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Do commercial fisheries display optimal foraging? The case of longline fishers in competition with odontocetes.

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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

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. 2015). 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. 2007; 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. 2015; 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. 2015).

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, 2015). 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. 2015). 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. 2015).

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.

Material and Methods

Data collection and field sites

From January 2008 to July 2015, 22 captains operating on eight legal longliners (50 m long vessels) hauled 6,387 longlines within the Crozet Islands Exclusive Economic Zone (hereafter EEZ) and 19,480 longlines within the Kerguelen Island EEZ (Fig. 1). Fishing occurs all year round and a fishing season spans from September to August. For a given vessel, a fishing season is composed of 3 trips of 3 months each during which the fish caught is 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.

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.

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.

Modelling captains’ decision to stay: 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):

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

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*’:

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

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.

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:

$$\alpha + \beta_1 \text{Fishing success} + \beta_2 (\text{Competition or Nb individuals}) + \beta_3 \text{Fishing success} \times (\text{Competition or Nb individuals}) + \varepsilon = \text{constant}$$

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

$$\Leftrightarrow (\beta_2 + \beta_3 \text{Fishing success}) \times (\text{Competition or Nb individuals}) = \text{constant}$$
$$\Leftrightarrow \beta_2 + \beta_3 \text{Fishing success} = 0$$

Results

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 (Fig. 2 and Table S1).

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 (Fig. 2 & Table S1). 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 (Fig. 2 & Table S1).

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 (Fig. 3). 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 (Fig. 2 & Table S1).

Modelling captains' decision to stay: GLMM

According to the AIC selection (Table S2), 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 (Table S2), but included a random effect on both the slope of the fishing success ($\beta_1 + b_j$) and the intercept ($\alpha + a_j$):

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

The probability to leave, π_{ij} , in absence of cetacean decreased significantly when fishing success increased both at Crozet ($z = -6.49$, $p < 0.001$, Fig. 4.a & Table 1) and at Kerguelen ($z = -8.00$, $p < 0.001$, Fig. 4.b & Table 1). This correlation was independent from cetacean depredation as the interaction term was not significant (Table 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 (Fig. 4 & Table 1), both at Crozet (Fig. 4.a) and Kerguelen (Fig. 4.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: $t = 3.79$, $p = 0.003$, Fig. 5). 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 (Fig. 5).

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 (Fig. 4 & Table 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 ($z = 3.16$, $p = 0.002$, Fig. 4.a. & Table 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 ($z = 2.10$, $p = 0.04$, Fig. 4.a. & Table 1) and at Kerguelen ($z = 6.06$, $p < 0.001$, Fig. 4.b. & Table 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 (Fig. 4.a.). Although this difference was not significant ($z = 1.03$, $p = 0.3$, Table 1).

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 (Table S3):

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

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 Table S3):

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

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 (Table S3):

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

whereas at Kerguelen the random effect was obtained over the slope of the fishing success (Table S3):

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

The fishing success had a significant negative effect on the probability of captains to leave, for all the models (Table 2). 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 (Fig. 6.a. & Table 2). In addition, high between-captain variability in the probability to leave an area in response to the variation in fishing success was detected (Fig. 6.a. & Table 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 (Fig. 7.a. & Table 2) and at Kerguelen (Fig. 7.b. & Table 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 (Fig. 7.b. & Table 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 (Fig. 7.a. & Table 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 ($z=1.75$, $p=0.08$, Fig. 8. & Table 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, Figs. 6.b. & 6.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 (Fig. 6.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 (Fig. 6.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 (Fig. 6.c.). Besides, this relationship changed from positive to negative for a given toothfish daily mass (Fig. 6.c., see following section for the threshold determination).

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 (Fig. 9.a) and $2,700\text{kg}\cdot\text{day}^{-1}$ at Kerguelen (Fig. 9.b). These results suggest that below these mean thresholds, captains were more likely to leave their patch.

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 (Fig. 6.c.). To define this threshold, we resolved the equation determining a constant probability to leave irrespective of the number of cetaceans:

$$(\beta_2 + \beta_3 \text{Fishing success}) \text{Nb cetaceans} = \text{constant}$$

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

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

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

331 $\Leftrightarrow \text{Fishing success} = 5866 \text{ kg.day}^{-1}$

332 As a result, we observed that the probability to leave a patch decreased when the number of cetaceans
333 increased for masses of toothfish caught per day above 5866 kg.day⁻¹ (Fig. 6.c).

336 *Discussion*

337 *Are fishers optimal foragers?*

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

343 *Influence of fishing success*

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

353 Decision making by fishers around Crozet and Kerguelen may reflect a passive adaptive
354 strategy as defined by Clark (Clark 1985), since fishers rely on the constantly updated information
355 provided by the patch to decide whether to leave it or not. Such strategy has been reported to be also
356 used by fishers in more traditional fisheries, resulting in an optimal use of foraging patches (Begossi
357 1992; Aswani 1998). This behaviour of optimal foraging has to be contrasted with a long-term
358 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 to operate 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. 2015) and by sperm whales (Janc et al. unpublished data). 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 (Abe and Iwami 1989). 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.

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 ($\sim 6\text{t}\cdot\text{day}^{-1}$), 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 ($1^\circ \times 0.5^\circ$), 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. in revision). 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. 2014; 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.

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.

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Captions of figures

Fig. 1. Map of Crozet and Kerguelen Islands, southern Indian Ocean, with fishing efforts, i.e. all longlines, positions (in orange). The map was realised with the package *marmap* through the software R.

Fig. 2. 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).

Fig. 3. 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.

Fig. 4. Probability to leave for captains, π , in response to the variation of the standardized toothfish weight caught per day and the competition variable, with the variability between captains in orange (Table 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 (coloured figures are available online).

Fig. 5. Linear regression between the slope ($\beta_l + b_j$) 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.

Fig. 6. 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), 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).

Fig. 7. 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).

Fig. 8. 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). The dashed line represents non-significant relationship (see Table 2).

Fig. 9. 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.

Crozet: threshold (km)
36

Kerguelen: threshold (km)
35

a) Crozet **b) Kerguelen**

a) Crozet

b) Kerguelen

a) Crozet

b) Kerguelen

TABLES

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

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

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

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