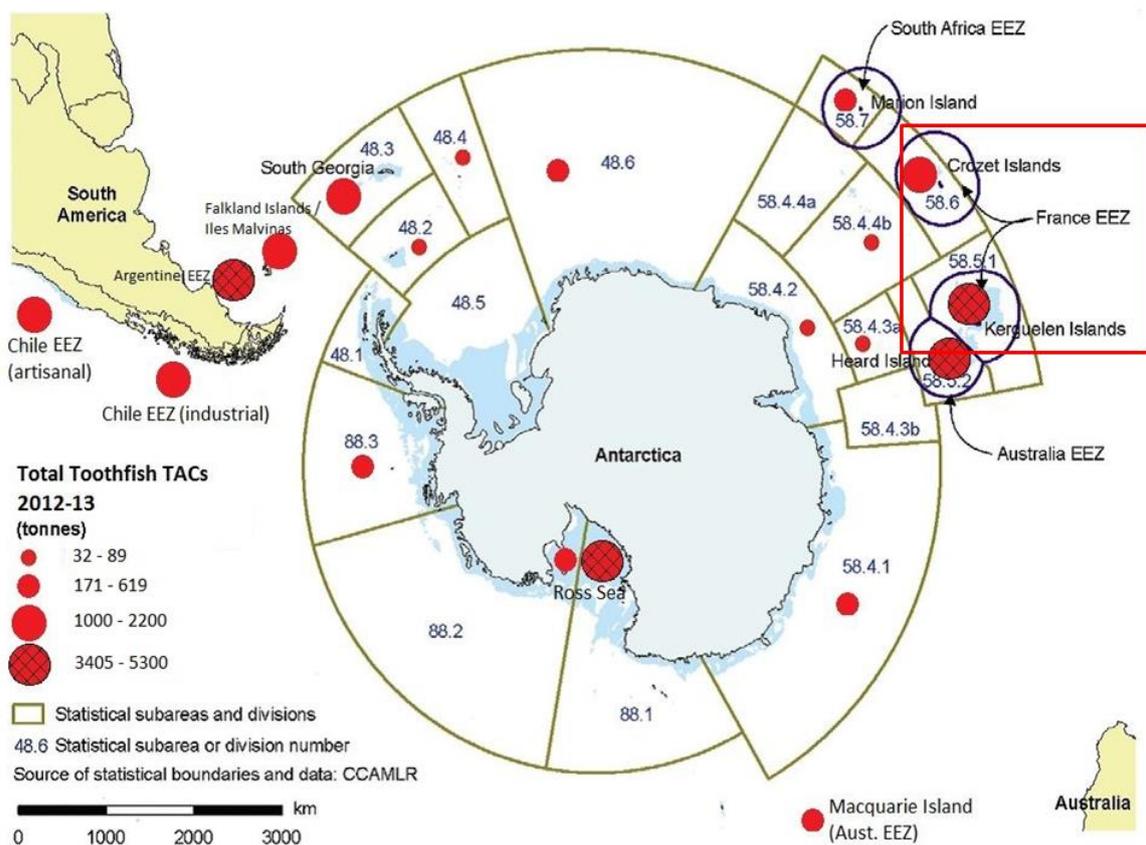


Figure 1-2 - Map from the Coalition of Legal Toothfish Operators (COLTO) of the toothfish fisheries sites with their total allowable catches (TACs), for the season 2015-2016, set by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) or by national authorities within their Economic Exclusive Zone (EEZ). The red square highlights French EEZs of Crozet and Kerguelen islands on which this thesis focused.

However, in most of these fishing areas, fisheries have experienced interactions with killer whales and/or sperm whales since the very beginning of their commencement (Nolan et al. 2000, Hucke-Gaete et al. 2004, Kock et al. 2006, Yates and Brickle 2007, Collins et al. 2010, Tixier et al. 2010, Roch et al. 2011, Arangio 2012, Guinet et al. 2015). In some fisheries the probability to haul a longline in presence of sperm whales have exceeded 50%, such as in Chile or around the French sub-Antarctic islands (Hucke-Gaete et al. 2004, Roche et al. 2007, Tixier et al. 2010, Janc et al. 2018). These interaction levels led to significant decrease to fishing success, with killer whales being the species causing greater fish losses than sperm whales (Hucke-Gaete et al. 2004, Roche et al. 2007, Tixier et al. 2010, Söffker et al. 2015). Therefore, these interactions with killer whales and sperm whales may have serious implications for the economic viability of the toothfish fisheries as well as for sustainable management of fish stocks, raising the necessity to find mitigation solutions.

The depredation conflict existing in the fishery operating in the French EEZs of Crozet and Kerguelen islands is a study case with suitable characteristics to address the aims of the thesis. Firstly, this fishery holds the largest Patagonian toothfish quota in the Southern Ocean (Guinet et al. 2015, COLTO 2016) and experiences the highest depredation levels of all other toothfish fisheries, with more than 30% and 9% of the total annual catch taken by killer and sperm whales, respectively at Crozet and Kerguelen (Roche et al. 2007, Tixier et al. 2010, Gasco et al. 2015, Janc et al. 2018). Secondly, this fishery is composed of 7 legal longliners ranging from 50 to 60 m long with crews composed of 30 fishermen and has been fully controlled and monitored since the early 2000s, with fishery observers monitoring 100 % of the fishing operations. The same fleet operates in both the Crozet and Kerguelen EEZs during a same fishing season, which greatly differ in catch limits (around 80% of the total annual catch is fished in Kerguelen) and in size (the Kerguelen fishing area is 5-7 times larger than the Crozet area). A fishing season runs from September to August, but the fleet is not allowed to fish in the Kerguelen EEZ for a 45-day period from the 1st February to mid-March to comply with seabird conservation measures. A season is composed of 3 to 4 trips lasting between 2.5 and 3 months. During a trip, vessels fish continuously through a diel pattern. Longlines are set at night and mostly hauled during the day, since fishing regulations prohibit setting at daylight to avoid seabird bycatch (Weimerskirch et al. 2000). These vessels use auto-weighted longlines set between two anchors and linked to buoys at the surface for retrieval. The lines are composed of sections of 750 hooks spaced every 1.2 m (Figure 1-1). The length of these lines can vary

from 1 to 40 km, averaging 8 km. The hooks are automatically baited and set on the seafloor at depths ranging from 500 to 2500 m. Fishing in waters shallower than 500 m is prohibited to avoid the capture of juvenile toothfish (Collins et al. 2010, Gasco 2011). Since 2003 the two EEZs are also subject to a high level of surveillance by the French government, which has resulted in negligible levels IUU fishing, further enhancing the representativeness of the data collected from licensed vessels (Guinet et al. 2015). Besides, interaction levels are sensitively different between the two EEZs since sperm whales are present around both islands but at different densities (Labadie et al. 2018), whereas killer whales are almost exclusively found in Crozet (Tixier et al. 2010, Guinet et al. 2015). Furthermore, the Crozet Archipelago is one of the few locations in the Southern hemisphere where killer whales have long been studied, allowing a monitoring of the population before and after the fishing activity started (Guinet et al. 2015). This unique study case gives the opportunity to understand the impact of the fishing activity on an odontocete population. Indeed, in Crozet the fishery started in 1996 with a lot of IUU fishing vessels which negatively impacted the killer whale population (Guinet et al. 2015, Tixier et al. 2017).

This example of depredation issue has been studied since 2007 by the research project named OrcaDepred. This project also assesses depredation by cetaceans on pelagic longline fishery targeting swordfish and tuna around Reunion Island and on demersal longline fishery fishing the blue-eye trevalla around St Paul and Amsterdam Islands. The project is led by Dr. Christophe Guinet (CEBC, CNRS-University of La Rochelle, France) and involved 8 partner-institutions (CEBC-CNRS, MNHN, ENSTA Bretagne, UBO, IFREMER, UMI 2958 GT-CNRS, AMURE, IRD UMR MARBEC) as well as one industrial provider (SATIM). OrcaDepred is supported by the ANR, the Fondation d'Entreprise des Mers australes, the Syndicat des Armements Réunionnais des Palangriers Congélateurs, fishing companies, the Direction des Pêche Maritimes et de l'Aquaculture, Terres Australes et Antarctiques Françaises (TAAF : the Natural Reserve and Fishery unit).

The objectives of OrcaDepred are to better understand the depredation behaviour and ecology of cetacean species involved to offer fishing companies operational and technological solutions to depredation. Thus, the project aims at:

1. Better understanding the natural feeding and interaction behaviours with the fishery cetaceans interacting with the lines, and in the case of pelagic longlines identify the cetacean species involved.
2. Assessing the bio-economic consequences of depredation through an ecological economic modelling exercise for the sustainable management of these fisheries taking into-account depredation.
3. Assessing the ecological consequences of fishing-depredation at the ecosystem level.
4. Assessing if the levels of interaction between cetaceans and ships are related to fishing practice differences between captains and/or vessel characteristics, with a special focus on acoustic noise generated.
5. Implementing a technological approach to remove depredation. In partnership with industry, new prototypes of fish protection devices on the lines and not harmful to cetaceans.

The OrcaDepred project is conducted in collaboration with the Australian research project: “Developing global solutions to marine mammals – fisheries interactions”, conducted by Dr Paul Tixier and Prof. John Arnould at Deakin University (Melbourne) and Prof. Mark Hindell and Dr Mary-Anne Lea at Institute for Marine and Antarctic Studies (University of Tasmania, Hobart), and funded by the Australian Research Council grant. This project focuses on objectives similar to OrcaDepred’s on other Patagonian toothfish fisheries (Heard and McDonald Islands, southern Chile, the Falklands, South Georgia, Prince Edward and Marion Islands) and on the blue-eye trevalla demersal longline fishery in South East Australia.

1.3.3. THESIS OBJECTIVES

My PhD thesis contributes to the OrcaDepred project, and to the French-Australian collaboration on longlines’ depredation. Indeed, my thesis is set as a cotutelle between the University of La Rochelle (Chizé, France) and Deakin University (Melbourne, Australia).

My work mostly focused on the 1st and 4th purposes previously described (section 1.3.2), using the French Patagonian toothfish fishery as a study case. More specifically, the aim of my thesis was to bring new insights on the interaction between odontocetes and demersal longlines using both human and animal behaviours at individual scales. My first objective was

to examine the drivers of observed variations of interaction rates between captains. This problematic was assessed through a human behavioural ecology approach (chapter 2) and an acoustic approach (chapter 3). My second objective was to assess how, when and where depredation occurs on demersal longlines. A passive acoustic monitoring and a biologging approach were suggested to bring some answers to this question (chapter 3 and chapter 4). Thus the thesis was organised around the three methodological approaches based upon research articles and technical protocol:

- Chapter 2: The first approach aimed at better understanding the behaviour of captains facing the depredation and which factors drive their foraging strategies, using operational data collected on fishing boats and methods of behavioural ecology.
- Chapter 3: This chapter focused on passive acoustic monitoring. I assessed what this method could bring on the understanding of depredation in the underwater dimension and I specifically focused on the underwater detectability of the fishermen to bring insights for the first problematic.
- Chapter 4: I finally assessed how bio-logging technologies could bring important information on the interaction between longlines and odontocetes. Bio-loggers were deployed on odontocetes but also on the fishing gear to bring an original double perception of the interaction.

Altogether, these new insights are expected to bring new perspectives for fisheries assessment and mitigation solutions, which are discussed in Chapter 5.

Pre-existing data were really scarce at the beginning of my thesis. To fulfil my objectives, I aimed at: *(i)* deploying an acoustic array to assess acoustic tracking and record vessels acoustic (chapter 3); *(ii)* deploying loggers (accelerometers) on longlines (chapter 4); *(iii)* deploying loggers on odontocetes with on-board processing acceleration data. Conducting experiments at sea was thus an important part of my PhD. My contribution covers experimental design, planning, logistics, and at-sea realization. This will be briefly summarized below.

1.3.4. THESIS FIELD EFFORT

No hydrophone and no loggers (both on longline and odontocetes) have ever been deployed from the French and Australian longliners to investigate depredation before my thesis. The first step of my PhD was therefore to choose adapted instrumentation, set the protocols and prepare the missions for the deployments. I did this in close collaboration with both instrument manufacturers and fishermen. An important point here was to ensure that scientific activities would minimally disturb fishing activities, in order to maintain collaboration with fishermen. As part of an experimental design, I have tested an acoustic tracking methods during my master thesis (prior to this PhD) to determine the best setting for an acoustic array (see Appendix 1). The setting was imparted to a French acoustic company (RTSYS) which designed the array.

Another experimental design, assessed at the beginning of this PhD, was to test whether a method derived from acceleration analyses on southern elephant seals could be used on sperm whales (section 4.2). The results and method adapted to a sperm whale dataset was then transmitted to Wildlife Computer, a biologging company. The company embedded this algorithm on new generation of loggers to be deployed on marine predators, *e.g.* for odontocetes in our study but also new tags for fish and sharks. As for the loggers deployed on longlines, they have been directly developed by Dominique Filippi (Sextant Technology, New Zealand). In a second step, I personally conducted the sea-trials from the French fishing fleet. I have therefore conducted two missions of 3 months each during the fishing seasons of 2016-2017 and 2017-2018, aboard three longliners during the first mission and two longliners during the second mission (see Table 1-1).

Table 1-1 – Summary of the field work conducted within this thesis.

Mission	Vessel host	Duration	Field work
First mission 2016-2017	Mascareignes 3 (SAPMER)	53 days 08/12/16 - 30/01/17	- Acoustic array
	Ile De La Reunion (COMATA)	28 days 03/02/17 - 03/03/17	- Loggers on longlines - Biopsy sampling
	Albius (SAPMER)	11 days 03/03/17 - 14/03/17	- Photo-identification
Second mission 2017-2018	Ile De La Reunion (COMATA)	35 days 14/12/17 - 18/01/18	- Acoustic array - Loggers on longlines - Odontocete tagging
	Mascareignes 3 (SAPMER)	48 days 18/01/18 - 07/03/18	- Protection systems - Biopsy sampling - Photo-identification - Fishery observer (1 month on MAS 3)

Loggers on longlines have been deployed during the two missions (Table 1-1). The first mission allowed testing and improving the protocol and during the second mission I had more loggers to increase the sampling effort. This experiment works well, but with a higher number of loggers I experienced an increase number of losses and breaks. The loggers on odontocetes have been deployed only during the second mission (Table 1-1) since it took some times to receive the new logger generation. Tagging condition on fishing vessels has been revealed to be very complicated. A successful tagging requires very good condition both from the weather and the approach of individuals. As the shoot occurs on the deck at 5 m above the water (without any swell), individual should be close enough to keep enough power when the dart hit the skin to fix the tag. Besides, the wind should be low to avoid strong deviation of the dart trajectory and allow hitting perpendicularly the individual. Despite these constraints, my experience revealed that it is doable to equip killer whales. Although sperm whales are seen more often, good tagging opportunities are less common than for killer whales.

The acoustic array was deployed during both mission (Table 1-1), but the setting evolved between the two missions to deal with several issues. The first mission allowed noticing that the acoustic array composed of 4 hydrophones connected through cables to one recorder was not adapted to the conditions experienced on a longliner within the southern ocean. The array was therefore changed during the second mission by 4 independent acoustic recorders (Soundtraps, Ocean Instruments, NZ). Using independent hydrophones facilitate the deployments. Additionally, I have set a protocol to deploy a single independent hydrophone by fishermen and fishery controllers on all the longliners for every trip (7 French vessels and 4 Australian vessels). Besides, the protocol is also used on both French and Australian blue-eye trevalla longline fisheries to monitor interactions with killer whales. The purpose of this protocol is to assess vessel acoustics and allow a passive acoustic monitoring of odontocetes. The hydrophones stay on-board and are deployed by fishermen under the supervision of the fishery observers who collect the data. The protocol will improve through fishermen and observers feedbacks to allow a future long term acoustic monitoring of the interaction between longliners and odontocetes.

In addition, I have processed photo-identification and biopsy sampling which were not analysed in this thesis but important for the OrcaDepred objectives. Besides, during the second mission I have also tested individual protection systems for hooks (Chapter 5), designed by an industrial provider (SATIM). The tests were not conclusive but were important to focus on

better countermeasures for the future. This experience has indeed allow the SATIM company to work on a new generation of protection system easier to implement considering all the constraint from the setting and hauling processes. I have finally experienced the role of fishery observer during a month, observation which fuel the PECHKER dataset (Martin and Pruvost 2007) managed by the Museum d'Histoire Naturelle de Paris. This dataset was graciously shared by the MNHN, allowing the study on captains' behaviour (section 2.2). Through the different steps of the missions' management I have been able to interact with the different protagonist of the fishery: fishermen, fishing companies, fishery observers, units of the TAAF and MNHN allowing a better understanding of the depredation issue from the different points of views.

2. FISHERMEN BEHAVIOURAL ECOLOGY

Most of previous studies have relied on large spatio-temporal scales and at the fleet scale to improve our understanding of these conflicts assessing the impact of depredation on fisheries and within fisheries how some practices, *i.e.* operational factors, could influence depredation rates. However, these studies did not really dissociate the fishing gear from the fishermen within fisheries, whereas fishermen (especially captains) are the decision makers playing on the operational factors. This chapter aims therefore at reviewing within the French Patagonian toothfish fisheries how an operational approach might help toward some mitigation measures. Additionally, the purpose of this chapter is to focus on the decision makings of captains and to suggest a finer scale could ensue from this operational approach through a human behavioural ecology.

2.1. INTRODUCTION

2.1.1. WHAT IS AN OPERATIONAL APPROACH?

Operational factors include all variables controlled by captains, and that can therefore be adjusted to act on either the probability of interaction with odontocetes or the extent of depredated fish during interactions. Mitigating depredation through operational approaches involves adapting the fishing practice in a way that it reduces depredation while maintaining high fishing success. Developing operational mitigation strategies therefore involves determining the causal connections between operational factors, depredation and fishing success. Such research is often challenging to implement since it requires an extensive monitoring of the fishing practices and of the occurrence of depredation. The French Patagonian toothfish fishery (*cf.* section 1.3.3.) is subject to a long-term full monitoring of fishing operations, allowing such approach.

Aboard the French longliners, fishing operations are monitored by fishery observers mandated by the administration of the French Antarctic and Southern Territories (TAAF), tasked for scientific monitoring by the National Museum of Natural History (MNHN) (Gasco 2011). The MNHN is the entity in charge of conducting the fish stock assessments and

estimating the Total Allowable Catch (TAC) used to define quotas. The data collected by fishery observers are stored within the so-called PECHEKER database (Martin and Pruvost 2007), which includes data on the species targeted, the quantity of fish caught and fishing locations (setting depths and geographic positions, see Gasco 2011). Observers also sample fish length and weight for resources assessments and record all by-catch of non-target species (*e.g.* grenadiers species, antimora, or skates species), as well as interactions with protected seabirds and marine mammals (Gasco 2011). Thus, the PECHEKER dataset provides information on operational variables such as the time, location, setting depth, number of hooks, as well as information on the total weight of toothfish caught, the occurrence of depredation and the number of depredating sperm whales and killer whales for every longline set. Visual observation of odontocetes around the vessels during hauling defines an interaction. These observations enable later estimation of interaction rates at different temporal scale (daily, monthly, per trip, per fishing season, etc) or at different spatial scale (longlines, sectors EEZ).

The first step of the operational approach is to assess whether some fishing practices (*e.g.* location, setting depth, length of longlines, fishing season...) may influence the probability of odontocetes to interact with longlines. The second step is to assess, when interaction is unavoidable, whether some fishing practice may reduce the impact of depredation on the fishing success. The catch per unit effort (CPUE, in g.hooks^{-1}) is a relevant proxy of the fishing success. The fishing effort is considered as the number of hooks (H) set, and the catch is the sum of the biomass (M in g) of Patagonian toothfish hauled for the given number of hooks. The CPUE for a given unit i (longline, sector, trip, etc.) is estimated as:

$$\text{EQUATION 2-1: } CPUE (i) = \frac{\sum M (i)}{\sum H(i)}$$

The CPUE is also used to estimate depredation rate, *i.e.* the loss of biomass due to odontocetes. The depredation rate is then assessed as the difference of CPUE on longlines hauled in absence of odontocete (set as the reference or the resource availability) and the CPUE on longlines hauled in presence of odontocetes (Gasco et al. 2015). Depredation rate can also be estimated by the change in proportion of by-catch species such, as grenadier species, which are not depredated by killer whales and sperm whales, in presence or absence of toothfish depredation (Gasco et al. 2015).

2.1.2. RECOMMENDATIONS ON FISHING PRACTICE TO MITIGATE DEPREDAATION

From the PECHEKER database (Martin and Pruvost 2007), probabilities of interactions and depredation rates for sperm whales and killer whales have been assessed in previous studies at different levels: longline set, fishing vessel, fishing fleet. These studies aimed at identifying correlations between operational variables and interaction/depredation rates (Roche et al. 2007, Tixier et al. 2010, Tixier 2012, Gasco et al. 2015). From results obtained at the longline level, advice has been given to fishermen on their fishing practice. For instance, fishermen should haul their longlines at a greater speed ($\text{hooks}\cdot\text{min}^{-1}$) since it reduces depredation rates by making the interaction with the hooks more difficult for both species but increasing hauling speed can also induce a greater loss of lightly hooked fish (Tixier et al. 2015c, Janc et al. 2018 see Appendix 4). Similarly, shorter longlines were shown to have lower depredation rate with killer whales as these longlines are fully hauled within shorter time frames and thus limit the time needed by odontocetes to detect, arrive and interact with the longline (Tixier et al. 2015c), but this practice become inefficient once killer whales or sperm whales have started to interact with a fishing vessel in a given location. Shorter soaking time was also shown to reduce opportunities for sperm whales to arrive to remove large amount of fish from longlines (Janc et al. 2018, see Appendix 4). Another factor influencing interaction and depredation rates for both species is the setting depth (Tixier et al. 2015c, Janc et al. 2018). However, this variable depicts the environment since the depth may reflect some parts of the shelves or seamounts where the odontocetes may forage naturally and are thus overlapping with fishing activity. As the contrary, deeper sets than 1000 m are beyond the foraging range of killer whales (Towers et al. 2018). At the fleet level, seasonal trends in the probabilities of interaction with odontocetes around Crozet and Kerguelen have been observed for both species (Tixier et al. 2015c, 2016, Janc et al. 2018). For instance, fishermen were advised to fish in Crozet around November-December where the interaction rate with Crozet killer whales are the lowest (Tixier et al. 2016). This might be explained by the breeding period of southern elephant seals, *Mirounga leonina*, from October to December, during which some killer whales units feed upon newly weaned elephant seal pups (Guinet 1992, Guinet and Bouvier 1995, Guinet et al. 2015, Tixier et al. 2016). Fishermen were also advised to focus their effort during winter (June-August) when the interactions rates with sperm whales become insignificant within Kerguelen EEZ and two times lower than summer within the Crozet EEZ (Labadie et al. 2018, Janc et al. 2018), since individuals migrate to warmer waters in low latitudes for reproduction purposes (Madsen et al.

2002, Mellinger et al. 2004, Teloni et al. 2008). However, for fishermen, some of these recommendations may be challenging to implement since other parameters shape their fishing timing. For instance, during winter the conditions are rough in these high latitudes, making fishing not always possible for safety reason. Variations of odontocetes occurrence may not only be temporal but also spatial. However, first insights on spatial distribution of interactions revealed that no fishing spots used by fishermen were free of odontocete depredation (Tixier et al. 2010, 2016, Tixier 2012, Labadie et al. 2015, 2018). Besides, as fishermen are in competition with odontocetes, it is more likely that predators already forage naturally within areas with high toothfish densities. First spatial analyses emphasize the necessity to better understand the natural ecology and behaviour of these species as it may help to predict their occurrence on fishing areas. At a finer spatial scale, the effect of the distances travelled by vessels after hauling a longline on the probability to experience interaction on the longline next hauled was also examined to determine the efficacy of “move-on” strategies (Tixier et al. 2015c, Janc et al. 2018). From these studies, fishermen were advised to cover at least 60 km in presence of sperm whale (Janc et al. 2018) and 100 km in presence of killer whales (Tixier et al. 2015c) to avoid new interaction with these species.

Altogether, these results have brought useful insights on the relationship between some fishing practices and interaction/depredation rates of odontocetes. Identifying better fishing practices may work as an easy-to-implement mitigation measures. However, these recommendations may involve changing several fishing practices inconsistent within a fishing strategy. For instance, suggesting to set shorter longlines at deeper depths may be unproductive for fishermen as it would result in spending more time to haul the ropes between the buoys and the anchors than hauling the longline. Thus, further investigations should be conducted at a finer scale exploring optimal fishing strategies made of a combination of fishing practices.

2.1.3. BEHAVIOURAL ECOLOGY OF CAPTAINS

The monitoring of an optimal combination of fishing practices requires assessing the strategies of the decision-makers: the captains. As the operational approach consists to assess whether some fishing practices may influence the probability of interaction with predators, it is therefore essential to assess in a first step whether captains reveal differences of interaction rates. Using the PECHKER dataset (Museum d'Histoire Naturelle de Paris; Martin and Pruvost 2007), I assessed the mean daily interaction rate per trip with killer and/or sperm whales for 22 captains whom had operated on 8 different vessels between January 2008 and July 2015 at Crozet and Kerguelen, represented on Figure 2-1. The daily interaction was estimated as the ratio of longlines hauled in presence of odontocetes and the total number of longlines hauled per day. I then represented the variations mean daily interaction rates per trip for each captain on a given vessel through boxplots (McGill et al. 1978). The boxplots depicted the median with the 25th and 75th percentiles (the two hinges). Also a 95% of confidence interval through was represented (the two whiskers) with the outlying points shown individually (McGill et al. 1978). Captains who performed at least one fishing season (*i.e.* 3 different trips) with a same vessel were kept for the graphic representation to allow median and percentiles estimations. Boxplots were assessed with the function `geom_boxplot` (package `ggplot2`) through the software R (R Development Core Team 2015). Firstly, this exploratory analysis showed on Figure 2-1 that in some cases, different captains working on the same vessel had a similar interaction rate but different to other vessels, *e.g.* between vessels 5 and 8 with sperm whales at Crozet. These differences of interaction rates might be related to vessels' specificities. A hypothesis which will be tested in this thesis is that vessels may have different acoustic signatures and thus different detectability by odontocetes (see section 3.3). Secondly, I also observed on Figure 2-1 inter-captains variability for a same vessel, *e.g.* between captains lighter green, darker green and purple for vessels 5 with sperm whales at Kerguelen. This variability suggests that captains' fishing strategies may involve different interaction rates. The purpose is then to determine what decisions made by captains, and therefore what fishing strategies, may induce or avoid depredation.

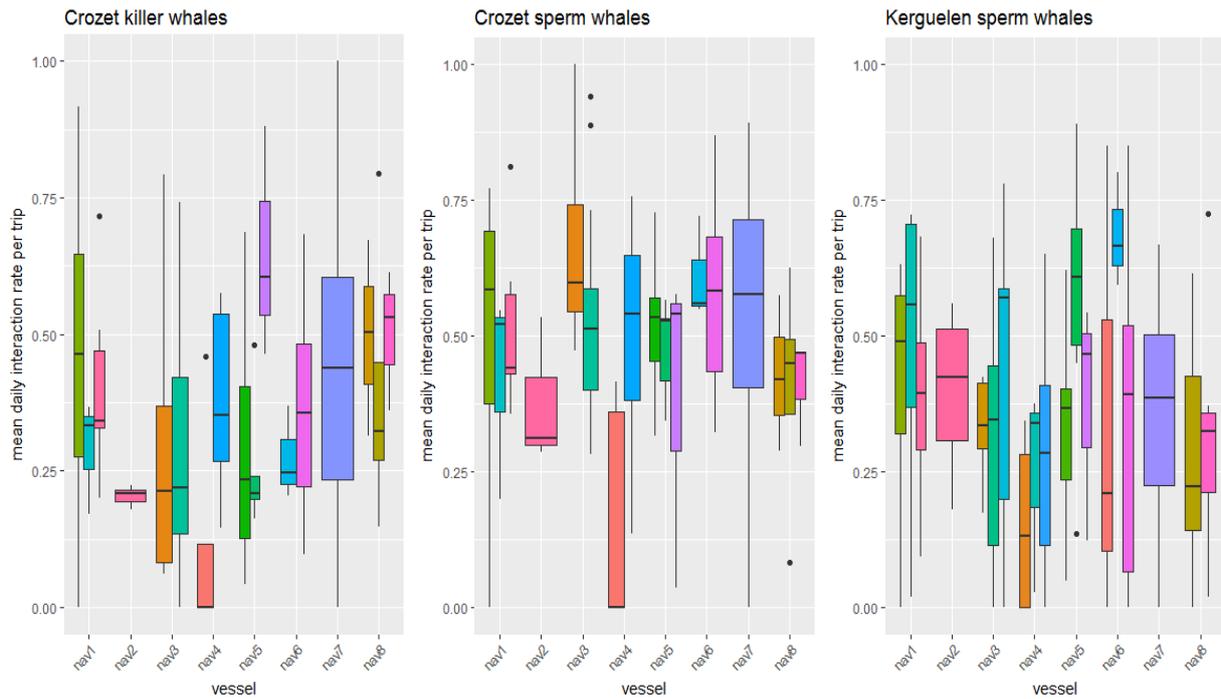


Figure 2-1 – Boxplot of the mean daily interaction rates per trip for every captain (colour) with a given fishing vessels.

Relationships between fishermen and their environment have mostly been assessed through the causalities between the operational factors and fishing success and/or depredation (section 2.1.2). Distinction between fisheries, fishermen and fishing gears has indeed not always been carried out. However, fishermen adapt the operational factors to the environmental conditions, such as the abundance of toothfish or the presence of odontocetes, to optimise their cost-benefit ratio of the fishing practices. Their purpose is thus to maximise their fishing success for a lowest associated costs, for instance gas consumption while navigating. The combinations of these practices define strategies and are more likely to vary between fishermen according to their perception of the environment. Thus, further investigations should focus on the decision makers of the fishing strategies: *i.e.* the captains of the French longliners. I suggested in this thesis to use a behavioural ecology approach to study captains' decisions (Nettle et al. 2013) : *i.e.* the optimal foraging theory (Pyke 1984, Real and Caraco 1986, Kamil 1987, Charnov and Orians 2006, Nettle et al. 2013). According to the optimal foraging marginal value theorem (Charnov 1976) as foragers, captains' decisions should maximise their “energetic” return. As the strategy of the captains is not to feed themselves but rather to fish for their company, the “energy” is in fact “money” in the broad sense (economical value with the fish and cost of

fishing operations). The captains' decisions should then maximise the money return, which is perceived on the fishing boat as an optimisation of the fishing success. During the different stages of the fishing process, captains have choices to make: *i*) while prospecting for the fish resource (*i.e.* setting) and *ii*) when exploiting the resource once found (*i.e.* hauling). The aim of this chapter was therefore to understand captains' decision-makings at these *i*) inter-patch (section 2.2) and *ii*) intra-patch (section 2.3.1) scales within a context of competition with odontocetes. The hypothesis is that they should optimise their prospection and maximise the exploitation of the resource and aim at minimising the competition. An assessment of how depredation impacts captains' behaviours may enable using an optimal strategy as a mitigation solution. This human behavioural approach aimed to modelise captains' decisions with ecological theories independently to captains' feedbacks. In a further stage, captains can provide ground truth to confirm models.

2.2. ARTICLE: DO COMMERCIAL FISHERIES DISPLAY OPTIMAL FORAGING? THE CASE OF LONGLINE FISHERS IN COMPETITION WITH ODONTOCETES

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2.2.1. ABSTRACT

Depredation in longline fisheries by odontocete whales is a worldwide growing issue, having substantial socio-economic consequences for fishers as well as conservation implications for both fish resources and the depredating odontocete populations. An example of this is the demersal longline fishery operating around the Crozet Archipelago and Kerguelen Island, southern Indian Ocean, where killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) depredate hooked Patagonian toothfish (*Dissostichus eleginoides*). It is of great interest to better understand relationships of this modern fishery with its environment. Thus, we examined the factors influencing the decision making process of fishers facing such competition while operating on a patch. Using optimal foraging theory as the underlying hypothesis, we determined that the probability captains left an area decreases with increasing fishing success whereas, in presence of competition from odontocete whales, it increases. Our study provides strong support that fishers behave as optimal foragers in this specific fishery. Considering that captains are optimal foragers and thus aim at maximising the exploitation of the resources, we highlight possible risks for the long-term sustainability of the local ecosystems.

Keywords: cetacean depredation, longline fishery, Patagonian toothfish, optimal foraging theory, fishing strategies

2.2.2. INTRODUCTION

The way humans acquire marine living resources from the environment has become, over the past 60 years, a major field of research (Flaaten et al. 1995, Coleman and Williams 2002, Wezel et al. 2009). While previous efforts have largely been oriented towards improving technology, the processes of decision making and strategy choices have recently received growing attention (Hamer et al. 2012, Holt-Giménez and Altieri 2012, Straley et al. 2015, Tixier et al. 2015c). In commercial fisheries, the increasing difficulty in predicting the variation of a resource abundance and distribution, mostly due to climate change (Simpson et al. 2011, Pinnegar et al. 2016), paired with growing economic competition, makes optimizing strategies challenging for fishers. Indeed, the marine environment is unpredictable and resource evaluation and decision making for fishing activity appear to be difficult (Acheson 1981).

To increase our understanding of fish stocks and their ecosystems, as well as to improve fishing strategies, human ecologists have used the “optimal foraging theory” (OFT) to investigate the behaviour of fishers (McCay 1978, 1981, Begossi 1992, Aswani 1998). The OFT was derived from economic models and has been broadly implemented in studies of animal foraging behaviour to examine various ecological issues as adaptation, competition and energy flow (Pyke 1984, Real and Caraco 1986, Kamil 1987, Charnov and Orians 2006). Within the OFT framework, energy flow is a key component of ecological systems. Fused with natural selection principles, whereby feeding strategies may evolve by natural selection, foragers choose the behavioural option that maximizes energy intake while minimizing costs (Charnov 1976).

Fishers primarily rely on environmental clues, paired with their perception about stock availability, to decide whether to stay or leave a resource patch (Begossi 1992). Consequently, the OFT is useful to predict the movement and decisions of fishers, helping to understand their environment and, more precisely, the resource availability (Aswani 1998). Previous studies focusing on traditional fisheries showed that fishers harness their environment as effectively as possible, which results in a short-term goal of energy maximization, *i.e.* fishing success (Begossi 1992, Aswani 1998). However, this occurs with low concern of the marine environment’s long-term sustainability (Begossi 1992, Aswani 1998).

Modern fishers are confronted with increasing competition and interactions with marine wild predators for the same resources, thus influencing fishers’ strategic choices (DeMaster et al. 2001, Donoghue et al. 2002, Gilman et al. 2006, Read 2008). Odontocetes depredation (*i.e.*, toothed whales removing fish from fishing gear) has been described as the greatest impact on decisions made by fishers (Sivasubramaniam 1964, Dahlheim 1988, Peterson and Carothers 2013). In some fisheries, fishers are forced to modify their fishing behaviour and to implement strategies of avoidance of odontocetes resulting in substantial losses for the fishing industry (Peterson and Carothers 2013, Tixier et al. 2015c, Werner et al. 2015). One example is the Patagonian toothfish (*Dissostichus eleginoides*) demersal longline fishery operating around the Crozet Archipelago and Kerguelen Island, southern Indian Ocean (Tixier et al. 2015c).

Since 2003, interactions with killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) have been reported on > 75% of the longline sets that were hauled around Crozet Archipelago (Roche et al. 2007, Tixier et al. 2010, 2015c). The amount of depredated fishes was estimated to be 30% and 9% of the total catch of Patagonian toothfish at Crozet and

Kerguelen, respectively (Gasco et al. 2015). Such high level of depredation paired with the small size of the fishing fleet (i.e. only 7 licensed 50-metres long longliners) and the long-term full monitoring of the fishery have made the Crozet and Kerguelen situations a unique opportunity to identify solutions to mitigate interactions with odontocetes. Previous studies have resulted in a number of recommendations being made to the fishing industry to avoid/reduce depredation by cetaceans (Hamer et al. 2012, Straley et al. 2015, Tixier et al. 2015c). For instance, one of these recommendations was to move away from patches when depredation occurs and to travel more than 100 km (Tixier et al. 2015c).

However, preliminary analyses of data collected around Kerguelen and Crozet showed that depredation may not be the only factor driving decisions made by fishers. For instance, in some cases fishers may decide to stay on a patch although depredation by killer whales is occurring and, conversely, they may leave and travel between patches when depredation is not reported. These travel phases are costly for the operators because fishers do not catch fish but still incur costs (e.g. fuel and wages). In terms of OFT, the vessel has null energy intake (fishing success) but increasing energy expenditure (fuel) when traveling. At the fishers' scale, these non-fishing phases are also costly since the major part of their salary is based upon the quantity of fish caught during a trip. Fishers have indeed a minimum fixed salary for their whole trip, whether they fish or travel, but if they fish more then they will earn more money. As an analogy with foragers, fishers have a null energy intake (no additional wages) when travelling whereas during fishing phase they have a positive energy intake (additional wages due to fishing success). We therefore hypothesised that fishers should aim to reduce the distances and the time spent travelling between patches to follow an optimal foraging strategy. In the present study, the aim was thus to identify the factors influencing the fishers' decision making process while they are operating on a patch. More specifically, we examined the respective role of fishing success (the daily mass of toothfishes hauled) and the depredation by killer whales and sperm whales on the probability that fishers leave or stay on a given patch. Ultimately, the aim was to determine whether their decision to stay or to leave matches with the OFT predictions.

2.2.3. MATERIAL AND METHODS

2.2.3.1. DATA COLLECTION AND FIELD SITES

From January 2008 to July 2015, 22 captains operating on eight legal longliners (50 m long vessels) hauled 6387 longlines within the Crozet Islands Exclusive Economic Zone (hereinafter EEZ) and 19 480 longlines within the Kerguelen Island EEZ (Figure 2-2). Fishing occurs all year round, and a fishing season spans from September to August. For a given vessel, a fishing season is composed of three trips of 3 months each during which the fish caught are processed, frozen, and stored on board.

For every longline set, fishery observers collected data for resource assessment (*e.g.* such as fish mass) and data about interactions with marine predators. Data were available through the PECHEKER database (Museum d'Histoire Naturelle de Paris; Martin and Pruvost 2007). An interaction was defined as when cetaceans were observed making repeated dives within an approximate 500 m range from the vessel. This was further quantified using three classes: (i) whales absent (condition suitable for a confident observation), (ii) whales present and (iii) uncertain-observation (conditions unsuitable and/or no observation undertaken). Only 9% and 13% of all longlines were assessed as uncertain-observation for killer whales and for sperm whales, respectively. These longlines were kept in the dataset to determine hauling session (see next section) and to estimate fishing success. Since we worked at a scale of several longlines (*cf.* hauling sessions) these uncertain-observation did not skew the estimation of interaction for our unit of analysis. In addition, when longlines were hauled in presence of whales, observers provided an estimation of the minimum and maximum number of individuals interacting with the boat.

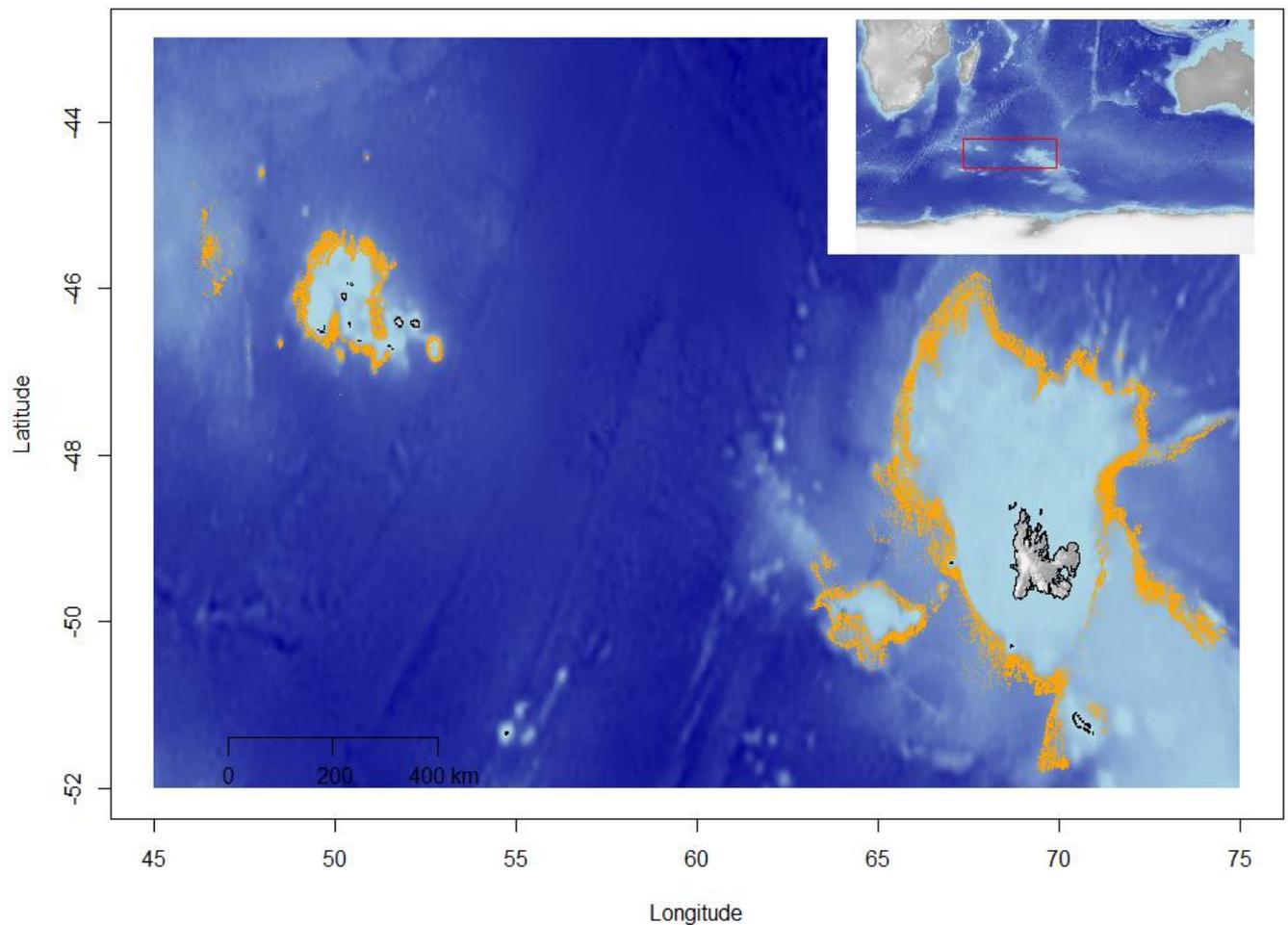


Figure 2-2 - Map of Crozet and Kerguelen Islands, southern Indian Ocean, with fishing efforts, i.e. all longlines, positions (orange). The map was realised with the package *marmap* through the software *R*.

2.2.3.2. DETERMINATION OF HAULING SESSION

Fishers can set longlines only at night to avoid birds' by-catch issues. Such constraint shapes their fishing activity as during the day, they can only haul the longlines. At nighttimes, captains can decide either to carry on hauling longlines or to set new ones. Using this alternation of fishing operations between hauling and setting, we defined a hauling session as a temporal succession of hauled longlines. In other word, a hauling session starts with the first hauled longline after a setting and it ends with the last hauled longline before setting new ones. We defined a longline hauling session carried out by a captain as the unit of analysis for our statistical models (see below). In addition, we only considered hauling sessions with at least 3 longlines to be able to estimate mean values from the dataset, since in statistics a mean could not be obtained from $n < 3$.

From the fishery observer dataset, we assessed for each hauling session the daily mass of toothfish caught ($\text{kg}\cdot\text{day}^{-1}$) and the distance covered at the end of the hauling session (km) before starting setting new longlines. We also recorded whether cetaceans were present during the session, *i.e.* whether cetaceans interacted at least with one recorded longline, and the mean number of individuals present during the session.

2.2.3.3. DEFINITION OF THE DECISION TO STAY OR LEAVE A PATCH

Our purpose was to describe the decision of captains to leave or stay in a patch. Considering that resource could not be clearly spatially defined in the ocean, we determined a ‘patch’ as defined in the optimal foraging theory (OFT). In other words, a patch is a spatial area where fishers are foraging, since a patch of toothfish cannot be determined. We, thus, defined a ‘patch’ as the localization where fishers haul longlines during a hauling session. We then determined whether captains “stay” or “leave” their current patch at the end of a hauling session before setting new lines. To do so, we applied a piecewise regression over the distribution of the distances after hauling sessions to identify a threshold (Toms and Lesperance 2003) defining whether captains leave a patch or not. The same method was applied both in Crozet and in Kerguelen, using the package *SiZer* (Sonderegger et al. 2009) through the software R (R Development Core Team 2015). Thus the threshold determined a variable: ‘stay’ or ‘leave’, for both EEZ. We named this variable ‘*Leave*’ and we set for this variable either 0 if a captain stays or 1 if a captain leaves after a hauling session.

2.2.3.4. MODELLING CAPTAINS’ DECISION TO STAY: GENERALIZED LINEAR MIXED MODEL (GLMM)

We aimed at assessing the relationship between the decision of captains to leave a patch, at the end of a hauling session, and the fishing success paired with competition encountered during this session. Thus, the unit of analysis of our model was a hauling session. The fishing success was expressed as the daily mass of toothfish caught per hauling session ($\text{kg}\cdot\text{day}^{-1}$) within a patch. This proxy of the fishing success was chosen as it is the metric used by captains to determine if they have reached the daily economic threshold (between 2 and 3 tons $\cdot\text{day}^{-1}$) and to assess the progress on their allocated fishing quota. The competition is a categorical variable, defined by the occurrence of cetaceans. Four categories were considered: presence of

killer whales only, presence of sperm whales only, presence of both species simultaneously, or absence of cetacean (set as the reference category). We also assessed the effect of the interaction between both predictive variables: fishing success and competition. Captains were considered as a random effect to investigate variations of decision between them. The variables were identified to translate our hypothesis to a statistical model (Johnson and Omland 2004). However, we could not use a simple linear model since the variable *Leave* follows a Bernoulli distribution, with a probability π to take the value 1 (leave) and the probability $1-\pi$ to take the value 0 (stay). As a result, we used a generalized linear mixed model: GLMM (Zuur 2009). We thus investigated the relationship between the probability to leave for a captain at the end of a hauling session (π) with the fishing success and the competition, using the link function *logit*, which is the canonical link for a Bernoulli distribution (Zuur 2009):

$$\text{EQUATION 2-2: } \text{logit}(\pi_{ij}) = \alpha + a_j + (\beta_1 + b_j)\text{Fishing success}_{ij} + \beta_2\text{Competition}_{ij} \\ + \beta_3\text{Fishing success}_{ij} \times \text{Competition}_{ij} + \varepsilon_{ij}$$

with π_{ij} the probability that a captain j leaves a hauling session i , α the intercept, a_j the random intercept for captain j , $\beta_{1,2,3}$ the coefficients of the predictive variables, b_j the random effect for captain j on the slope of fishing success and ε_{ij} the residual for hauling session i and captain j . Besides, using a top-down approach (Zuur 2009), we assessed first the most complex model, *i.e.* with the interaction between the two predictive variables and the random effect (captain j) set both on the intercept (α) and on the slope (β_1) of the continuous variable (fishing success). Then, we determined whether the random effect should be applied only on the intercept ($a_j \neq 0$ and $b_j = 0$) through the Akaike Information Criterion (AIC) selection (Akaike 1974, Zuur 2009). Because *Competition* is a categorical variable, no slope could be applied, so we did not assess a random effect on β_2 and β_3 . Once the random effect was determined, we removed the non-significant variables to select the best model, through the AIC selection, in agreement with the top-down approach. We also compared our models to the null model ($\text{logit}(\pi_{ij}) = \alpha$), using the AIC, to be able to interpret the results. The statistical model was implemented through the software R with the function *glmer* (package *lme4*).

Based on the assumption that the random effect for each captain j (b_j) on the slope of the fishing success (β_1) is significant, we assessed the variability of decision for each captain to stay or leave a ground between both EEZs. We aimed at comparing the slopes of each captain's relationship between the probability to leave an area and fishing success ($\beta_1 + b_j$) both at Crozet and Kerguelen. Thus, we assessed a linear regression between these slopes at Crozet and at

Kerguelen. To get sufficient number of sessions for each captain on both locations, we considered only captains who spent more than 2 seasons both at Crozet and Kerguelen, resulting in 14 captains. This may enlighten some between-captain variability of decision, according to the fishing area (EEZ).

In addition, we assessed a similar model using the mean number (Nb) of cetaceans present per longline within hauling sessions for killer whales alone, sperm whales alone, or both species simultaneously, instead of the categorical variable ‘*Competition*’:

$$\text{EQUATION 2-3: } \text{logit}(\pi_{ij}) = \alpha + a_j + (\beta_1 + b_j)\text{Fishing success}_{ij} + (\beta_2 + c_j)\text{Nb individuals}_{ij} \\ + (\beta_3 + d_j)\text{Fishing success}_{ij} \times \text{Nb individuals}_{ij} + \varepsilon_{ij}$$

with c_j and d_j the random effects for captain j on the slope of the number of individuals and on the slope of the interaction between the two predictive variables. All continuous variables were standardized. We used again a top-down approach to select the best model, using the AIC.

2.2.3.5. DESCRIPTION OF A FISHING SUCCESS’ THRESHOLD FOR CAPTAINS’ DECISION

Finally we monitored the distributions of the fishing success ($\text{kg} \cdot \text{day}^{-1}$) among hauling sessions for both cases when captains decide to “stay” and “leave” after the session. The purpose was to compare between the two decisions’ cases: how the number of sessions evolve with the increase of the daily mass of toothfish caught. We could then determine for which values of fishing success we have more sessions followed by the decision to stay or by the decision to leave. We thus fitted smoothing splines to both distributions of fishing success (sessions followed by a decision to stay and by the decision to leave), using the function *smooth.spline* (package *stats*) through the software R, with a smoothing coefficient of 0.5 to keep at least 50% of the variation. As a result, the intersection between both smoothed distributions approximates the threshold mass of toothfish caught per day at which captains change their decision to stay or leave. Indeed, below the threshold captains may decide to leave their patch. Conversely, above this threshold they may stay on the current patch.

Besides, within the assumption that we would obtain significant interactions between the predictive variables: fishing success and the presence of cetaceans, either as a categorical variable (*Competition*) or as a continuous variable (*Nb individuals*), we could determine a

threshold of fishing success above which the cetaceans' influence might become ineffective. To define this threshold, we resolve the equation determining a constant probability to leave irrespective of the competition/number of individuals:

$$\text{EQUATION 2-4: } a + \beta_1 \text{Fishing success} + \beta_2 (\text{Competition or Nb individuals}) + \beta_3 \text{Fishing success} \times (\text{Competition or Nb individuals}) + \varepsilon = \text{constant}$$

Since only the number of cetaceans can vary, we aimed at resolving:

$$\Leftrightarrow (\beta_2 + \beta_3 \text{Fishing success}) \times (\text{Competition or Nb individuals}) = \text{constant}$$

$$\Leftrightarrow \beta_2 + \beta_3 \text{Fishing success} = 0$$

2.2.4. RESULTS

2.2.4.1. HAULING SESSIONS

Data used in this study included 1,241 hauling sessions within the Crozet EEZ and 4,302 hauling sessions within the Kerguelen EEZ (Figure 2-3 and Supp. data 1).

The competition at Crozet was considered either in presence of killer whales alone, in presence of sperm whales alone, or in presence of both species simultaneously (Figure 2-3 & Supp. data 1). At Kerguelen, we only considered sessions with sperm whales alone, since the number of sessions in presence of killer whales only (6) and the number of sessions in presence of both species simultaneously (19) were both too small to conduct statistical analyses (Figure 2-3 & Supp. data 1).

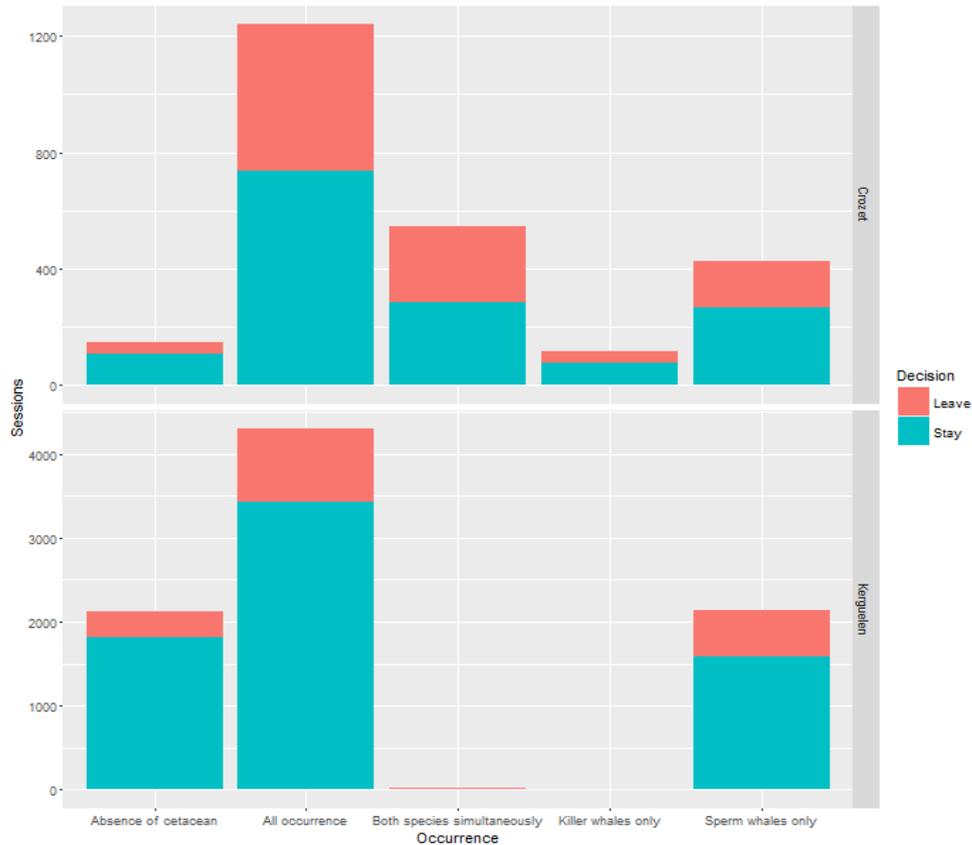


Figure 2-3 - Number of sessions in both EEZs with decision to stay or leave, in absence of cetacean, or in presence of cetaceans (each species alone or both simultaneously).

2.2.4.2. DEFINITION OF THE DECISION TO STAY OR LEAVE A PATCH

We defined through the breaks on the piecewise regression that a captain covering less than 36 km in Crozet and less than 35 km in Kerguelen after a hauling session stayed on the same patch (Figure 2-4). According to this threshold, 737 and 3,430 hauling sessions, respectively at Crozet and Kerguelen, were followed by a decision to stay. Conversely, 504 and 872 hauling sessions (respectively at Crozet and Kerguelen) were followed by a decision to leave (Figure 2-3 & Supp. data 1).

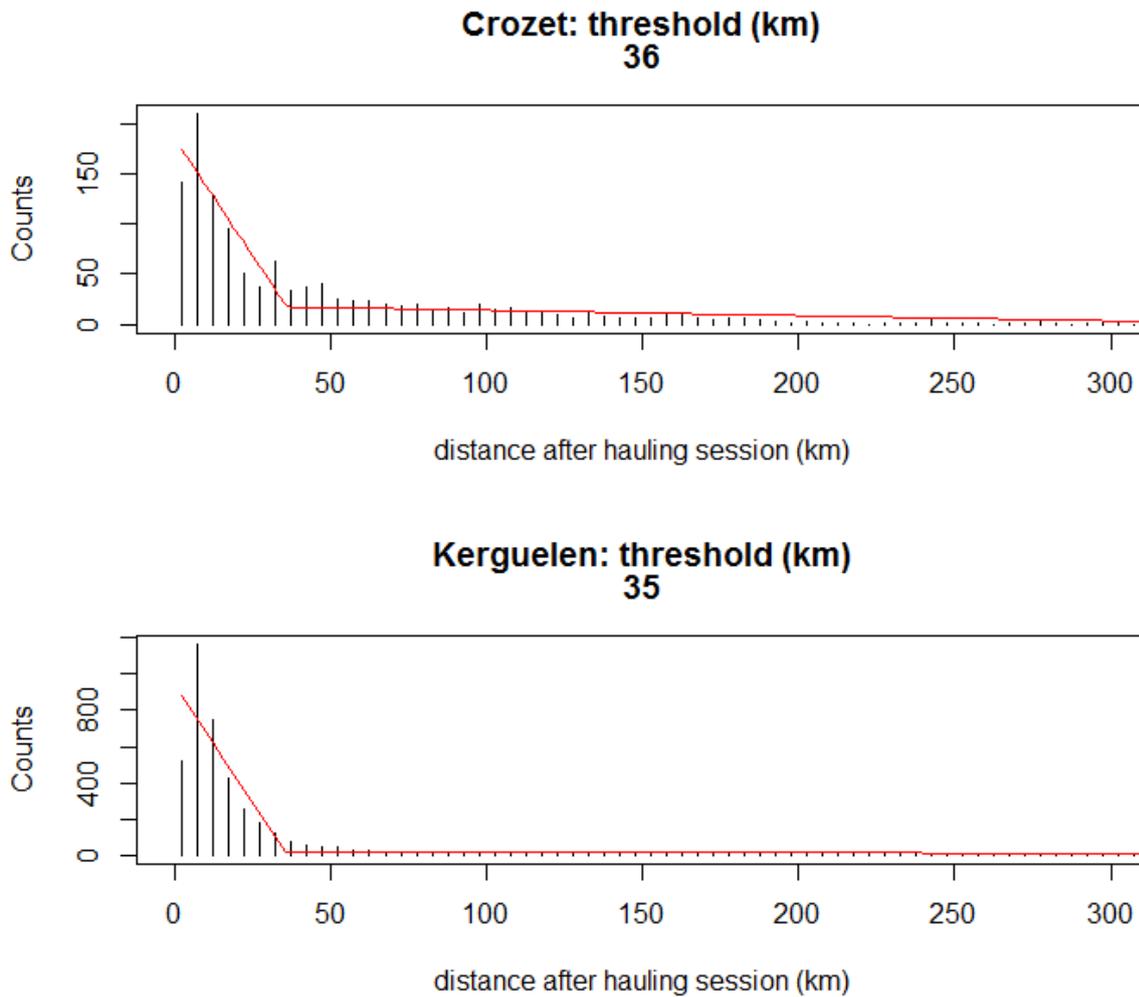


Figure 2-4 - Distributions of the distance after hauling sessions with piecewise regressions fitted to determine the distance threshold to consider a vessel 'leaving' in Crozet and Kerguelen.

2.2.4.3. MODELLING CAPTAINS' DECISION TO STAY: GENERALIZED LINEAR MIXED MODEL (GLMM)

According to the AIC selection (Supp. data 2), all models explaining the probability for captains to leave were better than the null model. The best model for both the Crozet and Kerguelen EEZ excluded the interaction between the fishing success and the competition (Supp. data 2), but included a random effect on both the slope of the fishing success ($\beta_1 + b_j$) and the intercept ($\alpha + a_j$):

$$\text{EQUATION 2-5: } \text{logit}(\pi_{ij}) = \alpha + a_j + (\beta_1 + b_j)\text{Fishing success}_{ij} + \beta_2\text{Competition}_{ij} + \varepsilon_{ij}$$

The probability to leave, π_{ij} , in absence of cetacean decreased significantly when fishing success increased both at Crozet ($z = -6.49$, $p < 0.001$, Figure 2-5.a & Table 2-1) and at Kerguelen ($z = -8.00$, $p < 0.001$, Figure 2-5.b & Table 2-1). This correlation was independent from cetacean depredation as the interaction term was not significant (Table 2-1).

In absence of cetaceans, high between-captains variability was detected on the probability to leave in response to the variation of the fishing success (Figure 2-5 & Table 2-1), both at Crozet (Figure 2-5.a) and Kerguelen (Figure 2-5.b.). As a result, for the 14 captains who spent more than 2 seasons both at Crozet and Kerguelen, we obtained a correlation of 0.74 between the slopes ($\beta_1 + b_j$) at Crozet and at Kerguelen, (Pearson's test: $t = 3.79$, $p = 0.003$, Figure 2-6). This indicates that captains with the greater negative slope of their probability to leave with a given increase of fishing success at Crozet were the same at Kerguelen (Figure 2-6).

Nevertheless, for a given fishing success, all captains showed a higher probability to leave in presence of cetaceans than in absence of interaction, regardless of the species encountered (Figure 2-5 & Table 2-1). For a given foraging success, the probability that captains leave a patch in the Crozet EEZ was 1.6 times higher in presence of both cetacean species than in absence of cetacean ($z = 3.16$, $p = 0.002$, Figure 2-5.a. & Table 2-1). Similarly, when sperm whales were the only depredating species, the probability of captains to leave a patch was nearly 1.5 times higher than the probability to leave in absence of cetacean both at Crozet ($z = 2.10$, $p = 0.04$, Figure 2-5.a. & Table 2-1) and at Kerguelen ($z = 6.06$, $p < 0.001$, Figure 2-5.b. & Table 2-1). At Crozet, the probability of captains to leave when killer whales were the only depredating species was 1.2 times higher than in absence of cetacean (Figure 2-5.a.). Although this difference was not significant ($z = 1.03$, $p = 0.3$, Table 2-1).

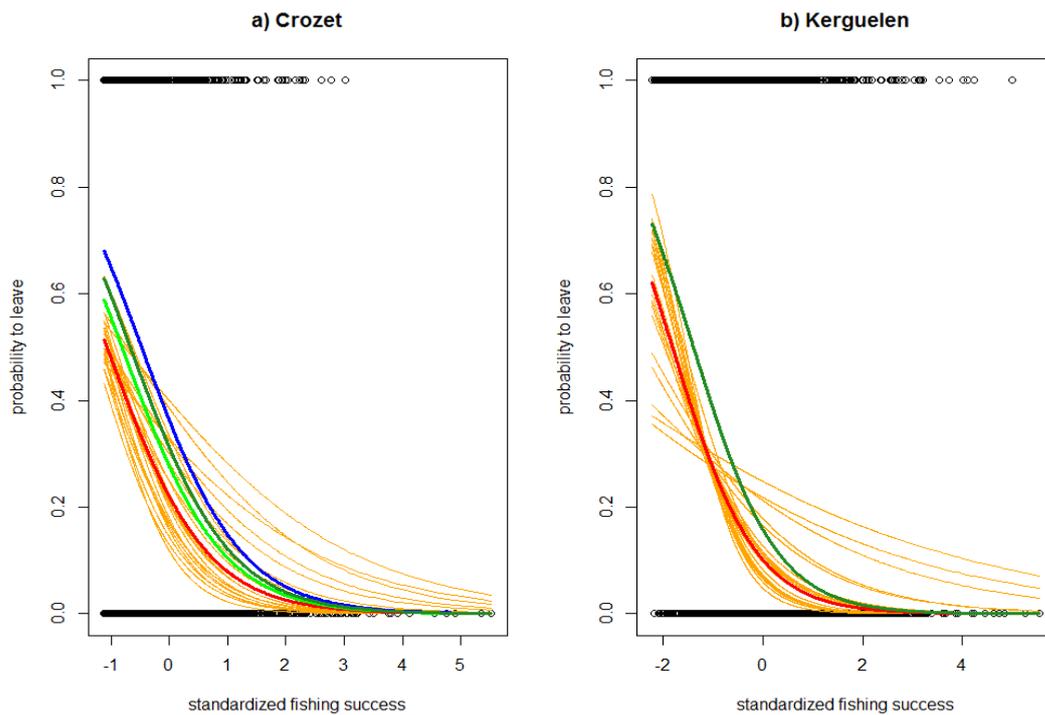


Figure 2-5 - Probabilities to leave for captains, π , in response to the variation of the standardized toothfish mass caught per day and the competition variable, with the variability between captains in orange (Table 2-1). The probability to leave in absence of cetaceans is represented in red, in the presence of killer whales only in light green, in the presence of sperm whales in dark green, and in the presence of both species simultaneously in blue.

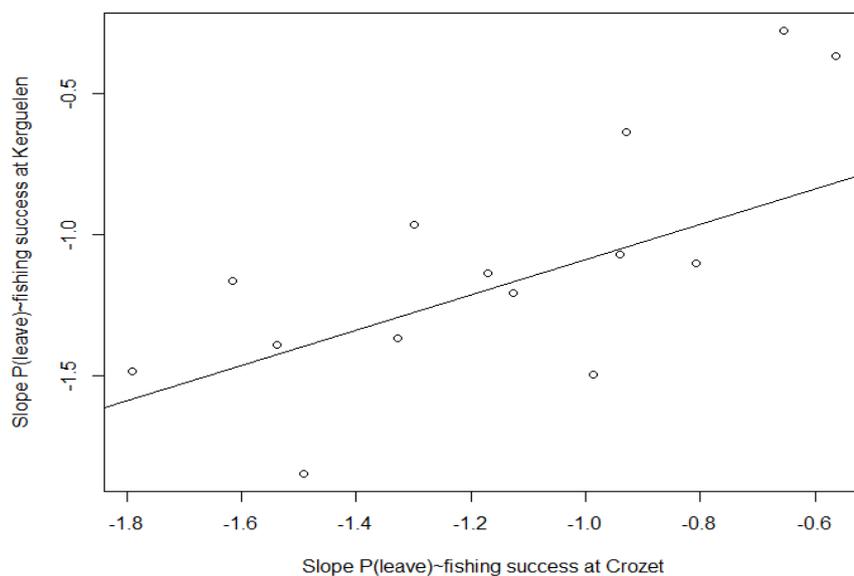


Figure 2-6 - Linear regression between the slope ($\beta_1 + \beta_j$) of the probability to leave as a function of the fishing success at Crozet and the one at Kerguelen for each captain j ($R^2=0.54$). We considered only captains who spent more than 2 seasons both at Crozet and Kerguelen.

Table 2-1 - Results of the GLMMs of the probability to leave for a captain in relation to the fishing success and the competition, with “absence” as the baseline, and random effects were set between captains (intercept) and on the daily weight of toothfish caught (slope).

	Parameter	Value	SE	z-value	p-value
	<i>Intercept</i>	-1.26	0.24	-5.17	<0.001
CROZET					
<i>N=1241</i>	<i>Fishing success</i>	-1.18	0.18	-6.49	<0.001
<i>Random effects:</i>					
<i>Intercept's variance=0.33</i>	<i>Presence of both species</i>	0.70	0.22	3.16	0.002
<i>Slope's variance=0.23</i>	<i>Presence of killer whales only</i>	0.30	0.29	1.03	0.30
	<i>Presence of sperm whales only</i>	0.47	0.22	2.10	0.04
KERGUELEN					
<i>N=4277</i>	<i>Intercept</i>	-2.19	0.17	-13.24	<0.001
<i>Random effects:</i>	<i>Fishing success</i>	-1.20	0.15	-8.00	<0.001
<i>Intercept's variance=0.36</i>	<i>Presence of sperm whales only</i>	0.51	0.08	6.06	<0.001
<i>Slope's variance=0.31</i>					

According to the AIC selection, the best model explaining the probability for captains to leave in relation to the daily mass of toothfish caught and the mean number of cetaceans (regardless of the species at Crozet) included the interaction between the two predictive variables as well as the random effect on both the slope and the intercept (Supp. data 3):

$$\text{EQUATION 2-6: } \text{logit}(\pi_{ij}) = \alpha + a_j + (\beta_1 + b_j) \text{Fishing success}_{ij} + \beta_2 \text{Nb cetaceans}_{ij} + \beta_3 \text{Fishing success}_{ij} \times \text{Nb cetaceans}_{ij} + \varepsilon_{ij}$$

For the model assessing the number of killer whales (at Crozet), the best model was the simplest model (*i.e.* no interaction and the random effect on the intercept, see Supp. data 3):

$$\text{EQUATION 2-7: } \text{logit}(\pi_{ij}) = \alpha + a_j + \beta_1 \text{Fishing success}_{ij} + \beta_2 \text{Nb killer whales}_{ij} + \varepsilon_{ij}$$

Finally, the best model assessing the probability to leave with the fishing success and the number of sperm whales alone excluded interaction between predictive variables, and it included a random effect over the slope of the number of individuals at Crozet (Supp. data 3):

$$\text{EQUATION 2-8: } \text{logit}(\pi_{ij}) = \alpha + a_j + \beta_1 \text{Fishing success}_{ij} + (\beta_2 + c_j) \text{Nb sperm whales}_{ij} + \varepsilon_{ij}$$

whereas at Kerguelen the random effect was obtained over the slope of the fishing success (Supp. data 3):

$$\text{EQUATION 2-9: } \text{logit}(\pi_{ij}) = \alpha + a_j + (\beta_1 + b_j) \text{Fishing success}_{ij} + \beta_2 \text{Nb sperm whales}_{ij} + \varepsilon_{ij}$$

The fishing success had a significant negative effect on the probability of captains to leave, for all the models (Table 2-2). In addition, for a given fishing success, the probability to leave was significantly and positively influenced by the number of cetaceans, regardless of the species (Figure 2-7.a. & Table 2-2). In addition, high between-captain variability in the probability to leave an area in response to the variation in fishing success was detected (Figure 2-7.a. & Table 2-2). The same positive and significant relationship was obtained between the probability of captains to leave and the number of sperm whales alone, both at Crozet (Figure 2-8.a. & Table 2-2) and at Kerguelen (Figure 2-8.b. & Table 2-2). At Kerguelen, high between-captain variability (*i.e.* random effect) in the probability to leave was observed upon the response to the fishing success in presence of sperm whales (Figure 2-8.b. & Table 2-2). Conversely, at Crozet, the between-captain variability (*i.e.* random effect) in the probability to leave was observed on the response to the number of sperm whales (Figure 2-8.a. & Table 2-2).

For the sessions with only killer whales, the correlation between the probability of captains to leave and the number of killer whales was positive but not significant ($z=1.75$, $p=0.08$, Figure 2-9. & Table 2-2).

In addition, when considering any of the two cetacean species, the interaction term between the two explanatory variables (daily mass of toothfish caught and number of cetaceans) was negative and significant ($z=-2.39$, $p=0.02$, Table 2-2, Figure 2-7 b & c). The slope of the relationship between the daily mass of fish caught and the probability to leave decreased when the number of cetaceans increased (Figure 2-7.b.). This result suggests that when the fishing success increased in presence of a high number of cetaceans, the probability to leave decreased at a faster rate than when the fishing success increased with a few cetaceans interacting (Figure 2-7.b.). Conversely, the slope of the relationship between the number of cetaceans and the probability to leave decreased when the daily mass of fish caught increased (Figure 2-7.c.). Besides, this relationship changed from positive to negative for a given toothfish daily mass (Figure 2-7.c., see following section for the threshold determination).

2. FISHERMEN ECOLOGY

Table 2-2 - Results of the GLMMs of the probability to leave in relation to daily weight of toothfish caught (fishing success) and the number of individuals for the different cetaceans' occurrence possible (both species, killer whales alone and sperm whales alone), with random effects set between the captains and in some models on the slope (according to the model selection based upon the AIC).

Localisation	Occurrence	Parameter	Value	SE	z-value	p-value
CROZET	Cetaceans N=790	<i>Intercept</i>	-0.64	0.20	-3.24	0.001
	<i>Random effects:</i> <i>Intercept's variance=0.42</i>	<i>Fishing success</i>	-1.21	0.25	-4.85	<0.001
	<i>Fishing success</i> <i>variance=0.56</i>	<i>Number of cetaceans</i>	0.21	0.09	2.27	0.02
		<i>Interaction</i> <i>fishing success x nb</i> <i>cetaceans</i>	-0.25	0.11	-2.39	0.02
	Killer whales N=78	<i>Intercept</i>	-1.04	0.29	-3.62	<0.001
	<i>Random effects:</i> <i>Intercept's variance=0</i>	<i>Fishing success</i>	-0.80	0.36	-2.21	0.03
		<i>Number of killer whales</i>	0.46	0.26	1.75	0.08
	Sperm whales N=457	<i>Intercept</i>	-0.77	0.16	-4.68	<0.001
	<i>Random effects:</i> <i>Intercept's variance=0.11</i> <i>Nb ind variance=0.17</i>	<i>Fishing success</i>	-0.64	0.13	-4.92	<0.001
		<i>Number of sperm whales</i>	0.54	0.18	2.99	0.003
KERGUELEN	Sperm whales N=3126	<i>Intercept</i>	-1.78	0.14	-12.58	<0.001
	<i>Random effects:</i> <i>Intercept's variance=0.24</i>	<i>Fishing success</i>	-1.07	0.14	-7.44	<0.001
	<i>Fishing success</i> <i>variance=0.23</i>	<i>Number of sperm whales</i>	0.40	0.05	8.78	<0.001

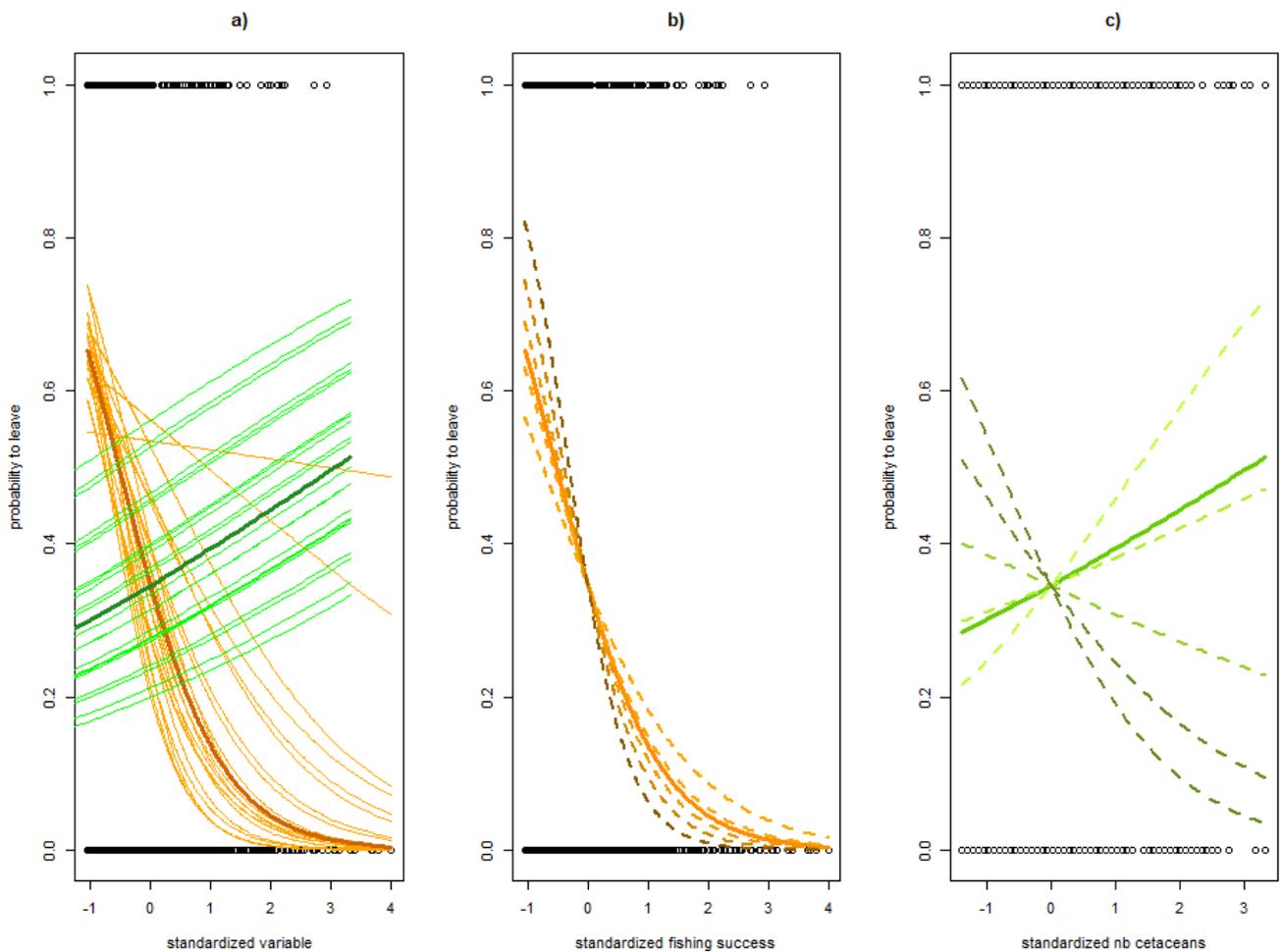


Figure 2-7 - a) Probability to leave a ground for captains, π , at Crozet in response to the variation of the standardized fishing success (orange) and the standardized number of cetaceans (green). Lighter thin lines represent captains' probabilities to leave on the left box. b&c) Dashed lines represent the interaction results (see Table 2-2), showing the probabilities to leave a ground as a function of one of the two standardized variable, and the color's gradients of dashed lines from light to dark represent variation of the other variable from minimum value to maximum value. b) The lightest orange dashed lines represent the probability to leave a ground as a function of fishing success the minimum number of cetaceans (i.e. in absence), and the darkest orange dashed line for the maximum number of cetaceans (i.e. 29 individuals). c) The lightest green dashed lines represent the probability to leave a ground as a function of the number of cetaceans for the minimum fishing success (i.e. a null success), and the darkest green dashed line for the maximum fishing success (i.e. 15650 kg).

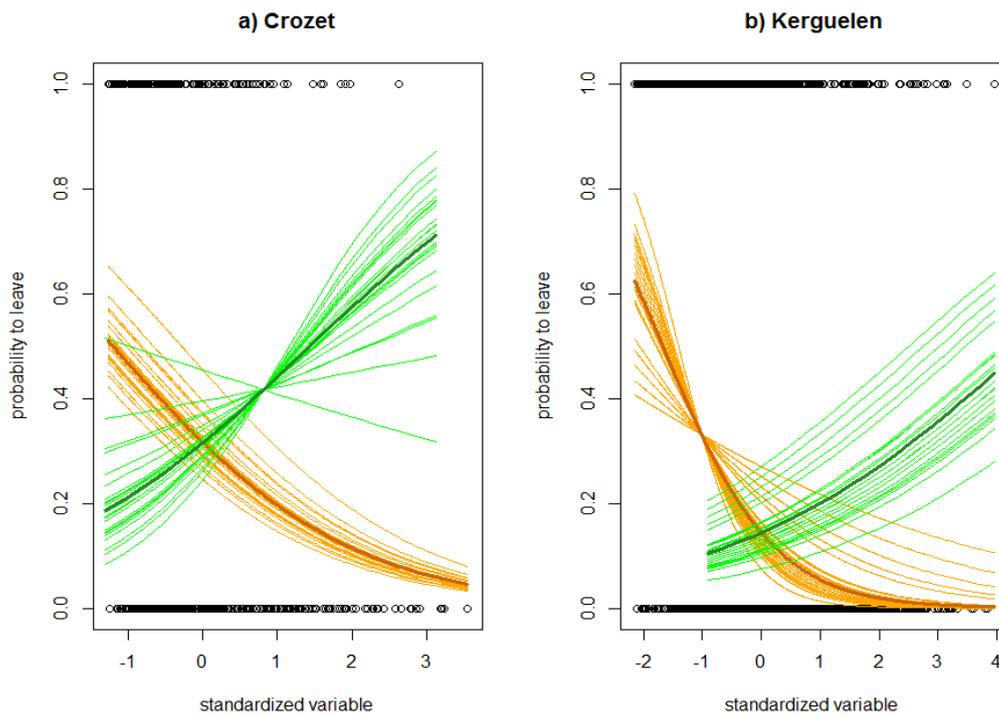


Figure 2-8 - Probabilities to leave a ground, π , at Crozet (a) and at Kerguelen (b) in response to the variation of the standardized fishing success (orange) and the standardized number of sperm whales (green). Lighter thin lines represent variability between captains (see Table 2-2).

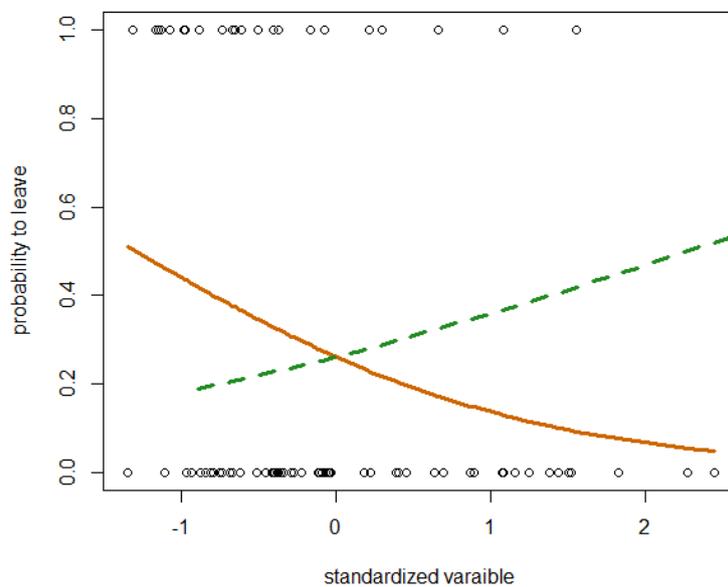


Figure 2-9 - Probability to leave a ground, π , at Crozet in response to the variation of the standardized fishing success (orange) and the standardized number of killer whales (green), (Table 2-2). The dashed line represents non-significant relationship (see Table 2-2).

2.2.4.4. DESCRIPTION OF A FISHING SUCCESS' THRESHOLD FOR CAPTAINS' DECISION

By assessing the intersection between smoothed distributions of the fishing success, for both hauling sessions followed by a decision to stay and sessions followed by a decision to leave, we obtained a threshold of approximately $500\text{kg}\cdot\text{day}^{-1}$ at Crozet (Figure 2-10.a) and $2,700\text{kg}\cdot\text{day}^{-1}$ at Kerguelen (Figure 2-10.b). These results suggest that below these mean thresholds, captains were more likely to leave their patch.

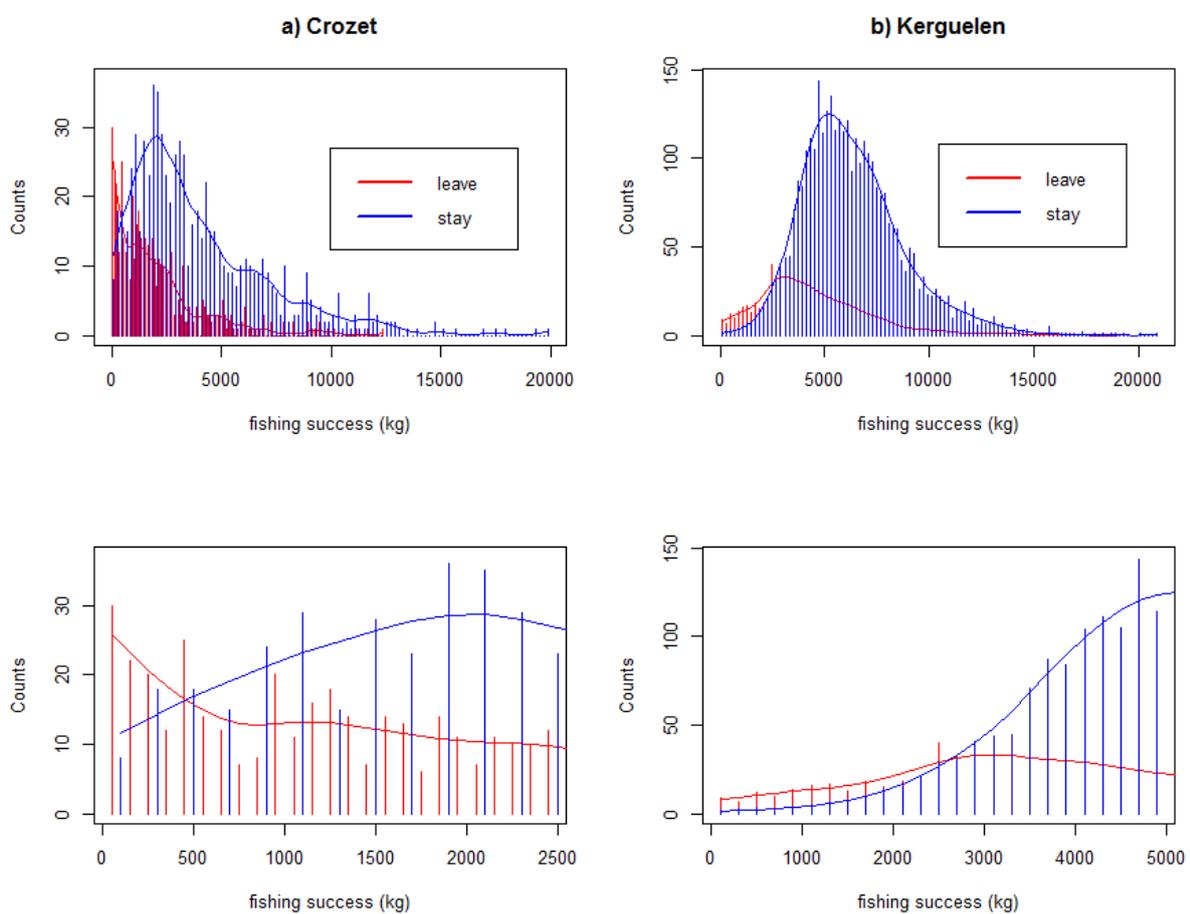


Figure 2-10 - Distributions of the weight of toothfish caught per day for every session, both at Crozet (a) and Kerguelen (b), followed both by a decision to stay (light grey) and by a decision to leave (black), with smoothing splines (coefficient=0.5). On the top we represented the global distributions and on the bottom we showed a zoom of the first values, allowing us to assess the threshold of the fishing success determining the captains' decision to stay or leave.

These values allowed for the determination of the mean fishing success regardless of the competition, which defined the global captains' decision to stay or leave, either at Crozet or at Kerguelen. Using the significant coefficient of the interaction term between the fishing success and the number of cetaceans in the GLMM, we estimated the threshold of fishing success above which the competition did not positively influence the decision to leave anymore (Figure 2-7.c.). To define this threshold, we resolved the equation determining a constant probability to leave irrespective of the number of cetaceans:

$$\text{EQUATION 2-10: } (\beta_2 + \beta_3 \text{Fishing success}) \text{Nb cetaceans} = \text{constant}$$

$$\Leftrightarrow \beta_2 + \beta_3 \text{Fishing success} = 0$$

$$\Leftrightarrow 0.21 - 0.25 \times \text{Fishing success standardized} = 0$$

$$\Leftrightarrow \text{Fishing success standardized} = 0.84$$

$$\Leftrightarrow \text{Fishing success} = 5866 \text{ kg.day}^{-1}$$

As a result, we observed that the probability to leave a patch decreased when the number of cetaceans increased for masses of toothfish caught per day above 5866 kg.day^{-1} (Figure 2-7.c).

2.2.5. DISCUSSION

2.2.5.1. ARE FISHERS OPTIMAL FORAGERS?

Using OFT, we were able to describe the decision process of longline fishing vessel captains. Our results provided strong support for the assumption that captains act as optimal foragers during fishing operations. We highlighted that decisions made by captains to stay or leave a patch were primarily driven by their fishing success, which is analogous to foraging success in OFT, but was also influenced by cetacean depredation.

Influence of fishing success

Our study showed that fishing success clearly stood as the main driver of the decision of captains to stay or leave a patch, both at Kerguelen and at Crozet, for any level of competition with cetaceans. Daily thresholds of 500 kg and 2,700 kg were suggested as driving the decision of captains to leave a patch at Crozet and at Kerguelen, respectively, *i.e.* below these masses of toothfish caught during a day, fishers were more likely to leave for another patch. In addition, in the presence of cetaceans, we showed a threshold effect of the fishing success upon the relationship between the number of cetaceans and the decision to stay. From our results, the number of cetaceans had no influence on the captain's probability to leave a fishing area if the fishing success was higher than 5,866 kg of fish caught per day.

Decision making by fishers around Crozet and Kerguelen may reflect a passive adaptive strategy as defined by Clark (1985), since fishers rely on the constantly updated information provided by the patch to decide whether to leave it or not. Such strategy has been reported to be also used by fishers in more traditional fisheries, resulting in an optimal use of foraging patches (Begossi 1992, Aswani 1998). This behaviour of optimal foraging has to be contrasted with a long-term sustainable strategy of the resource.

Maximizing catch rates by staying in a locally productive fishing area may be explained by a combination of factors involving both the socio-economic constraints of the fishing activity and the difficulty to find the fish. Vessels allowed operating in the Crozet and Kerguelen EEZs are subject to annual quotas, which are the highest of all Patagonian toothfish fisheries of the Southern Ocean (*e.g.*, 6,300 tonnes shared between the 7 licensed vessels in 2015-2016). The full completion of quotas during a given season ensures the economic viability of the fishing companies, and also demonstrates the capacity of these companies to complete their quotas, which is used to determine the quotas of the following season. In addition, fishery regulations, which are partly defined by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), restrict access to EEZs for a portion of the year and impose both fishing time limits (in days) to local patches within EEZs and minimum fish size policies.

Paired with the costs of fishing operations (fuel, gear, food, crew salaries), the toughness of fishing conditions and the remoteness of the fishing areas (on average vessels spend 3 consecutive months at sea before returning to port, with 7 days steaming each way from Reunion island), these socio-economic constraints lead captains to favour a short-term and local

catch rate maximization strategy when finding a productive fishing area meeting all regulations. This strategy may be further enforced by the specific difficulty to find productive fishing areas since Patagonian toothfish lack a gas-filled swimbladder and detection of fishable numbers can be difficult (Foote 1980). In addition, the quota allocation between the two localisations is asymmetric: 90% of the quota is set at Kerguelen and the 10% remaining is done at Crozet, and the Kerguelen fishing area is substantially greater than the Crozet fishing area. These features may explain the differences of daily mass threshold (500kg at Crozet and 2700kg at Kerguelen) driving the decisions made by captains. As more fishing effort is required at Kerguelen, captains may seek more productive areas in Kerguelen than in Crozet. Consequently, for captains, a given fishing success may be acceptable in Crozet but not in Kerguelen.

Influence of cetacean depredation

Although fishing success was found to be the primary driver of decisions by captains, the present study also showed the importance of cetacean depredation on the probability of fishers to stay on or to leave patches. For a given fishing success (*i.e.* the same mass of fish caught per day), captains were more likely to leave a patch when depredation occurred and when the number of depredating individuals increased. The number of depredating individuals also influenced the rate at which decisions were made: captains took the decision to leave sooner as the number of cetaceans increased. These results highlight the fishers' perception of both sperm whales and killer whales as competitors and, similarly to the findings of Goldstone et al. (2005), fishers react to competition by avoidance.

The competition effects of cetaceans underlined in our study is line with previous studies assessing the impact of cetacean interactions on the fishing success of fishers. In Crozet, killer whales and sperm whales were found to be responsible for the removal of 30% of the total catch of toothfish between 2003-2013, whether the two species interacted alone or simultaneously with vessels (Gasco et al. 2015). However, killer whales are likely to be considered by fishers as a more serious competitor than sperm whales, since the biomass loss when killer whales depredate alone has been estimated to be twice the biomass loss when sperm whales depredate alone (Gasco et al. 2015). In addition, our results suggested that the number of both depredating sperm whales and killer whales may positively influence the probability of captains to leave a fishing area. However, for killer whales alone, this relationship, which was based on a small

sample size ($n = 78$ fishing sessions), was only close to significance in the models. An increased number of depredating killer whales and sperm whales was shown to result in increased amount of depredated fish (Gasco, 2013) and is, therefore, likely to increase the probability of fishers to leave.

Factors explaining between-captain variability

Our result emphasized high between-captain variability in the probability to leave an area, either as a response to the fishing success or as a response to the competition with cetaceans. In addition, between-EEZs variability per captain of the probability to leave a ground as a response to the fishing success was low, which suggests that captains are consistent in their decision to leave a ground according to a same variation of fishing success wherever they fish. Together, these results underlie the importance of individual captain personalities over their decision to stay or leave a patch. We observed that the probabilities to leave a fishing area varied differently between captains according to their fishing success, suggesting differences either in fishing strategies or in perception about what is an acceptable level of fishing success. Within the context of OFT strategies, captains may play upon different technical variables, such as the number of hooks set, the setting depth, the soaking time, the hauling speed and so on. Nevertheless, differences in quotas between vessels may lead to differences in captains' decision making. For instance, during the season 2014-2015, quotas varied between the seven fishing vessels from 100 to 140 tonnes at Crozet and from 630 to 820 tonnes at Kerguelen (French Antarctic and Austral Territories Prefectural Decree n° 2014-76).

Differences in experience may also play a role in the variation of decision making between captains, either in response to a decrease of fishing efficiency or to the presence of cetaceans. We assume that more experienced captains may know how to react to both situations. While facing competition, some captains may indeed try to adapt their fishing techniques in presence of cetaceans. They can increase hauling speed or shorten longline length in order to limit the depredation rate both by killer whales (Tixier et al. 2015c) and by sperm whales (Janc et al. 2018). We may thus assume that fishers who successfully limit the competitive effect of cetaceans may be less sensitive to them. Conversely, less experienced captains who face depredation for the first time may react differently than more experienced captains.

Species may also be a factor determining differences of decision making between captains. Killer whale depredation is more obvious for fishers than sperm whale depredation, as killer whales leave some fish remains on longline. In addition, killer whales are usually observed depredating in larger groups than sperm whales, even though killer whales interact less with vessels than sperm whales. These differences of depredation perception by fishers may make killer whales more annoying to them (Gasco 2013). Furthermore, since killer whales cause greater fish losses than sperm whales, it could explain the null between-captains variability in the decisions when confronted with depredation by killer whales alone compared to the variability observed when confronted with sperm whale depredation alone.

Captains may be differently sensitive to the presence of sperm whales, as we observed high variability of decision between captains in our models while facing sperm whales competition. In addition to lower losses caused by sperm whales, previous studies have shown that sperm whales are naturally distributed on highly productive patches (Tixier 2012, Gasco 2013). Unlike killer whales, for which it is still not clear whether they naturally feed on Patagonian toothfish, the latter has been confirmed as an important prey item of sperm whales in the Southern Ocean (Yukhov 1982). As such, the presence of numerous sperm whales could sometimes be associated with rich fishing areas, which may result in a diluted impact of depredation in catch rates remaining high and which may, thus, influence the perception of fishers.

2.2.5.2. WHAT MAY BE THE CONSEQUENCES OF FISHERS' OPTIMAL STRATEGIES ON ECOSYSTEMS?

Consequences on local fish resources

Considering that fishers act like optimal foragers, since they aim at maximizing their fishing efficiency, we may wonder if this behaviour could be a risk for the long-term sustainability of local ecosystems, which include both the fish resource and the depredating whale populations. Fishers' choices seem to be only based upon short-term strategies, so there could be a risk of local depletion of Patagonian toothfish on patches. The foraging success clearly stands as the main driver of patch use even in the presence of cetaceans, and until recently the incorporation of the amount of depredated fish has remained limited in quotas allocation processes (Roche et al. 2007, Gasco et al. 2015). For instance, considering that 30% of the total catch in Crozet is lost to depredation (Gasco et al. 2015) and for a given quota of 850 t.year⁻¹ (e.g. season 2014-2015 within the Crozet EEZ), an additional 365 tonnes of Patagonian toothfish are caught but removed by cetaceans. The optimal strategies combined with the depredation may then become an issue to fishing stocks, within the condition that these amounts of depredated fish would not have been eaten in natural condition by cetaceans. We may indeed expect an overexploitation of the resource at the local scale due to the maximisation strategy of captains coupled to the loss due to depredation.

Furthermore, depredation may create bias in the length-frequency distributions used in fish stock assessment procedures since Gasco (2013) revealed that killer whales and sperm whales tend to depredate large Patagonian toothfish. Additionally, fishers concentrate their effort in fish-rich areas, where depredation is more likely to occur, especially in presence of sperm whales (Tixier 2012, Gasco et al. 2015). The decision to leave is then less likely to happen in such areas, as our results suggested that for a high fishing success (~6t.day⁻¹), fishers stay on a patch due to their optimal foraging strategy. Hence, a resource crunch is to be considered at finer scale than considering an EEZ range or even at a Small Scale Management Unit (1° X 0.5°), for instance at a seamount, a plateau or a slope level.

Consequences on local cetacean populations

Although fishers are more likely to avoid competition with cetaceans, we observed that captains do not leave fishing areas if their fishing success is high, even with an increasing number of cetaceans. Such decision may, therefore, provide cetaceans with large amounts of fish to depredate and, thus, with highly energetic and easily accessible resource in abundance. The consequences of artificial food provisioning on the sperm whale population has not been yet assessed since this population has been monitored only recently (Labadie et al. 2018). However, artificial food provisioning from fisheries was shown to result in increased survival and reproduction for the depredating killer whales of the Crozet population (Tixier et al. 2015a, Guinet et al. 2015).

We may also assume that the optimal foraging strategies of fishers reinforce cetaceans' depredation behaviour. If we now consider cetaceans as optimal foragers and depredation behaviour as a cost-effective strategy, due to the low foraging effort and the high energetic intake from toothfish (Collins et al. 2010), it is more likely that whales favoured interactions with longlines instead of natural hunting. Depredation may have been learned independently by some killer whale matriline and sperm whale individuals, and then socially transmitted to other individuals for both species by mimicry (Schakner et al. 2014). A cost-effective behaviour is more likely to be spread within a population of highly social cetaceans (Rendell and Whitehead 2001), especially as apprenticeship is important for cetaceans and relies on both vertical and horizontal cultural transmission (Guinet 1991, Ford et al. 1998, Deecke et al. 2000, Whitehead et al. 2004). Thus, killer whales and sperm whales might become more and more dependent of the longliners' activity. An increasing dependency of cetaceans to fisheries might become a concern if whales search for longliners outside the EEZs, where illegal fishing activity is still observed (Thierry Clot, pers. comm., from the French Antarctic and Austral Territories Administration) and is assumed to respond to depredation by cetaceans using lethal techniques.

2.2.5.3. CONCLUSION

In agreement with human ecological studies using OFT, our study showed that optimal patch modelling is a useful tool to analyse fishing strategies. However, we bring here new evidence of the possibility to monitor modern fishing activity according to the OFT, whereas previous studies focused on more traditional fisheries.

2.2.5.4. ACKNOWLEDGEMENTS

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2.3. WHAT INTEREST TO ASSESS HUMAN BEHAVIOUR?

2.3.1. CAPTAINS BEHAVIOUR WHILE EXPLOITING A PATCH

Using the optimal foraging theory, I observed that although captains' decision to use a patch is mainly driven by the fishing success, competition with odontocetes can strongly influence their decision (section 2.2). However, this article only focused on captain's prospection behaviour, *i.e.* setting decision, but it did not assess their foraging behaviour within a patch, *i.e.* the hauling decision. Thus, we may also wonder whether captains forage optimally within a patch. Thus, I aimed at assessing the decision to haul a longline when a choice is available. An optimal foraging strategy would consist in covering the shortest distance in order to haul the next longline among several ones set on the seafloor. The purpose was then to explain the hauling choice of the next longline for captains according to the optimal foraging theory. Similarly to our article (section 2.2), I hypothesised that the fishing success may influence positively the decision to haul the closest longline whereas the competition with

odontocetes may drive away the captains. I thus defined an optimal distance score (ODS) to estimate whether the captain made the most optimal choice by choosing the closest distance to haul the next longline ($score = 1$) or the least optimal choice by choosing the furthest distance ($score = 0$). The optimal distance score was estimated at the end of every longline hauled before another one (without any setting phases in between) and when at least 2 longlines remained on the seafloor, *i.e.* when a choice was available. Thus, I measured distances between the position of the fishing vessel at the end of the hauling and all extremities of longlines still soaking, considered as all the possible distances (d_p). From these values, d_p , I kept the minimum and the maximum from which I compared to the real distance (d_r) covered by the fishing vessel between the end of the hauled longline and the beginning of the next one. Thus, $ODS \in [0,1]$ and was defined as:

$$\text{EQUATION 2-11 : } ODS = \frac{\max(d_p) - d_r}{\max(d_p) - \min(d_p)}$$

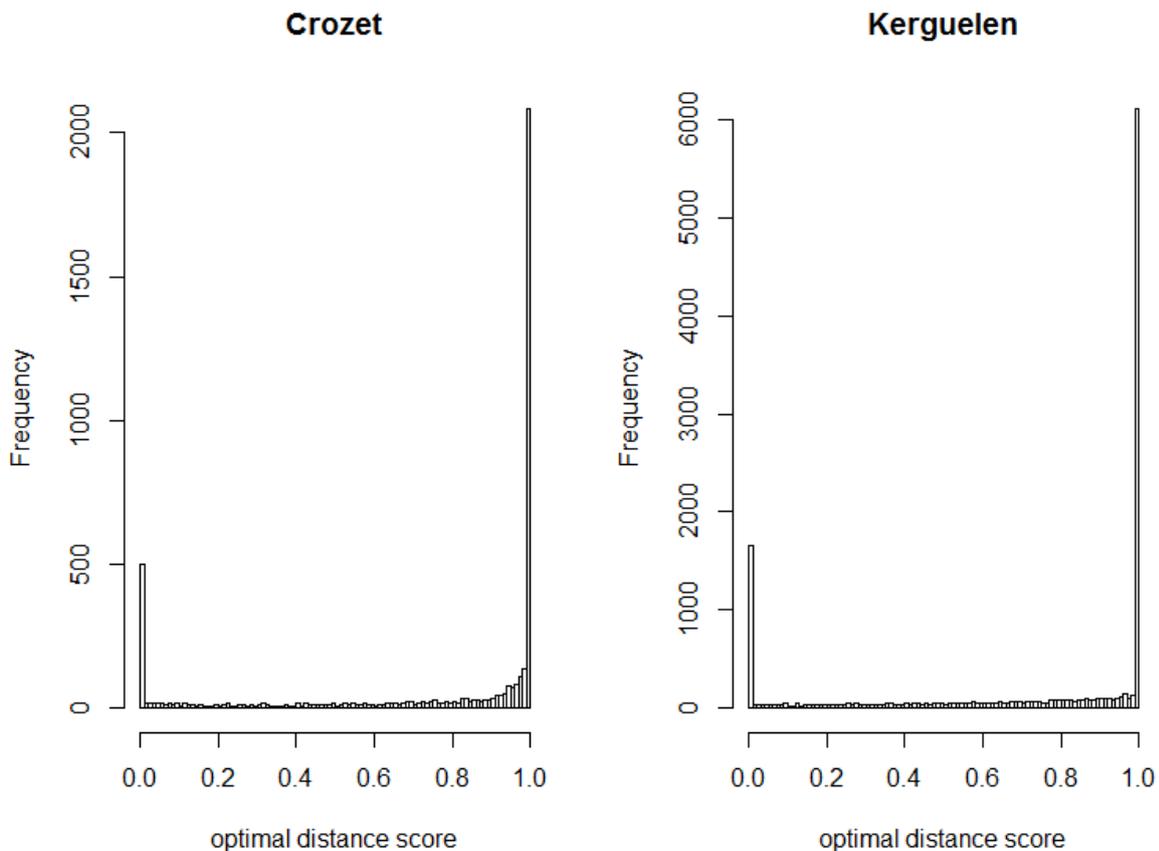


Figure 2-11 – Histograms of the optimal distance score (Equation 2-11) for all captains both at Crozet and Kerguelen.

I assessed the influence of the fishing success and the occurrence of depredation on the *optimal distance score*. The *optimal distance score* $\in [0,1]$ since it represented the proportion of optimality within captains choice. I thus investigated the logistic regression between the proportion to make the optimal choice (π) with the fishing success and the competition (Zuur 2009). The fishing success was expressed as the mass of toothfish caught on the hauled longline (kg), and the competition was set as a categorical variable with odontocetes occurrence (presence of species and absence of odontocetes). I also assessed the effect of the interaction between both predictive variables: fishing success and competition. Captains were considered as a random effect to investigate variations of decision between them.

$$\text{EQUATION 2-12 : } \text{logit}(\pi_{ij}) = \alpha + a_j + (\beta_1 + b_j)\text{Fishing success}_{ij} + \beta_2\text{Competition}_{ij} \\ + \beta_3\text{Fishing success}_{ij} \times \text{Competition}_{ij} + \varepsilon_{ij}$$

with π_{ij} the proportion to make the optimal decision for a captain j at the end of the hauled longline i , α the intercept, a_j the random intercept for captain j , $\beta_{1,2,3}$ the coefficients of the three predictive variables, b_j the random effect for captain j on the slope of fishing success and ε_{ij} the residual for the hauled longline i and captain j . Besides, using a top-down approach (Zuur 2009), I assessed first the most complex model, *i.e.* with the interaction between the two predictive variables and the random effect (captain j) set both on the intercept (α) and on the slope (β_1) of the continuous variable (fishing success) through the Akaike Information Criterion (AIC) selection (Akaike 1974, Zuur 2009). The statistical model was implemented through the software R with the function *glmer* (package *lme4*).

According to the AIC selection, only the models for the Crozet EEZ were better than the null model. The best model for Crozet was obtained with the competition as the only explanatory variables (excluding the fishing success) with a random effect of the captains on the intercept ($\alpha + a_j$):

$$\text{EQUATION 2-13 : } \text{logit}(\pi_{ij}) = \alpha + a_j + \beta_2\text{Competition}_{ij} + \varepsilon_{ij}$$

Interestingly, the model selection dropped out the fishing success, thus this variable did not explain the hauling decision of captains. However, the proportion of optimal decision in absence of odontocete was significantly different from 0, *i.e.* the least optimal choice ($\pi_{ij} = 0.79$, $p < 0.001$, Figure 2-12), with a significant variability between captains ($\text{std} = 0.27$). The optimal distance score decreased in presence of odontocetes with a significant difference between the

optimal distance scores in absence of competition and in presence of killer whales ($p_{kw} < 0.001$, Figure 2-12) whereas the optimal distance score in presence of sperm whales alone was not significantly different than in absence of odontocetes ($p_{kw} = 0.146$, Figure 2-12). When both species were present, the difference with the score in absence of odontocete was close to be significant ($p_{both\ sp} = 0.07$, Figure 2-12).

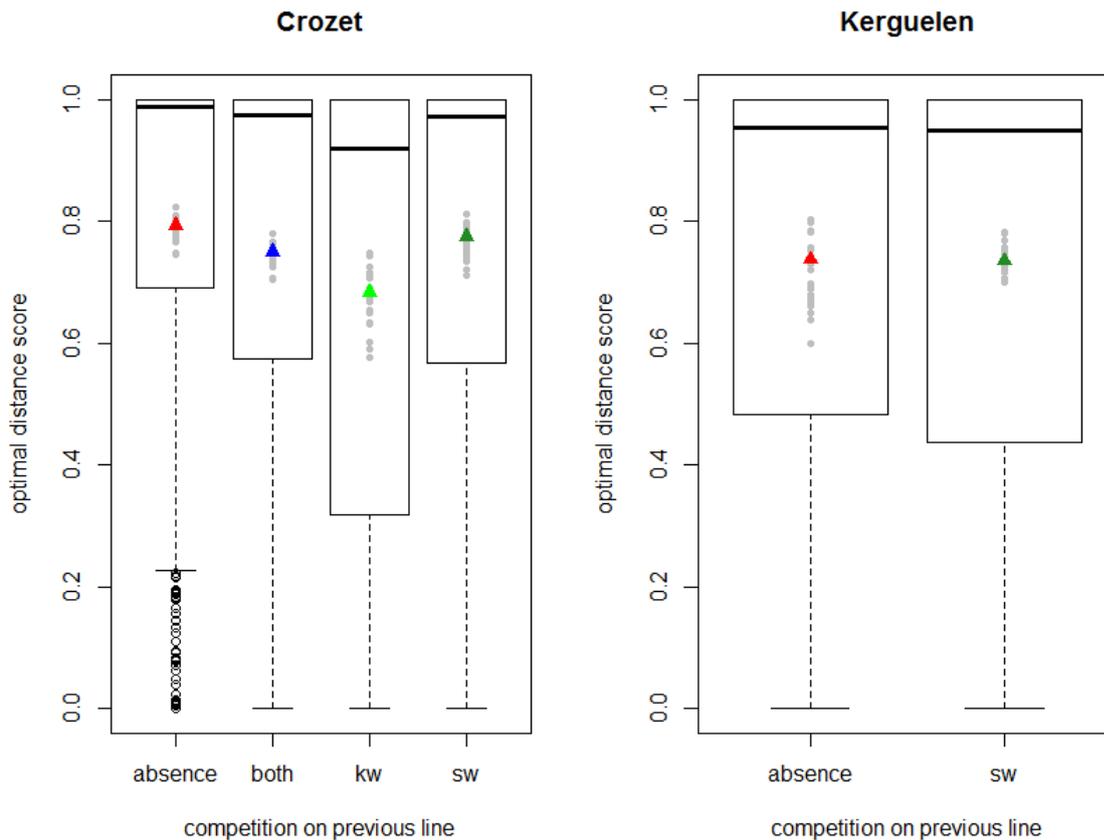


Figure 2-12- Boxplot of the optimal distance score per odontocete occurrence between Crozet and Kerguelen with mean scores represented by the coloured triangles and captains' variability by the grey dots.

These results revealed that captains display an optimal foraging behaviour within a patch since they tend to choose the closest longline whatever the fishing success and the competition. However, the models highlight that competition generated by the occurrence of killer whales impacts negatively the optimality of captains' hauling decision. This competition effect was not detected for sperm whales. Indeed, no competition effect was perceived in Kerguelen, where only sperm whales are present, as revealed by the mean value (absence in red and presence in dark green) on Figure 2-12 (right panel). Similarly, no significant differences between the

scores in absence of odontocete, in red on Figure 2-12 (left panel), and in presence of sperm whales alone, in dark green on Figure 2-12, was observed at Crozet. Besides the estimates revealed that in absence of odontocetes captains are more likely to choose the closest distances after 79% of the longlines hauled, in red on Figure 2-12, whereas in the presence of killer whales optimality decreases to 68% of the longlines, in light green on Figure 2-12. Additionally the inter-captains variability of optimal distance scores strengthen the hypothesis that they do not perceive their environment similarly and have different sensitivity to the competition (see captains variability in presence of killer whales on Figure 2-12)

Altogether, these observations show that competition decreases the optimality of captains decision as captains are either more likely to leave a patch in the presence of cetaceans or more likely to choose a further longline when killer whales are present. However, I did not assess the costs of implementing a non-optimal strategy in response to killer whales. Nevertheless, as interaction with odontocete may engage captains to cover larger distances than they should have done (*optimal distance score* < 1), this extra distance may be used as a proxy of an induced depredation cost. Thus, the extra distance (d_e) covered was measured as the difference between the real distance covered to haul the next longline and the minimum distance with the closest longline set on the seafloor that the captains could have covered:

$$\text{EQUATION 2-14: } d_e = d_r - \min(d_p)$$

I then estimated the mean (\pm sd) extra distance covered in presence of odontocetes at Crozet that I compared to the mean extra distance covered in absence of odontocete, as a reference of non-optimality in captains' hauling decision due to other parameters. I obtained extra distances of: 8.9 ± 13.4 km/longline in absence of cetacean, 11.1 ± 16.8 km/longline in presence of both species, 11.2 ± 15.6 km/longline in presence of sperm whales alone and 13.5 ± 20.4 km/longline in presence of killer whales alone (Figure 2-13). Thus, in presence of killer whales for instance, when captains chose to not haul the closest longline they cover 51% more distance than in absence of odontocete. This increase of distance begets considerable costs such as a rise of fuel consumption. However, additional fuel consumption is not the only cost that may be generated by the decrease of the fishermen optimality, but an increase of fishing effort, either by time or by fishing gear deployed may result in huge expenses (Peterson et al. 2014). Thus, further investigations should assess more precisely some captains' foraging strategies as a combination of the decision to deploy to haul and to use certain fishing practices according to their environment.

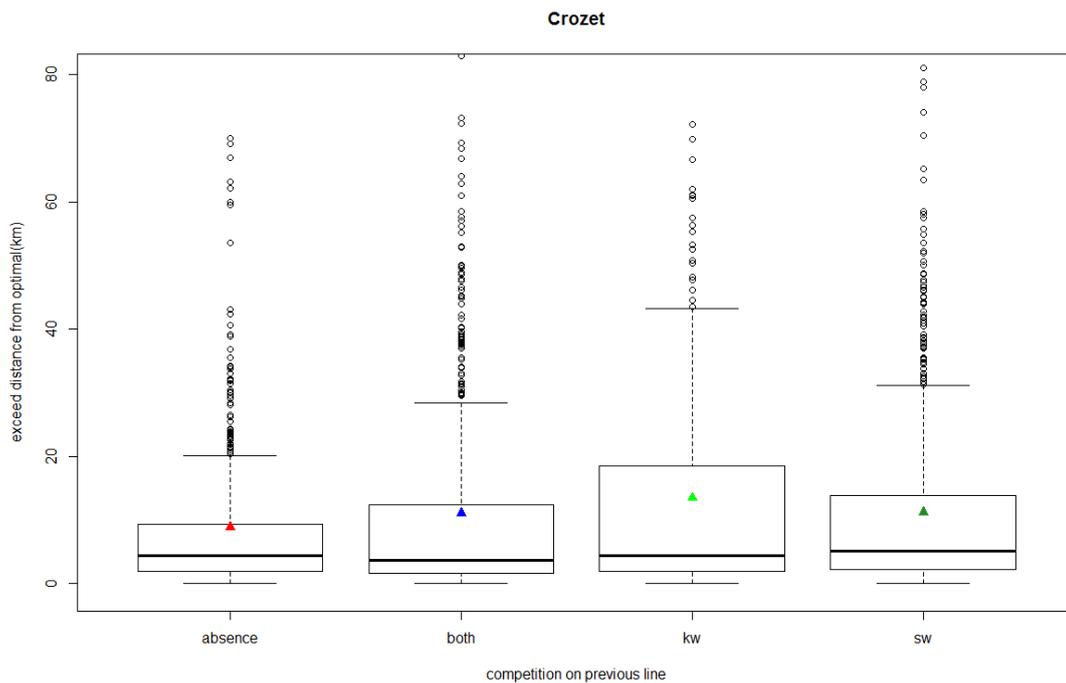


Figure 2-13 - Boxplot of the extra distance covered after a longline when captains do not chose the optimal decision (i.e. optimal distance score < 1) per cetacean occurrence at Crozet, with mean values represented by the coloured triangles.

2.3.2. CONCLUSION

In summary, this chapter confirms that fishermen behave like optimal foragers as their decisions are driven by variation of the environmental conditions. Captains face indeed decision-making with different implication term. When setting longlines, captains are prospecting for the resource. Their decision to set longline is therefore mostly based upon a long term strategy to find the best resource abundance (section 2.2). Once longlines are set captains could not improve anymore the catchability of the resource. However, during the hauling captains' decision will be important to reduce fishing costs and so captains rely mostly on direct environmental information, such as the presence of competitors (section 2.3.1). Besides, the behavioural ecology approach also revealed a large variability between captains, suggesting the importance of individual perception. However, further investigation should also assess the effect of captains' experience. Such approach would consist to determine whether captains behave more similarly to a different captain with the same experience than to himself with a different experience. I hypothesise that captains during their first trip behave like naïve

foragers. Then with experience fishing strategy should become more efficient and the perception of competition may evolve.

A better understanding of fishermen behaviour is thus essential toward a finer investigation of direct costs due to depredation. These costs could be quantified through the loss of optimality in captains foraging behaviour. Additionally, such an approach may also bring a new lead for mitigation measures by assessing the most optimal strategy in presence of odontocetes. Our studies showed the necessity to work at individual scale to assess captains' fishing strategies. Differences of personal sensitivity of the competition by captains, as revealed on Figure 2-5, Figure 2-7 and Figure 2-8 may explain a part of their inter-individual variation of interaction rates depicted on Figure 2-1. Thus, these results suggest that some captains may display foraging strategies which are more sensitive to interaction with odontocetes than strategies of other captains.

Apart from the fishing practices, we may wonder what type of behaviours may change the detectability of captains. As odontocetes mostly rely on acoustic to forage, captains could also display different navigation behaviours. As previously hypothesised, the acoustic signatures may explain differences of interaction rates between vessels (Figure 2-1), therefore different acoustic signature through the manoeuvrability of their vessels may explain another part of the inter-captains variability of interaction rates. This assumption was examined using a passive acoustic monitoring approach and results are presented in the following Chapter 3.

3. PASSIVE ACOUSTIC MONITORING

The previous chapter focused on the interest to study human behavioural ecology to better understand relationship between fishermen and the competition. This approach notably revealed differences of interaction rates between captains on Figure 2-1. This inter-captain variability was partially explained through differences of decision making and by different competition perception, suggesting that captains less sensitive would be less likely to leave in presence of odontocetes and thus would increase their interaction rates. This approach assessed in a way the consequence of the risk of interaction with odontocetes upon captains' behaviour; however the consequence of captains' behaviour upon the risk of interaction remains unclear. Using this opposite view of the issue would target how behaviour of captains may increase the risk of interaction, such as through an augmentation of their detectability. An assumption is that differences of detectability could be due to extrinsic signals, related to the vessels' navigation (*i.e.* captains sailing behaviour) or to intrinsic signals, related to vessels' specificities themselves. Intrinsic signals may then explain the inter-vessels variabilities observed on Figure 2-1. Thus, this chapter focuses on the acoustic signals as an explanation the detectability of fishing activity by odontocetes, through a passive acoustic monitoring approach. In a further extent, this chapter also determines how passive acoustic monitoring could bring a better understanding on the underwater dimension of the odontocete depredation behaviour.

3.1. INTRODUCTION

3.1.1. PASSIVE ACOUSTIC MONITORING TO STUDY DEPREDATION

Stimuli of any kind propagate differently underwater than in the air. Species like cetaceans have sensory and communication systems adapted to a fully aquatic environment (Watkins and Wartzok 1985, Wartzok and Ketten 1999). As beams of light are scattered and absorbed by water at closer range than in the air, the vision of marine mammals allows them to primarily distinguish their environment only at very close range (Watkins and Wartzok 1985, Wartzok and Ketten 1999). These predators need therefore to rely on other environmental clues

and other senses than vision to detect their preys. One reliable information signal underwater is sound. In the aquatic environment, sound travels five times faster than in the air, circa 1500 m.s⁻¹ instead of circa 300 m.s⁻¹. Sound can travel from a few metres to a hundreds of kilometres within the oceans depending on their intensity and their frequency, while light usually does not propagate for more than dozens of meters. It is then not surprising that evolution has driven cetaceans to primarily rely on acoustic signals (Wartzok and Ketten 1999). All cetaceans produce communication signals. Pieces of information contained in cetacean communication signals are still poorly understood since a broad range of sounds could be produced across species, contexts, behavioural states, etc. Indeed, signals, either random or stereotyped, can vary from short pulses to multi-themed songs including whistles and calls (Zimmer 2011). Some of these sounds are produced to be heard by prey in order to scare them within a foraging purpose. For instance some population of killer whales and bottlenose dolphins produce feeding-specific calls to manipulate preys and facilitate capture (Janik 2000, Simon et al. 2006). Another example of feeding-specific sounds but different to calls are produced by humpback whales when bubble-net feeding on herring (Cerchio and Dahlheim 2001). More specific sounds related to feeding and at larger extent to foraging activities are the echolocation signals. Echolocation is the use of a signal's echoes from an emitting animal to estimate the direction and the range of an object (Griffin 1958, Zimmer 2011). Echolocation signals, such as clicks, have first been described in bats (Griffin 1958), and in odontocetes to localise prey (Backus and Schevill 1966, Zimmer 2011). A click of echolocation is a broad-band sound, for instance circa 100 Hz to 150 kHz depending on odontocetes species, and is produced during a very short duration (*i.e.* a few to some twenty milliseconds). Altogether, communication and echolocation signals are good acoustic clues to interpret the behaviour of individuals, leading researchers to increasingly use passive acoustic monitoring (PAM) as a tool to study odontocete species

Within the context of longline depredation, PAM can be used as a reliable approach to assess the temporal and spatial behaviour of cetaceans around fishing gear. For instance, the deployment of acoustic recorders on longlines may allow a more comprehensive monitoring of the presence of depredating odontocetes, improving therefore accuracy in the estimation of interaction rates (Thode et al. 2014, 2015). PAM may also be implemented through multiple hydrophone deployments allowing tracking of individuals underwater (McPherson et al. 2004, Zimmer 2011, Mathias et al. 2013a). Odontocetes are most likely to rely on acoustic to detect vessels and fishing activity. Thus, another interest to use PAM within a fishing context is to identify the specific sounds that may attract depredating species. Although PAM offers

interesting insights, for the last 40 years the field of acoustic in a fishery context has mostly focused on deterrents and harassment devices (Shaughnessy et al. 1981, Jefferson and Curry 1996, Tixier et al. 2015b, Wild et al. 2017). This was partly explained by unwieldy acoustic recorders with high power and memory consumption, allowing only short recording duration, until the 2000s. With recent technological developments it has become easier to deploy autonomous devices on longlines, which lead to an increased use of the PAM approach to study depredation (Thode et al. 2015). Yet, only a few studies have used this approach to observe and measure depredation (McPherson et al. 2004, Hernandez-Milian et al. 2008, Thode et al. 2014, 2015). Among these studies, the Southeast Alaska Sperm Whale Avoidance Project (SEASWAP) has dedicated extensive efforts on PAM to investigate sperm whale depredation on Alaskan longline fisheries (see review Thode et al. 2015). This project used PAM through four distinct approaches aiming at: (i) better estimating of depredation rates by using distinctive echolocation sounds by sperm whales (Mathias et al. 2012, Thode et al. 2014, 2015); (ii) developing localisation and tracking methods of depredating whales from hydrophones arrays deployed on longlines' buoy (Thode 2004, 2005, Tiemann et al. 2006, Mathias et al. 2013a, 2013b, Thode et al. 2015); (iii) determining acoustic cues produced by fishing boats to determine how sperm whales detect and localise fishing activity (Thode et al. 2007, 2015); (iv) testing and evaluating potential countermeasures such as acoustic decoys and passive deterrents (O'Connell et al. 2015, Thode et al. 2015, Wild et al. 2017). SEASWAP revealed the large potential of PAM to understand, measure and mitigate odontocete depredation (Thode et al. 2014, 2015) .

Despite this research potential, PAM has never been implemented as a tool to study odontocete depredation on the Patagonian toothfish longline fisheries in the Southern hemisphere. During my PhD, I introduced PAM to the French and Australian toothfish fisheries with the purpose to collect long-term acoustic data from fishing vessels and longlines.

3.1.2. PAM WITHIN THE ORCADEPRED PROJECT

In our depredation study case, we focused on two odontocete species: sperm whales and killer whales. These species both produce echolocation clicks (Norris 1968, Barrett-Lennard et al. 1996, Madsen et al. 2002, Au et al. 2004, Miller et al. 2004, Simon et al. 2007, Zimmer 2011), which can be used as a reliable acoustic clue to identify foraging events. Using clues like ‘buzzes’ or ‘creaks’, described as an acceleration of click rates (Madsen 2004) and found to be associated with prey catch attempts (Miller et al. 2004, Watwood et al. 2006), we may detect fish removal from longlines (Thode et al. 2014, 2015). Killer whales, which have a more diverse acoustic repertoire than sperm whales, may also be detected by clues other than echolocation clicks, such as stereotyped pulsed calls and whistles, which they primarily use as communicative signals (Ford 1989, 1991, Thomsen et al. 2002, Riesch et al. 2006, 2012). These types of signals may therefore be reliable to determine socializing behaviour (Ford 1989, 1991, Deecke et al. 2000, Miller and Bain 2000, Filatova et al. 2013). Communication sounds have also been reported in sperm whales but through clicks echolocation sequences, called ‘coda’ (Pavan et al. 2000, Rendell and Whitehead 2003, 2004).

Knowing these species’ acoustic repertoire we could monitor their presence and identify their behavioural states around hydrophones deployed on longlines. With acoustic proxies of foraging behaviour, such as clicks of echolocation (Thode et al. 2014, 2015), we could determine when depredation events start. Aside from answering at which fishing stage (*i.e.* setting, soaking or hauling) odontocetes could depredate Patagonian toothfish, PAM might also specify depredation rates during interactions (Thode et al. 2014). PAM may also be useful when depredation is not occurring yet. If the presence of odontocete can be acoustically detected immediately when setting the longlines, this would inform that individuals were already present on the fishing area. Otherwise, if predators are acoustically detected after the setting, PAM can assess their arrival time on longlines. Such pieces of information are crucial to highlight predators’ natural distribution. Altogether, we expect to bring new insights on how odontocetes detect the fishing activities. Indeed, we wonder how far vessels could be detected and whether their activities, for instance setting or hauling, influence their detectability. A more direct approach to assess this detectability issue is to monitor vessels’ acoustics. We suggest that vessels might be detected either through their own signatures, *i.e.* intrinsic signals, which could vary between fishing phases (Thode et al. 2007, 2015), or through sounds induced by captains’ navigation, *i.e.* extrinsic signals. An increase of the acoustic detection range of fishing vessels

should increase the risk of interactions with odontocetes. The determination of intrinsic and extrinsic signals is thus crucial to better understand how odontocetes detect fishing activities.

As no acoustic deployment had previously occurred from Patagonian toothfish longliners, the setting of the acoustic monitoring constituted a first important work during this PhD, as presented hereafter. The first step before assessing the objectives to monitor odontocetes and vessels acoustics was to deploy hydrophones. Two different setting was used: a multi-hydrophones array to allow acoustic tracking and a single hydrophone to allow friendly deployment by fishermen and fishing controllers without scientific oversight on-board. This second setting has then allowed to install a long-term acoustic monitoring from the longliners.

3.2. PROTOCOLS AND FIELD METHODS, TOWARD A LONG TERM MONITORING

3.2.1. FIRST RECORDINGS WITH AN ACOUSTIC ARRAY

Within the purpose to answer when and where depredation occurred, the use of PAM for acoustic tracking is of great value (Mathias et al. 2013a, 2013b, Thode et al. 2015). This approach requires deploying an acoustic array to allow measuring time difference of the sounds' arrival between several hydrophones. A preliminary work was therefore conducted before this PhD to prepare the acoustic tracking tool, described in Appendix 1. The method and results from the models detailed in Appendix 1 were used to determine the best setting for an array of hydrophones. The acoustic array and its mooring were designed by RTSYS, a French acoustic company. This setting was composed of four synchronized hydrophones connected through 100 m cables to a single recorder (model EA-SDA14) as depicted on the Figure 3-1. After a preliminary test within the Brest bay to train manipulating the array, I worked with RTSYS and the captains of the French longliners to find an alternative mooring system more adapted to the fishing context. The array was then deployed on longliners during a first field mission from end December 2016 to early March 2017. The array was attached on the downline connecting the buoy to the ballast of a longline as represented on the Figure 3-1. The whole system was actually too complex to be conveniently deployed in the Southern Ocean from a fishing vessel that also conducts fishing operation. The use of the 100 m-cables added logistical constraints and was time consuming to recover. I have then switched to a simplest model with two hydrophones

connected with 10 m cables. Using 2 hydrophones instead of 4 can still be useful for acoustic tracking, especially to localise sperm whales using the difference of arrival time between a click and its echo (see Appendix 1). Nevertheless, I deployed the array 4 times with 4 hydrophones and then 13 times with 2 hydrophones, for a total recording duration of 656 h, as revealed in the first part of Table 3-1.

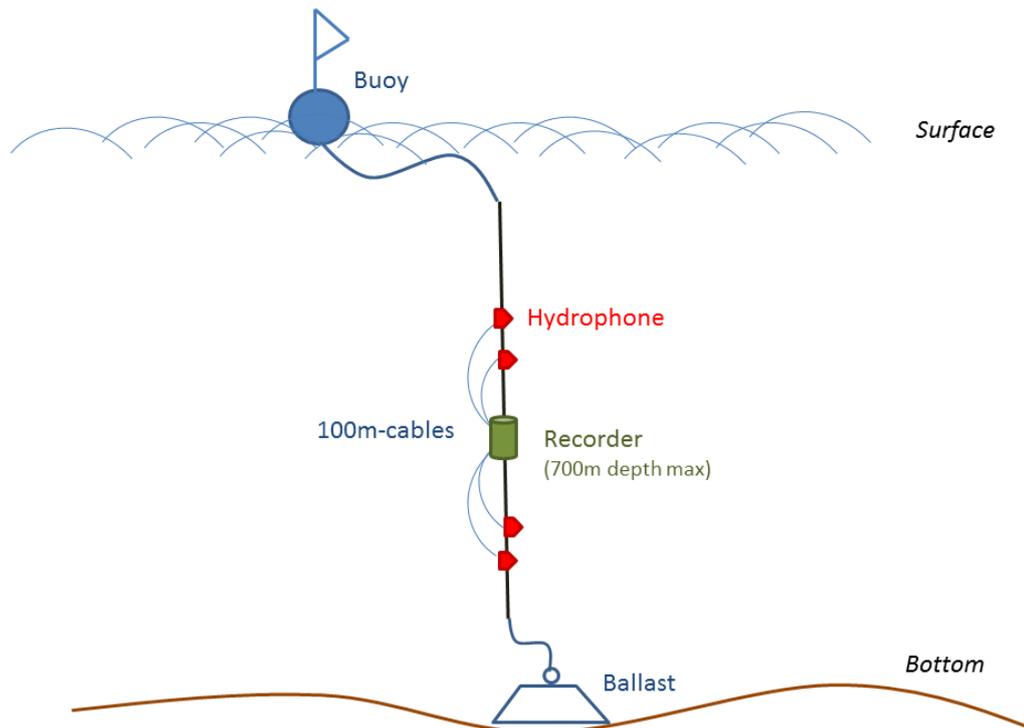


Figure 3-1- Scheme of the acoustic array designed by RTSYS deployed during the first mission (2016-2017).

From this first experience, we decided to change the acoustic array during a second mission (from end December 2017 to early March 2018). We then used 4 independent self-contained underwater sound recorders (SoundTrap 300, Ocean Instruments, NZ). The inconvenience was that each recorder has its own base time. We set therefore a pinger (V9-69kHz, VEMCO) between 2 SoundTraps to allow further time recalibration as suggested by Mathias et al. (2013). Each SoundTrap was permanently attached to a small rope which was clipped to the downline below the buoy as depicted on Figure 3-2. Hydrophones were deployed

3. PASSIVE ACOUSTIC MONITORING

similarly to the first season, *i.e.* they were associated in pairs at 100 m and 200 m with a space of 10 m between hydrophones of the same pair. However, for this new setting I paired each hydrophone with an 3-axis accelerometer/pressure sensor data loggers (Sextant Technology, New Zealand, see section 4.3) to get information of their position within the water column through the whole deployment. These information will be useful to perform the acoustic tracking since hydrophones positions are essential for the algorithm described in the Appendix 1. This new setting was simple to set and to recover as there were no electronic cables between sensors. As a result I deployed the array, composed of the 4 independent hydrophones, 26 times for a total recording duration of 882 h as shown in the Table 3-1.



Figure 3-2 – Picture of the attachment of the SoundTrap on the downline (green rope). The SoundTrap is set permanently on a small rope (the blue one) to facilitate the deployment on the downline.

3. PASSIVE ACOUSTIC MONITORING

Table 3-1 – Summary of the dataset acquired during this PhD from personal mission and through the deployments by fishermen and fishery controllers on French and Australina longliners. The Australian fishermen record 15 min every 30 min, so the recording durations are not equivalent to the deployments durations (twice higher than values in the table).

Operator	Fishery	Vessels	Number of trips covered	Number of deployments	Total recording duration (hours)
Personal contribution	French	Mission 2016-2017 (Mascareignes 3, Ile De La Réunion, Albius)	1	17	656
	French	Mission 2017-2018 (Ile De La Réunion, Mascareignes 3)	1	26	882
Fishermen and fishery observers	French	Albius	2	14	652
	French	Cap Horn	1	6	189
	French	Cap Kersaint	1	7	246
	French	Ile De La Réunion	2	18	737
	French	Ile Bourbon	1	20	695
	French	Mascareignes 3	1	2	72
	French	Saint André	2	22	469
	Australian	Antarctic Chieftain	1	15	332
	Australian	Atlas Cove	1	18	405
	Australian	Corinthian Bay	2	17	360
	Australian	Isla Eden	2	21	390
TOTAL			18	203	6085

3.2.2. LONG TERM MONITORING

Within the purpose to assess a long term monitoring of both odontocetes and vessels acoustics, I set an acoustic monitoring program for the whole fleet (section 1.3). In order to be applied on a large scale the protocol disturbance on fishing activities must be minimal. It is therefore essential to have a friendly deployment and an easy monitoring. The longlines are therefore equipped with a single independent hydrophone (SoundTraps), the same as I have deployed during my second mission. A protocol, detailed in Appendix 3, was provided with the hydrophone to the fishery observers before the trip. Within the protocol I have then described how to set the mounting system as showed on Figure 3-2 and where to deploy the hydrophone on the longline as depicted on Figure 3-3. The single hydrophone is set at 100 m to avoid strong noise from sea surface. A consistency between all deployments will allow comparing acoustic recordings between vessels. The protocol advises deploying as often as possible the hydrophone with a continuous recording, without adding excessive work for both fishermen and fishery observer, whom also download the data from the SoundTrap on-board once recovered. During the deployment, information such as environmental conditions, observation of odontocetes and occurrence of navigation manoeuvres made by the captains are asked to be notice by fishermen and fishery observers within a deployment sheet, provided at the end of Appendix 3.

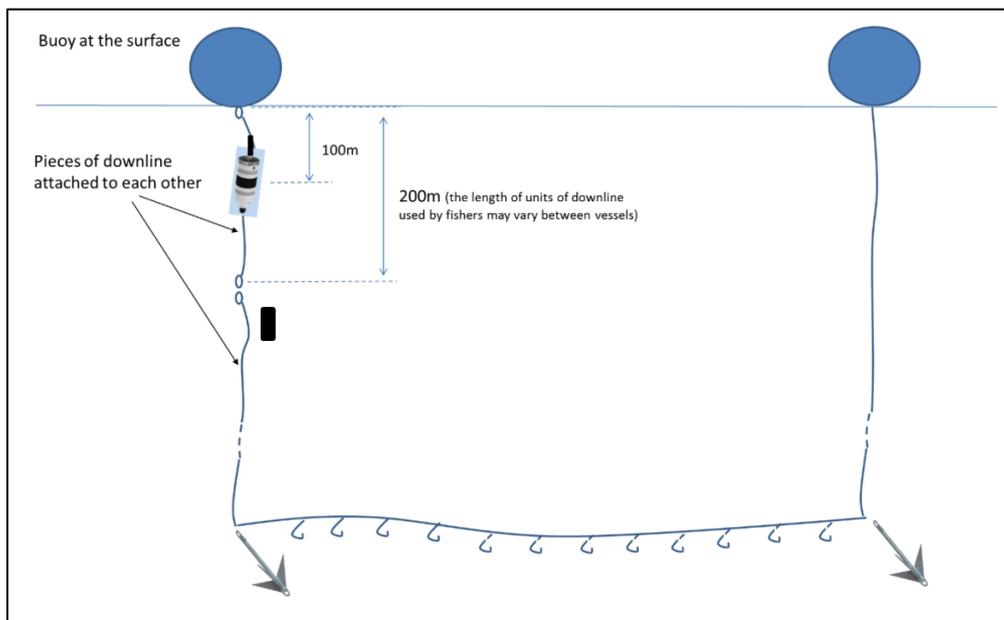


Figure 3-3 - Position of the recorder during deployment, that is attached to a piece of downline under the buoy.

A similar monitoring was also assessed around Heard and McDonald Islands (HIMI, 53°05' S, 73°31' E, Australian EEZ). I have provided my protocol to Dr. Paul Tixier so he could translate the protocol for the Australian fishermen, as part of his depredation program. Conversely to the French protocol, the recordings are not continuous (15 min on every 30 min) to avoid filling the intern memory too fast, since data could not be downloaded on-board. However, PAM around HIMI would allow adding a further level of comparison, *i.e.* between the two fleets. Indeed, while the two EEZs are adjacent and both experience sperm whale depredation, the frequency of the latter is substantially lower in HIMI than in Kerguelen (Welsford and Arangio 2015, Janc et al. 2018). Thus, it might be interesting to assess whether some differences in acoustic between the two fleets exist and if they might explain differences of detectability. Additionally, my protocol is also applied on the French longline fishery operating around Saint Paul and Amsterdam (38° 16' S, 77° 32' E, Southern Ocean) and South East of Australia, both targeting blue eye trevalla (*Hyperoglyphe Antarctica*) and both impacted by killer whale depredation (Tixier et al. 2018).

Deployments by fishermen and fishery observers started in December 2017 on French longliners and have been covering 3060 h over 89 longlines. As for the Australian longliners, deployments started in August 2017 with 2974 h covered by the hydrophone (but 1487 h of recordings) over 71 longlines. The details of the deployments per vessel are described in Table 3-1. The recording effort should be going as long as possible. The next step would be indeed to integrate the deployment sheet within the fishery observer notebook to facilitate the process and maintain the deployment on the long-term. At least data will be maintain until 2020, and the end of the ANR OrcaDepred.

These recordings have allowed the first recordings of killer whales and sperm whales within the French EEZ around the longliners. At a first sight we recovered some interesting recordings in absence of fishing activity on the equipped longline with killer whales and sperm whales around as their vocalises and clicks are observable on the spectrogram in

Figure 3-4. For instance, a group of killer whales was first visually observed interacting with a longline hauled nearby the one equipped and then the group was encountered again during the hauling of the equipped longline. Between these two hauling sessions the fishermen went further to haul a third longline but with no visual observation of this group. The acoustic recording of this period revealed then that this killer whale's unit staid around the buoy as vocalisations are audible during the whole time. This simplistic example demonstrates that

visual observation is not enough to assess presence/interaction of odontocetes around longlines in absence of the fishing vessel. It is not clear whether the group of killer whales or sperm whales heard on the acoustic recording were depredating. However, this presence in the vicinity of longlines may question estimation interaction rates, as it is computed through the visual observation of these species nearby the fishing vessels during hauling. Further investigation should focus on such cases to quantify the foraging activity of individuals around the longline monitored.

Additionally, all these recordings allowed preliminary analyses on vessels' acoustics, presented in this thesis in the next section 3.3. The purpose was to bring some first insights on possible acoustic explanation on differences of interaction rates between vessels and captains (Figure 2-1). These leads would then allow further investigation with more robust statistical analyses on possible cues.

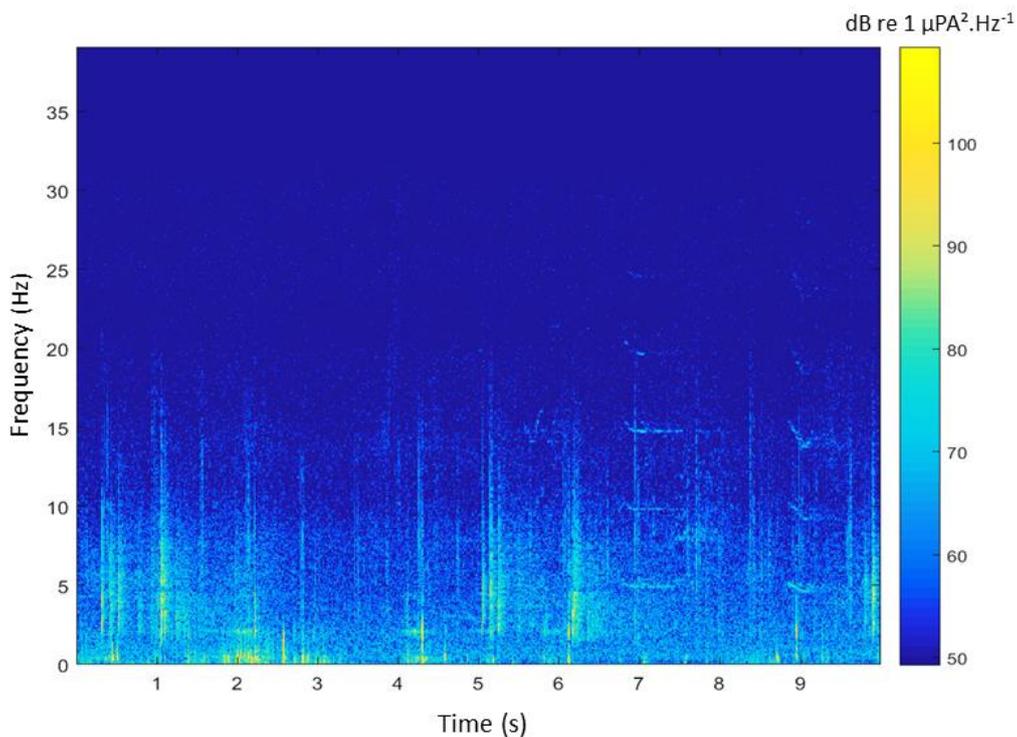


Figure 3-4 - Spectrogram of sperm whales' clicks (broadband frequencies produced during a very short duration) and killer stereotyped calls (e.g. at 7 s and 9 s). The colour scale represents the square modulus of the acoustic pressure in units of power spectral density (in dB re 1 $\mu\text{Pa}^2 \cdot \text{Hz}^{-1}$). The recording was made during the first mission, the 27th of in February 2017 on the vessel Ile de La Réunion at Crozet.

3.3. A FIRST APPLICATION: FISHERY ACOUSTIC

3.3.1. VESSELS' ACOUSTIC SIGNATURES

3.3.1.1. INTRODUCTION

The main component of vessels acoustic is due to the rotation of the propeller blades (Ross and Kuperman 1989, Richardson 1995, Hildebrand 2009). The sound produced by the propeller is characterized by two components: (i) tonal sounds at specific frequencies which related to mechanical noise from the blade rotation, named the propeller singing; (ii) a broadband noise related to the cavitation as bubbles explode when propeller blades increase the pressure water while rotating, which can be characterized as boiling seawater (Ross and Kuperman 1989, Richardson 1995, Hildebrand 2009). Sounds of machineries are also part of vessel signature (Richardson 1995, Thode et al. 2007), for instance the hydraulic winch, used to haul the longline, from vessels produce a narrow-band tones (Thode et al. 2007). However, sounds produced on-board do not propagate well underwater and may not cover more than 1 km as observed for the hydraulic winch tones around 200 Hz on longliners in Alaska (Thode et al. 2007).

3.3.1.2. METHODS

To investigate longliners acoustic signatures, I focused upon the propeller cavitation and singing propellers. I then compared the frequencies of these two types of noise between vessels. First, I assessed spectrograms over a minute. Second, I assessed the power spectrum (in dB re 1 μ Pa) to highlight tonal sounds of singing propeller. The power spectrum was estimated through the PAM Guide tool on Matlab (Merchant et al. 2015) in order to assess the root means square (RMS) with their quantiles. The power spectrum statistics were run per vessels for batched recording files of 3 min when the distance from the hydrophone was estimated around 1 km while hauling. I used 7 and 8 recording files of 3 min for 5 vessels and 3 recording files for the last vessel (because of the quality recording).

In this thesis I provided a preliminary and descriptive result of the analysis of vessels signatures. This aspect, along with the analysis of propagation ranges of the signals produced by vessels, will be treated in depth in the near future. In particular, the determination of detection ranges requires precise information on the distance between fishing vessels and the

hydrophones to reliably estimate transmission loss components. Data on vessels trajectories such as AIS would be of great interest; however such dataset was not available during this PhD. Indeed, AIS vessels data combined to the PECHEKER dataset for longlines (Martin and Pruvost 2007) deployed around hydrophones would allow to increase the accuracy of the models. In this thesis distance between the vessel and the hydrophone was estimated from the length of the longlines, knowing on which buoy the hydrophones were deployed. When the vessel was hauling a longline equipped with a hydrophone, I could estimate the distance from the hydrophone using a mean speed of the vessel calculated thanks to the beginning and ending times of the process. I also had access to the PECHKER dataset until the end of my first on-board mission, allowing assessing distances between longlines and hydrophones for the deployments made during the mission 2016-2017.

3.3.1.3. PRELIMINARY INSIGHTS

Broadband noises of the propellers cavitation of all six longliners concentrate the main energy from circa 100 to 2000 Hz, as observed on the spectrograms and DSP of Figure 3-5 and in Supp. data 4. This is consistent with the frequency range previously described for boats of same size (Scrimger and Heitmeyer 1991, Richardson 1995, McKenna et al. 2012). All vessels show from 1 to 3 distinctive ray at around 1 kHz, which stand out on the spectrograms of Figure 3-5 and Supp. data 4. This rays reflect the signals produced by propeller singing (Richardson 1995). However, the numbers of rays paired with their exact frequencies are specific to each vessel (see Figure 3-5 and Supp. data 4). For instance, spectrograms and DPS on Figure 3-5 reveal that vessel #1 has 3 rays which could be confounded as a strong tone around 1 kHz while vessel # 3 shows 2 very distinct tone around 900 Hz and another one above 1 kHz, as depict on Figure 3-5. I thus assume that odontocetes may be able to identify vessels through their distinct features resulting from propeller singing. As different acoustic signatures could propagate at different ranges, we suggest that vessels may potentially have different detectability. Assuming that detectability strongly influence interaction rate, this differences of signatures between vessels may explain some differences of interaction rates between some of them observed on the Figure 2-1 such as the variation of interaction rates with sperm whales between vessels 3 and 8 at Crozet. Indeed, sounds produced at low frequencies usually propagate further than at high frequencies (Fisher and Simmons 1977, Ainslie and McColm 1998). However, the difference of propagation range between a ray at 900 Hz and another one at 1 kHz may not be

high, thus only high differences of intensities would increase vessels' detectability. It would then be of interest to monitor the propagation of each tonal sound to estimate whether some vessels might be detected significantly further than other ones. However, the noise level statistics made through a power spectrum varies according to the duration of the recording. To integrate noise level statistics over the appropriate duration, it would require knowing how the hearing systems of these species integrate acoustic signals. Further investigation will focus on this aspect. Also, it would be interesting to assess whether two sister-ships have differences of interaction rates with odontocetes, since these vessels have similar manufacturing characteristics and so should similar signature acoustic. Among the other French vessels some sister-ships exist, but the vessels' identity in the Figure 2-1 are not known preventing to assess interaction rates between sister-ships. Besides, in this preliminary analysis, there are no sister-ships among the 6 vessels investigated (Figure 3-5 and Supp. data 4), avoiding the possibility to compare acoustic signatures. However, because the singing propeller varies according to the condition of the propeller, for instance damage propellers may produce more tones and at higher intensities (Richardson 1995), it more likely that sister-ships reveal different signatures.

3. PASSIVE ACOUSTIC MONITORING

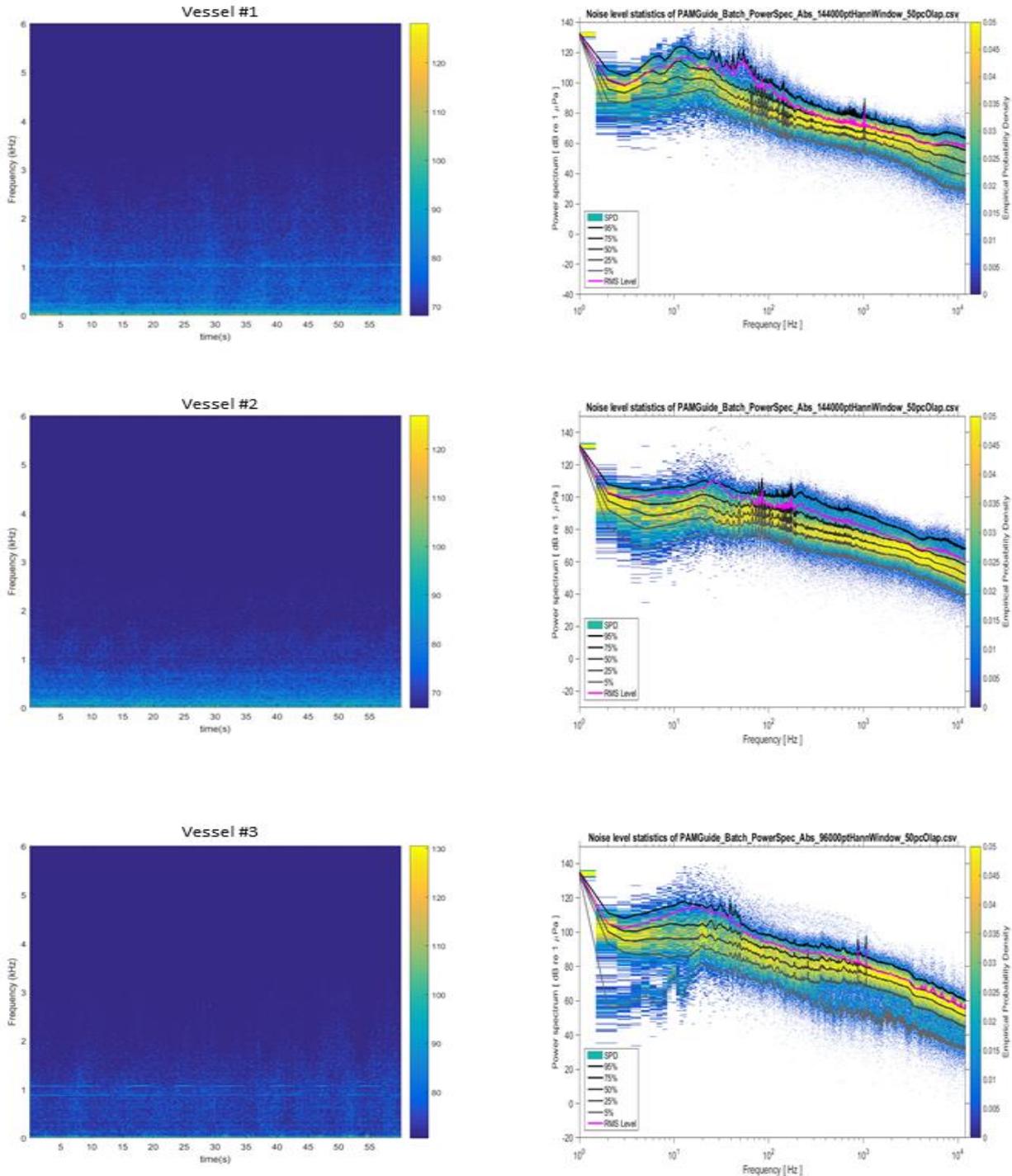


Figure 3-5 - Spectrograms (left panels) and power spectrum densities (right panels) of 2 French (vessel #1 and vessel #2) and 1 Australian (vessel #3) longliners (one vessel per line). The spectrograms were made over 1 min for vessels at 1 km for the hydrophone, with a colour scale representing the square modulus of the acoustic pressure in units of power spectral density (in dB re $1 \mu\text{Pa}^2 \cdot \text{Hz}^{-1}$). The power spectrum (in dB re $1 \mu\text{Pa}$) were assessed through PAM guide with batched recording files of 3 min for vessels at 1 km of the hydrophone (Merchant et al. 2015). See Supplementary data for the 3 other vessels.

3.3.2. ACOUSTIC CUES

3.3.2.1. INTRODUCTION

An acoustic cue could be defined as a signal with a distinct signature associated to a specific navigating behaviour or fishing phase. Although the vessel acoustic signature described through the propeller cavitation and the propeller singing was considered as the main source of detectability (section 3.3.1), an acoustic cue should be an acoustic signal different from this signature. A cue must hold information for the listener and should be recognised through its frequencies components and intensities. In this thesis, a first approach of the behavioural aspect of the detectability of vessels by odontocetes is raised. The purpose was to assess a first description of potential clues over a few fishing events. I therefore examined the variations in the frequency intensities of the signals produced by vessels at 3 different scales: (i) depending on the type of operation: setting *vs.* hauling; (ii) depending of the state of operation: setting *vs.* post setting; (iii) depending of the manoeuvrability during an operation: forward *vs.* backward. Additionally, I aimed at determining how far the information held within a cue could reach the odontocetes.

3.3.2.2. METHODS

I used data from a single vessel to allow for the interpretation of sound differences while avoiding any skew from vessel acoustic signatures. Broadband noise levels were estimated through power spectral densities (PSD, in dB re $1 \mu\text{Pa}^2\cdot\text{Hz}^{-1}$). I used the Welch's method in Matlab to visually compare PSD values and I conducted noise level statistics on PAM Guide (Merchant et al. 2015) to retrieve the noise values.

I first compared PSD over 15 s of a vessel between a setting and a hauling, from two different recording files but at a similar distance (circa 1 km) from the hydrophone. I then compared over a single recording file, a setting and a post-setting. The PSD of the setting was assessed over 15 s, during which the longline is dropped in the water from the stern of the vessel while the latter heads forward at a high speed (between 6 to 10 knots). The PSD of the post-setting was also assessed over 15 s, 45 s after the setting, *i.e.* after the last buoy has been dropped off. Lastly, I assessed 30 s of a hauling while the vessel was at 4 km from the hydrophone. The distance between the vessel and the hydrophone was estimated through the longlines positions,

accessible in the PECHEKER dataset. During these 30 s the vessel was moving forward and manoeuvred 2 times backward while hauling a same longline. I thus compared the PSD of these two manoeuvres estimated with PAM Guide. I used the two sound samples of the boat going backward batched together of a total duration of 4 s and 2 samples of the boat going forward before and after the two backward events, of the same duration.

I finally aimed at assessing the differences in the propagation ranges of the signals produced by fishing vessels between backward and forward manoeuvres. I used the transmission loss (TL) over the estimated distance between the vessel and the hydrophone to estimate the source level (SL) from the received level (RL) on the hydrophone:

$$\text{EQUATION 3-1 : } SL=RL+TL$$

Transmission loss is the attenuation of sound intensity as the sound propagates underwater. I used a transmission loss model considering the combination between the loss due to geometrical spreading of the sound wave-front and the absorption loss due to propagation (Fisher and Simmons 1977, Ainslie and McColm 1998). A simple model for underwater geometrical spreading is a spherical propagation until waves reach the surface and then follows a cylindrical propagation as they are constraint by the limit of the water column. Thus, I considered the transition range from which the sound switches from spherical to cylindrical spreading as one-half of the channel depth, H (Urick 1998). The absorption loss is sound's frequency dependent (Fisher and Simmons 1977, Ainslie and McColm 1998). The total transmission loss model was then defined as:

$$\text{EQUATION 3-2 : } TL = 20\log_{10}\left(\frac{H}{2}\right) - S_c\log_{10}\left(\frac{H}{2}\right) + S_c\log_{10}(R) + \alpha(f)R$$

with R the range source-hydrophone, H the depth of the water column, α the absorption component and f the sound frequency and S_c set at 10 or 17 to test a more permissive *vs* a more rigorous attenuation model through the cylindrical spreading ($S_c.\log_{10}(R)$).

The RL was measured as the root mean square (RMS) of the PSD estimated through PAM Guide. I finally resolved the SONAR equation to estimate for which range the TL would reduce the signal to be heard from the ambient noise above a certain threshold (dB):

$$\text{EQUATION 3-3: } SNR = \text{threshold} \Leftrightarrow SL - TL - NL = \text{threshold}$$

with NL the ambient noise level estimated through 40 minutes from 7 different recording files when the vessel was between 30 and 50 km, the furthest distances obtained between the vessel and the hydrophone on our recordings. I then considered the ambient noise level as the 50th percentile of the PSD.

As I used a frequency dependent TL model (Equation 3-2), I assessed the differences of propagation range for different frequencies. I first chose 250 Hz since it seems to represent the higher received sound levels (Supp. data 5) and since low frequencies propagate further than high frequencies. This frequency might thus be the component of the vessel acoustic audible by both species at the furthest range. Indeed, both species should be able to heard this low acoustic vessel frequency since killer whales can produce some pulsed calls around 100 Hz (Ford 1987). Similarly, sperm whales should also hear such frequency (250 Hz), as they are not known to produce clicks of echolocation lower than 200 Hz (Backus and Schevill 1966, Zimmer et al. 2005). I then assessed the propagation range at 1000 Hz, since this frequency has a high energy on the Welch' PSD (Supp. data 5) and is certainly audible by both species. Finally, I assessed the propagation range at 2750 Hz as the vessel produce sound above 2 kHz only when going backward.

3.3.2.3. PRELIMINARY INSIGHTS

Interestingly, I did not observe any clear difference between PSDs during setting and hauling, especially for frequencies below 2 kHz (Supp. data 6). This first observation confirmed that vessel signatures are mostly composed by propeller sounds (*cf.* 3.3.1). At both setting and hauling, a strong tone was observed around 1 kHz (Supp. data 6), which matches with the singing propeller signals identified for this vessel (Vessel #1 on Figure 3-5). Additionally, it may not be able to distinguish the hydraulic winch's acoustic signature since these sounds do not propagate further than 1 km (Thode et al. 2007). Between 2 and 10 kHz PSD values were slightly higher at setting than at hauling. A finer-scale investigation would be required to assess whether the acoustic signals produced by the vessel during setting and hauling propagate on different distance ranges. Also it should be confirmed whether the difference of signals between setting and hauling are actually due to the fishing activity, rather than a possible difference of condition, such as sea state (Wenz 1962, Hildebrand 2009) since both phases were recorded at different moment.

However, when closely examining the setting phase, I noticed a slight change in the soundscape after the end of setting, at 38 s on the recording (Figure 3-6). I noticed indeed that PSD values were slightly higher at setting than at post-setting. This difference was especially visible for frequencies above 2 kHz until 18 kHz, *i.e.* the maximum frequency recordable, *i.e.* half of the sampling frequency (Supp. data 7). As a result, the increase of intensities between 2 kHz and 18 kHz could not be due to the propeller cavitation (signature below 2 kHz, see section 3.3.1). Also, the difference of intensities may be less likely due to a difference of distances with the hydrophone between the two phases. Indeed, with a maximum speed around 10 knots, the boat could not cover more than 230 m in 45 s. I thus assumed that this increase of sound intensity between 2 kHz and 18 kHz may be produced by the longline itself dropping off the boat and hitting the sea surface. This observation may also explain the difference of acoustic signals observed between the setting and the hauling previously described (Supp. data 6). Consequently, this acoustic difference between setting and post-setting may be an interesting cue for odontocetes to indicate when and where a longline has been deployed.

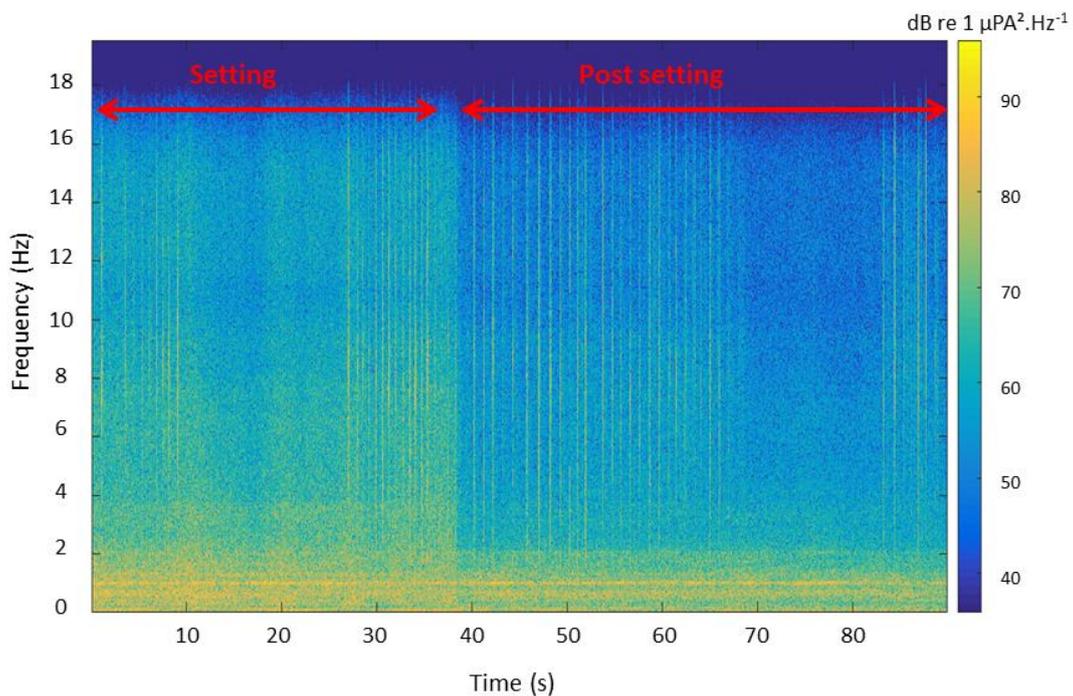


Figure 3-6 – Spectrogram of the boat ending its setting (until 38 s) and moving forward (defined as ‘post-setting’). The colour scale represents the square modulus of the acoustic pressure in units of power spectral density (in $\text{dB re } 1 \mu\text{Pa}^2 \cdot \text{Hz}^{-1}$). Clicks of sperm whales are also present (broadband frequencies produced during a very short duration).

When focusing on manoeuvres during hauling, I observed large differences in both frequencies and intensities between the sounds produced while going forward and while going backward (Figure 3-7 & Supp. data 5). Indeed, the backward manoeuvre produced sounds in broadband frequencies, with the main energy reaching until circa 6 kHz, whereas the main energy of the sound when going forward does not exceed 2 kHz (Figure 3-7 & Supp. data 5). While on the vessel I have noticed that the hull vibrates more during backward manoeuvres. The hull might enter in resonance creating these broadband frequencies sounds. This has been confirmed by a French navy expert (Legris personal communication).

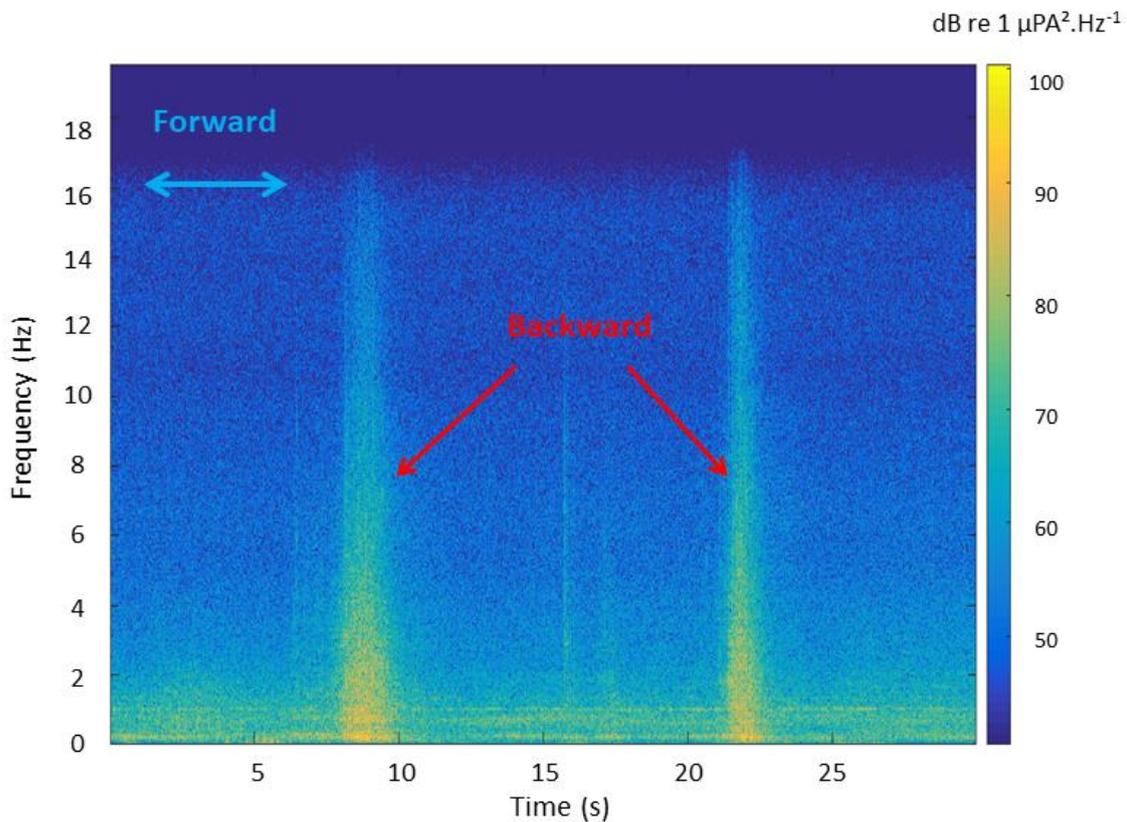


Figure 3-7- Spectrogram of the boat hauling a longline with two backward manoeuvres at 8 s and 21 s of the recording. The colour scale represents the square modulus of the acoustic pressure in units of power spectral density (in dB re 1 $\mu\text{Pa}^2 \cdot \text{Hz}^{-1}$).

I estimated the propagation range for two thresholds: 5 and 10 dB re $1 \mu\text{Pa}^2\cdot\text{Hz}^{-1}$ above the ambient noise level. From the results, the range of detectability of the vessel during a forward manoeuvre was estimated between 7 and 35 km (Table 3-2). This range is consistent with previous studies that did not use acoustics, suggesting that sperm whales and killer whales may lose track of a vessel when the latter travels over at least 30 to 40 km between two hauled longlines (Tixier et al. 2010, Tixier 2012, Janc et al. 2018). The backward manoeuvre was found to propagate on a larger distance range, with an estimated range between 30 and 270 km, at 250 Hz (Table 3-2). While a better modelling of the transmission loss (*e.g.* running beam-tracing acoustic propagation model) paired with accurate ambient noise and whale sensitivity parameters would be required, this preliminary analysis suggested that the sounds produced by a backward manoeuvre propagate circa 4 to 8 times further than those produced by a forward manoeuvre during hauling (Table 3-2). These analyses also show that a predator detecting a vessel from 8 to 18 km could also determine whether it is manoeuvring (Table 3-2). As a result, in addition of being an acoustic cue of the vessel's presence, such manoeuvre could also be a cue of the activity. Indeed, going backward is done sometimes when fishermen miss to catch the buoy or when the longline is stuck and the captain tries to orientate properly the vessels to avoid a break of the longline. Thus, some captains with less experience might manoeuvre more and be therefore more detectable by odontocetes. This hypothesis could partially explain the inter-captains variability of interaction rates for a same vessel, *e.g.* for vessel 4 at Crozet with killer whales (Figure 2-1). Further investigation should quantify any differences in the sound levels between captains to answer this hypothesis. Nevertheless, going backward seems unusual so other cues must be defined in order to assess any inter-captains detectability. A good candidate might be the approach of the longlines before hauling, which seems to vary according to captains sailing techniques. Indeed, while approaching longlines, fast deceleration or strong direction change is more likely to increase the sound production by the vessels (Trevorrow et al. 2008). Anyway, these preliminary results would suggest that avoiding too many manoeuvres, such as going backward, when it is possible should reduce the risk of vessels' detectability.

Table 3-2 – Summary of sounds levels and propagation range estimations for the vessels acoustic while going forward or manoeuvring backward.

Frequency (Hz)	RL (dB re 1 $\mu\text{Pa}^2\cdot\text{Hz}^{-1}$)		Propagation range estimations (km) Forward	Propagation range estimations (km) Backward
	Forward	Backward	[Min; Max]	[Min; Max]
250	78.2	89.6	[7 ; 35]	[30 ; 270]
1000	74.1	82.9	[5 ; 15]	[10 ; 55]
2750	60.3	75.6	[0 ; 2]	[5 ; 20]

3.4. CONCLUSION

PAM is an interesting tool to assess the interaction between odontocetes and fishermen, as it allows observing what we can't see. In this chapter, I exposed some preliminary analyses on how PAM may bring insights on interaction at the “fishermen-odontocetes” scale through the vessels acoustics for the Patagonian toothfish fishery. The results are encouraging but the amount of data analysed is too small to draw strong conclusion. It is therefore important to consider these results as interesting leads to follow for further investigations. Whereas previous studies have shown interesting results while focusing on vessels acoustic during hauling (Thode et al. 2007, 2015), here I have brought a new hypothesis that the acoustic signals during setting might play an important informative role for odontocetes on fishing activity detection. Assessing precisely how far and based on which cues predators detect the fishing activity could bring important leads toward appropriate countermeasures. A reduction of vessels' detectability may indeed decrease the risk of interaction with these odontocetes. Additionally, using the longlines as support for hydrophones could also bring fine insights on the interaction at the “longlines-odontocetes” scale through the odontocetes acoustic monitoring (Thode et al. 2014, 2015). This approach has been only presented through example of odontocetes acoustic recording as no analyses has been processed yet. However, the example shows the interest to assess PAM on our dataset, especially to affine the estimation of interaction rates, which is very likely to be underestimated, as revealed with the same method in Alaska (Thode et al. 2014).

The acoustic analyses have only been exploratory as the setting of the PAM on this fishery has constituted an important part of this thesis. The process has been laborious but fruitful I have collected around 1538 h of recordings with the acoustic array, which should allow to test and implement the tracking tools presented in the Appendix 1. Also these efforts have allow to set a friendly deployment process from longliners, which has already provided 4547 h of recording, collected by fishermen and fishery observers. Besides, the OrcaDepred funding is running until 2020, the deployments will pursue during this period and should considerably increase the dataset. Next effort should then focus on the application of an automatic detector (*e.g.* Deteclis see summary in Appendix 2) over this growing dataset to assess the presence of odontocetes around longlines and allow robust conclusions. With a long term monitoring a temporal dimension may also be add to further analyses. As for the vessel signatures, it is expected to cover all longliners and cover also most of the captains still in activity. Such dataset would allow completing the investigation upon the inter-captain variability of interaction rates, through the acoustic approach.

4. BIO-LOGGING

The previous chapter used a passive acoustic approach to assess the underwater dimension of the depredation. Within this purpose, a preliminary analysis was conducted on the fishing activity detectability, and some methods were discussed to show how PAM, while assessing odontocetes' acoustic, should bring in the future fine insights on the interaction at the “longlines-odontocetes” scale. Within the same purpose, this chapter aims at assessing when, where and how depredation occurs on the longline through a bio-logging approach. A first bio-loggers analysis is described in this chapter with a double perception of the interaction at a very fine “longlines-odontocetes” scale, since loggers were deployed on both odontocetes and on fishing gears. Additionally, this chapter proposes an experimental design for new loggers which would bring more insights on the foraging behaviour of odontocetes, either natural or in the depredation context.

4.1. INTRODUCTION

A good understanding of the odontocetes' foraging behaviours when interacting with longlines and when naturally foraging are needed to comprehensively assess the depredation conflict. Indeed, this comparison between both situations may reveal how opportunities to depredate modify the behaviour of odontocetes. Simultaneously, a fine-scale monitoring of odontocetes' behaviour in presence of fishing activity should assess their interaction behaviours and may bring more insight on how they detect vessels and longlines, and more precisely how they remove the fish from gears. To answer questions such as when, where and how odontocetes remove the toothfish from the fishing gears is essential to target efficient mitigation measures.

Investigating the fine-scale behaviour of odontocetes is challenging because of the inaccessibility of their environment. To overcome this issue, scientists have developed a broad-range of bio-logging tools. While the first time depth recorder was created in the 1960s (Kooyman 1965), the bio-logging technology has substantially evolved and been made broadly available over the last 30 years (Ropert-Coudert et al. 2009, McIntyre 2014). Bio-loggers have

allowed a better understanding of predators' spatial use of their environment either by following their horizontal displacements through ARGOS and GPS technologies or by assessing their vertical movements within the water column through time depth recorders (for examples see reviews Ropert-Coudert et al. 2009, McIntyre 2014). Then, with technological advances, devices have progressively decreased in size and increased in life-span and precision of the sensors. These improvements allow now fine assessment of marine predators foraging behaviours. For instance, the emergence of accelerometers, which measure orientation and movement dynamics of predators, have allowed measurements of fine temporal and spatial scale of predators' movements (Shepard et al. 2008, Brown et al. 2013). Indeed, from fine movements monitoring it is possible to assess sharp acceleration and to determine feeding events of marine predators (Viviant et al. 2010, Gallon et al. 2013, Ydesen et al. 2014, Volpov et al. 2015). However, these new device loggers are also memory consuming and must be recovered, which is difficult for some marine predators, especially cetaceans. Indeed, the main studies on marine mammals have been conducted on pinnipeds (Ropert-Coudert et al. 2009, McIntyre 2014) since these species are partially terrestrial making the deployment and recovering easier than for cetaceans who are accessible only when breathing. In addition to this limited accessibility, the limitation in the use of loggers on exclusively aquatic species has been the attachment techniques (Hooker and Baird 2001, McIntyre 2014). Two techniques are currently used: a long-term fixation, using stainless steel barbs to penetrate the skin, preventing tags recovering, and short-term fixation using suction-cups and allowing tags recovering. There is thus a trade-off between the quantity and the quality of data attainable for cetaceans. However, satellite transmission of data is possible, which allviates the need to retrieve loggers. Although the amount of information that can be successfully transmitted is limited, previous implementations have included the execution of simple algorithms capable of extracting basic behavioural metrics such as dive duration or maximum depth. The next step in bio-logging is to implement within loggers some methods developed by the community in order to transmit summarized information from these large data-sets. A recent study assessed this new possibility of transmittion by satellites the number of prey capture events made by southern elephant seals during their trip at sea from an on-board processing of accelerometry (Cox et al. 2018). This method is highly promising for other marine mammals' studies, especially cetaceans, but the method should be tested for other species since the algorithm implemented on the tag has been developed for elephant seals (Vacquié-Garcia et al. 2015, Richard et al. 2016, Cox et al. 2018).

Although the number of bio-logging studies is constantly increasing (McIntyre 2014), only a few studies have used bio-loggers to study marine mammals depredation behaviour (Mathias et al. 2012, Straley et al. 2014, Towers et al. 2018). The limited number of logger deployments to study this issue is easily explained by the technical and logistical constraints imposed by the fishing context. Indeed, odontocetes do not necessarily approach vessels with a range close enough to allow tagging. Moreover, during hauling, vessels are not manoeuvrable to help for tagging. First biologging studies on depredation have described some sperm whales interaction behaviours: sperm whales following fishing boats (Straley et al. 2014) and changing diving behaviour with shallow dives while depredating on hauled longlines (Mathias et al. 2012). Biologging studies are encouraging to study more species in different fisheries as they allow for data to be collected during interaction phases when individuals are sighted close to the boat (<500m, see Mathias et al. 2012) but also during potential interaction phases occurring when the boat is away from the fishing gear. Fine spatio-temporal scale of marine mammals movements still require more investigation to highlight how animals spot fishing activities and to improve our understanding of interaction behaviours. Another interesting use of loggers to investigate marine mammals' depredation is by deploying loggers on longlines, which is much easier than tagging marine mammals. For instance, accelerometers deployed on pelagic longlines paired with video cameras have revealed that odontocete depredation may occur not only on the catch, but also on the baits (Thode et al. 2016). Camera deployment is more complicated on demersal longlines because of low light conditions. Preliminary trials have revealed depredation by southern elephant seals on Patagonian toothfish fishery during soaking time (van den Hoff et al. 2017) although the seals might have been attracted by the light explaining the fortunate video footages. Thus, deployment of accelerometers on demersal longlines should be more workable than camera, similarly to the first deployments on pelagic longlines in Hawaii (Thode et al. 2016).

In this thesis I used both animal-borne behavioural data loggers and longline-attached data loggers to assess the interactions between the odontocetes and the fishing gear. My contributions are two-fold: both methodological and experimental. On the first hand, I assessed a method to estimate prey catch attempts by large odontocetes to be embedded within a logger for on-board processing (section 4.2). The method was assessed using DTAGs' data from SMRU (Dr. Johnson) and was then sent to Wildlife Computers during this PhD to be implemented into new loggers. On an experimental point of view, I personally deployed bio-

loggers during my second field mission, and subsequently analysed their data. In particular, I deployed 4 of the new loggers with my algorithm implemented by Wildlife Computers, but none emitted any signal. This failure is currently being investigated by Wildlife Computers. I also deployed 4 classical ARGOS tracking loggers (SPLASH 10 and SPOT 5 from Wildlife Computers) on killer whales. One of the loggers remained only a few hours on the individual because the anchors were not pegged deep enough on the individual's skin. Among the 3 loggers correctly deployed, two had pressure sensors (SPLASH 10) and were analysed in this thesis paired with the data provided by accelerometer/pressure sensor loggers (section 4.3).

The number of loggers deployed on odontocetes may look relatively small, when compared to the length of the field mission (3 months). However, the number of loggers was limited because of the costs of the loggers (10 available), and opportunities were quite rare (8 deployments). Indeed, a successful deployment requires gathering good conditions both from the weather and the approach of individuals. As deployments are made by crossbow from the deck at 5 m above the water (without any swell), individuals should swim along the hull to enable a good shot with enough power to peg the tag in individuals' skin. On the one hand, although sperm whales were seen quite often (present around 75% of my mission, both at Crozet and Kerguelen) they did not approach close enough. On the other hand, although killer whale came close enough to the boat, they were not seen very often (observed 10 days during my mission at Crozet). My experience confirmed the difficulty to deploy loggers from fishing boats, but the success on some killer whales is encouraging for further deployments. However, new deployments would require rethinking the material to optimise success, based upon this experience on such condition.

For the accelerometer/pressure loggers attached on the swivel of a hook (see description on section 4.3.3 and Supp. data 8), deployments were found easy to process directly on the operational fishing gear. Deployment did not require any intervention of the fishermen, as the hooks equipped with loggers were baited as the other hooks. The recovery was also easy but necessitated the help of the fishermen, as they removed the loggers from the mainline while hauling the fish. However, the recovery was a little bit time consuming and for the sake of fishermen's work it was preferable to not deploy too many loggers on the same section. The deployment could be constraining when the longline had to be hauled fast (for instance in presence of odontocetes) or within bad weather conditions, increasing then the risk to lose or to miss a logger and damaged it through the winch. As the deployment of these loggers did not

required to set experimental sections of longline, the number of deployments could be sizable. Thus 556 hooks were equipped over the two missions. However, although the number of loggers is important, it is questionable whether it is representative of the whole fishing effort and thus whether such effort could quantify what is happening underwater, which would be approached in section (section 4.3).

4.2. ON-BOARD PROCESSING ACCELERATION DATA TO ASSESS PREY CATCH ATTEMPTS

4.2.1. INTRODUCTION

The purpose of this first study was to test a method to estimate prey catch attempts from acceleration data, similarly to the methods implemented on pinnipeds (Cox et al. 2018). I used data from DTAGs, combining acoustic recording with acceleration data (Johnson and Tyack 2003). Sperm whales use echolocation to forage, and more precisely, they produce "buzzes", which have been described as click trains with high click rate, while attempting to catch a prey (Madsen 2004, Miller et al. 2004, Watwood et al. 2006, Fais et al. 2016). Indeed, Fais et al. (2016) observed through acceleration data that sharp movements occurred at the end of buzzes, which may revealed the prey engulfment. Thus, buzzes are good acoustic clues for prey catch attempts. While this previous study focused at the scale of buzzes (Fais et al. 2016), I wonder whether acceleration only would enable estimation of the number of prey catch attempts per dive. Our purpose was to assess a simple model to estimate sharp movements, which could be easily implemented within a tag. I then required a model with two constraints. First, acceleration would be processed at a dive scale and not over the whole logger dataset. Second, the method must be fully automatic, *i.e.* it must determine a threshold to estimate whether acceleration values define a prey catch attempts. Finally, I tested the accuracy of our method by assessing the correlation between our estimation of prey catch attempts from acceleration data and the number of buzzes, another good proxy of feeding events.

4.2.2. METHODS

4.2.2.1. PREY CATCH ATTEMPTS ESTIMATIONS

Acceleration data were provided by Dr. Mark Jonson (SMRU, St Andrews, UK) and were obtained from DTAGs deployed on 6 sperm whales in Mediterranean sea. The DTAG is an archival device that records acceleration at 25 Hz, pressure at 1 Hz and acoustic data with sampling-rate programmable between 2–200 kHz (Johnson and Tyack 2003). DTAGs were attached on sperm whale body thanks a square array of 4 suction cups and after the release of the tag from the whale, a VHF radio within the tag aided recovering the tag. A dive was considered for a depth below 50 m. For every dive, buzzes were counted thanks to acoustic recording by the DTAG. The acoustic recordings were process by Dr Mark Johnson and he directly provided us the buzzes' timings.

During buzzes made by sperm whales, it has been described through acceleration jerks that prey captures or maybe prey engulfment last around 1.5 s (Fais et al. 2016). Using a similar approach implemented on pinnipeds, I assessed the standard deviation of acceleration (Viviant et al. 2010, Gallon et al. 2013) every second within a moving window lasting twice the duration of the jerk event (3 s) described by Fais et al. (2016):

$$\text{EQUATION 4-1 } \mathbf{d}(t) = \frac{\sigma[a_x(t)] + \sigma[a_y(t)] + \sigma[a_z(t)]}{3}$$

with a_x , a_y and a_z the acceleration value (in g) along the x , y and z axes, and $\sigma[a_i(t)]$ the standard deviation of acceleration (a_i) for time between $t-1.5$ to $t+1.5$ seconds (*i.e.* during 3 s).

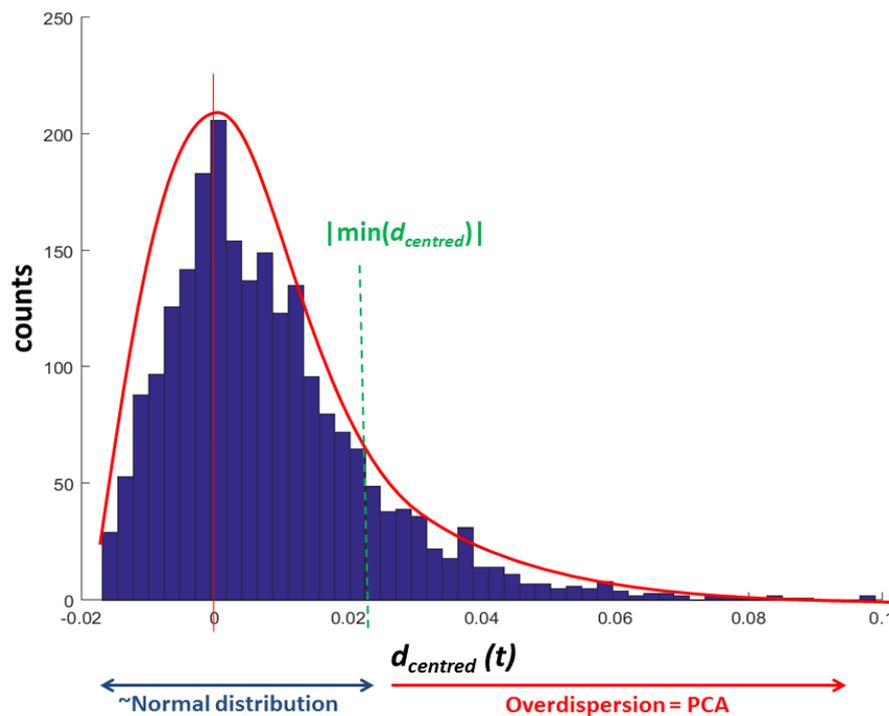


Figure 4-1 - Distribution of d (Equation 4-1) centred on 0: $d_{centred}(t) = d(t) - \text{mean}(d)$.

The amplitude of the movement recorded over this 3 s is represented through $d(t)$ (Equation 4-1). The purpose was then to assess how the amplitudes of movements over 3 s were distributed per dive (Figure 4-1). Empirically, I found that $d(t)$ has a quasi-Gaussian distribution components with an over-dispersion for positive high values and no negative values. No true statistical distribution was sought to describe $d(t)$, as a simple description based on empirical mean and standard deviation was enough to fulfil my objective.

I interpreted that the Gaussian part of the distribution of d (Equation 4-1) represents values of the movements' amplitude the most regular of a dive (*i.e.* values with the highest counts Figure 4-1). Considering sperm whales behaviour while diving, I hypothesised that these values of low acceleration amplitudes occurring regularly transcribe the swimming pattern. Conversely, the over-dispersion represents some sharp movements occurring at low frequency (Figure 4-1). As prey catch attempts are punctual compared to the swimming pattern and may be sharp movements, I hypothesised that the PCA are described through the over-dispersion of d (Figure 4-1).

Finally, within the purpose of defining the threshold above which the spurt would be considered as a PCA, I computed the distribution (*i.e.* histogram) of d at the scale of a dive, and centred the distribution around 0 (Figure 4-1). From the obtained distribution of d centred on 0, I retrieved the minimal negative value. Its absolute value (*i.e.* the positive mirror image) was finally used as the threshold (threshold= $|\min(d)|$) to categorise the over-dispersion (Figure 4-1). This approach allowed an easy automatic threshold determination per dive to assess the PCA

Once the PCAs were estimated, I monitored their occurrence at the same time as buzzes on sperm whales' dive profiles. I then assessed whether both events are associated. They were considered as associated if the PCA occurred within 10 s before the end of the buzz and 2 s after the end of the buzz.

Data were processed through the software Matlab (version R2015, The MathWorks, Natick, MA, USA).

4.2.2.2. RELATIONSHIP BETWEEN PREY CATCH ATTEMPTS AND BUZZES

To evaluate the relevance of our PCA detection method, we assessed the linear regression between the number of buzzes B_{ij} and the number of PCA P_{ij} for every individual i and dive j :

$$\text{EQUATION 4-2 } B_{ij} = \alpha + a_j + (\beta + b_j)P_{ij} + \varepsilon_{ij}$$

with α and β the global intercept and slopes of the regression, a_j the random effect on the intercept for the individual j , b_j the random effect on the slope and ε_{ij} the residual for a given dive i of the individual j . The random effect was tested first on the intercept only ($b_j = 0$), meaning that the regression is the same between individuals but there might be overestimation or underestimation of the number of PCA due to the accelerometer. I then tested the random effect also on the slope ($b_j \neq 0$), to see if the relation between the number of buzzes and the number of PCA is random, and so the method could not be implemented. After checking the normality of residuals, I compared the linear model to the null model and assessed a step backward approach to determine the best model (with or without random effect) through the Akaike Information Criterion (AIC) selection (Akaike 1974, Zuur 2009). The mixed linear models were assessed with a Gaussian distribution, using the function *lmer* of the package *lme4* through the software R (R Development Core Team 2015).

Once a proper model is determined, the regression should allow approximation of the number of buzzes from the estimated PCAs. Indeed, the purpose is to implement this method within a tag without any acoustic data. Thus, I processed to a leave-on-out cross validation with the 6 individuals. I ran the model by removing one individual, such as his numbers of buzzes per dive were unknown. For this individual I then estimated the number of PCA using acceleration data only. Then, the coefficients of the model obtained with the 5 other individuals were used to find back the number of buzzes for the 6th individual from its number of PCA. I finally calculated the difference between the accurate number of buzzes of this individual and the number of buzzes estimated by the regression from the 5 other individuals. I repeated the process for each individual.

Finally, I assessed whether the PCA determined through the acceleration data occurred at the same time than the buzzes. I measure a percentage of association for both proxies compared to the other one. In other word I estimated the proportion of PCA produced within the vicinity of a buzz and conversely, the proportion of buzzes occurring near PCA. I set this 2 s flexibility within the hypothesis that the acceleration may detect the prey engulfment after a catch and that sperm whale may stop buzzing instantly once the prey is caught.

4.2.3. RESULTS

4.2.3.1. PREY CATCH ATTEMPTS ESTIMATIONS

The number of prey catch attempts was estimated for 31 dives recorded among the 6 tags. I observed that the distribution of d , for all the dives and all individuals, followed a the same quasi-normal distribution with some over-dispersion (Figure 4-2). The threshold estimated as the absolute of the minimum dispersion value (red line Figure 4-2), allowed us to determined prey catch attempts over the diving profile (red points Figure 4-2). As I added buzzes on the diving profile (green points Figure 4-2), I observed that most of PCA and buzzes overlapped (Figure 4-5). I finally tested whether the observation of these overlaps between our estimation of PCA and the buzzes are consistent over every dive for every individual.

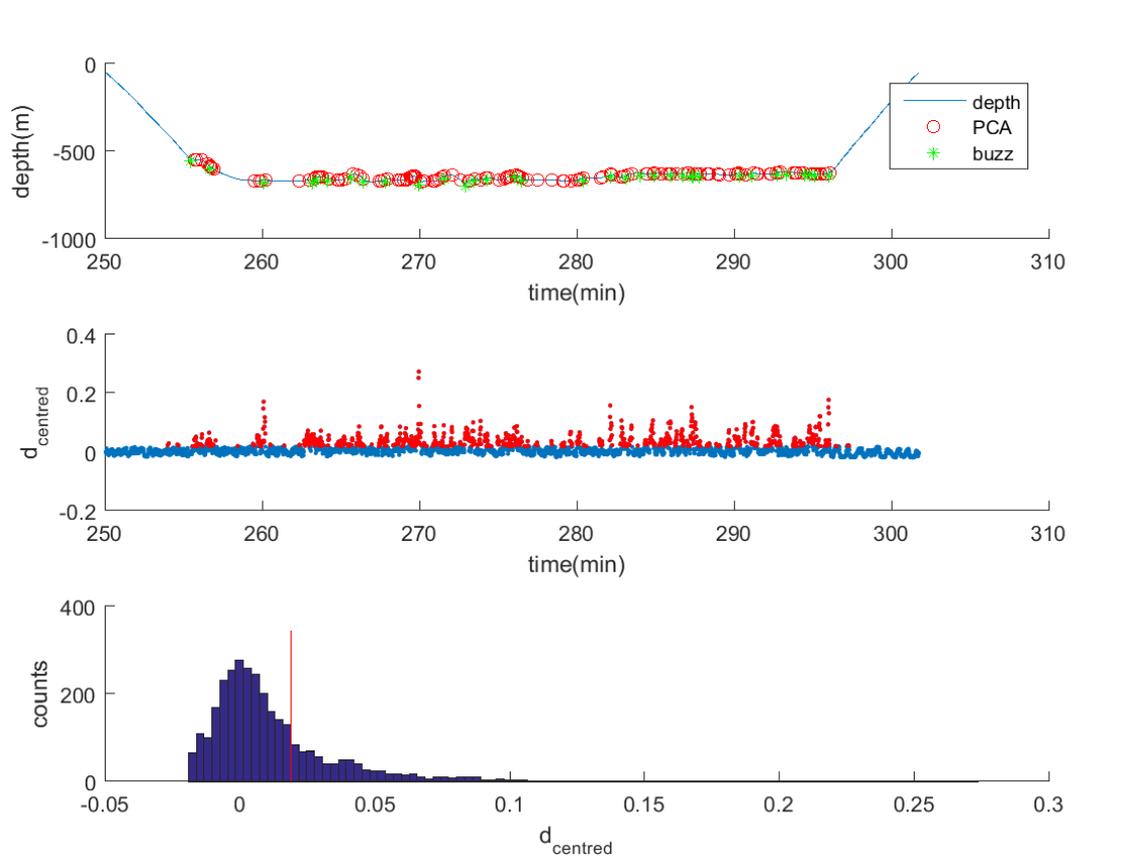


Figure 4-2 - Example of prey catch attempts estimations, in red, over a dive profile with buzzes events, in green (top panel). Value of $d(t)$ over the dive, with the over-dispersed values considered as PCA in red (middle panel). Distribution of d , with the threshold ($|\min(d)|$) estimation represented by the red line (bottom panel).

4.2.3.2. RELATIONSHIP BETWEEN PREY CATCH ATTEMPTS AND BUZZES

The residuals followed a normal distribution and according to the AIC selection the best regression was found for the linear mixed model assessing a random effect on the intercept only (Table 4-1). The regression between the number of buzzes and the number of PCA was significantly positive ($p < 0.001$, Figure 4-3), and the intercept of the model is not significantly different from 0 because of the variance due to individuals (Intercept = 2.9 ± 6.2).

Table 4-1 – Summary of the models' AIC.

Model	AIC	degree of freedom
<i>Number of buzzes</i> _i = α	238	2
<i>Number of buzzes</i> _i = $\alpha + \beta PCA_{ij} + \varepsilon_i$	209	3
<i>Number of buzzes</i> _{ij} = $\alpha + a_j + \beta PCA_{ij} + \varepsilon_{ij}$	192	4
<i>Number of buzzes</i> _{ij} = $\alpha + a_j + (\beta + b_j) PCA_{ij} + \varepsilon_{ij}$	196	6

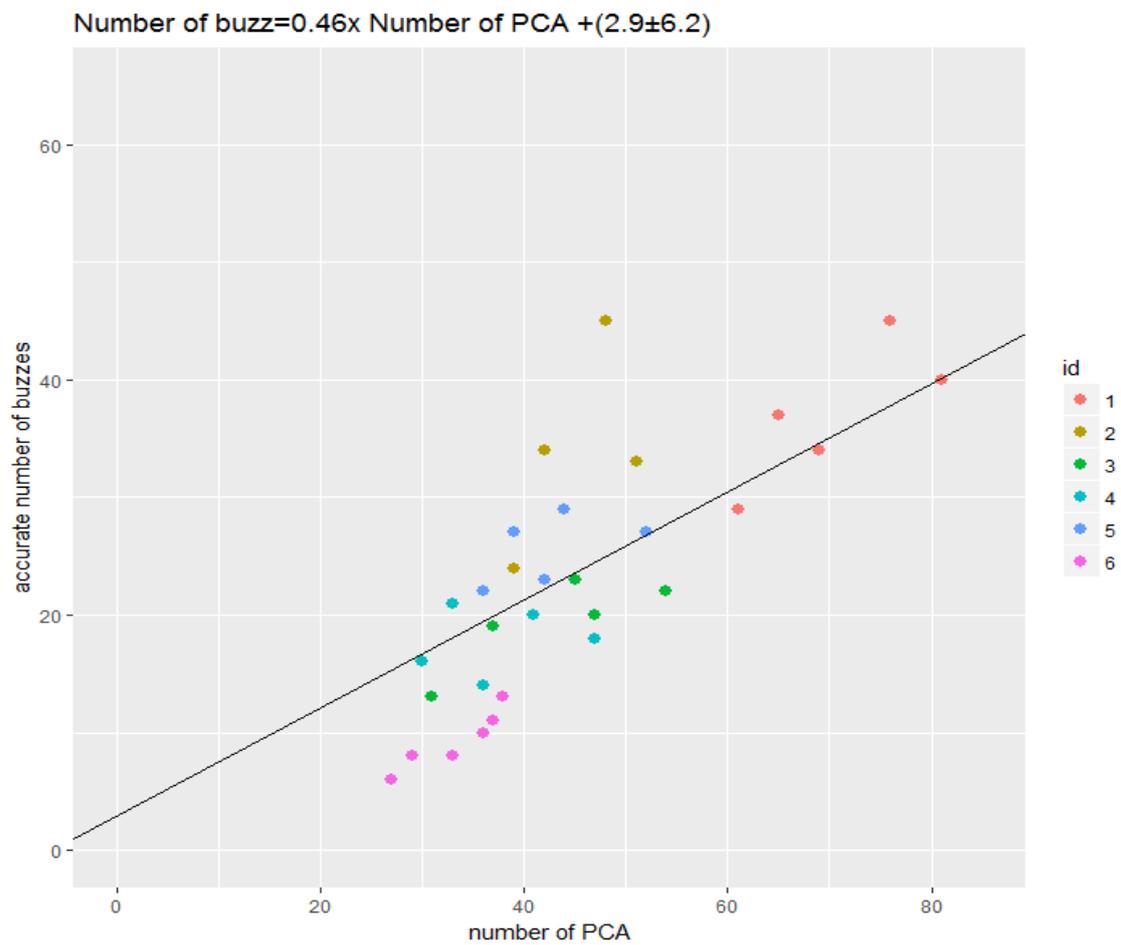


Figure 4-3 - Regression between the number of buzzes and the number of prey catch attempts estimated by our method. The mixed linear model equation (black line) was: $B_{ij} = 0.46x P_{ij} + (2.9 \pm 6.2)$.

The differences of intercept between individuals suggest that the model may underestimate or overestimate the number of buzzes from a same estimation of PCA between tags. However, the relationship between the number of buzzes and the number of PCA was the same between individuals since adding a random effect on the slope did not improve the regression. As a result, I only have to take into account the intercept variance between individuals to correct the estimation of buzz using the number of PCA determined. I then estimated the number of buzzes for each individual with a regression calculated from the 5 other individuals (Figure 4-4).

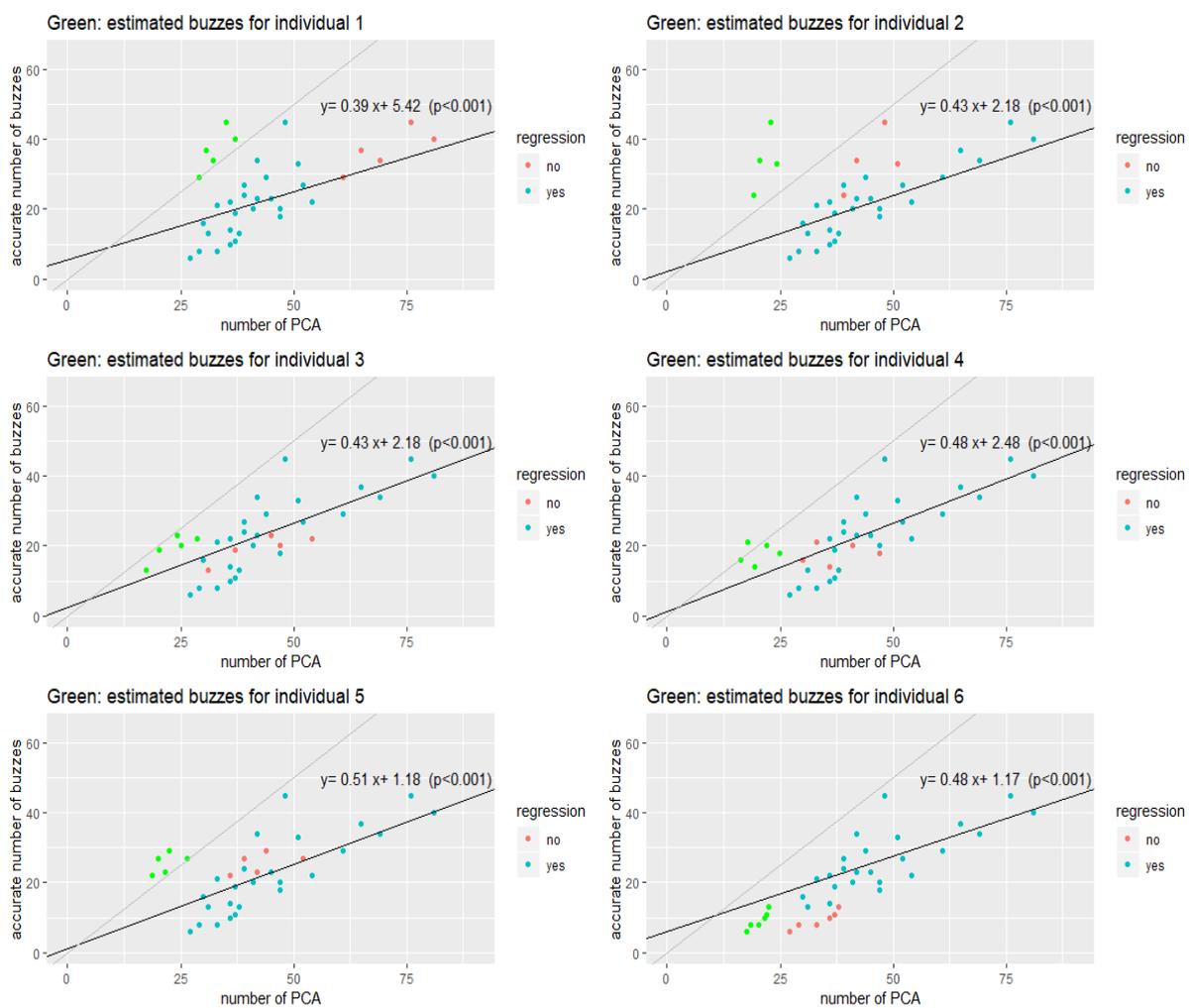


Figure 4-4 - Estimation of the number of buzzes (green) for each individual from the linear regression (dark line) estimated by the 5 other individuals (blue). Equation for each regression with the slope's p-value were noticed on each graph. The numbers of PCA of each individual not considered in the regression were represented in red. The estimated number of buzzes for each individual (green) should follow the equation $y=x$ (grey line) for a correct estimation.

The application of the regression coefficients obtained with 5 individuals on the PCA numbers of the 6th individual approximated well the accurate number of buzzes (Figure 4-4, Table 4-2), except for one individual (ID 6) for which I estimated a number of buzzes twice higher than the accurate number of buzzes (Table 4-2). However, for the other individuals I underestimated or overestimated the number of buzzes by 15% of the accurate number (*i.e.* ~ 5 buzzes, see Table 4-2).

Table 4-2 – Sumamry of the error estimation of the buzzes numbers per dive per individuals (Figure 4-4).

ID	Mean accurate number of buzzes per dive	Mean estimated number of buzzes per dive	Mean error number of buzzes	% of error
1	37	35.3±6.2	-1.7±3.8	-3.7±9.5%
2	33.8	24.1±6.2	-9.7±6.6	-26.5±12.7%
3	19.4	22.6±6.2	3.2±2.3	17.6±13.2%
4	17.8	20.1±6.2	2.3±3.8	14.9±22.4%
5	25.6	22.5±6.2	-3.1±2.8	-11.7±9.8%
6	9.3	18.2±6.2	8.9±0.9	102.8±34.5%

I estimated per dive that 51±14 % of the PCAs were associated with a buzz, and the minimum percentage of association for a dive was observed at 30% for and the maximum was obtained at 73 % (Figure 4-5). Conversely, 61±15 % of buzzes were associated with a PCA, and the minimum percentage of association for a dive was observed at 36% for and the maximum was reached 100 % (Figure 4-5).

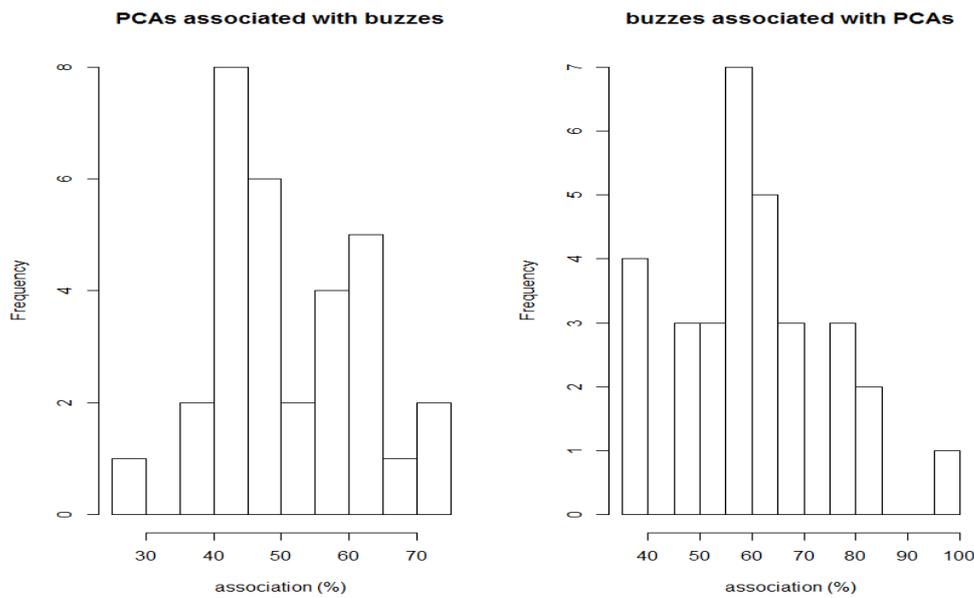


Figure 4-5 – Histograms of association (%) between buzz and PCA for the 6 individuals' dives.

4.2.4. DISCUSSION

Our study assessed by a simple way the prey catch attempts (PCA) using only acceleration data. The method described and implemented on pinnipeds (Viviant et al. 2010, Gallon et al. 2013, Cox et al. 2018) could be also implemented on sperm whale and probably on other large cetaceans. Indeed I observed a good relationship between the PCA estimated by the acceleration data and the buzzes. The method also brought an easy threshold determination of the prey catch attempts on the acceleration data, allowing then a simple automation within a logger for on-board processing. However, I obtained more PCA than buzzes and 49% of them were not associated to buzzes, *i.e.* false positives, which may be explained by other fast body movements or by attempts that occur without buzzes. Indeed, sperm whales might not use buzzes for every feeding attempts as they may only accelerate rhythm of clicks production while foraging, but not fast enough to be considered as a buzz (Madsen et al. 2002). By listening to the acoustic data from the DTAGs it would be possible to define whether the rhythm of clicks accelerates without ending in a buzz to confirm our hypothesis. Thus, either this PCA method may be more precise than the estimation of buzzes, or a lot of false alarms are detected. However, not all buzzes were associated with PCA suggesting either a miss of the feeding attempt occurred during these buzzes or the body movement to catch the prey was not sharp enough to be detected through our method.

Further investigation should focus on other proxies to estimate prey catch attempts in order to assess different kind of movements realised by the odontocetes. The purpose would be to allow discrimination between acceleration signals which components belong to which movement behaviours. This may allow describing different feeding attempts as individuals hunt differently according to the kind of prey. Nevertheless, the implementation of this method seems interesting enough to assess sperm whales foraging activities as results showed that it would be possible to apply correction coefficients from the linear regression used to approximate the number of buzzes. Although the feeding attempts might be overestimated or false alarms could be detected, the results suggest that we may at least interpret with confidence variation of PCA between dives for same individuals as a variation in feeding activity. Additionally, different prey types may lead to different ratios between PCA and buzzes too. One limitation of this study could be the difference of diet between sperm whales equipped with DTAG and individuals in Crozet and Kerguelen waters. Thus, further investigations on other populations with closer ecology than in French sub-antarctic islands should be of great interest to confirm the results described in this chapter. However, within the context of our project on depredation, such loggers implanting this method would allow to assess differences of rapid body movements as a proxy of individuals' foraging activity in presence or absence of fishing gear.

The method has been implemented in new loggers by Wildlife Computers and they were available for the second field mission. Unfortunately, none of the 4 loggers deployed on sperm whales transmitted any signal, avoiding the possibility to collect any of these data. Hopefully, the tampering of these loggers should be corrected by Wildlife Computers and new loggers should be deployed in the future. Nevertheless, other more classical ARGOS tracking loggers have been deployed on killer whales and data have been recovered. These bio-logging data have then been analysed paired with the dataset obtained from loggers deployed on longlines. The results revealed new insights of the underwater interactions between toothed whales and fishing gears, as presented hereafter.

4.3. EVIDENCE OF DEEP-SEA INTERACTIONS BETWEEN TOOTHED WHALES AND FISHING DEMERSAL LONGLINES.

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4.3.1. ABSTRACT

Toothed whales (odontocetes) feeding on fish caught on hooks in longline fisheries is a growing issue worldwide. The substantial impacts that this behaviour, called depredation, can have on the fishing economy, fish stocks and odontocetes populations raise a critical need for mitigation solutions to be developed. However, information on when, where and how odontocete depredation occurs underwater is still limited, especially in demersal longline fisheries (fishing gear set on the seafloor). In the present study, we investigated depredation by killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) on demersal longlines in the French Patagonian toothfish fishery (Southern Ocean). Using a combination of animal-borne behavioral and longline-attached data loggers, we revealed that both species are able to depredate longlines on the seafloor. This study suggests, therefore, that odontocete whale-longline interaction events at depth may be unrecorded when assessing depredation rates from surface observations during hauling phases only. This result has implications for the management of fisheries facing similar depredation issues as underestimated depredation rates may result in unaccounted fish mortality in fish stock assessments. Therefore, while further

research should be conducted to assess the extent of deep-sea whale-longline interaction events during soaking, the evidence that depredation can occur at any time during the whole fishing process as brought by this study should be considered in future developments of mitigation solutions to the issue.

Keywords: depredation, killer whales, sperm whales, demersal longlines, Patagonian toothfish, bio-logging

4.3.2. INTRODUCTION

The intensification of fishing activity over the last decades has been associated with an increase in direct interactions between fisheries and marine top predators worldwide (Northridge 1991; Northridge and Hofman 1999; Read et al. 2006; Read 2008). Depredation, which occurs when marine predators remove or damage fish from fishing gear, is a type of interaction often resulting in substantial impacts on fishing activity, depredating species and fish stocks (Donoghue et al. 2002; Gilman et al. 2006; Read 2008). Longlines are composed of a main line with baited hooks attached at intervals by means of branch lines called snoods. The main line is either deployed in the water column, *i.e.* pelagic longlines, or on the seafloor, *i.e.* demersal longlines. Therefore, longlining is a fishing technique that makes caught fish easily accessible for depredating animals. It has been reported to be the fishing technique most impacted by depredation, especially by toothed whales, *i.e.* odontocetes (Northridge and Hofman 1999; Donoghue et al. 2002; Gilman et al. 2006; Hamer et al. 2012). Indeed, at least 31 species of odontocetes have been reported to interact (either through depredation or bycatch) with longline fisheries worldwide (Werner et al. 2015). Depredation on fisheries leads to greater costs for fisheries. This is due to damaged fishing gear, damaged fish losing economical value, and increased effort to both avoid competition and reach quota limits (Peterson and Carothers 2013; Peterson et al. 2014; Tixier et al. 2015c; Werner et al. 2015). For odontocetes, interactions with longlines may increase risks of mortality, either by entanglement in fishing gear, *i.e.* bycatch (Northridge 1991; Trites et al. 1997; Read et al. 2006; Hamer et al. 2012), or by the use of lethal methods by illegal fisheries to eliminate competitors (Poncelet et al. 2009; Guinet et al. 2015). Also, depredation often involves access to new and easy-to-catch prey resource for predators, which may modify both the energy balance of odontocetes and the natural predator-prey dynamics of local ecosystems (Trites et al. 1997; Northridge and Hofman 1999; Boyd

2002; Guénette et al. 2006; Morissette et al. 2012; Tixier et al. 2017). For fish stocks, depredation may result in biased assessments and over-exploitation if the amount of depredated fish is not precisely estimated (Roche et al. 2007; Read 2008). Together, these multiple impacts of depredation, may jeopardize the sustainability of local fishing activity. Currently, there is a critical need for mitigation solutions. However, when, where and how fish are removed from longlines by odontocetes remains poorly understood yet is crucial to developing effective countermeasures to depredation. For instance, some mitigation devices may be efficient only during specific fishing phases, such as hauling. This is the case of the ‘Cachalotera’, a floating net sleeve sliding down over individual fish caught on a hook when the longline is hauled to protect it from depredating whales (Hucke-Gaete et al. 2004; Moreno et al. 2008). Another example is the SAGO, a catching pod going down the longline to collect the fish during hauling (Arangio 2012).

Depredation has been described to occur during both soaking and hauling phases for pelagic longlines (Dalla Rosa and Secchi 2007; Forney et al. 2011; Rabearisoa et al. 2012; Passadore et al. 2015; Thode et al. 2016) whereas this behavior has only been assumed to occur during hauling phases for demersal longlines (*e.g.* Mathias et al. 2012, Tixier 2012, Werner et al. 2015). In demersal longline fisheries, depredation rates are assessed from visual observations of depredating animals in the vicinity of fishing boats, or counting the number of damaged fish on hauled longlines (*e.g.* Hucke-Gaete et al. 2004, Purves et al. 2004, Roche et al. 2007, Rabearisoa et al. 2012, Straley et al. 2015, Söffker et al. 2015, Passadore et al. 2015). However, some studies using alternative types of data, such as underwater videos or acoustics, have showed that odontocetes can depredate baits and remove the whole fish from the hook (Mathias et al. 2009; Thode et al. 2014; Guinet et al. 2015; Thode et al. 2015; Thode et al. 2016). Therefore, methods using indirect approaches have been implemented to assess the extent of depredation in demersal longline fisheries. For instance, Gasco et al. (2015) proposed to estimate depredation rates based on the difference in fishing efficiency in the absence and in the presence of odontocetes within a restricted geographical area. Such approach requires an accurate and reliable monitoring of the presence of depredating animals during the fishing operations. However, there are still large knowledge gaps on the underwater depredation behaviour of odontocetes. Specifically, it is not known if the odontocetes depredate on demersal longlines soaking on the seafloor while the fishing vessel is potentially hundreds of kilometres away. Although interacting with longlines on the seafloor would require individuals to dive

deeper and, therefore, to expend greater energy than when depredating on longlines in the water column, both killer and sperm whales have diving capabilities that fully or partly encompass the depth range at which longlines are set on the seafloor. Indeed, killer whales have been recorded diving at maximum depths circa 1000 m (Reisinger et al. 2015; Towers et al. 2018) and sperm whales at maximum depths of circa 2000 m (Teloni et al. 2008; Fais et al. 2015; Guerra et al. 2017).

In the present study, we approached this problem by using fine-scale bio-logging technology deployed on both depredating odontocetes (ARGOS satellite tracking tags equipped with depth sensors) and longline sets (accelerometers paired with depth sensors) from commercial demersal longline fisheries. By combining these two approaches, our primary aim was to investigate the occurrence of odontocetes depredation events on demersal longlines in the underwater dimension during both soaking and hauling phases of the fishing process. The initial objective was to use the two methods to study both killer whales and sperm whales. Unfortunately, this turns out to be impossible. In the following, we will see that accelerometers deployed on longlines have been useful to study sperm whales (Sec. “longline accelerometry”), while tags deployed on animals were useful to study killer whales only (Sec. “Odontocetes tracking data loggers”).

4.3.3. METHODS

4.3.3.1. RESEARCH CONTEXT

The study focused on a depredation conflict involving the French Patagonian toothfish fishery with killer whales and sperm whales. The Patagonian toothfish is a long-lived (>50 years) and a large (> 200 cm in length and > 200 kg in weight) species (Collins et al. 2010), with high-quality flesh making the species economically highly valuable (Collins et al. 2010; Grilly et al. 2015). The French longline fishery is of particular scientific interest since it holds the largest Patagonian toothfish quota in the Southern Ocean (COLTO 2016) allocated between the subantarctic islands of the Crozet Archipelago (46°25'S, 51°59'E) and Kerguelen Islands (49°20'S, 70°20'E, see Figure 4-6). Additionally, this fishery also experiences the highest depredation levels of all toothfish fisheries, with more than 30% and 9% of the total annual catch taken at Crozet and Kerguelen, respectively, by killer and sperm whales (Roche et al.

2007; Tixier et al. 2010; Gasco et al. 2015; Janc et al. 2018). Interaction levels are fundamentally different between the two EEZs with sperm whales being present around both islands but at different densities (Labadie et al. 2018) and killer whales being almost exclusively found at Crozet (Tixier et al. 2010; Guinet et al. 2015).

Fishing seasons last a year, starting in September and ending in August. A fishing season consists of 3 or 4 trips of approximately 3 months each. During a trip, vessels fish continuously through a diel pattern. Longlines are set at night and primarily hauled during the day, since fishing regulations prohibit setting at daylight to avoid seabird bycatch (Weimerskirch et al. 2000). During trips, all longline positions (latitude and longitude), bathymetry at deployments (500 – 2000 m), and setting and hauling times are recorded. Fishing in waters shallower than 500 m is prohibited to avoid the capture of juvenile toothfish (Collins et al. 2010; Gasco 2011). Vessels use auto-weighted longlines set between two anchors and linked to buoys at the surface for retrieval. The lines are composed of sections of 750 hooks, with 1.2 m between hooks. The length of the longlines varies from 1 to 40 km, with an average of approximately 8 km. For each longline hauled, the presence of cetaceans (killer whales and/or sperm whales) is monitored according three classes: (i) whales absent (condition suitable for a confident observation); (ii) whales present; and (iii) uncertain-observation (conditions unsuitable and/or no observation undertaken). Data were available through the PECHEKER database (Museum National d'Histoire Naturelle de Paris; Martin and Pruvost 2007).

Data collection for this study was conducted from two commercial demersal longline fishing vessels during two summer trips (December - March) in 2016-2017 and in 2017-2018.

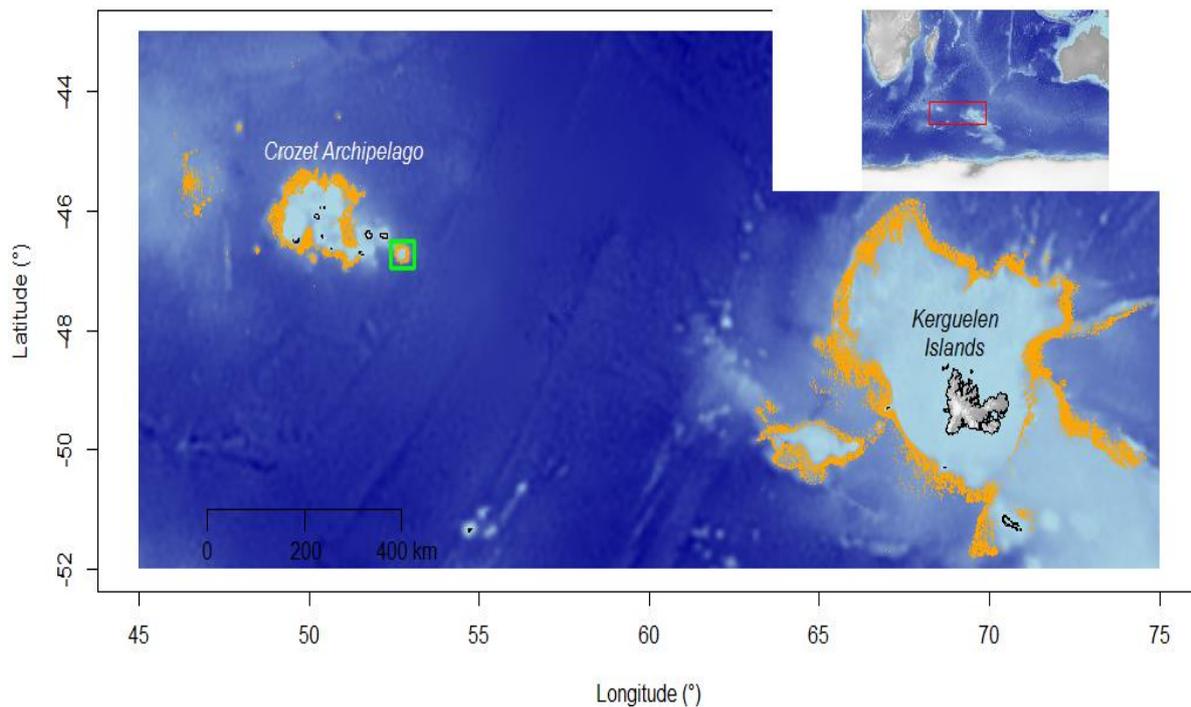


Figure 4-6 - Map of the study area with the locations of the fishing activity (orange dots) around Crozet and Kerguelen. The green rectangle indicates the seamount where the deployment of instruments on killer whales occurred.

4.3.3.2. ODONTOCETES TRACKING DATA LOGGERS

We deployed six ARGOS satellite tracking tags equipped with depth sensors (2 SPLASH10-292A units and 4 SCOUT-DSA units, Wildlife Computers, Redmond, Washington, USA) on 3 killer whales and 3 sperm whales. The 6 loggers were deployed from the fishing boat during longline hauling operations using modified crossbow arrows (Wildlife Computers) and fired from a 68 kg draw weight crossbow (Barnett Rhino, Barnett Outdoors Inc., Tarpon Springs, Florida, USA). The devices recorded diving depths using a pressure sensor every 2.5 minutes, with an associated error band. Between dives, the instruments were set to transmit geographic positions and depth data every 2 h through the ARGOS system (Collecte Localisation Satellites, Toulouse, France).

Position estimates were categorized into five estimated accuracies: (i) class with no estimate; (ii) class 0: $\geq 1\ 500$ m; (iii) class 1: 500-1 500 m; (iv) class 2: 250-500 m; (v) class 3: ≤ 250 m (Collecte Localisation Satellites, Toulouse, France). These accuracies were used to

determine a confidence area around the ARGOS positions. Position without uncertainty estimates (classes i) were removed from the dataset. ARGOS positions were processed using the software R (version 3.4.4, R Development Core Team). We mapped every position using a buffer function (*create.buffer*, package *marmap* version 1.0.2) to account for potential location accuracy errors. Bathymetric data were obtained from the ETOPO1 dataset (NOAA) and plotted using a custom R code. For a given ARGOS position and associated date/time, all longlines at sea and their status (soaking, hauling) were also plotted on the map. We then estimated the distance from the instrumented animal to the closest longline using the ARGOS positions and the longline coordinates.

From there, we defined interactions between an individual and the fishing gear based on the geographic proximities of both entities. We used a method that defines odontocete interactions with fishing vessels at hauling in other studies (Roche et al. 2007; Tixier et al. 2010; Mathias et al. 2012). Animals were considered to be interacting with a longline if they were within a 1.5 km proximity, independent of the fishing activity. Thus, we determined two behavioral states for every individual's ARGOS position: (i) 'interaction' with a longline; and (ii) 'no interaction' with any longline. Simultaneously, we monitored the individual's depth profile of every ARGOS position. We also added the depths of the closest longlines to the diving profile when the individual was in 'interaction'. Moreover, if the closest longline was being hauled, we also monitored bathymetry under the boat during the hauling. As the equipped individual was in interaction with the boat at this time, we considered it to be in waters with the same bathymetry than the fishing vessel.

All instrument deployments followed the ethics policies of the Terres Australes et Antarctiques Françaises (TAAF) and were authorized by the Réserve Naturelle Nationale (RNN des TAAF) through approval A-2017-154.

4.3.3.3. LONGLINE ACCELEROMETRY

We deployed 3-axis accelerometer/pressure sensor data loggers (Sextant Technology, New Zealand) on longlines to detect activity events at the hooks (fish catch and/or depredation events) and the depth at which they occurred during soaking and hauling. Accelerometer/depth data loggers were deployed singularly on snoods (*i.e.* short lines connecting individual hooks to the main longline; Supp. data 8). In the 2016/2017 field season, the data loggers were attached to snoods by a snap connector fixed on the mainline (Supp. data 8) while in 2017/2018 they were attached with a thick rope to the swivel between the snood and the main line (Supp. data 8), allowing the data loggers to roll around the mainline as normal snoods do. We used two different versions of data logger: 2016/2017 recorded acceleration at 10 Hz with a precision of 10 bits; 2017/2018 recorded acceleration at 12.5 Hz with a precision of 12 bits. In both versions, the acceleration range was set at ± 16 g per axis and, to conserve battery life and memory capacity, an acceleration threshold (2016/2017 0.03 g, 2017/2018 0.01 g) was set to start recording when a movement occurred on the hook. The pressure sensor recorded continuously at 0.2 Hz.

Sets of accelerometers were deployed along a longline on every hook (*i.e.* every 1.2 m), or separated by 3, 5 or 10 unequipped hooks. When the equipped longline was retrieved on the vessel, the presence of a captured fish (and its species) on an equipped snood was recorded. For equipped hooks without any capture, we recorded whether the bait was still present and the condition of hook (undamaged, twisted or ripped off the snood).

To assess the potential for detecting events on non-equipped snoods, the distance from equipped hooks to nearest capture along the longline was recorded, counting 0 when a catch occurred on the equipped hook. Simultaneously, we monitored the amplitude of the movement received on the loggers nearby. Thus, we estimated the norm of the acceleration vector:

$$\text{EQUATION 4-3 Norm} = \sqrt{ax^2 + ay^2 + az^2}$$

with ax , ay and az the 3 components of the acceleration vector. Acceleration data were extracted using the software Hermes DeepG (Sextant Industry, New Zealand). Accelerometer data and pressure profiles were processed using custom-built routines in Matlab (version R2015, The MathWorks, Natick, MA, USA).

We then examined how the acceleration norm (Equation 4-3) varied with respect to the distance (in number of hooks) of the closest capture. To do so, we produced boxplots depicting the median with the 25th and 75th percentiles (McGill et al. 1978). Also a 95% of confidence interval was represented (the two whiskers) with the outlying points shown individually (McGill et al. 1978). The dataset did not allow for linear regressions to be assessed because of a violation of independence when a same catch was monitored on several accelerometers nearby. The low number of accelerometers recording signals from a same catch did not allow for nested linear models to be used to correct the violation of independence. Boxplots were developed per season because of the difference in the sampling schedule of the loggers and their method of attachment to the longlines between the two field seasons

Finally, we assessed the depth profile of each accelerometer and mean norm acceleration. We manually looked for any depth anomalies and assessed the distance of closest capture to equipped hooks. Our aim was to determine if the acceleration/depth data could reveal depredation events for hooks that were hauled without fish.

4.3.4. RESULTS

4.3.4.1. ODONTOCETES TRACKING DATA LOGGERS

Only two loggers of the six deployed transmitted correctly. The other 4 loggers failed to transmit, most likely because of an on-board software issue. The two operational loggers were deployed on two adult female killer whales in February 2018 near the seamount located 40 km south-east from East Island, Crozet Archipelago (Figure 4-6). The two instruments provided 28 and 65 ARGOS locations during 3 and 7 days, respectively, before they stopped transmitting (*i.e.* fell off the animal or battery expired). Of these locations, 20 and 31, respectively, had an accuracy estimates and, thus, were included in further analyses.

Out of the 20 useful locations from the first logger, 9 locations were identified as “interactions” with 5 different longlines. For the second logger, 14 points were identified as “interactions” with 11 different longlines. Among the ‘interactions’ positions of the first individual, 3 were recorded during the hauling of 3 different longlines and 6 were recorded as overlapping with 2 different longlines during soaking. For the second individual, 6 positions

were recorded during the hauling of 5 different longlines and 8 positions overlapped with 6 different soaking longlines.

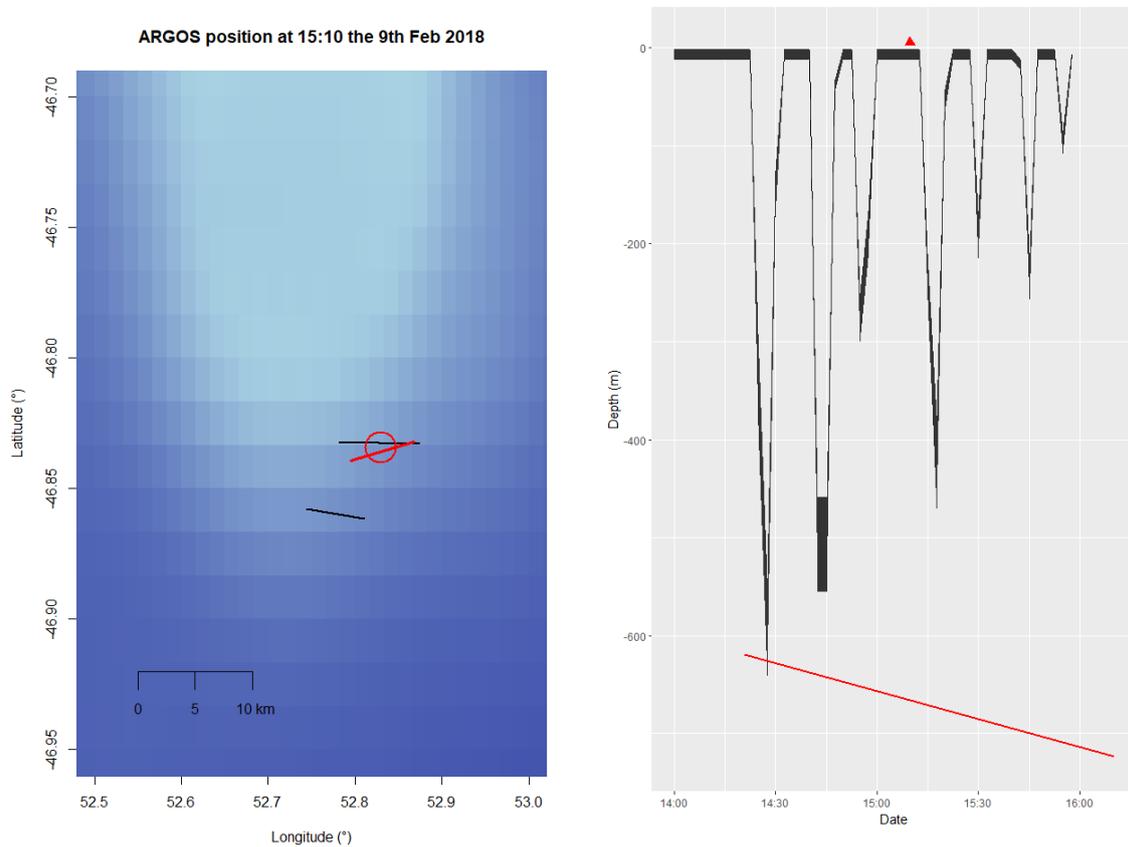


Figure 4-7 - ARGOS position (left panel) of an ‘interaction during hauling’ with its associate dive profile (right panel). The ARGOS position is indicated on the map by the red circle with the diameter representing the location estimate error buffer (cf. CLS classes). The color shade depicted the bathymetry. The soaking longlines are shown in black and the longline being hauled is shown in red at the given transmission time of the ARGOS position (left panel). The dive profile assessed the depth range estimated by the tag through the thickness of the drawing (right panel). On the dive profile the transmission time of the ARGOS position is represented by the red triangle and the bathymetry recorded by the boat during the hauling session is indicated by the red line, as the killer whale was interacting with the boat the red line represented then the bathymetry below the individual for a given time (right panel).

The dive data corresponding to the 9 ‘interaction’ positions on longlines being hauled indicated that killer whales started diving at the beginning of hauling activities and stopped diving once all hooks were landed onboard the vessel (Figure 4-7 and Supp. Data 10 to 14). Interestingly, during the hauling operations, the diving depths of the killer whales ranged throughout the entire water column (from the surface to the sea-floor).

The dive data corresponding to the 14 “interaction” positions on soaking longlines indicated that the killer whales mostly performed shallow dives (<50 m). An exception to this behavior occurred for one “interaction” position, where a killer whale performed a dive to 502 ± 22 m only 1:30 h after the “interaction” position time (Figure 4-8). This “interaction” position was the last of a series of 6 consecutive positions recorded within a 4.5 h window and all overlapping with the same cluster of longlines soaking within a 6 km radius (Figure 4-8). The next position was recorded 20 h later and at 4 km from the last position of previous series. During this 20 h time window, the killer whale conducted 8 dives deeper than 450 m in <6 h, with 5 of these being consecutive dives to the same estimated depth (502 ± 22 m) within 2 h (Figure 4-8). These dive depths correspond to the bathymetry at the extremity of the closest longline (set at 515 m; Figure 4-8). All these events occurred around the soaking longlines (*i.e.* the ARGOS positions and the recorded dives within the 15 h window; Figure 4-8) while no vessel was in the area. Indeed, after setting the longlines, the fishing vessel left the area and traveled 140 km away. It then returned to haul the considered longline, 3 h after the last deep dive (502 ± 22 m) was recorded. In addition, no other fishing vessel was active in this sector.

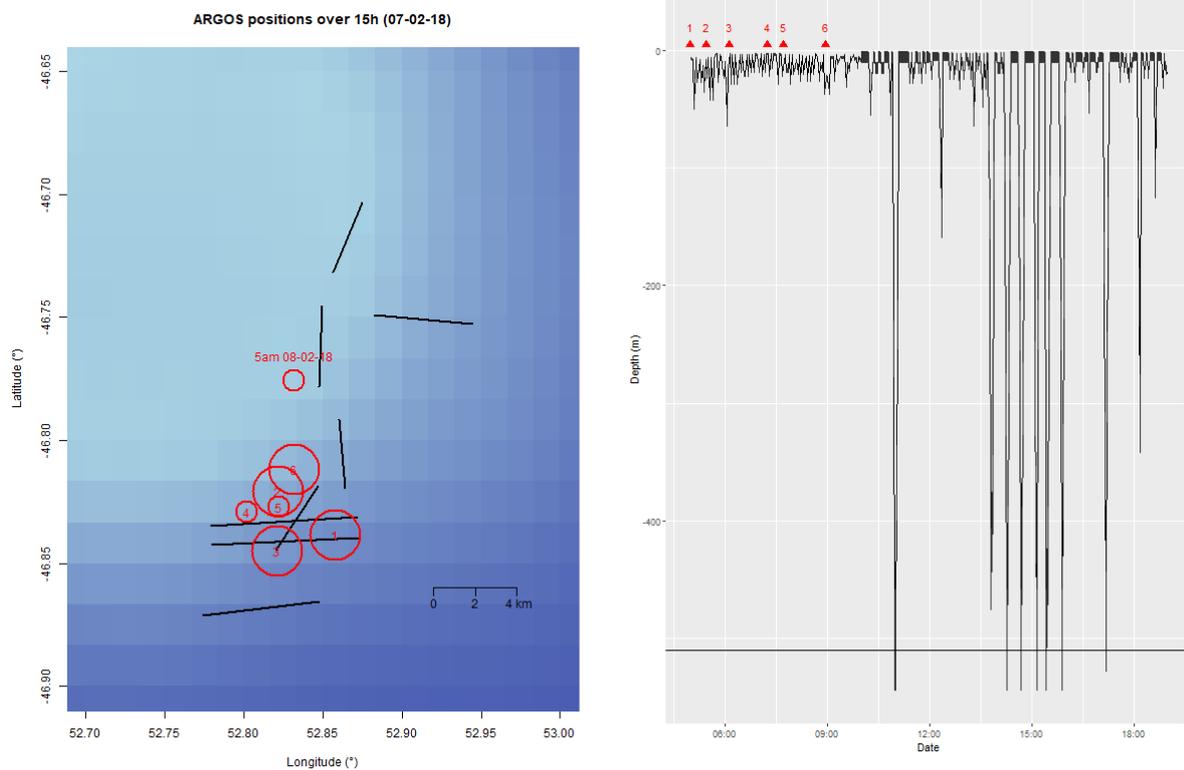


Figure 4-8 - ARGOS positions (left panel) of an ‘interaction before hauling’ with their associate dive profile (right panel) within a 15 hour-window. The ARGOS positions are indicated on the map by the red circles (numbered chronologically along track) with the diameter representing the location estimate error buffer (cf. CLS classes). The soaking longlines are indicated by the black lines on the map, and the closest soaking longlines to the most recent transmitted positions are in green (left panel). The dive profile assessed the depth range estimated by the tag through the thickness of the drawing (right panel). On the dive profile, the transmission times of the ARGOS positions are represented by the red triangles and the bathymetry of the closest longlines (at their extremities) at the time of the most recent ARGOS determined positions are outlined in green (right panel).

We observed with the two loggers that 68% of the ARGOS positions with ‘no interaction’ were associated with shallow dives (< 50 m) and occurred between two positions with ‘interaction’. However, for one of the two instrumented individuals, 9 “no interaction” positions coincided with 7 relatively deep dives. The maximum depths were between 200 and 325 m, and 3 of these dives were performed within a 3 h period (Figure 4-9 and Supp. data 15). This specific event occurred on a seamount. The area is characterized by steep slopes reaching a plateau at depths of approximately 200-300 m, with two peaks rising to depths of up to 100

m. As fishermen are not allowed to set longlines on the seafloor shallower than 500 m, these deep dives could not be associated to longline depredation.

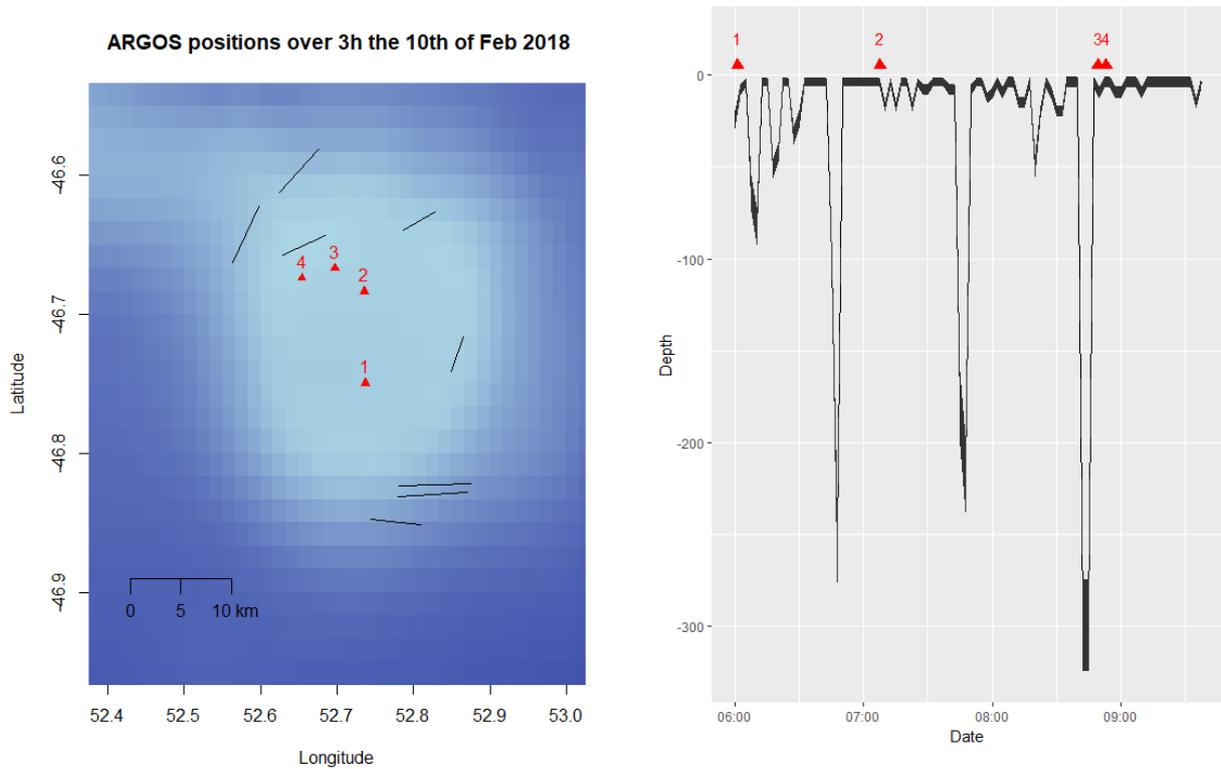


Figure 4-9 - ARGOS positions (left panel) within a 3 hour-window of 'no interaction' with the associate dive profile (right panel). The ARGOS positions are represented on the map by the red buffers with the diameter standing for the estimate error (cf. CLS classes) and the numbers assessed the chronology of the track. The longlines at sea during these 3 hours are plotted in black on the map (left panel).. The dive profile assessed the depth range estimated by the tag through the thickness of the drawing. On the dive profile the four transmission times of the ARGOS positions are represented by the red triangles (right panel).

4.3.4.2. LONGLINE ACCELEROMETRY

Accelerometer/depth data loggers were deployed on 556 hooks across 126 sections for 115 longline sets. Equipped hooks captured 38 fish, including 19 Patagonian toothfish. Other captures included grenadier (*Macrourus spp.*), antimora (*Antimora rostrata*) and skate species (*Bathyraja spp.*). The catch rate of Patagonian toothfish on the equipped hooks (3.42%) was similar to the catch rate of all longlines for the whole fleet for the same period (3.85%). However, due to device malfunctions, accelerometer data were obtained for only 13 toothfish captures.

Acceleration norms recorded during the second season were higher than those recorded during the first season (Figure 4-10). This is likely due to modifications in the newer generation of accelerometers that were used on the second year of the study, and to modifications in the way accelerometers were attached to longlines. In the second year, a smoother attachment was used, allowing a complete rotation of the snood around the mainline. However, for both field seasons, the accelerometer data showed the same feature: the accelerometer norm globally decreases when the distance of the closest capture increases (Figure 4-10).

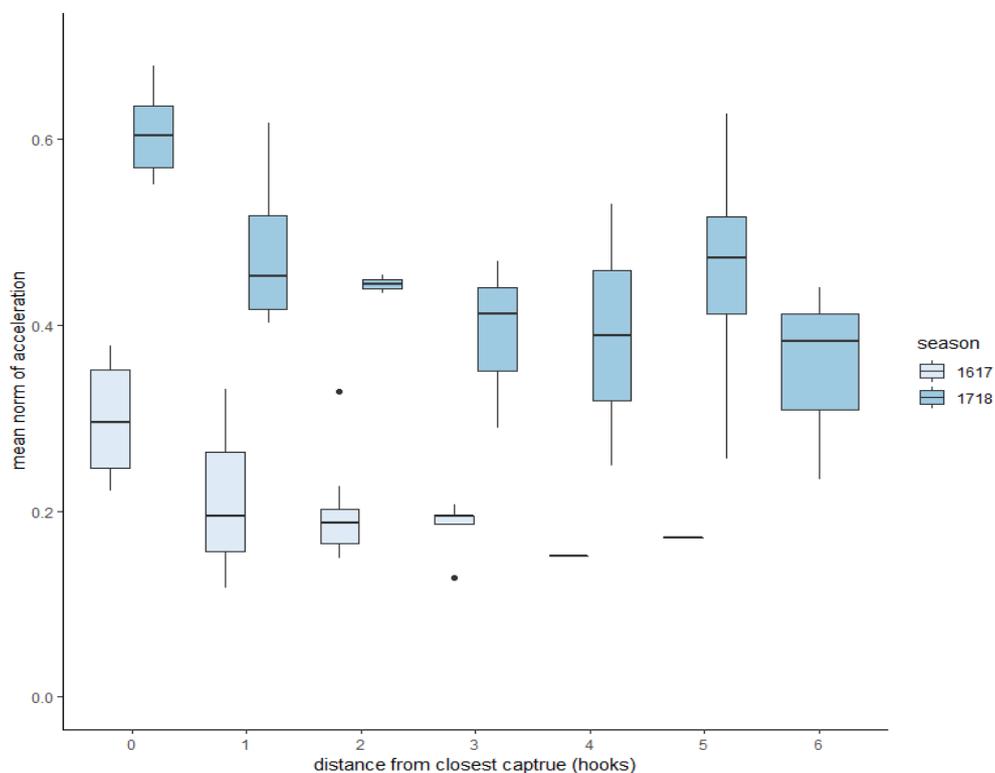


Figure 4-10 - Boxplots of the mean acceleration norm recorded during the bottom phase on accelerometers with the closest distance and for the two different season.

Over the total 126 sections of data logger deployments, we observed 3 events of significant depth variation during three separate longline soaking phases, one at Kerguelen in January 2017, one at Crozet in February 2017 and one at Crozet in February 2018 (Figure 4-11). These events occurred at depths of 600, 1600 and 1800 m, respectively, while the lines were soaking on the seafloor. The elevation events lasted 6, 9 and 52 minutes, respectively (Figure 4-11). The first event in Kerguelen occurred 1 h before the arrival of the fishing vessel at the longline (Figure 4-11.A.B.). The second event happened just after fishermen stopped hauling the longline half way through and let it fall back to the seafloor (Figure 4-11.C.D.). The third event occurred 1 day after the longline was set and 3 days before the hauling (Figure 4-11.E.F.). During these events, longlines were elevated by 30 m, 40 m and 300 m, respectively, above the seafloor (Figure 4-11). Sperm whale presence was confirmed on the first event (Figure 4-11.A.B.) by visual observations and passive acoustic recordings (obtained as part of concurrent studies). No such cues of sperm whale presence were detected near the set during the second event, though no passive acoustic monitoring occurred in the area at that time (Crozet 2016-2017, Figure 4-11.C.D.). However, a sperm whale was found entangled and dead (Fig. S2) on the longline of the third event (Figure 4-11.E.F.). The logger was located 1km from the dead sperm whale. During the three events, all equipped hooks were hauled without caught fish and one of the equipped hooks was hauled in a row of ten hooks twisted or ripped off the snood.

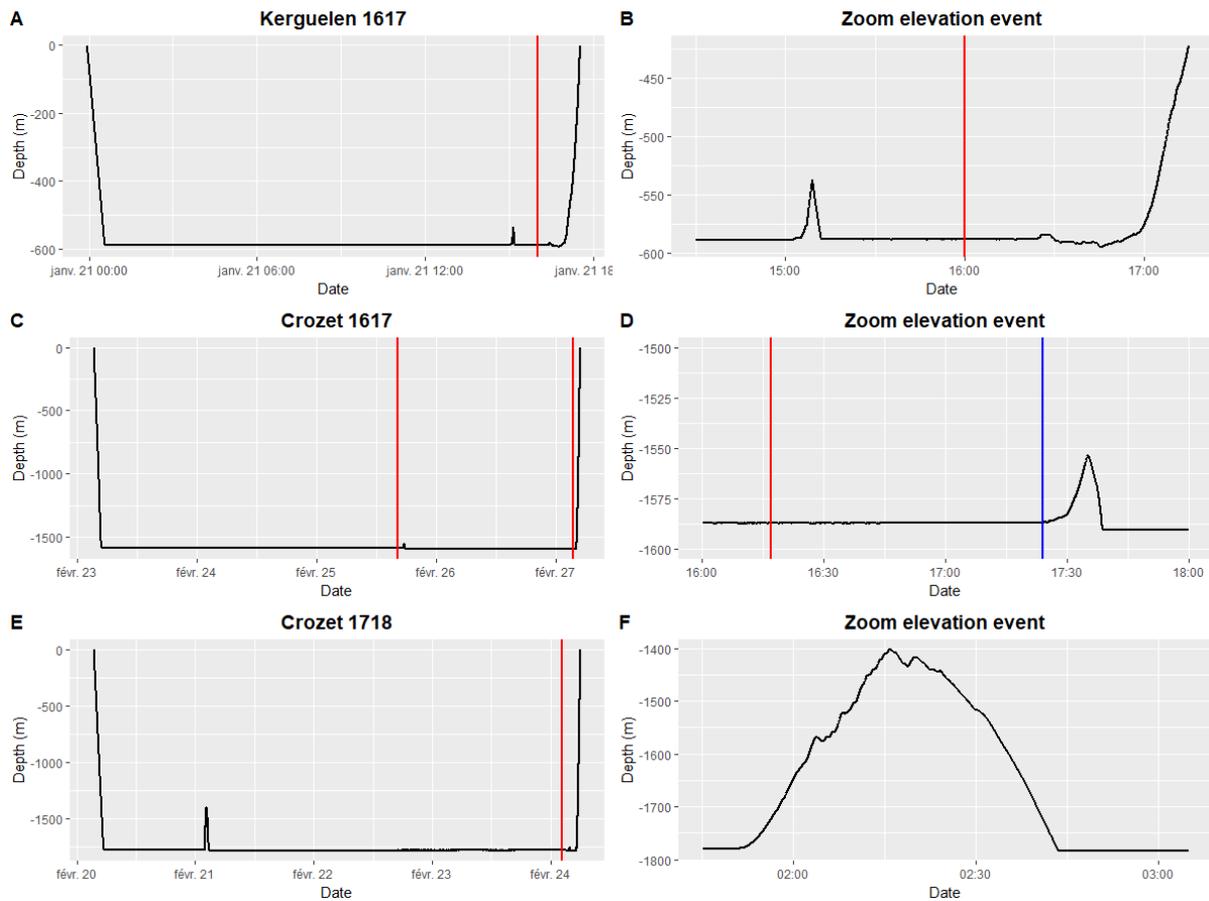


Figure 4-11 - Dive profiles (A,C,E) of three accelerometers hauled without any fish and showing some depth anomalies, zoomed on the right column (B,D,F). Each row represent a different logger monitoring a precise event: the first line represents the event which occurred at Kerguelen during the first field season (2016-2017); the second line represents the event which occurred at Crozet the same field season (2016-2017); and the third line represents the event with the dead sperm whale hauled at Crozet in February 2018. We assessed on the depth profiles and elevation zooms the arrival time of the fishing boat on the longline (red line), and for the second event (D) we also monitored the time at which fishermen stopped the fishing activity and cut the longline (blue line) before leaving.

The accelerometer of the third elevation event (*i.e.* with the dead sperm whale) did not reveal any acceleration activity while the longline was on the sea floor. This suggests that no fish were captured on any of the hooks located near the logger. However, the loggers monitoring the two other events revealed acceleration occurring before each elevation event and then stopped recording any activity until the hauling process began. This indicates the occurrence of a fish capture and then depredation. We then compared the mean acceleration norm of the

equipped hook during the soaking phase until these elevation events with the boxplot of mean acceleration norm per closest capture (Figure 4-12). These comparisons allowed for the distances of the activities recorded on the accelerometers to be roughly estimated before the elevation events occurred. We observed that the mean acceleration norm before the second elevation event (Crozet 1617) was higher than the lower quartile of the boxplot at a distance of 0, *i.e.* fish hauled on the equipped hook (Figure 4-12). This revealed that the equipped hook, hauled undamaged and with no fish, probably caught a fish during the soaking and before the elevation event. In contrast, the the mean acceleration norm before the elevation first event (Kerguelen 1617) was too low to indicate a capture on the equipped hook, suggesting some activity further away (Figure 4-12).

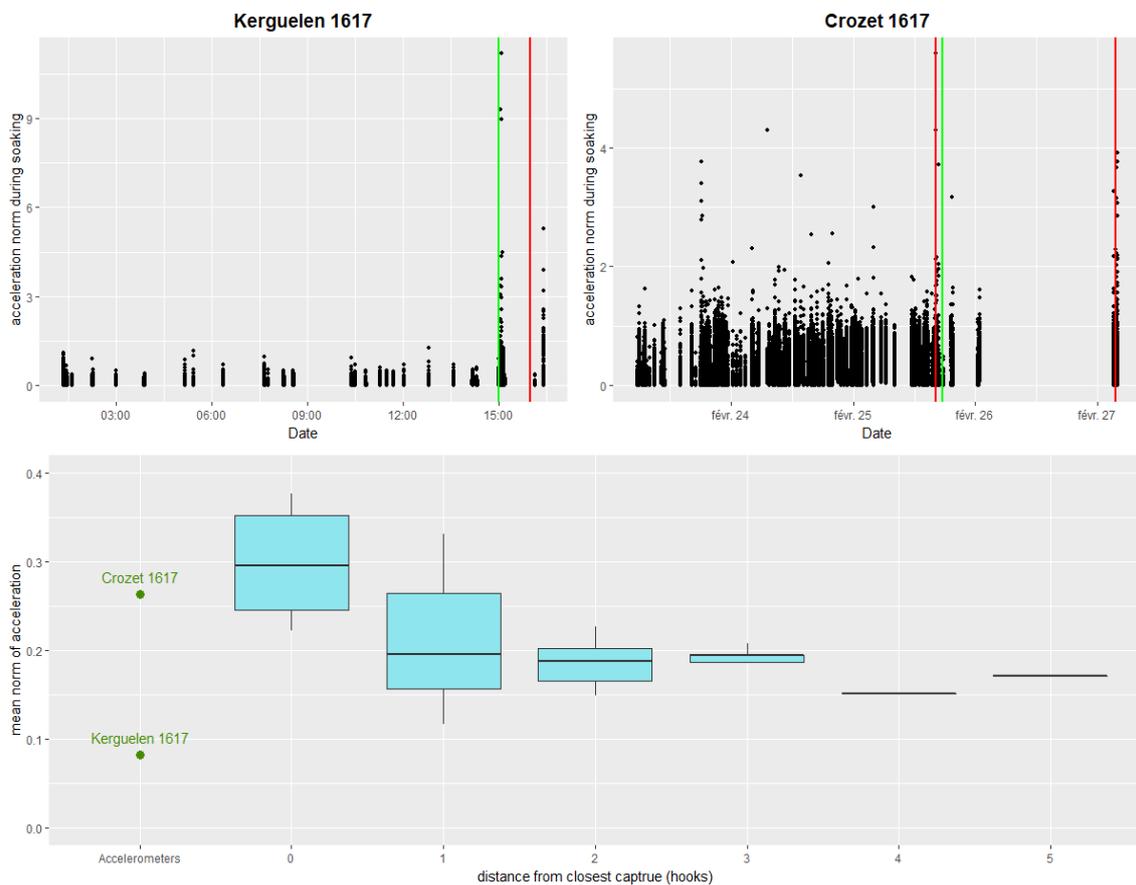


Figure 4-12 - The first row depicts acceleration norm over the dive of the two equipped hooks showing activity before the elevation event (green line). The mean acceleration norm before the elevation event (green line) was compared for each accelerometer with mean acceleration norm estimated with the distance of the closest toothfish capture.

4.3.5. DISCUSSION

4.3.5.1. INSIGHTS INTO DEPREDATION BEHAVIOR DURING HAULING AND SOAKING PHASES OF LONGLINES

The diving behavior of instrumented killer whales showed that individuals actively and repeatedly dived to depths matching those of longlines while they were being hauled onto vessels. Interestingly, these dives were performed as soon as hauling was initiated by fishermen, with the first dives being the deepest (on occasions >600 m) and matching the seafloor depth. Together, these findings suggest that depredating killer whales readily expend high amounts of energy in deep, short-spaced successive dives and that these costs are likely outweighed by the benefits gained from feeding on toothfish caught on hooks. These benefits may be maximized if individuals are the first to access the resource offered on the hooks, potentially with a choice of bigger fish. It may therefore be hypothesized that deep dives performed at the beginning of hauling is a response to both intra- and inter-specific competition. Competition is likely generated by a highly localized, short-term availability of easy-to-catch resource, such as toothfish caught on longlines. The large concentrations of both killer whales and sperm whales (sometimes co-occurring) around fishing vessels suggests such competition (Roche et al. 2007; Tixier et al. 2010). Deep diving behavior while depredating on longlines being hauled has also been reported for killer whales off South Georgia (Towers et al. 2018) and for sperm whales in Alaska (Mathias et al. 2012), suggesting competition for the hauled resource in both cases.

In the present study, the diving/tracking data for the killer whales and the longline accelerometry/depth data for the sperm whales suggest that these species also interact with longlines during soaking. For killer whales, interactions with longline sets on the seafloor during soaking phases are suggested by the matched maximum dive depths and bathymetry when positions of individuals overlapped with those of longlines. Additionally, the repeated deep dives within a short duration (5 dives in 2 hours) to the same depth, strongly suggests a foraging activity on a highly localized resource remaining available at the same depth for extended periods of time, strengthening the idea that the killer whale was foraging on the soaking longlines. While more data are required to fully address these issues, our dataset demonstrates that killer whales can forage on soaking longlines and suggests that they do.

The unfortunate by-catch of a sperm whale entangled in a longline equipped with a logger confirms the species does depredate on soaking longline. The event also helps the interpretation of the other longline logger data. The elevation signals detected on loggers were identified as interaction events and confirmed by additional cues such as toothfish capture events on the same portion of sets, wrested and twisted hooks, and the presence of sperm whales in the vicinity of sets. While such cues were undetected for one of the nominally identified events, the depth of the event (1600 m) makes it unlikely to be the result of killer whales as they are not known to dive deeper than 1100 m (Reisinger et al. 2015; Towers et al. 2018). In contrast, sperm whales are known to be able to reach depths of 1500-2000m (Teloni et al. 2008; Fais et al. 2015; Guerra et al. 2017).

In addition, the variation in depth data obtained during longline soaking suggests how depredation events may occur. The two elevations of longlines up to 30 and 40 m off the seafloor indicate a significant pull must have been exerted directly on the line, and not on a hooked toothfish. Pulling on a hook or a fish may only support an elevation of 1 or 2 m, as observed in video data obtained by Van den Hoff et al. (2017) showing an elephant seal pulling a toothfish to unhook it. Furthermore, sperm whales depredating hauled lines near Alaska appear to bite and scrape sections of lines in order to remove fish instead of directly targeting hooked fish (Mathias et al. 2009; Mathias et al. 2012). In the present study, the observation of twisted and wrested hooks in a row, even if no fish captures were recorded in the accelerometry record, suggests that sperm whales rake the mainline while lifting it from the seafloor. Such a hypothesis may also explain why the dead sperm whale hauled on a longline with equipped hooks had the mainline wrapped around its jaw. It is also known from subsurface video data that killer whales are more likely to pull fish to remove them from lines (Guinet et al. 2015) such that it is unlikely this species was involved in elevation events of soaking longlines.

4.3.5.2. FISHERIES MANAGEMENT AND ODONTOCETE CONSERVATION IMPLICATIONS

This study has major implications for the way depredation is estimated and incorporated into fish stock assessment as well for the conservation of depredating odontocete populations. Our results demonstrate that visual observations from fishing vessels are not enough to correctly quantify depredation rates. Indeed, depredation rates are estimated by the difference between

catch per unit effort on longlines in absence of cetacean and longlines in presence of cetaceans (*e.g.* Hucke-Gaete et al. 2004, Purves et al. 2004, Roche et al. 2007, Gasco et al. 2015). Within cases that seafloor depredation occurs on longlines hauled in the absence of cetaceans, depredation rates will be underestimated. This insight has significant implications for fish stock management, since even with the recent efforts to consider depredation in quota management (Roche et al. 2007; Gasco et al. 2015), our study shows that the fishing stock might be more impacted than previously assumed. Furthermore, to clearly estimate the impact of depredation on the fish stock it is essential to know whether the targeted fish belong to the natural diet of the depredating odontocetes.

While Patagonian toothfish has previously been described as a natural prey of sperm whales (Yukhov 1982), doubts remain about killer whales naturally feeding upon this prey. In the present study, we observed killer whales diving to the seafloor of a seamount, where no longlines were set. This suggests that killer whales naturally forage in this area, though it is not known on what prey. Killer whales at Marion Island have been similarly observed foraging on the seafloor of a seamount at 800 m depth, where they were considered as preying upon squids or Patagonian toothfish (Reisinger et al. 2015). Thus, we also assumed that Crozet killer whales may naturally forage either on squids or on Patagonian toothfish. This hypothesis was already suggested since this population immediately learned to depredate toothfish in 1996 (Guinet et al. 2015). Under this assumption, depredation may therefore have a limited impact on the toothfish stocks but it nonetheless suggests that fishermen and odontocetes are clearly in competition for the same resource.

The dead sperm whale found entangled in the gear and reported here highlights the potential risk of bycatch. This incident is the fifth of its kind reported at Crozet between 2007 and 2018, which represents a bycatch rate of 0.04 % individual per longline over that period. Among these 5 bycatch events, three resulted in the death of a sperm whale, which represents 2.6 % of the 114 known individuals of the Crozet population (Labadie et al. 2018). While this proportion is low, it still may significantly impacts this low fecundity, long-lived marine mammal (Whitehead 2009). In addition, the increase of sperm whale bycatch rate in recent years (4 of the 5 reported events occurred in the past 3 years) raises concern about a potentially increased competition between the fishing activity and the local whale populations, which may be due to a greater dependency to depredation and/or a depletion of the toothfish stock. Although the easy-to-get food provided by longlines may complement an individual's energy

intake and improve reproduction (Tixier et al. 2015b; Tixier et al. 2017), seafloor depredation may pose serious threats to odontocete populations by an increase in entanglement risk.

Previous efforts to minimize odontocetes depredation on demersal longline fisheries have primarily relied on the assumption that fish were removed from hooks only during hauling of longlines (Gilman et al. 2006; Werner et al. 2015). However, if both killer and sperm whales depredate fish on the seafloor as suggested by the present study, efforts to develop new mitigation techniques should be re-orientated to the development of deterrence/protection systems of the longline/hooks throughout the whole soaking and hauling periods. Until now, solutions have mostly been targeted at hauling operations where it might be easier to apply systems to protect the caught fish, such as acoustic deterrent devices to switch on while hauling longline, *e.g.* the ‘OrcaSaver’ system (Tixier et al. 2015a), or floating net sleeves sliding down over individual caught fish when the longline is hauled to protect it from depredating whales, *e.g.* the ‘Cachalotera’ (Moreno et al. 2008). However, these mitigations solutions may be costly and difficult to implement if they require changing fishing gear, or they may be efficient only for a while before odontocetes understand how to bypass these devices (Tixier et al. 2015a). Rather, our results suggest changing the fishing system with a global protection of the targeted fish, such as fishing pots, may be needed. However, new fishing methods may not be as efficient as the conventional fishery. For instance, in Alaska pot fisheries have been approved and seem to be effective in preventing sperm whale depredation but they are more expensive when compared to conventional longlines (Sullivan 2015; Peterson and Hanselman 2017). The same conclusion has been drawn after a preliminary trial performed as part of the ORCASAV program in 2010 around Crozet Archipelago (captains communications, personal observations and see Bavouzet et al. 2011; Gasco 2013).

Further investigations should examine whether the occurrence of sea-floor depredation is negligible compared to depredation during hauling. Such quantification would allow for the extent to which depredation rates are underestimated to be assessed and this information would help in determining whether efforts should be put to develop mitigation devices that protect the hooks during hauling only or during the whole fishing process to reduce the economic losses caused by depredation. This study provided preliminary insights to this aspect by suggesting that seafloor depredation might occur more sporadically for killer whales than for sperm whales. With three interaction events recorded for sperm whales over a low coverage of the fishing effort by accelerometers (~0.02% of hooks set by fishermen), we might assume that depredation

on longlines on the seafloor during soaking may be relatively frequent for that species. Increasing the bio-logging effort on individuals with longer logger deployment might bring more cues on the occurrence of this behaviour. Alternatively, the use of passive acoustic monitoring may help quantifying depredation at seafloor, since killer whales and sperm whales are vocal animals and use echolocation to forage (Norris 1968, Barrett-Lennard et al. 1996, Madsen et al. 2002, Miller et al. 2004, Watwood et al. 2006, Zimmer 2011). Thus, the clicks can be used as an acoustic proxy of the depredation behaviour, which can help to assess the depredation rates during interactions between soaking and hauling (Thode et al. 2014).

4.3.6. CONCLUSION

Using bio-logging technology on both odontocetes and demersal longlines, this study brought new behavioral insights into sperm whale and killer whale depredation behavior on demersal longlines. Depredation was confirmed during hauling phases from the observations of killer whales diving behavior around the fishing gear in the water column during that phase as described at South Georgia (Towers et al. 2018). More importantly, although the capabilities of sperm whales to interact with the longline on the seafloor has been previously suggested (Janc et al. 2018) our results confirm that sperm whales do, and that killer whales very likely also, depredate on longlines while they are soaking on the seafloor. Although seafloor depredation still needs to be accurately quantified, we have demonstrated the occurrence of this behavior which has major implications both for past depredation assessment and management, and for future mitigation developments.

4.3.7. ACKNOWLEDGMENTS

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4.4. CONCLUSION

Biologging techniques are useful tools to assess the depredation conflict because these techniques allow for a monitoring of interactions at the “longlines-odontocetes” scale, which is finer than the “fishery-odontocetes” scale. Deployments on longlines have brought a new lead for a “fishing gears behaviour” monitoring, especially while soaking. Within this thesis we provided evidence of seafloor depredation on soaking demersal longlines by odontocetes (section 4.3), but the extent to which this behaviour occurs remains unknown. Nevertheless, with 3 interaction events recorded for sperm whales over a low coverage of the fishing effort by accelerometers (~0.02% of hooks set by fishermen have been equipped), we might assume that depredation on longlines on the seafloor during soaking may be relatively frequent. Therefore, an acoustic approach would be interesting to assess interaction during soaking time as killer whales and sperm whales are vocal animal and used echolocation to forage (Norris 1968, Barrett-Lennard et al. 1996, Madsen et al. 2002, Miller et al. 2004, Watwood et al. 2006, Zimmer 2011). Thus, the combination of hydrophones (section 3) and accelerometers (section 2) on longline would enable to have a better covering of interaction when fishing boats are not around the longlines and to estimate the soaking depredation rates.

Despite the small number of individuals equipped, the short duration of loggers deployed on killer whales and low data resolution, results from this study demonstrate that animal-borne biologging techniques are determinant in understanding the underwater dimension of the depredation conflict. Additional deployments of loggers with longer lifespan and better resolution, on both killer and sperm whales, would help further characterisation of the depredation behaviour of these species underwater. For instance, with a higher spatio-temporal resolution of tracking data, we should be able to characterise the time and the distance at which odontocetes detect and make the decision to head towards fishing activities (Collet et

al. 2015). By recording tracking data over extended periods of time, bio-logging may provide insights on where these odontocetes naturally forage in absence of vessels. For killer whales, although they can be seasonally observed from the Crozet islands while foraging on penguins or pinnipeds (Guinet 1991, Guinet and Bouvier 1995, Tixier 2012, Guinet et al. 2015) they may feed on other prey items which are yet to be determined. As for sperm whales it would allow to confirm their fidelity to some foraging grounds as suggested from photo-identification (Labadie et al. 2015, 2018) and to assess whether they are preferentially distributed on spots of high toothfish density. As sperm whale is a migratory species, long duration tracking would help to identify breeding sites, which remains unknown to date. Combined to satellite tracking, depth recorders are essential to assess the use of the water column by these predators, either while depredating or while foraging naturally. Similarly to killer whales around Crozet (section 4.3), it would be important to describe whether sperm whales could perform depredation both near the surface and close to the bottom, such as observed on sperm whales depredating on halibut fisheries in Alaska (Mathias et al. 2012). Loggers on sperm whales could also add some complementary description to the sea-floor depredation and may quantify the recurrence of this behaviour for an equipped individual. Although we have been able to observe some natural diving behaviour for an equipped killer whale, the amount of data available during times when there was no fishing activity was not sufficient to investigate natural foraging behaviours. We also did not dispose of a bathymetric dataset precise enough to assess whether the whales forage on the seafloor. This aspect is also of great interest since dives in different layers strongly suggest that individuals forage on different prey types. Further investigation would also require deploying new generations of loggers processing on-board acceleration on both species (section 4.2). Information on prey catch attempts is crucial to accurately determine where the odontocetes focus their foraging strategies and would allow comparing foraging efficiency between natural and depredating behaviours. Estimation of prey catch attempts would enable to quantify the number of fish remove at an individual scale, similarly to the use of buzzes of echolocation in Alaska to quantify depredation rates (Thode et al. 2014, 2015). Investigation of the natural foraging behaviour may also highlight how these species found their food and on which prey they naturally forage. In a further extent, knowing whether these predators forage on Patagonian toothfish naturally and how much this prey represent in their diet proportion would allow a quantification of the impact of depredation on fish stocks. On-board accelerometers could also transmit some proxies of swimming effort (Cox et al. 2018). As observed with southern elephant seals, such proxies could directly be correlated with body

condition (Richard et al. 2014, 2016). Although depredation has been described to have benefits on killer whales reproduction (Tixier et al. 2015a), such loggers may quantify differences of foraging costs at an individual scale between natural and depredation behaviours. Altogether, these investigations may bring then crucial information on the influence of depredation on odontocetes behaviours.

5. DISCUSSION

A clear identification of the actors involved in a conflict is necessary to achieve the correct management (Treves et al. 2006, Young et al. 2010, Colyvan et al. 2011, Redpath et al. 2013, 2015). Within fisheries depredation conflicts, the actors are mostly described between the “depredating species” and the “depredated fishery”. The “fishery” gathers “fishermen” and their “fishing gear” as the interaction is commonly observed when fishermen recover their fishing gear. Although depredation is known to occur during soaking time on pelagic longlines (Dalla Rosa and Secchi 2007, Forney et al. 2011, Rabearisoa et al. 2012, Passadore et al. 2015, Thode et al. 2016), the distinction between longlines and fishermen has never been clearly expressed. Indeed, “interactions” for demersal longline fisheries have been assumed to primarily occur during hauling phases when animals are visually observed from the vessels (Mathias et al. 2012, Tixier 2012, Werner et al. 2015). The underwater dimension of the conflict has then never been clearly investigated. Thus, questions such as when, where and how odontocetes interact with demersal longlines remain unclear. These gaps of knowledge have raised uncertainties both on the estimation of depredation rates and on the way to find suitable mitigation measures.

The purpose of this thesis was to bring new insights on the depredation conflict with a finer definition of the actors involved in the “fishery-odontocetes” interaction. In this thesis, the distinction was made for the interactions between the three actors: fishermen, fishing gears and odontocetes. This categorisation of entities allowed assessing individual behavioural ecology for both fishermen and odontocetes, which has also been sparsely explored. From this approach I aimed at bringing new insights on these competition/ interactions between these actors. In this discussion I will outline in which extent this thesis answered some of these questions using the study case of the Patagonian toothfish longline fishery around French Sub Antarctic islands. Although some gaps are filled, new ones open up. As a result this discussion ends with new perspectives on the depredation issue.

5.1. HOW TO EXPLAIN INTER-CAPTAINS VARIABILITIES OF INTERACTION RATES?

Within the purpose to monitor the perceptions of conflicts as well as the behaviours of the involved actors (Treves et al. 2006, Redpath et al. 2013, Blackwell et al. 2016), the use of human behavioural ecology (Nettle et al. 2013) can bring new highlights on the relationships between “fishermen-odontocetes” and “fishermen-fishing gear”. This approach aims at assessing whether fishermen behaviours may influence the probability of interaction with predators based upon the optimal foraging theory (McCay 1978, Pyke 1984, Nettle et al. 2013). As other foragers, fishermen behaviour could be assessed through their exploration and exploitation of resources, or through finer scale with their navigation behaviour, *i.e.* the use of their fishing vessels, to avoid detectability. As captains are the decision-makers, variations of their behaviour may explain part of the between-captains observed variability in interaction rates with odontocetes highlighted on Figure 2-1. Firstly, I showed in Chapter 2 that although all captains behave like optimal foragers, they have different fulfilment of a fishing success and they perceive the competition differently. As such, a captain being less sensitive to depredation, *i.e.* with a lower probability to leave a patch or with a higher probability to haul the following closest longlines in presence of odontocetes, would consequently show higher interaction rates. Secondly, as I introduced in Chapter 3, captains frequently manoeuvring vessels and decelerating roughly may increase their acoustic detectability by odontocetes, suggesting then an increase of their interaction rate. A change in this behaviour, *i.e.* hiding the fishing activity, would be akin to stealth behaviour or camouflage.

Altogether, these results suggest that the behaviour of captains is likely to be an important driver of their probability to interact with odontocetes. More broadly, these results emphasize the importance of human behavioural ecology approaches in studies addressing human-wildlife conflicts (Treves et al. 2006, Redpath et al. 2013, Blackwell et al. 2016). These new insights would be useful to further optimize fishermen behaviour to reduce depredation as they could be combined to other aspects of captains’ behaviour (e.g. operational variables) to develop effective and easy-to-implement mitigation strategies. Besides, since the optimal foraging theory is an ecological method derived from economy fields, I suggest using such human behavioural ecology approach to assess the socio-economic impacts of the conflict. Quantifying the economic impact of depredation on fisheries and modelling the various costs

generated by this conflict would allow determining better ways to optimise fishing success while minimising the risk of interaction with odontocetes. Further studies on the fishing success optimisation should also include the level of experience of captains. As an analogy to a juvenile forager naïve towards its environment, we may consider that captains fishing for the first time have to learn how to find fish stocks and how to face depredation. However, most of captains when commanding during their first trip have already some experience as chief officer and have learned from former captains. As such, increased experience and apprenticeship with experienced captains is expected to result in changes in the fishing strategy to minimize depredation and optimise fishing success. The variables composing this improved strategy should be therefore identified. In addition, increased experience may also improve the captains' manoeuvrability of their vessel. Differences of detectability according to different way captains use the vessel's acoustics should also receive further attention to confirm such hypothesis.

While the identification of optimal fishing strategies and stealthier navigation behaviour would be critical for mitigation measures to be developed, odontocetes may potentially learn to overcome these strategies and hence maintain a competitive pressure on captains. As such, systems providing captains with real-time information about the presence of odontocetes would allow them to adjust their fishing strategy accordingly. The example of odontocetes acoustics exposed in Chapter 3, revealed the interest of PAM to provide presence information around the buoy prior to hauling. This measure would require to implement an automatic detector (*e.g.* Deteclis, see summary in Appendix 2) with a real-time processing on hydrophones (*e.g.* PAMGUARD *cf* Gillespie et al. (2009), in the Soundtraps) and to transmit predators' presence information around the longline via VHF, satellite or mobile phone signals (Van Parijs et al. 2009). Another approach would consist to use a towed array from the fishing vessel to detect the presence of odontocete (Thode 2004, Weir and Dolman 2007, Van Parijs et al. 2009, Yack et al. 2013), before starting to set new longlines. Whatever the chosen technology solution, a real-time PAM should give captains one step ahead of their competitors. Inspired by the work conducted in this thesis, a fishing company has bought a towed hydrophone and will make the first trials during the fishing season 2018-2019.

5.2. WHEN, WHERE AND HOW DO INTERACTIONS OCCUR?

Until now, depredation on demersal longlines was assumed to only occur during the hauling (Hucke-Gaete et al. 2004, Gilman et al. 2006, Read 2008, Mathias et al. 2012, Rabearisoa et al. 2012, Söffker et al. 2015, Guinet et al. 2015, Passadore et al. 2015, Tixier et al. 2015c, Werner et al. 2015). Additionally, how odontocetes detect longliners and fishing activity has only been investigated on sperm whales in Alaska and with focus limited on acoustic cues produced during hauling activity (Thode et al. 2007, 2015). In Chapter 4, I showed that both killer whales and sperm whales depredate on longline while soaking on the seafloor. This brings new insights on the capacity of odontocetes to interact with longlines at depth. The results also suggest that sperm whales take the longline into their mouth, rake it to unhook and then catch toothfish as depicted in Alaska (Mathias et al. 2013). However, the ‘deep’ depredation behaviour occurring on hauling longlines described by Mathias et al. (2013) might also depict some seafloor depredation. These findings also indicate that odontocetes can localise fishing activity long before the hauling, and more precisely where the longlines are being deployed at sea. Through the preliminary acoustic analyses in Chapter 3, I observed that odontocetes are likely to know when a longline is being deployed, as vessels produce specific acoustic cues during the setting operation. Further investigation are required to accurately estimate the distance at which these cues propagate, and whether they propagate on a broader range than the cues produced during hauling. For now, I can only speculate that odontocetes may be able to detect the vessel within a 7-35 km range, and then through acoustic signature of the setting operation they may understand when a longline is deployed.

These results strongly suggest that mitigation devices should protect the fish caught on hooks not only during hauling but also during the whole soaking time. As such, a first experimental deployment of fish protective devices was conducted during my second field trip (2017-2018). The devices were designed by the industrial supplier SATIM to protect individual hooks from odontocetes while allowing the toothfish to enter in the tube and grab the bait (Figure 5-1). Forty six devices were deployed over 36 sections of longlines *i.e.* 1 to 2 devices per section of 750 hooks. The toothfish had then a choice between easy accessible free hooks and a protected hook harder to access, thus the likelihood of toothfish to enter in the device was assumed to be almost null. A second test was, therefore, conducted with a small section of 15 hooks all equipped with this systems. However, the deployment went wrong and fishermen had to cut the longlines after the 10th systems dropped off the boat. Because of safety, the experiment was not conducted again. No catch occurred on hooks equipped with the device over 56 deployments. Based on the capture rates obtained with the accelerometers during the same trip (circa 4%), one would assume that 2 toothfish should have been caught over the 56 hooks equipped with the device. A possible explanation of the failure of the test could be that toothfish do not seem to be able to swim backwards (fishery observers and personal observations from fish alive in tagging tank), they are less likely to enter in a tube without possible exit.

Deployments of these devices proved to be challenging and imposed security concerns at sea. The main issue is that the fishing vessels are optimised for one kind of fishing practice. It is then not possible to modify techniques on-board. One solution could be to change the fishing practice and to switch to fish traps. Although this solution would solve the depredation issue, a preliminary trial performed as part of the ORCASAV program in 2010 revealed that none of the 12 fish trap models tested allowed a fishing success high enough to be economically sustainable (captains and Guinet personal communications, and see (Bavouzet et al. 2011, Gasco 2013).

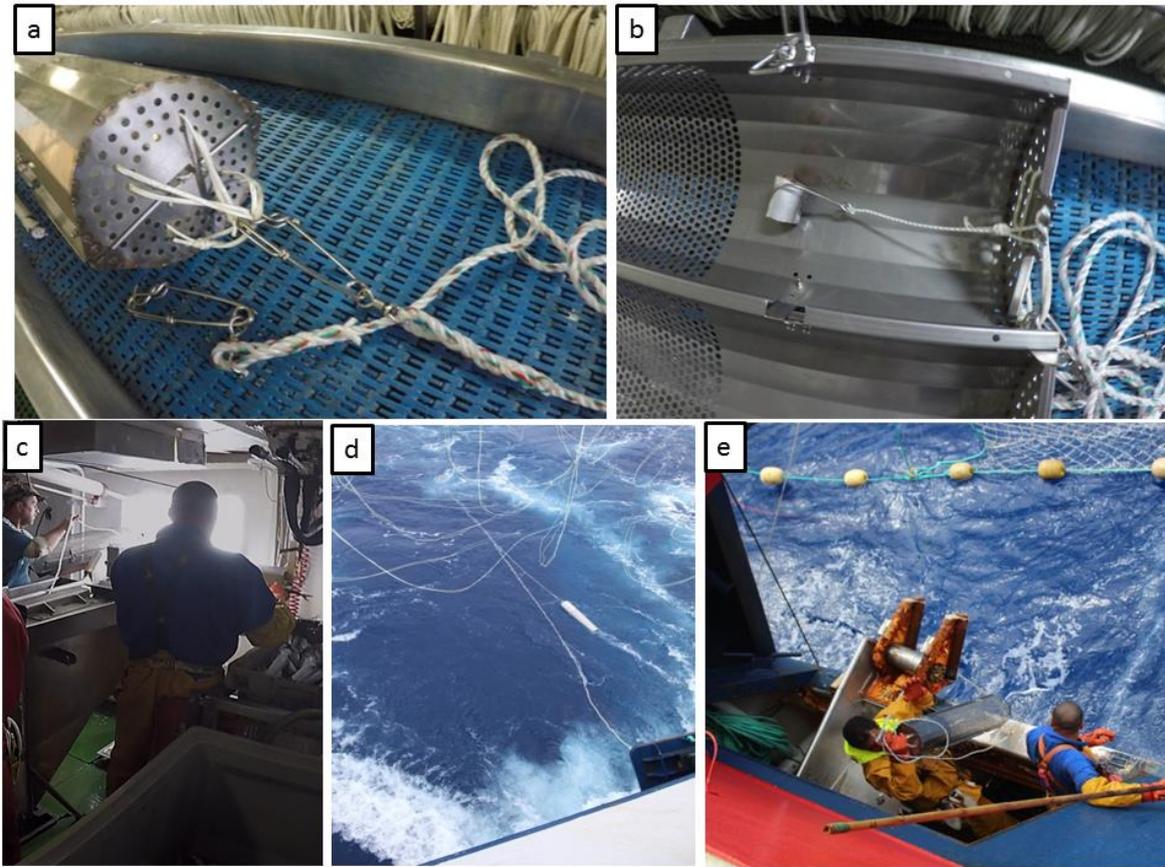


Figure 5-1 – Pictures of the protection device deployed during my second field work. a) device close with its attach system; b) system open with the position of the hook baited; c) system set on the longline and ready to be deployed by the window from which longline is dropped off; d) system dropped off the window at the rear side of the longliners during the setting; e) system being hauled at the bunker.

Because of these difficulties, further investigation should assess whether the impact of sea-floor depredation is negligible compared to the hauling depredation. Within this assumption, mitigation devices protecting the hooks during the hauling only such as the ‘Cachalotera’, a floating net sleeves sliding down over individual caught fish when the longline is hauled to protect it from depredating whales (Hucke-Gaete et al. 2004, Moreno et al. 2008) or the SAGO, a catching pod going down the longline to collect the fish (Arangio 2012), could be enough to reduce the loss in default of deleting depredation. First insights highlighted in the Chapter 4 suggest that seafloor depredation might occur more sporadically for killer whales than sperm whales, but this needs to be accurately quantified. Results obtained from loggers on killer whales, on Figure 4-8, paired with the recording of this species presented on

Figure 3-4, suggested that they are more likely to wait for the longline being hauled to start depredating. For sperm whales, the three events observed on the equipped hooks seem noticeable compared to the deployment effort. Besides, depredation behaviour while the line was soaking on the seafloor was suggested in a previous study analysing the PECHKER dataset and described in Appendix 4 (Janc et al. 2018). In absence of sperm whales at hauling absolute catch per unit effort (CPUE) increases with increasing soaking time. This correlation decreased with an increasing number of sperm whales present during hauling. When more than 5 sperm whales were present, the CPUE decreased with increasing fishing time (Janc et al. 2018). This change in the relationship was interpreted as an indication that sperm whales may depredate toothfish from longline at the bottom while the line was fishing and the higher the number of sperm whales the greater the number of fish removed during soaking (Janc et al. 2018). The quantification of this depredation on the seafloor would then require deeper investigation. Within this purpose bio-logging on odontocetes should allow comparing number of depredation events between soaking time and hauling time through an individual perception. Indeed, the bio-loggers deployed on killer whales revealed both depredation behaviours during hauling and during soaking (Chapter 4), thus with an increased dataset it may be possible to compare the number of dives during the hauling as observed on Figure 4-7 with the number foraging dives on soaking longlines as on Figure 4-8. Thus, increasing the bio-logging efforts on both species should allow assessing at an individual scale whether the impact of sea-floor depredation is negligible compared to the hauling depredation. Additionally, using clicks as acoustic proxies of depredation behaviour a PAM approach could specify depredation rates during interactions between soaking and hauling (Thode et al. 2014).

Considering fishermen and the fishing gear as separate entities, I provided preliminary insights on fishermen detectability and longline depredation on the seafloor but I did not consider how odontocetes may detect the fishing gear. Although future research efforts should focus on vessels detectability and how to make them stealthier, further investigation should also assess detectability of the longlines. Knowing how odontocetes find and see the longline could lead to new countermeasures, such as passive acoustic deterrent to reduce depredation by repelling or by masking the longline. For instance, a deterrent supposed to simulate a swim bladder of a rockfish (*Sebastes spp.*), species not consumed by sperm whales in Alaska, was tested on longlines targeting halibut (O'Connell et al. 2015). Although the results have not been very conclusive yet (O'Connell et al. 2015), such approach might be replicated on Patagonian

toothfish fisheries. Indeed, similarly to Alaska sperm whales also avoid to depredate a species with a swim bladder, the grenadiers (*Macrourus spp.*), whereas toothfish are deprived of one. Additionally, other repelling aspect might be tested, such as deterrent simulating a heap of hooks which seems to hinder odontocetes to depredate (fishermen personal communication). Further investigation could assess the acoustic target strength of longline to bring important insights on how longline could be perceived through odontocetes' echolocation. However, a good understanding of how odontocetes see through their biosonar would be essential to determine whether such mitigation approach is assessable.

5.3. ECOLOGICAL IMPLICATIONS

The fishermen optimal foraging behaviour paired with the seafloor depredation behaviour of odontocetes strongly suggest that depredation is underestimated. The amount of fish depredated by odontocetes is currently estimated from the difference of the catch per unit effort, *i.e.* the quantity of fish caught per hook (CPUE in $\text{g}\cdot\text{hook}^{-1}$), between longlines in absence of competition and longlines on presence of odontocetes within a fine spatial scale (Gasco et al. 2015). This method is based upon the assumption that the longlines hauled without odontocetes gave a baseline of the natural resource abundance. However, some depredation events may be not accounted for, since whales can interact with the longline soaking on the seafloor when the vessel is away from the gear, and therefore when no visual observation effort is made. Additionally, captains are more likely to keep fishing in presence of whales if the success is high. This type of decision may lead to large numbers of longlines hauled in presence of whales with high CPUEs compared to longlines without competition showing lower fishing success which may generate a bias in depredation estimations.

Further assessment of depredation rates should take into consideration the consequence of captains' decision to stay on a patch in presence of odontocetes. However, such consideration would be difficult to quantify. Conversely using a PAM, as previously described, should allow refining the number of depredation events during the whole fishing process (Thode et al. 2014). Within this purpose, the long-term acoustic monitoring set on the whole French and Australian fleets could provide an effective dataset. Besides, PAM will allow the estimation of odontocetes arrival time on longline. From the intensities of received sounds produced by odontocetes

compared to sound emission levels of these species, a transmission model loss should allow a range estimation of the source production. Additionally, displacements of predators could be modelled based upon their swimming speed and the hypothesis that they may head straight to the longline once this one is fishing, to estimate where odontocetes were prior to line setting. These spatial models should bring insights upon the natural distribution of predators yet poorly known. Although some insights on both species spatial distribution have been brought thanks to photo-identification (Tixier et al. 2014, Labadie et al. 2018). Additionally, a recent analysis underlined large spatio-temporal variations of sperm whale–vessels interaction levels with French and Australian commercial Patagonian toothfish on the Kerguelen Plateau, as detailed in Appendix 5 (Tixier et al. submitted in *CCAMLR Sc*). The observed spatial gradient of interaction rates raised the question whether this reflect a natural variation in sperm whale distribution through the Kerguelen Plateau or if this behaviour has been learned by ease in some the north and likely transmitted across individuals of populations through social pathways (Schakner et al. 2014). Investigation of the spatial factors influencing odontocetes' distribution paired with the understanding of the social behaviour transmission are essential to better predict the occurrence of interactions to implement effective strategies of avoidance in the future. However, it is important to keep in mind that odontocetes distribution is slightly skewed by observation efforts made from longliners when interactions occur. It is then difficult to clearly determine whether the presence in this area is because of the fishing activity or because of the resource abundance. Therefore, causality between the fishing success and the interaction rates might be difficult to understand, as a good fishing success may occur where individuals naturally forage or could attract depredating species. Within this purpose a PAM approach, such as a multi-month monitoring of acoustic occurrence of cetaceans using an acoustic recording station could be used to assess the importance of fishing grounds for natural foraging of sperm whales and killer whales in absence of any fishing activity. One limitation to use a stationary hydrophone is to monitor one spot and to confound individuals using it. An individual monitoring is therefore essential to precise the habitat use at a finer scale. Bio-logging is then an interesting tool to follow where odontocetes focus their natural foraging effort. Thus further efforts should be increased to deploy loggers, and especially the model with PCA estimation processing on-board described in Chapter 4. Additionally, a comparison between foraging effort and the habitat exploration should highlight cues on the natural diet of these predators, in particular whether toothfish is a natural prey remained unclear. However, an increasing number of cues strongly suggest that both species naturally forage on Patagonian toothfish. Sperm

whales has been described to naturally feed on toothfish obtained from stomachs contents of harpooned sperm whales (Abe and Iwami 1989). As for killer whales, results from this study showing that individuals equipped with loggers dive to the seafloor at 300 m depth in absence of longlines suggest that they naturally forage on toothfish (Chapter 4). Additionally, an isotopic analysis has been assessed by Tixier et al. (submitted) revealing that Patagonian toothfish is likely a natural prey item in the diet of killer whales at Crozet. There is not so much doubt left about Patagonian toothfish being a natural diet of both predators. Nevertheless, the question is therefore to estimate the importance of the toothfish in these species' diet to assess whether depredation behaviour may impact the fish stock if it added a supplementary predatory pressure on the toothfish population compared to their natural consumption.

Furthermore, a finer-scale analysis using bio-loggers paired with movement data of vessels would allow to assess the extent at which odontocetes modify their natural behaviour in response to fishing operations. More specifically, it is still unknown whether depredation behaviour is an opportunistic behaviour, *i.e.* odontocetes interact with longlines when their distribution spatio-temporally overlaps with that of the fishing operations, or an active behaviour, *i.e.* odontocetes follow fishing vessels, or a combination of both. To highlight whether interactions result from opportunistic or active behaviour, a preliminary meta-analysis was conducted between the different Patagonian toothfish fisheries of the Southern Ocean in order to better understand the spatio-temporal variations of interaction rates, as described in Appendix 6 (Tixier et al. submitted in *Scientific Report*). Besides, the preference towards an opportunistic or an active behaviour should be driven by the most optimal depredation strategy. Although depredation behaviour is energetically more rewarding than a natural behaviour (Tixier et al. 2015a), at some points the efforts to pursue fishing vessels might be higher than to forage naturally. Assuming that behaviours may evolve to become more active than opportunistic, it would raise the question on these predators' ecosystem health and their capacity to find their resource, urging the necessity of a well-managed fishery leaving sufficient fish resources for their natural predators. In that case the long term monitoring of demographic performances, in particular calving rate and early survival of killer whales, along the body condition monitored through drone aerial picture of both sperm whales and killer whales may reveal if both of these natural predators of Patagonian toothfish are under nutritional stress or not.

5.4. CONCLUSION AND PERSPECTIVES

The behavioural ecology approaches of fishermen and odontocetes assessed in this thesis filled gaps in our understanding of the depredation conflicts on demersal longline fisheries. Results may be extrapolated beyond the study cases of Crozet and Kerguelen, and have implications for other Patagonian toothfish demersal longline fisheries in the Southern Ocean, and also for other demersal longline fisheries experiencing depredation in other parts of the world. For instance, the findings on the way odontocetes interact with longlines in the underwater dimension, with interactions occurring during both hauling and soaking phases, may substantially change the way depredation was previously assessed in demersal longline fisheries. Other findings from the novel approaches used in this thesis such as passive acoustic monitoring, bio-logging and human behavioural ecology brought insights on depredation with broad implications, for both other fisheries experiencing this conflict. Although it is impossible to generalise the issue across fisheries as different predators are involved within different environments, all conflicts have in common the human activity. I therefore strongly suggest considering fishermen as actors to be included in ecosystem based studies of depredation in addition to fish and odontocete species. These models based upon the optimal foraging strategies should account for impacts of depredation on fishermen through socio-economic costs. Further studies should also focus on the behaviour of fishermen at fine scales. For instance, the analysis of the behavioural factors influencing the acoustic detectability of captains, which was introduced here, may help to identify easy-to-implement ways to decrease probabilities of interaction with odontocetes. Such analyses will be finalised in a nearby future using data from both Australian and French Patagonian toothfish longliners. Additionally, the acoustic signatures of vessels will be investigated on the demersal longline fisheries targeting the blue-eye trevalla around St Paul and Amsterdam Islands and in Southeast Australia.

The PAM approach developed in this thesis therefore proved to be a useful tool to investigate both human and odontocetes behaviour. To study odontocete behaviour, which understanding still needs to be improved for mitigation, conservation and general ecology purposes, PAM should be combined with other approaches. For example, using information on depredating odontocete individuals, long-term studies can help to identify the mechanisms leading predators to switch from natural to depredation behaviour. Although the identification

of these mechanisms may constitute an important step to find appropriate mitigation measures, as described in Appendixes 5 and 6; it could also help to predict the possibility of depredation to develop in other regions and/or fisheries. This might be the case of the Greenlandic halibut fishery where fishermen and killer whales foraging activity co-occurrence in space is growing with the decrease of the sea-ice range, as detailed in Appendix 7 (Lennert and Richard 2017). This forecasting study emphasizes the importance to share the knowledge as a better understanding of the conflicts' mechanisms may also prevent depredation. Thus, collaborative work should increase as depicted in Appendixes 5 and 6. Within this purpose OrcaDepred also includes the pelagic longline fishery targeting swordfish and tuna around Reunion Island to broaden the expertise.

In a further extent, this thesis revealed the importance to use a behavioural ecology approach for both human and wildlife to assess a conservation conflict (Treves et al. 2006, Redpath et al. 2013, Blackwell et al. 2016). Assessing the impact of the human impacts on wildlife but also the wildlife impacts of human is crucial to tend toward a win-win solution (Redpath et al. 2013). Indeed, conservation conflict's solution should be a situation where both parties can coexist with a decrease of the human-wildlife impact (Treves et al. 2006, Redpath et al. 2013, Sarrazin and Lecomte 2016). Therefore, this thesis with all collaborative works of the OrcaDepred project aim altogether at determining and contributing to the sustainability of the longlines fisheries within a depredation context. The goal is to conciliate a cost-effective activity for fishermen with the longline, one of the most fish-selective methods available to date, while preserving the fish stock and allowing the odontocetes populations to be maintained using natural prey resources. A mitigation solution cannot come from a simple and isolated measure. The knowledge garnered by scientific studies is crucial to lead in the good direction countermeasure research, but the work must be conducted with industrial providers and in collaboration with fishermen, fishing companies and the policy makers.

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SUPPLEMENTARY DATA

Supp. data 1 - Summary of the number of sessions in both EEZs with decision to stay or leave, in absence of presence of cetaceans (each species only or both simultaneously).

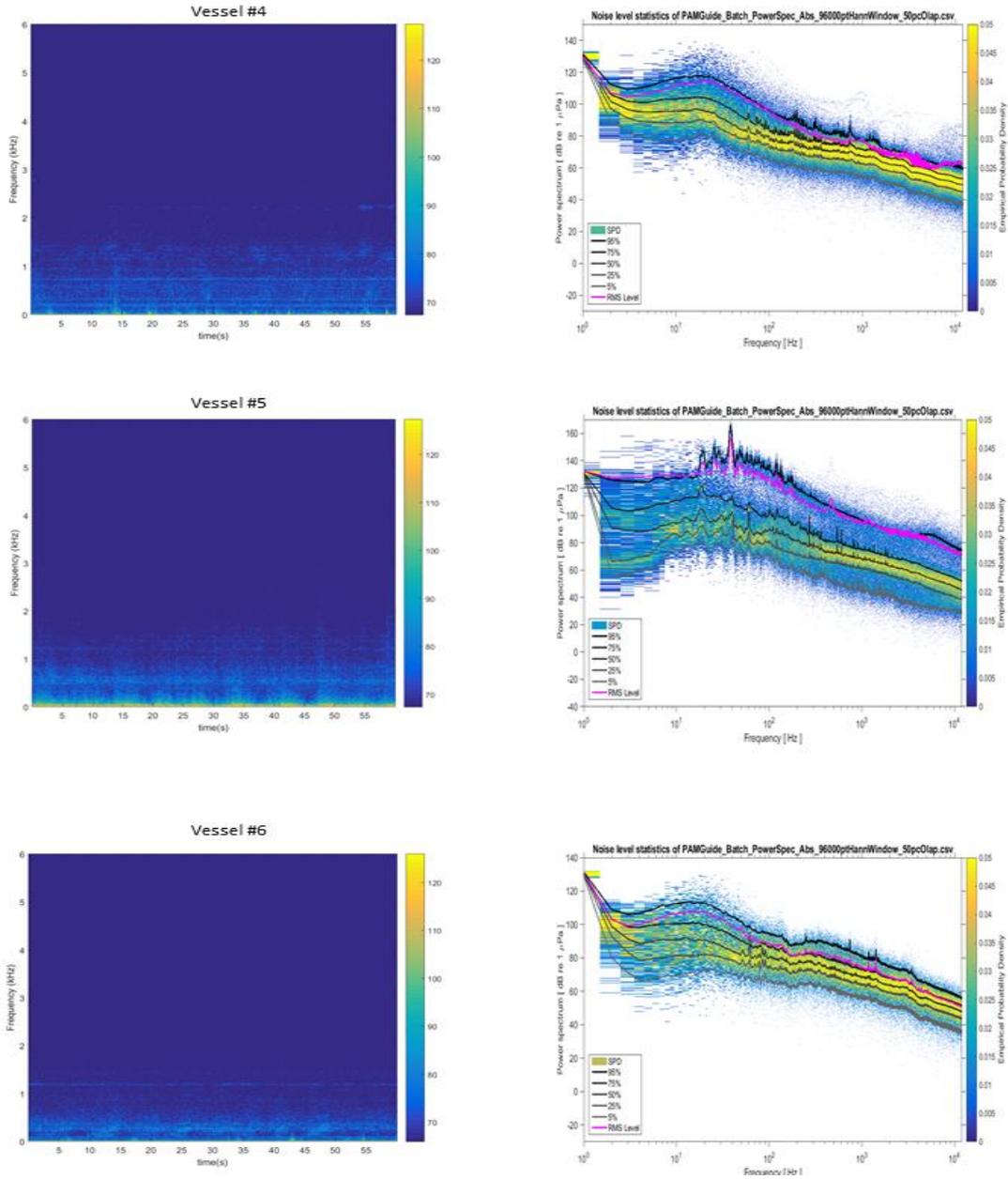
<i>Occurrence:</i>	Crozet			Kerguelen		
	<i>Stay</i>	<i>Leave</i>	<i>All sessions</i>	<i>Stay</i>	<i>Leave</i>	<i>All sessions</i>
Absence of cetacean	108	41	149	1818	312	2130
Killer whales only	77	38	115	5	1	6
Sperm whales only	267	162	429	1586	561	2147
Both species simultaneously	285	263	548	5	14	19
<i>All occurrence</i>	<i>737</i>	<i>504</i>	<i>1241</i>	<i>3430</i>	<i>872</i>	<i>4302</i>

Supp. data 2 - Akaike Information Criteria of the generalized linear mixed models of the probability of captains to leave in relation to the fishing success and the competition for both Crozet and Kerguelen. Best AIC are in bold.

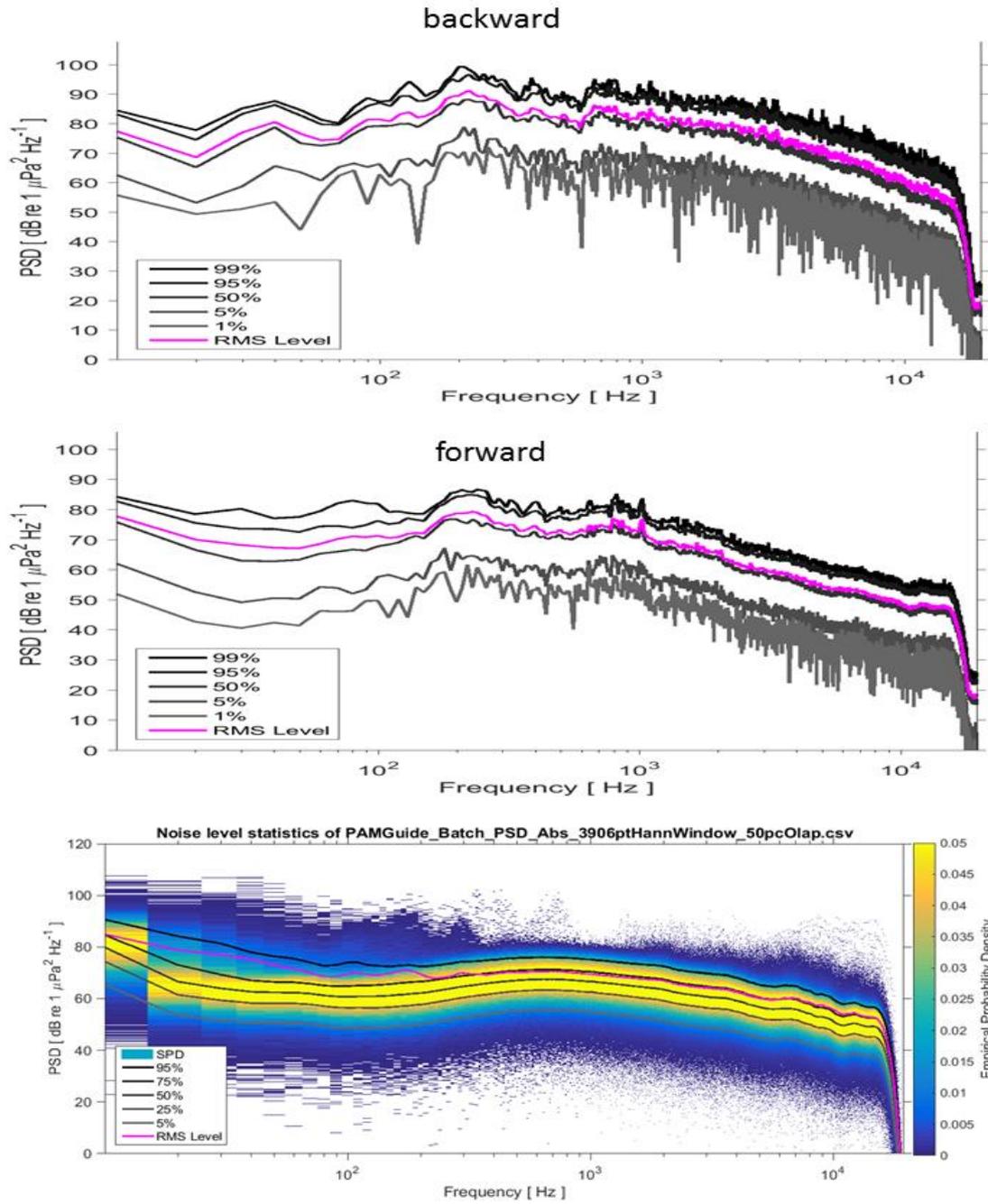
Models	Crozet		Kerguelen	
	<i>df</i>	<i>AIC</i>	<i>df</i>	<i>AIC</i>
<i>Null</i>	4	1532	4	3889
<i>Fishing success * competition</i> <i>random= Fishing success captain</i>	11	1501	7	3823
<i>Fishing success * competition</i> <i>random=1 captain</i>	9	1510	5	3897
<i>Fishing success + competition</i> <i>random= Fishing success captain</i>	8	1499	6	3822
<i>Null</i>	4	1532	4	3889

Supp. data 3 - AICs of the GLMMs of the probability to leave in relation to the fishing success and the number of individuals for both Crozet and Kerguelen. Best AIC are in bold.

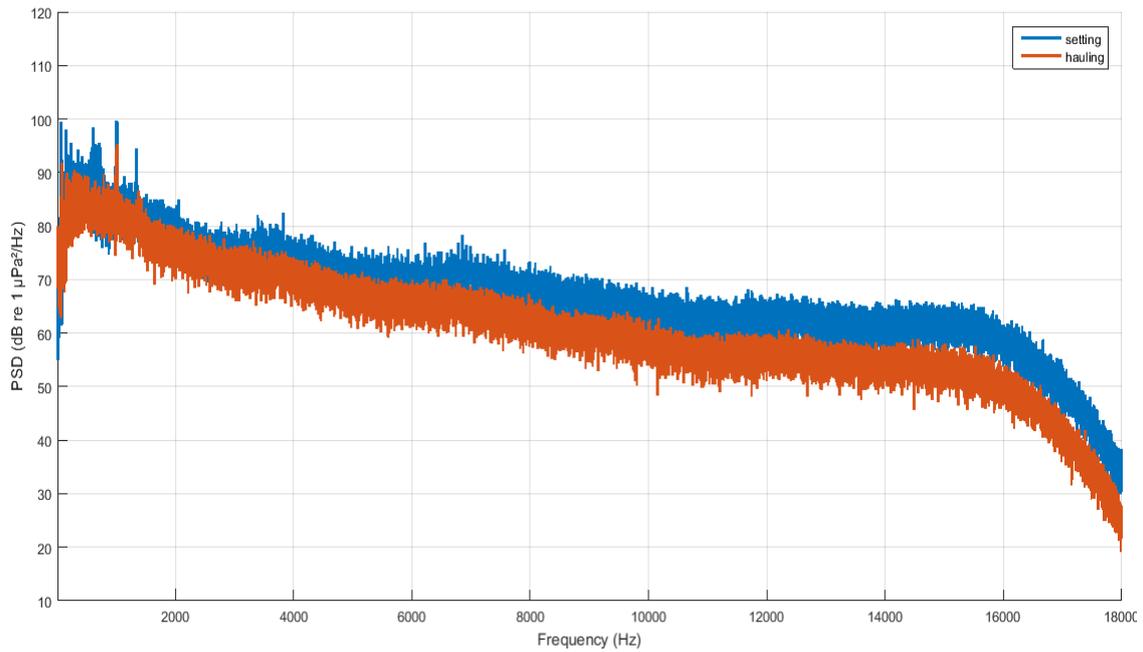
Models	Crozet				Kerguelen			
	<i>Cetaceans</i>		<i>Killer whales</i>		<i>Sperm whales</i>		<i>Sperm whales</i>	
	<i>df</i>	<i>AIC</i>	<i>df</i>	<i>AIC</i>	<i>df</i>	<i>AIC</i>	<i>df</i>	<i>AIC</i>
<i>Fishing success * nb individuals</i>								
<i>random= Fishing success * nb ind captain</i>	14	965	14	115	14	575	14	2858
<i>Fishing success * nb individuals</i>								
<i>random= Fishing success + nb ind captain</i>	10	956	10	103	10	566	10	2852
<i>Daily weight of toothfish * nb individuals</i>								
<i>random= nb individuals captain</i>	7	969	7	99	7	562	7	2894
<i>Fishing success * nb individuals</i>								
<i>random= Fishing success captain</i>	7	952	7	97	7	566	7	2850
<i>Fishing success * nb individuals</i>								
<i>random=1 captain</i>	5	969	5	95	5	564	5	2891
<i>Fishing success + nb individuals</i>								
<i>random= Fishing success captain</i>	6	956	-	-	-	-	6	2849
<i>Fishing success + nb individuals</i>								
<i>random= nb individuals captain</i>	-	-	-	-	6	561	-	-
<i>Fishing success + nb individuals</i>								
<i>random=1 captain</i>	-	-	4	93	-	-	-	-
<i>Null</i>								
<i>Null</i>	2	1073	2	99	2	600	2	3262



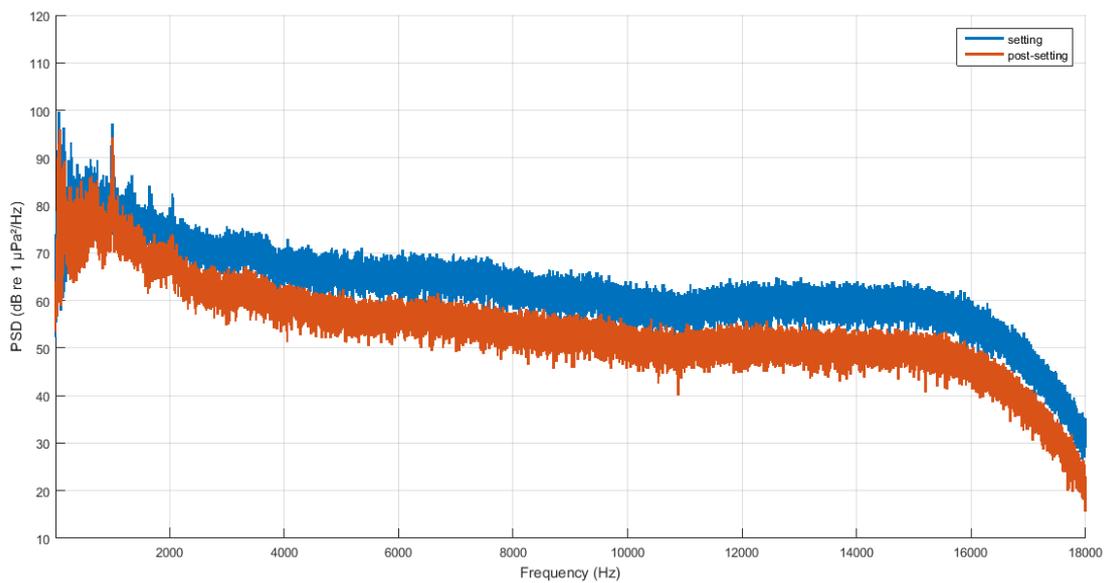
Supp. data 4 - Spectrograms (left panels) and power spectrum densities (right panels) of 3 Australian longliners (Vessel #4 to #6, one vessel per line). The spectrograms were made over 1 min for vessels at 1 km for the hydrophone, with a colour scale representing the square modulus of the acoustic pressure in units of power spectral density (in dB re $1 \mu\text{Pa}^2 \cdot \text{Hz}^{-1}$). The power spectrum (in dB re $1 \mu\text{Pa}$) were assessed through PAM guide with batched file of 3 min for vessels at 1 km of the hydrophone (Merchant et al. 2015).



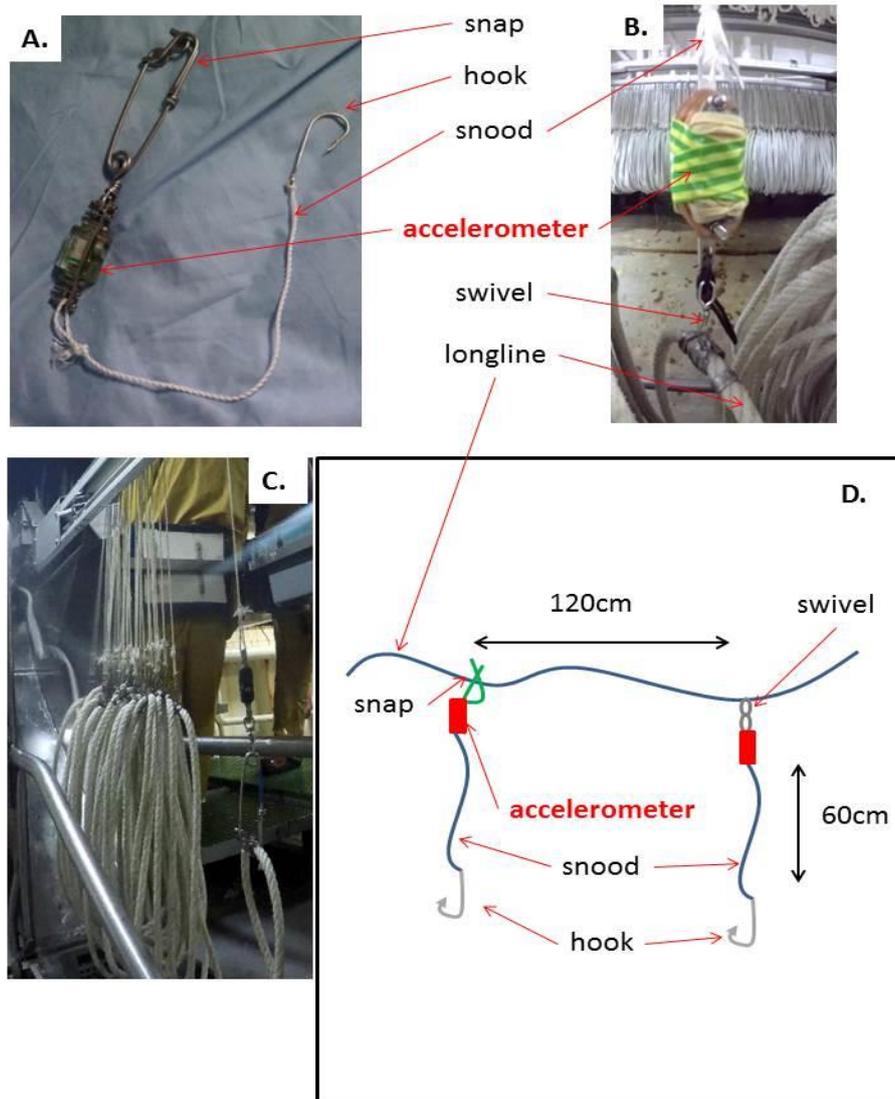
Supp. data 5 - Welch's power spectral densities of the forward, backward and ambient noise estimated with PAM Guide.



Supp. data 6 - Welch's power spectral densities (in dB re 1 μPa².Hz⁻¹) of a vessel while setting and hauling. During both phases the fishing vessel was at circa 1 km to the hydrophone.



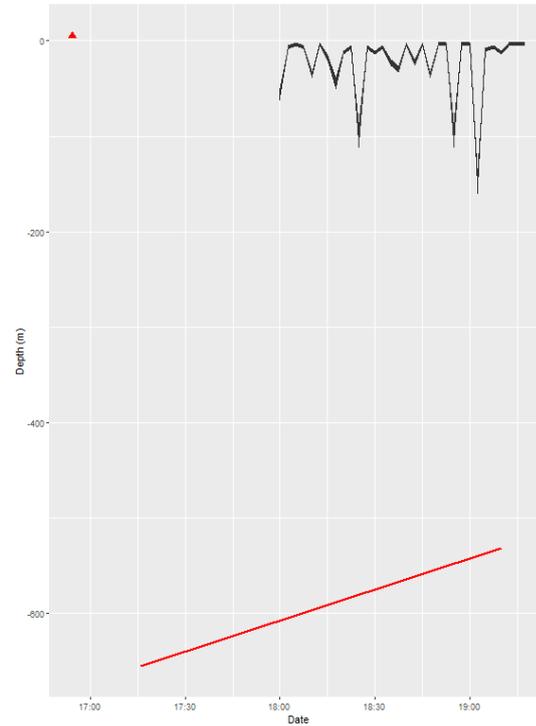
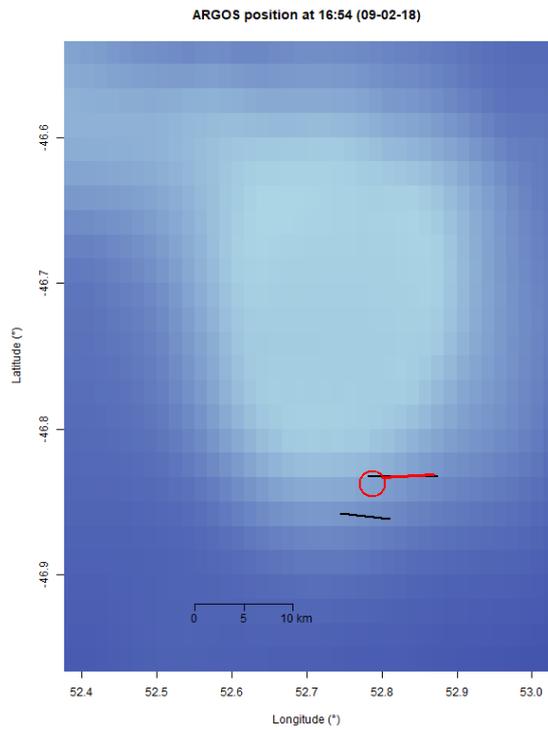
Supp. data 7 - Welch's power spectral densities of the setting and the post setting estimated over 15 s each at 45 s from each other, *i.e.* the setting PSD and post setting PSD were run respectively from 10 to 25 s and 65 to 80s over the spectrogram on Figure 3-6.



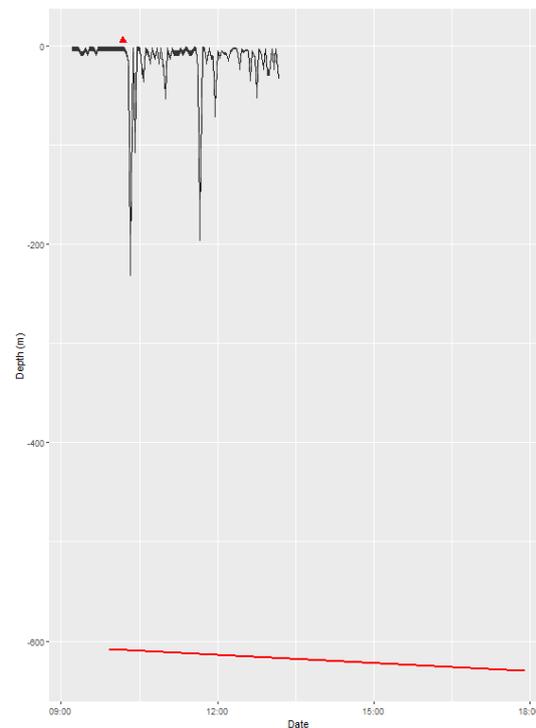
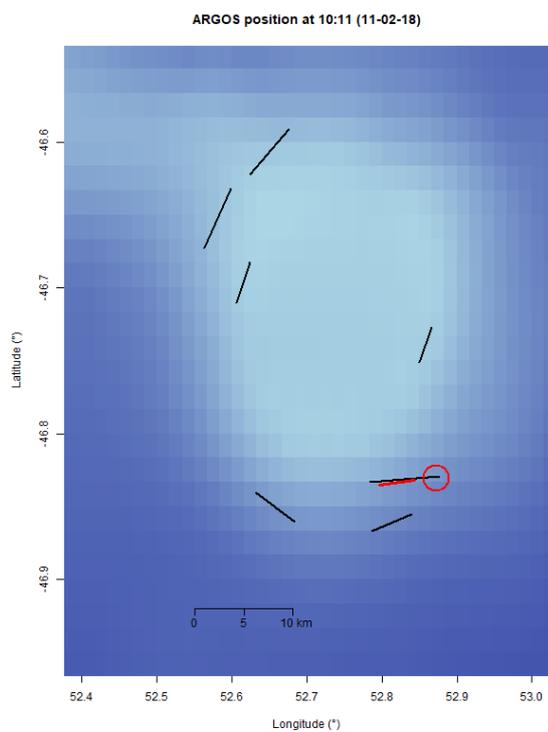
Supp. data 8 - Setting of the accelerometers deployment on the longline. A) picture of the first setting (2016-2017). B) picture of the second setting (2017-2018). C) picture of the first setting hanged on the longline. D) scheme of the accelerometers attached on the longline with both settings example.



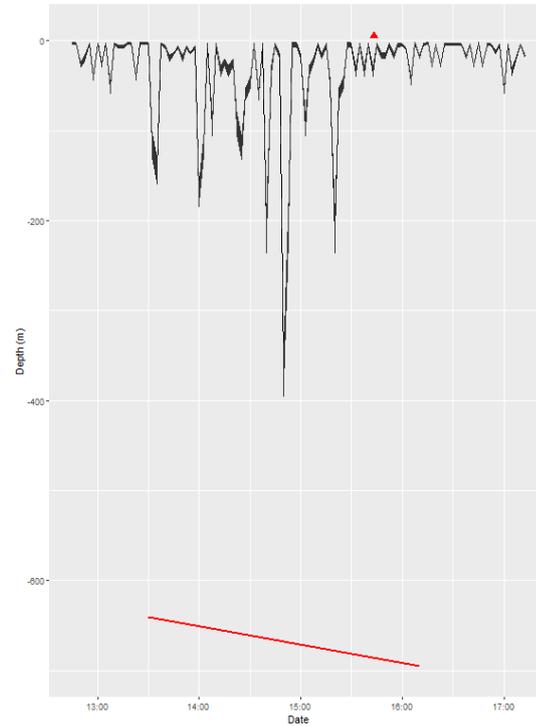
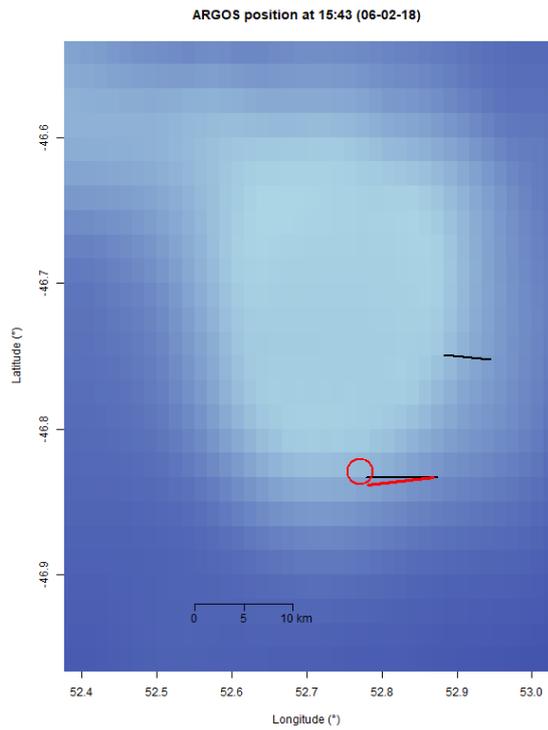
Supp. data 9 - Picture of an entangled dead sperm whale (by Gabriel DEVIQUE, fishery controller).



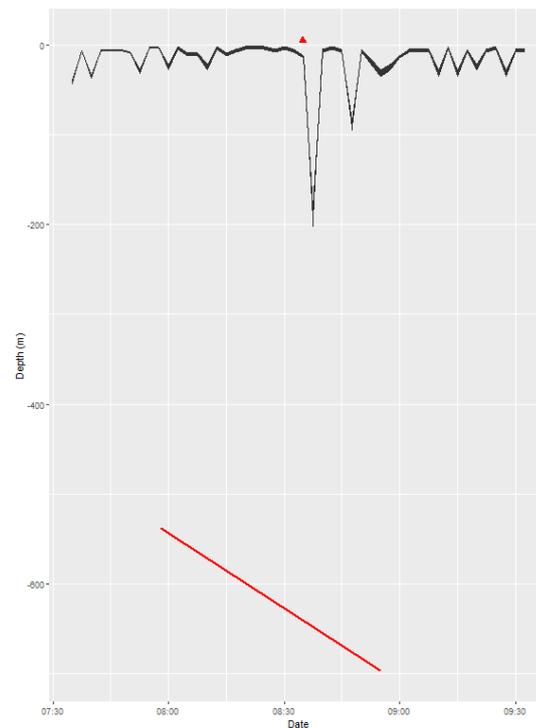
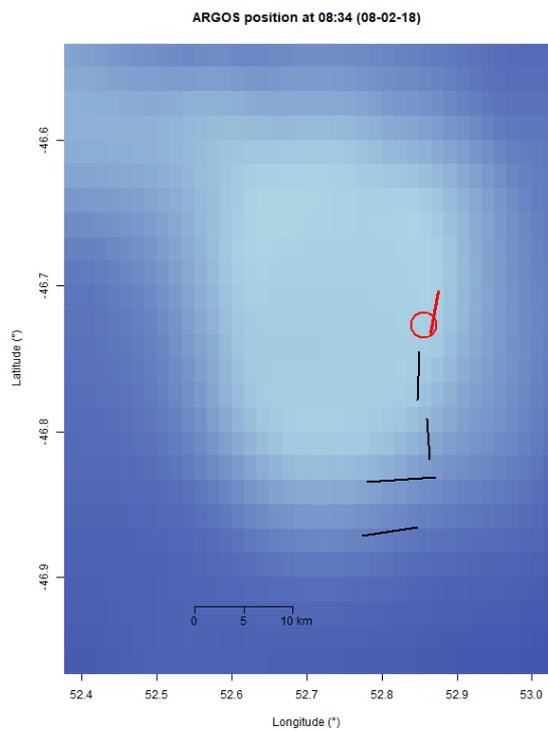
Supp. data 10- ARGOS position (left panel) of an ‘interaction during hauling’ with its associate dive profile (right panel).



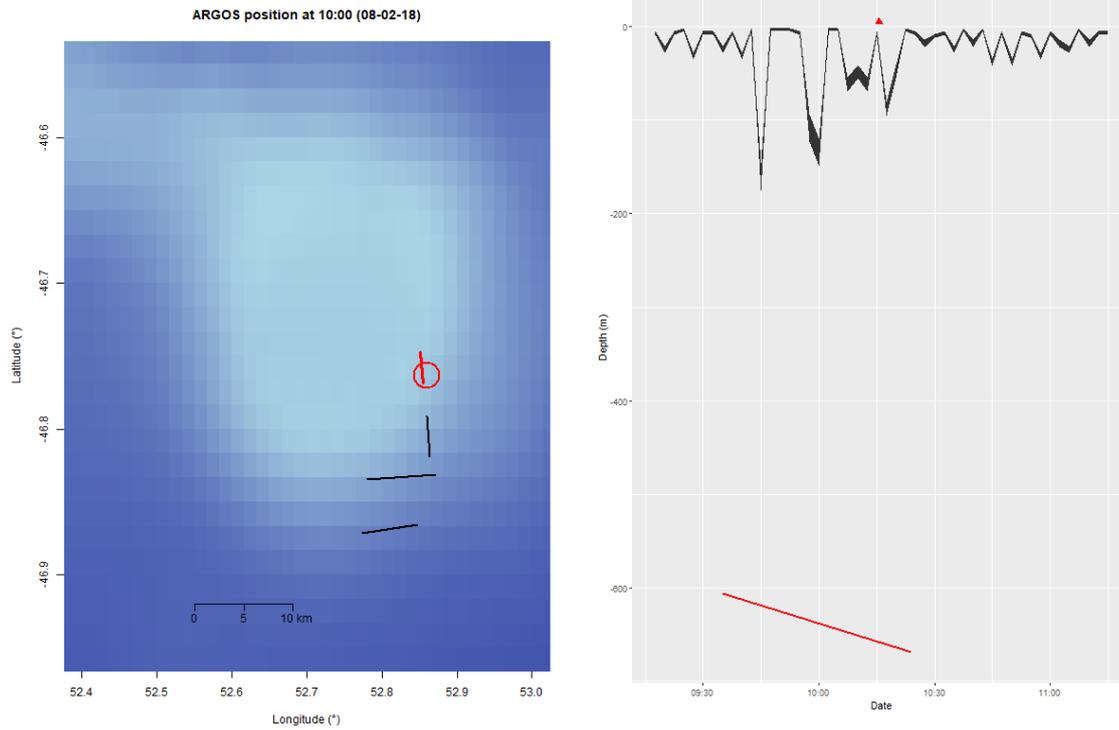
Supp. data 11- ARGOS position (left panel) of an ‘interaction during hauling’ with its associate dive profile (right panel).



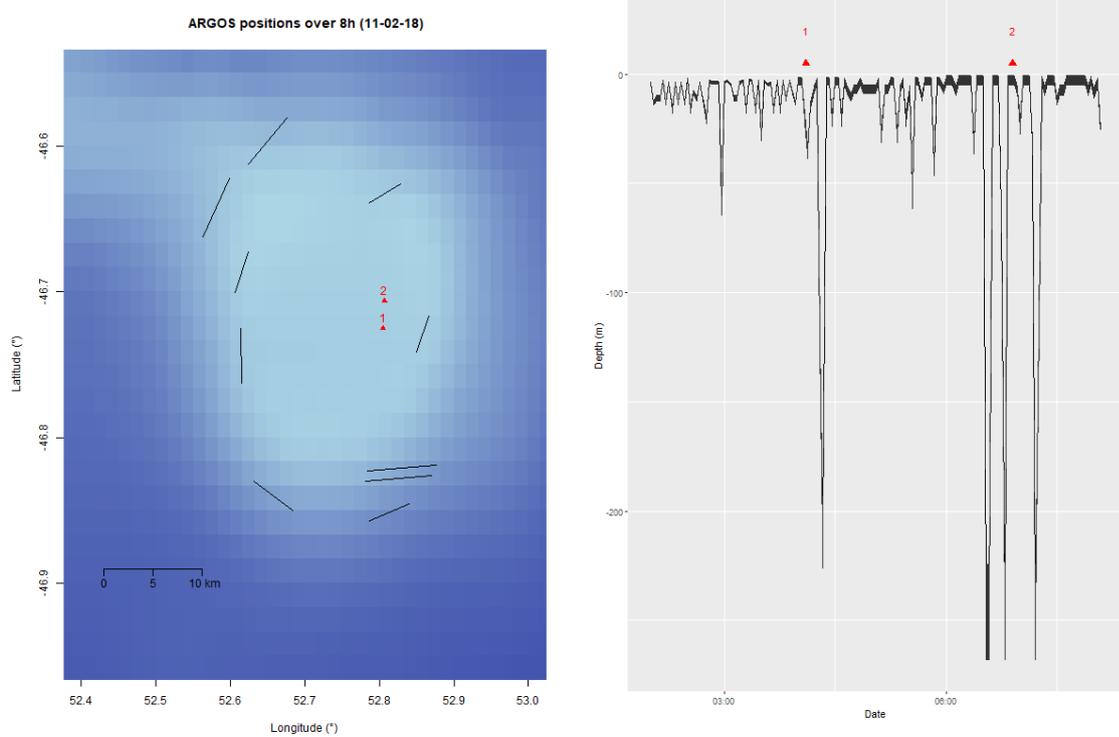
Supp. data 12- ARGOS position (left panel) of an ‘interaction during hauling’ with its associate dive profile (right panel).



Supp. data 13- ARGOS position (left panel) of an ‘interaction during hauling’ with its associate dive profile (right panel).



Supp. data 14- ARGOS position (left panel) of an ‘interaction during hauling’ with its associate dive profile (right panel).



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APPENDIX 1 – MASTER THESIS

Internship Report



Year: **2**
Semester: **4**

Acoustic tracking of sperm whales and killer whales in a context of fisheries interaction.

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Total number of words in the report: 2999

Abstract

Interactions between marine mammals and fisheries are real issues both ecological and economical. For instance, killer whales and sperm whales around Crozet Archipelago and Kerguelen Islands have learned to remove fish from longlines causing high economical loss and modifying survival rates. Our study fitted into this context as a preliminary step to better understand cetacean depredation behaviour. A way to assess cetacean behaviour is to monitor their acoustic activity. Indeed, cetaceans use echolocation clicks while foraging, thus these sounds enable animal localisation by passive acoustic monitoring. By implementing an acoustic tracking algorithm, our purpose was to predict the setting of 4-hydrophone array so that tracking capacity was optimal, while respecting constraints on the length of the cables and the maximal depth of the recorder. We associated the hydrophones in two pairs, and demonstrated that the deeper the first pair was and the longer the distance between the pairs was, the better the precision of localisation was. These results will allow optimal deployments of hydrophones among longlines, so that depredating cetaceans could be localized accurately, and thus the depredation issue better understood.

Introduction

Interactions between marine top predators and fisheries are global phenomena, and in most of the cases are sources of conflicts (Northridge and Hofman, 1999). For instance, some marine mammals have learned how to remove fish from lines or nets, such as sperm whales, *Physeter microcephalus*, and killer whales, *Orcinus orca* (Donoghue et al., 2002; Gillman et al., 2006; Hamer et al., 2012; Kock et al., 2006). This activity of depredation (Donoghue et al., 2002) could lead to significant financial cost for fisheries (Read, 2008) and to biological cost for marine mammals, such as higher risks of mortality and modification of energy balances (Northridge and Hofman, 1999).

Our study focused on the context of depredation off the Crozet (46°25'S, 51°40'E) and Kerguelen (49°20'S, 70°20'E) Islands, Southern Indian Ocean. In these waters, killer whales and sperm whales depredate on longline fisheries targeting a high commercial valuable fish, the Patagonian toothfish, *Dissostichus eleginoides*. Indeed, a recent study estimates a financial loss around €60M in 10 years due to the depredation of killer whales and sperm whales in the Crozet and Kerguelen Exclusive Economic Zones, EEZ hereafter (Gasco, 2013).

Patagonian toothfish is a demersal fish presenting a large bathymetric distribution during their life. Indeed, they spawn in deep water, and after hatching, larvae become pelagic and remain in upper water layers (<500m) until their juvenile stage when they become benthopelagic. Juveniles migrate into deeper water while growing (Collins et al., 2010). Thus, in order to avoid catches of juveniles, demersal longlines are deployed deeper than 500m and up to 2500m (Tixier et al., 2010, 2014). It is known that sperm whales can reach such depth and that they can naturally feed on toothfish (Yukhov, 1982), whereas it is unknown whether toothfish is a natural component of killer whales diet. Indeed, Crozet killer whales feed on penguins, seals, baleen whales and fish (Guinet, 1992), and a recent study revealed that killer whales could occasionally reach depth up to 900m (Pitman et al. pers. comm.), so they might also have natural access to toothfish. However, it is still unknown how sperm whales and killer whales interact with the longline fisheries within the EEZ.

It is thus necessary to find a way to assess whales' behaviour while interacting with the longlines in order to be able to address the depredation issue, by determining if this behaviour is taking place when hauling out the line and/or when the line is fishing. Monitoring whales' behaviour is hardly accessible because of logistical constraints. However, passive acoustics can provide a good alternative to direct observations and data-loggers. Indeed, toothed whales, such as killer whales and sperm whales, produce echolocation clicks while foraging (Barrett-Lennard et al., 1996; Miller et al., 2004; Zimmer, 2011) in repeated trains and with a high broadband intensity. These sounds can be detected by hydrophones several kilometres away from the clicking animal.

Acoustic tracking of toothed whales

Thus, clicks allow fine temporal and spatial scales localization by acoustic tracking (Gassmann et al., 2013; Roy et al., 2010; Thode, 2005; Zimmer, 2011).

The purpose of our study was to define the best hydrophones setting, constrained by the number of hydrophones (4), the length of the cables and the depth of the recorder, to localize killer whales and sperm whales in the depredation context. Thus, we developed a two-dimensional acoustic tracking algorithm, using a ray-tracing propagation model environment-dependant. Then, by simulating hypothetical clicks at different range and depth from the receivers, we statistically tested the efficiency of different hydrophones settings.

Material and method

We implemented our acoustic tracking algorithm following a commonly used model-based ranging method (Baggeroer et al., 1993; Mathias et al., 2013; Tiemann et al., 2006; Zimmer, 2011), which was divided into three steps: (i) modelling multipath arrivals within a research grid at a fine spatial scale, using a ray-tracing propagation model; (ii) measurement of the multipath arrival pattern for each click on each receiver; (iii) comparison of the measured arrival pattern with the predicted ones among the grid. The researched source localisation was finally determined by the localisation on the grid of the hypothetical source with the pattern matching most closely the measured one. To be more selective our algorithm associated the estimations of time delays and of the arrival angles.

In our study we developed the acoustic tracker without real data, so we simulated the “measured” data.

Setting of the environment

Underwater sound propagation is highly dependent of the speed of sound which is also dependent of oceanic environment parameters. We used temperature and salinity data from the World Ocean Database (NOAA) within the EEZ. Thus, for a given GPS point we had temperature, T (Celsius), and salinity, S (PSU), as functions of depth, z (m), and then we used the following formula to obtain the sound speed profile, c in $\text{m}\cdot\text{s}^{-1}$ (Clay and Medwin, 1977, see Fig.1):

$$c = 1449.2 + 4.6T - 0.0557T^2 + 0.00029T^3 + (1.34 - 0.017T)(S-35) + 0.016z, \quad (1)$$

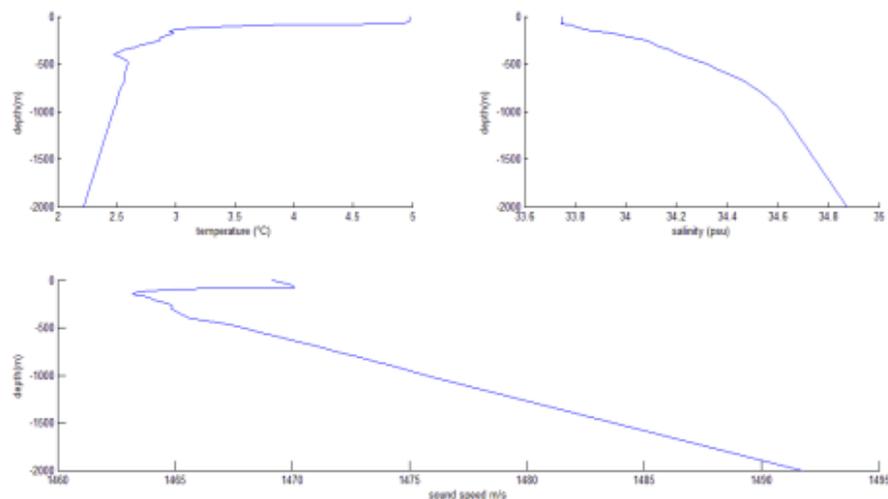


Figure 1. Temperature (top left) and salinity profiles (top right) used to calculate the sound speed profile (bottom) for this study.

The sound profile is required to model the sound propagation within a two-dimensional research area. We ran the Gaussian beam-tracing acoustic propagation model, BELLHOP (Porter and Bucker, 1987), through the software Matlab, in order to simulate hypothetical sources among a research grid, received by the hydrophones (Mathias et al., 2013; Tiemann et al., 2006). This modelled research grid served as a reference to localise sounds recorded, since for each point BELLHOP outputs the arrival times and angles of simulated rays.

Fisheries within the EEZ use longlines measuring in average 8000m and generally deployed between 500 and 2000m depth (Guinet et al., 2014; Tixier et al., 2010, 2014). Consequently, we defined a research grid of 10000m in range and 2000m in depth (Fig.2.a.), with a resolution of 20x10m (range x depth). We did not modelled difference of bottom depth as our model was independent of bottom reflected rays. For each simulated source on the grid, 50000 rays were launched between -89° and $+89^\circ$ from the horizontal. BELLHOP outputted arrival time and arrival angle (which do not depend on the source frequency) on each receiver and bounce numbers on the surface or on the bottom for every ray of each source among the grid. The receivers were modelled on the vertical axis at the beginning of the grid.

The recording device is a vertical array composed of 4 hydrophones linked to a centrally located receiver by 100m-long cables. Our tracking algorithm was based on two models, a time-delays estimation, commonly used with widely spaced hydrophones, and a beam-forming method (estimation of arrivals angles), requiring closely spaced hydrophones (Gassmann et al., 2013; Mathias et al., 2013; Zimmer, 2011). Thus, we associated the hydrophones in two pairs, within which hydrophones were separated by 10m (Mathias et al., 2013) and with variable distance between the pairs (Fig.2.b.). As our purpose was to find the best setting, we tested 4 different distances between the pairs, limited by cables (60, 90, 160, 190m), at 5 different immersion depths for the first pair, restricted by the recorder's pressure resistance (150, 250, 350, 450 and 550 m depth), so we tested 20 different settings.

Acoustic tracking of toothed whales

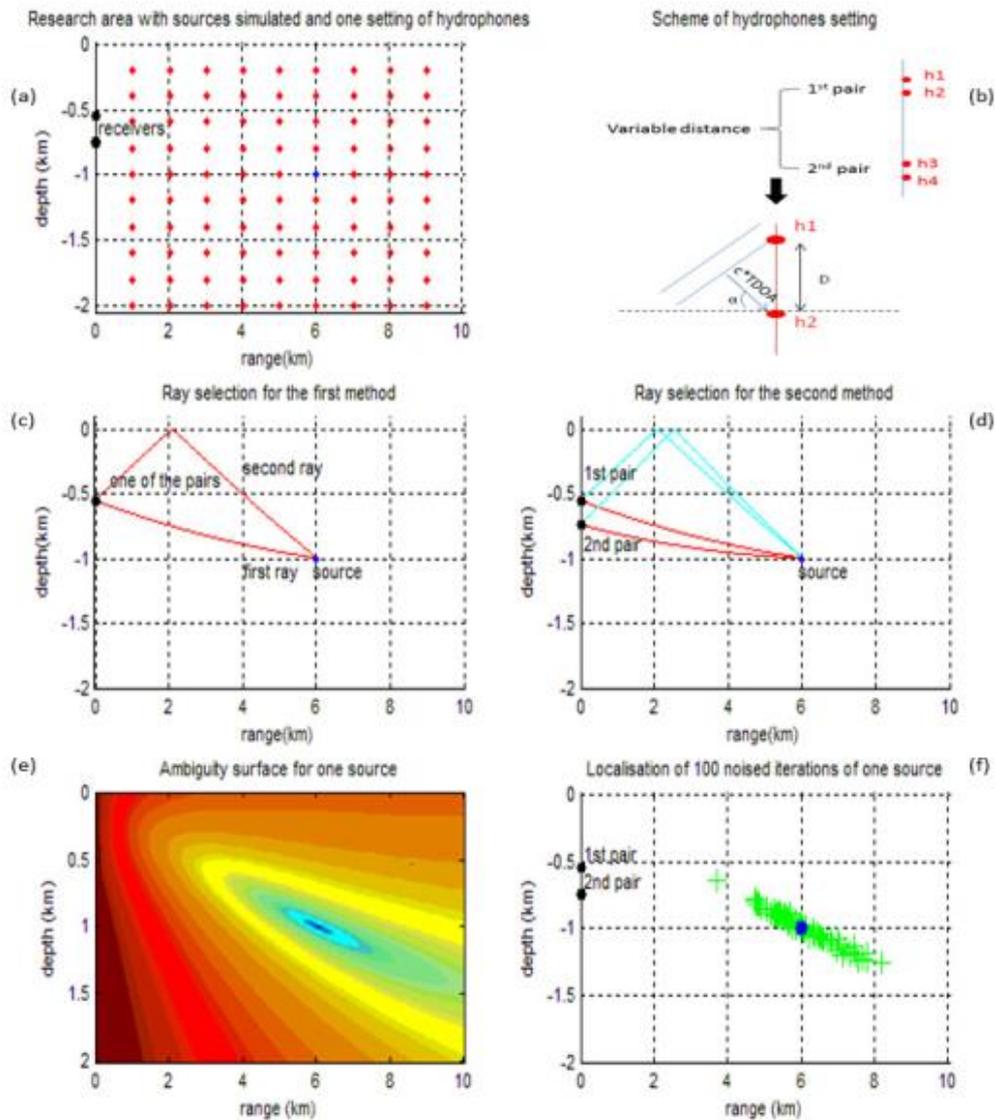


Figure 2. Method summary. The setting defined the beginning in range of the research grid, within which we simulated 90 sources (a). The hydrophones were associated in 2 pairs, with $D=10\text{m}$ in order to estimate rays' arrival angles (b). We varied the distance between pairs and the setting's depth (a, b). To compute the ambiguity surface, we used the comparison of arrival patterns between the first and the second arrival rays in one receiver (c, in red) and the comparison of arrival patterns of the first arrival rays between two receivers (d, in red). By combining both methods, we calculated one ambiguity surface for each source (e), the coldest colours represent the lowest L_{rms} values, *i.e.* the most likely position of one researched source. To test the settings efficiency, we randomly simulated 100 noisy signals per each source position, the 100 noisy signals lead to 100 estimated sources' position in green (f), and can be compared with the true source position, in blue.

Measured data

We simulated 90 sources within the grid, every 1000m in range (from 1000 to 9000m) and every 200m in depth (from 200 to 2000m depth, Fig.2.a.). For each source, we ran BELLHOP to obtain the arrival time on each hydrophone. This measure was then noised to copy the possible estimation error of a real measure, estimated from Zimmer (2011). We added a random normalised value with a standard deviation of 150 μ s on each "measured" ray and repeated the operation 100 times per measure. To be closer to the reality, we removed bottom reflected rays (Mathias et al., 2013), and kept the two first arriving rays on receivers for each source for our tracking algorithm. Then we calculated the rays' vertical arrival angles on each pair of receivers (Eq.2). Considering that clicks propagate as a plane wave on short range (Fig.2.b.), we used the time difference of arrival (dT) of the same ray between two hydrophones closely spaced, $D=10$ m, to compute the incident angle, α in radian (Gassmann et al., 2013; Mathias et al., 2013):

$$\alpha = \text{asin}\left(\frac{c \cdot dT}{D}\right), (2)$$

with c the mean sound speed ($\text{m} \cdot \text{s}^{-1}$).

Ambiguity surface

An ambiguity surface is a two-dimensional function comparing the measured rays' pattern with modelled rays' patterns among the reference grid (Fig.2.e.). We used two different comparison models using weighted mean-square error. For each points of the grid (r, z), both methods estimated the mean-square error between the measured and modelled time difference of arrival between two arriving rays (dT), and the mean-square error between measured and modelled arrival angles (α) of these rays.

The first method used the first and second arriving rays (i, j) measured on one receiver (Mathias et al., 2013, see Fig.2.c.). We computed the weighted mean-square error ($Lwms$) between the measured rays (i, j), using all possible combination of the modelled rays (A, B) on one receiver, for each point of the grid (r, z):

$$Lwms_{\text{pair } 1 \text{ or } 2}(r, z) = \min_{A, B} \left[\left(\frac{dT_{A, B}(r, z) - dT_{i, j}}{\sigma_{\text{time}}} \right)^2 + \left(\frac{\alpha_A(r, z) - \alpha_i}{\sigma_{\text{angle}}} \right)^2 + \left(\frac{\alpha_B(r, z) - \alpha_j}{\sigma_{\text{angle}}} \right)^2 \right], (3)$$

with σ_{time} the standard deviation of the measured arrival time differences and σ_{angle} the standard deviation of the measured angle. For each point of the grid (r, z), we selected the modelled arrival combination (A, B) minimizing $Lwms$. We applied the first method on each pair, so we obtained two different ambiguity surfaces.

The second method is similar to the first one, but we only considered the first arriving rays on two receivers (Fig.2.d.). We computed the $Lwms$ between the first measured rays of each pair of hydrophones ($i1, i2$), using all possible combination of the modelled rays between the two pairs ($A1, A2$), for each point of the grid (r, z):

$$Lwms_{\text{2pairs}}(r, z) = \min_{A1, A2} \left[\left(\frac{dT_{A1, A2}(r, z) - dT_{i1, i2}}{\sigma_{\text{time}}} \right)^2 + \left(\frac{\alpha_{A1}(r, z) - \alpha_{i1}}{\sigma_{\text{angle}}} \right)^2 + \left(\frac{\alpha_{A2}(r, z) - \alpha_{i2}}{\sigma_{\text{angle}}} \right)^2 \right], (4)$$

Finally, we combined the three $Lwms$ obtained by the two methods to compute one $Lwms$. Thus, we considered all the comparative factors (time difference of arrival and arrival angles) available thanks the two pairs of hydrophones, and so we strengthened our selective criteria:

$$Lwms_{\text{mix}}(r, z) = Lwms_{\text{pair } 1}(r, z) + Lwms_{\text{pair } 2}(r, z) + Lwms_{\text{2pairs}}(r, z), (5)$$

The lowest values L_{wms} in the ambiguity surface revealed the likeliest position of the researched source (Fig.2.e.).

Statistical analysis

The ambiguity surface computation was realised for the 90 simulated researched sources. For each source position, 100 noisy signals were generated so that localisation was reiterated 100 times per source position. The reiterations were used to estimate the mean errors of localisation in depth and range for each source as we know precisely the source localisations (Fig.2.f.). As we had 20 settings of hydrophones, we tested the errors of localisation between these configurations. We tested the accuracy of localisation for the 20 settings separately, for the distance between pairs regardless the immersion depth and, conversely, the immersion depth regardless the distance between pairs. Besides, once the best setting estimated, we tested whether sources are localised differently according to the depth of the source or/and the distance from the hydrophones.

We used ANOVA tests coupling with multiple comparison tests through Matlab (*anova1* and *multcompare*) to test the mean errors divergence.

Results

The ANOVA tests, which compared mean errors regardless sources' position on the grid, revealed significant differentiations ($p < 0.001$) between the distance between pairs, between depths of the first hydrophone and between the 20 settings. Then, the multiple comparison tests showed that the deeper is the first pair of hydrophones and the longer is the distance between pairs, the lower are the mean errors both in depth and in range (Fig.3.). Indeed, we observed an additive effect between the distance between pairs of hydrophone and the first pair. Thus, the 20th settings, *i.e.* first pair at 550m with a distance of 190m between pairs, showed the lowest mean errors, both in range and depth regardless the sources' position, and significantly different from 18 other settings ($p < 0.05$), after applying a Bonferroni correction (Fig.3.).

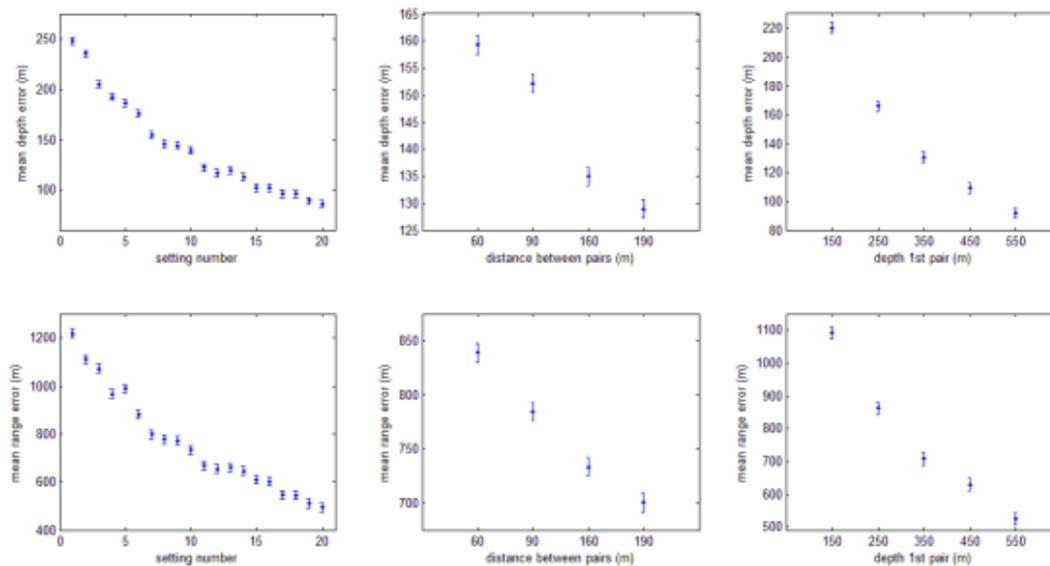


Figure 3. Mean errors of localisation, both in depth (top) and in range (bottom), as a function of the settings (left column), of the distance between pairs (middle column) and of the depth of the first pair (right column).

Acoustic tracking of toothed whales

Once the best setting estimated, it was interesting to assess how positions of the sources could impact on the localisation precision.

When the source depth increased, regardless to its distance from hydrophones, we observed an increase of the mean depth error, from 38.4m at 400m depth to 148m at 1800m depth (Fig.4.a.), but a low variation of the mean range error. Indeed, there was no significant difference, according to the multiple comparison tests, between the mean errors (estimated around 515m) from 400m to 1800m depth (Fig.4.b.). Similarly, when the range between the sources and the hydrophones increased, we observed a slight increase of the mean depth error and a high increase of the mean range error (Fig.4.c. and d.).

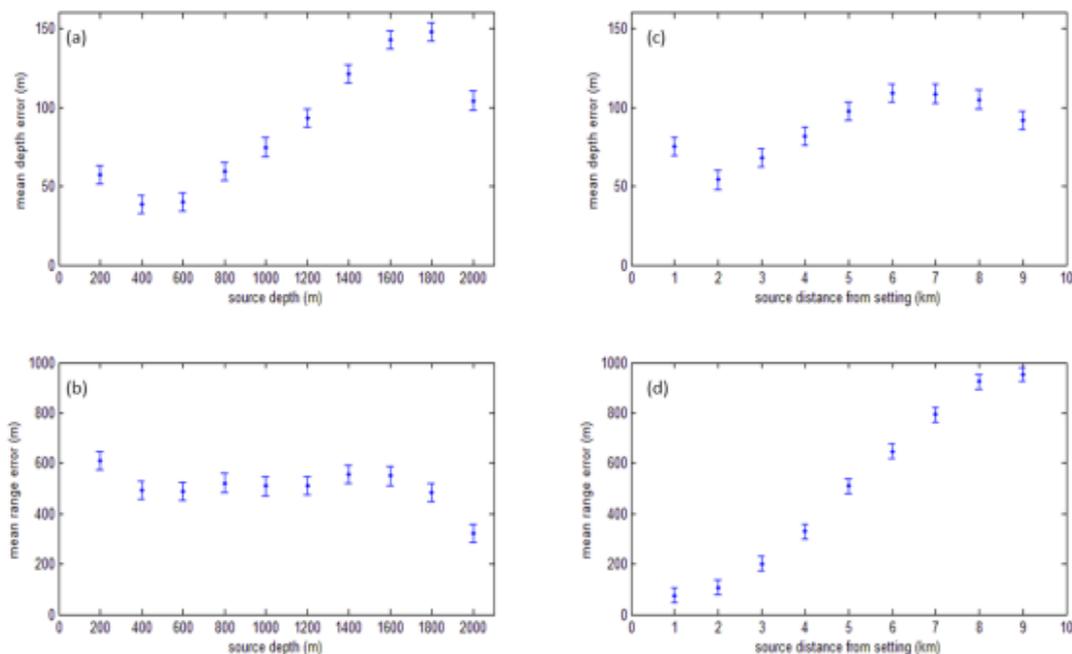


Figure 4. Mean errors of localisation with the 20th setting (1st pair at 550m with a distance between pairs of 190m), both in depth (top) and in range (bottom), as a function of the sources depths (left column) and of the horizontal distance between the sources and the setting (right column).

Discussion

This study was a preliminary work of a project which will focus on a better understanding of sperm whales and killer whales' depredation behaviour, through an acoustic approach. Indeed, no acoustic data is currently available, thus, our goal was to develop an optimised method to collect and assess acoustic data. To study depredation, a critical issue is to know at which depth animals are interacting with the longlines, so one focus of our study was to better localize cetaceans rather in depth than in range.

We based our tracking algorithm on the method exploited by Mathias et al. (2013), which revealed good localisation precisions with one pair of hydrophones for real data. As we implemented one more pair and use the two pairs to add selective criteria, we expected to also have a strong localisation resolution. Besides, we voluntarily overestimated the error of localisations by using relatively strong noises on the measure of arrival time. Indeed, we expected to have a better accuracy on the arrival time estimation with real data than with the simulated values in this study.

Acoustic tracking of toothed whales

We revealed that to have the most accurate setting, hydrophones should be deployed as deep as allowed by the pressure constraint and with the maximum distance possible between pairs.

In our model, we considered the setting of hydrophones aligned with the longline, so range error of localization would still positioned whales on the longline. We assumed that killer whales should interact with longlines close to the surface, during hauling (Tixier et al., 2010, 2014), with a maximum possible depth at 900m, whereas sperm whales could be more likely to interact with longlines at the bottom. As a result, we should localize killer whales in depth with a maximum mean error of 75m, and sperm whales with a mean depth error of 100m, which are both enough to define whether whales interact mostly at the surface or at the bottom. It is thus essential to equip longlines with loggers recording pressure, temperature and salinity to correctly monitor the environment and set the most realistic acoustic propagation model according to local oceanographic conditions. Furthermore, by adding accelerometer among the longline and by tagging several individuals, we will be able to assess the removal of fish from cetacean and to calibrate our tracking algorithm.

Author contribution and acknowledgment

The author managed the tracking algorithm's coding, using a ray-tracing propagation, which was implemented to the algorithm with the help of Rémi Emmetière. The author also assessed the statistical analysis.

I am very grateful to Dr. J.Bonnell for allowing me to join his team and have this great experience in this very interesting research field, and I warmly thank him for his guidance during my internship. I am also grateful to R.Emmetière for his collaborative work and to B.Picard for sharing environmental data from the CEBC. I also thank Dr. C.Guinet, for his insightful comments.

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APPENDIX 2 – ABSTRACT DETECLIC

8th DCLDE WORKSHOP

DeteClic: a user-friendly and comprehensive automated click detector to monitor odontocetes

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Passive acoustic monitoring is now intensively used to study cetaceans. Given the growing amount of collected data, it is of interest to implement automatic methods to monitor cetaceans' sounds. In that aim, we developed DeteClic, a transparent and user-friendly odontocetes click detector on Matlab. This detector takes the form of an intuitive interface to analyze pulsed and loud acoustic signals. DeteClic can be used along the entire bioacoustics analyzing process, from the display of graphic representations to the click detection and their understanding. Our detector allows for (i) manual labeling, based on both listening and visualization, and (ii) automatic detection. DeteClic includes 4 different automatic click detection approaches: (i) a Teager-Kaiser energy operator [1], (ii) an intercorrelation computation with a given reference signal, (iii) a spectrogram analysis [2], and (iv) a kurtosis-based statistical detection [3]. Combining the results of these 4 methods enhances the automatic detection robustness. To assess its performances, we equipped DeteClic with an evaluation tool, relying on automatic comparison of manually- and automatically-detected clicks. DeteClic can therefore be used to compare the results of the methods (i.e. recall and precision rates [4]) depending on acoustic environments and recordings. In addition to the clicks detection and based on how the user defines a train of clicks (using criteria in time between clicks and train duration [5]), DeteClic enables a presence event analysis. Finally, we provide a series of outputs easily reusable for any further statistical or visual analysis. We first tested DeteClic on sperm whale clicks, recorded during longline fishing campaigns around the Kerguelen Islands (southern Indian Ocean). Considering clicks detected by at least three methods was the most efficient approach (average recall of $71\pm 5\%$ and precision of $54\pm 5\%$). Discriminating click trains allowed for a greater precision in detecting echolocation events and an accurate presence event analysis.

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APPENDIX 3 – HYDROPHONE PROTOCOL

DEPLOIEMENT D'UN ENREGISTREUR ACOUSTIQUE A PARTIR DES PALANGRIERS FRANÇAIS DANS LES ZEE DE CROZET ET KERGUELEN.

Ce protocole a été réalisé par Gaëtan RICHARD, doctorant au CEBC (UMR CNRS – Université La Rochelle) et à l'ENSTA Bretagne (Brest) sous la direction de Dr. Christophe GUINET (CEBC, UMR CNRS – Université La Rochelle) et Dr. Julien BONNEL (Woods Hole Oceanographic Institution, USA) et en collaboration avec Dr. Paul TIXIER (Deakin University, Melbourne, Australia).

Pourquoi récolter des données acoustiques ?

Le projet ORCADEPRED mené par Dr. Christophe GUINET (CEBC, UMR CNRS – Université La Rochelle) vise à mieux comprendre le phénomène de déprédation réalisé par deux espèces de cétacés (les orques et les cachalots) sur la pêcherie à la légine dans les ZEE de Crozet et Kerguelen. Ces interactions entraînent de nombreux problèmes, aussi bien socio-économiques qu'écologiques. L'objectif à long terme est donc de trouver des solutions pour réduire voire empêcher la déprédation.

Jusqu'à présent les études du projet ont été réalisées sur les données de pêche et les observations de surface réalisées par les COPECs. Ces informations ont permis d'apporter de nombreuses réponses sur la quantification du phénomène et du suivi des populations de cétacés. Cependant une dimension reste mal connue : le comportement sub-surface. Or il est difficile « d'observer » ce qu'on ne peut voir, c'est pour cela que le projet a mis en place une étude acoustique. Le but est donc d'équiper les palangres avec des hydrophones.

Les orques et cachalots sont des mammifères qui produisent de nombreux sons, que ça soit pour communiquer ou pour chasser. En effet ces animaux évoluent dans un milieu où la lumière est rare et donc ils utilisent l'écholocation (principe du sonar) pour rechercher leur nourriture. En déployant des hydrophones (i.e. des microphones sous-marins) sur les palangres, il est possible de surveiller la présence des cétacés autour des lignes même en absence du navire. De plus, comme indiqué précédemment, l'acoustique est très importante pour ces mammifères marins, c'est donc essentiellement de cette manière qu'ils repèrent les navires. Il est donc important d'enregistrer les palangriers pour quantifier et qualifier leur signature acoustique et d'évaluer si les différents bruits générés lors des opérations de pêches permettent une détection, et à quelle distance, des navires de pêche par les cétacés.

Description de l'enregistreur



Accessoires fournis avec le Soundtrap :

- 1 bouchon en caoutchouc
- 1 télécommande waterproof
- 1 câble USB pour connecter le Soundtrap
- 1 disque dur externe LACIE

Données à collecter

Avant tout déploiement créer un dossier sur le disque dur externe dont le nom portera les informations du déploiement :

⇒ ***A_XXX_ZEE_CAP_NAV_AAMMJJ_PALXXX***

- *A = acoustique*
- *XXX = le numéro de la manip : 001, 002...020 (toujours avoir 3 chiffres)*
- *ZEE = les 3 initiales de la ZEE où le déploiement a lieu*
- *CAP = les 3 initiales du capitaine*
- *NAV= les 3 initiales du bateau*
- *AAMMJJ=année mois et jour de la mise à l'eau*
- *PALXXX=numéro de la palangre sur lequel l'hydrophone est mis : PAL001, PAL045, PAL123 (toujours avoir 3 chiffres)*

Dans ce dossier vous viendrez ensuite :

- **enregistrer une impression écran des configurations (cf section configuration), et renommer l'image : « A_XXX_ZEE_CAP_NAV_AAMMJJ_PALXXX_config »**
- **enregistrer la fiche déploiement, et renommer le doc word : « A_XXX_ZEE_CAP_NAV_AAMMDD_PALXXX »**
- **enregistrer les données acoustiques après le déploiement.**

Mise à l'eau

Il est important pour nous de bien connaître la position de l'hydrophone pour ensuite connaître les distances navire-hydrophone lors des analyses acoustiques.

Les conditions météo et océanographiques sont aussi importantes car cela représente une part majeure du paysage sonore (*i.e.* du bruit ambiant sous-marin). Ces informations sont à compléter dans la fiche de déploiement.

Pour la présence/absence des cétacés bien souvent vous ne les aurez pas puisque la nuit il n'y a pas d'observation de nuit, mais dans certains cas leur présence peut être noté, sinon indiquer 'non obs'.

Récupération

Les mêmes informations que la mise à l'eau sont nécessaires. L'observation des cétacés est ici très importante. Bien remplir la fiche de déploiement.

⚠ En cas de présence d'orque : un effort important de PHOTO-IDENTIFICATION est nécessaire.

La photo-identification couplée aux enregistrements acoustique nous permettront d'établir sur du long terme le répertoire acoustique des orques de Crozet. Ne pas mettre les photos sur le disque dur destiné pour l'acoustique, suivre le protocole normal de photo-identification.

Evènements acoustiques

Une part importante de notre étude consiste à déterminer des signaux acoustiques susceptibles d'attirer les cétacés. Pour cela veuillez noter tous les évènements de manœuvre du bateau lorsque l'hydrophone est à l'eau.

Nous considérons comme manœuvres avant tout la croche d'une bouée lors du virage d'une palangre, **veuillez noter l'heure et minute de l'arrivée du navire sur la bouée et indiquer « Croche palXXX »**, cette information est différente du début de palangre trouvé dans le CP (=1^{er} hameçon à bord). Aussi veuillez indiquer des changements de conduite du capitaine tels que des demi-tours ou encore marche arrière (=signaux acoustique forts). Tout bruit inhabituel entendu à bord est également un évènement important à noter, même si l'origine est inconnue. Veuillez noter aussi les rencontres avec d'autres espèces de cétacés que les orques et les cachalots, afin de récolter les sons qu'ils produisent.

⚠ La fiche de déploiement sera plus facilement rempli par les officiers. Veuillez imprimer une version papier à mettre en passerelle et après chaque déploiement, lors du téléchargement de données, remplissez la version numérique à enregistrer dans le dossier du déploiement.

Configuration de l'enregistreur

La configuration nécessite le logiciel SoundTrap Host présent sur votre disque dur fourni.

Installation de SoundTrap Host sur votre PC

Ne pas brancher le Soundtrap sur votre ordinateur. Lancer l'exécutable : « SoundTrapHostinstaller».

Une fois installé, lancez le logiciel SoundTrap Host.

Connecter le SoundTrap au PC

Connecter le Soundtrap à l'ordinateur avec le câble USB fourni, l'appareil va alors apparaître dans la liste du logiciel après quelques minutes (Figure 1). Le sélectionner en cliquant dessus.

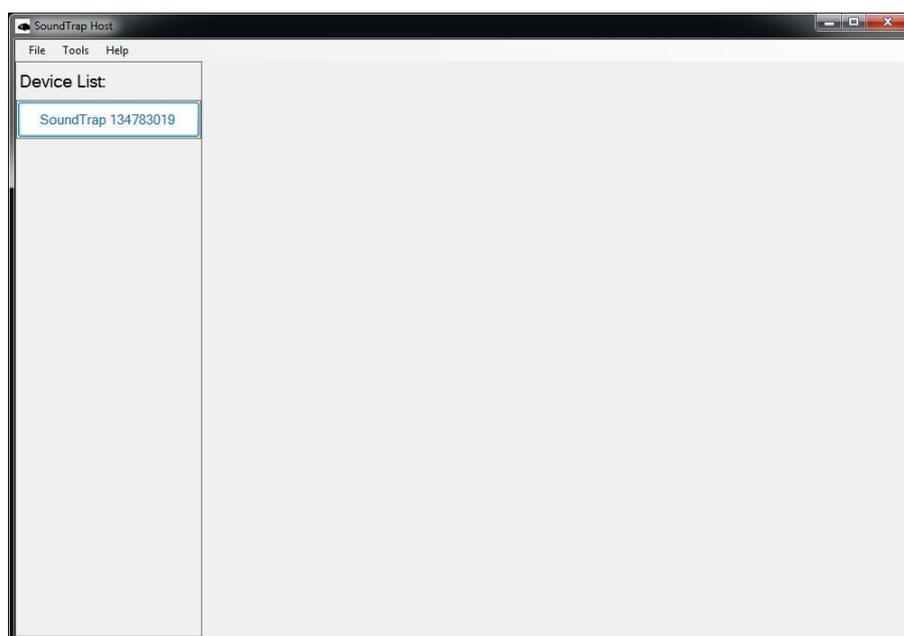


Figure 1 : Liste des appareils

Control du statut du Soundtrap

Vous pouvez vérifier l'état de la batterie, de la mémoire ou encore de l'heure de l'appareil (synchronisé à celle de l'ordinateur) dans l'onglet 'Status' (Figure 2). Avant un déploiement faites en sorte que la mémoire soit vide et la batterie pleine.

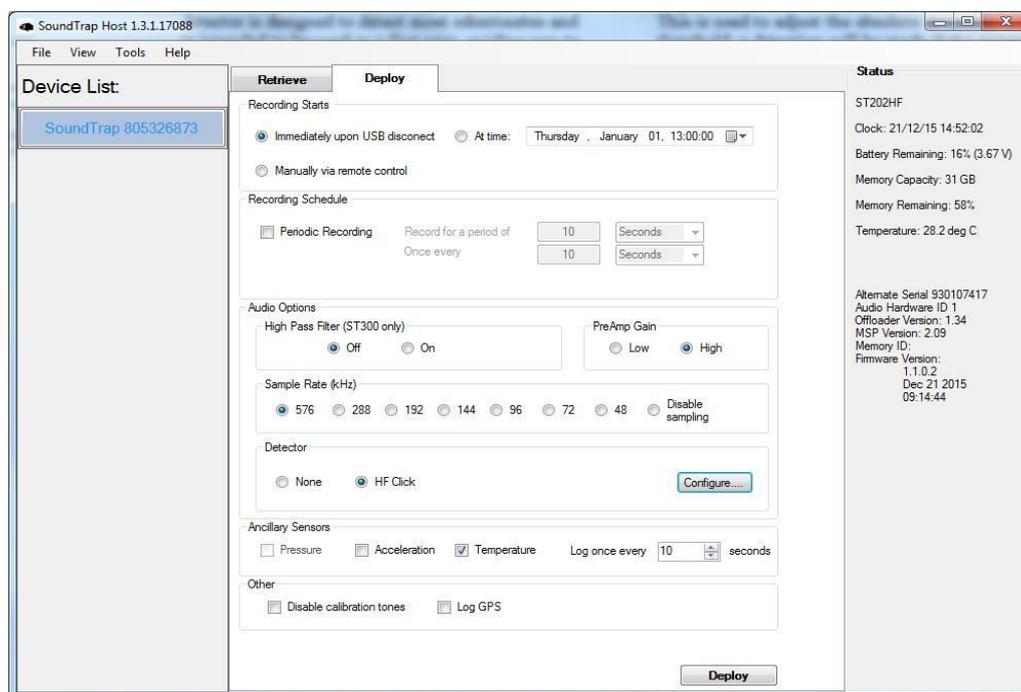


Figure 2 : Fenêtre de contrôle pour le déploiement

Configuration de l'enregistreur

Sélectionner l'onglet 'Deploy' comme montré dans la Figure 2. Configurer l'enregistreur comme indiqué ci-dessous:

Paramètres	Configuration requise	Commentaires
Recording Starts	<p>Cocher <i>Manually using the IR remote control</i></p> <p>Ou Cocher 'At time' et indiquer l'heure de démarrage souhaité</p> <p>Attention ! l'heure doit être la même que celle du navire</p>	<p>Choisissez le mode de démarrage que vous souhaitez, idéalement il faut que l'hydrophone démarre un peu avant son entrée dans l'eau</p> <p>Voir avec les marins pour la télécommande ou avec le capitaine pour l'heure de mise à l'eau.</p>
Recording Schedule	Décocher "<i>Periodic Recording</i>"	Permet de sélectionner un enregistrement cyclique ou continu.
Audio Options		
Preamp Gain	Cocher: <i>HIGH</i>	
High pass filter.	Cocher: <i>OFF</i>	
Sample Rate	Cocher: <i>96 kHz</i>	Cette configuration permet de couvrir les bandes de fréquences des sons

		émis par les orques et les cachalots.
Detector	<p>Cocher: HF Click</p> <p>Click on 'Configure...'</p> <p>Select: Threshold 12 dB</p> <p>Integration time: 10 000 μs</p> <p>Blanking time: 65 000 μs</p> <p>Store Snippets: leave as it is</p>	Détecteur automatique de clics d'écholocation des cétacés
Ancillary sensor	<p>Cocher: Temperature et Pressure</p> <p>Log once every: 10 s</p>	Si vous avez ces possibilités, sinon cocher ce que vous pouvez.

- Une fois les paramètres réglés, cliquez sur le bouton : 'Deploy' et l'hydrophone est prêt, débranchez et mettez le bouchon prévu pour (cf encadré ci-dessous).
- Si vous avez besoin de faire un changement ou vérifier les paramètres il vous suffit de reconnecter l'appareil et de recommencer.

!/ Ne pas oublier de faire un imprimer écran de la fenêtre de control (Fig2) et remplir la section de la fiche déploiement.



Le SoundTrap est fourni avec un bouchon en caoutchouc qui se branche sur l'entrée de l'hydrophone, n'oubliez pas de le mettre afin de protéger l'appareil et pour plus de sureté ajouter une bande de scotch/duct tape pour bien le maintenir connecté !

Vous pouvez aussi mettre de la graisse siliconé pour protéger les connectiques.



Recharge de la batterie

La batterie du Soundtrap est une batterie Lithium-ion rechargeable. La recharge s'effectue avec le câble USB soit sur un ordinateur soit sur une prise acceptant le port USB. Une LED bleue s'allume lorsque le Soundtrap recharge. Il faut environ 8h pour recharger entièrement une batterie vide, et la charge s'effectue plus rapidement lorsque le Soundtrap n'est pas connecté au logiciel SoundTrap Host. Lorsque la batterie est rechargée, la LED s'éteint.

Déploiement et récupération de l'enregistreur sur une palangre

⚠ Ne pas oublier de remplir la fiche déploiement

Système d'attache

Pour venir fixer l'hydrophone à l'orin de la palangre il faudra au préalable préparer un système d'accroche sur le Soundtrap (Figure 3). Prendre un bout d'orin d'1m de long et de petit diamètre de préférence, mettre 2 mousquetons aux extrémités enfermés dans des boucles/yeux. Venir fixer l'hydrophone au centre. Sur la Figure 3 est proposé un système mais si vous pensez à d'autres systèmes plus fiable n'hésitez pas, les marins sont de bon conseils. Mais attention, bien maintenir l'hydrophone contre la corde, le plus sûr étant de venir sécuriser l'attache avec du duck tape/ scotch, ne pas hésiter à faire plusieurs tours pour bien consolider la fixation.

Ce système d'attache sera permanent et viendra se fixer/retirer sur l'orin d'une palangre à **100m de profondeur sous la bouée** (Figure 4). Le plus simple étant de préparer une section d'orin qui sera dédié à l'accroche de l'hydrophone et qui viendra en premier en dessous de la bouée. La plupart des navires possèdent des sections de 200m, mais cela peut varier. Sur ce bout d'orin, préparer des yeux à 100m de profondeur et espacé d'environ 1m pour venir fixer l'hydrophone via les mousquetons.

IMPORTANT: éviter toute liaison metal/metal (e.g. deux mousquetons consécutifs) qui produirait des bruits "clic-clic" parasites.



Figure 3 : système permanent d'accroche du soundtrap

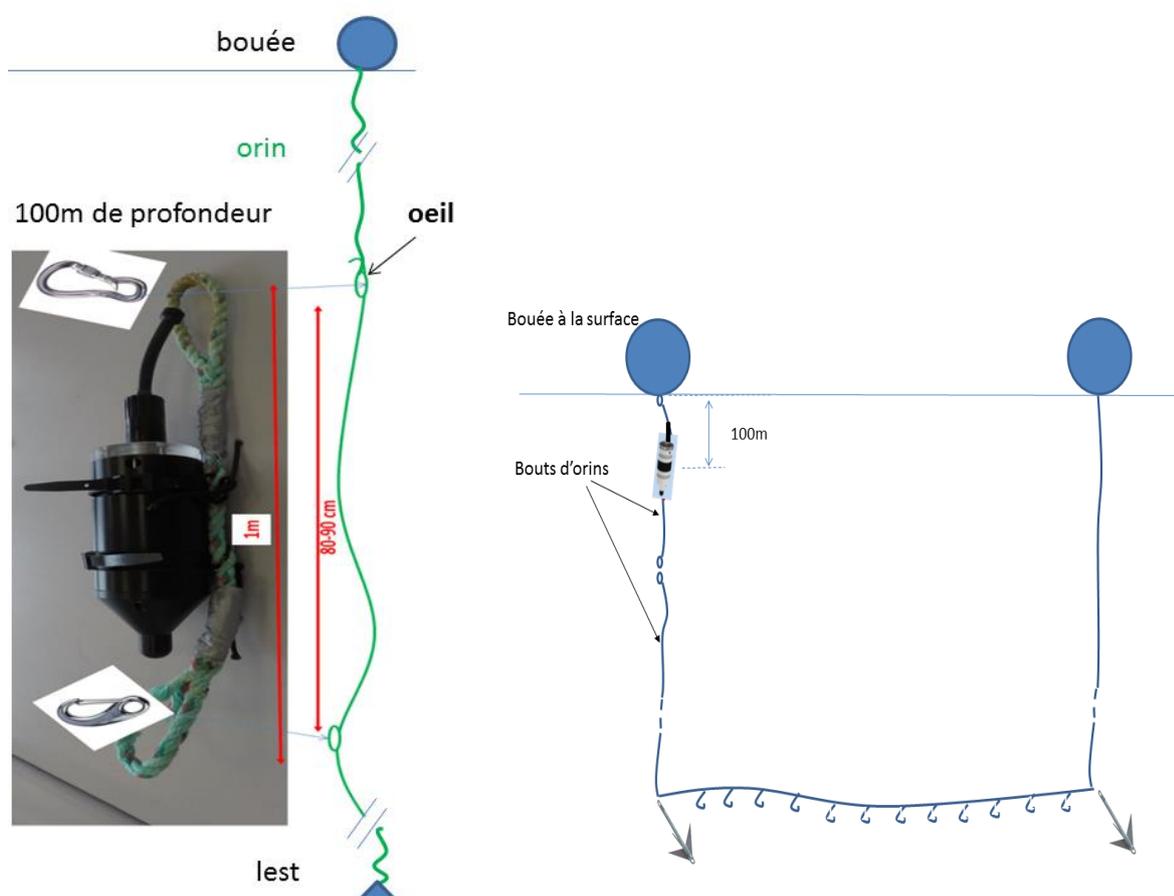


Figure 4 : insertion du système d'accroche dans l'orin.

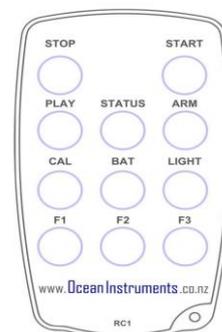
Récupération : rincer à l'eau douce le Soundtrap avant d'enlever le capuchon.

Démarrer et arrêter le Soundtrap

Les palangres étant déployés de nuit, vous ne serez pas présent, donc soit vous demandez aux marins de démarrer l'hydrophone avec la télécommande fournie, soit vous programmez le début d'enregistrement à l'heure prévu de la mise à l'eau par le capitaine.

Pour la télécommande, il faut :

- Appuyer sur 'START' pour démarrer l'enregistrement juste avant le déploiement de la palangre.
- Appuyer sur 'STOP' une fois l'hydrophone remonté
- La télécommande est waterproof, mais ne supporte pas une immersion complète.
- **Une fois allumé l'hydrophone se met à clignoter lentement avec une LED verte, bien vérifier cela pour un démarrage manuel.**



Pour un démarrage programmé, voir avec le capitaine l'heure du début du filage, indiquer dans 'Recording starts' la date et l'heure de démarrage souhaité. Bien vérifier la date qui ne s'actualise pas automatiquement.

Retrieve

Deploy

Recording Starts

Immediately upon USB disconnect
 At time:

Manually via remote control

Pour arrêter l'hydrophone, utiliser la télécommande ou brancher à l'ordinateur.

Où, quand, comment déployer et récupérer le Soundtrap ?

Déployez l'hydrophone aussi souvent que possible. **L'objectif étant d'avoir au moins une dizaine de déploiement, soit environ un déploiement par semaine.**

Déployez en particulier pendant le **premier filage d'un nouveau secteur.**

Il est préférable de mettre l'hydrophone sur une palangre qui sera remontée en dernière d'une zone ou d'une session de virage. Il est du plus grand intérêt d'avoir **l'hydrophone le plus longtemps à l'eau** afin de pouvoir enregistrer le plus de virages possible (moment où il y a déprédation).

Au niveau de la palangre, il est préférable de **mettre l'hydrophone sous la bouée qui sera remontée en second**, afin d'enregistrer le virage de la palangre équipée. Cependant, si la bouée avec l'hydrophone peut être quelque fois remontée en premier cela est aussi intéressant pour enregistrer l'approche du navire. Ainsi essayez d'avoir au moins **3 enregistrements avec l'hydrophone remonté avec la première bouée** de la palangre équipée.

Téléchargement des données de l'enregistreur

Lancer le logiciel Soundtrap Host et connecter le disque dur externe sur lequel les fichiers seront téléchargés. Par défaut les fichiers seront téléchargés dans un dossier créé automatiquement dans ‘Documents’ qui est nommé ‘SoundTrap’. **Changez la destination par défaut** du téléchargement à partir du menu ‘Tools’ pour que le téléchargement se fasse directement sur le disque dur externe (ne sera à aire qu’une fois).

Connecter le soundtrap à l’ordinateur de la même manière que lors de la programmation de l’appareil, et ouvrir l’onglet ‘Retrieve’ où vous verrez tous les fichiers créés lors du déploiement (Fig.5)

Décochez ‘Decompress’ pour que le téléchargement soit plus rapide et moins lourd. Sélectionnez tous les fichiers en cliquant sur le premier puis dernier fichier en maintenant la touche shift enfoncée, puis cliquez sur ‘Download’.

Une fois le téléchargement finit ouvrez le dossier avec les fichiers en cliquant sur ‘open save folder’. Le téléchargement a produit des fichiers ‘.sud’ qui sont des fichiers brut. Ce format de compression permet un stockage moins lourd et un téléchargement plus rapide. Une fois que vous avez vérifié que le téléchargement s’est bien effectué, videz la mémoire du Soundtrap en cliquant sur ‘Delete All’.

Si vous souhaitez vérifier les sons enregistrés téléchargés quelques fichiers en cochant la case ‘Decompress’ vous pouvez lire le fichier ‘.wav’. Utiliser votre lecteur audio classique ou avec le logiciel Audacity qui vous permet de visualiser les formes d’ondes et spectrogrammes du fichier.

NB : si vous avez assez de place sur votre ordinateur veuillez faire une copie de sauvegarde des enregistrements sur votre ordinateur.

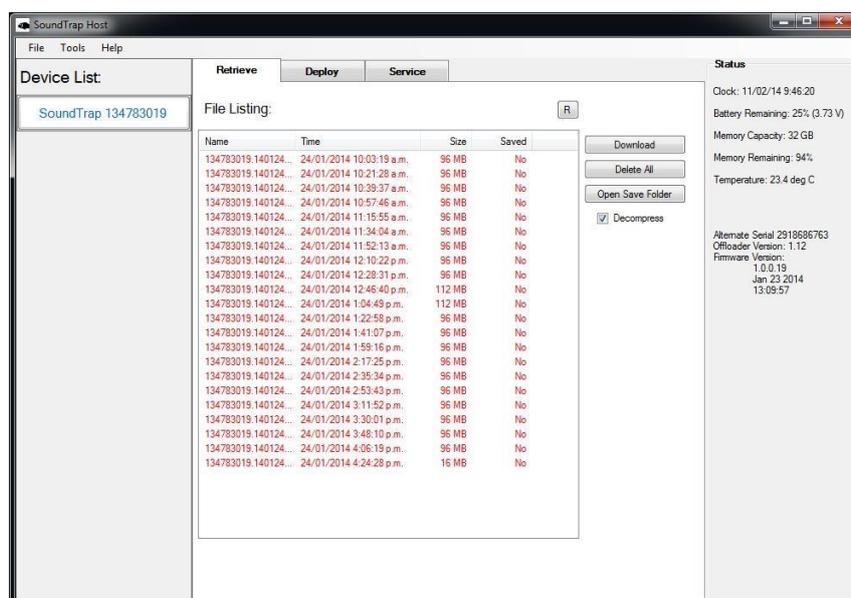


Figure 6 : Fenêtre de téléchargement.

Remerciements

De la part de tous les acteurs du projet OrcaDepred, nous vous remercions, ainsi que les capitaines et leur équipage, de votre aide à la bonne réalisation de cette étude, contribuant à une meilleure compréhension de ce phénomène de déprédation.

Soundtrap

Fiche de déploiement

APPENDIX 3

Mouillage

Numéro de la palangre

Profondeur Enregistreur

NB : enregistrer le fichier avec le code

A_XXX(num manip)_ZEE_CAP_NAV_AAMMJJ(déployé)_PALXXX

Mise à l'eau	
Officier au filage	
Position soundtrap sur la palangre filée	<input type="checkbox"/> début de la palangre filée <input type="checkbox"/> fin de la palangre filée
Présence cétacé	<input type="checkbox"/> abs <input type="checkbox"/> orques <input type="checkbox"/> cachalots <input type="checkbox"/> les 2 <input type="checkbox"/> non obs
COMMENTAIRES	

Récupération	
Officier au virage	
Rang du virage lors de la remontée de l'hydrophone	
Date et heure remontée Soundtrap	
Condition océano	Etat de la mer : Taille vague : Force du vent : Direction du vent : Météo : Beaufort (0-12) :
Présence cétacé	<input type="checkbox"/> abs <input type="checkbox"/> orques <input type="checkbox"/> cachalots <input type="checkbox"/> les 2 <input type="checkbox"/> non obs
COMMENTAIRES	

Evènements acoustiques		
Date dd/mm/yy -heure hh :mm (remettre la date que si elle change)	Position GPS	Evènement <i>Croche Pal XXX/ Demi-tour/ marche arrière/ autre manœuvre/ cétacés (autre que orque et cachalots)</i>

APPENDIX 4 – JANC ET AL. (2018)

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How do fishing practices influence sperm whale (*Physeter macrocephalus*) depredation on demersal longline fisheries?



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ABSTRACT

Marine mammal depredation on fisheries (animals removing fish caught on fishing gear) is a worldwide issue involving socio-economic and ecological consequences. Longline fisheries are the most impacted by odontocete (toothed whales) depredation. While technological means have provided limited efficacy in reducing depredation, this study examined the fishing practices influencing both the proportion of depredated longline sets and the amount of fish removed by whales. We used an 8-year dataset from the Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries operating in Crozet and Kerguelen Economic Exclusive Zones (EEZs) (South Indian Ocean) and GLMMs to investigate sperm whale (*Physeter macrocephalus*) depredation. Sperm whale depredation occurred on 61% of 5260 sets in Crozet and 41% of 16,902 sets in Kerguelen, and resulted in minimum estimated toothfish losses of 702 tons and 2649 tons, respectively, in the two areas. The probability of depredation decreased in winter months, increased with depth fished and decreased when vessels travelled over distances of > 60 km from fishing grounds with encountering depredation. These findings suggest the natural spatio-temporal distribution of sperm whales and their ability to follow vessels over limited ranges influence the number of captured fish removals. The amount of depredated toothfish decreased with the speed at which longline sets were hauled and increased with the soaking time of sets suggesting that whales may depredate sets during both hauling and soaking operations. Together, these observations indicate that rates of depredation may be influenced by the conditions of fishing operations and could therefore be employed to implement strategies of avoidance in all fisheries facing similar depredation impacts.

1. Introduction

Human-wildlife conflicts, which often result from competition between animals and humans over the same resources, are as old as humankind (Anand and Radhakrishna, 2017; Treves et al., 2006; Woodroffe et al., 2005). In the marine environment, the global expansion of fisheries over the last fifty years has led to the over-exploitation of many fish stocks and major changes in fishing techniques. It also has resulted to changes in food-search behavior of some predators such as marine mammals that has resulted in the emergence of direct marine predators–fisheries interactions, including depredation on fishing gears (Augé et al., 2012; Fertl, 2008; Kaschner and Pauly,

2004; Plagányi and Butterworth, 2002; Read, 2008). Depredation on fisheries is defined as the partial or total removal of captured fish from fishing equipment by marine predators (Donogue et al., 2002; Fertl, 2008; Read, 2005) and has received growing attention over the past five decades (Northridge, 1991). Marine mammals were reported as the taxa with the broadest range of depredating species. These species have been documented to depredate on a wide variety of fishing gears such as purse seines, trawls, gill nets, pots and baited longlines (Bearzi, 2002; Donogue et al., 2002; Fertl, 2008; Gales, 2003; Gilman et al., 2007; Hamer et al., 2012; Read, 2005; Werner et al., 2015).

Marine mammal depredation on fisheries often results in major socio-economic and ecological issues (Gilman et al., 2007). Economic

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issues for fisheries include both direct costs (i.e., catch losses) and indirect costs (i.e., additional fishing time, fuel consumption and payroll needed to complete fishing quotas, the implementation of strategies of marine mammals avoidance) (Maccarrone et al., 2014; Peterson et al., 2014). Ecological and conservation issues may include the over-exploitation of the targeted fish resources (i.e., the amount of depredated fish are often not accounted for in fish stock assessments and quota allocation processes) and effects on the survival of marine mammal populations (e.g., increased risks of by-catch on fishing gear; lethal responses from illegal, unreported and unregulated fishers who may perceive these animals as competitors; habituation to an artificial foraging behavior; modification of energy balance; etc.) (Baird et al., 2002; Gasco et al., 2015; Gilman et al., 2007). For instance, artificial food provisioning from fisheries may increase prey availability for depredating predators, and was shown to positively influence the survival and reproduction of individuals in various populations (Oro et al., 2004; Tixier et al., 2015a, 2017; Ward et al., 2009). Together, these ecological consequences of marine mammal depredation were recently suggested as important to consider when managing fisheries, fish stocks and marine mammal populations through ecosystem-based approaches (Boyd, 2002; Guénette et al., 2006; Morissette et al., 2012; Trites et al., 1999; Williams et al., 2011).

Longline gear is a fishing device which is made up of a horizontal line, to which are attached droppers ending in baited hooks and takes fish by hooking (Brock, 1962). Longlining progressively emerged as the most selective fishing technique for large fish species during the 1980s and 1990s (Løkkeborg and Bjordal, 1992). Unlike other techniques, this fully exposes the hooked fish in the water column, making this catch easily accessible for depredating marine mammals (Fertl, 2008). Both pelagic and demersal longlining are subject to depredation worldwide (Forney et al., 2011; Mesnick et al., 2006; Muñoz-Lechuga et al., 2016; Passadore et al., 2015; Rabearisoa et al., 2012; Roche et al., 2007; Straley et al., 2006; Visser, 2000). While the issue on depredation remains sporadic in some fisheries, it has spread and substantially increased in others, jeopardizing their sustainability (Powell and Wells, 2011; Schakner et al., 2014) and raising a critical need for solutions to minimize or suppress it (Hamer et al., 2012).

Extensive efforts have been made by fishers and ship-owners to develop technological solutions to either deter marine mammals from fishing gear or to protect the fish caught on hooks. However, most trials of such devices have showed limited efficacy (Dyb, 2006a; Hamer et al., 2012; Mooney et al., 2009; O'Connell et al., 2015; Tixier et al., 2015b). The development of fishing strategies for avoiding interactions has provided more promising insights into ways to reduce depredation levels. For instance, increased knowledge of local marine mammal populations ecology has allowed some fisheries to target the timing or areas of low marine mammal presence and, thus, lower the probability of depredation (Guinet et al., 2015; Straley et al., 2015; Tixier, 2012; Tixier et al., 2016). Other studies have focused on the behavior of fishing vessels and operational factors that can be controlled. For instance, Tixier et al. (2015b) showed that the depth at which longlines are set, longline length, the hauling speed and the distance travelled by vessels between fishing grounds can significantly influence the proportion of fishing gear depredated by killer whales (*Orcinus orca*) and the impact of this depredation on the Catch Per Unit Effort (CPUE) of the target species.

The influence of such operational factors on sperm whale (*Physeter macrocephalus*) depredation, however, has remained poorly investigated despite several reports on significant depredation in the majority of longline fisheries operated in high latitudes (Mesnick et al., 2006; Taylor et al., 2008). In both hemispheres, demersal longline fisheries are primarily depredated by adult male sperm whales whose natural foraging grounds often overlap with fishing areas (Ashford et al., 1996; Best, 1979; Mesnick et al., 2006; Whitehead, 2003). Sperm whale depredation has been reported in the North Pacific on fisheries targeting Pacific halibut (*Hippoglossus stenolepis*) and sablefish

(*Anoplopoma fimbria*) (Hill et al., 1999; Peterson and Carothers, 2013; Schakner et al., 2014; Sigler et al., 2008; Straley et al., 2006), in the North Atlantic on fisheries targeting Greenland halibut (*Reinhardtius hippoglossoides*) (Dyb, 2006b) and in the Southern Ocean on fisheries targeting Patagonian toothfish (*Dissostichus eleginoides*) (Duhamel, 2003). For the latter, sperm whale depredation occurs off Chile (Hucke-Gaete et al., 2004; Moreno et al., 2008), the Falklands/Malvinas (Goetz et al., 2011; Nolan et al., 2000), South Georgia (Ashford et al., 1996; Moir Clark and Agnew, 2010; Purves et al., 2004; Söffker et al., 2015), Prince Edward Island (Kock et al., 2006; Tilney and Purves, 1999), Heard and McDonald Islands (Arangio, 2012) and Crozet and Kerguelen Islands (Ashford et al., 1996; Capdeville, 1997; Gasco et al., 2015; Roche et al., 2007; Tixier et al., 2010).

The Patagonian toothfish longline fishery operating off the Crozet and Kerguelen Islands has been reported as one of the most impacted by sperm whale depredation, with an estimated reduction of 8–12% in the toothfish CPUE between 2003 and 2013 (Gasco et al., 2015; Roche et al., 2007; Tixier et al., 2010). These estimates were recently incorporated in the Crozet and Kerguelen fish stock assessments and used to increase accuracy of quota allocation processes. This fishery, with a fleet comprised of seven commercial vessels, is highly regulated, closely monitored by onboard fishery observers at all times, and benefits from a long-term fishing dataset covering 100% of fishing operations. This fully controlled environment has proved to be particularly suitable for studies on operational factors influencing depredation by killer whales, the other major depredating species of demersal longline fisheries in high latitudes (Gasco et al., 2014; Guinet et al., 2015; Tixier et al., 2010, 2016).

Therefore, the long-term datasets from the Crozet and Kerguelen Patagonian toothfish fisheries were here used as a unique opportunity to investigate the spatio-temporal and operational factors of fishing practices influencing the level of sperm whale depredation on demersal longlining. The aims of this study were to test for the effects of these factors on (i) the proportion of fishing gear depredated by sperm whales, and (ii) the CPUE during sperm whale depredation events.

2. Material and methods

2.1. Study areas and data collection

During the study period (1 January, 2008–25 July, 2015), seven commercial fishing vessels were authorized to operate in the Crozet (between 44° and 48°S–46° and 54°W) and Kerguelen (between 45° and 52°S–63° and 75°W) Exclusive Economic Zones (EEZs). These vessels all used auto-weighted longlines that were set between two anchors at each end of the mainline, on which 375–47,250 hooks were positioned with an individual hook every 1.2 m. These hooks were automatically baited and dropped to the bottom at depths ranging from 500 to 2300 m (i.e., legal depth range to avoid the capture of juvenile toothfish (Collins et al., 2010)). Fishing regulations also imposed fishers to set their lines at night to avoid seabird bycatch (Cherel et al., 1996; Weimerskirch et al., 2000). Hauling, which was allowed at any time of the day, took between 00:30–9:58 to be completed depending on the number of hooks on the longline and the hauling speed. The fishing fleet was allowed to operate all year round in the Crozet, but is closed for a 45-day period from the 1st February to mid-March in the Kerguelen EEZ to comply with seabird conservation measures (CCAMLR, 2015a, 2015b).

All data used in the study were collected by fishery observers and were provided by the Muséum d'Histoire Naturelle de Paris (MNHN – PECHEKER database (Martin and Pruvost, 2007)). The unit of this dataset was the longline set. Each set was affiliated with one captain, one vessel and one fishing trip. A fishing trip (lasting 2–3 months) was defined as the time between the departure of a vessel with a given captain from Reunion Island and its return to the port. The date, time, number of hooks set and hauled, spatial coordinates and depth of downlines at the beginning and the end of both setting and hauling

processes were recorded for each longline set. The total number and the biomass of fish caught and landed for Patagonian toothfish was assessed as well as for three bycatch species groups (bigeye grenadier, *Macrourus carinatus*; blue antimora, *Antimora rostrata* and skate species grouped into a single group, *Bathyraja eatonii*, *Bathyraja irrasa*, *Bathyraja murrayi* for Kerguelen and *Amblyraja taaf* for Crozet). From these data, the CPUE was calculated as the biomass of entire caught fish in grams divided by the number of hauled hooks (g.hook^{-1}) for each hauled longline, for Patagonian toothfish and for each of the three bycatch species groups:

$$\text{CPUE}_i (\text{g.hook}^{-1}) = \Sigma \text{Biomass of entire caught fish}_i / \Sigma \text{hauled hooks}_i$$

CPUE_i is the obtained CPUE on longline *i*

Concurrently, fishery observers visually monitored odontocetes (i.e., sperm whales and killer whales) depredating on longlines during hauling. Depredation was classified according to three states for each of the two depredating species: (i) “Depredation” – depredation of whales on the fishing gear was confirmed by whales repeating long dives (> 15 min) within a 500 m radius from the vessel and surrounded by seabirds when surfacing, slicks of fish oil visible at the surface of the water and/or chunks of fish observed in the mouth of whales; (ii) “No depredation” – no whales sighted from the vessel or if sighted, whales were in transit with no indicators of depredation (see above) observed; (iii) “not observed” – observations were not possible due to weather, sea state and/or visibility conditions (e.g., night). For sets for which depredation was recorded during hauling, fishery observers provided minimum and maximum estimates of the number of whales present around the vessel. For the purposes of this study, and to limit bias due to overestimated numbers, only the minimum estimate was used to test the number of depredating sperm whales as an explanatory variable in the models presented below.

2.2. Models on the proportion of fishing gear depredated by sperm whales

Generalized Linear Mixed Models (GLMM) (Zuur et al., 2009, 2013) were used to explore the relationship between the proportion of hauled sets depredated by sperm whales out of all hauled sets (noted “Pr(set)”) and three spatio-temporal predictors. Temporal predictors included a year (“Year” – continuous) and a month (“Month” – discrete) effects to respectively test for annual trends and intra-annual variations of the proportion of sets depredated by sperm whales. The depth at which sets were hauled was considered here as the vertical spatial predictor (“Depth” – continuous and expressed in meters). As observers recorded one depth value for each of the two ends of a set, we used the mean of these two values in the model. The continuous explanatory predictors were centered at their mean and scaled by their standard deviation (i.e., standardized). Data were restricted to longline sets with confirmed presence (“Depredation”) or absence (“No depredation”) of depredating sperm whales during hauling and fitted with a binomial distribution and a logit link function, which was defined as follows:

$$\text{logit}(\pi_{ij}) = \eta_{ij} \leftrightarrow \pi_{ij} = \exp(\eta_{ij}) / (1 + \exp(\eta_{ij}))$$

in which π_{ij} represented the expected value of Pr(set) for each longline *j* in trip *i* (i.e., the mean of $\text{Pr}(\text{set})_{ij}$) and $\text{Pr}(\text{set})_{ij}$ took values of 0 or 1 for each longline *j* in trip *i*.

The fishing trip (“Trip”) was used as a random intercept to impose a correlation structure on the presence of depredating sperm whales because of multiple observations recorded for each trip (Zuur et al., 2013). The model was extended with a temporal auto-correlation structure to account for the fact that the interaction of sperm whales with a given longline set could depend upon their interaction with the previously hauled longline (Tixier, 2012). The full model (Model 1) was separately fitted on data from Crozet and Kerguelen using the function *glmmPQL* in packages MASS (Venables and Ripley, 2002) and *nlme* (Pinheiro et al., 2016) in R (R Core Team, 2015) as follows:

$$\text{Model 1: } \eta_{ij} = \text{Intercept} + \beta_1 \text{Year} + \beta_2 \text{Month}_{ij} + \beta_3 \text{Depth}_{ij} + a_i + \varepsilon_{ij}$$

in which a_i and ε_{ij} were the residuals: $a_i \sim N(0, \sigma_{\text{Trip}}^2)$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$, and $\beta_{1,2,3}$ were the coefficients of the explanatory variables.

Cleveland dot plots were used as an alternative to bar charts to inspect the outliers of variables. Collinearity between continuous variables was assessed using pair plots and variance inflation factor (VIF) values calculated as the ratio of variance in a model with multiple terms, divided by the variance of a model with one term alone (Zuur et al., 2009, 2010; Zuur, 2012). Model selection was performed by using backward stepwise selection, dropping the least significant interaction term from the model and refitting the model until terms were significant at 5% level (Zuur et al., 2013).

Using the same modeling approach, a second GLMM was developed to investigate the effect of the distance travelled by fishing vessels from one hauled set depredated by sperm whales to the set hauled next in time. Previous studies have shown depredating odontocetes follow fishing vessels between fishing operations, sometimes over great distances (Tixier et al., 2015c). Preliminary analyses of photo-identification data collected in Crozet and Kerguelen suggested that sperm whales also follow vessels from one haul to the next, likely because vessels remain within the acoustical detection range of the whales (Thode et al., 2015). Fishing vessels travel at speeds ranging from 8 to 12 knots, which exceed the average swimming speed of sperm whales during travelling (1.5–3 knots; Aoki et al., 2007; Whitehead, 2003). Hence, increased distances between sets may result in vessels being able to outrun the depredating sperm whales which may eventually lose the acoustical detection of vessels. To test this assumption, *Pr(set)* was here fitted with data restricted to pairs of sets that were hauled successively in time (by the same fishing vessel during the same fishing trip) after the first set was hauled in presence of depredating sperm whales. Longlines hauled with in presence of killer whales, whether depredating alone or simultaneously with sperm whales, were not included in the analysis to limit the bias due to the effect of killer whale depredation on the distance travelled by fishing vessels. Assuming that there is a straight trajectory of the vessel between the two sets, the distance between pairs of sets (“Distance” – continuous and expressed in kilometers) was calculated from the GPS coordinates of the mid-point between the two ends of the first set and the mid-point of the second set. The number of sperm whales recorded depredating on the previous set (“Nb.ind.set₁” – continuous) was also entered in the model and tested both as a single term and in interaction with *Distance*. We assumed that the greater *Nb.ind.set₁*, the more likely that at least one individual would be depredating again on the next set. As 99% of the values by *Nb.set₁* were comprised between 1 and 8 individuals, the dataset was restricted to 8 sperm whales recorded on the previous set to avoid bias due to extreme values while maintaining statistical power. The full model (Model 2) was also separately fitted on data from Crozet and Kerguelen with a binomial distribution and a logit link function as follows:

$$\text{Model 2: } \eta_{ij} = \text{Intercept} + \beta_1 \text{Distance}_{ij} + \beta_2 \text{Nb.ind.set}_{1ij} + \beta_3 \text{Distance}_{ij} \times \text{Nb.ind.set}_{1ij} + a_i + \varepsilon_{ij}$$

in which a_i and ε_{ij} were residuals: $a_i \sim N(0, \sigma_{\text{Trip}}^2)$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$, and $\beta_{1,2,3}$ were the coefficients of the explanatory terms.

2.3. Modelling the CPUE of longline sets

As an exploratory analysis, and prior to modelling the CPUE, the fishing data on Patagonian toothfish and on bycatch were initially used to statistically identify which fish species were primarily removed by sperm whales from longline sets when depredating. Several *t*-test comparisons were performed on mean CPUEs of 4 groups of species caught on longlines (Patagonian toothfish and 3 bycatch groups: blue antimora, bigeye grenadier and skate species) between sets hauled without (absence of any odontocete species) and sets hauled in the presence of depredating sperm whales over the 2008–2015 period.

Longlines hauled with in presence of killer whales were not included in the analysis to limit the bias due to the effect of killer whale depredation on the CPUE.

GLMMs were then developed to examine the relationship between the CPUE of the depredated fish species and 4 operational predictors depending on the number of sperm whales simultaneously depredating during hauling of a given set. This number (“*Nb.ind*”) ranged from 0 for sets hauled in absence to 16 for Crozet and 15 individuals for Kerguelen. However, as 93% of the values taken by this variable were comprised between 0 and 5 for Crozet and 94% were comprised between 0 and 4 for Kerguelen; the data used in models on the CPUE were restricted to a maximum number of 5 individuals for Crozet and 4 for Kerguelen to avoid bias due to extreme values while maintaining statistical power. *Nb.ind* was tested both as a single term because it was hypothesized that increasing *Nb.ind* negatively influenced on the CPUE of the depredated fish species. *Nb.ind* was also tested in interaction with the following operational predictors. First, we tested for the effect of the length of longline sets (“*Length*” – continuous and expressed in

kilometers). Here, it was hypothesized that shorter sets, for which hauling time is reduced, may decrease the amount of depredated fish by sperm whales, usually approaching the longline after the hauling has started (Tixier et al., 2015c). Second, we tested for the effect of the hauling speed of sets (“*HaulingSpeed*” – continuous and expressed in number of hauled hooks per minute (hooks.min^{-1})), which was calculated as the total number of hooks hauled on a given set divided by the total hauling time of that set. If sperm whales depredate on the catch only during hauling, we assumed that while reducing the time available for whales to access the catch, a simultaneous increase in hauling speed may also make the removal of captured fish from the sets more difficult for them (Tixier et al., 2015c). Third, we tested for the effect of the soaking time of sets (“*SoakingTime*” – continuous and expressed in hours), which was the time elapsed between the end of setting and the start of hauling. This variable was used to specifically investigate the possibility that sperm whales may also depredate on sets before hauling while the line is still at the bottom of the sea. If it is the case, shorter soaking time can also reduce the time available for whales

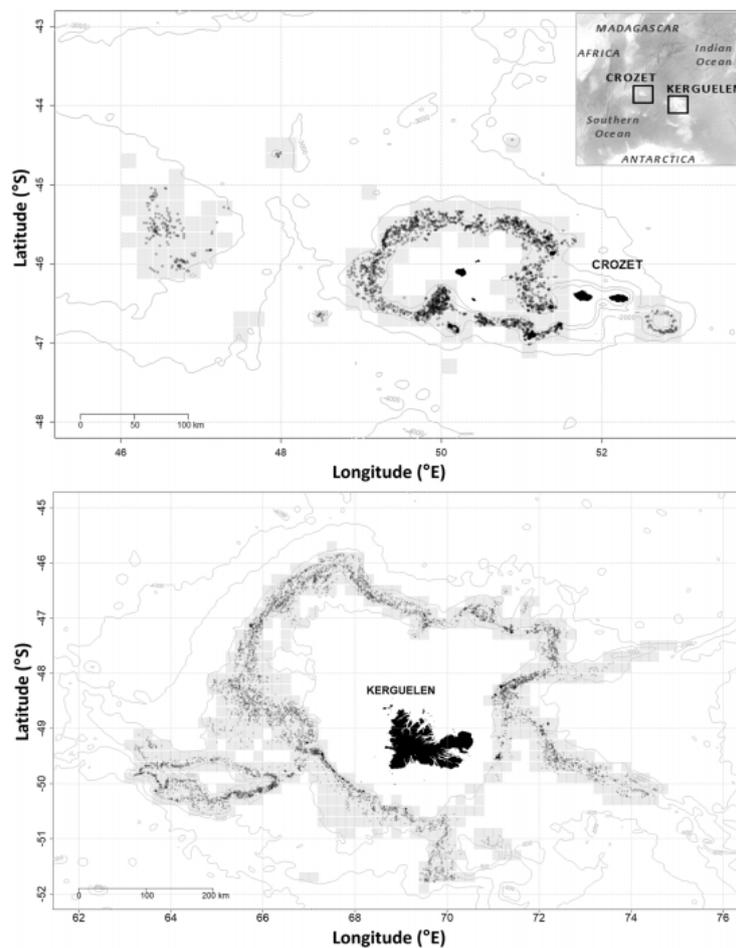


Fig. 1. Distribution of longline sets hauled in presence of depredating sperm whales (black dots) and fishing grounds ($0.2' \times 0.2'$ squares in which at least one set was hauled over the 2008–2015 period – grey squares) in Crozet (top) and in Kerguelen (bottom). Thin grey lines are the 500, 1000, 2000 and 4000 m isobaths.

to access the catch and, therefore, reduce the amount of depredated fish. Lastly, the effect of the depth at which sets were hauled (“Depth” – continuous and expressed in meters) was also entered in the models to account for bathymetric variations of fish abundance. The continuous predictors were centered at their mean and scaled by their standard deviation. The fishing trip (*Trip*) was then used as a random intercept. Using the function *glmer* in package *lme4* (Bates et al., 2015) in R (R Core Team, 2015), models were fitted with a Gamma distribution and the logarithmic link function, which was defined as follows:

$$\log(\mu_{ij}) = \eta_{ij} \leftrightarrow \mu_{ij} = \exp(\eta_{ij})$$

in which μ_{ij} represented the expected value of CPUE of longline *j* in trip *i* (i.e., the mean of $CPUE_{ij}$).

The full model (*Model 3*) was separately fitted on data from Crozet and from Kerguelen as follows:

$$\begin{aligned} \text{Model 3: } \eta_{ij} = & \text{Intercept} + \beta_1 \text{Nb.ind}_{ij} + \beta_2 \text{Length}_{ij} + \beta_3 \text{Depth}_{ij} \\ & + \beta_4 \text{Soaking Time}_{ij} + \beta_5 \text{Hauling Speed}_{ij} + \beta_6 \text{Length}_{ij} \times \text{Nb.ind}_{ij} \\ & + \beta_7 \text{Depth} \times \text{Nb.ind}_{ij} + \beta_8 \text{Soaking Time}_{ij} \times \text{Nb.ind}_{ij} \\ & + \beta_9 \text{Hauling Speed}_{ij} \times \text{Nb.ind}_{ij} + a_i + \varepsilon_{ij} \end{aligned}$$

in which a_i and ε_{ij} were residuals: $a_i \sim N(0, \sigma_{trip}^2)$ and $\varepsilon_{ij} \sim N(0, \sigma^2)$, and $\beta_{1,2,3,4,5,6,7,8,9}$ were the coefficients of the explanatory terms.

Cleveland dot plots were also used to inspect the outliers of variables and collinearity between continuous variables was assessed using pair plots and VIF values (Zuur et al., 2009, 2010; Zuur, 2012). Model selection was performed using backward stepwise selection by dropping the least significant term interaction from the model and refitting the model until terms were significant at 5% level (Zuur et al., 2013).

3. Results

3.1. Data summary

During the study, a total of 25,715 longlines were set and hauled in both study areas: 6343 (25%) in Crozet and 19,372 (75%) in Kerguelen. A total of 42,688 tons of Patagonian toothfish were landed during the study with 5622 tons (13%) in Crozet and 37,066 (87%) in Kerguelen. The absence or presence of depredating odontocetes was confirmed for 83% and 87% of all longline sets hauled in Crozet and Kerguelen, respectively. Sperm whales depredated on 60.5% and 40.7% of these sets in Crozet and Kerguelen, respectively (Fig. 1).

In Crozet, $34.7\% \pm 2.1\%$ SE of the sets were hauled in the presence of sperm whales as the only depredating species and $25.8\% \pm 1.4\%$ SE ($n = 8$ years) with sperm whales and killer whales depredating simultaneously. In Kerguelen, sets were primarily depredated by sperm whales alone at $40.6\% \pm 1.1\%$ SE while $0.1\% \pm 0.05\%$ SE ($n = 8$ years) in presence of both sperm whales and killer whales. When depredation occurred, the average number of depredating sperm whales per set was significantly different between Crozet and Kerguelen (Student *t*-test: $t = -16.87$, $df = 10038$, $P < 0.001$) and was estimated at 3.5 ± 2.9 SD individuals per set in Crozet ($n = 3188$ sets) and 2.6 ± 1.9 SD individuals per set in Kerguelen ($n = 6852$ sets). The average number of depredating sperm whales per set varied between months in both areas. In Crozet, it was the highest in December (5.31 ± 4.02 SD) and the lowest in September (1.89 ± 1.15 SD, Fig. 2a). In Kerguelen, it was the highest in April (3.17 ± 2.40 SD) and the lowest in July (2.00 ± 1.01 SD, Fig. 2a).

3.2. Models on the proportion of fishing gear depredated by sperm whales

Results from *Model 1* indicated in Table 1 showed that no significant annual trend in the proportions of sets depredated by sperm whales from 2008 to 2015 was observed in either area. However, significant inter-month variations were detected. Predicted probabilities of sperm whale depredation from the model were the highest between November

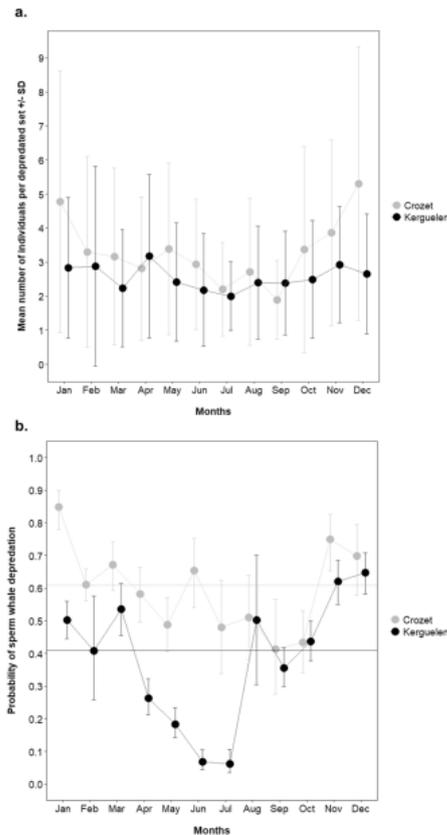


Fig. 2. Intra-annual variations of a. the number of sperm whale individuals depredating the same set (mean \pm SD calculated from observed values) and b. the probability and confidence interval at 95% (error bars) of sperm whale depredation to occur during hauling of sets as predicted by *Model 1* outputs of the month as a discrete predictor in Crozet (grey) and in Kerguelen (black). The mean proportions of sets depredated by sperm whales per year over the study period (horizontal lines) are also depicted.

(0.75 [95% CI: 0.65–0.83]) and January (0.85 [95% CI: 0.78–0.90]) in Crozet and between November (0.62 [95% CI: 0.55–0.69]) and December (0.65 [95% CI: 0.59–0.71]) in Kerguelen (Fig. 2b). These probabilities were the lowest between July (0.48 [95% CI: 0.34–0.63]) and October (0.44 [95% CI: 0.35–0.54]) in Crozet and between April (0.27 [95% CI: 0.22–0.33]) and July (0.06 [95% CI: 0.03–0.11]) in Kerguelen (Fig. 2b).

The depth at which longlines were set had no effect on the proportion of depredated sets in Crozet (Table 1). However, the depth effect was significant and positive in Kerguelen ($t = 7.94$, $df = 16559$, $P = 0.00$). For a typical trip in Kerguelen, the probability of sperm whale depredation increased from 0.30 [95% CI: 0.09–0.50] for sets hauled 506 m deep to 0.48 [95% CI: 0.27–0.70] for sets hauled 2140 m deep.

Results from *Model 2* indicated in Table 2 showed that the number of depredating sperm whales recorded during the hauling of the first longline had a significant and positive effect on the proportion of subsequent sets hauled with depredation, both in Crozet ($z = 4.04$, $P < 0.001$) and in Kerguelen ($z = 12.18$, $P < 0.001$). In the same case, the distance travelled by vessels between the two sets had a

Table 1
Numerical outputs from *Model 1* testing the effects of the year (*Year*) and the depth (*Depth*) at which longline sets were hauled as continuous standardized predictors, as well as the effect of the month (*Month*) as discrete predictor on the proportion of sets depredated by sperm whales out of all sets hauled in Crozet and in Kerguelen. The baseline is represented by the month having the lowest probability of interaction and is the level with which the estimated probabilities of sets to be depredated of the other months are compared. The fishing trip (*Trip*) was added as a random term in *Model 1* along with an autocorrelation structure AR1 within each *Trip*.

	CROZET (N = 5217 sets)					KERGUELEN (N = 16738 sets)				
	Value	SE	df	t	P	Value	SE	df	t	P
Intercept	-0.35	0.32	5094	-1.11	0.27	-2.74	0.31	16559	-8.86	0.00
Year	-	-	-	-	NS	-	-	-	-	NS
January	2.09	0.39	5094	5.30	0.00	2.76	0.33	16559	8.37	0.00
February	0.81	0.33	5094	2.45	0.01	2.28	0.46	16559	4.91	0.00
March	1.07	0.36	5094	2.99	0.003	2.89	0.35	16559	8.38	0.00
April	0.69	0.36	5094	1.91	0.06	1.74	0.33	16559	5.24	0.00
May	0.33	0.36	5094	0.92	0.36	1.24	0.32	16559	3.86	< 0.001
June	1.00	0.40	5094	2.51	0.01	0.10	0.32	16559	0.30	0.76
July	0.28	0.44	5094	0.65	0.51	Baseline	Baseline	Baseline	Baseline	Baseline
August	0.39	0.41	5094	0.95	0.34	2.79	0.47	16559	5.91	0.00
September	Baseline	Baseline	Baseline	Baseline	Baseline	2.11	0.34	16559	6.28	0.00
October	0.10	0.37	5094	0.28	0.78	2.48	0.33	16559	7.41	0.00
November	1.44	0.39	5094	3.71	< 0.001	3.23	0.34	16559	9.41	0.00
December	1.19	0.41	5094	2.88	0.004	3.36	0.34	16559	9.90	0.00
Depth	-	-	-	-	NS	0.18	0.02	16559	7.94	0.00
	Random intercept: 0.51					Random intercept: 0.77				
	Residual variance: 0.98					Residual variance: 0.96				
	Auto-correlation parameter estimate: 0.36					Auto-correlation parameter estimate: 0.51				

Table 2
Numerical outputs from *Model 2* testing the effects of the distance travelled by fishing vessels between two successively hauled sets (*Distance*) and the number of sperm whales recorded depredating during the hauling of the first of these two sets (*Nb.ind.set₁*) as continuous standardized predictors on the proportion of next sets depredated by sperm whales. The fishing trip (*Trip*) was entered in *Model 2* as a random term.

	CROZET (N = 1180 sets)				KERGUELEN (N = 4223 sets)			
	Estimate	SE	z	P	Estimate	SE	z	P
Intercept	1.65	0.11	14.70	< 0.001	1.91	0.10	19.74	< 0.001
Nb.ind.set ₁	0.42	0.10	4.04	< 0.001	0.90	0.07	12.18	< 0.001
Distance	-0.76	0.08	-9.62	< 0.001	-0.66	0.04	-14.74	< 0.001
Distance:Nb.ind.set ₁	-0.19	0.08	-2.40	0.02	-0.24	0.04	-5.26	< 0.001
	Random intercept: 0.28				Random intercept: 0.77			

significant and negative effect on the proportion of the next sets depredated by sperm whales, both in Crozet ($z = -9.62, P < 0.001$) and in Kerguelen ($z = -14.74, P < 0.001$). The interaction term between the variables *Distance* and *Nb.ind.set₁* was significant and negative both in Crozet ($z = -2.40, P = 0.02$) and in Kerguelen ($z = -5.26, P < 0.001$). From the model outputs, the effect of the number of depredating sperm whales during hauling of the first set on the proportion of next sets depredated became negligible if vessels travelled more than 55.8 km in Crozet and 48.6 km in Kerguelen (Fig. 3). Based on an average number of sperm whales depredating on the first set, the estimated probabilities of the next sets to be depredated in Crozet was decreased by 10.7% when vessels travelled 20 km from the previous set, and by 39.8% when vessels travelled 50 km. This rate was greater in Kerguelen. The probability of the next sets to be depredated was decreased by 15.9% when vessels travelled 20 km from the previous set and by 65.2% when vessels travelled 50 km (Fig. 3).

3.3. Modelling the CPUE of longline sets

A significant decrease of CPUE of Patagonian toothfish between non-depredated and depredated longline sets by sperm whales was detected both at Crozet (Student *t*-test: $t = -3.07, df = 402, P = 0.002$) and at Kerguelen (Student *t*-test: $t = -4.58, df = 1194, P < 0.001$) while no effect could be detected on monitored bycatch species (Fig. 4).

Results from *Model 3*, which was therefore run on Patagonian

toothfish CPUE, indicated in Table 3 showed that the number of depredating sperm whales per set had a significant and negative effect on toothfish CPUE for both study areas ($t = -8.56, P < 0.001$ for Crozet and $t = -14.09, P < 0.001$ for Kerguelen). From the model output, the CPUE loss was estimated at 24.72 g.hook⁻¹ in Crozet and 17.65 g.hook⁻¹ in Kerguelen per sperm whale individual (see Supplementary Data for details on calculations). For both areas, the interaction term between the number of sperm whales interacting *Nb.ind* and the variable *Length* or the variable *Depth* had no significant effect on toothfish CPUE.

The soaking time had no effect on toothfish CPUE in absence of cetaceans in Crozet ($t = 0.91, P = 0.36$) whereas it had a significantly positive effect in Kerguelen ($t = 9.83, P < 0.001$). The interaction term between the number of sperm whales and the variable *SoakingTime* had no significant effect on toothfish CPUE in Kerguelen. However, this interaction term was significant and had a negative effect on toothfish CPUE in Crozet ($t = -1.97, P = 0.05$). For instance, soaking times of 10 and 60 h, respectively, resulted in toothfish CPUEs of 169.68 and 168.27 g.hook⁻¹ (e.g., CPUE reduction of 0.8%) when two sperm whales simultaneously depredated on a given set. CPUEs further decreased to values of 134.94 and 105.45 g.hook⁻¹ (e.g., CPUE reduction of 21.9%) when five sperm whales simultaneously depredated on a given set (Fig. 5).

The hauling speed had a significant negative effect on toothfish CPUE in the absence of cetaceans both at Crozet ($t = -3.74, P < 0.001$) and at Kerguelen ($t = -16.16, P < 0.001$). In interaction

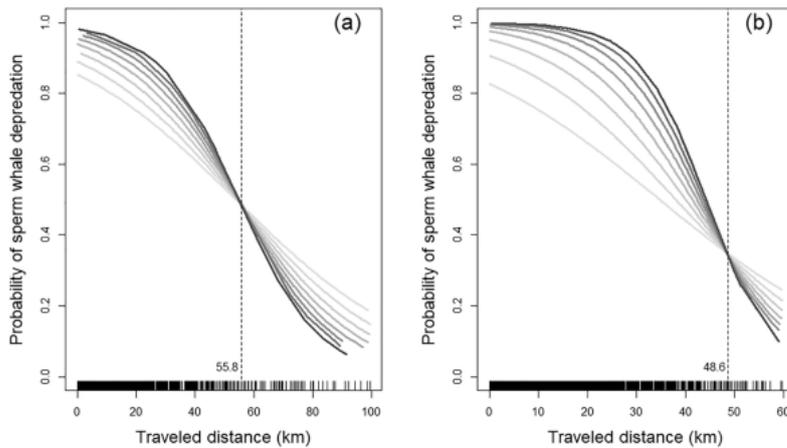


Fig. 3. Predicted probabilities from Model 2 outputs of sperm whale depredation to occur during hauling of the second of two successively hauled sets against the interaction effect between the distance travelled by vessels between these two sets and the number of sperm whales depredating on the first set in Crozet (a) and in Kerguelen (b). Each curve corresponds to a given number of sperm whales simultaneously depredating the first set, ranging from 0 (light grey) to 8 (dark grey).

with the number of sperm whales, the hauling speed had no significant effect on the toothfish CPUE in Crozet, but the effect was significant and positive in Kerguelen ($t = 3.54$, $P < 0.001$). For instance, the presence of 1 and 4 depredating whales on a given set resulted in toothfish CPUEs of 288.50 and 229.69 g.hook^{-1} (e.g., CPUE reduction of 20.4%), respectively, when using a hauling speed of 20 hooks.min^{-1} . A further decrease was observed at 199.48 and 185.07 g.hook^{-1} (e.g., CPUE reduction of 7.2%) when a hauling speed of 50 hooks.min^{-1} was used (Fig. 6). The model also estimated that the effect of the number of sperm whales on the amount of depredated toothfish became negligible for speeds greater than 60 hooks.min^{-1} (Fig. 6).

4. Discussion

This study provided evidence that sperm whales specifically remove Patagonian toothfish from longlines when depredating on fisheries of the Crozet and Kerguelen EEZs. This depredation varied in space and time and was influenced by a number of operational variables. The proportion of depredated sets depended upon the season and the depth at which longlines were set and was influenced by the distance travelled by vessels when switching from one fishing ground to another while trying to avoid depredation. This study also demonstrated that the amount of Patagonian toothfish depredated by sperm whales varied with (1) the number of individuals co-occurring around the vessels, (2) the speed at which longline sets were hauled, and (3) the soaking time of sets. These findings provide interesting insights to the understanding of factors that may influence and mitigate sperm whale depredation on the studied fisheries, as well as for other longline fisheries facing similar sperm whale interactions.

4.1. Sperm whale depredation levels

The proportions of longline sets hauled in presence of depredating sperm whales in Crozet (61%) and Kerguelen (41%) are among the highest ever recorded in the Southern Ocean region and in other demersal longline fisheries experiencing depredation. For example, sperm whales have been reported depredating on 18–25% of Patagonian toothfish longline sets in South Georgia (Moir Clark and Agnew, 2010; Purves et al., 2004; Söfker et al., 2015) and 35% of the sets in the Falklands (Goetz et al., 2011; Yates and Brickle, 2007). In Alaska, 10–35% of all longline sets were depredated by sperm whales on the sablefish fisheries (Hill et al., 1999; O'Connell et al., 2015; Peterson and Carothers, 2013; Straley et al., 2006, 2015; Thode et al., 2015).

The proportions of sets depredated by sperm whale reported here, which were calculated over the 2008–2015 period, are consistent with estimates from other studies including years preceding the study period considered in this work (Gasco et al., 2015; Roche et al., 2007; Tixier et al., 2010). In addition, no annual trend in the proportion of depredated sets was detected in this study. Together, these results suggest that the proportion of fishing gear depredated by sperm whales in Crozet and Kerguelen remains relatively constant over a period of nearly 13 years.

While sperm whales may naturally forage on other prey items such as large cephalopods that are not caught on longlines (Clarke and MacLeod, 1974; Kawakami, 1980), Patagonian toothfish has been observed as being part of their natural diet (Abe and Iwami, 1989; Duhamel et al., 2005; Gon and Heemstra, 1990; Yukhov, 1972, 1982). During depredation events, sperm whales primarily removed Patagonian toothfish from longlines despite the presence of other species caught as by-catch. Greater numbers of toothfish on longline sets and its larger size compared to bycatch species may respectively increase the probability of sperm whales to encounter toothfish and facilitate its detection during depredation events, which may therefore contribute to this selectivity. However, the latter is more likely to be explained by the optimal energetic intake sperm whales may gain when feeding on this fish species, which energetic richness is higher than that of other fish species caught on longlines (Capdeville, 1997; Collins et al., 2010; Duhamel, 2003; Fertl, 2008; Péron et al., 2016). As selective depredation towards Patagonian toothfish was also reported for killer whales in Crozet (Tixier et al., 2016), interspecific competition for the same resource can also likely occur when two odontocete species simultaneously depredate on the same longline sets.

Decreases in Patagonian toothfish CPUE caused by sperm whale depredation were detected both in Crozet and Kerguelen (i.e., 24.72 g.hook^{-1} and 17.65 g.hook^{-1} per sperm whale individual, respectively). If multiplied by the number of hooks hauled and the number of individuals for each of the longline sets hauled in presence of sperm whales as the only depredating species, such declines in toothfish CPUE resulted in estimated total losses of 702 tons in Crozet and 2649 tons in Kerguelen for the period of 2008–2015. However, the extent of this CPUE decrease is likely to be underestimated. First, as the distribution of sperm whales is often correlated with highly productive fishing grounds (Gasco et al., 2015; Goetz et al., 2011; Hucke-Gaete et al., 2004; Purves et al., 2004; Tixier, 2012), simple comparisons between the CPUE of all sets hauled in the absence and in the presence of depredating sperm whales are likely to be biased upward. Second,

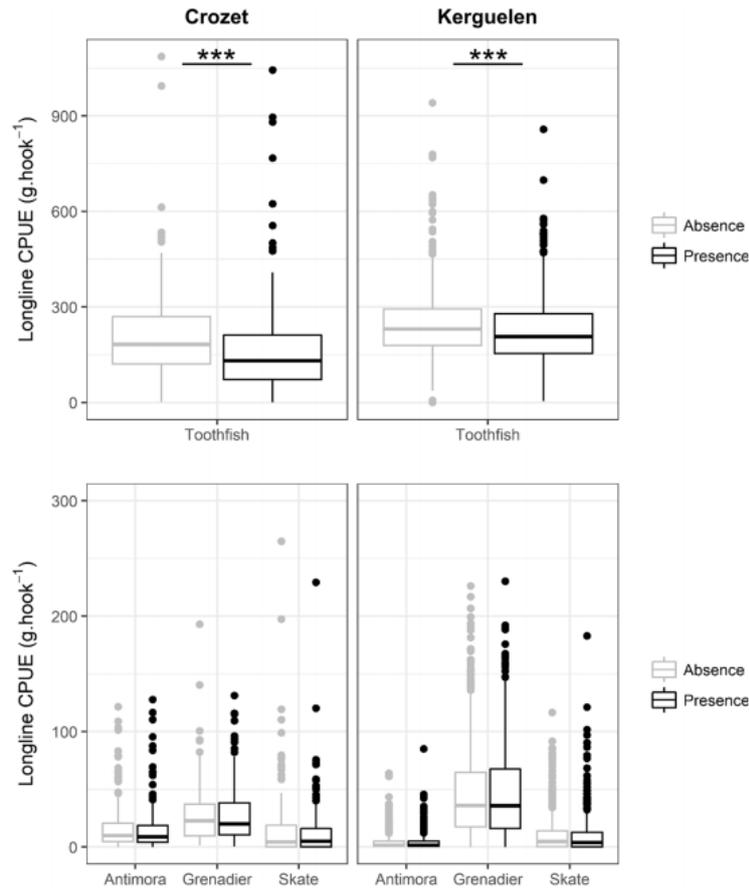


Fig. 4. Boxplots of observed CPUE values per longline set for Patagonian toothfish (top) and for the bycatch species groups (Antimora, Grenadier and Skate, bottom) when sets were hauled without depredation (absence of any odontocete species confirmed – light grey) and with confirmed depredation by sperm whales as the only depredating species (black) in Crozet (left) and in Kerguelen (right). Points are the outliers of the boxplots. *** indicate a significant difference ($P < 0.001$) in CPUE values between sets hauled in absence and in presence of sperm whales (Student *t*-test comparisons).

Table 3

Numerical outputs from Model 3 testing the effects of the number of sperm whales simultaneously depredating the same set (*Nb.ind*), the length of longline sets (*Length*), the soaking time (*SoakingTime*), the speed (*HaulingSpeed*) and the depth (*Depth*) at which sets were hauled as continuous standardized predictors on the Patagonian toothfish CPUE. The fishing trip (*Trip*) was entered in Model 3 as a random term.

	CROZET (N = 2695 sets)				KERGUELEN (N = 15080 sets)			
	Estimate	SE	t	P	Estimate	SE	t	P
Intercept	5.20	0.05	97.39	< 0.001	5.49	0.02	305.25	< 0.001
Nb.ind	-0.15	0.02	-8.56	< 0.001	-0.07	0.005	-14.09	< 0.001
Length	-0.14	0.02	-6.30	< 0.001	-0.08	0.005	-16.63	< 0.001
Depth	-0.06	0.02	-2.78	0.005	-	-	-	NS
SoakingTime	0.02	0.02	0.91	0.36	0.05	0.005	9.83	< 0.001
HaulingSpeed	-0.09	0.02	-3.74	< 0.001	-0.10	0.006	-16.16	< 0.001
Length:Nb.ind	-	-	-	NS	-	-	-	NS
Depth:Nb.ind	-	-	-	NS	-	-	-	NS
SoakingTime:Nb.ind	-0.03	0.02	-1.97	0.05	-	-	-	NS
HaulingSpeed:Nb.ind	-	-	-	NS	0.02	0.004	3.54	< 0.001
Random intercept: 0.15					Random intercept: 0.02			
Residual variance: 0.56					Residual variance: 0.25			

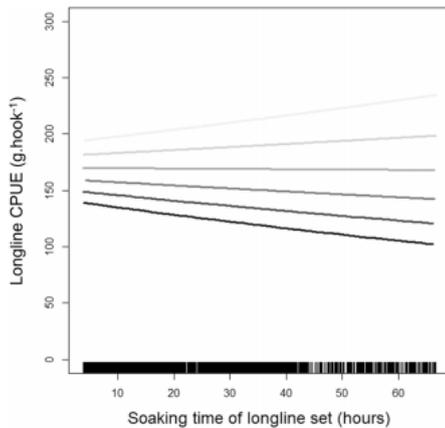


Fig. 5. Predicted estimates from *Model 3* outputs of the interaction effect between the soaking time of longline sets and the number of sperm whales depredated the same set on the Patagonian toothfish CPUE in Crozet. Each curve corresponds to a given number of sperm whales depredated the same set, ranging from 0 (light grey) to 5 (dark grey).

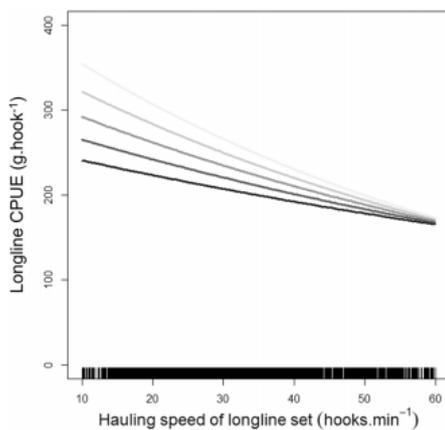


Fig. 6. Predicted estimates from *Model 3* outputs of the interaction effect between the hauling speed of longline sets and the number of sperm whales depredated the same set on the Patagonian toothfish CPUE in Kerguelen. Each curve corresponds to a given number of sperm whales depredated the same set, ranging from 0 (light grey) to 4 (dark grey).

visual monitoring may lead to some depredation events being missed and unrecorded. The diving behaviour and capabilities of sperm whales (Jaquet, 1996; Watkins et al., 1985) which allow them to interact with longline sets at greater depths, may result in individuals remaining at great distances from the vessels and for longer period of time underwater.

4.2. Spatio-temporal variations in the proportion of sets depredated

For both Crozet and Kerguelen, the models developed on the proportion of depredated sets indicated that sperm whales were significantly less likely to depredate on fishing gear in winter months. This

result was also reported in previous studies (Labadie et al., 2018; Tixier, 2012), and was attributed to the male sperm whale migration patterns of moving between feeding grounds in cold waters and reproduction grounds in tropical and sub-tropical waters (Jaquet et al., 2000; Madsen et al., 2002; Mellinger et al., 2004; Teloni et al., 2008).

The amplitude in the likelihood of sperm whale-fishery interaction between winter and summer months was lower in Crozet than in Kerguelen. However, variations in the mean number of sperm whales simultaneously depredated the same set were greater in Crozet than in Kerguelen, with increased numbers in summer months in Crozet. These differences may be explained by the size of the fishing area being smaller and the density of depredated sperm whales being greater in Crozet than in Kerguelen. The size of the Crozet fishing area is 20,512 km², a third of the Kerguelen fishing area (63,200 km²). From Labadie et al. (2018), the annual number of depredated sperm whales was estimated to 82 in Crozet and 106 in Kerguelen, which, if divided by the size of the fishing areas, resulted in 0.0040 sperm whale per km⁻² in Crozet, and 0.0017 sperm whale per km⁻² in Kerguelen. As a result, the likelihood of vessels to be detected and depredated may remain higher in Crozet than in Kerguelen.

Restricting the fishing activity to winter months is likely to minimize the rate of interaction of sperm whales with vessels, and therefore the amount of depredated toothfish. A possible evidence of such application is the extremely low proportion of sets depredated by sperm whales in the Australian Patagonian toothfish longline fishery operating around Heard and MacDonal Island (HIMI), at the Southern border of the Kerguelen EEZ. Unlike the Kerguelen longlining, which operates all year round, HIMI demersal longlining has been restricted to the April–November period. In the latter, the rate of depredation by sperm whales has remained lower than 5% ever since (CCAMLR, 2015c). However, this low depredation rate may also be explained by sperm whale densities being naturally low at the latitudes of HIMI fishing grounds and/or by the fact that trawling has been the primary fishing technique used in this area until longlining emerged in recent years.

Different sizes in fishing areas may also explain the fact that the depth at which longlines were set influenced the proportion of sets depredated in Kerguelen but not in Crozet. Paired with higher densities of depredated individuals and steeper bathymetric slopes, vessels are more likely to be detected and reached more quickly by sperm whales in the small fishing areas of Crozet than in Kerguelen. As such, the spatial variations in the proportion of sets depredated may better reflect the natural distribution of sperm whales in Kerguelen. Increased probability of depredation on sets hauled at greater depths may indicate that sperm whales are naturally distributed at the outer edge of the Kerguelen oceanic shelf, which corresponds to the type of feeding ground preferentially used by other males in other high latitude areas (Whitehead, 2003).

4.3. Operational means to mitigate sperm whale depredation

When leaving a given fishing ground where sperm whale depredation occurred, vessels were significantly less likely to have their next longline sets depredated if they travelled over large distances, on average greater than 60 km (*i.e.*, 32 nautical miles) because sperm whales may lose acoustical detection of vessels (G. Richard, pers. comm.). While further analysis would be required at the individual level using photo-identification, this result indicate that sperm whales do not follow fishing vessels over large distances and could be used as a mitigation measure to reduce depredation. From previous studies, implementing a “move-on” technique may be an effective strategy to avoid odontocete depredation (Peterson and Carothers, 2013; Tixier et al., 2015c). However, as indicated by a lower distance effect on sperm whale depredation in Crozet than in Kerguelen, this strategy may be highly dependent upon the size of the fishing areas and the densities of sperm whales as we explained in the previous section.

In Crozet, the hauling speed had no effect on sperm whale

depredation but increased soaking time of longline sets at the bottom combined with increased number of depredating sperm whales present around the vessel resulted in lower toothfish CPUE. Together, these results suggest that sperm whales may also depredate toothfish caught on longline sets before hauling. While this assumption remains poorly investigated, preliminary acceleration/acoustic data indicated that sperm whales were already present in the vicinity of the fishing gear prior to hauling and may interact with longlines at the bottom (A. Janc and G. Richard, pers. comm.). Sperm whales are deep diving animals and their diving range does overlap with the depths at which longlines are set (Fiscus, 1982; Jaquet et al., 2000; Jaquet and Gendron, 2002). As depredation can also occur when sets are soaked, depredation events can be missed, and therefore underestimated, if this process is only monitored visually from vessels during hauling operations.

In Kerguelen, the soaking time of sets had no effect on sperm whale depredation but the increased hauling speed was found to decrease sperm whale depredation. The extent of this correlation increased with increasing number of sperm whales simultaneously depredating on longline sets during hauling. Leaving toothfish caught on hooks in the water column for a shorter amount of time may prevent the whales from removing large proportions of toothfish. As a large body size reduces its maneuverability (Dial et al., 2008), a faster moving line may also make depredation more difficult for sperm whales. This assumption is supported by a lower hauling speed threshold above which CPUE remained unchanged for sperm whales (60 hooks.min⁻¹ – this study) than for killer whales (80 hooks.min⁻¹ – Tixier et al., 2015c).

Hauling speed and soaking time had different effects on sperm whale depredation depending on whether vessels operated in Crozet or Kerguelen. The influence of the soaking time detected in Crozet only suggests that sperm whales are more likely to depredate during soaking in this area than in Kerguelen. This difference can be interpreted by higher densities of sperm whales paired with high depredation by killer whales in Crozet (Gasco et al., 2015; Guinet et al., 2015; Tixier, 2012; Tixier et al., 2010, 2016), which are likely to increase both inter- and intra-specific competition for toothfish caught on longlines. Depredation on sets on the seafloor, which may be more energetically costly than depredation at shallow depths during hauling, may be a response of sperm whales to competition when the number of depredating odontocetes increases around vessels.

4.4. Conclusions

Together, the findings of this study could be used to develop operational fishing strategies that minimize odontocete depredation on longline fisheries of the Southern Ocean region. Targeting fishing periods of low depredating sperm whales presence, paired with other factors such as an increase in distance travelled between fishing grounds, an optimal depth at which longlines are set, a shorter soaking time at the bottom and a faster speed at which hooks are hauled may work as easy-to-implement mitigation measures to avoid or mitigate response to depredation. However, as these strategies may induce additional constraints for fishers (Maccarrone et al., 2014; Peterson et al., 2014), full bio-socio-economic assessments of the costs and benefits of changing fishing practices would be needed. For instance, the “move-on” technique may involve increased non-fishing time and motor-fuel consumption that can render this fishing strategy less advantageous to fishers or sustainable to the fishery itself. To increase profitability, these additional costs should not exceed the benefits gained by minimizing depredation (Trijoulet, 2016; Trijoulet et al., 2018). Further assessments are also needed to ensure that these operational adaptive measures are in agreement with fisheries regulations and resource management strategies, which is currently one of the key challenges for various stakeholders (Doyen et al., 2017, 2012; Gourguet et al., 2013; Nielsen et al., 2018). This study has also emphasized the various gaps of knowledge on odontocete depredation. For instance, sperm whales interaction with the fishing gear, and more importantly, the possible

occurrence of depredation when lines are still fishing before hauling. These may have direct implications on various aspects of the issue, including toothfish stock management, whale population conservation, and the ecosystem stability. Such information can also provide knowledge on other possible technical means and opportunities that can reduce depredation, such as the use of toothfish protecting devices which are currently receiving a growing attention and may be further developed in the future.

Author contributions

Study conception and design: AJ, CG, PT.
Acquisition of data: AJ, CG, PT.
Analysis and interpretation of data: AJ, GR, PT.
Drafting of manuscript: AJ, GR, CG, JA, MCV, GD, NG, PT.
Critical revision: AJ, GR, PT.

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Conflicts of interest

None.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.fishres.2018.04.019>.

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APPENDIX 5 – TIXIER ET AL. *CCAMLR SC*

ACCEPTED

1 **Fisheries interaction data suggest variations in the distribution of sperm whales on the**
2 **Kerguelen Plateau.**

3

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29

30 **Abstract**

31

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

46

47

48 **Keywords:** Fisheries interactions, Sperm whale, Patagonian toothfish, Kerguelen, Depredation

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57 **Introduction**

58

59 The emergence of longline fishing throughout the world's oceans is concomitant with increasing
60 reports of depredation interactions by marine top-predators, primarily odontocetes (toothed whales),
61 with fishing vessels (Northridge 1991, Northridge and Hofman 1999, DeMaster et al. 2001, Read
62 2008, Hamer et al. 2012). Depredation interactions occur when odontocetes feed on fish caught by
63 fishers on longline sets (Read et al. 2005, Hamer et al. 2012, Werner et al. 2015). These interactions
64 often result in socio-economic (financial losses for fishers), ecological (effects on depredating
65 species) and conservation issues (impacts on depredated resources) (Gasco et al. 2015, Tixier et al.
66 2015, 2017, Werner et al. 2015, Esteban et al. 2016, Peterson and Hanselman 2017, Hanselman et al.
67 2018).

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

76 On the Kerguelen Plateau, the two commercial Patagonian toothfish (*Dissostichus eleginoides*)
77 longline fisheries operating respectively around Kerguelen Island (French Economic Exclusive Zone
78 – EEZ) and around Heard Island and McDonald Islands (Australian EEZ) have experienced
79 depredation by two odontocete species: sperm whales (*Physeter macrocephalus*) and killer whales
80 (*Orcinus orca*). While both species have been reported interacting with vessels in the French EEZ,
81 only sperm whales were documented depredating on longlines in the Australian EEZ (Roche et al.
82 2007, Tixier et al. 2010, Guinet et al. 2014, Welsford and Arangio 2015, Janc et al. 2018). The French
83 fishery, for which commercial longlining started in the 1990s, has experienced consistent high sperm

84 whale depredation levels (> 40% of fishing operations) for over two decades (Roche et al. 2007,
85 Tixier et al. 2010, Janc et al. 2018). The seven licensed longliners of this fishery operate all year
86 round except in February and early March. Conversely, sperm whale depredation in the Australian
87 EEZ was first reported in 2011, although commercial longlining started in 2003 in this area, and have
88 remained low (<10 % of the fishing operations) over the following years (Welsford and Arangio
89 2015). This fishery includes four licensed fishing vessels and operates from April to November only.
90 Whether the large differences of sperm whale interaction levels between the French and the
91 Australian EEZs are explained by differences in fishing patterns or difference in the natural presence
92 of sperm whales, or a combination of both, remains unknown.
93 Therefore, as a first step in understanding these variations, the aims of this study were to investigate
94 the level of interactions between sperm whales and fishing vessels over an area encompassing both
95 the French and the Australian EEZs. Using a dataset including fishing and observation data from both
96 areas over the 2011-2016 period, this study assesses the spatio-temporal variations of sperm whale
97 interactions and provides preliminary insights on the role of sperm whale natural distribution in these
98 variations.

99

100 **Methods**

101

102 **Data**

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

108

109 The occurrence of sperm whale depredation interactions with longline sets was recorded during
110 hauling operations by visual cues. An interaction was confirmed when whales were sighted at the

111 surface within 500 m of the vessel with typical depredation behaviour: individuals made repeated
112 dives towards the line being hauled and throughout the hauling process; they were usually surrounded
113 by birds when surfacing after long dives; and slicks of fish oil were visible at the surface. True
114 depredation interaction events (recorded as 1) were, therefore, assumed to be monitored in a
115 standardised way across Kerguelen and HIMI fisheries. Observers distinguished between longline sets
116 with confirmed non-occurrence of depredation (recorded as 0) and sets with lacking information due
117 to insufficient or impossible monitoring effort (recorded as No data Available – N/A) caused by poor
118 weather (e.g. fog), sea or light conditions.

119

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

127

128 Statistical analyses

129 Spatial and temporal variations of sperm whale interactions with vessels were examined through
130 Generalized Linear Mixed Models (GLMM) fitted to the records of sperm whale presence/absence
131 data per set and per spatial cell with a binomial distribution and a logit link function. The null model
132 fitted at the set level included the interaction between the presence/absence of sperm whales on the set
133 that was previously hauled and the distance between this set and the next as a structural term to
134 account for spatio-temporal autocorrelation as previously reported in depredation data (Tixier et al.
135 2014, Janc et al. 2018). The null model fitted at the spatial cell level included the fishing effort,
136 calculated as the total number of hooks set per spatial cell per vessel per year and per season, as a
137 structural term to account for increased likelihood of vessels to experience interactions with increased
138 fishing time in cells (Janc et al. 2018). The null model, for models fitted both at the set and at the

139 spatial cell levels, included the vessel identification (ID) as a random term to account for unidentified
140 vessel-dependent variables influencing whale interactions with vessels (Tixier et al. 2010, 2014,
141 Richard et al. 2017, Janc et al. 2018). The fishery (Kerguelen or HIMI) and the latitude at which sets
142 were hauled were included as spatial fixed terms. Temporal terms included the year and the season
143 and were, respectively, tested as continuous and categorical fixed terms. The season was a 4-level
144 variable, defined as summer (December-February), autumn (March-May), winter (June-August) and
145 spring (September-November). Models best fitting the data were selected through a stepwise forward
146 Akaike Information Criterion (AIC) selection process. These models were then fitted to sperm whale
147 interaction data on sets and in spatial cells for each of the three seasons (autumn, winter, spring)
148 during which fishing occurred both in Kerguelen and HIMI to examine differences in the level of
149 sperm whale interaction between the two fisheries during a given season.

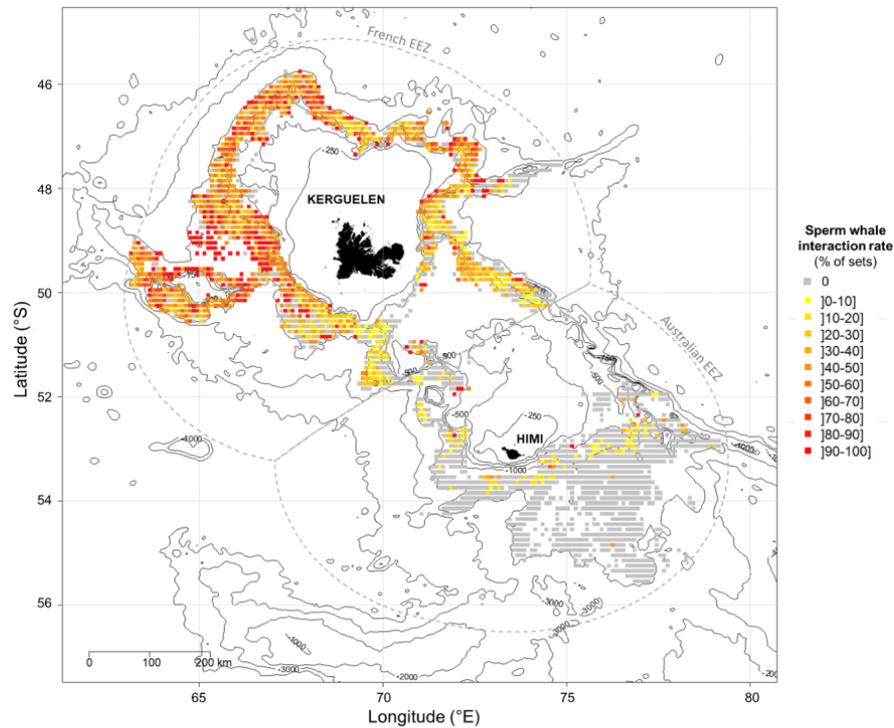
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151 **Results**

152

153 Data from a total of 20,163 longline sets hauled from January 2011 to December 2016 were available
154 for the study. Sperm whale interactions occurred on $\text{Pr}(\text{sets}) = 29.1\%$ of these longline sets and in
155 $\text{Pr}(\text{area}) = 49.4\%$ of all fished spatial cells ($n = 2,618$). Visual exploration of spatialized $\text{Pr}(\text{sets})$
156 showed large variations across the full area, but also within the Kerguelen and HIMI fisheries over the
157 study period (Figure 1). Concentrations of $0.1^\circ \times 0.1^\circ$ grid cells with high proportions of depredated
158 sets ($> 60\%$) were visible in the north-western part of Kerguelen, and these areas were consistent
159 across seasons (Figure 2).

160

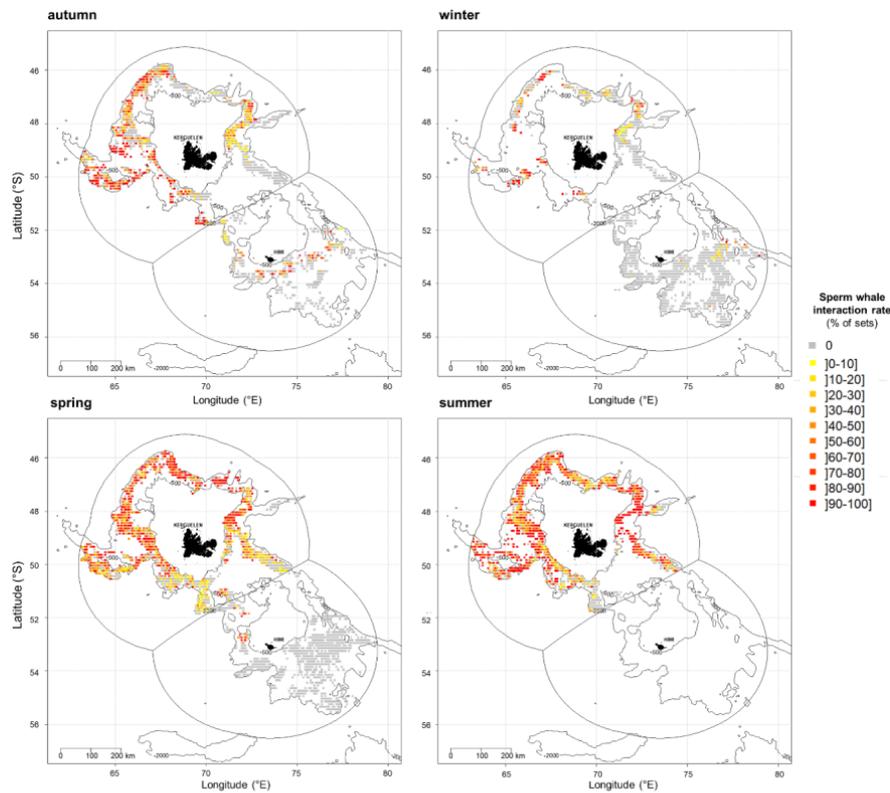


161

162 Figure 1. Map of spatialized interaction rates of sperm whales with fishing vessels on the Kerguelen
 163 Plateau. Interaction rates were calculated as the proportion of longline sets hauled in presence of
 164 sperm whales in a $0.1^\circ \times 0.1^\circ$ spatial cell out of all longline sets hauled in that cell between 2011 and
 165 2016. Grey filled cells indicate cells in which fishing occurred (at least one set was hauled) but sperm
 166 whale interaction was never reported. 250, 500, 750, 1000, 2000, 3000 and 4000 m isobaths are
 167 depicted (black lines) as well as the limits of the Exclusive Economic Zones (EEZ – dashed line) of
 168 Kerguelen (France) and Heard Island and McDonald Islands (HIMI – Australia).

169

170



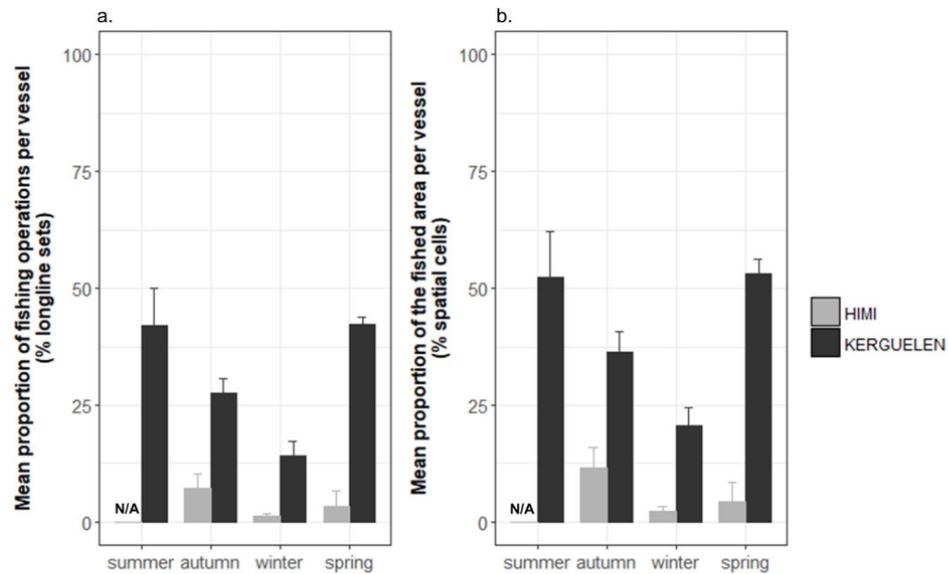
171

172 Figure 2. Map of spatialized interaction rates of sperm whales with fishing vessels on the Kerguelen
 173 Plateau per season. Interaction rates were calculated as the proportion of longline sets hauled in
 174 presence of sperm whales in a $0.1 \times 0.1^\circ$ spatial cell out of all longline sets hauled in that cell for each
 175 season between 2011 and 2016: autumn (March –May), winter (June –August), spring (September–
 176 November) and summer (December–February). Grey filled cells indicate cells in which fishing
 177 occurred (at least one set was hauled) but sperm whale interaction was never reported. The 500 m and
 178 1000 m isobaths are depicted (black lines) as well as the limits of the Exclusive Economic Zones
 179 (EEZ) of Kerguelen (France) and Heard Island and McDonald Islands (HIMI – Australia).

180

181 $Pr(\text{sets})$ and $Pr(\text{area})$ per vessel were significantly higher in Kerguelen than in HIMI (GLMM $z =$
 182 4.06 ; $P < 0.001$ and $z = 3.48$; $P < 0.001$ respectively, Table 1). Over the study period, sperm whales

183 interacted with an average of 33.2 ± 4.5 % of all sets per vessel in Kerguelen ($n = 9$ vessels) and $3.1 \pm$
184 1.2 % of all sets in HIMI ($n = 6$ vessels). Vessels experienced sperm whale interactions in $\text{Pr}(\text{area}) =$
185 5.4 ± 2.0 % of the spatial cells in HIMI and in $\text{Pr}(\text{area}) = 48.2 \pm 7.2$ % of the spatial cells in
186 Kerguelen. $\text{Pr}(\text{sets})$ and $\text{Pr}(\text{area})$ per vessel linearly and significantly decreased with the latitude
187 (GLMM $z = -10.47$; $P < 0.001$ and $z = -14.83$; $P < 0.001$ respectively) at which longlines were hauled.
188 No trend over the study period could be detected in $\text{Pr}(\text{sets})$ nor in $\text{Pr}(\text{area})$ per vessel as the year term
189 was not selected in the final models. However, significant variations of $\text{Pr}(\text{sets})$ and $\text{Pr}(\text{area})$ between
190 seasons were detected (Table 1). $\text{Pr}(\text{set})$ and $\text{Pr}(\text{area})$ per vessel were the highest in summer with
191 respectively $42.0 \pm 7.9\%$ of the sets and $52.3 \pm 9.8\%$ of the spatial cells, and the lowest in winter with
192 respectively $8.8 \pm 2.6\%$ of the sets and $12.9 \pm 7.7\%$ of the spatial cells.
193 Models run by season indicated that $\text{Pr}(\text{sets})$ and $\text{Pr}(\text{area})$ were consistently significantly lower for
194 vessels operating in HIMI than for vessels operating in Kerguelen during autumn, winter and spring
195 (Table 1 and figure 3a,b). In HIMI, $\text{Pr}(\text{sets})$ and $\text{Pr}(\text{area})$ per vessel were the highest in autumn with
196 $7.3 \pm 3.1\%$ of the sets and $11.6 \pm 4.3\%$ of the spatial cells, whereas for that season $\text{Pr}(\text{sets})$ and
197 $\text{Pr}(\text{area})$ in Kerguelen were $27.5 \pm 3.3\%$ of the sets per vessel and $36.3 \pm 4.6\%$ of the spatial cells per
198 vessel, respectively (figure 3a,b). In Kerguelen, sperm whale interaction rates were the highest in
199 spring for $\text{Pr}(\text{sets})$ with $42.3 \pm 1.6\%$ of the sets per vessel and for $\text{Pr}(\text{area})$ with 53.0 ± 3.1 of the
200 spatial cells per vessel. In HIMI in spring, $\text{Pr}(\text{sets})$ was $3.3 \pm 3.3\%$ of the sets per vessel and $\text{Pr}(\text{area})$
201 was $4.3 \pm 4.3\%$ of the spatial cells per vessel. While no fishing occurred in summer in HIMI, $\text{Pr}(\text{sets})$
202 and $\text{Pr}(\text{area})$ for that season in Kerguelen were high and similar to spring values for that area (Figure
203 3a,b).
204



205

206 Figure 3. Seasonal variations of the mean \pm SE level of sperm whale interaction with vessels in
 207 Kerguelen (black) and HIMI (grey). The interaction level was calculated per season a. as a proportion
 208 of longline sets and b. as a proportion of $0.1^\circ \times 0.1^\circ$ spatial cells in which fishing occurred. Seasons
 209 included summer (December–February), autumn (March–May), winter (June–August) and spring
 210 (September–November). “N/A” indicates season for which fishing did not occur. Comparisons
 211 between HIMI and Kerguelen were significant ($P < 0.05$ in GLMMs – Table 1) for each season where
 212 data were available.

213

214

215 Table 1. Summary outputs of the final GLMMs fitted with a binomial distribution and a logit link
 216 function to the presence/absence records of sperm whale interactions at the longline set level and at
 217 the $0.1^\circ \times 0.1^\circ$ spatial cell level. Models were fitted using all records available for the 2011-2016
 218 period, and for each of the three seasons (autumn, winter, spring) during which fishing occurred both
 219 in Kerguelen and HIMI. (-) indicates that the predictor was not tested in models.

220

221

Level	Predictor	All data			autumn			winter			spring		
		Est. \pm SE	z	P	Est. \pm SE	z	P	Est. \pm SE	z	P	Est. \pm SE	z	P
<i>set</i>	Intercept	-3.49 \pm 0.25	-13.76	< 0.001	-3.12 \pm 0.26	-11.85	< 0.001	-4.32 \pm 0.43	-10.12	< 0.001	-4.90 \pm 0.84	-5.80	< 0.001
	presence/absence * distance (previous set)	-0.46 \pm 0.04	-12.10	< 0.001	-0.34 \pm 0.08	-4.12	< 0.001	-0.70 \pm 0.21	-3.30	0.001	-0.50 \pm 0.07	-7.45	< 0.001
	area: Kerguelen	1.24 \pm 0.30	4.06	< 0.001	1.13 \pm 0.32	3.51	< 0.001	1.39 \pm 0.60	2.30	0.021	3.07 \pm 0.95	3.23	< 0.001
	latitude	-0.41 \pm 0.04	-10.47	< 0.001	-0.06 \pm 0.09	-0.65	0.516	-0.32 \pm 0.21	-1.52	0.128	-0.95 \pm 0.07	-14.02	< 0.001
	season: winter	-0.69 \pm 0.09	-7.79	< 0.001	-	-	-	-	-	-	-	-	-
season: spring	0.40 \pm 0.06	6.83	< 0.001	-	-	-	-	-	-	-	-	-	
season: summer	0.60 \pm 0.06	9.76	< 0.001	-	-	-	-	-	-	-	-	-	
<i>spatial cell</i>	Intercept	-2.78 \pm 0.37	-7.41	< 0.001	-2.11 \pm 0.34	-6.23	< 0.001	-3.42 \pm 0.48	-7.08	< 0.001	-4.61 \pm 1.20	-3.66	< 0.001
	fishing effort	0.30 \pm 0.03	12.00	< 0.001	0.34 \pm 0.05	6.49	< 0.001	0.15 \pm 0.06	2.45	0.014	0.42 \pm 0.05	8.54	< 0.001
	area: Kerguelen	1.61 \pm 0.46	3.48	< 0.001	1.35 \pm 0.42	3.24	0.001	1.53 \pm 0.66	2.30	0.022	4.06 \pm 1.35	3.01	0.003
	latitude	-0.61 \pm 0.04	-14.83	< 0.001	-0.06 \pm 0.09	-0.68	0.500	-0.52 \pm 0.22	-2.34	0.019	-1.38 \pm 0.08	-17.85	< 0.001
	season: winter	-1.09 \pm 0.10	-11.37	< 0.001	-	-	-	-	-	-	-	-	-
season: spring	0.63 \pm 0.06	10.45	< 0.001	-	-	-	-	-	-	-	-	-	
season: summer	1.02 \pm 0.06	15.89	< 0.001	-	-	-	-	-	-	-	-	-	

222

223 **Discussion**

224

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

230

231 The difference between Kerguelen and HIMI may be due to variations in the way vessels operate
232 when fishing. In previous studies, factors such as the time of year were found to significantly
233 influence the probability of vessels experiencing sperm whale depredation (Tixier et al. 2010, Janc et
234 al. 2018). In the Southern Ocean, this probability has been shown to decrease in winter and increase in
235 summer/spring months in areas such as Chile, South Georgia, Crozet and Kerguelen (Hucke-Gaete et
236 al. 2004, Clark and Agnew 2010, Janc et al. 2018). The present study confirmed this seasonal pattern
237 on the Kerguelen Plateau. However, for any given season, vessels operating in Kerguelen experienced
238 substantially higher rates of interaction with sperm whales than the vessels operating in HIMI. While
239 the HIMI fishery primarily operates during winter months and is closed to fishing in summer, which
240 could contribute to the low observed interaction rates, the results of the present study suggests other
241 factors are likely to explain the observed differences with Kerguelen. Among other operational
242 factors, differences in the distance travelled between longline sets, variations in the acoustic cues
243 produced by vessels used by sperm whales to locate them, or the decisions made by skippers when
244 confronted by sperm whale depredation between Kerguelen and HIMI should be further examined as
245 these factors have also been shown to influence the probability of sperm whales to depredate on
246 fishing gear (Thode et al. 2007, 2015, Tixier et al. 2010, 2014, Richard et al. 2017, Janc et al. 2018).

247

248 The large spatial variations reported in the present study, paired with a strong latitudinal gradient
249 detected in models fitted to the level of sperm whale interactions with vessels, suggests the degree of

250 spatial overlap between fishing operations and the natural distribution of sperm whales may have
251 major influence on the level of interactions. Areas of consistent high probability of sperm whale
252 interactions were identified in the northern reaches of the Kerguelen plateau, and this probability
253 decreased linearly as vessels operated further south. Previous studies based on whale–vessel
254 depredation interaction data suggested that spatial variables such as local bathymetry may influence
255 the probability of the fishing gear to be depredated (Janc et al. 2018). However, fishing operations in
256 HIMI and Kerguelen are conducted over similar depth frequency distributions (Péron et al. 2016),
257 which suggests that other spatial factors may influence the observed variation in sperm whale
258 interactions.

259 Sperm whales, as a species, are characterised by an age- and sex-dependent temporary segregation
260 patterns, with females and juveniles distributed in tropical and sub-tropical waters, and adult males
261 seasonally using high latitude areas as feeding grounds (Best 1979, Rice 1989, Jaquet 1996, Mellinger
262 et al. 2004, Whitehead 2009, Wong and Whitehead 2014). As such, factors influencing their
263 distribution are likely to involve a large extent of oceanographic features driving prey abundance and
264 availability. The natural diet of these adult male sperm whales feeding in the Southern Ocean is
265 poorly known but is believed to be made of a combination of cephalopods and fish (Kawakami 1980,
266 Rice 1989). These prey groups have also already been observed in the diet of sperm whales in
267 southern Australian waters (Evans and Hindell 2004) and in the Gulf of Mexico (Judkins et al. 2015).
268 The distribution of adult male sperm whales in other high latitude areas was found to be highly driven
269 by static oceanographic features such as the bathymetric slope and dynamic oceanographic variables
270 such as eddies and fronts (Whitehead et al. 1992, Jaquet 1996, Jaquet and Whitehead 1996, Jaquet et
271 al. 2000, Straley et al. 2014, Wong and Whitehead 2014). The high site fidelity of individual sperm
272 whales on small-scale ranges within the Kerguelen area over periods of nearly 10 years (Labadie et al.
273 2018) further supports that animals seek for specific feeding grounds, and the spatial variables
274 characterising these feeding grounds should be examined in details in the near future.

275

276 The Kerguelen longline fishery is older than the HIMI longline fishery and, consequently, it is
277 possible that sperm whales in HIMI are less experienced in interacting with fishing vessels. This

278 would lead to them being less likely to switch from natural feeding to depredation than sperm whales
279 in Kerguelen. Indeed, in other depredating sperm whale populations such behaviour has been shown
280 to progressively spread spatially and, possibly, across individuals over time (Schakner et al. 2014).
281 While sperm whale depredation is believed to have started as soon as longline fishing began in
282 Kerguelen in the early 1990s, the first reports of sperm whale depredation in HIMI occurred in 2011,
283 9 years after longline fishing started in that area. Whether the depredating sperm whales in HIMI are
284 the same individuals as the ones depredating in Kerguelen, or new ones, is still unknown, and should
285 be assessed and accounted for when investigating the spatial drivers of sperm whale interactions with
286 vessels.

287

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

293

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295

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307 Operators, Inc. (COLTO).

308

APPENDIX 6 – TIXIER ET AL. *SCI. REP.*

ACCEPTED

- 1 **Commercial fishing patterns influence odontocete whale-longline interactions in the Southern**
2 **Ocean**
3
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28 The emergence of longline fishing around the world has been concomitant with an increase in
29 depredation-interactions by odontocete whales (removal of fish caught on hooks), resulting in
30 substantial socio-economic and ecological impacts. The extent, trends and underlying mechanisms
31 driving these interactions remain poorly known. Using long-term (2003-2017) datasets from seven
32 major Patagonian toothfish (*Dissostichus eleginoides*) longline fisheries, this study assessed the levels
33 and inter-annual trends of sperm whale (*Physeter macrocephalus*) and/or killer whale (*Orcinus orca*)
34 interactions as proportions of fishing time (days) and fishing area (spatial cells). The role of fishing
35 patterns in explaining between-fisheries variations of probabilities of odontocete interactions was
36 investigated. While interaction levels remained globally stable since the early 2000s, they varied
37 greatly between fisheries from 0 to > 50% of the fishing days and area. Interaction probabilities were
38 influenced by the seasonal concentration of fishing effort, size of fishing areas, density of vessels,
39 their mobility and the depth at which they operated. The results suggest that between-fisheries
40 variations of interaction probabilities are largely explained by the extent to which vessels provide
41 whales with opportunities for depredation interactions. Determining the natural distribution of whales
42 is therefore the next step to better predict and better mitigate depredation.

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56 **Introduction**

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58 Over the last 60 years, the world's commercial fisheries have undergone substantial changes in
59 distribution, intensity, regulations and technology¹. Fishing techniques have evolved towards greater
60 efficiency but declines in catch per unit effort, paired with environmental impacts, have led some
61 fisheries to increase target selectivity in their technological development. A number of trawling and
62 gillnetting fisheries have progressively switched to longlining as a more selective fishing technique²⁻
63⁴. However, the emergence of longline fishing throughout the world oceans is concomitant with
64 increasing reports of depredation interactions by marine top-predators, primarily odontocete (toothed)
65 whales⁵⁻¹⁰, with fishing vessels.

66 Depredation interactions, hereafter termed interactions, are a form of human-wildlife conflict that
67 occurs when wild species consume a resource caught or raised/grown by humans. Here, odontocetes
68 directly remove fish from hooks on longlines, which results in a combination of socio-economic and
69 conservation impacts. Socio-economic impacts include financial losses and increased fishing time for
70 humans. Conservation impacts for the depredated fish include inaccurate stock assessments due to
71 difficulties in estimating the amount of fish taken by odontocetes. For the depredating species,
72 conservation impacts include negative effects due to increased risks of injury caused by fishing gear
73 or lethal responses from fishers, increased dependency to depredation and alteration of natural energy
74 intake balances, and positive effects from artificial food provisioning^{8,10-20}.

75 While odontocete interactions have been increasingly reported over the past decade, it is unclear
76 whether the issue is actually increasing in frequency and intensity¹⁰. In addition, the mechanisms
77 leading whales to change from natural foraging behaviours to depredation are poorly understood. This
78 change may be driven by two processes, occurring either separately or together. Firstly, depredation
79 may be a purely opportunistic behaviour simply resulting from the spatio-temporal overlap of fishing
80 operations with the natural distribution of whales and their normal prey. Secondly, depredation may
81 be an active behaviour occurring when whales modify their natural distribution by actively searching
82 for fishing vessels or by following them over great distances.

83 Whether interactions result from opportunistic or active behaviour, their occurrence may be highly
84 dependent upon the extent to which fishing vessels provide odontocetes with opportunities to
85 depredate, and therefore the spatio-temporal patterns of fishing operations. The present study used this
86 hypothesis to investigate the influence of fishing patterns of different commercial fisheries in the
87 Southern Ocean on the levels of interaction between fishing vessels and two odontocete species: killer
88 whales (*Orcinus orca*); and sperm whales (*Physeter macrocephalus*). These commercial fisheries
89 operating in the Exclusive Economic Zones (EEZ) of southern Chile, the Falklands (UK), South
90 Georgia and South Sandwich Islands (UK), Prince Edward and Marion Islands (“PEMI” – South
91 Africa), Crozet and Kerguelen (France), and Heard and MacDonal Islands (“HIMI” – Australia) all
92 use demersal longlines to catch Patagonian toothfish (*Dissostichus eleginoides*). Patagonian toothfish
93 longline fisheries emerged as commercial fisheries in the 1980s-2000s, replacing existing bottom-
94 trawling fisheries, and have all been subject to killer and/or sperm whale depredation interactions
95 since the first years following their commencement²¹⁻²⁸. These fisheries have now become the
96 primary economic activity of Southern Ocean^{29,30} but greatly vary in size of fleets and fishing area,
97 length of fishing seasons, quotas and longline fishing system. For instance, fisheries operating in
98 Chile, the Falklands and PEMI predominantly use the trotline system (longlines with clusters of
99 hooks) equipped with “cachalotera”, a fish protection device developed to reduce odontocete
100 depredation and seabird mortality³¹, whereas the other fisheries use the autoline system (weighted
101 longlines with individual hooks to reduce seabird mortality). Most EEZs also experienced substantial
102 Illegal Unreported and Unregulated (IUU) fishing in the 1980s and 1990s, resulting in an over-harvest
103 of local fish stocks and impacts on seabird and whale populations interacting with illegal vessels<sup>29,32-
104 38</sup>.

105 Depredation by killer whales and sperm whales represent a major challenge for the economic
106 viability of the toothfish fisheries, for the assessment of fish stocks and their management, and for the
107 conservation of whale populations in the Southern Ocean²⁸. Determining the role of fishing patterns
108 in explaining variations in the level of whale interaction with vessels would bring important insights
109 for fisheries to minimize depredation by adjusting their spatio-temporal fishing patterns. Therefore,
110 the aims of this study were to: i) assess the level and annual trends of whale-fishing vessel interaction,

111 both locally and globally in the Southern Ocean; and ii) examine the effect of variations in spatio-
 112 temporal fishing patterns on observed interaction levels.

113

114 **Results**

115

116 *Spatial and temporal variations in interaction levels*

117

118 Data from a total of 97,688 longline sets hauled in the seven study areas/fisheries (southern Chile,
 119 the Falklands, South Georgia, PEMI, Crozet, Kerguelen, HIMI, Fig. 1), were available for this study.
 120 Confirmed depredation interactions by killer whales occurred during hauling of 8,271 sets (8.5%) and
 121 30,875 sets (31.6%) for sperm whales. The mean level of interactions per vessel per year varied
 122 between the seven fisheries for both sperm whales and killer whales. *Pr(days)* and *Pr(area)* were the
 123 highest for vessels that operated in Crozet, for both sperm whales (0.77 ± 0.02 of fishing days, $0.68 \pm$
 124 0.02 of the fishing area with depredation, $n = 96$ vessels per year, Fig. 2a) and killer whales ($0.55 \pm$
 125 0.02 of fishing days, 0.49 ± 0.02 of the fishing area with interactions per vessel per year, $n = 96$
 126 vessels per year, Fig. 2b). HIMI was the only fishery where killer whale interactions were never
 127 recorded. Vessels that operated in HIMI also had the lowest mean *Pr(days)* and *Pr(area)* for sperm
 128 whales (0.04 ± 0.01 of fishing days, 0.05 ± 0.01 of the fishing area, $n = 20$ vessels per year, Fig 2.).
 129

130 At the vessel level, significant decreases of *Pr(days)* over time were detected in Chile, Crozet and
 131 Kerguelen for sperm whales ($t = -3.51$, $P < 0.01$; $t = -2.07$, $P = 0.04$; $t = -2.79$, $P < 0.01$ for the three
 132 fisheries, respectively, Table S1a; Fig. 3a). However, *Pr(days)* for sperm whales significantly
 133 increased in the Falklands ($t = 2.70$, $P = 0.01$), with 0.43 ± 0.12 of the fishing days per vessel in 2003
 134 ($n = 6$ vessels) to 0.59 ($n = 1$ vessel) in 2016 (Fig 3a.). *Pr(days)* for killer whales decreased
 135 significantly in Chile ($t = -2.31$, $P = 0.02$) but increased in South Georgia ($t = 2.88$, $P < 0.01$, Table
 136 S1b; Fig. 3b). In Chile, *Pr(days)* varied from 0.98 ± 0.02 of the fishing days per vessel with sperm
 137 whale interactions in 2006 ($n = 4$ vessels) to 0.22 ± 0.06 ($n = 5$ vessels) in 2016 (Fig. 3a), and from
 138 0.60 ± 0.19 in 2006 ($n = 4$ vessels) to 0.20 ± 0.06 in 2016 ($n = 5$ vessels) for killer whales (Fig 3.b).

5

139 At the fleet level, $Pr(days)$ decreased in South Georgia ($t = -3.23$, $P < 0.05$) and increased in HIMI (t
 140 $= 2.88$, $P = 0.04$) for sperm whales (Table S1a; Fig. 3a). In HIMI, $Pr(days)$ varied from 0.05 of the
 141 fishing days in 2011 to 0.17 in 2016 (Fig. 3a). No trend in $Pr(days)$ was detected at the fleet level for
 142 killer whales. No general trends were detected at either the vessel or the fleet level when using data
 143 from all fisheries combined (Table S1a,b).

144

145 Fisheries could be categorized into two groups based on the slope ($\hat{\beta}_1$) of the linear correlation
 146 between the spatial spread of fishing operations and the cumulative proportion of the full fishing area
 147 where interactions occurred during the study (Fig. 4). The spatial spread of sperm whale interactions
 148 increased at a rate of $\hat{\beta}_1 > 0.5$ with the spatial spread of fishing operation in all fisheries but HIMI ($\hat{\beta}_1 =$
 149 0.1). For killer whales, the spatial spread of interactions correlated with that of fishing operations at a
 150 rate of $\hat{\beta}_1 > 0.5$ in Chile, South Georgia and Crozet and at a rate $\hat{\beta}_1 < 0.1$ in the Falklands and
 151 Kerguelen (Fig. 4).

152

153 *Influence of fishing patterns on interaction probabilities*

154

155 Models best fitting the level of sperm whale interactions, at both the vessel and the fleet levels,
 156 included all predictors including the interaction between fishery and mobility (Data S1, Table 1, Table
 157 S2.1 & S2.2). These models indicated that $Pr(days)$ of sperm whales decreased with increasing size of
 158 the fishing area, proportion of effort in winter and depth of sets, and decreasing mobility of vessels
 159 and proportion of sets using trotlines equipped with cachalotera (Table 1). The density of vessels in
 160 fisheries decreased $Pr(days)$ at the vessel level (GLM $P = 0.04$) but increased $Pr(days)$ at the fleet
 161 level (GLM $P < 0.01$, Table 1).

162

163 For killer whales at the vessel level, $Pr(days)$ was best explained by the model including the
 164 fishery, the size of fishing areas, the density of vessels, their mobility, the depth of sets and an
 165 interaction between fishery and mobility (Data S2, Table 2, Table S2.3). The model without the

166 interaction term was within 2 AIC of the optimal model (Table S2.3), however, trends in the common
167 covariates were identical to the optimal model so it is not further discussed. At the vessel level,
168 *Pr(days)* decreased with increasing size of fishing areas (GLM $P < 0.01$), increasing mobility of
169 vessels (GLM $P < 0.01$) and increasing density of vessels (GLM $P < 0.01$, Table 2). At the fleet level
170 for *Pr(days)* six models were within 2 AIC of the optimal model (Data S2, Table S2.4) which
171 included the fishery, the density of vessels and the depth of sets and mobility (Data S2, Table 2, Table
172 S2.4). All models within 2 AIC of the optimal model included fishery and the depth of sets, while the
173 density of vessels was significant in five of the six models. Mobility of vessels was included in one
174 model other than the optimal model, while the size of the fishing area, proportion of effort in winter
175 and proportion of cachalotera errors were significant in one model each. For all models at the vessel
176 level within 2 AIC of the optimal model, *Pr(days)* increased with the density and mobility of vessels
177 and decreased with the depth of sets (Data S2, Table 2, Table S2.4).

178

179 **Discussion**

180

181 The present study demonstrated large variations in the level of killer whale and sperm whale
182 interactions with Patagonian toothfish fishing vessels between commercial fisheries in the Southern
183 Ocean, and indicated that some of this variation can be explained by the fishing patterns of vessels.
184 These findings suggest that the level of whale-fisheries interactions may primarily depend upon the
185 extent to which fisheries provide whales with opportunities to depredate in space and time. However,
186 the present study also demonstrated that some of the variability around whale-vessel interaction levels
187 was attributed to as yet unknown area-specific factors that are further discussed here as potential
188 directions for future research on odontocete depredation in the Southern Ocean.

189 Over the last 14 years, Patagonian toothfish fisheries operating in Chile, the Falklands, South
190 Georgia, PEMI, Crozet, Kerguelen and HIMI all experienced sperm whale interactions, and six of
191 them experienced killer whale interactions. In most fisheries, the level of interaction has remained
192 stable. Interactions, which were reported as soon as demersal longlining started in the Southern Ocean
193 in the 1980s and 1990s, are now an established behaviour for the majority of local whale populations.

7

194 The exception is sperm whale interactions at HIMI which were first reported in 2010 despite
195 longlining for Patagonian toothfish commencing in 2003³⁹.

196 Increased fishing effort by vessels in winter coincided with decreased sperm whale interaction
197 levels. This decrease is likely explained by seasonal shifts in the local abundance of mature male
198 sperm whales, possibly driven by ecological and/or reproduction factors, with smaller numbers of
199 individuals found at high latitudes in winter months⁴⁰⁻⁴⁴. As a result, lower densities of sperm whales
200 in winter months may contribute to interaction levels being the lowest with vessels at HIMI and South
201 Georgia, which are both primarily winter fisheries. As the fishing season at HIMI has extended in
202 recent years, vessels concentrating increasing proportions of their effort in spring may also explain the
203 emergence of sperm whale interactions in this fishery since 2010³⁹.

204 Larger fishing areas were associated with decreased levels of both killer and sperm whales
205 interaction with vessels. A larger fishing area is likely to decrease the probability of vessels being
206 detected by whales⁴⁵⁻⁴⁷, to decrease the predictability of the fishing activity^{28,48} and to increase the
207 effectiveness of move-on strategies which have been implemented to avoid/escape depredation^{26,49}.
208 However, these effects may be also driven by the density of vessels operating simultaneously in
209 fishing areas. At the fleet level, greater densities of vessels were associated with higher interaction
210 levels (present study). Increased number of vessels combined with a small fishing area may increase
211 the detectability of fleets as a whole. This combination is, therefore, likely to contribute to the high
212 interaction levels observed at Crozet, which, with 7 vessels operating in an EEZ of 17,900 km², hosts
213 one of the largest fleets and one of the smallest fishing areas of the Southern Ocean.

214 Interestingly, increased density of vessels in fishing areas was associated with decreased sperm
215 whale and killer whale interactions at the individual vessel level. This effect may result from a limited
216 number of depredating specialist individuals which, once they have found a vessel, may keep
217 interacting with its fishing gear until this vessel leaves and travels over distances sufficiently large to
218 outrun the whales. Consequently, increased numbers of vessels operating simultaneously in the same
219 region may generate a “dilution” effect decreasing the level of whale interaction per vessel⁴⁹.

220 Greater vessel mobility was associated with decreased interaction levels for killer whales.
221 Increased vessel mobility may reduce interaction levels either by limiting the

222 detectability/predictability of vessels prior to interactions and/or by working as an effective strategy to
223 outrun depredating whales in response to the occurrence of interaction events⁴⁹⁻⁵¹. However, for
224 sperm whales, greater mobility of vessels was associated with higher interaction levels. Firstly, this
225 result may be due to an ineffectiveness of vessels of avoiding interactions by being mobile because of
226 naturally large densities of sperm whales overlapping with areas of fishing operations. Varying
227 densities of sperm whales across areas used by different fisheries may also explain the significance of
228 the fishery-mobility interaction terms in models. For instance, vessels were more mobile at Crozet and
229 Kerguelen than in any of the other fisheries, but these two areas were recently described as hosting
230 densities of depredating sperm whales substantially larger than densities of killer whales^{17,52}. In such
231 areas, the probabilities of interaction with any sperm whale may be high across large proportions of
232 fishing areas and vessels may, therefore, experience high levels of interaction regardless of their
233 mobility. Secondly, this result may also be explained by sperm whales actively following vessels, and
234 vessels not moving on distance great enough to outrun these whales. In a recent study, Janc et al.
235 (2018) showed a drop in the probability of sperm whale interaction when vessels travelled over a
236 range of 40 to 60 km between sets. While this distance is lower than the distance estimated for killer
237 whale (100 km⁴⁹), it is likely that vessels are less incline to implement costly strategies of avoidance
238 of sperm whales given the lower impact of that species on catch rates compared to that of killer
239 whales^{15,26}.

240 Interestingly, the use of trotline equipped with cachalotera, a fishing system designed to prevent
241 whales from accessing fish caught on longlines³¹, did not significantly influence the level of killer
242 whale-vessel interactions, and was associated with higher levels of sperm whale-vessel interactions.
243 Therefore, it is unlikely that the significant decrease in both sperm and killer whale interaction levels
244 observed in Chile since 2006, when vessels switched from the autoline to the trotline and the
245 cachalotera system^{22,31}, may be attributed to that change in fishing system. While cachaloterias may
246 increase the difficulty for whales to remove fish from hooks^{53,54}, this study suggests that whales still
247 gain benefit from feeding off longlines equipped with such a system. In addition, if cachaloterias are
248 effective means to lower depredation and maintain high catch rates, vessels may be more likely to stay
249 and keep fishing despite the presence of depredating sperm whales, further increasing interactions

250 with this species. Further research is therefore needed to identify the causes of the decrease in killer
251 and sperm whale interactions in the Chilean fishery. As this fishery has undergone substantial
252 decreases in both quotas and fleet size⁵⁵, it is possible that lower numbers of vessels paired with the
253 implementation of fishing strategies being more effective in avoiding depredation have contributed to
254 this decrease.

255 Part of the variability in interaction rates across fisheries was due to unexplained area-specific
256 factors. The importance of such local factors was further emphasized by different levels of correlation
257 between the spatial spread of interactions and the spatial spread of fishing operations between
258 fisheries. Spatial variations in the natural presence and density of whales in the Southern Ocean are
259 likely to contribute to these differences. The depth at which longlines were set on the seafloor had a
260 negative influence on the levels of both killer and sperm whale interactions with vessels, suggesting
261 that depredating individuals in the Southern Ocean may be generally naturally distributed on the
262 shallowest part of the bathymetric range used by fishing vessels. However, the natural distribution of
263 the depredating whales is likely to be influenced by a number of other habitat drivers that have
264 characteristics which may differ between areas where fisheries operate. For instance, the distribution
265 of mature male sperm whales at high latitudes was found to be highly correlated with oceanographic
266 variables, such as frontal zones, bathymetric slope and primary productivity likely to drive the
267 abundance and availability of their natural prey items^{41,43,44}. These prey items may include Patagonian
268 toothfish but also cephalopods, a resource with a distribution and abundance that is highly influenced
269 by oceanographic processes. The variability of these processes across the Southern Ocean⁵⁶ may,
270 therefore, greatly influence the degree of overlap between sperm whales and fishing operations.

271 Among other unexplained area-specific factors, local ecological specializations may also influence
272 the natural distribution patterns and movements and, therefore, the degree of overlap of whales with
273 fishing operations. Such specializations have been extensively described across killer whale
274 populations, including among those involved in interactions in the Southern Ocean^{57,58}. For instance,
275 killer whales interacting with fisheries are all fish specialists or generalist foragers whereas
276 individuals feeding exclusively on marine mammals have never been observed undertaking this
277 behaviour^{14,59-61}.

278 Finally, the probability of whales to switch from natural foraging to depredation may also depend
279 upon the level of experience to this behaviour and, therefore, on the history of the fisheries and the
280 number of years whales have been exposed to fishing operations⁶². Depredation is assumed to be a
281 learnt artificial behaviour and likely transmitted across individuals of populations through social
282 pathways⁶². As such, and paired with natural individual heterogeneity in foraging behaviours, the
283 experience of depredating whales, their propensity to find/follow vessels and to efficiently remove
284 fish from longlines may vary between fisheries.

285

286 In summary, sperm whale and killer whale interaction with Patagonian toothfish fishing vessels is
287 a widespread and established issue in the Southern Ocean. The drivers of these interactions include
288 the spatio-temporal patterns of fishing operations and the extent to which these operations give
289 opportunities for whales to feed on fish caught on fishing gear. Changing the simple operational
290 aspects of fishing could, therefore, mitigate the issue. However, further research is needed to identify
291 the factors driving whale habitat selection, distribution, movements and the mechanisms leading these
292 whales to switch from natural foraging to depredation interactions. These drivers, which depend upon
293 the ecology of local whale populations, could be used to better predict the occurrence of interactions
294 and may, therefore, be used to implement effective strategies of avoidance in the future.

295

296 **Methods**

297

298 *Data collection and standardisation*

299

300 Fishing and whale interaction data from the seven study fisheries were collected by fishery
301 observers and/or crews over periods ranging from 3 to 14 years. These fisheries are all fully controlled
302 by local and/or international (Commission for the Conservation of Antarctic Marine Living Resources
303 – “CCAMLR”) management authorities and all fishing operations are monitored. Data from Chile and
304 the Falklands, although not under the CCAMLR supervision, were collected by fishery observers
305 following protocols based on those used by CCAMLR observers in the other fisheries of the study.

11

306 Data from all vessels legally operating in these fisheries and all fishing trips of these vessels were
307 therefore accessed for the study. In all fisheries, the base unit was the longline set *i.e.* a mainline
308 bearing series of hooks (autoline) or clusters of hooks (trotline) with, at each end, one anchor at the
309 bottom connected to a buoy at the surface by a downline. For each longline set, fishery observers
310 and/or crews collected the same data on the date and time, as well as GPS coordinates, at setting (*i.e.*
311 deployed at sea) and at hauling (*i.e.* retrieved and landed on-board), in the same way in all seven
312 fisheries.

313

314 The occurrence of whale depredation interactions with longline sets was recorded during hauling
315 operations by visual cues. An interaction was confirmed when one of these two species, or the two
316 species co-occurring with a typical depredation behaviour were sighted within a 500 m range from the
317 vessel. During depredation, individuals made repeated dives towards the line being hauled and
318 throughout the hauling process, they were usually surrounded by birds when surfacing after long
319 dives, and slicks of fish oil were visible at the surface. When all these cues were observed, true
320 depredation interaction events (recorded as 1) were monitored in a standardised way across all
321 fisheries. However, only the Crozet, Kerguelen and South Georgia fishery observers distinguished
322 between longline sets with confirmed non-occurrence of depredation (recorded as 0) and sets with
323 lacking information due to insufficient or impossible monitoring effort (recorded as "N/A") caused by
324 poor weather (e.g. fog), sea or light conditions. As Chile, Falklands and HIMI recorded zeros for sets
325 with either a true non-occurrence of depredation and/or a set for which the occurrence of depredation
326 was unknown, we consider all the Crozet, Kerguelen and South Georgia sets with N/A's as zeros for
327 the sake of between-fisheries standardisation needed for this study. As a result, the estimates of
328 depredation should be considered as minimum estimates.

329 Differences in spatial and temporal frequencies of killer whale and sperm whale interactions were
330 estimated using two indices, which were both calculated annually for each fishery per vessel (one
331 value for each vessel that operated in a given fishery during a given year), and per fleet (one value for
332 all data collected in a given fishery during a given year regardless of the vessel identity). Firstly, we
333 calculated the proportion of fishing days (days of hauling operations only) with a minimum of one

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334 depredated longline set during the day out of all fishing days per year ($Pr(days)$). Secondly, we
335 calculated a proportion of the fishing area for which depredation interactions occurred as the number
336 of 0.1° latitude x 0.1° longitude cells in which a minimum of one longline set was depredated out of
337 the total number of cells in which fishing occurred ($Pr(area)$).

338

339 *Statistical analyses*

340

341 Annual trends of whale-fishery interaction levels over the study periods were examined using
342 linear regressions. PEMI was excluded from this analysis due to the limited time series ($n = 3$ years of
343 data) available for that fishery. Trends were tested on $Pr(days)$ calculated per vessel (several values
344 per year depending on the number of vessels) or per fleet (a single value per year), separately for
345 killer whales and sperm whales, in each fishery and across all fisheries. In addition, a regression
346 analysis was conducted to investigate the inter-annual changes in $Pr(area)$ in relation to inter-annual
347 changes in the spatial spread of the fishing effort. For this analysis $Pr(area)$ was calculated annually
348 as a cumulative number of new $0.1^\circ \times 0.1^\circ$ cells in which interactions occurred every year, out of the
349 total number of $0.1^\circ \times 0.1^\circ$ cells fished during the respective study periods in the respective fisheries.
350 The spatial spread of fishing effort was calculated annually as the cumulative number of new $0.1^\circ \times$
351 0.1° cells in which fishing occurred every year, out of the total number of $0.1^\circ \times 0.1^\circ$ cells fished
352 during the respective study periods in the respective fisheries.

353

354 The influence of fishing operations on $Pr(days)$ was investigated using Generalised Linear Models
355 (GLMs). GLMs were developed for each species at both the vessel (using individual $Pr(days)$ values
356 per vessel per year per fishery) and the fleet (using individual $Pr(days)$ values per year per fishery)
357 levels. As fisheries differed in fleet size and study periods, the number of $Pr(days)$ values per vessel
358 per year varied between fisheries and ranged from 1.5 ± 0.3 vessels per year ($n = 5$ values) in PEMI to
359 8.4 ± 0.8 ($n = 109$ values at South Georgia, Table 3).

360 A series of binomial GLMs with logit link functions were fitted using the function `glm` in R 3.3.0⁵⁹ to
361 the proportion of total fishing days for each vessel, in each year (Table 3) where depredation was

13

362 observed. To account for variability in the number of days each vessel/fleet fished the total number of
363 days fished each year was used as the model weights (i.e. equivalent to using the *weights* argument in
364 the *glm* function in R) for each vessel/fleet. The fishery was included in models as a categorical
365 variable with seven levels for each of the studied fisheries, with Chile being the fishery compared to
366 each one of the others. The other predictors included were all continuous and were calculated as
367 annual values, either at the vessel or at the fleet level, as follows i) the spatial spread of fishing effort
368 calculated as the total number of 0.1° x 0.1° spatial cells in which at least one set was hauled by
369 vessels; ii) the mean density of vessels per fishing day, calculated as the mean number of different
370 vessels operating during the same day in the same fishery out of the spatial spread of fishing effort
371 previously calculated; iii) the seasonal spread of fishing effort, measured as the proportion of fishing
372 days during winter months (from 1 June to 31 Aug) out of all fishing days during a given year; iv) the
373 mobility of vessels, calculated as the ratio between the spatial spread of fishing effort and the total
374 number of fishing days during a given year; v) the mean depth at which longlines were set; and vi) the
375 fishing system, calculated as the proportion of sets using trotlines equipped with cachalotera out of all
376 sets (Table 3). In addition to the single predictors described above, we also tested an interaction
377 between fishery and mobility, when both were present in the optimal model. Collinearity between
378 continuous predictors was checked using Pearson tests and predictors were retained if $r < 0.8$ (Table
379 S3). All continuous predictors were centred then scaled using the *scale* function in R and variable
380 selection was conducted using stepwise forward selection of models with the lowest Akaike
381 Information Criterion (AIC)⁶³. When multiple models were within 2 AIC of the model with the lowest
382 AIC (i.e. the optimal model) we considered all of them. The proportion of the total variance explained
383 was quantified for each model using the pseudo r^2 statistic⁶⁴. Model estimates are presented as
384 probabilities with 95% confidence intervals by applying an inverse logit transformation.

385

386 *Data availability*

387

388 The datasets generated during and/or analysed during the current study are available from the
389 corresponding author on reasonable request.

390 *Guidelines and regulations*

391

392 All methods were carried out in accordance with relevant ethical guidelines and regulations of Deakin

393 University, Australia. Data used in this manuscript were collected by fishery observers under the

394 authority of CCAMLR in EEZs of South Georgia, PEMI, Crozet, Kerguelen and HIMI, Instituto de

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396

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- 553

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555

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566

567 **Author Contributions Statement**

568

569 P.T., P.B., G.R., K.O. and J.A. conceived the study. P.T. performed the primary analysis. P.T., P.B.,
570 G.R., K.O., D.W., M.A.L., M.H., C.G., A.J., N.G., G.D., M.C. V., L.S., R.A. and J.A. were involved
571 in developing the manuscript and P.T. took a lead role in writing.

572

573 **Competing interests**

574

575 The authors declare that they have no financial or non-financial competing interests.

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589 **Figure legends**

590

591 Figure 1. Location of the Exclusive Economic Zones in which the seven commercial Patagonian
592 toothfish demersal fisheries used in the study operate in the Southern Ocean.

593

594 Figure 2. Between-fisheries variations of whale-vessel interaction levels in the Southern Ocean.

595 Boxplots were calculated from *Pr(days)* and *Pr(area)* observed values per vessel per year in fisheries
596 for a. sperm whales and b. killer whales.

597

598 Figure 3. Observed annual variations of a. sperm whale and b. killer whale interaction levels with
599 fisheries. Interaction levels (*Pr(days)*) were calculated as a proportion of fishing days during which at
600 least one interaction was recorded out of all fishing days in a year, at the vessel level (mean \pm SE per
601 vessel per year, points and solid lines) and at the fleet level (dashed lines). Equations and r^2 values of
602 the linear regressions conducted at the fleet level (upper line) and at the vessel level (lower line) are
603 also provided for each plot.

604

605 Figure 4. Relationship between the spatial spread of fishing effort and the spatial spread of whale-
606 vessel interactions in fisheries (*Pr(area)*). The spatial spread of fishing effort and whale vessel
607 interactions were calculated as the cumulative proportion of $0.1^\circ \times 0.1^\circ$ cells over the full fished area
608 in which fishing occurred and interactions were recorded, respectively, per year per fishery for sperm
609 whales (grey) and killer whales (black). Linear regression equations are shown for each species and
610 fishery.

617 **Tables**

618

619 Table 1. Parameter estimates for the optimal GLMs fitted to yearly sperm whale interaction levels
 620 with fishing vessels in fisheries through index $Pr(days)$ at both the vessel and fleet level. Parameter
 621 estimates are presented as probabilities relative to the Chilean fishery which was the default fishery in
 622 all models. Covariates with interaction probabilities higher than the Chilean fishery are associated
 623 with an increase in whale interactions while those with lower with interaction probabilities are
 624 associated with a reduction in whale interactions.

Predictors	Vessel level			Fleet level		
	Est. [95% CI]	z	P	Est. [95% CI]	z	P
Fishery						
<i>Chile</i>	0.59 [0.55-0.63]	3.99	<0.01	0.99 [0.98-0.99]	12.57	<0.01
<i>Crozet</i>	0.66 [0.61-0.71]	2.56	0.01	0.78 [0.61-0.89]	-7.74	<0.01
<i>Falklands</i>	0.39 [0.35-0.43]	-9.35	<0.01	0.76 [0.59-0.87]	-8.85	<0.01
<i>HIMI</i>	0.06 [0.05-0.08]	-19.77	<0.01	0.12 [0.06-0.24]	-16.30	<0.01
<i>Kerguelen</i>	0.67 [0.61-0.71]	2.75	0.01	0.82 [0.71-0.90]	-8.85	<0.01
<i>PEMI</i>	0.04 [0.03-0.07]	-13.36	<0.01	0.14 [0-0.85]	-3.54	<0.01
<i>South Georgia</i>	0.36 [0.31-0.42]	-7.79	<0.01	0.63 [0.41-0.80]	-9.11	<0.01
Total size of fishing area	0.48 [0.46-0.50]	-11.50	<0.01	0.99 [0.98-0.99]	-2.65	0.01
Density of vessels	0.57 [0.56-0.59]	-2.09	0.04	0.99 [0.99-0.99]	3.75	<0.01
Mobility of vessels	0.70 [0.67-0.72]	8.19	<0.01	1.00 [1.00-1.00]	9.85	<0.01
Depth	0.58 [0.57-0.59]	-2.13	0.03	0.99 [0.99-0.99]	-5.29	<0.01
Proportion of effort in winter	0.56 [0.54-0.57]	-5.34	<0.01	0.99[0.99-0.99]	-3.30	<0.01
Proportion of effort using trotlines and cachalotera	0.62 [0.61-0.62]	5.52	0.00	0.99 [0.99-0.99]	1.95	0.05
Fishery * Mobility of vessels						
<i>Crozet</i>	0.49 [0.45-0.53]	-5.08	<0.01	0.74 [0.55-0.81]	-8.18	<0.01
<i>Falklands</i>	0.50 [0.46-0.55]	-4.08	<0.01	0.89 [0.79-0.94]	-6.38	<0.01
<i>HIMI</i>	0.57 [0.46-0.66]	-0.48	0.63	0.82 [0.70-0.90]	-8.38	<0.01
<i>Kerguelen</i>	0.49 [0.46-0.52]	-6.10	<0.01	0.75 [0.60-0.86]	-9.57	<0.01
<i>PEMI</i>	0.30 [0.20-0.42]	-4.36	<0.01	0.77 [0.14-0.99]	-2.16	0.03
<i>South Georgia</i>	0.49 [0.45-0.53]	-5.16	<0.01	0.84 [0.71-0.92]	-7.13	<0.01

625

648

649 Table 2. Parameter estimates for the optimal GLMs fitted to yearly killer whale interaction levels with
 650 fishing vessels in fisheries through index $Pr(days)$ at both the vessel and fleet level. Parameter
 651 estimates are presented as probabilities relative to the Chilean fishery which was the default fishery in
 652 all models. Covariates with interaction probabilities higher than the Chilean fishery are associated
 653 with an increase in whale interactions while those with lower with interaction probabilities are
 654 associated with a reduction in whale interactions.

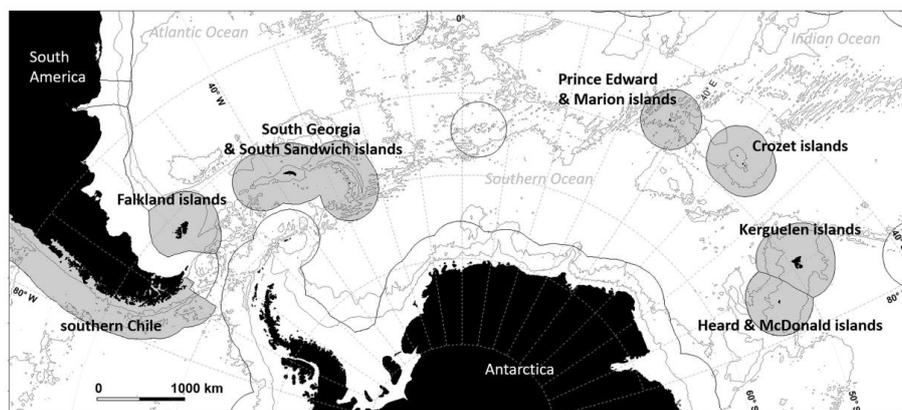
Predictors	<i>Vessel level</i>			<i>Fleet level</i>		
	Est. [95% CI]	z	P	Est. [95% CI]	z	P
Fishery						
<i>Chile</i>	0.31 [0.28-0.35]	-9.37	<0.01	0.66 [0.61-0.70]	6.37	<0.01
<i>Crozet</i>	0.37 [0.32-0.42]	2.15	0.03	0.63 [0.56-0.70]	-0.78	0.44
<i>Falklands</i>	0.02 [0.01-0.02]	-23.25	<0.01	0.05 [0.04-0.06]	-25.23	<0.01
<i>HIMI</i>	0.00 [0.00-1.00]	-0.04	0.97	0.00 [0.00-1.00]	-0.02	0.98
<i>Kerguelen</i>	0.01 [0.01-0.02]	-16.46	<0.01	0.01 [0.01-0.02]	-24.98	<0.01
<i>PEMI</i>	0.09 [0.07-0.12]	-8.54	<0.01	0.23 [0.18-0.29]	-12.03	<0.01
<i>South Georgia</i>	0.08 [0.07-0.10]	-14.19	<0.01	0.28 [0.23-0.33]	-11.51	<0.01
Total size of fishing area	0.17 [0.15-0.19]	-11.43	<0.01	NS		
Density of vessels	0.26 [0.24-0.27]	-6.78	<0.01	0.68 [0.66-0.70]	2.51	0.01
Mobility of vessels	0.28 [0.26-0.30]	-2.70	0.01	NS		
Depth	0.26 [0.25-0.27]	-8.51	<0.01	0.58 [0.56-0.61]	-5.79	<0.01
Proportion of effort in winter						
		NS			NS	
Proportion of effort using trotilines and cachalotera						
Fishery * Mobility of vessels						
<i>Crozet</i>	0.33 [0.29-0.36]	0.72	0.47			
<i>Falklands</i>	0.42 [0.35-0.49]	2.90	<0.01			
<i>HIMI</i>	0.36 [0.00-1.00]	0.00	1.00			
<i>Kerguelen</i>	0.40 [0.31-0.51]	1.79	0.07			
<i>PEMI</i>	0.36 [0.27-0.45]	0.94	0.35			
<i>South Georgia</i>	0.36 [0.32-0.41]	2.18	0.03	NS		

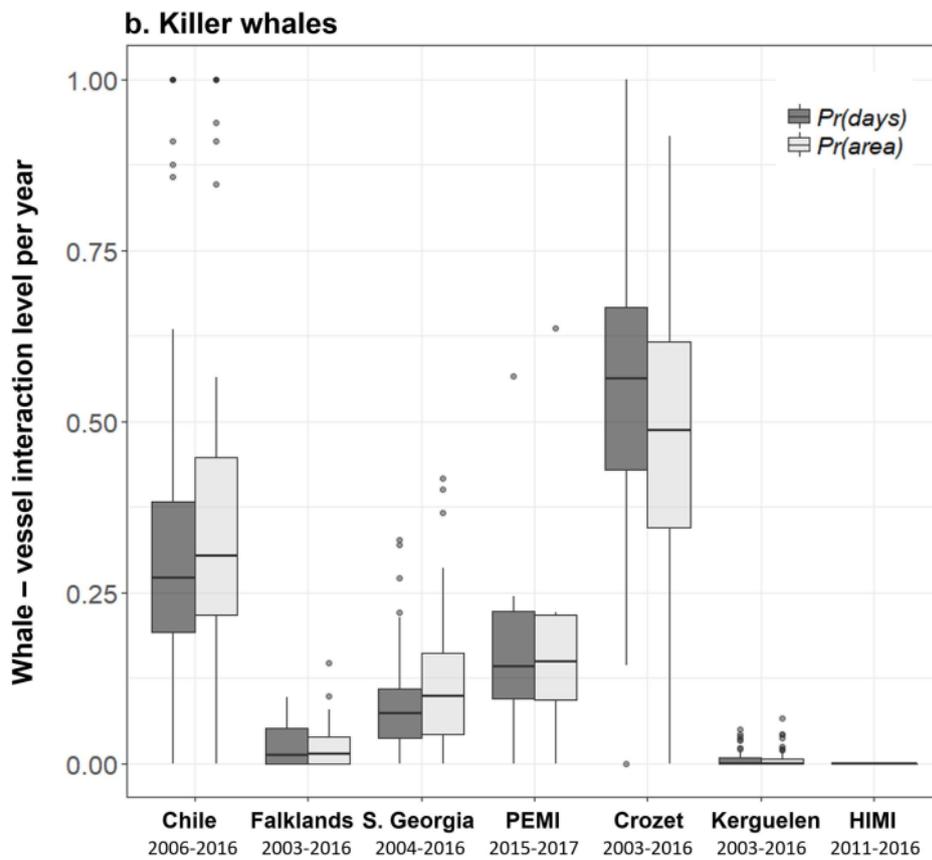
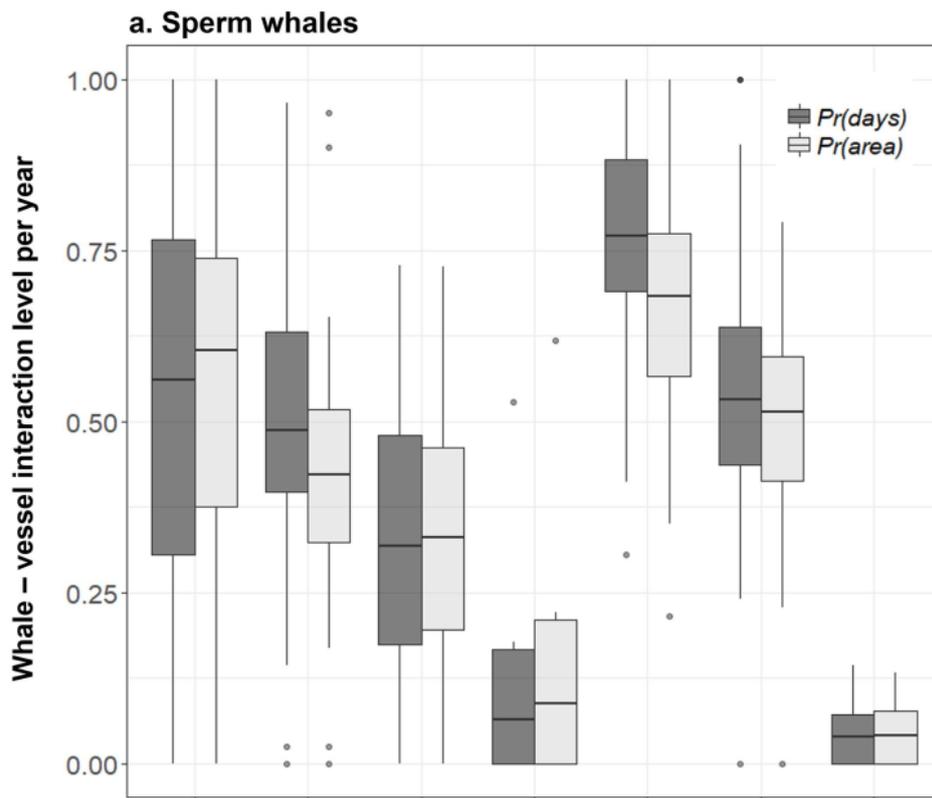
655

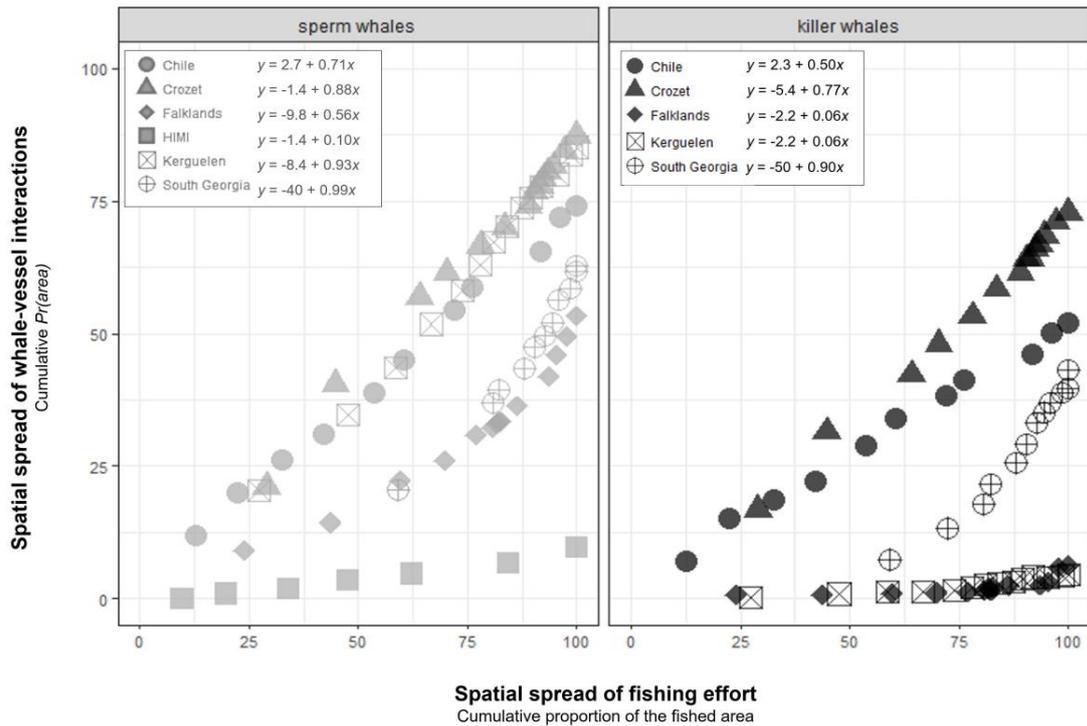
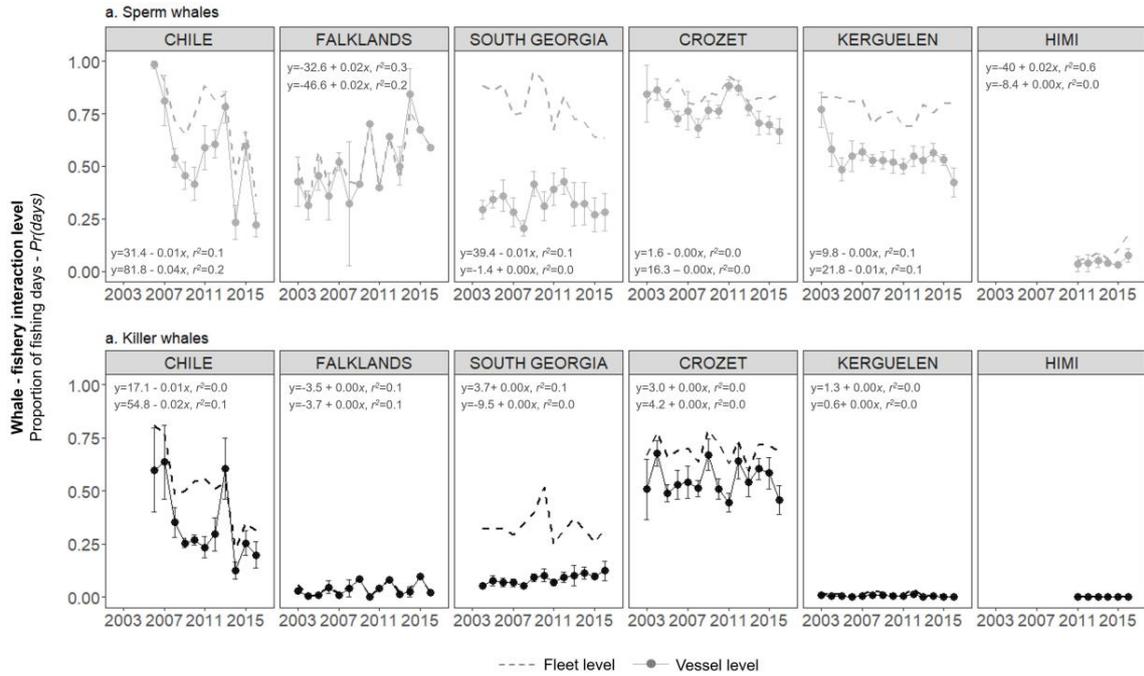
656 Table 3. Summary of terms used as fishing patterns variables and considered in GLMs fitted on the
 657 level of whale-vessels interaction levels. Mean \pm SE per vessel per year are here presented for each of
 658 the seven studied Patagonian toothfish fisheries of the Southern Ocean. N_{total} (total number of vessel
 659 per year values), the mean and the range of the number of vessels operating in fisheries per year are
 660 provided.

	Unit	Chile	Falkland s	South Georgi a	PEMI	Crozet	Kerguele n	HIMI
Term		$N_{total} = 60$	29	109	5	96	102	20
	vessels per year	mean = 5.5 ± 0.5 range = [3-8]	2.1 ± 0.4 [1-6]	8.4 ± 0.8 [6-16]	1.5 ± 0.3 [1-2]	6.9 ± 0.2 [5-8]	7.3 ± 0.2 [7-9]	3.3 ± 0.6 [2-6]
<i>Fishing effort</i>	n days	116 ± 9	101 ± 11	75 ± 2	83 ± 19	38 ± 2	131 ± 3	128 ± 8
<i>Spatial spread of effort</i>	n $0.1 \times 0.1^\circ$ cells	308 ± 12	248 ± 15	303 ± 3	127 ± 19	205 ± 4	750 ± 10	450 ± 37
<i>Density of vessels</i>	n vessels / 100 cells	1.04 ± 0.05	0.59 ± 0.05	2.00 ± 0.04	1.04 ± 0.2	1.19 ± 0.05	0.06 ± 0.02	0.06 ± 0.02
<i>Seasonal spread of effort</i>	proportion of days in winter	0.03 ± 0.02	0.24 ± 0.04	0.63 ± 0.02	0.31 ± 0.09	0.16 ± 0.02	0.10 ± 0.01	0.47 ± 0.05
<i>Mobility of vessels</i>	n cells / day	0.87 ± 0.03	1.2 ± 0.05	0.85 ± 0.02	1.07 ± 0.12	1.55 ± 0.03	1.43 ± 0.03	1.02 ± 0.04
<i>Depth of sets</i>	meters	1580 ± 20	1341 ± 25	1248 ± 14	1339 ± 43	1099 ± 19	1186 ± 14	1311 ± 51
<i>Fishing technique</i>	proportion of sets with trotline & cachaloter a	0.88 ± 0.04	0.48 ± 0.09	0 ± 0	0.52 ± 0.17	0 ± 0	0 ± 0	0 ± 0

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APPENDIX 7 – LENNERT AND RICHARD (2017)

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At the cutting edge of the future: Unravelling depredation, behaviour and movement of killer whales in the act of flexible management regimes in Arctic Greenland



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ABSTRACT

Fisheries are an important resource in many countries, across oceans and along coasts, and, even though it is usually neglected, they bring not only economic value with them but also social value, supporting an important web of cultural practices. Thus, any perturbation on the fish resources may cause a domino effect on both ecosystem and human populations. In this paper we focus on a marine mammal which is entering the Arctic in increasing numbers, the killer whales (*Orcinus orca*), a major predator that may not only reshape the rapidly changing marine ecosystems via top-down forcing but also affect fisheries and cultural costumes through a specific, socially transmitted behavioural factor: depredation. By assessing the current knowledge of the depredation issue at a global scale as well as the studies of killer whales in the North Atlantic and Arctic waters, we discuss whether an eventual emerging depredation on halibut fisheries in Greenlandic waters should be taken into consideration. We stress a more flexible and cutting edge management regime on the forefront of environmental change and future scenarios. We accentuate an increased recognition of wildlife management also including an understanding of people and that success will be determined largely by political, social and cultural factors. Finally, we conclude that Greenland, being on the cutting edge of change, has high potentiality for building research based on a co-production of knowledge of both natural science and traditional knowledge.

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1. Introduction

As emphasized in a new AMAP report (Jacobsen et al. forthcoming) as well as by work done by Delaney et al. (2012), fisheries are an important resource in many countries, across oceans and along coasts. Besides, even though it is usually neglected, the industry brings not only economic value with it but also social value. In northern Greenland as well as settlements along the coasts of West and East Greenland, fisheries are an integral part of the land-based activities that hold these social and cultural values. Fishing, processing, distributing and consuming local fish link people to their history and their present cultural settings. Living through subsistence fishing, hunting and through

an informal economy, these activities maintain individual well-being and social relationships and help define a sense of family and community (Nuttall, 2005). Fishing supports an important web of cultural practices, meeting social obligations as well as social relations due to its strong links to support hunting activities. In a mixed economy, which the majority of these settlements depend on, the small-scale fisheries serve as an ad hoc to cover expenses relating not only to fishing but also hunting and gathering for subsistence and cultural purposes (Delaney et al., 2012, Hendriksen and Jørgensen, 2015, Jacobsen et al. forthcoming), conducted with longlines— either by boat, by dog sledges (Fig. 1.) or snowmobiles.

Fisheries play a significant role in Greenland's national economy, producing over half of the total service and good export value, 57% of 4.2 billion in 2011 (Copenhagen Economics, 2013), financing the emergent welfare state and supporting national independence (Jacobsen et al. forthcoming). Consequently, a change of resource or a disturbance to the fisheries may not only have an impact on the

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Fig. 1. Hunter fishing with longline from the ice (Photo: Bjørn Stig Hansen).

national economy but also regional impacts on communities, cultures, social relations and well-being, which are of at least as imperative importance.

In the face of climate change, significant changes in biodiversity, movement of ecosystems, introduction of new species and increase in population of others pose a potential threat. Therefore, it is of the outermost importance to be prepared, to foresee and predict, and to learn from and be educated by scenarios as well as impacts and disturbances seen elsewhere, including potential readjustment of species distribution and abundance in the new open waters of the Arctic. Conservation programs and management regimes generally focus on the ecological and behavioural aspects of species and ecosystems, but there is an increasing recognition that wildlife management also includes an understanding of people (Decker et al., 2006) and that success will be determined largely by political, social and cultural factors (Clark et al., 1996; Clark and Rutherford, 2005; Decker et al., 2006; Bruskotter and Shelby, 2010; Westdal et al., 2013). Additionally, as the locals encompass knowledge from year-around surveillance and movement in a regional environment, it is important to build on their knowledge, their interactions with the environment and observations of animal behaviour, movement, variations, and changes to be able to meet the right and most precise management of resources.

In this paper, we wish to focus on a marine mammal which is entering the Arctic in increasing numbers, the killer whales (*Orcinus orca*); a major predator that may not only reshape the rapidly changing marine ecosystems via top-down forcing (Trites et al., 2006; Springer et al., 2008; Higdon and Ferguson, 2009; Higdon et al., 2012) but also affect fisheries through socially transmitted behavioural factors, such as depredation (Donoghue et al., 2003; Hamer et al., 2012). An increasing number of interaction incidents between marine mammals and fisheries have been reported throughout the world's oceans (Northridge and Hofman, 1999). The increasing numbers are not only due to more and wider anthropogenic movement but also caused by climate change and change of ocean currents. Among these conflicts fish depredation, defined as the removal of fish from lines by marine mammals, represents a worldwide major issue. Depredation has several consequences, such as socio-economic, including losses for fishers, and conservation complications for both marine mammals (risk of injuries and mortality, modification of energy balance, and foraging behaviour with new and easy prey sources) and for fish resources (losses due to depredation are mostly not accounted for in quota allocation processes and neither in stock assessments). These negative impacts stem from a marine mammal increasing in numbers, as well as interactions between fishermen and the killer whales (Orcas).

This observed behavioural trend might pose an immense threat to the cultural practices, the well-being of communities and the national economy. On the other hand, interactions with fisheries may have important conservation issues both for killer whales, due to a higher risk of mortality and a modification of energy balance by giving access to new prey sources, and for fish stocks, since the combination of both human and whales foraging may lead to an overexploitation to the stocks. Besides, at a larger scale we may expect disturbance of the ecosystem. Furthermore, in this study we emphasize that it is of significant importance to keep an eye open and collaborate in knowledge production – even though research may be conducted in areas that are spatially far apart, the problems they are facing are relatively close – in this way being at the forefront of developing both baseline data and feasible mitigation strategies towards the problem of depredation, which most likely will occur as ecosystems and environmental settings change. Thus, we advocate through our study that, thanks to the different knowledge, we might be able to anticipate the issue and take measures to avoid depredation to happen on Greenlandic fisheries. Indeed, prevention is better than cure, and as we observe at a worldwide scale solution, are difficult to implement.

We structure our reflection around a first statement of changing conditions in Greenland with the increasing number of killer whales observed, and then around a second statement about depredation at a worldwide scale. From these both statements, we finally discuss the impact of a possible depredation in Greenland, aiming on suggesting possible means to avoid this phenomenon.

2. Methods

This study is built on an ongoing PhD project at The Greenland Institute of Natural Resources and Climate Research Centre and a PhD project being conducted at the Centre d'Etudes Biologiques de Chizé (CNRS & Université de La Rochelle), France. It builds on natural and social sciences, as well as traditional knowledge. Moreover, it uses both a review of selected studies covering depredation seen around the Crozet Archipelago, as well as studies from the North Atlantic supplementing this review with local and traditional knowledge of killer whales, local perceptions, depredation, and encounters across the Arctic. This co-production of knowledge gives a divination and appliances to eventually meet both anthropogenic and marine ecosystem-based disturbances caused by more killer whales entering the Arctic ecosystems.

The local and traditional knowledge presented was collected through travels in Greenland and obtained by participant observations, informal interviews, and a notion of conversational

interviews with family, friends, local hunters and elders. Elements relevant for this study were coupled with the extensive review of selected studies covering depredation seen around the Crozet Archipelago, as well as studies from the North Atlantic, to meet the questions of contemporary concern presented.

Hereby, the study strives to meet the problems and solutions in relation to depredation of longline fisheries, which most likely will become a problem in Arctic Greenland. It serves as an eye opener and encourages how solutions may be found – meeting the local communities, quota allocation processes and stock assessments, co-management, the conservation complications and the well-being of the involved marine animals and humans – and, not least, to be prepared.

3. The new lead actor of the Arctic

Since the 1950s, the atmosphere and ocean have warmed unprecedentedly, leading to a decrease of the global amount of ice, to an increase of the sea level, and thus to multiple changes in ecosystems (IPCC, 2013). Based upon this warming up, predictions suggest that the Arctic sea ice cover will continue to shrink until the end of the 21st century, with an overall 94% surface reduction in the worst scenario. Consequently, former basins are now opening up, previously having been cut off. The effects, such as declining sea ice and warming, are likely to initially cause shifts in marine mammals' range and abundance. The killer whale has occasionally been hunting along ice edges and leads (Reeves and Mitchell, 1988) but typically avoiding heavy ice concentrations. The declining ice has now set the scene for a new lead actor, allowing the killer whale to penetrate farther into the Arctic environment and stay for longer periods of time (Higdon and Ferguson, 2009).

Thus, there have been made a large amount of studies on killer whales' distribution, behaviour and prey in Arctic Canada and Alaska (Laidre et al., 2006; Matthews et al., 2011; Higdon et al., 2012, 2014; Reinhart et al., 2013; Peterson et al., 2013; Higdon et al., 2014; Matthews and Ferguson, 2014). However, studies of this species along the coasts of Greenland are few (Jefferson et al., 1991; Higdon, 2007). Today only few abundance estimates, set by hunting reports and observations, set the basis of this knowledge (Lennert, 2016). Local observations, hold an important message of this species, and have to be exploited, as well as taken into account. Sightings of these whales have been increasing not only around Alaska and eastern Canada but also along the coasts of Greenland. The Ministry of Hunting, Fishing and Agriculture has experienced a significantly increasing rate in hunting of killer whales (Table 1). From being a rare hunting activity, it has now become regular, reflecting a change in abundance (Arvid-Rosing, 2013).

“There has come more Killer Whales along the east coast, and we have begun to take advantage of this. I was out on the first hunt where we were guided with knowledge of the animal, the hunt, the animals' movements, signals and reactions, through the VHF radio as the hunt went on (Fig. 2)”.

Per, hunter from Tasilaq

As this new lead actor has entered, minke whales have almost disappeared from certain areas, which also explains the more excessive hunt of the killer whale. The effects of the killer whale reshaping the rapidly changing Arctic ecosystem are already occurring and might occur in a more tenacious manner.

“This summer I was hunting narwhals together with local hunters in Qaanaaq. We caught a narwhale which's back was broken and the tale was crooked. The hunters began telling about a narwhale

where there had been taken a huge bite or lump from its neck area. They also said it had been a strange year. The narwhals' behaviours have been strange. They are “aalerivoq” nervous because of “aarluk” the killer whales that increased in numbers up north”

Lene Nielsen Holm, researcher from GCRC

This marine predator is known to consume a broad range of prey including mammals, fish and birds. However, in other regions, it is known to have a high level of dietary specialization, consuming a specific and narrow range of prey (Bigg et al., 1987, 1990; Guinet, 1992; Ford et al., 1998, 2011; Pitman and Ensor, 2003; Foote et al., 2009; Ford et al., 2011; Higdon et al., 2012, Foote, 2012; Foote et al., 2014). As this paper reflects, through depredation it might become a serious competitor to the Inuit fishermen and hunters of Greenland. A recent study revealed how the depredation by marine mammals might be perceived as a strong competition by fishermen and that it impacts their fishing strategies (Richard et al., 2017). A shift of fishing behaviour may lead to both economic and ecological issues. Competition would increase the foraging effort, and so the costs, for fishermen with a similar or even a lower payback than without killer whales (Peterson et al., 2014). As fishermen are optimal foragers, we assume they would harness their environment in a short-term goal of energy maximization (Begossi, 1992; Aswani, 1998; Richard et al., 2017). This may result as an increase of the fishing effort on a ground in absence of killer whales at the expense of the patch quality, with a threat of fishing stock depletion.

Inuit throughout the Arctic have a complex relationship with killer whales. Killer whales are disliked because they drive other marine mammals away (Higdon, 2007; Westdal et al., 2013) and blamed for declines in harvested species (e.g. Wilkinson et al., 1995). Statements are conflicting but generally view killer whales as competition for food resources:

“When killer whales come too close to the coast, we usually sail out and fire a rifle to scare them off”.

Hunter from Sisimiut

One can question if this relationship and tactic of scaring off killer whales has deeper roots of “packaged knowledge” from when killer whales in the past have been a competition with the hunters because of a larger abundance than today, as the Greenlandic Inuit philosophy of animal behaviour is already linked to this predator. *Aarluk* is the Greenlandic word for Orcas and when speaking of other animals that are either very shy, nervous, escaping or have disappeared –it grammatically and philosophy is linked to *Aarluk* even though it may be another predator or environmental setting doing the impact. *Aarluppai -the Orca has scared the animals away, aalerivoq-is nervous because of Orcas* or the term *aarluppoq -is escaping from Orcas*, are used in the description of behavioural changes. On the other hand, statements and perceptions considering them helpful, making hunting easier for the Inuit, also occur:

“Killer whales sometimes guard the outlets of fjords so that prey cannot come out. It, in some way, makes a treasure chest of food where it, when hungry, can go in and pick what it wishes to eat. Some hunters also take advantage of this. Actually, killer whales result in prey being closer to the coasts, making it easier for us to hunt. Therefore I do not understand why some hunters chase them away, when they actually are helping us”.

Apollo, hunter from Saattut

Table 1
Registered catch of killer whales along the coasts of Greenland.

Settlement	Year						Sum
	2009	2010	2011	2012	2013	2014	
<i>West Greenland</i>							
Aasiaat						1	1
Ilulissat		7		5	2		14
Kangaatsiaq			1		1	3	5
Manitssoq		4	2		12		18
Nanortalik		2		1	5		8
Narsaq							
Nuuk			2		1		3
Qaqortoq						5	5
Qeqertarsuaq				1			1
Sisimiut			2		2		4
Upernavik	9	1	22	8		1	41
Ummannaq			5	17	4		26
<i>East Greenland</i>							
Tasiilaq	5	1	5	12	11	6	47
Sum	14	15	39	44	38	16	173



Source: LULI Piniarneq, NELE 19/8 2016 (data still under validation)



Fig. 2. Killer whale caught by local hunters outside Tasiilaq, East Greenland (Photo: Frede Kilme).

Arctic seals and whales typically avoid killer whale predation by moving into shallow waters along shorelines (Westdal et al., 2013); this behaviour providing hunters with easy prey (Gonzalez, 2001; Westdal et al., 2013) as emphasized by Apollo. Besides, hunters always refer to the killer whales as being extremely clever, resulting in precautionary behaviour when being around this marine mammal.

"Killer whales are extremely clever and adaptive".

Hunter from the Disko Bay

Or even stories of them hunting hunters:

"I have heard stories of hunters in kayaks being hunted by killer whales as if they were seals"

Marianne from Nuuk

The one thing, though, that never came up when talking and travelling with hunters was how this major predator, known to reshape and control the rapidly changing marine ecosystems via top-down forcing (Trites et al., 2006; Springer et al., 2008; Higdon and Ferguson, 2009; Higdon et al., 2014), could possibly affect fisheries through the socially transmitted behavioural factor: depredation. Depredation by killer whales was never mentioned as a problem in the localities that were sustainably dependent on longline halibut fisheries.

This behavioural trend, seen in other regions of the world and potentially having immense impacts on not only national economy but also cultural practices and the well-being of communities in the future, was not addressed on any level. Why? When we know that climate change is pushing ecosystems, abundances, and distribution of animals, why are these potential negative impacts not at all in the interest or in the eye of the beholder? Why not see it as critical and essential to be at the forefront of both collecting baseline data and developing feasible mitigation strategies for the



Fig. 3. Killer whales eating fish from longlines of the coasts of Crozet Island (Photo: B. Loyer © St Thomas Production).

problem of depredation and top-down effects, which most likely will occur as ecosystems and environmental settings change?

4. Cutting edges of new issues

As Greenland keeps on living, inattentive to potential problems moving up along the coasts, other countries and fishermen struggle to cope with depredation (Fig. 3). Orcas are a large problem in the southern oceans around the Crozet Archipelago where these whales have revealed a high level of dietary specialization. Around the Crozet Islands, depredation by killer whales accounted for 75% of the total depredation, which from an economic point of view showed a catch per unit of effort (CPUE: mass of fish caught per hook) reduction around 30% due to killer whale interaction between 2003 and 2013 (Gasco et al. 2015). This issue seems to be growing around Crozet Island. Indeed, Tixier (2012 and pers. comm.) has observed an increasing number of matrilineal interacting with longlines over the years. As the relationships between matrilineal are known, a further approach will be to determine whether the apparition of the depredation behaviour between matrilineal follow the social relationship between them. This correlation should give information whether the depredation behaviour is socially transmitted or learned randomly around Crozet Archipelago. For comparison, Schakner et al. (2014) revealed that sperm whales in Alaska have learned the behaviour of depredation by social transmission. In a similar extent, depredation on traditional Greenland halibut fisheries by sperm whales has been observed in Norway since August 2014. This depredation behaviour used to be observed on demersal longlines in open waters off Norwegian coasts but never close to shore. There has been a major shift in the distribution pattern of sperm whales off the islands of Vesterålen in Norway, where a previously favoured feeding ground (a deep water canyon) has become less interesting for the whales. They have moved a bit closer to shore, adding yet another odontoceti to take into account. The Greenland halibut spawns at around 600 m off the continental shelf, and this is the area where depredation takes place (Simila pers. comm.). Is the change in the distribution pattern of killer whales related to migration of their resource due to climate change? Finally, it is of interest to understand that depredation behaviour may be opportunistically self-taught by some individuals. For instance, a poorly-known ecotype of killer whales, named Type D (Pitman et al., 2011), have been

interacting for less than 10 years with the French longlines (Tixier et al., 2016), while this ecotype did not mix with the Crozet killer whales, avoiding any social transmission, the depredation behaviour has to have been opportunistic. However, this behaviour was then quickly spread within the rest of the populations of Crozet killer whales or Type D by social transmission. Apprenticeship is crucial for killer whales, especially to master foraging techniques which could be complex, such as intentional beaching (Lopez and Lopez, 1985; Guinet and Bouvier, 1995). It is thus not surprising to see females teaching juveniles how to depredate longlines as observed by fishermen around Crozet archipelago:

"Worse than seeing killer whales eat Patagonian toothfish on our longlines, is seeing juveniles remove the fish and play with them before letting them go"

Lieutenant of a French longliner.

Like the situation in southern oceans, in the North Pacific depredation has become a large problem in the Sea of Okhotsk. Fishermen report killer whale consumption up to 100% of the catch from bottom nets of halibut fisheries and 20–80% of longline fisheries (Belonovich pers. comm.). Likewise, after decades of a relative peaceful coexistence with cod and halibut fishers of the coast of Alaska, killer whales are now stalking individual fishing boats. The killer whales will wait all day for a fisher to accumulate a catch of halibut, to the lead in fishers on a high-speed chase to get away, robbing them blind (Hopper, 2017).

"We've been chased out of the Bering Sea"

Paul, co-owner of F/V Augustina (Hopper, 2017).

How would this impact the Greenlandic fisheries playing a significant role in the national economy of Greenland, producing over half of the total service and goods export value, 57% of 4.2 billion, and where halibut is one of the main sources? The number of killer whales is increasing in the North Atlantic and possibly Arctic Greenland. Therefore it is of uttermost importance to be at the forefront in a precautionary manner to not only meet the local fishermen but also quota allocation processes and stock assessments, co-management and the conservation complications as well as the well-being of the involved marine mammals getting an easy

meal.

Depredation along the coast of Greenland might additionally cause an increase in the level of trophic interactions due to increased competition for the same fish stock, resulting in either direct reduction (through removal of fish) or indirect reduction (through trophic cascades) of the targeted fish stock; both scenarios reducing the overall quantity of fish available.

As a result, this would hit the economy built on fishing abundance, and would cause critical issues for management agencies with important implications for fishermen, affect cultural practices, and influence other cetaceans, such as narwhals (*Monodon monoceros*). These odontocetes are, as killer whales, top predators especially feeding on halibut. These of which also are interacting with the catch distribution and movement of halibut as Apollo describes;

"When the Narwhals enter our area, the halibut disappear, they hide. In old days we would stop fishing because it would be a waste of time".

Apollo, hunter from Saattut

Having a circumpolar distribution, narwhals share on a history with the Inuit through traditional knowledge as well as being an important food resource. The hunting of this marine mammal is not only associated with provision of food but involves the aspects of travelling, and community values. The Greenlandic word for food, Kalaaminernit (piece of a Greenlander), does not only refer to meat or fish but has a cultural manifestation built on multisensory and multiple meanings (Petersen, 1985; Sowa, 2015; Lennert, 2016). The subsistence activities are not only of economic or nutritional significance but also an important element regarding both physical and mental well-being, as well as being an essential asset in preserving one's cultural roots and identity (Poppel and Kruse, 2009). Many of the coastal communities rely on these food sources because of poor infrastructure and low access to fresh food supply in the local stores. Therefore, a competition between killer whales and humans for resources, being fish or marine mammals, may have critical effects on the usually isolated communities relying not only on fisheries but meat resources that only can be obtained through hunting. In a mixed economy, which the majority of these settlements depend on, the small-scale fisheries serve as an ad hoc to cover expenses relating not only to fishing but also hunting and gathering for subsistence and cultural purposes (Delaney et al., 2012; Hendriksen and Jørgensen, 2015; Jacobsen et al. forthcoming). These fisheries and settlements will be affected and experience immense feedback effects; accentuating the importance of being on the cutting edge of which future scenarios might be met as well as solutions.

5. A test of solutions

Off the Crozet Islands, acoustic harassment devices (AHDs) have been increasingly implemented in various fisheries that suffer significant losses caused by depredation. However, the effect of AHD activation was generally most effective when the killer whales were exposed to the device for the first time, as they seemed to become habituated to AHD (Tixier et al., 2014).

"We've tried all kinds of electronic sounds, music, whatever; anything that would confuse them. But whatever you do, it seems they adapt to it. They know the sound of everybody's propeller screw out there".

Fisherman from Alaska (Peterson et al., 2013)

Likewise, the F/V Augustine of the shores of Alaska tried electronic noisemakers to ward off the animals, but the killer whales simply got used to them;

"It became a dinner bell,"

Paul, co-owner of F/V Augustina (Hopper, 2017)

In Arctic Alaska, the use of dummy buoys has achieved limited success. Nevertheless, acoustic decoys are being tested in field trials by SEASWAP, who are using playbacks to drive animals away from the fishing site during the terminal phase by either broadcasting biological meaningful sounds (e.g. sounds of marine mammal eating killer whale) that generate an avoidance response, or generating sounds intended to "jam" the bio sonar of species (Thode et al., 2015), or masking the sound signature of fishing vessels that are thought to attract the killer whales (McPherson et al., 2008; Hamer et al., 2012).

Physical mitigation technologies such as "net sleeves", pots, chain and cage devices have yielded mixed results as they generally require complex moving parts. Indeed, implementation of fish pots as an alternative fishing technique to longline suppressed depredation but did not provide economically sustainable catch per unit effort for the French automated longliners (Gasco et al., 2010). However, in the toothfish fishery off the Chilean coast, fishermen developed a manual longline method with fish protection through a 'net sleeve' called 'cachalotera' from the Spanish name of sperm whale (Moreno et al., 2008). Even though this method requires a lower fishing effort, i.e. a lower number of hooks deployed per day, it was revealed efficient to avoid depredation by sperm whales (Moreno et al., 2008). Thus, this physical mitigation approach on longlines seems to be rather possible on manual longlines/more traditional fisheries. Furthermore, Derek J. Hamer et al. (2012) emphasizes that development of approaches should not only be focused on one certain "tool" but rather on compiling a "toolbox" of various strategies and solutions, because a single panacea for the problem of depredation is unlikely to emerge.

The question here is if these solutions will be accessible, manageable or affordable for the local fishermen operating from small dinghies during summer and fishing at ice margins from dog sledges in extreme cold weather (Fig. 1). Furthermore, are the acoustic suggestions accessible when taking spontaneous trips out when weather, ice and other circumstances allow it? Also, how does one travel with pots, net sleeves, chain and cage devices when having 400 hooks to deploy? Can pots, nets, sleeves, chain and cage devices be modified to meet the ways of travel, fishing and depredation all together? Can these be built by fishers own innovative solutions and knowledge? In most cases it is hard to find good devices to avoid depredation, so another approach is to understand how whales interact and if some techniques, e.g. choice of environmental setting as used by the fishermen, could reduce the depredation by avoiding detection or limiting the number of fish withdrawn from the longlines. Such a technique might have the greatest potential as the traditional knowledge and observations already define local management regimes of resources within the small communities along the coasts. We thus suggest implementing a combined policy looking for physical mitigation solutions and for appropriate fishing strategies to avoid depredation. This policy should be discussed with fishermen since they are the first protagonists and are the most competent to find devices to protect the hooks on their longlines, as did the Chilean fishermen with the cachalotera (Moreno et al., 2008). However, scientists might bring better understanding to fishermen on their fishing strategies by using human ecology and assess which techniques may bring the

better catch per unit effort.

Known to consume a broad range of prey, including mammals, fish and birds, in some regions, but also to feed highly specialized, consuming a specific and narrow range of prey, in other regions (Foote, 2012), another important query is what would the natural diet of this marine mammal be along the coasts of Greenland, and how would it differ between Greenlandic regions (e.g. north v.s. east coast)? Would they feed on marine mammals only, or would they feed also on fish and on halibut specifically? In other words, would they be more likely to learn depredation on halibut fisheries by opportunism or by ease? This question is of main interest to foresee the potential impact of this new behaviour upon the Greenlandic halibut fishing stocks but also on other top predators that are important for sustainable living of Inuit. This problem emphasizes the importance to modify research and management to better understand the foraging behaviour, the movement and the distribution of this toothed whale. This crucial act would allow an evaluation of killer whales' potential impact on top predators and ecosystems, as well as the threat they face.

In the North-East Atlantic, killer whales are known to follow specific prey stock; nevertheless, their seasonal movement is still poorly understood. In the North Pacific, two genetically distinct populations forage on distinct prey and both types don't change their diet: the *transient* feeding on marine mammals and the *resident* feeding on fish. Around the Crozet Islands, scientists are more convinced that killer whales, known to hunt penguins, elephant seals and other marine mammals (Guinet, 1992; Guinet et al., 2000, 2014), were already feeding on Patagonian toothfish as a natural diet since killer whales immediately interacted with longlines, when the fishery was started in 1996, to remove toothfish whereas they have never touched to the grenadiers (*Macrourus* spp.), a by-catch fish commonly hauled. However, Crozet killer whales show a decrease of interaction with fisheries from October, when southern elephant seals come back to land for the reproduction period, to December, when weaned pups leave for sea (Tixier et al., 2016). Killer whales switching between fish and mammals when travelling from Iceland to Scotland (Samarra and Foote, 2015) and Norway has also been observed (Vongraven and Bisther, 2014). This type of preying might be the best tactic, i.e. preying on whatever resource is available and most abundant at a given environmental setting or location. This observation recognizes that the killer whale has an ability to shift between specialized feeding strategies adapted to different prey resources (Similä and Ugarte, 1993; Beck et al., 2012; Samarra and Foote, 2015). It also recognizes that a potential prey shift might occur in relation to resource availability along the coast of Greenland. Even though their movement follows a specific life stock, the new selection of prey could potentially change their foraging. Taking into account the hunter's quote about the killer whale being extremely clever and adaptive – this founded on his own observations and shared knowledge – it does not contradict this potential; it actually reinforces the theory. Understanding the extent of behavioural plasticity in foraging strategies and to what extent killer whales may switch prey types requires future studies, particularly combining seasonal behavioural observations and diet assessments in different feeding contexts (Samarra and Foote, 2015).

The Greenlandic killer whales seen in extensively larger numbers along the east coast of Greenland are most likely a sign of recent substantial changes in the ecosystems such as a change in the distribution and abundance of mackerel (*Scomber scombrus*). Killer whales are known to feed on this species (Nøttestad et al., 2014), thus, it emphasizes the importance of knowing the dynamics of killer whales' diet to better understand and predict their responses to variations in the availability of various prey (Samarra and Foote, 2015). The killer whales caught off the east coast had

only remains of marine mammals in their stomach contents. This leads to the question if these whales have changed their diet from fish to marine mammals? Contrariwise, do they represent a separate group already feeding on marine mammals, since having increased in numbers because of the change of ice patterns and temperatures (Arvid-Rosing, 2013)? Another question is to what extent killer whales are moving in relation to the changes happening due to climate change affecting ecosystems. Just as ecosystems are altering and moving, killer whales must potentially move too. In the Disko Bay, West Greenland, a pod size of 40 individuals was caught in 2001 (Arvid-Rosing, 2013). This size corresponds to the pod sizes of the *resident* killer whales (fish-eating) studied off British Columbia and Washington State's coasts (Baird et al., 1992). Pods of killer whales are generally rare in such large numbers in these western North Atlantic and Arctic areas but might just indicate a natural (or unnatural) movement of fish-eating killer whales, as an analogy to the *resident* killer whales in the North Pacific. In this case it is important to build on management regimes handling this question, as hunting such large groups would have a crucial impact on the population, since pods are built on matrilineal family groups comprising one to four generations of individuals. Furthermore, explanation of the drop in caught numbers in 2014 (Table 1) is unknown as hunters from both the east and northwest coast of Greenland did not observe any major change in ice, break-up or movement of marine mammals. Explanations can lie in the movement of mackerel, capelin, other marine species feeding on these, excessive hunting or just as well anthropogenic disturbances such as increased ship traffic and tourism; disturbances that the hunters address themselves when it comes to other cetaceans and how they have changes distribution and movement. Even more so, understanding their movement will aid the knowledge of this whale's potential impact on local prey resources, being marine mammals or depredations, as well as ecosystems.

Indeed, it is unknown if killer whales visiting the west coast of Greenland are the same individuals as the orcas in eastern Canadian Arctic, since movements of killer whales in the western North Atlantic are complex (Heide-Jørgensen, 1988; Reeves and Mitchell, 1988; Lawson et al., 2008; Matthews et al., 2011). However, killer whales off the eastern Canadian coast are predominantly observed during summer, whereas killer whales off the western and south-western coasts of Greenland seem present throughout the year (Heide-Jørgensen, 1988), suggesting a possible migration from Canada to Greenland during winter. Additionally, Matthews et al. (2011) revealed a satellite track of a killer whale going through the Davis Strait from the Arctic waters (Prince Regent Inlet) to the open North Atlantic off Newfoundland, reinforcing hypotheses from previous studies of possible migration from Arctic waters to the Labrador Sea and the East Atlantic off Newfoundland, or along the North American coast (Katona et al., 1988; Reeves and Mitchell, 1988). In these waters, killer whales are mostly known to feed on marine mammals, but some killer whales have also been observed feeding on bluefin tuna (*Thunnus thynnus*), herring (*Clupea harengus*) and discarded fish near vessels fishing for Greenland halibut (Lien et al., 1988; Lawson et al., 2008). In an isotopic analysis Matthews and Ferguson (2014) confirmed that killer whales in the eastern Canadian Arctic forage upon narwhal, beluga, bowhead whales, and seals, but also revealed that killer whales off the coast of Newfoundland and Labrador may feed on both marine mammals and fish. Some genetic analysis and more tracking studies should allow for a better understanding of the killer whales' complex movements and their little-known population structure in this Arctic region.

By combining natural scientific studies with the knowledge already embedded in the waters along the coasts of Greenland, solutions might be found. Inspired by perceptions, this holistic

approach is not only a matter of data and observations but as much a matter of a process of community engagement, education as well as transmission of knowledge (Lennert and Berge, 2016). This approach is also implied by Hamer et al. (2012) and Gilman et al. (2006), who note that an acknowledgement of the conceptualization and development of some solutions may lie with the fishermen whose knowledge, experience and enthusiasm should not be underestimated or under-evaluated. There is already much local observation and knowledge along the coasts of Greenland covering movement, behaviour and variations of prey. The solution might even just build on a natural one, as expressed by Apollo: Just as narwhals cause a redistribution of halibut disappearing from an area, killer whales might have the same effect, therefore, in a natural way, not causing depredation conflicts. Again, Apollo's knowledge (see section 3.) contributes to understanding the distribution of stocks in a given environment as well as the variations of these; an important asset when striving to develop sustainable management regimes.

6. Conclusion

The degree and consequence of any impact is a function of the characteristics of the fishing community. As many Greenlandic communities built on fishing and hunting are remote and have limited economic opportunities of resident, the critical points are the vulnerability of a community to negative repercussions of management actions and the resilience the community has in being able to absorb these repercussions. Consequently, it is important to understand the ability and vulnerability of a community in order to successfully anticipate the impact, as well as to proceed at a pace that everybody can follow.

It is of paramount importance to hence an alternative understanding and perception by virtue of how organisms function and interact with their environment in order to prime our awareness of how systems might change in the future and to accentuate a flexible management approach.

Depredation is a problem that most likely will hit local fisheries of Greenland in the future. It is important that not only researchers but also policy makers and management agencies are at the forefront; that they meet the problem rather than be surprised; that they are proactive about not only dealing with depredation but also technologies to accurately assess the fish stocks and manage these if the depredation problem should occur to be in the same range as around the Crozet Archipelago, Alaska and the Sea of Okhotsk. Furthermore, only sparse knowledge covers the understanding of the movement and distribution of this toothed whale. Building on this knowledge is important for evaluating their impacts on top predators and ecosystems, as well as the threat they face. An understanding of killer whale movement will aid the understanding of prey specialization as well as the whales' potential impacts on local prey resources and ecosystems. Wrong handling of this may not only threaten the conservation of this cetacean population but also have an impact on the economic viability of longline fisheries and communities along the coasts of Greenland.

Indigenous and local observations deserve serious attention, especially when we seek to understand this dynamic world. In combination, the increased need for data, promotion of locally relevant knowledge, and management actions suggest that there are substantial prospects for more local engagement around the Arctic in the decades to come, and that an increase will contribute to more effective local conservation actions. Fishers, hunters and other communities relying on natural resources, as well as environmentally interested people are already using their own

observations, thereby obtaining small-scale and regional management regimes following the variations of nature.

Greenland is privileged to already have communities conducting local management regimes of resources built on traditional knowledge and observations. Greenland has the opportunity to be a role model: Successfully combining this knowledge, already embedded in the waters along the coasts, with natural scientific studies, solutions might be found, inspired by perceptions and holistic approaches, which are not only being a matter of data and observations. Greenland has the potentiality to encourage the process of community engagement, education as well as transmission of knowledge. Hamer et al. (2012) and Gilman et al. (2006) noted it as crucial to acknowledge that the conceptualization and development of some solutions may lie with the fishermen. That their knowledge, experience and enthusiasm should not be underestimated or under-evaluated. Furthermore, when community members, fishers and hunters present their natural resource observations and knowledge to leaders, community-based documentation of natural resources can be a very effective tool in enabling communities to achieve a greater "voice" in municipal, national and corporate decision-making (Norden 2015).

Greenland, being on the cutting edge of change, has the potentiality for building research on the topics touched upon in this paper, basing the research on natural science as well as traditional knowledge. The question now is who has the audacity to take up this intriguing challenge that might answer not only questions in the regions around Greenland but in a spatial and global scale.

The purpose of this study was to draw a statement of the current knowledges about killer whales around Greenland and what is known around the world on this species, especially about their behaviour of depredation. Thus, through this statement paired with the current knowledge of environmental changes in arctic and more precisely around Greenland, we aimed at predicting possible scenarios of a depredation issue happening on the Greenlandic halibut fishery. However, our study is mainly speculative even though it is based on strong statements; so further studies are encouraged to strengthen our hypothesis and at least avoid the phenomenon of depredation to appear. Thus, we recommend that biologists lead serious studies on killer whales ecology in Greenland by setting up at first a follow-up of the population using photo-identification coupled with biopsy samples to assess the genetic diversity of these individuals. Thanks biopsies, it is also possible to get a better idea of killer whales' diet through isotopic analyses. Additionally to their diet, monitoring it is of interest to study their foraging behaviour using for instance bio-loggers or passive acoustic devices, since they are highly vocal animals. Besides, as we underlined in our study, it is essential to benefits from traditional and local knowledge. Indeed, hunters and fishermen are the first observers of the environment and so they have a special expertise which is precious to science. We then suggest opening a dialogue and collecting traditional and local knowledges within a database in order to depict a better picture of the situation, and engage them in innovatively finding solutions, meet changes, impacts and opportunities that might occur in the future.

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