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Long-term studies of Crozet Island killer whales are fundamental to understanding the economic and demographic consequences of their depredation behaviour on the Patagonian toothfish fishery

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This paper provides a synthesis of results obtained as part of a long-term collaborative study involving biologists, fishers, and resource managers—centring on the occurrence of killer whales in the Crozet Archipelago before and after the implementation of a demersal longline fishery for Patagonian toothfish. Depredation behaviour was reported as soon as the fishery was initiated, with dramatic effects on both the demographic trajectories of the killer whales and on the amount of fish lost by the fishers. Killer whales interacting with the fishery exhibited very high mortality rates when illegal fishing took place, while killer whales not interacting were unaffected. However, after illegal fishing ended, killer whales interacting with the fishery exhibited both higher fecundity and survival rates compared with killer whales not interacting. Since whales typically removed fish entirely from the hooks, an adapted methodology that did not rely on determining the number of damaged fish was developed to estimate depredation rates. In the Crozet EEZ over a 10-year period, 33.9% of the total amount of Patagonian toothfish caught, representing a total of 28 million €, was estimated to be lost due to the combined effects of killer whale and sperm whale depredation. In an effort to reduce depredation losses, modifications to fishing methods, such as changing the fishing season, changing fishing areas when exposed to depredation and changing longline length and hauling speed were successfully tested. Acoustic deterrent devices were ineffective in deterring killer whales from depredating longlines. Alternative fishing gears, such as fish pots, were also tested. However, while providing encouraging results regarding the suppression of depredation and seabird bycatch, fish pots were not efficient enough to sustain an economically viable fishery. In conclusion, we discuss how the findings of this comprehensive study can be used elsewhere in fisheries confronted with depredation.

Keywords: crozet archipelago, demersal longlines, depredation, killer whales, patagonian toothfish, sperm whales.

Introduction

Many studies have documented the consequences of the development of human activity on ecosystems and species; this is particularly true for terrestrial ecosystems (see Sala *et al.*, 2000 for review). For marine ecosystems, a number of studies have reported major changes related to pollution and fisheries (Pauly *et al.*, 1998, 2002). Furthermore, as fisheries expand throughout the world's oceans, an increasing number of interaction events between fisheries and marine mammals have been reported (Northridge and Hofman, 1999).

Among such conflicts, marine fish depredation, which is defined as an operational interaction and concerns the removal of fish from lines or from nets by marine mammals, represents a major and increasing issue worldwide (see Donoghue *et al.*, 2002; Gilman *et al.*, 2006; Read, 2008; Hamer *et al.*, 2012). Depredation is distinguished from predation, which is defined as the taking of free-swimming fish by cetaceans (Donoghue *et al.*, 2002). Fishery depredations have important socio-economic consequences, including significant losses for fishers and fishing companies, as well as conservation implications for both fish resources (losses due to depredation are generally not accounted for in fish stock assessments and quota allocation processes; Roche *et al.*, 2007; Read, 2008), and for marine mammal species (risk of mortality by entanglement, modification of energy balance by giving access to new prey sources) (Secchi and Vaske, 1998; Northridge and Hofman, 1999; Fertl, 2002; Goldsworthy *et al.*, 2003). While losses to fishers have historically been the primary focus when assessing depredation cases, the direct consequences of interactions for the marine mammal populations involved have received less attention and remain poorly documented. Killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), false killer whales (*Pseudorca crassidens*), and pilot whales (*Globicephala macrorhynchus*) are the species most commonly implicated in depredation events (Donoghue *et al.*, 2002; Hamer *et al.*, 2012). These species may depredate fishing gear because the catch is part of their natural diet and is made more available by fisheries because their natural prey species have been reduced (Donoghue *et al.*, 2002; Guinet *et al.*, 2007). As a consequence, they have switched foraging behaviour to newly accessible and easy to catch resources. Once some whales in a population have learnt to feed this way, depredation behaviour can be rapidly transmitted through the population via social learning (Rendell and Whitehead, 2001; Allen *et al.*, 2013). Very few studies with concomitant long-term longitudinal monitoring datasets on both demographic parameters of interacting cetaceans and fishery history are available, and even fewer when the fishery started after demographic monitoring of cetaceans species involved in fishery interactions had been initiated. Here we summarize one of the few studies available worldwide, if not the only one, that documents the demographic changes and depredation behaviour of a previously studied killer whale population in a newly implemented fishery.

In the ‘Terres Australes Françaises’ Exclusive Economic Zone (hereafter EEZ), killer whale researchers, the fishing industry and resource managers confronted the depredation situation that had developed since 1996 by forming a partnership to investigate the interactions and to assess their consequences both on the killer whale population and the fishery. By combining killer whale photo-identification efforts and fish catch datasets, the primary aims were to estimate the amount of fish lost to depredation and to propose mitigation measures for recommendation to the resource managers and the industry. This unique collaboration was enhanced with the involvement of fishery observers in the collection of photoidentification data on both killer whales and sperm whales.

Here we present a case study with a review and synthesis of findings that demonstrate the effects of depredation on the demographics of the whales, as well as the consequences to the fishery in terms of economic losses. We also provide an example of how the combination of behavioural ecology data on killer whales and the fine scale monitoring of fishing activity and yields allowed the design of mitigation measures to reduce both the level of interaction and the amount of fish lost to depredation. In conclusion, we will discuss the application of our findings in addressing the social, economic, and political aspects of the depredation issue in fisheries confronted with depredation around the world.

The French Patagonian toothfish fishery

The Patagonian toothfish, marketed as Chilean sea bass in the United States and Canada, is a fish found in cold waters (1–4°C) in the Southern Ocean on seamounts and continental shelves around most Subantarctic Islands (Collins *et al.*, 2010). While juveniles are found on the continental shelf, adults are generally found at depths ranging from 500 to 2000 m (Duhamel *et al.*, 2005). The legal French fishery is currently the largest toothfish fishery in the world with a total quota of 5800 t distributed between the Crozet and Kerguelen Archipelagos (EEZ) (with quotas of ∼700 and 5100 t yr^{-1}, respectively). The average weight of a commercially caught Patagonian toothfish is 7–10 kg, depending on the fishery, with large adults occasionally exceeding 100 kg. They are thought to live up to 50 years and to reach lengths of up to 2.3 m. Patagonian toothfish are currently fished by the use of demersal longlines (see Collins *et al.*, 2010 for review on Patagonian tooth fish biology and fishery). The length of these lines varies from 1 to 40 km, averaging 8 km. The lines are composed of a succession of 1.2 km-long sections, each with 1000 hooks. Longlines are generally set at depths ranging from 500 to 2000 m; the 500 m minimum depth has been set as a regulation to protect juvenile Patagonian toothfish stocks (Collins *et al.*, 2010). Although started as a trawl fishery, most toothfish are now caught by longline. Longline fishing for Patagonian toothfish in the the Subantarctic first commenced during summer of 1988/89 in the vicinity of South Georgia, Atlantic sector of the Southern Ocean (Dalziell and De Poorter, 1993) and was soon followed by fishing around Kerguelen, Indian sector, in 1990/1991 (Cherel *et al.*, 1996; Duhamel, 2003), then extended to the Marion (Purves, 1997; Nel *et al.*, 2002) and Crozet (Duhamel, 2003) Islands in 1996.

Killer whales strip fish from the line only when the vessels are pulling in their lines and both killer whales and sperm whales selectively retrieve larger sized fish from the lines (Gasco, 2013). From 1996 to 2000, this fishery was dominated by illegal fishing vessels (Duhamel, 2003) but navy patrols and legal actions completely stopped illegal fishing by 2003. Currently, there are seven licensed fishing vessels operating within the French subantarctic EEZ, with fishery observers on each. Fishing observers collect information on each line set and hauled, such as the time and location of setting, the number of hooks set, the number and total tonnage of targeted Patagonian toothfish caught, the length and mass of individual fish, species and numbers of bycatch, as well as the duration of both setting and hauling operations. Furthermore, during hauling, observers monitor killer whale and/or sperm whale interactions and, if present, count the number of both species of whales. They also ensure that seabird deterrent devices, such as streamer lines, are used and properly set (Delord *et al.*, 2005). All seabird bycatch (mortality on hooks, injured birds) is also recorded. These data are recorded, checked, then stored in a database KERPECHE managed by the Museum National d’Histoire Naturelle (G. Duhamel and P. Pruvost). When sperm whales and/or killer whales are observed, fishery observers will take photographs to allow the identification of individual whales involved in the interaction with the line. All photographs taken are provided to the Centre d’Etudes Biologiques de Chizé (CEBC)-CNRS where the identification work is performed and the data are stored in an Access database.

Crozet Killer Whales

The Crozet Archipelago (46°25′S, 51°40′E) is one of the few locations in the Southern hemisphere where killer whale occurrence has long been documented and monitored. The first recorded sighting there occurred in 1825, when 22-year-old captain Lesquin (1840) was stranded on East Island after his shipwreck of ‘l’Aventure’ and reported what he called the ‘butcher’ seizing young elephant seals on the beach (Figure 1). Guinet (1991a) reported how that behaviour was learned through social transmission and practice. The first systematic behavioural observations were made in the 1970s (Voisin, 1976). A dedicated killer whale study was conducted from 1986 to 1990 on the Crozet Archipelago. As part of this study, 65 killer whales organized in 18 social units, averaging 4.2 ± 1.5 (mean ± SD) individuals each were photoidentified from the coasts of Possession Island (Guinet, 1988, 1991b). This study revealed that the recruitment rate of 1-year-old calf of this population was abnormally low (on the order of 0.02 neonates reaching the age of 1 year per adult female killer whale per year, i.e. one 1-year-old offspring produced every 50 years per adult female) (Guinet, 1991b; Poncelet *et al.*, 2010).

In contrast to many other studies that have found a high level of dietary specialization among individual populations, individual killer whales at Crozet have been observed attacking and feeding on a broad range of prey types including fish, penguins, pinnipeds (elephant seals *Mirounga leonina* and fur seals *Arctocephalus* sp.), and cetaceans (Guinet, 1992; Guinet and Tixier, 2011). Starting in 1996, longliners began fishing for Patagonian toothfish (*Dissostichus eleginoides*) within the Crozet Exclusive Economic Zone (Duhamel, 2003), and almost immediately killer whales and sperm whales started to take fish from the longline hooks as the lines were coming up (Figures 2–4). Although the longline fishery started earlier on Kerguelen Island, the first killer whale depredation event reported at this location by fishery observers did not occur until April 2004 (KERPECHE Database). Furthermore, such events remain uncommon within the Kerguelen EEZ, and some of the depredating killer whales involved in those events were known to interact with the Patagonian toothfish fishery operating in Crozet waters (Roche *et al.*, 2007; Tixier *et al.*, 2010). Although killer whales immediately learned to interact with the fishery, it was not clear whether killer whales were naturally feeding on Patagonian toothfish before the fishery (Guinet and Tixier, 2011). This hypothesis is most likely, as killer whale dietary shifts are thought to be a slow process. Some killer whale populations, such as the AT1 population in the Gulf of Alaska, were reported to disappear following multiple years of extremely low breeding success that coincided with the collapse of their main food resources as well as other anthropogenic factors (Matkin *et al.*, 2003, Saulitis *et al.*, 2005).

Larger adult Patagonian toothfish were thought to be distributed in waters too deep (>500 m) to be reached by diving killer whales, whereas juvenile Patagonian toothfish live at relatively shallow depths (<300 m) until reaching 6–7 years of age (i.e. 500–700 mm total length; Collins *et al.*, 2010) and are therefore more

Figure 1. A killer whale works its way back into deeper water after taking an elephant seal pup at the water's edge; this kind of 'intentional stranding' can be dangerous for the prey and predator alike. Baie Américaine, Possession Island, Crozet Archipelago (© Guinet).

Figure 2. A killer whale surfaces next to a Patagonian toothfish longliner as the fishers haul in their lines (© Tixier).

Figure 3. A killer whale surfaces next to a longline vessel with a Patagonian toothfish in her mouth that she has just removed from a hook (© Tixier).

Figure 4. Underwater view of killer whales from Crozet Island interacting with a demersal longline during hauling. Those videos allowed to show that killer whales were selectively retrieving Patagonian toothfish on the line while letting grenadier (or rattail fish) untouched (B. Loyer © St Thomas production).

likely to be accessible to killer whales. However, the view that adult Patagonian toothfish were mostly inaccessible to killer whales was recently challenged by diving data showing that killer whales around the Antarctic Peninsula (Pitman *et al.*, pers. comm.) and the Prince Edward Islands (R. Reisinger *et al.*, pers. comm.) were able to repeatedly dive to depths exceeding 600 m. This provided indirect support for the possibility that killer whales from Crozet Islands could be feeding naturally, at least under certain circumstances, on high energy content adult Patagonian toothfish. We hypothesize that differences in diet composition likely existed between killer whales from different social units observed in Crozet waters prior the fishery. Social units were known to differ greatly in their use of space (Guinet, 1992) and in the amount of time dedicated to hunting elephant seals from shore. Some social units were never observed alongshore and were identified for the first time after the fishery started. However, all social units are thought to all belong to the same population as they associate with each other (Tixier, 2012). Two distinct and genetically segregated morphotypes (Foote *et al.*, 2013) are observed in Crozet waters the type D killer whales (Pitman *et al.*, 2011; Tixier *et al.*, 2014a) and the 'Crozet killer whales' (Tixier *et al.*, 2014b) more similar to type A Antarctic killer whales (Pitman *et al.*, 2011). Type D killer whales were uncommonly observed interacting with the fishery in Crozet waters and the two morphotypes were never observed to associate with each other.

Until the mid-1990s and before longline fishing resumed, Crozet killer whales were observed and studied almost exclusively from the shore of Possession Island (one of the five main island groups in the archipelago). Individual monitoring was made possible by photoidentification, a technique that was developed by Bigg in the early 1970s (Bigg, 1982; Bigg *et al.*, 1987). In addition to dorsal fin shape and saddle-patch pigmentation, the shape of the anterior part of the white eye patch was also used for identification purposes in this study (Guinet, 1991b). Individual photoidentified whales have demonstrated long distance, longitudinal movements ranging nearly 3000 km (1864 mi), with movements between the Marion, Crozet, and Kerguelen Archipelagos (Roche *et al.*, 2007; Tixier, 2012; Reisinger and de Bruyn, 2014, Tixier *et al.*, 2014b).

Demographic trajectory of the Crozet Killer whale population

Between 1964 and 1986, many photographs of killer whales were taken opportunistically from the shore of Possession Island by the staff wintering at the Alfred Faure Research Station. Since 1987, a dedicated shore-based photoidentification effort has been carried out as part of a long-term programme conducted by CEBC to monitor marine bird and mammal populations in the Terres Australes Françaises. Since 1998, this work has been supplemented by a second dedicated photoidentification effort by fishery observers on licensed fishing vessels operating in Crozet waters. Each useable photograph is included in our long-term photoidentification database, along with information on the location of the sighting, total number of individuals photographed, identity code of each individual positively identified in each picture, and a rating of the photographic quality of the individual in the picture. Currently, our photoidentification database includes over 60 000 killer whale pictures. From this, we have created catalogs of all identified killer whales at Crozet (Tixier *et al.*, 2014a, b, c). Individual whales are organized into long-term stable social units, which according to the whales born during the scope of this long-term study, are likely to be matrilines (i.e. a family unit with individuals likely related through a common matriarch; Tixier *et al.*, 2014b). Social analyses of photoidentification data revealed that the Crozet killer whale social units were composed of 2–7 individuals that were constantly associated over time with no detected dispersal. Mean size (mean ± SD) of social unit decreased from 4.2 ± 1.5 individual during the late 1980s (Guinet, 1991b) to 3.5 ± 1.4 individuals 20 years later (Tixier, 2012; see also Tixier *et al.*, 2014b).

Killer whales occurred year-round in Crozet waters, but were more frequently encountered alongshore from October to December (the elephant seal breeding season) and to a lesser extent during March–April (Guinet, 1991b; Tixier, 2012). An analysis of photographic data from 1987 to 1990, before the start of any commercial fishing, suggested a decrease in the overall number of individuals observed at Possession Island (Guinet, 1991b). Furthermore, an extremely small number of calves was reported (Guinet, 1991b), suggesting that the recruitment of juveniles into the adult study population was probably negligible.

Shortage of natural prey in the region was suggested as a possible cause for this period of slow decline before the start of illegal fishing in the area. For unknown reasons, the elephant seal population at Crozet declined by 80% from 1970 to 1990, falling to its lowest documented number in 1997. Killer whale predation is thought to have contributed to the decline, but is not thought to be the main driving factor of this decline (Guinet *et al.*, 1999, Authier *et al.*, 2011). In addition, the whaling industry exploited large whale populations in the southwestern Indian Ocean (among other areas) until 1978 (Mikhalev, 1997; Branch *et al.*, 2008) and may have impacted the local killer whales by lowering the abundance of other potentially important prey. At Crozet, for example, killer whales were previously observed preying on Minke whales (*Balaenoptera acutorostrata*; Guinet *et al.*, 2000), southern right whales (Eubalaena australis) and chasing large balaenopterid whales (Guinet, 1992).

A mark recapture study performed by Poncelet *et al.* (2010) revealed that apparent survival (estimated from the CJS models for well-marked individuals which were, according to their size, mostly mature during the study) decreased from ~0.94 in 1977 to 0.90 in 2002. This suggested that the part of the Crozet Killer whale population that was identified from shore before the start of illegal fishing declined sharply from an estimated 98 individuals to 37 individuals by the end of the illegal fishing period (Poncelet *et al.*, 2010). Compared with other well-studied killer whale populations, such as 'residents' in the eastern North Pacific, which had survival rates of 96 and 99% in mature males and females, respectively (Olesiuk *et al.*, 1990), the apparent survival rate of the Crozet killer whales known to interact with the fishery during that period was strikingly low for both sexes compared with killer whales belonging to social units not interacting with the fishery. None of the missing Crozet whales were later observed either from the coast or from fishing vessels (Poncelet *et al.*, 2010; Tixier *et al.*, in revision). Furthermore, individuals and not complete social units were missing (Poncelet *et al.*, 2010, Tixier *et al.*, in revision). Dispersal of individuals (permanent emigration) was unlikely, given the social cohesion of these animals—like the 'resident' ecotype killer whales in the north Pacific, the evidence suggests that Crozet killer whales stay with their social units for their entire lives (Guinet, 1991b; Tixier, 2012; Tixier *et al.*, 2014b). Based on this evidence, we suggested that death was the most reasonable explanation for these permanent, abnormally high losses and that these probably resulted from the active killing of killer whales by Patagonian toothfish poachers during the late 1990s early 2000s. One vessel, the 'Praslin' was arrested and accused 'of illegal fishing by outrageous means' by F. Garde (head administrator of the TAAF in 2003) for the use of explosives to repel the killer whales coming to their longlines to feed on hooked fish (Ponchelet, 2003).

The increased mortality rate likely impacted the social organization of Crozet killer whales. For example, the number of lone individuals increased and the social unit size decreased, changes in social structure group composition during the study (Tixier, 2012). This modification in social structure was interpreted as the result of a strong disruption induced by the 'loss' of a large number of individuals (Tixier, 2012), as observed in Alaska following the Exxon Valdez oil spill (Matkin *et al.*, 2008).

Extensive photoidentification work over the past 15 years (performed both from shore and fishing vessels) revealed that among the 25 regularly observed social units (totalling 85 large juvenile and adult individuals in 2011; Tixier *et al.*, 2014c), 21 units were interacting to some extent with the Patagonian toothfish fishery. Of these 21 social units, 10 were also observed to varying degrees from the Possession Island shore, including three units that were regularly monitored from Possession Island preying on elephant seals before the fishery. Eleven social units were only observed and therefore 'discovered' from fishing vessels over the 1998–2008 period (Tixier *et al.*, 2010b, 2014b, in revision).

Since 2008 nine previously unobserved social units totalling 32 subadult–adult individuals (not included in the previous demographic studies from Tixier *et al.*, 2014d and Tixier *et al.*, in revision) were first observed interacting with the fishery. Three social units totalling 12 individuals, 4 social units totalling 13 individuals, and 2 social units, 7 individuals were first observed in 2009, 2010, and 2013, respectively (Tixier *et al.*, 2014b). The discovery of new individuals reveals that the number of individual within the 'Crozet Island' killer whale population is likely to be larger than the number of individuals regularly observed from the coasts of Possession Island and fishing vessels. This is not surprising as these means of observation provide access only to a limited part of their range. These observations also suggest that an increasing number of social units are interacting with this fishery overtime. These newly identified killer whales belong to the same population of the so-called 'Crozet killer whales' as they share the same morphotype (Type A) and they socially interact and associate with previously known killer whales.

The level of interaction with the fishery exhibited by the different social units was correlated with their level of social association (Tixier, 2012), providing support for the horizontal transmission of depredation behaviour between social units. In this way, depredation behaviour has spread throughout the Crozet killer whale population. Only four social units have never been observed interacting with the fishery and were only observed from shore. Of these, two social units (one of them known since the early 1980s) have not been observed since 2005 and their fate is unknown. One social unit progressively lost all of its members except one individual that currently associates with the only remaining social units not interacting with the fishery and still regularly observed from the shore of Possession Island.

A reassessment of survival rates was made using a robust design demographic model with a trap dependence effect (Tixier *et al.*, in revision). Before the inception of the fishery (i.e. 1996), Crozet killer whales demonstrated high survival rates (0.98–0.99; Tixier *et al.*, in revision) comparable with those observed in the North Pacific (Olesiuk *et al.*, 1990) but a very low reproductive output (Poncelet *et al.*, 2010). This also suggests that the apparent survival rates before the illegal fishery were likely to be underestimated by Poncelet *et al.* (2010). After the fishery started, Tixier *et al.*, (2014c, in revision) found that killer whales interacting or not interacting with the fishery exhibited major differences in their demographic trajectories. Killer whales belonging to social units known to interact with the fishery experienced a sharp decline in survival rate (down to 0.90) during the course of the illegal fishing period in Crozet waters, while individuals belonging to social units not known to interact maintained a higher (but still declining) survival rate (Tixier, 2012; Tixier *et al.*, in revision; Figure. 5). However, since the end of illegal fishing in 2003, the opposite trend has been observed. The survival rate of killer whales belonging to social units known to interact with the fishery rose back to a constant 0.95, while the survival rate of killer whales not interacting exhibited an accentuated decline (Figure 5). Furthermore, the recruitment rate of depredating killer whales was found to increase in relation to their level of interaction (Tixier, 2012; Tixier *et al.*, 2014c), while killer whales not interacting exhibited a dramatically low recruitment rate. The accentuated decline of survival rates for killer whales belonging to social units not interacting with the fishery is thought to be the direct consequence of the absence of recruitment for nearly three decades (Guinet, 1991b; Poncelet *et al.*, 2010; Tixier, 2012; Tixier *et al.*, in revision). Consequently, these social units were mainly composed of ageing adult killer whales experiencing greater mortality rates, with most females likely to be post-reproductive. The loss of additional members to ageing in the absence of any recruitment, accompanied by greater mortality rates possibly due to poorer foraging performance, may lead to extinction of these social units (see also Foster *et al.*, 2012).

Killer whales interacting with the fishery from 2003 to 2011 exhibited a higher survival rate (0.95) compared with the non-interacting whales. However, this value is still lower than survival rates observed in stable or slightly increasing populations, as reported in British Columbia for 'resident' or salmon eating killer whales (0.97–0.98; Olesiuk *et al.*, 2005) or in Norway (0.98; Kuningas *et al.*, 2013). Furthermore, these killer whales exhibit a calving (one

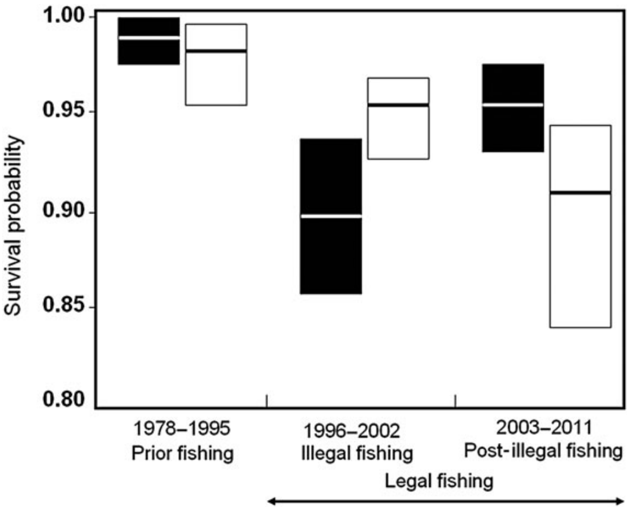

Figure 5. Survival probability by period (before longline fishing; during illegal fishing and after illegal fishing within the Crozet EEZ) of killer whales not interacting (white boxes) or interacting (black boxes) with longliners. Mean is represented by the bolded middle line of the box and the 95% CI of model parameter estimates represent the upper and lower extents of the box (from Tixier *et al.*, in revision).

year old calf) rate estimated to 0.195 ± 0.044 calves $\text{female}^{-1}\ \text{yr}^{-1}$ with a positive relationship between depredation level and calving rate at the female level (Tixier *et al.*, 2014d). This calving rate is similar to the calving rate reported in British Columbia for the increasing northern resident killer whale population (0.18 calves $\text{female}^{-1}\ \text{yr}^{-1}$; Olesiuk *et al.*, 2005). The fact that these killer whales exhibit a fecundity rate higher than reported for that population before the fishery but associated with survival rate lower to what was observed before the fishery (Tixier *et al.*, 2014c, in revision) suggests that these killer whales are likely to be exposed to an unknown cause of mortality. Indeed, for long-lived predators, survival should be favoured over reproduction (Cairns, 1987; Gaillard *et al.*, 1989, , 1998) and in the Crozet situation, the opposite is currently observed. We speculate that this increased mortality might be related to the interaction of the whales with illegal fishing vessels outside the EEZ (some illegal fishing activity was recently reported at the limits of the French EEZs by the Terres Australes et Antarctiques Françaises Administration (Thierry Clot, Personal communication; http://www.taaf.fr/Peche-illicite)). An unbalanced age structure after years of very low recruitment may also drive this trend. However, the latter hypothesis is less likely because killer whales interacting with the fishery have a much lower proportion of post-reproductive females (0.241; Tixier *et al.*, in revision) than the growing North Pacific resident killer whales (0.324; Brault and Caswell, 1993), which exhibit a higher survival rate (Olesiuk *et al.*, 1990). But the small proportion of post-reproductive (i.e. older) females in the Crozet population may in fact contribute in explaining the low survival performances as in North Pacific resident, older post-reproductive females were found to be beneficial to other age categories, in particular to their older sons, likely by assisting them in foraging (Foster *et al.*, 2012).

Crozet killer whales present a unique situation, where a killer whale population was monitored before and during a fishery. This allowed us to assess the effect of fishery interactions on whale recruitment and mortality. This study also points out the importance of assessing the impact of social units (matriline)-specific foraging preferences (which are most likely culturally transmitted across generations) on matriline fitness, as suggested by Whitehead (1998).

Killer whale depredation on the Crozet Patagonian toothfish fishery

Part of the killer whale work conducted in collaboration with the fishery aims at understanding the behavioural processes of depredation and possible mitigation measures to reduce its impact. From 2003 to 2012, killer whales were found to interact with 42% of the lines set by fishers in Crozet waters. For 29% of the total lines set, both killer whales and sperm whales were observed simultaneously, while in 13% of cases only killer whales were observed. In the absence of killer whale interactions, sperm whale interactions occurred with 33% of the lines, and only 25% of the lines were unattended by cetaceans (Tixier *et al.*, 2010; Tixier, 2012; Gasco, 2013).

When depredating, the mean number of killer whales and sperm whales observed interacting on longline was 8.2 ± 4.7 (range 1–25) and 4.1 ± 3.4 (range 1–30) individuals, respectively, with typically two or more killer whale social units simultaneously present per line set (Roche *et al.*, 2007; Tixier *et al.*, 2010). Both killer whales and sperm whales are suspected to selectively remove larger Patagonian toothfish caught on the line as the mean length of Patagonian toothfish is higher on non-depredated lines compared with the depredated ones (Gasco, 2013).

Depredation levels cannot be reliably assessed by recording the number of fish damaged or partly eaten by killer and sperm whales. When depredating longlines, both species entirely remove most fish from the hooks. Therefore, enumerating only damaged fish would lead to serious underestimation of depredation levels. Depredation rates were first estimated by comparing cpue between lines hauled in the absence and in the presence of cetaceans over the whole Crozet Islands EEZ. From 2003 to 2012, a total of 5054 t of Patagonian toothfish were landed and an additional 2589 t of Patagonian toothfish (i.e. average loss of 259 t yr^{-1}) were estimated to have been lost to killer whales and sperm whales at Crozet. Sperm whales alone, killer whales alone, and sperm whales and killer whales interacting together were responsible for 25, 22, and 53% of the fish lost to depredation, respectively (Gasco, 2013). This estimate is larger than those previously provided for the 2003–2005 (Roche *et al.*, 2007) and the 2003–2008 periods (Tixier *et al.*, 2010): 150 and 114 t yr^{-1} average annual losses of Patagonian toothfish, respectively. The differences in estimates of depredation levels require further investigation. It may partially result from the fact that the periods covered do not completely overlap, and therefore may reflect some variation in the level of depredation between periods. The most recent study (Gasco, 2013) would suggest increasing depredation levels in recent years, which is supported by the fact that new social units were found to have started interacting with the fishery (Tixier *et al.*, 2014b). The discrepancies may also be partly due to different methodological approaches. In the first two studies, depredation was estimated only for geographical units (i.e. cells) of varying size, but for which enough longlines in the presence and absence of depredation were available for analysis. As a consequence, many cells were excluded due to the lack of suitable data (either too few lines or all lines were depredated) and therefore the total amount of fish lost was likely to be underestimated. In Gasco (2013) study, the mean yield (cpue in g hooks^{-1}) was calculated for each cells in the absence of cetaceans, in the presence of killer whales only, in the presence of both killer whales and sperm whales simultaneously, and in the presence of sperm whales only. In cells for which all lines were depredated, the mean yield in the absence of depredation over the whole Crozet ZEE was used to compare with the yield obtained for the three different combinations of depredating cetaceans (killer whale, sperm whale, killer whale, and sperm whale) for that cell.

Killer whales were estimated to be responsible for the largest part of this loss (>75% of the amount of fish loss), while sperm whales had a lower impact (>25%, Tixier *et al.*, 2010). These results indicate that depredation levels by killer whales and sperm whales in Crozet exceeded by far the level of depredation reported for the same species elsewhere in the Southern Ocean and in other parts of the world. The depredation levels estimated from the differences in mean yield were supported by the implementation of a new method to estimate the amount of fish lost. Underwater videos of killer whales depredating longlines revealed that killer whales selectively retrieved Patagonian toothfish from hooks but let rattail fish or grenadier (*Macrourus* sp.) untouched (B. Loyer pers. comm., see Figure 4). Therefore, this method relies on estimating the proportion of a commonly encountered bycatch species, the rattail fish on lines in the absence and presence of cetacean depredation. The proportional increase of rattail fish due to the selective removal of Patagonian toothfish by killer whales on depredated lines compare with non-depredated lines, when controlling for the fishing location, produced extremely consistent results (see Gasco, 2013).

Altogether, depredation around the Crozet Islands from 2003 until 2012 was estimated to represent an economic loss >28 million € or 2.8 million € yr^{-1} (Gasco, 2013). Although over 70 killer whales are known to currently interact to some extent with the fishery, the photoidentification data revealed that the majority of interactions with the fishery (81.3%) involved only 35 killer whales belonging to five different social units (Tixier *et al.*, 2010; Tixier, 2012).

Operational and technological approaches to reduce the level of depredation

Exposure to depredation according to fishing practices revealed that six fishing variables could affect killer whale depredation levels on Patagonian toothfish longlines set in the Crozet EEZ (Tixier *et al.*, 2010, Tixier, 2012, Tixier *et al.*, 2014e). Four variables had an influence on the probability that killer whales would interact with a fishing vessel: (i) fishing season (i.e. spring, summer, fall or winter), (ii) number of vessels operating simultaneously, (iii) depth of longline sets, and (iv) distance travelled by a vessel between a depredated set and the following set. Two variables were found to influence the amount of fish losses caused by depredation: (i) length of longline sets and (ii) hauling speed. Some relatively simple measures were sufficient to significantly reduce killer whale depredation rates. These included reducing longline length, increasing line hauling speed, travelling a minimum of 40 miles from an area where killer whales are present, and fishing during seasons when killer whale social units tend to forage on other prey resources (e.g. during elephant seal breeding season). By acting on these operational variables, fishing captains can significantly reduce both the level of interaction with killer whales and the amount of fish lost (Tixier *et al.*, 2010; Tixier, 2012; Tixier *et al.*, 2014a). However, this does not take into account the additional costs associated with the implementation of these measures, such as increased fuel consumption and/or increased non-fishing time, which would require a cost–benefit analysis (see Peterson *et al.*, 2014). In a location where depredation has not yet started, it is of the utmost importance to adopt a 'no-reward policy' by stopping fishing operations, let the line sank to the seabed and leaving the fishing area for at least a few days. This policy has been strictly enforced within the Kerguelen Island EEZ, where killer whales have rarely been seen interacting with the fishery. So far, these measures appear to have been successful, as the killer whale depredation behaviour has not spread throughout the population. However, although such approaches can reduce the level of depredation, they cannot suppress it entirely (Tixier *et al.*, 2014e).

These operational approaches can be complemented by developing technological methods that aim to prevent cetaceans from accessing the fish. The use of acoustic deterrent devices to produce high noise levels that frighten the whales has been proposed as a possible way to discourage whales from depredating. A powerful acoustic deterrent, the Orcasaver® (Mustad) has received considerable attention from the Patagonian toothfish fishery industry. Test trials performed with this device within the Crozet EEZ provided mixed results: after an initial phase during which the killer whales were repelled, they habituated quickly and within a few days the system was completely ineffectual at preventing depredation (Tixier *et al.*, 2014f). Continued use of acoustic deterrents could pose a threat to the whales' hearing as they expose themselves to very high levels of powerful sound while depredating (see Tixier *et al.*, 2014f). We suggest that such an approach could only work with whales that were naive to depredation and if a no-reward policy is enforced. However, as the Crozet killer whales have long been interacting with the fishery this method of repelling whales is not advisable.

Fish pots were thought to represent a possible alternative to demersal longline operations in the Crozet EEZ confronted by both cetacean depredation and seabird bycatch during gear deployment, which is also a major issue within the Patagonian toothfish subantarctic longline fisheries (Dalziell and De Poorter, 1993; Cherel *et al.*, 1996; Weimerskirch *et al.*, 2000; Nel *et al.*, 2002). Although the bycatch of white-chinned petrels (*Procellaria aequinoctialis*), in longlines was reduced from several thousand to <100 individuals by implementing a range of mitigation procedures such as the deployment of streamer lines to prevent the birds approaching the line before it has sunk; increasing the sinking rate of the line by adding extra weight and setting the line in total darkness), seabird mortality has remained a conservation issue. It was a secondary objective of a Crozet experimental fish pot trial (Gasco *et al.*, 2010; Bavouzet *et al.*, 2011) to assess its effectiveness in reducing the residual accidental bycatch of pelagic birds attracted by baited hooks (Barbraud *et al.*, 2008).

Pots are used to fish some demersal species and were successful in reducing sablefish (*Anoplopoma fimbria*) losses in the North Pacific due to both killer and sperm whale depredation (Sigler *et al.*, 2006). Previous pot trials targeting Patagonian toothfish were conducted in South Georgia in 2001 (Agnew *et al.*, 2001), Prince Edward Islands in 2004–2005 and Chile in 2006 (Guerrero and Arana, 2009). Major differences were observed between these trials in terms of both the Patagonian toothfish harvest and the bycatch rates of non-target species, particularly crustaceans (*Litodes* sp.). To find a solution to these issues, a 25-day pot trial cruise was conducted in the Crozet EEZ on-board the vessel 'Austral Leader II' from January 22 to February 17, 2010 (Gasco *et al.*, 2010; Bavouzet *et al.*, 2011). This pot trial period was chosen to match the longline closure period for the main French fishing grounds, the Kerguelen EEZ. This closure is a conservation measure enforced to reduce bird mortality during this high-risk white-chinned petrel bycatch period in Kerguelen waters. This allowed commercial longliners and the experimental pot fishing vessels to operate simultaneously in the Crozet waters to compare catches provided by both fishing methods. On a number of occasions, the longlines and pot lines were set in the same locations with a 48-h lag for direct comparisons. Eleven different models of pots were trialled and some were modified with weights, floats (to lift the pots from the bottom), or by adding escape devices for stone crab (*Lithodides murrayi* and *Paralomis aculeata*). These modifications resulted in the testing of 20 different models in attempts to improve catch per unit of effort (CPUE) and to reduce the undesirable bycatch of crustaceans.

Several issues were identified in the use of the pots: first, none of the pot models reached a CPUE high enough to be economically sustainable (i.e. 10 kg of fish/pot). Second, fish were more difficult to locate since the pot lines, totalling a maximum of 100 pots, were short (<5 km) compared with longlines, making it difficult to search for fish. In Crozet waters, the use of pots induced an extremely high level of stone crab (*Lithodides murrayi* and *Paralomis aculeata*) bycatch, which would need to be addressed to ensure their conservation if a pot fishery was implemented. In addition, compared with demersal longlines, pot catches of Patagonian toothfish were biased toward larger individuals, which are mainly females. Finally, the handling of pots on-board the vessel during fishing operations raised some safety and social concerns, such as greater fatigue among the crew. Implementation of pots fishing would therefore require specially designed and larger vessels with a conveyer belt to move the traps from the hauling to the setting platforms. As expected, pots were efficient at suppressing the depredation from sperm whales and killer whales and no incidental mortality of seabirds was observed. Despite elimination of cetacean depredation and seabird mortality, the use of pots is currently not an economically viable alternative to demersal longline fishing for Patagonian toothfish (Gasco *et al.*, 2010; Bavouzet *et al.*, 2011) in Crozet waters (see also Supplementary material).

Conclusion and perspectives

Interactions between marine mammals and Patagonian toothfish fishery operations have been reported to occur in the Southern Ocean (Hucke-Gate *et al.*, 2004; Kock *et al.*, 2006), off South Georgia Island (Ashford *et al.*, 1996; Purves *et al.*, 2004), and the Falkland (Nolan and Liddle, 2006), Crozet, and Kerguelen (Capdeville 1997; Roche *et al.*, 2007; Tixier *et al.*, 2010) Islands. Killer whales and sperm whales are the two main cetacean species reported to interact with the Crozet fishery, which is heavily exposed to depredation (Gasco, 2013). This review determined that depredation behaviour had strong implications for both the demographic trajectories of the killer whales and the socio-economics of the fishery in terms of significant financial losses caused by reduced fishing yields. There is also evidence that both sperm whales and killer whales are competing to some extent with the fishery. Future work should investigate how much killer whales naturally rely on Patagonian toothfish in their diet in the absence of fishery depredation. Preliminary nitrogen stable isotope studies suggest that, despite the high levels of observed fishery interactions, adult size Patagonian toothfish do not represent a major prey item of the Crozet killer whales (Tixier, 2012, unpublished data).

Currently, no technological approach has been able to solve the depredation issue, and future work should be conducted in that area to find ways to protect the fish on the line and prevent them from being depredated. The Norwegian company A. S. Fiskevegn is currently performing some research on a system they call SAGO, aimed at collecting the fish on the bottom during the hauling process to protect it from depredation (see Arangio, 2012). In addition, the 'cachaletora' system to protect fish at the hook level has been tested by some Chilean fishers (Moreno *et al.*, 2008). However, both these approaches are thought to be difficult to implement on industrial fishing vessels.

Therefore, with our current understanding of the depredation issue, altering fishing operational behaviour is the only certain method to reduce depredations on Patagonian toothfish. It can provide a substantial reduction of depredation levels, but not its complete elimination. Most of these changes in fishing behaviour were tested for killer whales, although sperm whales also represent a significant part of the depredation issue within the Patagonian toothfish fishery. Some techniques, such as the hauling speed, were found to be very efficient at reducing losses from both cetacean species. However, a complete socio-economic assessment of such measures needs to be conducted to properly evaluate the net benefit for fishers.

On the conservation side, it is necessary to assess the ecological consequences of this artificial provisioning on the foraging and reproductive success of killer whale social units that engage in depredation, according to their level of interaction. The longer term effects of this 'supplementary' feeding on killer whale populations will be an important focus of future research. Our knowledge of this population is still limited to observations from opportunistic and passive platforms. Our current understanding of depredation would benefit from the use of satellite tracking techniques and activity recorders that would yield important information about whale movements, natural feeding areas, prey types and diving behaviour in the presence and absence of fishing vessels. In addition, acoustic recorders would allow us to determine at what depth both sperm whales and killer whales tend to interact with longlines.

It is still too early to know the ultimate fate of the Crozet killer whale population, but we do know that the population declines documented over the last few decades would have gone unnoticed (and unexplained) without the continuous and ongoing collection of data at Crozet from the fishing vessels, illustrating once again the value of long-term datasets. Although both the whales that visit the longlines and those that do not belong to the same population; killer whales belonging to social units that do not interact with longliners are likely to disappear in the years to come. As these animals have unique cultural traditions, such as the use of the intentional stranding technique to capture elephant seals on shore (Guinet, 1991a, Guinet and Bouvier, 1995), this could represent a significant loss in the cultural foraging repertoire of this population as a whole (Whitehead, 1998).

Implications for other fisheries confronted with depredation

The results presented here have a direct application to vessels in the Crozet EEZ as an impetus to change their fishing behaviour. These findings are also directly applicable to many other fisheries, since the fishing methods used by Patagonian toothfish longliners in the Crozet EEZ are identical with those used by Patagonian toothfish fisheries off South Georgia Island (Ashford *et al.*, 1996; Purves *et al.*, 2004; Clark and Agnew, 2011), the Prince Edward Islands (Tilney and Purves, 1999), the Falkland Islands (Nolan and Liddle, 2006), and Chile (Hucke-Gaete *et al.*, 2004). They are also very similar to demersal longlining methods used in Alaskan waters (Yano and Dahlheim, 1995; Peterson *et al.*, 2013; Peterson *et al.*, 2014). This study illustrates the need for close collaboration between researchers, fishers and resource managers to address the depredation question. Because experimental trials are difficult to implement due to time and economic constraints, recommendations based on the Crozet findings can be made to fishers elsewhere to mitigate depredation. Full access to fishing data may *a posteriori* allow for assessment of the resulting benefits of such changes as mitigation solutions. For instance, length of longline sets, hauling speed, longline depth and the 'move on' technique may be easy changes for demersal longline fishers to implement on a voluntary basis to reduce killer whale depredation. However, local features of fishing gear, fishing grounds and the killer whale populations involved in depredation may influence the expected results of such trials. Furthermore, a good understanding of the ecology of the depredating species involved was critical in identifying all aspects of this issue and detailing the contribution of each killer whale social unit to the depredation problem. We also strongly recommend supporting technological research aimed at protecting the catch on the line, which might be the only way to completely solve the depredation issue on a longer term basis.

The findings here are not applicable to all longline fisheries. Although odontocete species involved in depredation on tuna and swordfish (i.e. pilot whales *Globicephala* spp. and false killer whales *Pseudorca crassidens*) are genetically closely related to killer whales (Hamer *et al.*, 2012), the fishing techniques differ and rely on the use of pelagic longlines. Most of the mitigation techniques for demersal longline fisheries are likely to be inadequate for solving depredation issues in pelagic fisheries, as fish are accessible to depredating cetaceans during the duration of the fishing operation and whales can remove fish far away from the vessels, thus preventing the completion of photoidentification work (Rabearisoa *et al.*, 2012). Dedicated studies are therefore required to better understand the depredation behaviour of cetacean species interacting with pelagic longlines and to find appropriate solutions specific to this fishery.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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References

Agnew, D. J., Daw, T. M., Purves, M. G., and Pilling, G. M. 2001. Fishing for toothfish using pots: Results of trials undertaken around South Georgia, Mars – Mai 2000. CCAMLR Science, 8: 93–105.

Allen, J., Weinrich, M., Hoppitt, W., and Rendell, L. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science, 340: 485–488.

Arangio, R. 2012. Minimising whale depredation on longline fishing Australian toothfish fisheries. Repport Nuffield Australia Project No 1201. 43 pp. http://www.nuffieldinternational.org/rep_pdf/1353965947Rhys_Arangio_final_report.pdf (last accessed 2 December 2014).

Ashford, J. R., Rubliar, P. S., and Martin, A. R. 1996. Interactions between cetaceans and longline fishery operations around South Georgia. Marine Mammal Science, 12: 452–457.

Authier, M., Delord, K., and Guinet, C. 2011. Population trends of female Elephant Seals breeding on the Courbet Peninsula, îles Kerguelen. Polar Biology, 34: 319–328.

Barbraud, C., Marteau, C., Ridoux, V., Delord, K., and Weimerskirch, H. 2008. Demographic response of a population of white-chinned petrels *Procellaria aequinoctialis* to climate and longline fishery bycatch. Journal of Applied Ecology, 45: 1460–1467.

Bavouzet, G., Morandeau, F., Mouchel, M., Méhault, S., Duhamel, G., Guinet, C., Roullot, J., *et al.* 2011. Rapport de la campagne casier Orcasav: Une campagne innovante de pêche aux casiers dans la ZEE de Crozet pour lutter contre la déprédation des orques et la mortalité aviaire.

Bigg, M. A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Report of the International Whaling Commision, 32: 655–666.

Bigg, M. A., Ellis, G. M., Ford, J. K. B., and Balcomb, K. C. 1987. Killer whales – A study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press, Nanaimo, BC.

Branch, T. A., Allison, C., Mikhalev, Y. A., Tormosov, D., and Brownel, R. L. 2008. Historical catch series for Antarctic and pygmy blue whales. Int. Whaling Comm., The Red House, Sta. Rd., Impington, Camb., U.K., Pap. SC/60/SH9 11p. http://swfsc.noaa.gov/publications/cr/2008/2008branch.pdf (last accessed 2 December 2014).

Brault, S., and Caswell, H. 1993. Pod-specific demography of killer whales (*Orcinus orca*). Ecology, 74: 1444–1454.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography, 5: 261–271.

Capdeville, D. 1997. Interaction of marine mammals with the longline fishery around the Kerguelen Islands (Division 58.5.1) during the 1995/96 cruise. CCAMLR Science, 4: 171–174.

Cherel, Y., Weimerskirch, H., and Duhamel, G. 1996. Interactions between longline vessels and seabirds in Kerguelen waters and a Method to reduce seabird mortality. Biological Conservation, 75: 63–70.

Clark, J. M., and Agnew, D. 2011. Estimating the impact of depredation by killer whales and sperm whales on longline fishing for toothfish (*Dissostichus eleginoides*) around South Georgia. CCAMLR Science, 17: 163–178.

Collins, M. A., Brickle, P., Brown, J., and Belchier, M. 2010. The Patagonian toothfish: Biology, ecology and fishery. Advances in Marine Biology, 58: 227–300.

Dalziell, A. J., and De Poorter, M. 1993. Seabird mortality in longline fisheries around South Georgia. Polar Record, 14: 231–241.

Delord, K., Gasco, N., Weimerskirch, H., Barbraud, C., and Micol, T. 2005. Seabird mortality in the Patagonian toothfish longline fishery around Crozet and Kerguelen Islands, 2001–2003. CCAMLR Science, 12: 53–80.

Donoghue, M., Reeves, R., and Stone, G. (Ed.). 2002. New England Aquarium Aquatic Forum Series Report. 03–1. Report of the workshop on interactions between cetaceans and longline fisheries. Apia, Samoa, November 2002. New England Aquarium Press, Boston, USA.

Duhamel, G. 2003. La légine, pêcherie conflictuelle. Pêche légale et braconnage organisé. Cas du secteur indien de l'océan Austral: 177–187. In: Exploitation et surexploitation des ressources marines vivantes. Rapport sur la Science et la Technologie n°17. Académie des Sciences éditions Tec & Doc Lavoisier Paris, 503 pp.

Duhamel, G., Gasco, N., and Davaine, P. 2005. Poissons des îles Kerguelen et Crozet, guide régional de l'océan Austral. Patrimoines naturels, 63, 419 pp.

Fertl, D. 2002. Interference with fisheries. *In* Encyclopedia of marine mammals, Ed. by W. F. Perrin, B. Würsig, and H. Thewissen. Academic Press, San Diego.

Foote, A. D., Morin, P. A., Pitman, R. L., Ávila-Arcos, M. C., Durban, J. W., van Helden, A., Sinding, M. H. S., *et al.* 2013. Mitogenomic insights into a recently described and rarely observed killer whale morphotype. Polar Biology, 36: 1519–1523.

Foster, E. A., Franks, D. W., Mazzi, S., Darden, S. K., Balcomb, K. C., Ford, J. K. B., and Croft, D. P. 2012. Adaptive Prolonged Postreproductive Life Span in Killer Whales. Science, 33: 1313.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. G. 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. Trends in Ecology and Evolution, 13: 58–63.

Gaillard, J.-M., Pontier, D., Allainé, D., Lebreton, J.-D., Trouvilliez, J., and Clobert, J. 1989. An analysis of demographic tactics in birds and mammals. Oikos, 56: 59–76.

Gasco, N. 2013. Déprédation de la légine (*Dissostichus eleginoides*) par les orques (*Orcinus orca*), les cachalots (*Physeter macrocephalus*) et les otaries (*Arctocephalus* spp.) à Kerguelen et Crozet (Océan indien sud). Conséquences sur la gestion de la pêcherie et évaluation de solutions. Diplôme de l'Ecole Pratique des Hautes Etudes. 92p.

Gasco, N., Tixier, P., and Guinet, C. 2010. Results of trials undertaken around Crozet Island using pots to target Patagonian toothfish CCAMLR WG-FSA-10/10. https://www.ccamlr.org/en/wg-fsa-10/10 (last accessed 2 December 2014).

Gilman, E., Brothers, N., McPherson, G., and Dalzell, P. 2006. A review of cetacean interactions with longline gear. Journal of Cetacean Research and Management, 8: 215–223.

Goldsworthy, S. D., Bulman, C., He, X., Larcombe, J., and Littnan, C. 2003. Trophic interactions between marine mammals and Australian fisheries: An ecosystem approach. *In* Marine mammals: Fisheries, tourism and management issues, pp. 62–99. Ed. by N. Gales, M. Hindell, and R. Kirkwood. CSIRO, Collingwood, Australia.

Guerrero, A., and Arana, P. 2009. Fishing yields and size structures of Patagonian toothfish (*Dissostichus eleginoides*) caught with pots and long-lines off far Southern Chile. Latin America Journal of Aquatic Resources, 37: 361–370.

Guinet, C. 1991a. Intentional stranding apprenticeship and social play in Killer Whales (*Orcinus orca*). Canadian Journal of Zoology, 69: 2712–2716.

Guinet, C. 1991b. L'orque autour de l'archipel Crozet, comparaison avec d'autres localités. Revue d' Ecologie (la Terre et la Vie), 46: 321–337.

Guinet, C. 1992. Comportement de chasse des orques (*Orcinus orca*) dans l'archipel Crozet. Canadian Journal of Zoology, 70: 1656–1667.

Guinet, C., Barrett-Lennard, L., and LOYER, B. 2000. Attacks of a minke whale and a southern elephant seal by killer whales at Crozet Archipelago, with underwater observations of feeding and prey sharing. Marine Mammal Science, 16: 829–834.

Guinet, C., and Bouvier, J. 1995. Development of intentional stranding hunting techniques in Killer whale (*Orcinus orca*) calves at Crozet Archipelago. Canadian Journal of Zoology, 73: 27–33.

Guinet, C., Domenici, P., de Stephanis, R., Barrett-Lennard, L., Ford, J. K. B., and Verborgh, P. 2007. Killer whale predation on bluefin tuna: Exploring the hypothesis of the endurance-exhaustion technique. Marine Ecology Progress Series, 347: 111–119.

Guinet, C., Jouventin, P., and Weimerskirch, H. 1999. Recent population change of the southern elephant seal at îles Crozet and îles Kerguelen: The end of the decrease? Antarctic Science, 11: 193–197.

Guinet, C., and Tixier, P. 2011. Crozet Killer Whales: A remote but changing environment. Whalewatcher, 40: 33–38.

Hamer, D. J., Childerhouse, S., and Gales, N. J. 2012. Odontocete bycatch and depredation in longline fisheries: A review of available literature and of potential solutions. Marine Mammal Science, 28: 345–374.

Hucke-Gaete, R., Moreno, C. A., and Arata, J. 2004. Operational interactions of sperm whales and killer whales with the Patagonian toothfish industrial fishery off Southern Chile. CCAMLR Science, 11: 127–140.

Koch, K. H., Purves, M. G., and Duhamel, G. 2006. Interactions between cetacean and fisheries in the Southern Ocean. Polar Biology, 29: 379–388.

Kuningas, S., Similä, T., and Hammond, P. S. 2013. Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003. Journal of the Marine Biological Association of the United Kingdom, doi:10.1017/S0025315413000933

Lesquin, W. 1840. Voyage aux Iles Marion et Crozet. *In* André le voyager, avec des notes nouvelles comprenant le naufrage aux Iles Crozet suivi du Brahme, pp. 125–185. Ed. by F. Denis. L'Editeur, Paris (in French).

Matkin, C. O., Ellis, G., Barrett-Lennard, L. B. L., Yurk, H., Saulitis, E., Scheel, D., Olesiuk, P., *et al.* 2003. Photographicand acoustic monitoring of killer whales in Prince William Sound and Kenai Fjords. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 030012 Final Report). North Gulf Oceanic Society, Homer, Alaska.

Matkin, C. O., Saulitis, E. L., Ellis, G. M., Olesiuk, P., and Rice, S. D. 2008. Ongoing population-level impacts on killer whales *Orcinus orca* following the 'Exxon Valdez' oil spill in Prince William Sound, Alaska. Marine Ecology Progress Series, 356: 269–281.

Mikhalev, Y. A. 1997. Additional information about the catches of Soviet whaling fleet Sovetskaya Ukraina. Reports of the International Whaling Commission, 47: 147–150.

Moreno, C., Castro, R., Mújica, L. J., and Reyes, P. 2008. Significant conservation benefits obtained from the use of a new fishing gear in the Chilean Patagonian toothfish fishery. CCAMLR Science, 15: 79–91.

Nel, D. C., Ryan, P. G., and Watkins, B. P. 2002. Seabird mortality in the Patagonian toothfish longline fishery around the Prince Edward Islands, 1996–2000. Antarctic Science, 14: 151–161.

Nolan, C. P., and Liddle, G. M. 2000. Interactions between killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) with a longline fishing vessel. Marine Mammal Science, 16: 658–664.

Northridge, S. P., and Hofman, R. J. 1999. Marine mammal interactions with fisheries. *In* Conservation and Management of Marine Mammals, pp. 99–119. Ed. by J. R. Twiss, and R. R. Reeves. Smithsonian Institution Press, Washington, DC.

Olesiuk, P., Bigg, M., and Ellis, G. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission, Special Issue, 12: 209–243.

Olesiuk, P. F., Ellis, G. M., and Ford, J. K. B. 2005. Life history and population dynamics of northern resident killer whales in British Columbia. Research document 2005/45. Canadian Science Advisory Secretariat, Fisheries and Oceans Canada, Ottawa, Canada.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. Science, 279: 860–863.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R., *et al.* 2002. Towards sustainability in world fisheries. Nature, 418: 689–695.

Pitman, R. L., Durban, J. W., Greenfelder, M., Guinet, C., Jorgensen, M., Olson, P. A., Tixier, P., *et al.* 2011. Observations of a distinctive morphotype of killer whale (*Orcinus orca*, Type D) from subantarctic waters. Polar Biology. doi: 10.1007/s00300-010-0871-3.

Peterson, M. J., Mueter, F., Criddle, K., and Haynie, A. C. 2014. Killer whale depredation and associated costs to Alaskan sablefish, Pacific halibut and Greenland turbot longliners. PLoS ONE. doi: 10.1371/journal.pone.0088906.

Peterson, M., Mueter, F., Hanselman, D., lunsford, C., Matkin, C., and Fearnbach, H. 2013. Killer whale (*Orcinus orca*) depredation effects on catch rates of six groundfish species: Implications for commercial longline fisheries in Alaska. ICES Journal of Marine System, 70: 1220–1232.

Poncelet, E., Barbraud, C., and Guinet, C. 2010. Population dynamics of killer whales in Crozet Archipelago, Southern Indian Ocean: A mark recapture study from 1977 to 2002. Journal of Cetacean Research and Management, 11: 41–48.

Ponchelet, H. 2003. On achève bien les orques. Le point. http://www.lepoint.fr/actualites-sciences-sante/2007–01–19/on-acheve-bien-les-orques/919/0/53633 (last accessed 2 December 2014).

Purves, M. G. 1997. Catch rates and length composition data of the longline fishery for Dissostichus eleginoides at the Prince Edward Islands: 1996/97. SC-CCAMLR-XVI/BG/ZI, Hobart, 18 pp.

Purves, M. G., Agnew, D. J., Balguerias, E., Moreno, C. A., and Watkins, B. 2004. Killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) interactions with longline vessels in the Patagonia toothfish fishery at South Georgia, South Atlantic. CCAMLR Science, 11: 111–126.

Rabearisoa, N., Bach, P., Tixier, P., and Guinet, C. 2012. Pelagic longline fishing trials to shape a mitigation device of the depredation by toothed whales. Journal of Experimental Marine Biology and Ecology, 432–433: 55–63.

Read, A. J. 2008. The looming crisis: Interactions between marine mammals and fisheries. Journal of Mammalogy, 89: 541–548, Reisinger, R. R., and de Bruyn, P. J. N. 2014. The Prince Edward Islands Killer whales 2006–2013. Photoidentification Catalogue. 31 pp. doi: 10.6084/m9.figshare.971317.

Rendell, L., and Whitehead, H. 2001. Culture in whales and dolphins. Behavioural Brain Science, 24: 309–382.

Roche, C., Gasco, N., Duhamel, G., and Guinet, C. 2007. Marine mammals and demersal long line fishery interactions in Crozet and Kerguelen Exclusive Economic Zones: An assessment of the depredation level. CCAMLR Science Series, 14: 67–82.

Sala, O. E., Chapin, F. S., III, Armesto, J. J., Berlow, R., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., *et al.*2000. Global biodiversity scenarios for the year 2100. Science, 287: 1770–1774.

Saulitis, E. L., Matkin, C. O., and Fay, F. H. 2005. Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in Southern Alaska. Canadian Journal of Zoology, 83: 1015–1029.

Secchi, E. R., and Vaske, J. T. 1998. Killer whale (*Orcinus orca*) sightings and depredation on tuna and swordfish longline catches in Southern Brazil. Aquatic Mammals, 24: 117–122.

Sigler, M. F., Lunsford, C. R., Straley, J. M., and Liddle, J. R. 2006. Sperm whale depredation of sablefish longline gear in the northeast Pacific Ocean. Marine Mammal Science, 24: 16–27.

Tilney, R., and Purves, M. G. 1999. The status of integrated fisheries monitoring in South Africa. *In* Proceedings of the International Conference on Integrated Fisheries Monitoring, pp. 343–356. Ed. by C. P. Nolan. Sydney, Australia, 1–5 February 1999, FAO, Rome.

Tixier, P. 2012. Déprédation par les orques (*Orcinus orca*) et les cachalots (*Physeter macrocephalus*) sur les palangriers à la légine australe dans la ZEE de l'archipel de Crozet. Thèse de Doctorat Université d'Aix Marseille II. 367 pp. http://www.cebc.cnrs.fr/Fthese/PUBLI/Tixier.pdf (last accessed 2 December 2014).

Tixier, P., Gasco, N., Authier, M., and Guinet, C. 2014d. Influence of artificial food provisioning from fisheries on killer whales reproductive output. Animal Conservation, doi: 10.1111/acv.12161.

Tixier, P., Gasco, N., Duhamel, G., and Guinet, C. 2014f. Habituation to an acoustic harassment device (AHD) by killer whales depredating demersal longlines. ICES Journal of Marine Science. doi: 10.1093/icesjms/fsu166.

Tixier, P., Gasco, N., Duhamel, G., Viviant, M., Authier, M., and Guinet, C. 2010. Interactions of Patagonian toothfish fisheries with killer and sperm whales off the Crozet islands: An assessment of depredation levels and insights on possible mitigation solutions. CCAMLR Science Series, 17: 179–195.

Tixier, P., Gasco, N., Roche, C., and Guinet, C. 2014c. Killer whales of the Crozet Islands Austral and Antarctic French Territories. Photo-identification catalogue 2003-2011. doi:10.6084/m9.figshare.1085960.

Tixier, P., Gasco, N., and Guinet, C. 2014b. Killer whales of the Crozet islands, photo-identification catalogue 2014. doi: 10.6084/m9.figshare.1060247.

Tixier, P., Gasco, N., Poupart, T., and Guinet, C. 2014a. Type-D killer whales of the Crozet Islands. doi: 10.6084/m9.figshare.1060259.

Tixier, P., Pardo, D., Barbraud, C., Gasco, N., Duhamel, G., and Guinet, C. (in revision). Demographic consequences of behavioral heterogeneity and interaction with fisheries within a generalist killer whale population. Oecologia.

Tixier, P., Vacquié-Garcia, J., Gasco, N., Duhamel, G., and Guinet, C. 2014e. Mitigating killer whale depredation on demersal longline fisheries by changing fishing practices. ICES Journal of Marine Science. doi:10.1093/icesjms/fsu137.

Voisin, J. F. 1976. On the behaviour of the killer whale, *Orcinus orca*. Norwegian Journal of Zoology, 24: 69–71.

Weimerskirch, H., Capdeville, D., and Duhamel, G. 2000. Factors affecting the number and mortality of seabirds attending trawlers and long-liners in the Kerguelen area. Polar Biology, 23: 236–249.

Whitehead, H. 1998. Cultural Selection and Genetic Diversity in Matrilineal Whales. Science, 282: 1708–1712.

Yano, K., and Dahlheim, M. 1995. Killer whale, *Orcinus orca*, depredation on longline catches of bottomfish in the southeastern Bering Sea and adjacent waters. Fishery Bulletin, 93: 355–372.

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