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Fishing behaviours and fisher effect in decision- making processes when facing depredation by marine predators

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Abstract :

Fishers aim to optimise cost–benefit ratios of their behaviour when exploiting resources. Avoidance of interactions with marine predators (i.e. their feeding on catches in fishing gear, known as depredation) has recently become an important component of their decisions. How fishers minimise these interactions whilst maximising fishing success is poorly understood. This issue is addressed in a sub-Antarctic, long-line fishery confronted with extensive depredation by sperm whales Physeter macrocephalus and killer whales Orcinus orca by examining a 15-year data set. Whereas a broad range of behaviours was identified from spatio-temporal and operational descriptors, none combined high fishing success with low frequency of interactions. With experience, fishers favoured exploitation of productive patches with high frequencies of interactions over avoidance behaviours. Such decisions, although potentially optimal in the short term, are likely to intensify pressures on fish stocks and impact depredating whales. Therefore, the present study provides additional evidence to inform management decisions pertaining to the coexistence between fisheries and marine predators.

Keywords : experience, individual perceptions, optimal foraging theory, skipper behaviour, sustainability of fish stocks, whale–fisheries interactions

1. INTRODUCTION

Fishers are decision-makers who have a top predator-like foraging behaviour when searching and exploiting patchily distributed fish resources (Bertrand et al. 2007; Bez et al. 2011; Planque et al. 2011). Decision-making processes may be driven by both external factors (e.g. resource availability, environmental conditions, economic circumstances, fishing regulations, presence of other predators, etc.), and internal factors (e.g. fishers' skills/personality and characteristics of boats – Holley & Marchal, 2004; Marchal et al. 2006; Simpson et al. 2011). To model these human behaviours, ecologists have used the optimal foraging theory (OFT) to inform the decision-making process as regards alternatives for optimising cost-benefit ratios (McCay, 1981; Begossi, 1992; Aswani, 1998). Decisions made by fishers, in keeping with the OFT to harvest animal species, aim to maximise the economic benefits by selecting highly-productive patches and to minimise operational costs by limiting travels between patches (Dorn, 2001; Richard et al. 2018).

The propensity of fishers to optimise this cost-benefit ratio through their decisions was found to be greatly influenced by fishers knowledge acquired through past experience and his/her individual perception (Vázquez-Rowe & Tyedmers, 2013; Richard, 2018). Fishers increase their knowledge of the profitability of resources experientially by accumulating and applying a range of acquired information, such as previous fishing successes (both theirs and those of other fishers), fish distributions, expected fishing costs and management regulations (Johannes & Hviding, 2002; Salas & Gaertner, 2004; Andersen et al. 2012). However, variations in individual perceptions, preferences and personality traits, such as patience and risk-taking, across fishers may also influence the decision-making processes (Eggert & Lokina, 2007; Carpenter & Seki, 2011).

Collapses in the world’s fish stocks over the past five decades, combined with increased fishing and environmental regulations, have resulted in a broader and more complex range of factors influencing decisions made by fishers (Cai et al. 2005; Arlinghaus & Cooke, 2009; Gaines et al. 2010). Amongst such factors, interactions with marine predator species in the form of bycatch or depredation (i.e. predators feeding on catches on fishing gear) have grown in severity and have become a major driver of decision-making processes in artisanal and commercial fisheries (Read, 2008; Tixier et al. 2021). Depredation, which primarily involves sharks and marine mammals, has increased considerably in long-line fisheries worldwide (Gilman et al. 2007, 2008; Tixier et al. 2021) and often results in adverse socio-economic and ecological impacts such as (i) greatly reduced catch rates for fishers, (ii) larger uncertainties in stock assessments and (iii) depredating species being accidentally by-caught on gear (Tixier et al. 2021). In anticipation of, or in response to, these impacts, fishers generally implement fishing behaviours (i.e. a set of decisions and strategies related to fishing) aimed to maximise fishing success and minimise depredation-type interactions (hereafter referred to as “interactions”). This is achieved by spatial and temporal avoidance of depredating species and/or by operational changes in the way they use the fishing equipment (Hamer et al. 2012; Werner et al. 2015). For example, avoidance behaviours include the selection of areas and/or time of the year during which the risks of interactions are low, and, when an interaction occurs, the displacement of fishing operations to new fishing grounds located large distances away (Straley et al. 2015; Tixier et al. 2016; Janc et al. 2018). However, avoidance behaviours generate additional socio-economic costs, which are primarily operational, e.g. fuel consumption, non-fishing time and time spent at sea (Peterson et al. 2014; Guinet et al. 2015). Assessing the relationship between these costs and the benefits from preventing interactions is, therefore, essential to identify mitigation solutions that are both economically sustainable for fisheries and environmentally sustainable for the resource and marine predators. However, the extent to which avoidance and operational practices may affect the optimality of fisher behaviours remains poorly known.

The demersal long-line fisheries for Patagonian toothfish *Dissostichus eleginoides* (Smitt, 1898) that operate in the Economic Exclusive Zones (EEZs) of the Crozet and Kerguelen Islands, which are highly regulated and closely monitored, have experienced interactions since their beginning in the mid-1990s. Fishers of this fleet, which has a Total Allowable Catch (TAC) limit set to 6,000 tonnes for the fishing season 2019–2020, face substantial catch losses due to two odontocete species, sperm whale *Physeter macrocephalus* (Linnaeus, 1758) and killer whale *Orcinus orca* (Linnaeus, 1758). Together, these two species remove several hundred tonnes of Patagonian toothfish (henceforth simply ‘toothfish’) from lines every year (Roche et al. 2007; Gasco et al. 2015; Tixier et al. 2020). Multiple aspects of fishing behaviours (i.e. spatio-temporal and operational factors) minimising interactions levels were identified from empirical evidence (Tixier et al. 2015, 2019a; Janc et al. 2018). However, the fishing success was often found to be more important than interactions in influencing decisions made by fishers, whereas large inter-individual variation in the way these fishers perceived the issue was observed (Richard, 2018; Richard et al. 2018). From these findings, the extent to which fishing behaviours, which aim to minimise interactions and maximise fishing success, may affect the fishing global optimality, and the role of fishers effect in choosing one fishing behaviour over another, have yet to be examined.

Using the comprehensive long-term fishing datasets from the toothfish fisheries in EEZ Crozet and EEZ Kerguelen, the aim of the present study was to identify which fishing behaviours were optimal in minimising interactions and maximising fishing success, and the role of that fisher effect had on achieving this optimality. The specific objectives of this study, using a broad range of spatio-temporal and operational descriptors, were to: (i) identify and describe the different fishing behaviours implemented by the fishers; (ii) assess the effects of the fishing behaviours implemented on both the fishing success as “benefit” and the frequency of interactions as “cost”; and (iii) explore the influence of fisher effect on the fishing behaviours implemented.

2. MATERIAL AND METHODS

2.1 Study fisheries and data collection

The data used for this study were collected by fishery observers on-board eight different commercial long-liner boats (lengths: 50–60 m) fishing legally for toothfish in EEZ Crozet (44°–47°S; 48°–54°W) and EEZ Kerguelen (45°–54°S; 62°–76°W) under both national (French) and international (Commission for Conservation of Antarctic Marine Living Resources – CCAMLR) jurisdictions (Figure 1). These data were retrieved from the PECHEKER database (Muséum d’Histoire Naturelle de Paris; Martin & Pruvost, 2007). Long-liner boats operated year round in both EEZs except from 1 February to mid-March in EEZ Kerguelen (closure as seabird bycatch mitigation measure; CCAMLR, 2013). During fishing seasons, from September to August, boats conduct three to four fishing trips, their duration delineated by port departure and return times (Reunion Island). Each fishing trip lasted two to three months during which one fisher was in charge of the fishing – this was generally the skipper, though collective decision-making by a boat crew cannot be excluded. Fishers typically operated by alternating between lines deployment sessions (i.e. setting sessions) and retrieval sessions (i.e. hauling sessions).

The base unit of the dataset is a long-line, each consisting of series of 375 to 47,250 individual hooks automatically baited and attached every 1.2 m from each other on the main line with, at each end, one down-line fitted to one anchor at the bottom and one buoy at the surface. Setting operations were always conducted at night as a seabird conservation measure, at depths ranging from 500 to 3,000 m, and hauling operations were performed mainly during daylight after leaving baited hooks at the bottom from eight hours to five days (soaking duration). For each line, the date, time, number of hooks, GPS coordinates and depth of down-lines at each end of fishing (i.e. setting and hauling) operations, as well as the biomass of toothfish caught, were recorded.

During hauling operations, fishery observers also monitored interactions with sperm whales and/or killer whales by visual surface cues as follows: (i) “Interaction”, whales were observed making repeated dives within an ≈ 500 m radius from the long-liner boat; (ii) “No interaction”, no whales sighted from the long-liner boat or if sighted, then whales were in transit with no observed indicators of interaction with the fishing gear; and (iii) “Uncertain”, observation effort was not provided or not possible due to poor weather, sea or visibility conditions. Catch shares and management policies are established independently for EEZ Crozet and for EEZ Kerguelen. Therefore, when a boat operated in both EEZs during the same trip, two separate trips were considered, one for each EEZ. Fishing trips with an uncertain frequency of interactions greater than 20% were withdrawn to avoid bias due to the high-unconfirmed frequencies (n = 153 of 557 fishing trips). As the frequency of killer whale interactions at EEZ Kerguelen is negligible (< 0.5% of lines; CCAMLR, 2013; Tixier et al. 2019a), sperm whales were considered as the only depredating species at EEZ Kerguelen. As interactions with killer whales were found to be substantially greater than those with sperm whales, in terms catch losses at EEZ Crozet (Gasco et al. 2015), fishers were assumed to respond primarily to the presence of killer whales when the two species simultaneously depredate the same line at EEZ Crozet.

2.2 Selection of fishing trip descriptors

Each fishing trip was characterised by a set of 16 temporal, spatial and operational continuous descriptors selected as potentially affecting the fishing success and/or the frequency of interactions based on current (Table 1) and previous studies (Tixier et al. 2015, 2016, 2019a; Janc et al. 2018; Richard, 2018).

Three temporal descriptors were selected to investigate how a fisher managed time during a fishing trip in a given EEZ, namely the time spent setting lines (*Prop.set.time*), hauling lines (*Prop.haul.time*) or travelling between lines (*Prop.travel.time*). These descriptors were calculated as proportions relative to the total duration of the fishing trip from dates and times of the start and end of the setting or hauling lines. The overall proportion of time allocated to fishing operations relative to non-fishing time (stand-by or travels between lines/patches) was calculated from cumulative time values over the entire fishing trip.

Eight spatial descriptors were selected to examine the use of the fishing zones of an EEZ during a fishing trip depending on whether the fisher tried to maximise the exploitation of the resource or avoid interactions. Two descriptors of the spatial extent and the density of the fishing effort (*Spatial.extent* and *Density.FE*, respectively) were calculated by using the GPS coordinates of the ends of the lines and by gridding the fishing EEZ into cells of 35 × 35 km. The choice of this cell size corresponded to the distance below which the fisher travelled between the end of a setting session and the start of a hauling session to maintain position within an optimal fishing patch (See Richard et al. 2018; for more details on the definition of staying or leaving an optimal fishing patch). *Spatial.extent* was the mean number of 35 × 35 km cells in which at least one line was hauled per day and *Density.FE* was the mean number of hooks set and hauled per 35 × 35 km cell. As Vessel Monitoring System (VMS) data could not be accessed for the study, the movements of the long-liner boat were alternatively examined by means of five descriptors using GPS coordinates of lines during successive fishing operations. Assuming that the boat travelled in a straight line between operations, the overall distance travelled during a fishing trip (*Travel.distance.per.day*) was calculated over all fishing operations as the mean of the distances cumulated per day. The distances travelled within setting sessions (*Inter.set.distance*, *Ai*), or within hauling sessions (*Inter.haul.distance*, *Bi*), were calculated as the mean distance between lines, either successively set or successively hauled, respectively. The mean distances travelled between the end of a setting session and the start of a hauling session (*Set.haul.distance*), and those between the end of a hauling session and the start of a new setting session (*Haul.set.distance*) were calculated. A descriptor assessing the variation in long-liner boat movements between setting and hauling sessions (*Ratio.hauling/setting*) was calculated as the ratio between the cumulative distances travelled between lines successively hauled ($\sum_{i=1}^{S} B_i$) and the cumulative distances travelled between lines successively set ($\sum_{i=1}^{S} A_i$), with S corresponding to the total number of set and hauled lines during the fishing trip. This ratio allowed for a deviation from optimality to be examined as an index ranging from 1 to > 1. The deviation was 1 when the fisher's decisions within hauling sessions were the same as those within setting sessions. This situation was assumed optimal because according to the OFT, the itinerary taken during setting sessions should be the straightest and the shortest between lines, and, therefore, the most optimal as not being subject to any environmental pressure such as interactions with whales. The deviation was > 1 when the fisher's decisions within hauling sessions deviated from optimal itineraries observed during setting sessions, possibly because of risks of interactions during hauling sessions.

Five operational descriptors were selected to describe the way the fisher used fishing equipment during the trip. These descriptors have been shown as factors influencing the frequency of interactions (Tixier et al. 2015; Janc et al. 2018). Mean values were calculated for the line length (*Length.longline*), the fishing depth (*Depth*), the soaking duration (*Soaking.time*) of lines, the hauling speed (*Hauling.speed*) of lines, and the number of lines hauled per day (*Nb.longlines.per.day*).

2.3 Identification and description of fishing behaviours

A fishing behaviour was defined here as a set of temporal, spatial and/or operational fishing descriptors. To explore the different fishing behaviours in each of the two EEZs, principal component analysis (PCA) were applied to the 16 standardised fishing trip descriptors to provide a geometric representation of the dataset structure with the location of observations (i.e. fishing trips) and variables (i.e. fishing trip descriptors) in principle component space (Lewy & Vinther, 1994; He et al. 1997; Pelletier & Ferraris, 2000). The between-fishing trip similarity in fishing behaviours was assumed to capture well within a component space formed by the first principal components (Palmer et al. 2009), being particularly efficient if > 50% of the total variance was captured in the first few principal components.

Hierarchical clustering analysis (HCA) was carried out on the scores derived from the retained principal components to group the fishing behaviours used by fishers into clusters based on similarities amongst them. The Euclidean distance and Ward’s minimum variance methods were used as a measure of similarity (Ward, 1963; Pelletier & Ferraris, 2000; Johnson & Wichern, 2002). The number of clusters that best represented the structure of the dataset was chosen according to the break of the inertia characterising the different levels of clustering in order to maximise the inter-cluster variance with a limited number of clusters. To ensure a representative presentation, clusters containing < 10% of the total number of fishing trips were avoided. The resulting clusters (i.e. fishing behaviours) took into account the variability observed between trips and were considered as similar entities (Alemany & Álvarez, 2003; Rodríguez, 2003; Tzanatos et al. 2006). These clusters could then be projected on PCAs to facilitate their interpretation (Pelletier & Ferraris, 2000).

Both PCA and HCA were implemented in R software (R Core Team, 2020). The function *PCA* in package *FactoMineR* (Lê et al. 2008), and the function *fviz_pca_biplot* in package *factoextra* (Kassambara & Mundt, 2016) were used for PCA. The function *dist* with the *"euclidean"* method and the function *hclust* with the *"ward.D2"* method in package *stats* (R Core Team, 2020), and the function *as.dendrogram* in package *dendextend* (Galili, 2015) were used for HCA. To describe the different fishing behaviours, mean values of fishing trip descriptors were calculated for each fishing behaviour identified and compared to the mean of all trips using Student *t*-test comparisons (Frontier, 1985).

2.4 Fishing behaviours variations with fishing success, interactions and fisher effect

The influence of fisher effect on fishing behaviour, the effect of this behaviour on fishing success and frequencies of interactions with predators were examined for each fishing behaviour identified. The fishing success was calculated as the daily biomass of fish caught throughout the duration of the trip (*Biomass.per.day*). The frequency of interactions was assessed as the proportion of fishing days of a fishing trip with at least one interaction with sperm whales (*Prop.days.sw.only*) or killer whales regardless of the presence of sperm whales (*Prop.days.kw*).

The level of fishers' experience (*Experience*), which was attributed to the skipper for the purposes of the analysis, was assessed during each fishing trip as the number of trips that the corresponding skipper had performed in a given EEZ. Fishing trips with a skipper's experience > 26 and 20 fishing trips at EEZs Kerguelen and Crozet, respectively, were removed (n = 59 of 404 remaining fishing trips) to always have at least three skippers for each level of *Experience*.

Temporal changes in the diversity of fishing practices with increasing skipper experience were measured by Shannon's diversity index (H) and Pielou's equitability index (J) that are defined as follows:

$$H = -\sum_{i=1}^{S} \rho_i \,.\, log_2(\rho_i)$$

$$J = H/H_{max}$$

with i the fishing behaviour, S the total number of fishing behaviours and ρ_i the proportional abundance of the fishing behaviour, defined as follows:

$$\rho_i = \eta_i \,/\, N$$

with η_i the number of fishing trips where the fishing behaviour i was observed and N the total number of trips of all fishing behaviours.

The Shannon's diversity index varied from 0 (when all fishing trips belonged to a single fishing behaviour, or a fishing behaviour dominated all the others) to $H_{max} = log_2(S)$ (when all fishing trips are evenly distributed over all fishing behaviours; Frontier, 1984, 1985; Legendre & Legendre, 1984; Odum, 2014). Pielou's equitability index measures the distribution of fishing trips within fishing behaviours, and varies from 0 (dominance of one fishing behaviour) to 1 (equal distribution of trips within behaviours; Pielou, 1969, 1975). A linear regression was used to explore the relationship between each of the two index (H and J) and the skipper's experience

(*Experience*) both as a single term and in interaction with the fishing zone (*EEZ*) using the function *lm* (Zuur et al. 2009, 2013) in package *stats* in R (R Core Team, 2020). The Pielou's equitability index, because it accounts for different total numbers of potential behaviours at EEZ Kerguelen and EEZ Crozet, allowed comparison of the difference in significance of the intercept and the slope between the two EEZs. The influence of the skipper's individual perception on the choice of one or several fishing behaviours was explored by comparing the frequency of use of different fishing behaviours between skippers sharing the same level of experience, i.e. fishers (*Experience*).

To assess the performance of different fishing behaviours and fisher effect on these behaviours, mean values of *Biomass.per.day, Prop.days.sw.only, Prop.days.kw* and *Experience* were calculated for each fishing behaviour identified and compared to the mean of all trips using Student *t*-test comparisons. Statistical analyses were performed using R (R Core Team, 2020). Means' precisions were represented by the standard error (SE).

3. RESULTS

Data from 63,036 lines from 345 fishing trips (196 and 149 at EEZs Kerguelen and Crozet, respectively) performed between September 2003 and July 2017 were analysed (Figure 1). Fishing trips were longer at EEZ Kerguelen (48 ± 18 [15–85] days, $n = 196$) than at EEZ Crozet (17 ± 10 [4–41] days, $n = 149$). Whereas the fishing success (*Biomass.per.day*) was the highest at EEZ Kerguelen, the extent of whale interactions was the largest at EEZ Crozet where killer whales and/or sperm whales interacted with lines during 72% of the fishing days in that area (*Prop.days.sw.only* and *Prop.days.kw* combined – Table 1).

The fishing success greatly varied between fishers, ranging from 3.2 ± 0.4 to 6.1 ± 0.3 t/day at EEZ Kerguelen, and from 1.3 ± 0.2 to 5.4 ± 1.1 t/day at EEZ Crozet (Supplementary Information document 1, Figure S1). Similarly, fishers experienced varying levels of interactions, ranging from 7 ± 7% to 63 ± 7% for interactions with sperm whales; and from 18 ± 7% to 81 ± 9% for interactions with killer whales (Supplementary Information document 1, Figure S2).

3.1 Identification of fishing behaviours

Three principal components were retained for EEZ Kerguelen, explaining 63% of the total variance (Supplementary Information document 1, Figure S3): PC1 was positively correlated with *Travel.distance.per.day*, *Set.haul.distance*, *Spatial.extent*, *Inter.haul.distance* and *Inter.set.distance*, distinguishing fishing trips spatially dispersed from those spatially concentrated (Figures 2a, 2b, Supplementary Information document 1, Table S1); PC2 was correlated positively with *Prop.set.time* and *Prop.haul.time* and negatively correlated with *Prop.travel.time*, identifying fishing trips during which fishers maximised fishing time and minimised travel time (Figures 2a, 2c, Supplementary Information document 1, Table S1); and PC3 was correlated positively with *Length.longline* and negatively correlated with *Nb.longlines.per.day*, segregating fishing trips during which fishers used fewer but longer lines from fishing trips during which fishers used more but shorter lines (Figures 2b, 2c, Supplementary Information document 1, Table S1).

Two principal components were retained for EEZ Crozet, explaining 55% of the total variance (Supplementary Information document 1, Figure S3): PC1 was correlated positively with *Travel.distance.per.day*, *Inter.haul.distance*, *Prop.travel.time* and *Set.haul.distance* and negatively correlated with *Prop.haul.time*, reflecting fishing trips during which fishers reduced the time spent hauling and increased the time travelling because their fishing operations were spatially dispersed (Figure 3, Supplementary Information document 1, Table S1); and PC2 was correlated positively with *Depth* and *Length.longline* and negatively correlated with *Nb.longlines.per.day*, separating fishing trips during which fishers used fewer but longer and deeper lines from fishing trips during which fishers used more but shorter and shallower lines (Figure 3, Supplementary Information document 1, Table S1).

Six and seven clusters were identified in the HCA for EEZs Kerguelen and Crozet, respectively, representing the different fishing behaviours; these were clearly separated in principle component space for each of the EEZs (Figures 2, 3, Supplementary Information document 1, Figure S4).

3.2 Description of fishing behaviours

At EEZ Kerguelen, fishing trips of clusters *K-1* and *K-2* showed similar spatial and temporal descriptors (both with effort spatially concentrated, more time spent fishing than traveling), but differed in operational descriptors such as the number and the length of long-lines (fewer but longer lines for *K-1*). Cluster *K-3* included trips during which fishers spent more time travelling than fishing, travelled short distances, spatially concentrated their effort, and set the lowest number of lines per day. Cluster *K-4* included trips during which fishers spent more time fishing than travelling, with a spatially dispersed effort, the use of short lines deployed at great depths, and hauled at low speed. Cluster *K-5* included trips whose descriptors were close to the overall mean value for all trips. Cluster *K-6* was characterised by considerable time spent travelling, a spatially-dispersed effort and elevated hauling speeds (Figures 2a, 2b, 2c, Table 2, Supplementary Information document 1, Figure S5a and Table S2).

At EEZ Crozet, clusters *C-1* and *C-2* corresponded to trips during which fishers spent more time travelling than fishing, spatially concentrating their effort, and leaving their lines soaking for long periods. These two clusters differed in the deviation from optimality between distances covered during hauling and setting sessions (greater deviation for *C-2*). For both clusters *C-3* and *C-7*, fishers spent as much time travelling as they did fishing; they travelled large distances, spatially concentrating their effort, and leaving their lines soaking for short periods. However, cluster *C-3* was characterised by the use of a greater number of shorter lines in shallow waters and by the lowest deviation from optimality. Trips in clusters *C-4*, *C-5* and *C-6* differed in their operational descriptors: *C-4* included trips whose descriptors were close to the overall mean value of all trips; *C-5* and *C-6* were differentiated by the number, the length and the depth of lines used (more but shorter lines set shallower for *C-5* – Figure 3, Table 3, Supplementary Information document 1, Figure S5b and Table S3).

3.3 Fishing behaviours variations with fishing success, interactions and fisher effect

At EEZ Kerguelen, the fishing success of clusters *K-3* and *K-4* was significantly lower and that of cluster *K-6* was significantly higher than the mean fishing success of all trips performed. In cluster *K-3*, the frequencies of sperm whale interactions were significantly higher, and those of cluster *K-5* were significantly lower, than the mean occurrence with sperm whales of all trips. The skipper's experience was the lowest in cluster *K-4* and the highest in cluster *K-6*, but these variations were not significantly different than the mean skippers' experience across all trips (Figure 4a, Table 2, Supplementary Information document 1, Table S2).

At EEZ Crozet, the fishing success of cluster *C-6* was significantly lower and that of cluster *C-5* was significantly higher than the mean fishing success of all trips. The frequencies of sperm whale interactions did not vary significantly between each of the seven clusters and the mean occurrence with sperm whales of all trips. However, frequencies of killer whale interactions were significantly lower in clusters *C-4* and *C-6* and significantly higher in cluster *C*-5 than the mean occurrence with killer whales of all trips. The skipper's experience was the lowest in cluster *C-4* and the highest in cluster *C-2*, but these differences were not statistically, significantly different with the mean skippers' experience for all trips (Figure 4b, Table 3, Supplementary Information document 1, Table S3).

The diversity of fishing behaviours used decreased significantly with skippers' experience in both EEZs (Shannon's diversity index: $t = –2.5$, $p = 0.02$ and $t = –4.2$, $p < 0.001$ for EEZs Kerguelen and Crozet, respectively). The tendency to use preferentially certain behaviours over others significantly increased with the skipper's experience (decrease in Pielou's equitability index: $t = –2.6$, $p = 0.02$ and $t = –4.2$, $p < 0.001$ for EEZs Kerguelen and Crozet, respectively; Figure 5, Supplementary Information document 1, Figures S6, S7 and Tables S4, S5). The coefficient and the intercept of the linear regression fitted to the Pielou's equitability were not significantly different between the two EEZs ($t = 1.1$, $p = 0.27$ and $t = –0.2$, $p = 0.82$ for the coefficient and the intercept, respectively; Figure 5b, Supplementary Information document 1, Figure S7 and Table S5). However, fishing behaviours varied across skippers of the same level of experience in both EEZs (Supplementary Information document 1, Figure S8 and Table S6). For example, at EEZ Kerguelen, fishing effort during trips performed by highly-experienced skippers ($Experience \geq 15$) was spatially concentrated for Skipper 7 but spatially diffusive for Skipper 4 (Supplementary Information document 1, Figure S8 and Table S6). These same highly-experienced skippers exhibited similar fishing behaviour regardless of the fishing EEZ (Kerguelen *vs* Crozet).

4. DISCUSSION

4.1 Diversity of fishing behaviours

Three general patterns in the way fishers spatiotemporally used the fishing zones of an EEZ during a fishing trip emerged from the different fishing behaviours identified in this study, with the exception of *K-3* and *K-4*: exploitation, exploration and mixed behaviours (Supplementary Information document 2 for details). Exploitation behaviours included the maximisation of the time allocated to fishing by spatially concentrating effort and the minimisation of patches switching and travelling time between patches. Fishing behaviours *K-1, K-2, C-3* and *C-7* shared this exploitation profile, which was also observed in previous studies and qualified as "area-specialist" behaviour (Hilborn, 1985). According to the OFT, this type of behaviour is expected to generate an optimal cost-benefit ratio if the fishing success of the exploited patches is significantly higher than the mean fishing success in a stochastic and uncertain environment (MacArthur & Pianka, 1966; Charnov, 1976; Danchin et al. 2005). However, fishing success was higher for only two of these exploitation behaviours than the mean success and was not related to lower frequencies of interactions or to the greater experience of fishers. Together, these results may be interpreted as behaviours resulting from fishing trips during which fishers of any experience level have found highly-productive fishing patches and have remained on these patches despite interactions.

Exploration behaviours (*K-6, C-1* and *C-2*) were characterised by increased spatial extent of fishing effort, number of fishing patches and travelling time between patches. According to the

OFT, such “movement-specialist” behavioural profile is expected to be optimal in terms of cost-benefit ratios only if the fishing effort is dispersed between several patches that are productive enough to avoid possible local depletions (Charnov, 1976; Dorn, 2001; Danchin et al. 2005). For fishers, the costs of increased travelling time include extra fuel expenses and costs associated with longer time spent at sea such as food or wages (Parsons, 2003), and these additional costs need to be counterbalanced by high fishing success in multiple patches. As such, this profile was shown to be optimal only when fishers have developed knowledge on the quality of any fishing patch and operated simultaneously in several patches (Hilborn, 1985). This was the case for *K-6*, which was associated with the most experienced fishers and the highest fishing success across all behaviours identified at EEZ Kerguelen. However, at EEZ Crozet, the increased experience of fishers detected for *C-2* did not result in greater fishing success, but instead in a lower frequency of killer whale interactions than that of fishers having the other exploration behaviour identified at EEZ Crozet (*C-1*). Additionally, *C-2* also included trips with greater distances travelled during hauling sessions than those during setting sessions compared to *C-1*. Together, these differences highlight the possibility that exploration behaviours may not only include trips associated with fishers travelling more, and switching patches frequently when searching for resources, but also doing so in response to interactions in order to mitigate them (Janc et al. 2018; Janc, 2019). Although this causality issue may challenge interpretations, fishers moving over large distances away from fishing gear between two successively-hauled lines has often been implemented; this has proved effective in outrunning whales that had depredated on the first hauled line (Peterson & Carothers, 2013; Tixier et al. 2015; Janc et al. 2018).

Mixed behaviours, showing characteristics from both exploration and exploitation behaviours, were identified (*K-5*, *C-4*, *C-5* and *C-6*). This profile may be interpreted as a stochastic fishing behaviour, which is often based on information obtained over short time-frames combining searching for new potentially highly-productive fishing patches; and, if necessary, then also their exploitation for a prolonged period during which higher earnings are anticipated (Allen & McGlade, 1986; Gaertner et al. 1999). In the present study, such rapid decision-making process was found primarily driven by the fishing success. However, it may also be influenced by individual perceptions of fishers towards both the fishing success and interactions with whales (Richard et al. 2018). Individual perceptions can be driven by the level of experience and a broad range of external variables including incentives to limit bycatch, fisheries management policies, and/or the fishing remuneration system (Béné, 1996). At EEZ Crozet and EEZ Kerguelen, variations in perceptions among fishers were reflected by differences in their behaviours being associated with fisher effect. Specifically, at EEZ Crozet, highly experienced fishers were observed to be capable of finding productive fishing patches that were being intensively depredated but decided not to leave these patches despite high frequency of killer whale interactions (behaviour *C-5*), whereas less-experienced fishers sought to minimise interactions but had lower fishing success (behaviour *C-4*).

4.2 Decision-making in response to interactions with marine predators

Amongst all identified fishing behaviours, none combined a high fishing success with low frequencies of predator interaction. Instead, the majority of highly-successful fishing behaviours was associated with high frequencies of predator interaction. This result may be explained by productive fishing patches overlapping with areas characterised by an elevated likelihood of whales' presence. This is supported by the fact that both sperm whales and killer whales are known to feed on toothfish at EEZ Crozet and EEZ Kerguelen (Yukhov, 1972; Tixier et al.

2019b), and therefore they are likely to congregate in patches of high natural density of toothfish. Additionally, the implementation of whale avoidance behaviours by fishers may generate costs that exceed the expected benefits associated with these specific patches, where the possibility of escaping interactions is limited by elevated whale densities and the relatively homogeneous distribution of whales over the fishing patches; this is especially the case at EEZ Crozet (Janc et al. 2018; Labadie et al., 2018). Consequently, fishers may prefer to operate on highly-productive patches whilst concentrating their efforts on mitigating depredation rather than on avoidance of interactions, possibly by trying to reduce the loss of fish to whales during interactions. This was typically the case for clusters *K-6* and *C-5* in which fishers used a greater number of shorter lines, shorter soaking times and/or higher hauling speed. Indeed, these operational practices have already been identified as those that minimise the amount of depredated fish by whales (Tixier et al. 2015; Janc et al. 2018).

Decisions to keep fishing despite the presence of depredating whales, by limiting the costs of travelling and non-fishing time, may be socio-economically optimal for fishers in the short-term if the exploited patches are productive enough and measures reducing catch losses effective enough (Guinet et al. 2015; Richard et al. 2018). However, these decisions may have a number of ecological consequences, which, in the long-term, may retroactively and negatively affect the fishing companies. On one hand, as fishing in the whales' presence increases the amount of depredated fish, this behaviour is likely to increase substantially the fishing pressure on fish stocks and may lead to local depletions of the resource. This effect may be especially strong since the amounts of depredated fish are often underestimated due to depredation events being missed by fishery observers (Towers et al. 2019; Richard et al. 2020). On the other hand, by allowing increased intake of depredated fish for whales, this fishing behaviour may not only modify the ecological role of these species in ecosystems by displacing predator-prey relationships, but also enhance the demographic performances of depredating populations through artificial food provisioning effects (Guinet et al. 2015; Tixier et al. 2015, 2017). Together, increased local depletions of the resource, paired with increased populations of depredating individuals caused by this type of human fishing behaviour, may result in an intensification of the depredation by marine predators. Indeed, a positive correlation between the reproductive output of killer whales and the extent to which they interact with the fishery was evidenced at EEZ Crozet. And, if this effect becomes sufficiently strong to numerically enhance the population, then it may lead to increased interactions and alterations of local ecosystem functioning (Tixier et al. 2015, 2017). Such possible effects are currently not evaluated in the Patagonian toothfish stock assessment and management models, and this would be worth investigating (Guinet et al. 2015). However, the killer whale population in EEZ Crozet, despite a relatively high reproductive output of mature females, is currently decreasing due to a low survival rate attributed to non-authorized long-liner boats, suspected to shoot whales interacting with their fishing activity (Guinet et al. 2015).

In addition to showing an increase of both fishing success and frequencies of interactions with the fishers' experience, the present study also indicated that fishers tended to specialise progressively towards one type of behaviour as they gained experience. A given fisher was also more likely to exhibit the same fishing behaviour regardless of the EEZ they were fishing. However, this type of behaviour varied between the most experienced fishers, further supporting the importance of accounting for fisher effect when modelling catch rates in fish stock assessments. Understanding fishers' perceptions and their associated motivations would also be crucial in determining the causal relationships across the range of variables examined as part of this study (Gaertner et al. 1999; Bertrand et al. 2007). Specifically, to understand better which of a fisher’s specific decisions lead to optimal fishing in a context of depredation by marine predators, it is necessary to determine the role for the observed spatio-temporal and operational components of fishing behaviours; were they responsible for the observed fishing success and frequencies of interactions, or were they implemented in response to fishing success and frequencies of interactions?

By providing a comprehensive description of variables composing the fishing behaviour of fishers, this study has demonstrated both the diversity and the complexity of decision-making processes in a situation where fishers have to maintain profitability of their activity while experiencing costs from interactions with marine predators. Although fishers at EEZ Crozet and EEZ Kerguelen increasingly prioritised greater fishing success over low interactions as they gained fishing experience, this behaviour could be unsustainable over the long-term, both ecologically and economically. However, some fishers were found to implement behaviours intended to minimise these interactions, and although these behaviours were associated with lower fishing success, they are the ones that should receive particular attention to find the compromises needed for a long-lasting management (Supplementary Information document 3 for details). A socio- and bio-economic simulation modelling framework may be a potential next step to the present study by using the combination of other approaches such as: qualitative surveys, discrete choice random utility models (RUM – Andersen et al. 2012), artificial neural networks (ANNs – Palmer et al. 2009), Markov decision processes (Puterman, 2005), or the Kalman filter (Dorn, 2001).

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Figure legends

Figure 1 Spatial distribution of lines hauled in presence of sperm whales as the only depredating species (grey dots), in presence of depredating killer whales whatever the presence of sperm whales (black dots) and fishing grounds (0.1° × 0.1° squares in which at least one line was hauled in the years 2003–2017, light grey squares) at: (a) EEZ Kerguelen (*n* = 196 fishing trips); and (b) EEZ Crozet (*n* = 149 fishing trips).

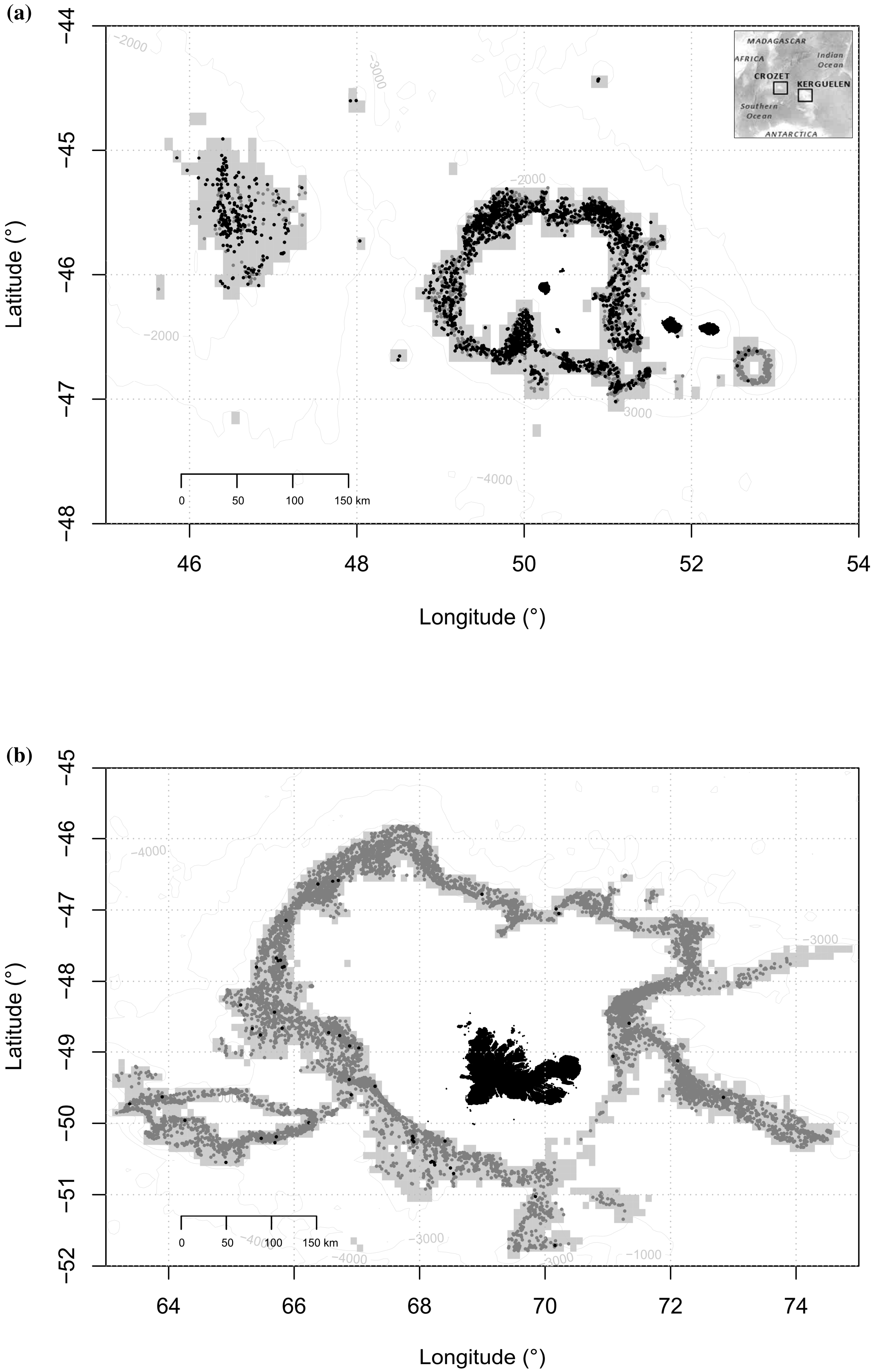
Figure 2 Projection of 16 fishing trip descriptors and observations (i.e. fishing trips) for EEZ Kerguelen (*n* = 196 fishing trips) in the Euclidean space of principal components (PC): (a) PC1 and PC2 (horizontal and vertical axes, respectively); (b) PC1 and PC3 (horizontal and vertical axes, respectively); (c) PC2 and PC3 (horizontal and vertical axes, respectively). Observations are coloured depending on the reference fishing behaviour identified by the hierarchical clustering analysis. Ellipses represent 95% confidence interval around cluster means.

Figure 3 Projection of 16 fishing trip descriptors and observations (i.e. fishing trips) for EEZ Crozet (*n* = 149 fishing trips) in the Euclidean space of principal components one and two (horizontal and vertical axes, respectively). Observations are coloured depending on the reference fishing behaviour identified by the hierarchical clustering analysis. Ellipses represent 95% confidence interval around cluster means.

Figure 4 Boxplots of fishing success, frequencies of interactions and fishers' experience for each fishing behaviour identified at (a) EEZ Kerguelen (*n* = 196 fishing trips); and (b) EEZ Crozet (*n*

= 149 fishing trips) with outliers (black dots), mean values of all trips (red dotted lines) and cluster mean values (black diamonds).

Figure 5 Linear regression lines of the correlation between fishers' experience and (a) Shannon's diversity index (*H*); and (b) Pielou's equitability index (*J*) applied to fishing behaviours identified at EEZ Kerguelen (*n* = 196 fishing trips, grey points and line) and at EEZ Crozet (*n* = 149 fishing trips, black points and line). See Supplementary Information document 1, Figures S6, S7 and Tables S4, S5 for more details on numerical outputs and validation plots for linear regression models.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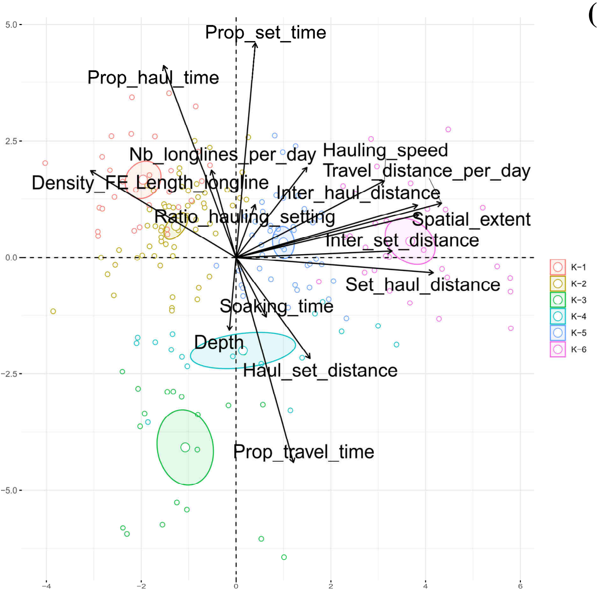
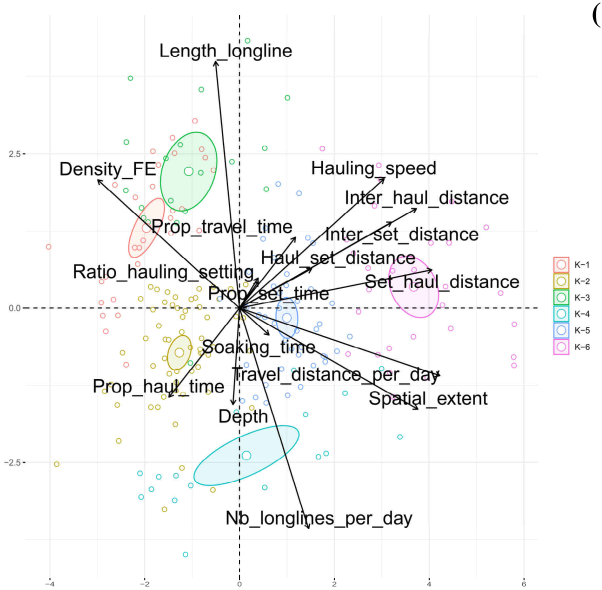
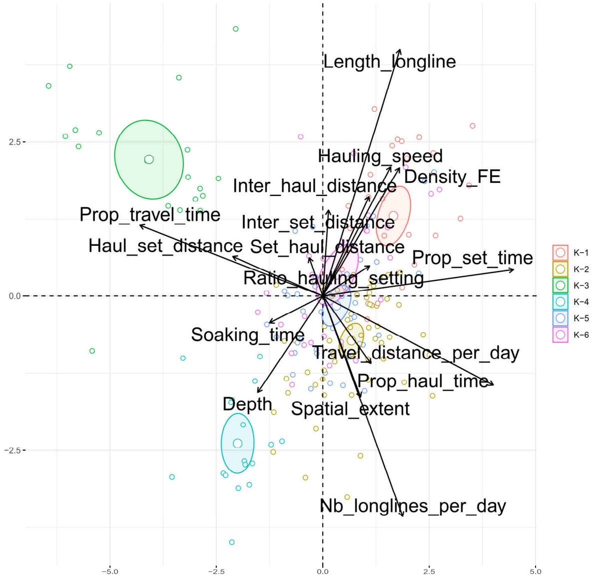
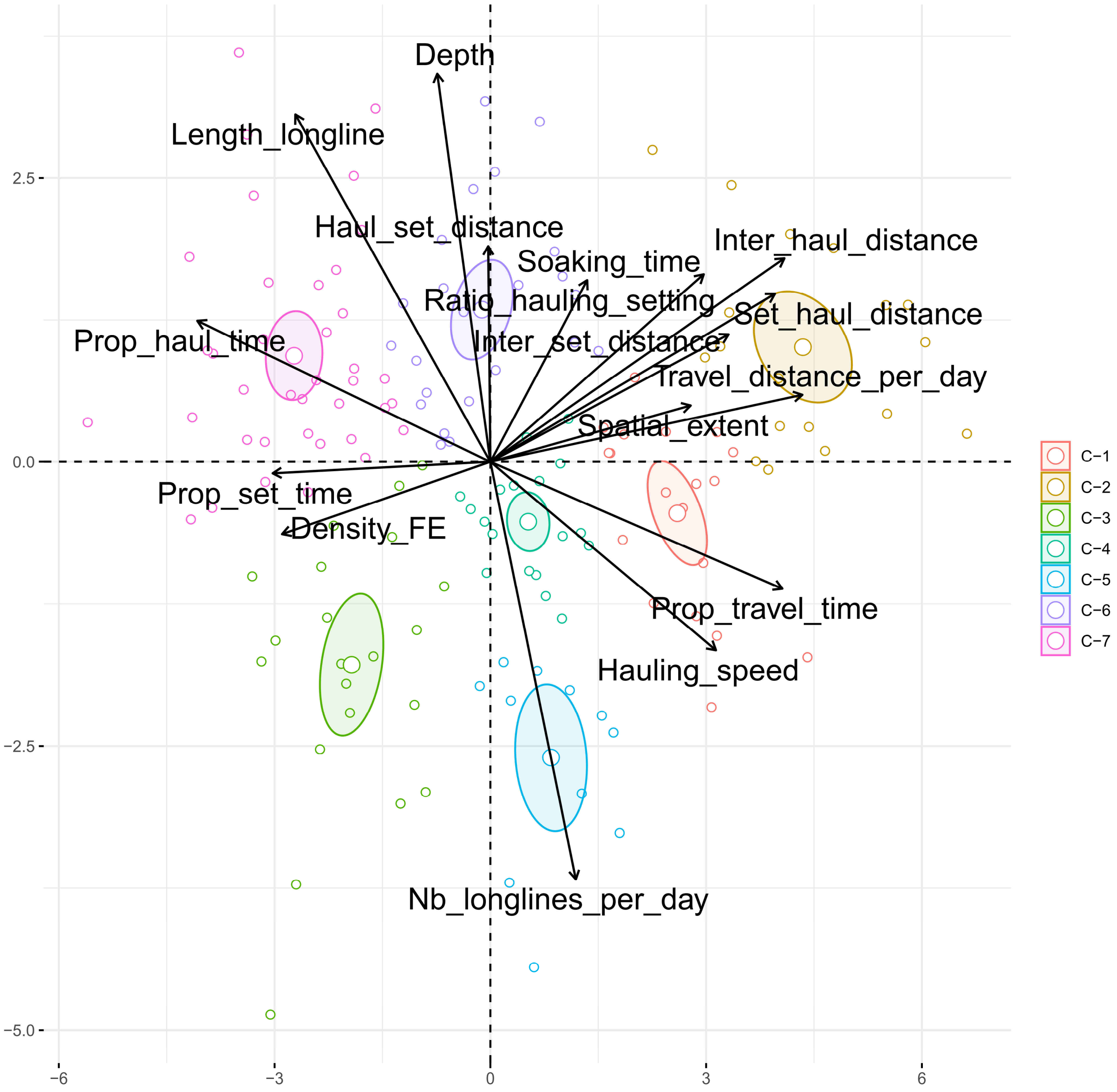

Prop_set_time
Prop_haul_time
Nb_longlines_per_day
Hauling_speed
Travel_distance_per_day
Density_FE
Length_longline
Inter_haul_distance
Ratio_hauling_setting
Spatial_extent
Inter_set_distance
Set_haul_distance
Soaking_time
Depth
Haul_set_distance
Prop_travel_time
5.0
2.5
0.0
-2.5
-5.0
-4
-2
0
2
4
6
K-1
K-2
K-3
K-4
K-5
K-6

(b)

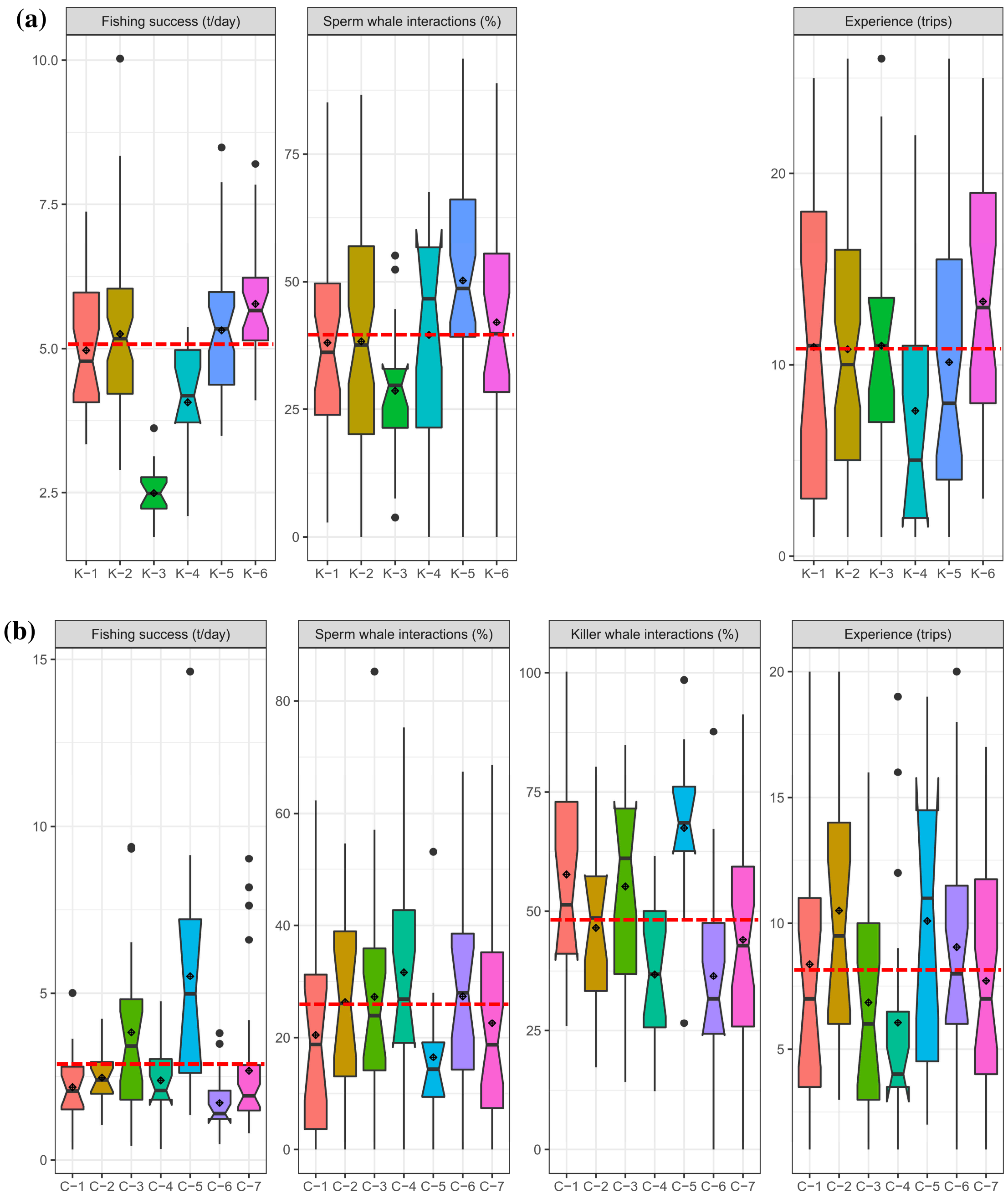

Length_longline
Density_FE
Hauling_speed
Inter_haul_distance
Prop_travel_time
Inter_set_distance
Haul_set_distance
Ratio_hauling_setting
Set_haul_distance
Prop_set_time
Soaking_time
Travel_distance_per_day
Prop_haul_time
Spatial_extent
Depth
Nb_longlines_per_day
2.5
0.0
-2.5
-4
-2
0
2
4
6
K-1
K-2
K-3
K-4
K-5
K-6

(c)

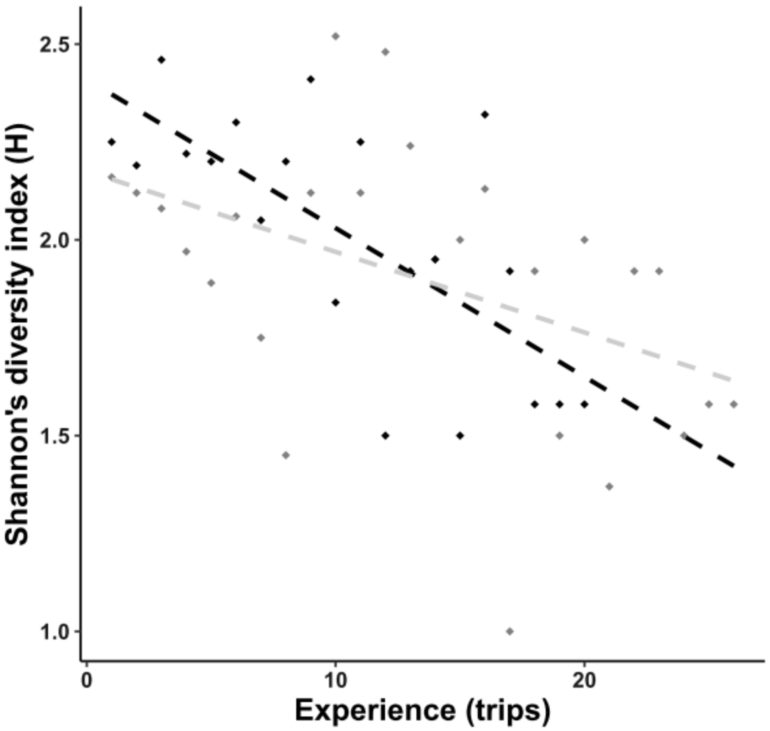

Length_longline
Hauling_speed
Inter_haul_distance
Density_FE
Prop_travel_time
Inter_set_distance
Haul_set_distance
Set_haul_distance
Prop_set_time
Ratio_hauling_setting
Soaking_time
Travel_distance_per_day
Prop_haul_time
Depth
Spatial_extent
Nb_longlines_per_day
2.5
0.0
-2.5
-5.0
-2.5
0.0
2.5
5.0
K-1
K-2
K-3
K-4
K-5
K-6



Depth
Length_longline
Haul_set_distance
Soaking_time
Inter_haul_distance
Ratio_hauling_setting
Set_haul_distance
Prop_haul_time
Inter_set_distance
Travel_distance_per_day
Spatial_extent
Prop_set_time
Density_FE
Prop_travel_time
Hauling_speed
Nb_longlines_per_day
2.5
0.0
−2.5
−5.0
−6
−3
0
3
6
C−1
C−2
C−3
C−4
C−5
C−6
C−7


(a)
Fishing success (t/day)
10.0
7.5
5.0
2.5
K−1 K−2 K−3 K−4 K−5 K−6
Sperm whale interactions (%)
75
50
25
0
K−1 K−2 K−3 K−4 K−5 K−6
Experience (trips)
20
10
0
K−1 K−2 K−3 K−4 K−5 K−6
(b)
Fishing success (t/day)
15
10
5
0
C−1 C−2 C−3 C−4 C−5 C−6 C−7
Sperm whale interactions (%)
80
60
40
20
0
C−1 C−2 C−3 C−4 C−5 C−6 C−7
Killer whale interactions (%)
100
75
50
25
0
C−1 C−2 C−3 C−4 C−5 C−6 C−7
Experience (trips)
20
15
10
5
C−1 C−2 C−3 C−4 C−5 C−6 C−7

(a)


Shannon's diversity index (H)
2.5
2.0
1.5
1.0
0
10
20
Experience (trips)

(b)

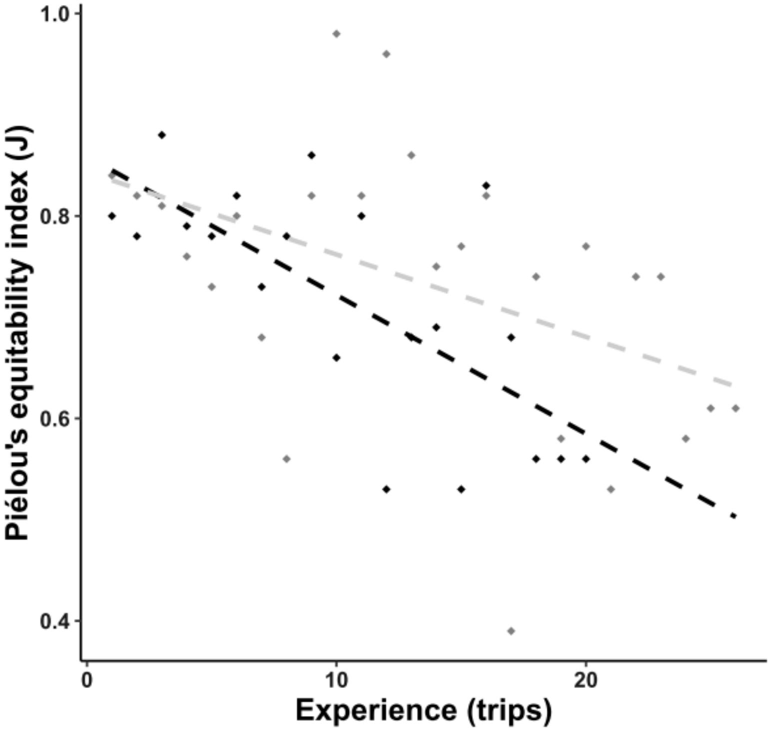

Piélou's equitability index (J)
1.0
0.8
0.6
0.4
0
10
20
Experience (trips)

Table 1 Description and statistical summary of 16 fishing trip descriptors (used for the identification of fishing behaviours) and optimality indicators (e.g. fishing success, frequencies of interactions and fishers' experience) at EEZ Kerguelen and EEZ Crozet.

			KERGUELEN (*n* = 196 fishing trips)						**CROZET** (*n* = 149 fishing trips)					
		Unit	**Mean**	**±**	**SE**	**Min**	**–**	**Max**	**Mean**	**±**	**SE**	**Min**	**–**	**Max**
Temporal descriptors	*Prop.set.time*	%	8.9	±	0.1	3.1	–	14.1	7.5	±	0.1	2.1	–	13.5
	Prop.haul.time	%	47.7	±	0.4	20.2	–	63.0	40.1	±	0.6	12.3	–	61.4
	Prop.travel.time	%	43.3	±	0.5	24.7	–	76.6	52.2	±	0.7	28.0	–	85.5
Spatial descriptors	*Spatial.extent*	No. of cells/day	0.4	±	0.01	0.1	–	0.9	0.6	±	0.01	0.1	–	1.5
	Density.FE	No. of hooks ($x10^3$)/cell	63.0	±	1.0	25.0	–	150.0	37.0	±	1.0	10.0	–	156.0
	Travel.distance.per.day	km/day	76.6	±	1.0	21.0	–	147.8	110.2	±	2.6	17.8	–	235.6
	Inter.set.distance	km	5.3	±	0.1	2.6	–	12.6	7.8	±	0.2	3.2	–	50.9
	Set.haul.distance	km	18.6	±	0.2	9.5	–	35.2	29.5	±	0.9	6.4	–	81.8
	Inter.haul.distance	km	11.0	±	0.2	4.7	–	22.0	16.7	±	0.6	3.2	–	50.9
	Haul.set.distance	km	40.2	±	0.7	9.1	–	90.2	44.5	±	1.4	5.8	–	182.4
	Ratio.hauling/setting	without unit	2.2	±	0.03	1.1	–	4.4	2.3	±	0.05	0.6	–	6.5
Operational descriptors	*Nb.longlines.per.day*	No. of lines set/day	2.6	±	0.03	0.8	–	4.3	3.0	±	0.04	0.9	–	5.9
	Length.longline	km	10.4	±	0.1	5.0	–	17.1	7.6	±	0.1	3.6	–	17.2
	Depth	m	1188.0	±	9.0	729.0	–	1802.0	1119.0	±	14.0	617.0	–	1702.0
	Soaking.time	h/line	22.9	±	0.2	14.2	–	50.3	26.0	±	0.6	10.9	–	53.4
	Hauling.speed	No. of hooks/min	32.0	±	0.3	18.4	–	45.1	32.3	±	0.4	17.5	–	51.8
Optimality indicators	*Biomass.per.day*	t/day	4.9	±	0.1	1.7	–	10.0	2.8	±	0.1	0.3	–	14.6
	Prop.days.sw.only	%	41.0	±	1.0	0.0	–	94.0	25.0	±	1.0	0.0	–	85.0

Prop.days.kw	%	0.4	±	0.1	0.0	–	9.0	47.0	±	1.0	0.0	–	100.0
Experience	No. of trips	10.8	±	0.4	1.0	–	26.0	8.2	±	0.3	1.0	–	20.0

Table 2 Summary of fishing behaviours and their respective optimality indicators (e.g. fishing success, frequencies of interactions and fishers' experience) for each identified fishing behaviour at EEZ Kerguelen (*n* = 196 fishing trips). "+++/——" indicate a significantly positive/negative difference ($p \leq 0.05$) relative to the mean of all trips, "+/–" indicate a positive/negative difference but no significant ($0.05 < p \leq 0.10$), and "ns" indicate no difference ($p > 0.10$). See Supporting Information document 1, Figures S5a, 4a and Table S2 to view boxplots of fishing trip descriptors and optimality indicators as well as for more details on Student *t*-test comparisons between each fishing behaviour and the set of trips.

		K-1	***K-2***	***K-3***	***K-4***	***K-5***	***K-6***
Temporal descriptors	*Prop.set.time*	+++	+++	——	——	ns	+++
	Prop.haul.time	+++	+++	——	——	ns	——
	Prop.travel.time	——	——	+++	+++	ns	+++
Spatial descriptors	*Spatial.extent*	——	——	——	+++	+++	+++
	Density.FE	+++	+++	ns	——	——	——
	Travel.distance.per.day	——	——	——	ns	+++	+++
	Inter.set.distance	——	——	ns	ns	ns	+++
	Set.haul.distance	——	——	ns	ns	+++	+++
	Inter.haul.distance	ns	——	——	ns	+++	+++
	Haul.set.distance	ns	——	+++	+++	ns	+++
	Ratio.hauling/setting	ns	ns	ns	ns	ns	ns
Operational descriptors	*Nb.longlines.per.day*	——	+++	——	+++	+++	+++
	Length.longline	+++	——	ns	——	ns	ns
	Depth	ns	ns	ns	+++	ns	ns
	Soaking.time	ns	ns	ns	ns	ns	ns
	Hauling.speed	ns	——	ns	——	+++	+++
Optimality indicators	*Biomass.per.day*	ns	+	——	——	+	+++
	Prop.days.sw.only	ns	ns	——	+	+++	ns
	Experience	ns	ns	ns	–	ns	+

Table 3 Summary of fishing behaviours and their respective optimality indicators (e.g. fishing success, frequencies of interactions and fishers' experience) for each identified fishing behaviour at EEZ Crozet (n = 149 fishing trips). "+++/——" indicate a significantly positive/negative difference ($p \leq 0.05$) relative to the mean of all trips, "+/–" indicate a positive/negative difference but no significant ($0.05 < p \leq 0.10$), and "ns" indicate no difference ($p > 0.10$). See Supporting Information document 1, Figures S5b, 4b and Table S3 to view boxplots of fishing trip descriptors and optimality indicators as well as for more details on Student t-test comparisons between each fishing behaviour and the set of trips.

		C-1	***C-2***	***C-3***	***C-4***	***C-5***	***C-6***	***C-7***
Temporal descriptors	*Prop.set.time*	——	——	+++	ns	ns	ns	+++
	Prop.haul.time	——	——	+++	——	——	ns	+++
	Prop.travel.time	+++	+++	——	+++	+++	ns	——
Spatial descriptors	*Spatial.extent*	+++	+++	ns	ns	ns	ns	——
	Density.FE	——	——	ns	ns	ns	ns	+++
	Travel.distance.per.day	+++	+++	——	ns	ns	ns	——
	Inter.set.distance	+++	+++	——	ns	ns	ns	——
	Set.haul.distance	+++	+++	——	ns	——	ns	——
	Inter.haul.distance	+++	+++	——	ns	——	ns	——
	Haul.set.distance	ns	ns	ns	ns	ns	ns	ns
	Ratio.hauling/setting	ns	+++	——	ns	ns	ns	ns
Operational descriptors	*Nb.longlines.per.day*	+++	ns	+++	ns	+++	——	——
	Length.longline	——	——	——	——	——	+++	+++
	Depth	ns	ns	——	ns	——	+++	+++
	Soaking.time	+++	+++	——	ns	——	ns	——
	Hauling.speed	+++	+++	——	ns	+++	——	——
Optimality indicators	*Biomass.per.day*	–	–	+	–	+++	——	ns
	Prop.days.sw.only	–	ns	ns	+	–	ns	–
	Prop.days.kw.only	+	ns	+	——	+++	——	ns
	Experience	ns	+	–	–	+	ns	ns

Supporting Information document 1

Fishing behaviours and fisher effect in decision-making processes when facing depredation by marine predators

Anaïs Janc, Christophe Guinet, David Pinaud, Gaëtan Richard, Pascal Monestiez, Paul Tixier

Figures and tables

Figure S1 Boxplots of fishing success per fishing trip for each skipper at EEZ Kerguelen (*n* = 196 fishing trips); and EEZ Crozet (*n* = 149 fishing trips) with outliers (black dots), mean values of all trips (red dotted lines) and skipper mean values (black diamonds).

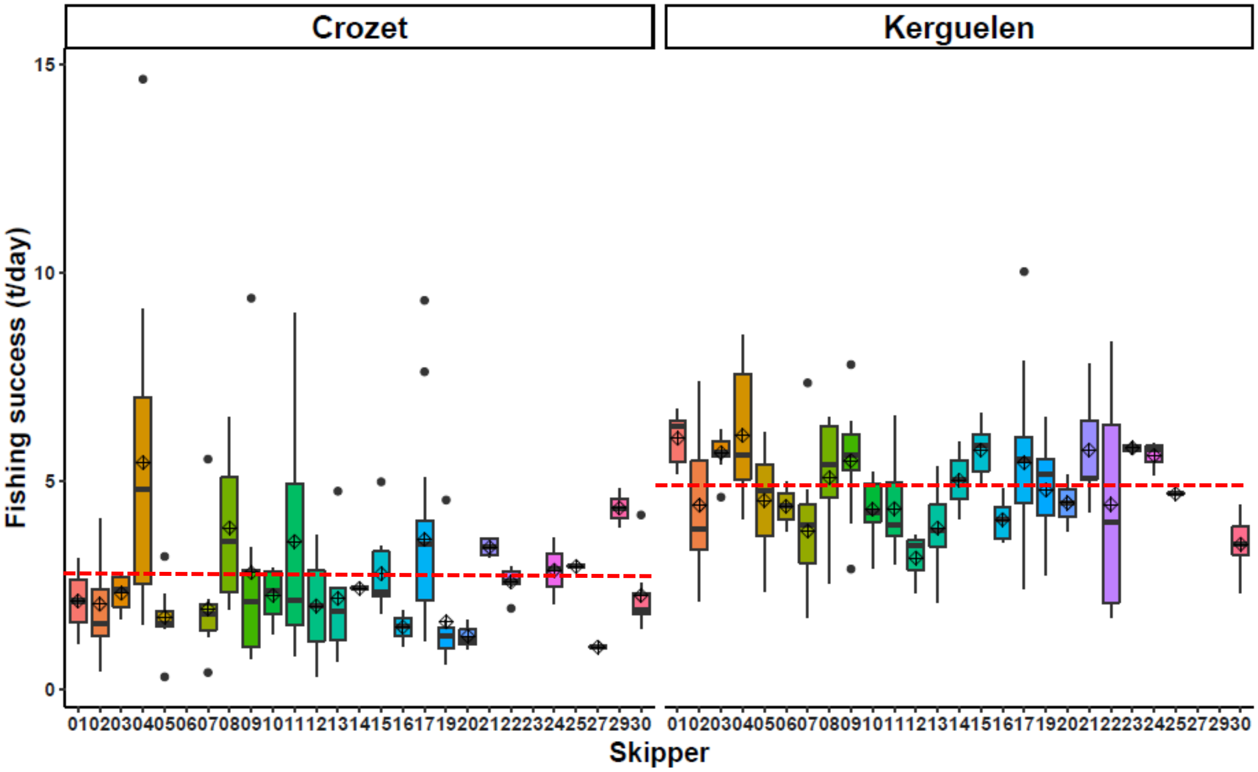


Figure S2 Boxplots of frequencies of interactions (as a proportion of the fishing days) when interactions occurred with (a) sperm whales only (*Prop.days.sw.only*); and (b) with killer whales regardless of the presence of sperm whales (*Prop.days.kw*) for each skipper at EEZ Kerguelen (*n* = 196 fishing trips); and EEZ Crozet (*n* = 149 fishing trips), with outliers (black dots), mean values of all trips (red dotted lines) and skipper mean values (black diamonds).

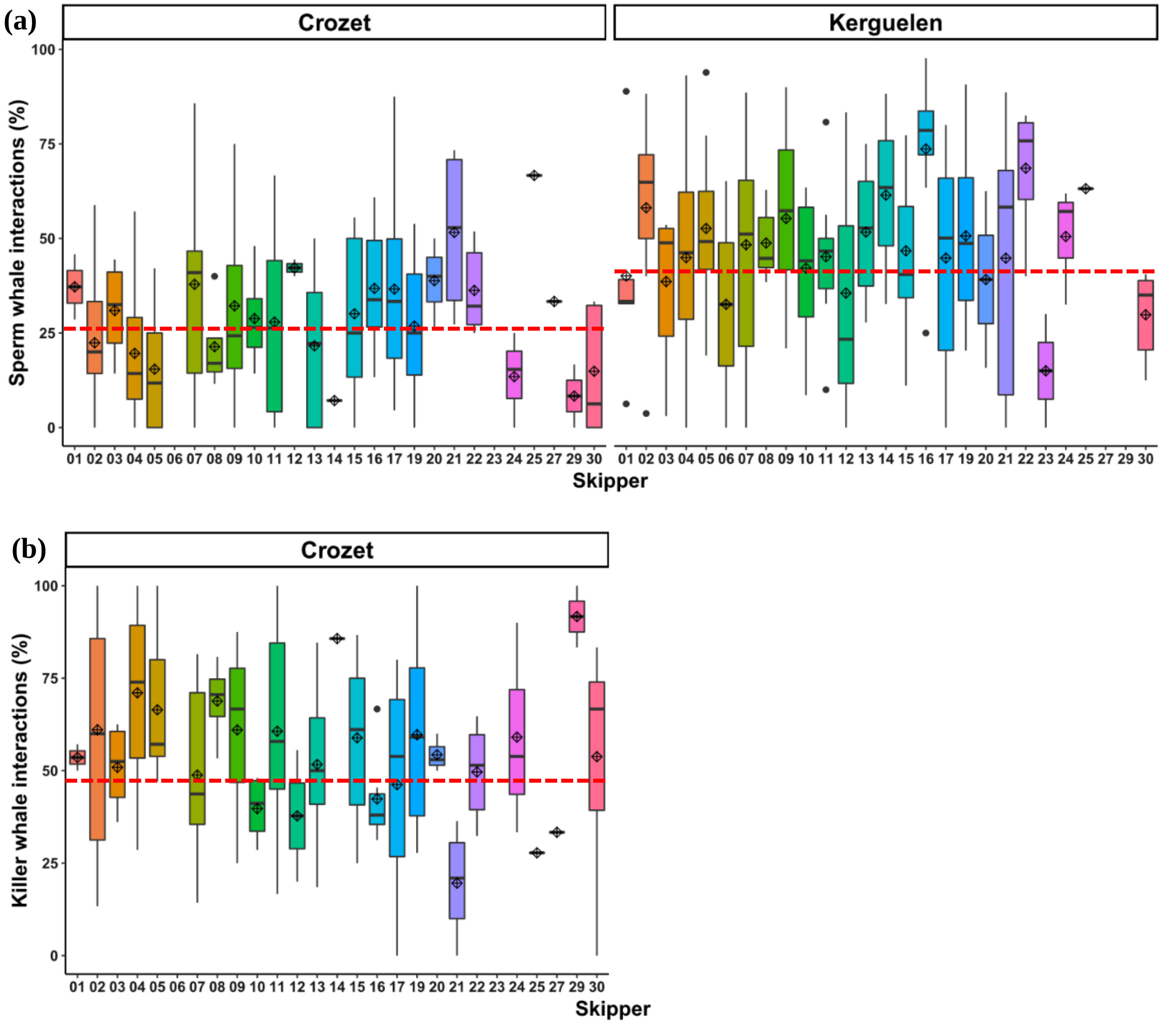


Figure S3 Percentage of total variance explained by each principal component for (a) EEZ Kerguelen (*n* = 196 fishing trips); and (b) EEZ Crozet (*n* = 149 fishing trips). The first three and two principal components were retained for EEZs Kerguelen and Crozet, respectively.

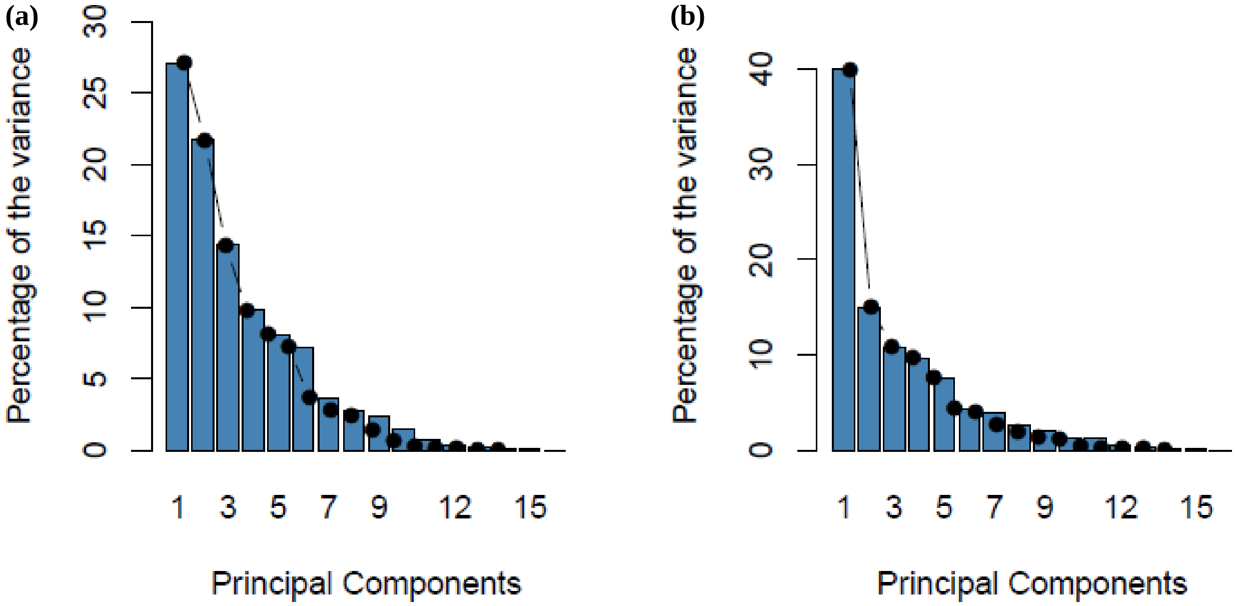


Figure S4 Dendrograms from the hierarchical clustering analysis conducted on fishing trip descriptors with: (a) six clusters at EEZ Kerguelen (*n* = 196 fishing trips); and (b) seven clusters at EEZ Crozet (*n* = 149 fishing trips). The Ward's hierarchical clustering method and the Euclidean distance function were used over the scores of the retained principal components. The inertia recorded for each cluster is indicated (top right). Clusters are coloured depending on the reference fishing behaviour identified by the hierarchical clustering analysis; and the composition of fishing trips are specified for each cluster. See Supporting Information document 1, Tables S2 and S3 for more details on the statistical description of fishing behaviours obtained at EEZs Kerguelen and Crozet, respectively.

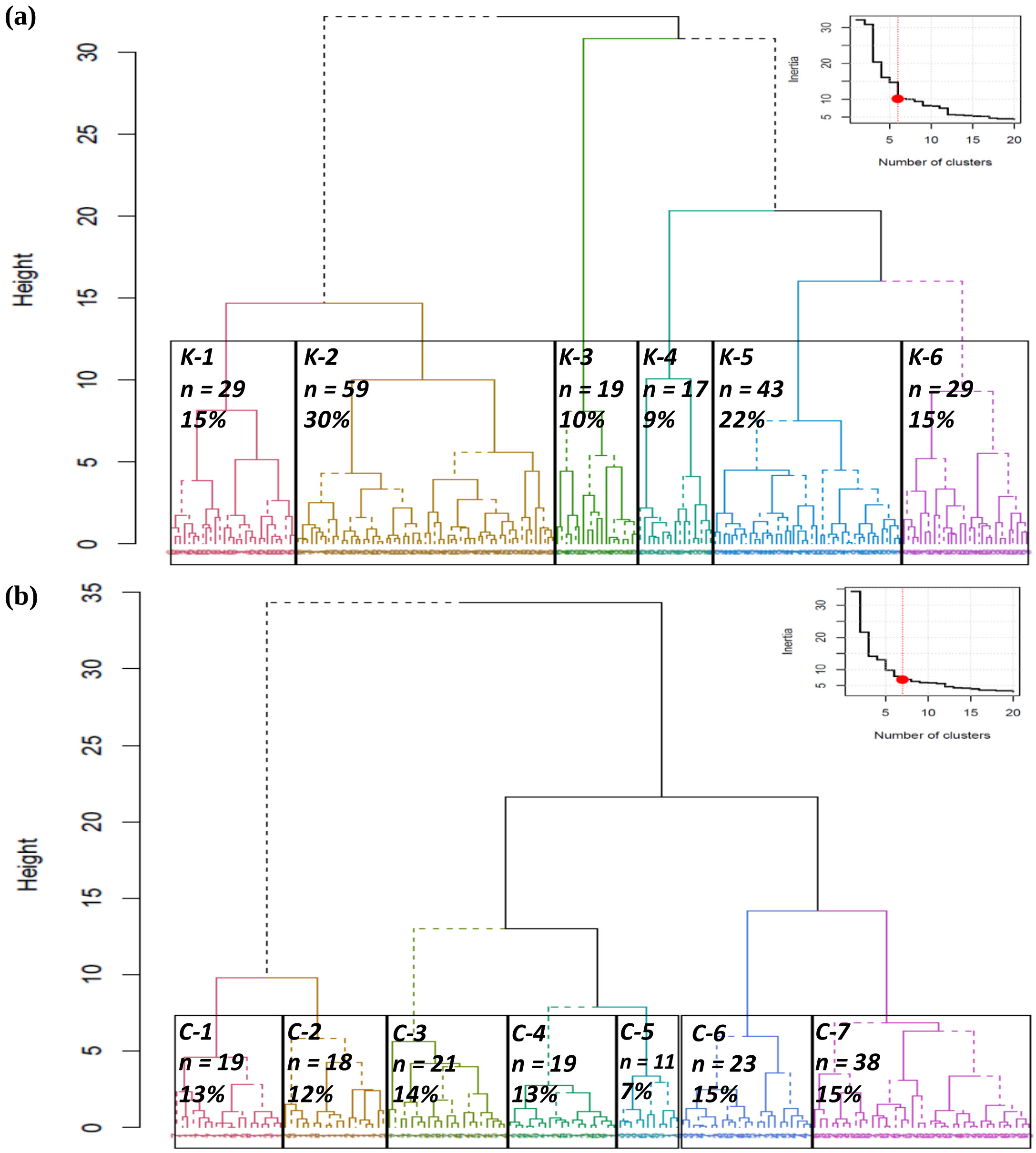
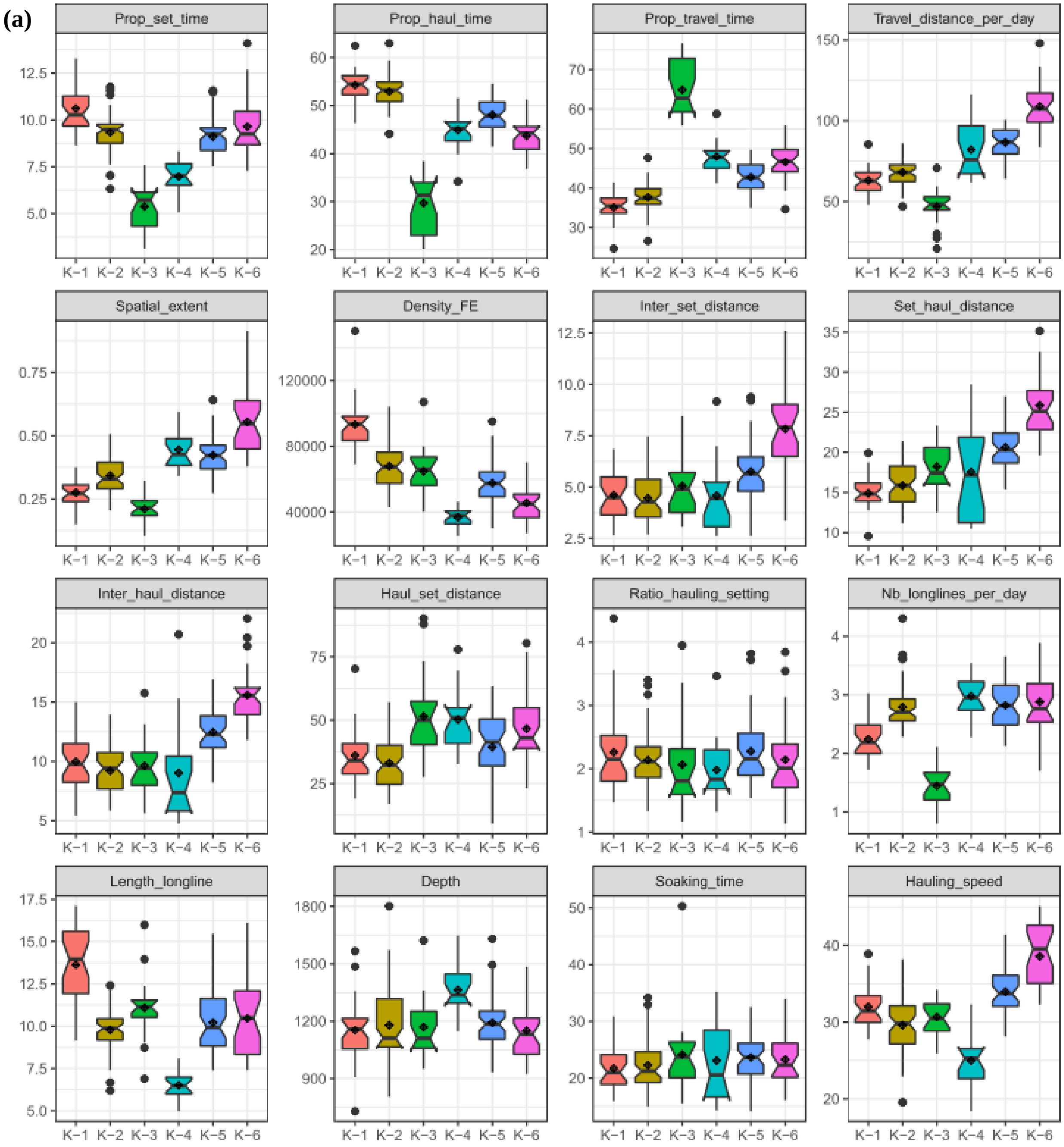


Figure S5 Boxplots of fishing trip descriptors for each fishing behaviour identified at (a) EEZ Kerguelen (*n* = 196 fishing trips); and (b) EEZ Crozet (*n* = 149 fishing trips) with outliers (black dots) and cluster mean values (black diamonds).



(b)

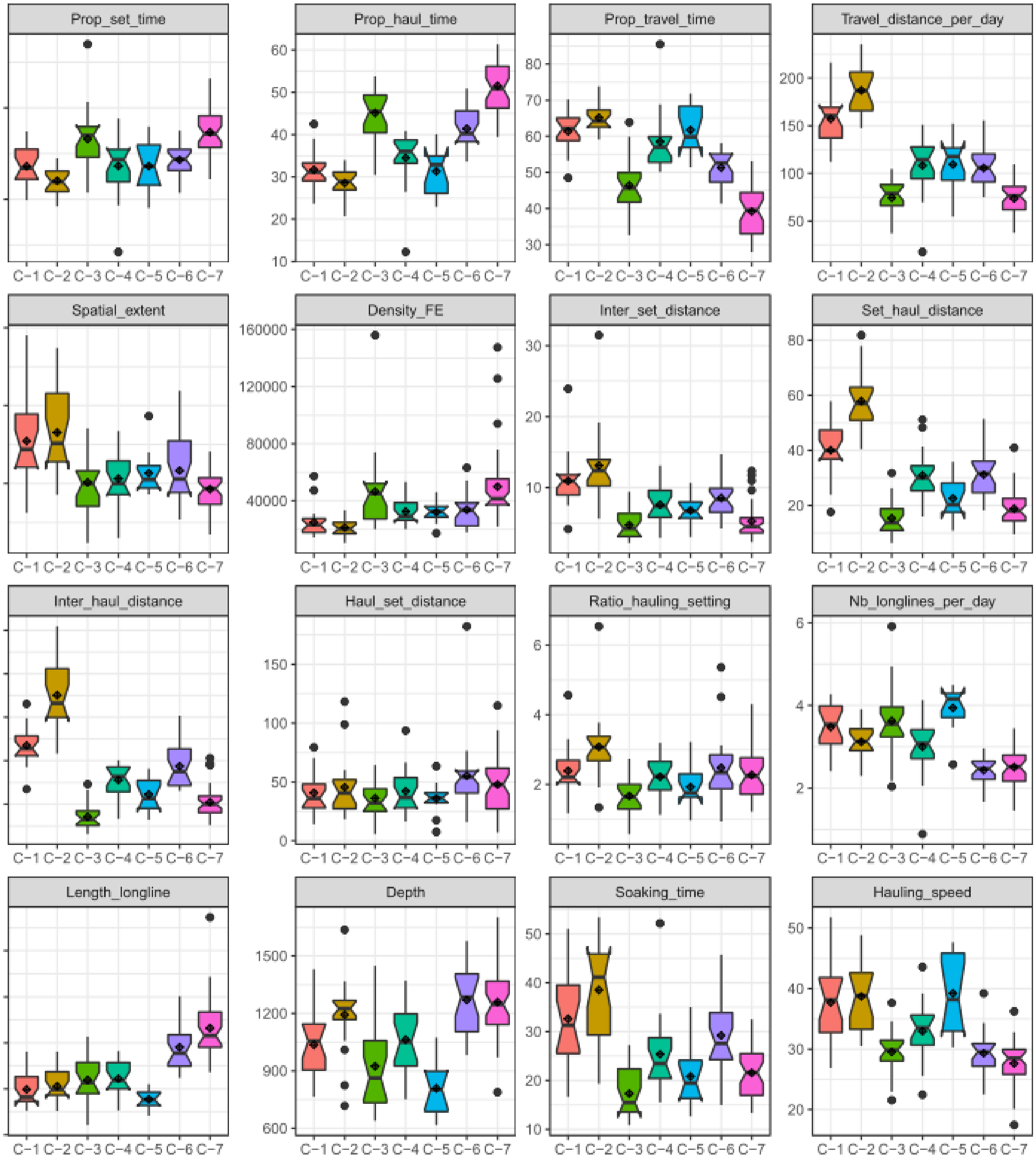
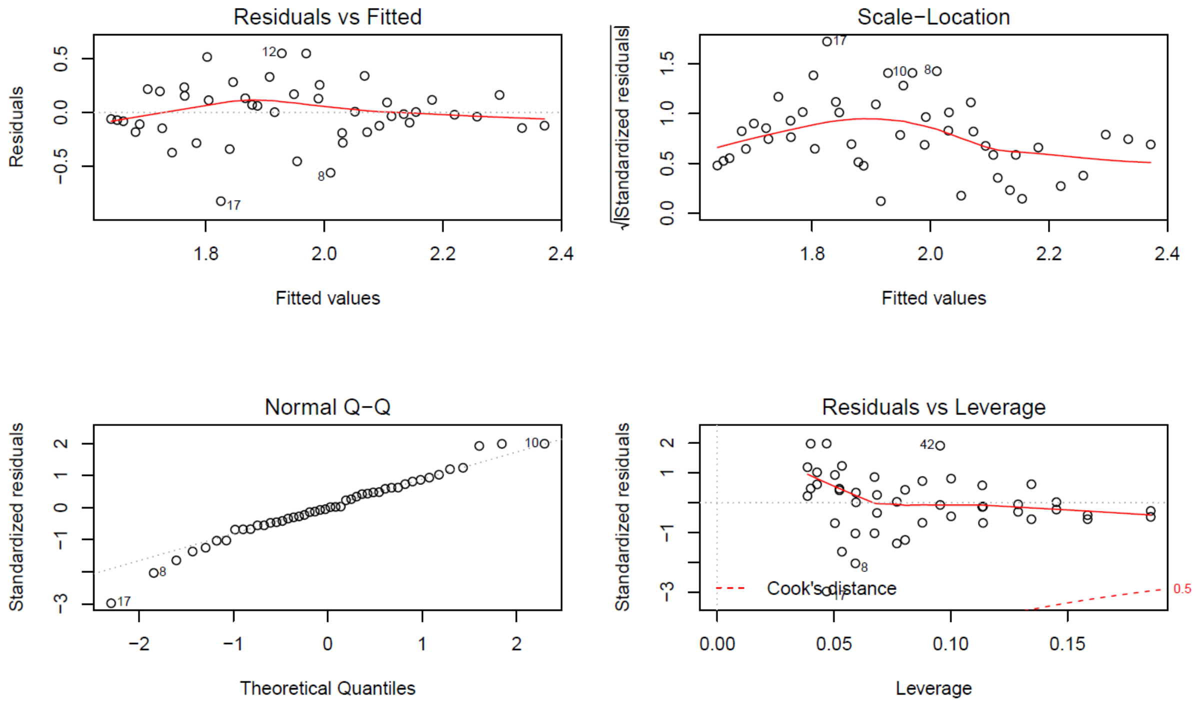

Prop_set_time
5
10
Prop_haul_time
10
20
30
40
50
60
Prop_travel_time
30
40
50
60
70
80
Travel_distance_per_day
50
100
150
200
Spatial_extent
0.5
1.0
1.5
Density_FE
40000
80000
120000
160000
Inter_set_distance
10
20
30
Set_haul_distance
20
40
60
80
Inter_haul_distance
10
20
30
40
50
Haul_set_distance
0
50
100
150
Ratio_hauling_setting
2
4
6
Nb_longlines_per_day
2
4
6
Length_longline
3
6
9
12
15
Depth
600
900
1200
1500
Soaking_time
10
20
30
40
50
Hauling_speed
20
30
40
50
C−1
C−2
C−3
C−4
C−5
C−6
C−7

Figure S6 Validation plots for the linear regression model fitted to the Shannon's diversity index (*H*). See Supporting Information document 1, Table S4 for more details on numerical outputs.



Details on testing assumptions about the linear model:

Shapiro-wilk normality test: $W = 0.98$, $p = 0.43$

Rainbow linearity test: $Rain = 1.18$, $p = 0.36$

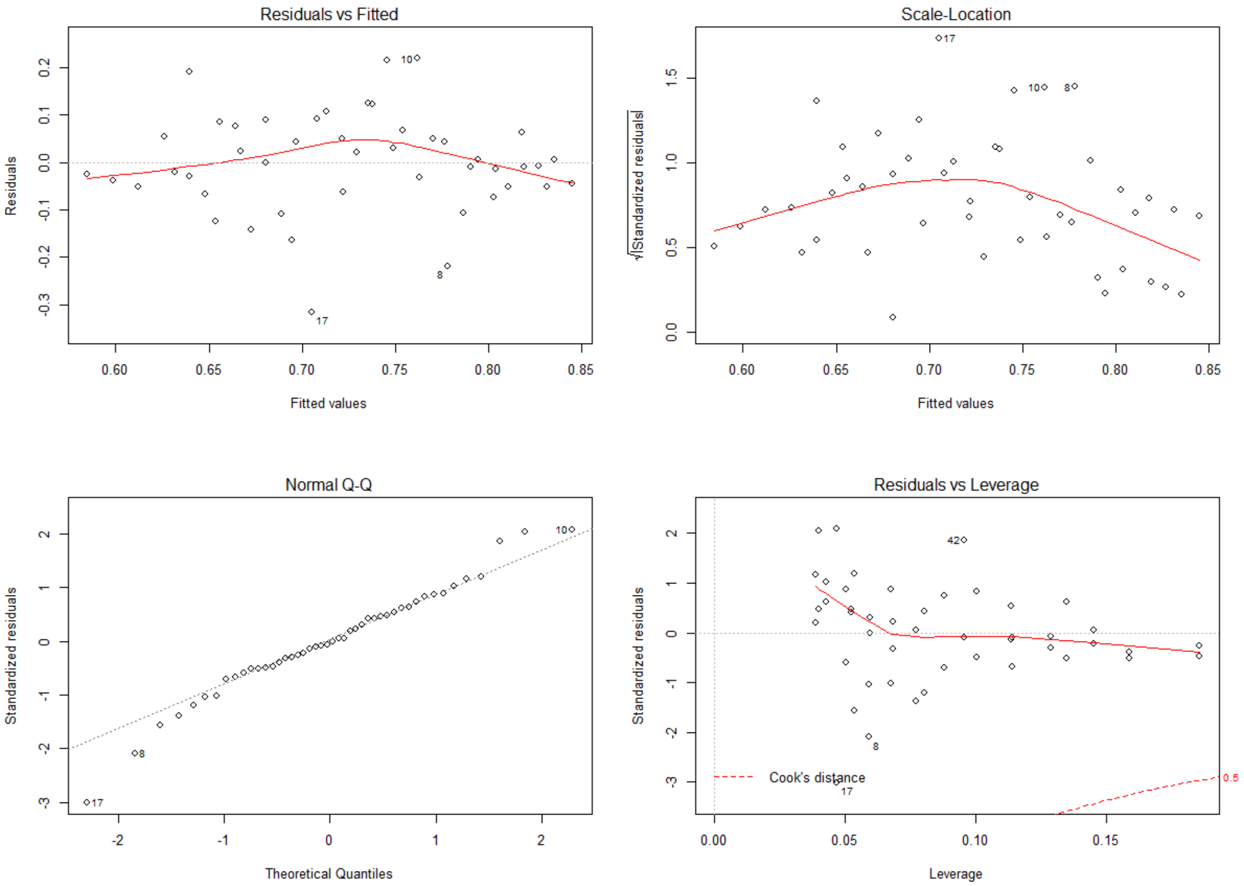
Goldfeld-Quandt variance homogeneity test: $QG = 0.42$, $p = 0.97$

Durbin-Watson residues independence test: $DW = 2.17$, $p = 0.55$

VIF (Variance Inflation Factors) values for collinearity absence test:

Experience = 3.35, *EEZ* = 4.28, *Experience:EEZ* = 7.71

Figure S7 Validation plots for the linear regression model fitted to the Piélou's equitability index (*J*). See Supporting Information document 1, Table S5 for more details on numerical outputs.



Details on testing assumptions about the linear model:

Shapiro-wilk normality test: *W* = 0.97, *p* = 0.39

Rainbow linearity test: *Rain* = 1.17, *p* = 0.37

Goldfeld-Quandt variance homogeneity test: *QG* = 0.37, *p* = 0.98

Durbin-Watson residues independence test: *DW* = 2.15, *p* = 0.52

VIF (Variance Inflation Factors) values for collinearity absence test:

Experience = 3.35, *EEZ* = 4.28, *Experience:EEZ* = 7.71

Figure S8 Frequencies of fishing behaviours observed in the different skippers at (a) EEZ Kerguelen (*n* = 196 fishing trips); and (b) EEZ Crozet (*n* = 149 fishing trips). Skippers are listed in ascending order of experience (*Experience*). See Supporting Information document 1, Table S6 for more details on the relative distribution of trips according to the three general spatio-temporal patterns emerged from the different fishing behaviours identified in this study (e.g. exploitation, exploration and mixed behaviours) for the most experienced skippers.

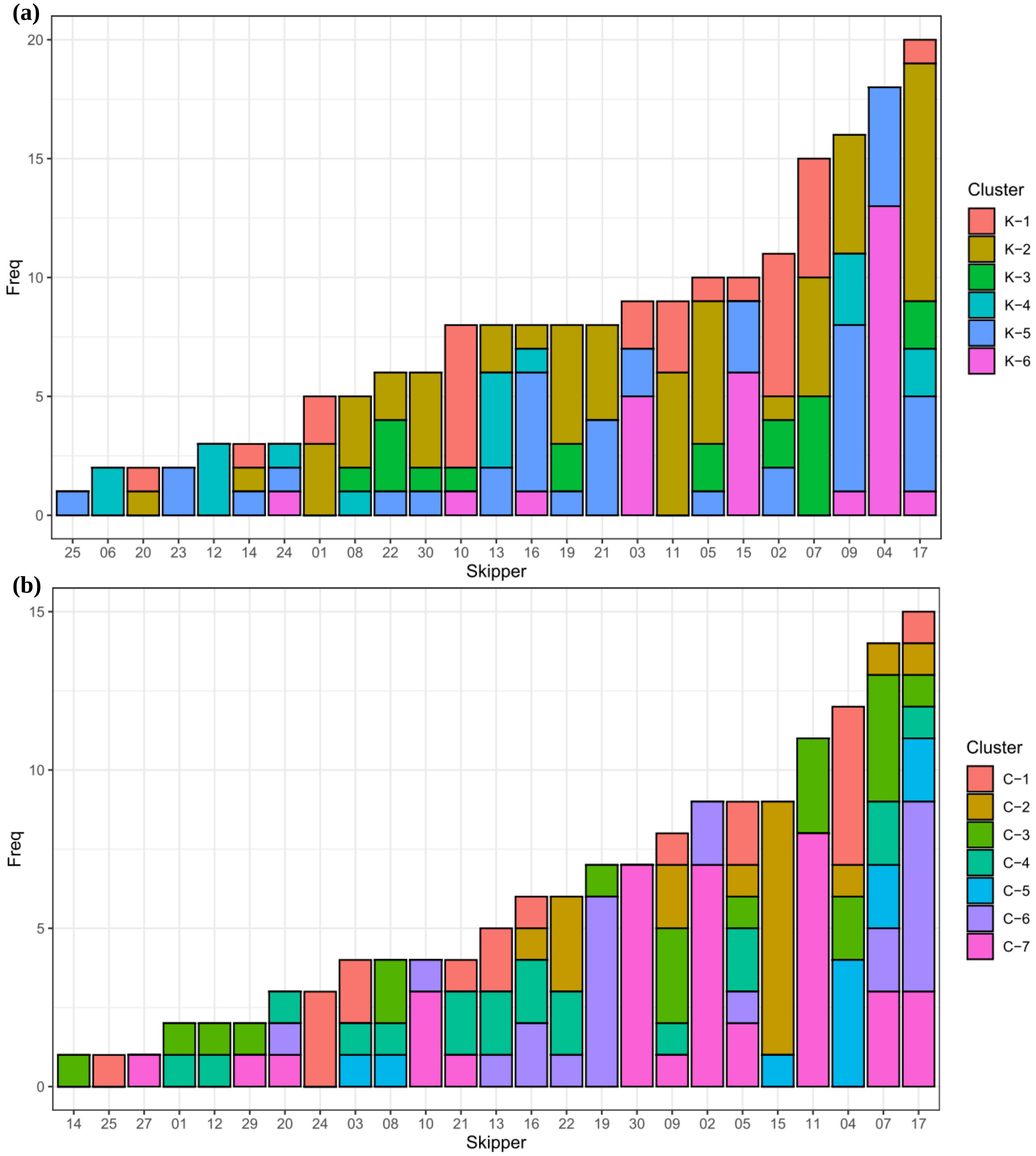
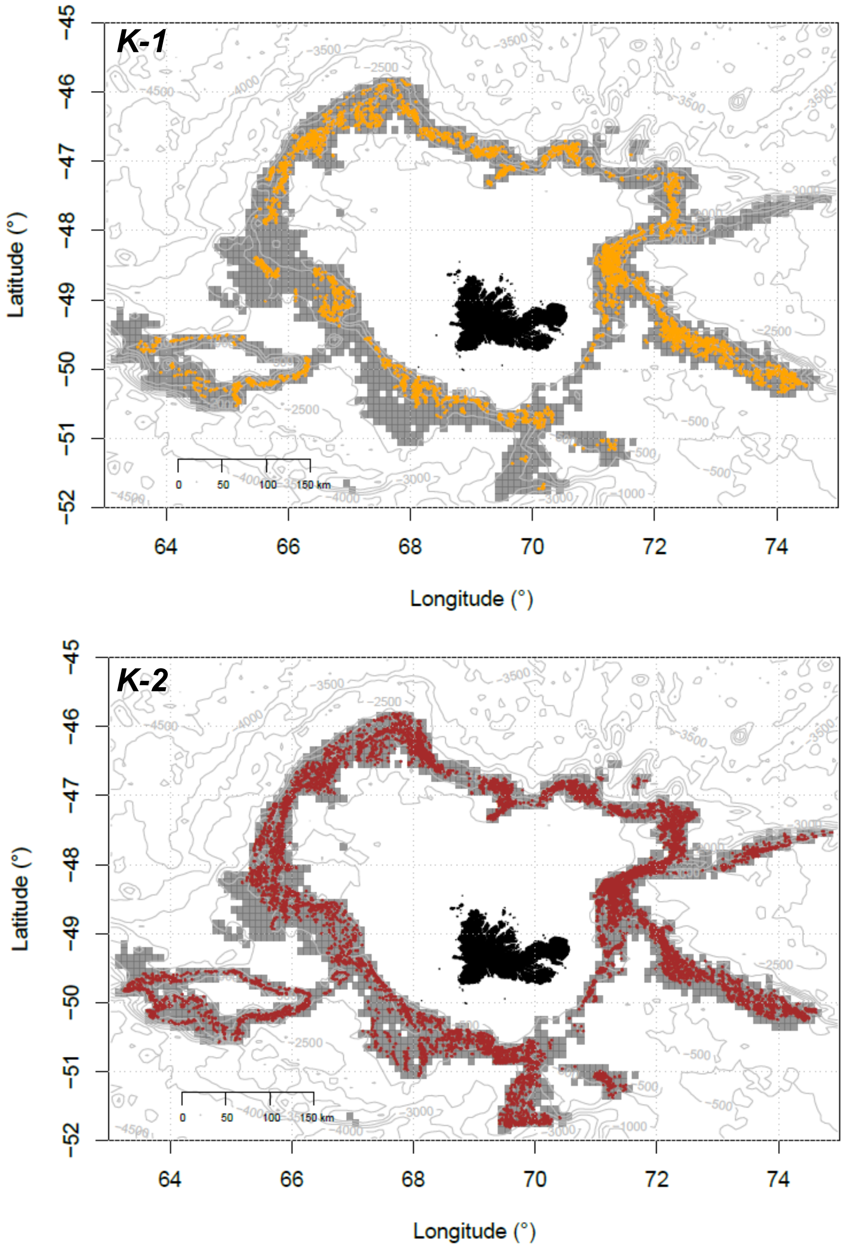
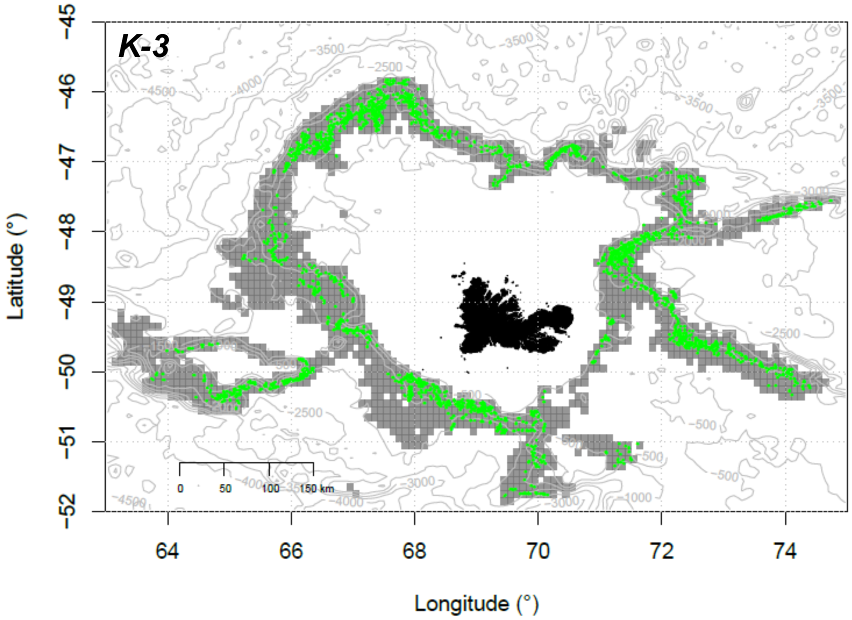
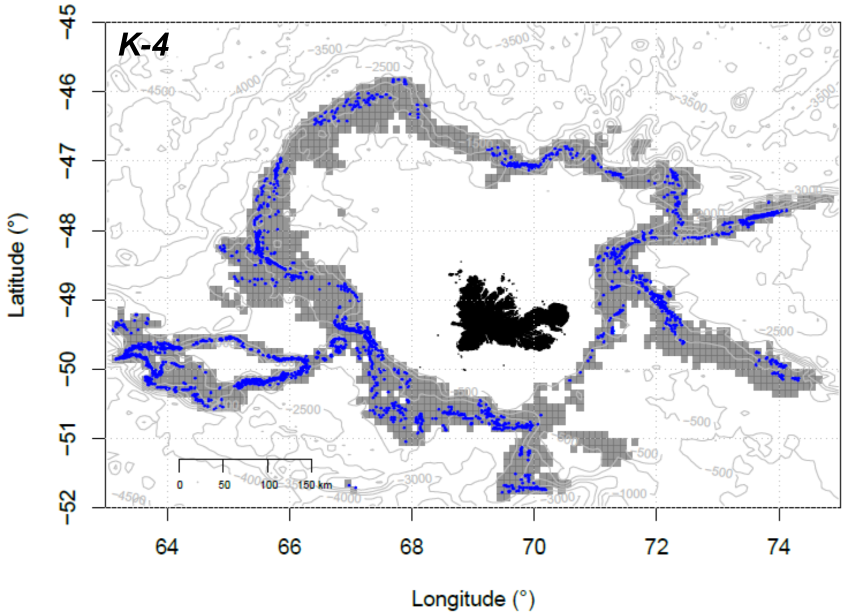
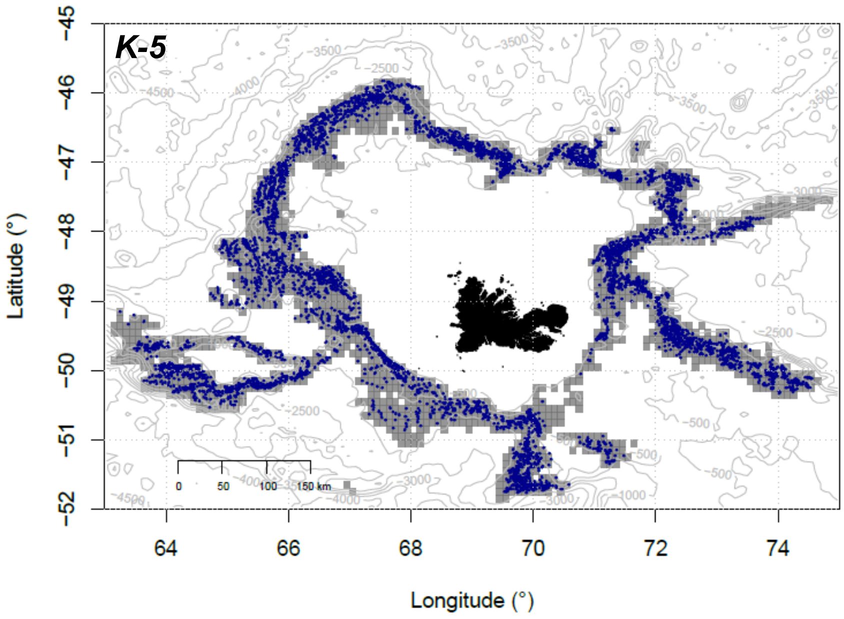


Figure S9 Spatial distribution of lines hauled for each fishing behaviour (coloured dots) and fishing grounds (0.1×0.1° grey squares in which at least one line was hauled over the 2003–2017 period) at EEZ Kerguelen (n = 196 fishing trips).




K-3
Latitude (°)
Longitude (°)
-45
-46
-47
-48
-49
-50
-51
-52
64
66
68
70
72
74
-3500
-2500
-4000
-4500
-3000
-500
-1000
0
50
100
150 km


K-4
Latitude (°)
Longitude (°)
-45
-46
-47
-48
-49
-50
-51
-52
64
66
68
70
72
74
-3500
-2500
-4000
-4500
-3000
-500
-1000
0
50
100
150 km


K-5
Latitude (°)
Longitude (°)
−45
−46
−47
−48
−49
−50
−51
−52
64
66
68
70
72
74
0
50
100
150 km
−4500
−4000
−3500
−3000
−2500
−1000
−500

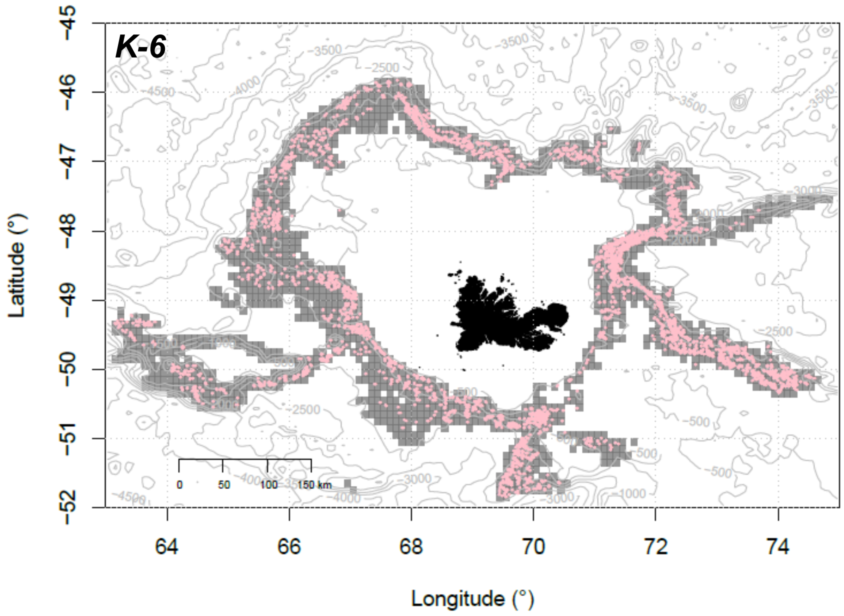
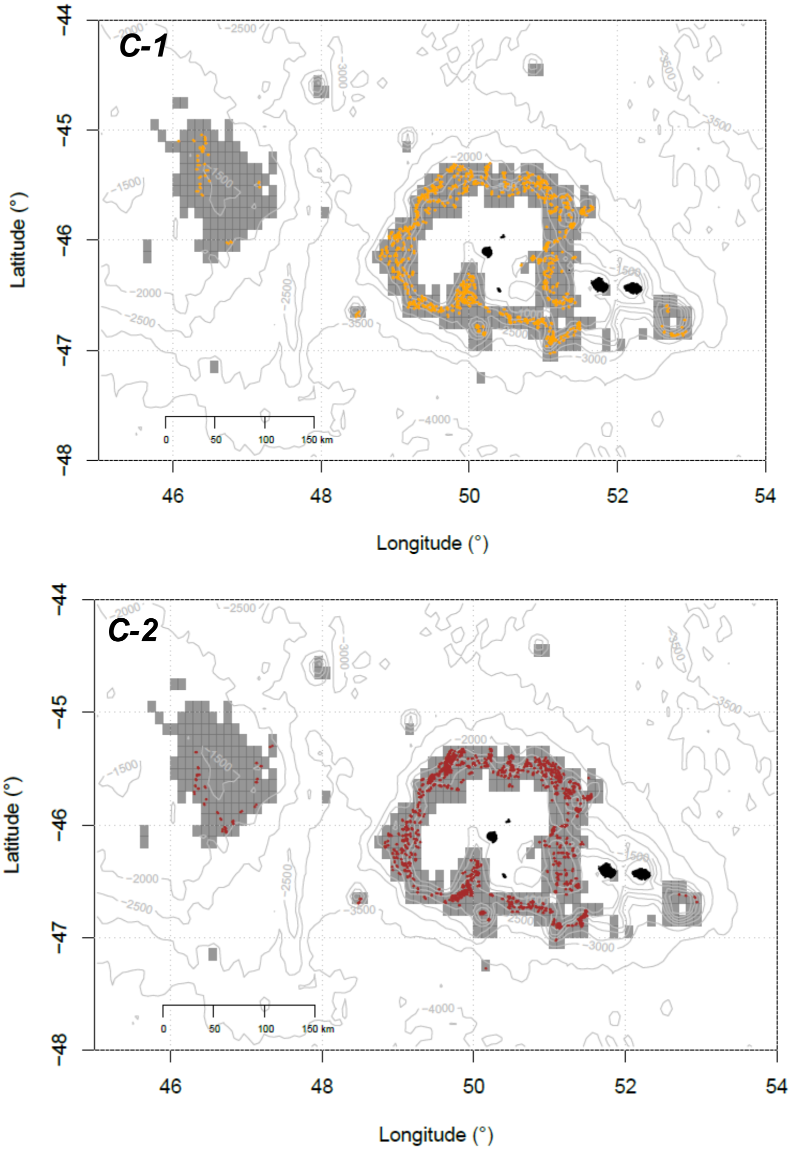
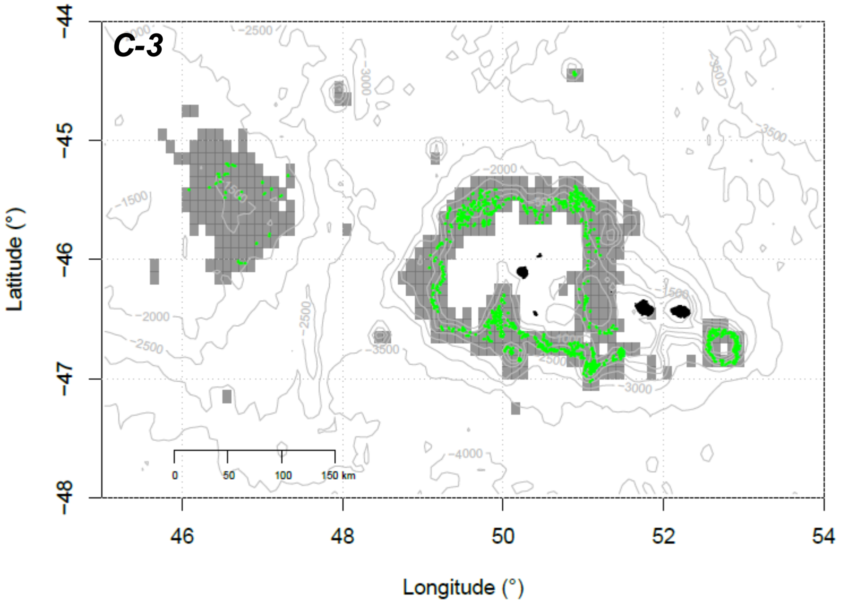
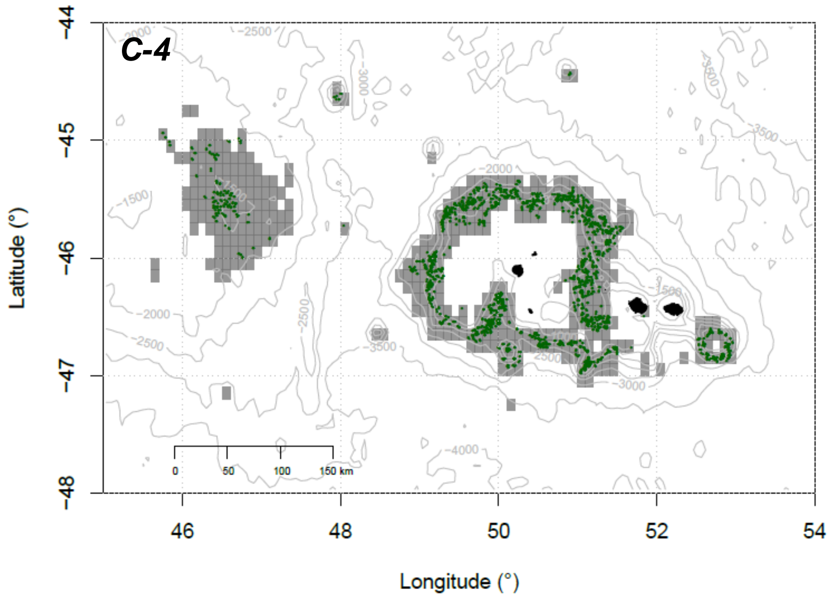

K-6
Latitude (°)
Longitude (°)
−45
−46
−47
−48
−49
−50
−51
−52
64
66
68
70
72
74
0
50
100
150 km
−4500
−4000
−3500
−3000
−2500
−1000
−500

Figure S10 Spatial distribution of lines hauled for each fishing behaviour (coloured dots) and fishing grounds (0.1×0.1° grey squares in which at least one line was hauled over the 2003–2017 period) at EEZ Crozet (n = 149 fishing trips).




C-3
Latitude (°)
Longitude (°)
−44
−45
−46
−47
−48
46
48
50
52
54
−1500
−2000
−2500
−3000
−3500
−4000
0
50
100
150 km


C-4
Latitude (°)
Longitude (°)
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−45
−46
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48
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52
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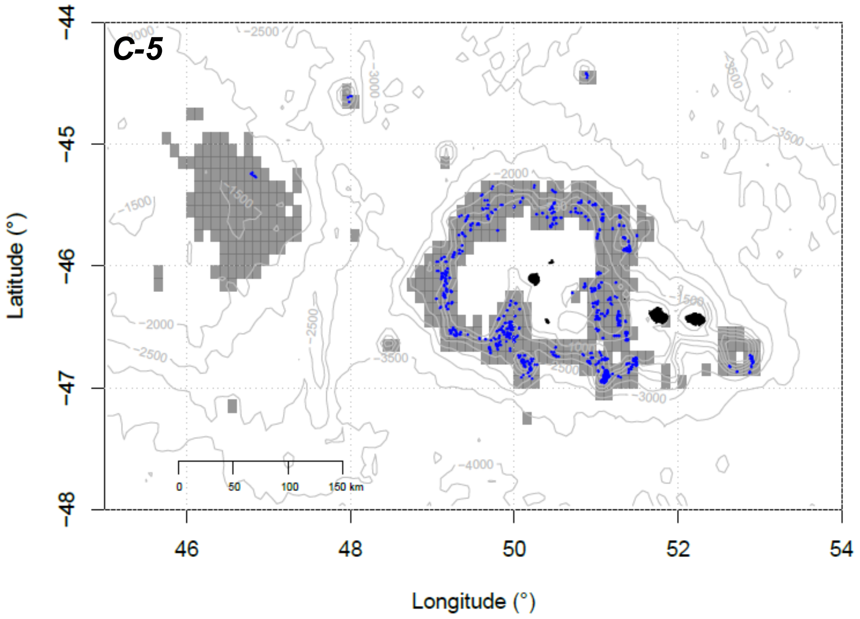
−2500
−3000
−3500
−4000
0
50
100
150 km


C-5
Latitude (°)
Longitude (°)
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−45
−46
−47
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46
48
50
52
54
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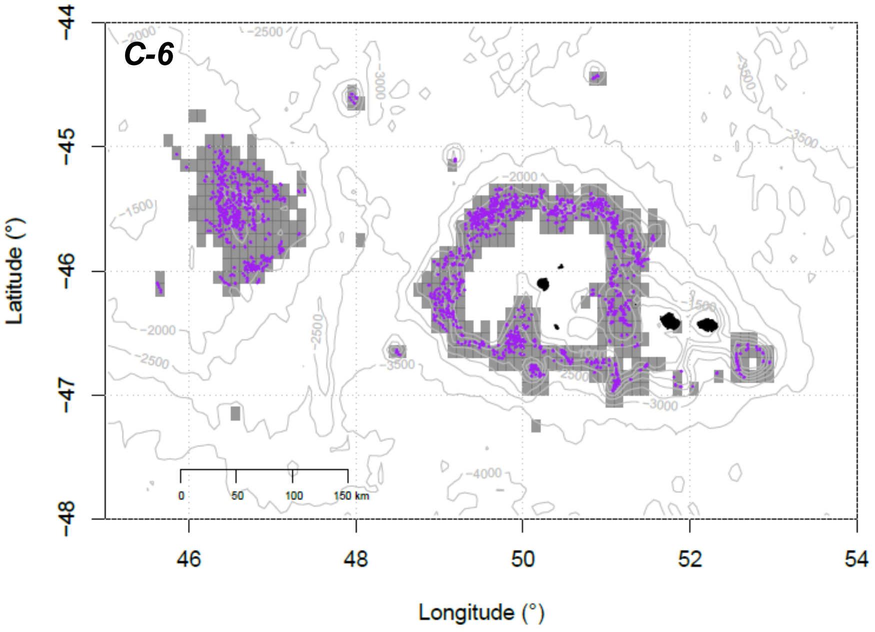
−2000
−2500
−3000
−3500
−4000
0
50
100
150 km


C-6
Latitude (°)
Longitude (°)
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52
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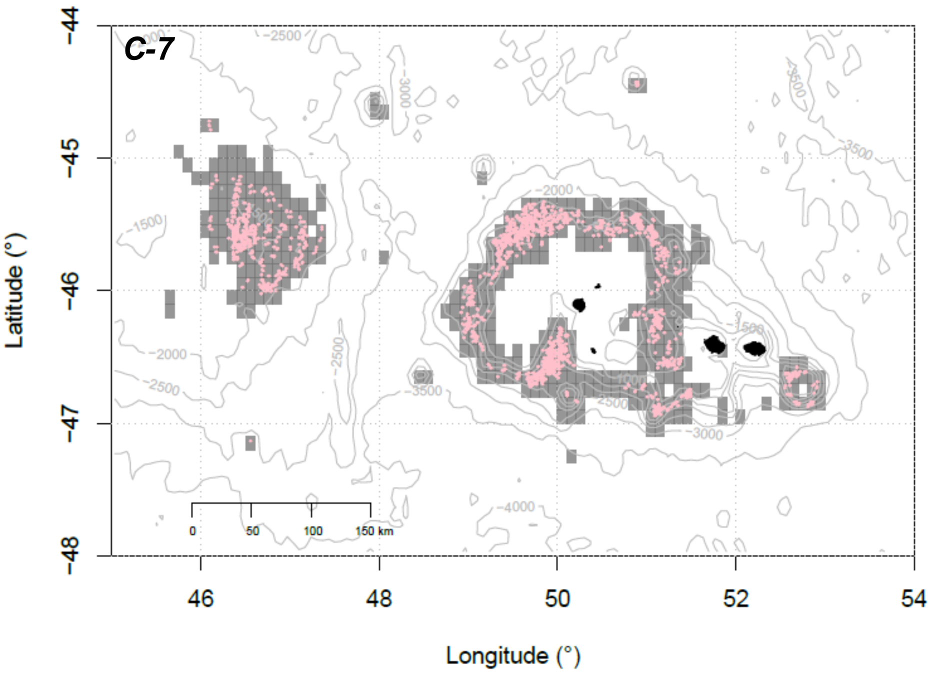
−2000
−2500
−3000
−3500
−4000
0
50
100
150 km


C-7
Latitude (°)
Longitude (°)
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−45
−46
−47
−48
46
48
50
52
54
−1500
−2000
−2500
−3000
−3500
−4000
0
50
100
150 km

104

Table S1 Correlation coefficients between each of the fishing trip descriptors and the retained principal components ($p < 0.05$). The contribution of each descriptor for each of the principal components is specified in brackets. The greatest contributions are in bold.

Fishing trip descriptors	**KERGUELEN** (*n* = 196 fishing trips)			**CROZET** (*n* = 149 fishing trips)	
	PC1 (27%)	**PC2 (22%)**	**PC3 (14%)**	**PC1 (40%)**	**PC2 (15%)**
Temporal descriptors					
Prop.set.time	ns	**0.93 (25%)**	ns	–0.62 (6%)	ns
Prop.haul.time	–0.31 (2%)	**0.83 (20%)**	–0.30 (4%)	**–0.84 (11%)**	0.26 (3%)
Prop.travel.time	0.25 (1%)	**–0.89 (23%)**	0.24 (2%)	**0.84 (11%)**	–0.23 (2%)
Spatial descriptors					
Spatial.extent	**0.78 (14%)**	0.18 (1%)	–0.34 (5%)	0.57 (5%)	ns
Density.FE	–0.62 (9%)	0.37 (4%)	0.43 (8%)	–0.59 (6%)	ns
Travel.distance.per.day	**0.88 (18%)**	0.24 (2%)	–0.23 (2%)	**0.89 (13%)**	ns
Inter.set.distance	**0.67 (10%)**	ns	0.29 (4%)	0.68 (7%)	0.23 (2%)
Set.haul.distance	**0.84 (16%)**	ns	ns	**0.82 (10%)**	0.30 (4%)
Inter.haul.distance	**0.78 (14%)**	0.23 (1%)	0.34 (5%)	**0.84 (11%)**	0.37 (6%)
Haul.set.distance	0.32 (2%)	–0.44 (6%)	ns	ns	0.38 (6%)
Ratio.hauling/setting	ns	0.23 (2%)	ns	0.28 (1%)	0.33 (5%)
Operational descriptors					
Nb.longlines.per.day	0.30 (2%)	0.39 (4%)	**–0.74 (24%)**	0.24 (1%)	**–0.75 (24%)**
Length.longline	ns	0.38 (4%)	**0.83 (30%)**	–0.56 (5%)	**0.63 (17%)**
Depth	ns	–0.32 (3%)	–0.32 (5%)	ns	**0.71 (21%)**
Soaking.time	ns	–0.26 (2%)	ns	0.61 (6%)	0.35 (5%)
Hauling.speed	0.63 (9%)	0.33 (3%)	0.44 (8%)	0.65 (7%)	–0.33 (5%)

Table S2 Description of the six fishing behaviours identified through the hierarchical clustering analysis for EEZ Kerguelen (*n* = 196 fishing trips). Student *t*-test comparisons were performed between cluster mean values and the mean value of all trips.

	KERGUELEN (*n* = 196 fishing trips)			
	Cluster Mean ± SE	**Sample Mean ± SE**	***t***	***p***
Cluster *K-1* (*n* = 29, 15%)				
Fishing trip descriptors				
Prop.set.time	10.6 ± 0.2	8.9 ± 0.1	6.29	< 0.001
Prop.haul.time	54.3 ± 0.6	47.7 ± 0.4	7.89	< 0.001
Prop.travel.time	35.1 ± 0.7	43.3 ± 0.5	–8.60	< 0.001
Spatial.extent	0.3 ± 0.01	0.4 ± 0.01	–7.58	< 0.001
Density.FE	93,000 ± 2,902	63,000 ± 1,000	9.25	< 0.001
Travel.distance.per.day	63.1 ± 1.5	76.6 ± 1.0	–6.40	< 0.001
Inter.set.distance	4.6 ± 0.2	5.3 ± 0.1	–2.97	0.004
Set.haul.distance	14.9 ± 0.4	18.6 ± 0.2	–7.39	< 0.001
Inter.haul.distance	10.0 ± 0.5	11.0 ± 0.2	–1.90	ns
Haul.set.distance	36.1 ± 2.0	40.2 ± 0.7	–1.80	ns
Ratio.hauling/setting	2.3 ± 0.1	2.2 ± 0.03	0.76	ns
Nb.longlines.per.day	2.2 ± 0.1	2.6 ± 0.03	–5.00	< 0.001
Length.longline	13.6 ± 0.4	10.4 ± 0.1	6.81	< 0.001
Depth	1,153 ± 31	1,188 ± 9	–1.08	ns
Soaking.time	21.7 ± 0.8	22.9 ± 0.2	–1.39	ns
Hauling.speed	32.0 ± 0.5	32.0 ± 0.3	0.06	ns
Optimality indicators				
Biomass.per.day	5.0 ± 0.2	4.9 ± 0.1	0.16	ns
Prop.days.sw.only	38 ± 4	41 ± 1	–0.58	ns
Experience	10.9 ± 1.5	10.8 ± 0.4	0.09	ns
Cluster *K-2* (*n* = 59, 30%)				
Fishing trip descriptors				
Prop.set.time	9.3 ± 0.1	8.9 ± 0.1	2.15	0.033
Prop.haul.time	52.9 ± 0.6	47.7 ± 0.4	7.44	< 0.001
Prop.travel.time	37.7 ± 0.5	43.3 ± 0.5	–6.91	< 0.001
Spatial.extent	0.3 ± 0.01	0.4 ± 0.01	–2.75	0.007
Density.FE	68,000 ± 1,792	63,000 ± 1,000	2.10	0.037
Travel.distance.per.day	68.1 ± 1.1	76.6 ± 1.0	–4.63	< 0.001
Inter.set.distance	4.5 ± 0.2	5.3 ± 0.1	–4.30	< 0.001
Set.haul.distance	15.9 ± 0.3	18.6 ± 0.2	–5.75	< 0.001
Inter.haul.distance	9.2 ± 0.3	11.0 ± 0.2	–5.05	< 0.001
Haul.set.distance	33.1 ± 1.4	40.2 ± 0.7	–4.15	< 0.001
Ratio.hauling/setting	2.1 ± 0.1	2.2 ± 0.03	–0.41	ns
Nb.longlines.per.day	2.8 ± 0.05	2.6 ± 0.03	2.67	0.008
Length.longline	9.8 ± 0.2	10.4 ± 0.1	–2.47	0.014
Depth	1,179 ± 26	1,188 ± 9	–0.35	ns
Soaking.time	22.3 ± 0.5	22.9 ± 0.2	–0.96	ns
Hauling.speed	29.6 ± 0.5	32.0 ± 0.3	–4.01	< 0.001
Optimality indicators				
Biomass.per.day	5.3 ± 0.2	4.9 ± 0.1	1.51	ns

Prop.days.sw.only	38 ± 3	41 ± 1	–0.74	ns
Experience	10.8 ± 0.9	10.8 ± 0.4	0.02	ns

Cluster *K-3* (*n* = 19, 10%)				
Fishing trip descriptors				
Prop.set.time	5.4 ± 0.3	8.9 ± 0.1	–11.93	< 0.001
Prop.haul.time	29.7 ± 1.4	47.7 ± 0.4	–11.81	< 0.001
Prop.travel.time	64.9 ± 1.7	43.3 ± 0.5	12.13	< 0.001
Spatial.extent	0.2 ± 0.01	0.4 ± 0.01	–10.77	< 0.001
Density.FE	65,000 ± 3,475	63,000 ± 1,000	0.45	ns
Travel.distance.per.day	46.8 ± 2.7	76.6 ± 1.0	–9.77	< 0.001
Inter.set.distance	5.1 ± 0.4	5.3 ± 0.1	–0.71	ns
Set.haul.distance	18.2 ± 0.7	18.6 ± 0.2	–0.51	ns
Inter.haul.distance	9.6 ± 0.6	11.0 ± 0.2	–2.24	0.034
Haul.set.distance	51.5 ± 4.0	40.2 ± 0.7	2.73	0.013
Ratio.hauling/setting	2.1 ± 0.2	2.2 ± 0.03	–0.57	ns
Nb.longlines.per.day	1.5 ± 0.1	2.6 ± 0.03	–12.85	< 0.001
Length.longline	11.1 ± 0.4	10.4 ± 0.1	1.48	ns
Depth	1,169 ± 37	1,188 ± 9	–0.50	ns
Soaking.time	24.2 ± 1.7	22.9 ± 0.2	0.74	ns
Hauling.speed	32.0 ± 0.5	32.0 ± 0.3	–1.95	ns
Optimality indicators				
Biomass.per.day	2.5 ± 0.1	4.9 ± 0.1	–15.96	< 0.001
Prop.days.sw.only	29 ± 3	41 ± 1	–3.49	0.002
Experience	11.0 ± 1.6	10.8 ± 0.4	0.12	ns

Cluster *K-4* (*n* = 17, 9%)				
Fishing trip descriptors				
Prop.set.time	7.0 ± 0.2	8.9 ± 0.1	–7.85	< 0.001
Prop.haul.time	44.9 ± 1.1	47.7 ± 0.4	–2.39	0.024
Prop.travel.time	48.0 ± 1.1	43.3 ± 0.5	3.71	< 0.001
Spatial.extent	0.5 ± 0.02	0.4 ± 0.01	3.05	0.006
Density.FE	37,000 ± 1,412	63,000 ± 1,000	–12.92	< 0.001
Travel.distance.per.day	82.1 ± 4.4	76.6 ± 1.0	1.19	ns
Inter.set.distance	4.6 ± 0.4	5.3 ± 0.1	–1.70	ns
Set.haul.distance	17.6 ± 1.5	18.6 ± 0.2	–0.68	ns
Inter.haul.distance	9.0 ± 1.0	11.0 ± 0.2	–1.88	ns
Haul.set.distance	50.3 ± 2.9	40.2 ± 0.7	3.29	0.004
Ratio.hauling/setting	2.0 ± 0.1	2.2 ± 0.03	–1.40	ns
Nb.longlines.per.day	3.0 ± 0.1	2.6 ± 0.03	3.69	0.001
Length.longline	6.5 ± 0.2	10.4 ± 0.1	–14.02	< 0.001
Depth	1,363 ± 32	1,188 ± 9	5.12	< 0.001
Soaking.time	23.1 ± 1.7	22.9 ± 0.2	0.10	ns
Hauling.speed	25.0 ± 0.9	32.0 ± 0.3	–7.54	< 0.001
Optimality indicators				
Biomass.per.day	4.1 ± 0.2	4.9 ± 0.1	–3.39	0.003
Prop.days.sw.only	40 ± 5	41 ± 1	–0.19	ns
Experience	7.6 ± 1.6	10.8 ± 0.4	–1.91	0.071

Cluster *K-5* (*n* = 43, 22%)				
Fishing trip descriptors				
Prop.set.time	9.1 ± 0.2	8.9 ± 0.1	0.90	ns

Prop.haul.time	48.1 ± 0.5	47.7 ± 0.4	0.45	ns
Prop.travel.time	42.8 ± 0.6	43.3 ± 0.5	–0.58	ns
Spatial.extent	0.4 ± 0.01	0.4 ± 0.01	2.95	0.004
Density.FE	58,000 ± 1,922	63,000 ± 1,000	–2.27	0.025
Travel.distance.per.day	86.6 ± 1.5	76.6 ± 1.0	4.79	< 0.001
Inter.set.distance	5.8 ± 0.2	5.3 ± 0.1	1.71	ns
Set.haul.distance	20.6 ± 0.4	18.6 ± 0.2	3.74	< 0.001
Inter.haul.distance	12.4 ± 0.3	11.0 ± 0.2	3.73	< 0.001
Haul.set.distance	39.4 ± 2.1	40.2 ± 0.7	–0.36	ns
Ratio.hauling/setting	2.3 ± 0.1	2.2 ± 0.03	1.20	ns
Nb.longlines.per.day	2.8 ± 0.1	2.6 ± 0.03	2.56	0.012
Length.longline	10.2 ± 0.3	10.4 ± 0.1	–0.51	ns
Depth	1,193 ± 23	1,188 ± 9	0.15	ns
Soaking.time	23.6 ± 0.6	22.9 ± 0.2	1.03	ns
Hauling.speed	34.0 ± 0.5	32.0 ± 0.3	3.23	0.002
Optimality indicators				
Biomass.per.day	5.3 ± 0.2	4.9 ± 0.1	1.90	0.062
Prop.days.sw.only	50 ± 3	41 ± 1	2.64	0.010
Experience	10.1 ± 1.1	10.8 ± 0.4	–0.53	ns
Cluster *K-6* (*n* = 29, 15%)				
Fishing trip descriptors				
Prop.set.time	9.7 ± 0.3	8.9 ± 0.1	2.37	0.023
Prop.haul.time	43.7 ± 0.6	47.7 ± 0.4	–4.78	< 0.001
Prop.travel.time	46.6 ± 0.9	43.3 ± 0.5	3.07	0.003
Spatial.extent	0.6 ± 0.02	0.4 ± 0.01	7.29	< 0.001
Density.FE	46,000 ± 1,966	63,000 ± 1,000	–7.15	< 0.001
Travel.distance.per.day	108.8 ± 2.6	76.6 ± 1.0	10.77	< 0.001
Inter.set.distance	7.8 ± 0.4	5.3 ± 0.1	6.60	< 0.001
Set.haul.distance	25.9 ± 0.8	18.6 ± 0.2	8.71	< 0.001
Inter.haul.distance	15.6 ± 0.4	11.0 ± 0.2	9.03	< 0.001
Haul.set.distance	46.7 ± 2.7	40.2 ± 0.7	2.20	0.034
Ratio.hauling/setting	2.2 ± 0.1	2.2 ± 0.03	–0.18	ns
Nb.longlines.per.day	2.9 ± 0.1	2.6 ± 0.03	2.42	0.020
Length.longline	10.5 ± 0.5	10.4 ± 0.1	0.14	ns
Depth	1,150 ± 28	1,188 ± 9	–1.25	ns
Soaking.time	23.3 ± 0.8	22.9 ± 0.2	0.41	ns
Hauling.speed	38.6 ± 0.7	32.0 ± 0.3	8.07	< 0.001
Optimality indicators				
Biomass.per.day	5.8 ± 0.2	4.9 ± 0.1	3.87	< 0.001
Prop.days.sw.only	42 ± 4	41 ± 1	0.37	ns
Experience	13.3 ± 1.2	10.8 ± 0.4	1.87	0.070

Table S3 Description of the seven fishing behaviours identified through the hierarchical clustering analysis for EEZ Crozet (*n* = 149 fishing trips). Student *t*-test comparisons were performed between cluster mean values and the mean value of all trips.

	CROZET (*n* = 149 fishing trips)			
	Cluster Mean ± SE	**Sample Mean ± SE**	***t***	***p***
Cluster *C-1* (*n* = 19, 13%)				
Fishing trip descriptors				
Prop.set.time	6.8 ± 0.2	7.5 ± 0.1	–2.33	0.027
Prop.haul.time	31.7 ± 1.13	40.1 ± 0.6	–6.02	< 0.001
Prop.travel.time	61.4 ± 1.3	52.2 ± 0.7	5.75	< 0.001
Spatial.extent	0.8 ± 0.07	0.6 ± 0.01	2.72	0.013
Density.FE	25,000 ± 2,537	37,000 ± 1,000	–3.85	< 0.001
Travel.distance.per.day	157.1 ± 5.9	110.2 ± 2.6	6.76	< 0.001
Inter.set.distance	10.9 ± 0.9	7.8 ± 0.2	3.26	0.003
Set.haul.distance	40.1 ± 2.4	29.5 ± 0.9	3.85	< 0.001
Inter.haul.distance	23.5 ± 1.1	16.7 ± 0.6	5.17	< 0.001
Haul.set.distance	40.8 ± 4.3	44.5 ± 1.4	–0.80	ns
Ratio.hauling/setting	2.4 ± 0.2	2.3 ± 0.05	0.51	ns
Nb.longlines.per.day	3.5 ± 0.1	3.0 ± 0.04	3.23	0.003
Length.longline	6.0 ± 0.3	7.6 ± 0.1	–4.94	< 0.001
Depth	1,036 ± 42	1,119 ± 14	–1.78	ns
Soaking.time	32.6 ± 2.2	26.0 ± 0.6	2.85	0.009
Hauling.speed	37.7 ± 1.5	32.3 ± 0.4	3.35	0.003
Optimality indicators				
Biomass.per.day	2.2 ± 0.3	2.8 ± 0.1	–1.91	0.063
Prop.days.sw.only	20 ± 4	25 ± 1	–0.97	ns
Prop.days.kw	58 ± 5	47 ± 1	1.90	0.070
Experience	8.4 ± 1.4	8.2 ± 0.3	0.13	ns
Cluster *C-2* (*n* = 18, 12%)				
Fishing trip descriptors				
Prop.set.time	6.0 ± 0.2	7.5 ± 0.1	–6.76	< 0.001
Prop.haul.time	28.6 ± 0.9	40.1 ± 0.6	–9.69	< 0.001
Prop.travel.time	65.1 ± 1.0	52.2 ± 0.7	9.66	< 0.001
Spatial.extent	0.8 ± 0.07	0.6 ± 0.01	3.23	0.004
Density.FE	21,000 ± 1,681	37,000 ± 1,000	–6.43	< 0.001
Travel.distance.per.day	187.1 ± 5.7	110.2 ± 2.6	11.39	< 0.001
Inter.set.distance	13.1 ± 1.3	7.8 ± 0.2	3.88	< 0.001
Set.haul.distance	57.9 ± 2.6	29.5 ± 0.9	9.83	< 0.001
Inter.haul.distance	35.0 ± 1.8	16.7 ± 0.6	9.47	< 0.001
Haul.set.distance	45.5 ± 6.2	44.5 ± 1.4	0.15	ns
Ratio.hauling/setting	3.1 ± 0.2	2.3 ± 0.05	3.02	0.007
Nb.longlines.per.day	3.1 ± 0.1	3.0 ± 0.04	0.80	ns
Length.longline	6.2 ± 0.3	7.6 ± 0.1	–4.38	< 0.001
Depth	1,193 ± 48	1,119 ± 14	1.42	ns
Soaking.time	38.5 ± 2.5	26.0 ± 0.6	4.79	< 0.001
Hauling.speed	38.7 ± 1.4	32.3 ± 0.4	4.21	< 0.001
Optimality indicators				
Biomass.per.day	2.5 ± 0.2	2.8 ± 0.1	–1.20	ns
Prop.days.sw.only	26 ± 4	25 ± 1	0.34	ns

Prop.days.kw	47 ± 4	47 ± 1	–0.17	ns
Experience	10.5 ± 1.2	8.2 ± 0.3	1.77	0.092
Cluster *C-3* (*n* = 21, 14%)				
Fishing trip descriptors				
Prop.set.time	8.3 ± 0.4	7.5 ± 0.1	2.10	0.046
Prop.haul.time	45.1 ± 1.3	40.1 ± 0.6	3.19	0.003
Prop.travel.time	46.4 ± 1.6	52.2 ± 0.7	–3.06	0.004
Spatial.extent	0.5 ± 0.04	0.6 ± 0.01	–1.69	ns
Density.FE	46,000 ± 6,372	37,000 ± 1,000	1.46	ns
Travel.distance.per.day	74.6 ± 4.1	110.2 ± 2.6	–6.47	< 0.001
Inter.set.distance	4.8 ± 0.4	7.8 ± 0.2	–5.41	< 0.001
Set.haul.distance	15.4 ± 1.4	29.5 ± 0.9	–7.33	< 0.001
Inter.haul.distance	7.1 ± 0.6	16.7 ± 0.6	–9.52	< 0.001
Haul.set.distance	36.1 ± 3.8	44.5 ± 1.4	–1.98	ns
Ratio.hauling/setting	1.7 ± 0.1	2.3 ± 0.05	–4.67	< 0.001
Nb.longlines.per.day	3.6 ± 0.2	3.0 ± 0.04	3.02	0.006
Length.longline	6.6 ± 0.3	7.6 ± 0.1	–2.62	0.013
Depth	924 ± 54	1,119 ± 14	–3.38	0.002
Soaking.time	17.3 ± 1.2	26.0 ± 0.6	–6.08	< 0.001
Hauling.speed	29.5 ± 0.9	32.3 ± 0.4	–2.74	0.009
Optimality indicators				
Biomass.per.day	3.8 ± 0.6	2.8 ± 0.1	1.81	0.083
Prop.days.sw.only	27 ± 4	25 ± 1	0.51	ns
Prop.days.kw	55 ± 5	47 ± 1	1.63	ns
Experience	6.9 ± 1.1	8.2 ± 0.3	–1.16	ns
Cluster *C-4* (*n* = 19, 13%)				
Fishing trip descriptors				
Prop.set.time	6.8 ± 0.4	7.5 ± 0.1	–1.59	ns
Prop.haul.time	34.5 ± 1.5	40.1 ± 0.6	–3.22	0.003
Prop.travel.time	58.5 ± 1.8	52.2 ± 0.7	3.07	0.005
Spatial.extent	0.5 ± 0.04	0.6 ± 0.01	–1.36	ns
Density.FE	33,000 ± 2,050	37,000 ± 1,000	–1.57	ns
Travel.distance.per.day	108.3 ± 6.9	110.2 ± 2.6	–0.24	ns
Inter.set.distance	7.6 ± 0.6	7.8 ± 0.2	–0.26	ns
Set.haul.distance	31.0 ± 2.1	29.5 ± 0.9	0.58	ns
Inter.haul.distance	15.6 ± 0.9	16.7 ± 0.6	–0.92	ns
Haul.set.distance	42.1 ± 4.4	44.5 ± 1.4	–0.50	ns
Ratio.hauling/setting	2.2 ± 0.1	2.3 ± 0.05	–0.57	ns
Nb.longlines.per.day	3.0 ± 0.2	3.0 ± 0.04	–0.12	ns
Length.longline	6.7 ± 0.3	7.6 ± 0.1	–2.84	0.007
Depth	1,064 ± 40	1,119 ± 14	–1.24	ns
Soaking.time	25.4 ± 1.9	26.0 ± 0.6	–0.32	ns
Hauling.speed	33.0 ± 1.1	32.3 ± 0.4	0.53	ns
Optimality indicators				
Biomass.per.day	2.4 ± 0.2	2.8 ± 0.1	–1.34	ns
Prop.days.sw.only	32 ± 5	25 ± 1	1.38	ns
Prop.days.kw	37 ± 4	47 ± 1	–2.58	0.015
Experience	6.1 ± 1.1	8.2 ± 0.3	–1.80	0.085

Cluster *C-5* (*n* = 11, 7%)				
Fishing trip descriptors				
Prop.set.time	6.8 ± 0.4	7.5 ± 0.1	–1.42	ns
Prop.haul.time	31.3 ± 1.8	40.1 ± 0.6	–4.47	< 0.001
Prop.travel.time	61.7 ± 2.1	52.2 ± 0.7	4.09	0.001
Spatial.extent	0.6 ± 0.05	0.6 ± 0.01	–0.41	ns
Density.FE	32,000 ± 2,364	37,000 ± 1,000	–1.59	ns
Travel.distance.per.day	109.3 ± 8.8	110.2 ± 2.6	–0.09	ns
Inter.set.distance	6.8 ± 0.7	7.8 ± 0.2	–1.26	ns
Set.haul.distance	22.6 ± 2.5	29.5 ± 0.9	–2.46	0.026
Inter.haul.distance	12.2 ± 1.3	16.7 ± 0.6	–2.93	0.009
Haul.set.distance	35.9 ± 4.4	44.5 ± 1.4	–1.78	ns
Ratio.hauling/setting	1.9 ± 0.2	2.3 ± 0.05	–1.84	ns
Nb.longlines.per.day	3.9 ± 0.2	3.0 ± 0.04	5.10	< 0.001
Length.longline	5.3 ± 0.2	7.6 ± 0.1	–8.49	< 0.001
Depth	809 ± 43	1,119 ± 14	–6.49	< 0.001
Soaking.time	20.8 ± 1.9	26.0 ± 0.6	–2.48	0.027
Hauling.speed	39.2 ± 2.1	32.3 ± 0.4	3.22	0.008
Optimality indicators				
Biomass.per.day	5.5 ± 1.2	2.8 ± 0.1	2.30	0.043
Prop.days.sw.only	17 ± 4	25 ± 1	–1.78	ns
Prop.days.kw	67 ± 6	47 ± 1	3.34	0.006
Experience	10.1 ± 1.7	8.2 ± 0.3	1.07	ns
Cluster *C-6* (*n* = 23, 15%)				
Fishing trip descriptors				
Prop.set.time	7.2 ± 0.2	7.5 ± 0.1	–1.36	ns
Prop.haul.time	41.4 ± 1.0	40.1 ± 0.6	1.01	ns
Prop.travel.time	51.3 ± 1.1	52.2 ± 0.7	–0.62	ns
Spatial.extent	0.6 ± 0.05	0.6 ± 0.01	–0.09	ns
Density.FE	34,000 ± 2,595	37,000 ± 1,000	–0.96	ns
Travel.distance.per.day	105.7 ± 4.6	110.2 ± 2.6	–0.76	ns
Inter.set.distance	8.6 ± 0.6	7.8 ± 0.2	1.11	ns
Set.haul.distance	31.2 ± 1.8	29.5 ± 0.9	0.76	ns
Inter.haul.distance	18.7 ± 1.0	16.7 ± 0.6	1.59	ns
Haul.set.distance	55.3 ± 6.5	44.5 ± 1.4	1.58	ns
Ratio.hauling/setting	2.5 ± 0.2	2.3 ± 0.05	0.86	ns
Nb.longlines.per.day	2.4 ± 0.1	3.0 ± 0.04	–6.17	< 0.001
Length.longline	8.7 ± 0.3	7.6 ± 0.1	3.08	0.004
Depth	1,270 ± 37	1,119 ± 14	3.60	< 0.001
Soaking.time	29.2 ± 1.6	26.0 ± 0.6	1.80	ns
Hauling.speed	29.3 ± 0.7	32.3 ± 0.4	–3.33	0.002
Optimality indicators				
Biomass.per.day	1.7 ± 0.2	2.8 ± 0.1	–4.31	< 0.001
Prop.days.sw.only	27 ± 4	25 ± 1	0.60	ns
Prop.days.kw	36 ± 4	47 ± 1	–2.34	0.026
Experience	9.0 ± 1.1	8.2 ± 0.3	0.71	ns
Cluster *C-7* (*n* = 38, 26%)				
Fishing trip descriptors				
Prop.set.time	8.7 ± 0.2	7.5 ± 0.1	4.81	< 0.001

Prop.haul.time	51.5 ± 1.0	40.1 ± 0.6	8.93	< 0.001
Prop.travel.time	39.2 ± 1.1	52.2 ± 0.7	–9.07	< 0.001
Spatial.extent	0.5 ± 0.02	0.6 ± 0.01	–4.19	< 0.001
Density.FE	50,000 ± 4,114	37,000 ± 1,000	2.95	0.005
Travel.distance.per.day	73.8 ± 2.9	110.2 ± 2.6	–7.69	< 0.001
Inter.set.distance	5.3 ± 0.4	7.8 ± 0.2	–4.67	< 0.001
Set.haul.distance	18.9 ± 1.1	29.5 ± 0.9	–6.29	< 0.001
Inter.haul.distance	10.4 ± 0.6	16.7 ± 0.6	–6.29	< 0.001
Haul.set.distance	47.8 ± 4.2	44.5 ± 1.4	0.71	ns
Ratio.hauling/setting	2.3 ± 0.1	2.3 ± 0.05	–0.19	ns
Nb.longlines.per.day	2.5 ± 0.1	3.0 ± 0.04	–5.44	< 0.001
Length.longline	10.0 ± 0.3	7.6 ± 0.1	6.46	< 0.001
Depth	1,259 ± 31	1,119 ± 14	3.84	< 0.001
Soaking.time	21.5 ± 0.8	26.0 ± 0.6	–3.87	< 0.001
Hauling.speed	27.6 ± 0.6	32.3 ± 0.4	–5.66	< 0.001
Optimality indicators				
Biomass.per.day	2.7 ± 0.3	2.8 ± 0.1	–0.28	ns
Prop.days.sw.only	23 ± 3	25 ± 1	–0.64	ns
Prop.days.kw	44 ± 4	47 ± 1	–0.76	ns
Experience	7.7 ± 0.7	8.2 ± 0.3	–0.55	ns

Table S4 Numerical outputs from the linear model fitted to the Shannon's diversity index (*H*) with the skipper's experience (*Experience*) as a continuous predictor and the EEZ (*EEZ*) as a discrete predictor at EEZ Kerguelen ($n = 196$ trips) and EEZ Crozet ($n = 149$ trips). EEZ Crozet represented the Intercept (baseline). See Supporting Information document 1, Figure S6 for more details on model validation.

	Value	**SE**	***t***	***p***
Intercept	2.41	0.13	18.28	< 0.001
Experience	–0.04	0.01	–3.45	0.001
EEZKerguelen	–0.23	0.17	–1.34	0.19
Experience:EEZKerguelen	0.02	0.01	1.31	0.20

Residual standard error: 0.28
R^2: 0.34

Table S5 Numerical outputs from the linear model fitted to the Piélou's equitability index (*J*) with the skipper's experience (*Experience*) as a continuous predictor and the EEZ (*EEZ*) as a discrete predictor at EEZ Kerguelen ($n = 196$ trips) and EEZ Crozet ($n = 149$ trips). EEZ Crozet represented the Intercept (baseline). See Supporting Information document 1, Figure S7 for more details on model validation.

	Value	**SE**	***t***	***p***
Intercept	0.86	0.05	17.23	< 0.001
Experience	–0.01	0.004	–3.29	0.002
EEZKerguelen	–0.02	0.07	–0.23	0.82
Experience:EEZKerguelen	0.01	0.005	1.11	0.27
Residual standard error: 0.11 R^2: 0.32				

Table S6 Relative distribution of the most experienced skippers' trips according to the three general spatio-temporal patterns emerged from the different fishing behaviours identified in this study (e.g. exploitation, exploration and mixed behaviours).

Spatio-temporal pattern	**Fishing behaviours**		**The most experienced skippers** (*Experience* ≥15 (Kerguelen) / 10 (Crozet))					
			Skipper 7		***Skipper 4***		***Skipper 17***	
	Kerguelen	*Crozet*	*Kerguelen*	*Crozet*	*Kerguelen*	*Crozet*	*Kerguelen*	*Crozet*
Exploitation	*K-1 / K-2*	*C-3 / C-7*	67%	50%	0%	17%	55%	27%
	K-3	-	33%	-	0%	-	10%	-
	K-4	-	0%	-	0%	-	10%	-
Mixed	*K-5*	*C-4 / C-5 / C-6*	0%	42%	28%	33%	20%	60%
Exploration	*K-6*	*C-1 / C-2*	0%	7%	72%	50%	5%	13%

Supporting Information document 2

Fishing behaviours and fisher effect in decision-making processes when facing depredation by marine predators

Anaïs Janc, Christophe Guinet, David Pinaud, Gaëtan Richard, Pascal Monestiez, Paul Tixier

Description and assumptions about two peculiar fishing behaviours identified at EEZ Kerguelen: *K-3* and *K-4*

Trips in cluster *K-3* were considered “trips with technical problems or encountering extreme weather conditions”. Regardless of fishers’ experience, long-liner boats spent most time not fishing, not moving over the EEZ, and the fishing success was the lowest. Moreover, Gaertner et al. (1999) confirmed that the bad weather conditions at sea negatively impacted on fishers’ motivations to chase fish schools because maneuvering possibility for setting lines is reduced. This could explain the very low frequencies of sperm whale interactions because under those weather and sea-state conditions sperm whales may lose the acoustical detection of boats (Misund, 1997; Jensen et al. 2011). This fishing behaviour was not observed at EEZ Crozet because most fishing is taking place in summer at EEZ Crozet (i.e. when EEZ Kerguelen is closed from 1 February to mid-March) and weather and sea conditions are often better.

Trips in cluster *K-4* were considered as “technically not optimal trips”. Boats spent more time travelling between over dispersed line setting patches and used the lowest hauling speed, and/or shortest lines set at the greatest depth. Indeed, the time necessary to haul a line is positively related to line setting depth and the deviation from optimality increases when the lines are shorter and fishing depth increases (i.e. they spend proportionally more time to haul the down-line versus the fishing mainline). This fishing behaviour resulting in very low fishing success was mainly observed in the less experienced fishers. A similar fishing behaviour was not identified at EEZ Crozet, and the reasons are not fully understood. This could possibly related to the smallest fishing zone in EEZ Crozet compared to EEZ Kerguelen, reducing the dispersion between line setting patches.

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Supporting Information document 3

Fishing behaviours and fisher effect in decision-making processes when facing depredation by marine predators

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Perspectives about further research

Different indices that reflected spatial characteristics of the fishers' fishing effort at the fishing trip level (i.e. indices of spatial diversity, spatial extent, and of spatial patchiness) could be used (Marchal et al. 2006). The use of linear modelling (Punsly & Nakano, 1992; He et al. 1997; Rodríguez, 2003) or Generalized Additive Models (GAM – Dorn, 1997) could improve the investigation of optimality indicators (e.g. fishing success, frequencies of whale interactions and fishers' experience) using fishing behaviours as explanatory variables. Non-hierarchical clustering methods were also used to classify fishing behaviours with partitioning around medoids (PAM – Duarte et al. 2012). The investigation of fishers' trajectories from VMS data to use specific speeds and turning angles in order to define better fishing spatial behaviours was also suggested (Vermard et al. 2010; Walker & Bez, 2010; Hintzen et al. 2012).

Further studies are needed to understand the factors explaining dissimilarities between fishing behaviours and their optimality indicators that could result from many other factors. For instance, fishing behaviours could be controlled by the duration of the fishing trip within the EEZ (Joo et al. 2015). External factors such as the diurnal and lunar periodicity of fishing effort, the presence of other long-liner boats operating nearby, or the fishing EEZ size decreasing the probability of boats being detected by whales may affect fishers' decision-making (Janc et al. 2018; Tixier et al. 2019a). Internal factors such as the belonging of the boat to fishing company could be investigated in defining of fishing behaviours (Gillis & Peterman, 1998; Rijnsdorp et al. 2000; Dorn, 2001). Indeed, some fishing companies have several boats and the fishers concerned may adopt collective exploitation due to information transfer between fishers. Conversely, other companies have only one boat, and fishers concerned are expected more likely to adopt an individual and competitive behaviour than a collaborative behaviour because of lack of existing information sharing (Allen & McGlade, 1986; Joo et al. 2015). Other studies emphasised the importance of fishing location and seasonality because fisheries could be characterised by both small-scale spatial and temporal variability of their fishing behaviours (Colloca et al. 2003; Massutí & Reñones, 2005; Bez et al. 2011). By a passive acoustic monitoring, the difference of boats' acoustics propagation and the difference of fishers' navigation behaviour may also influence frequencies of whale interactions (Richard, 2018).

Our study revealed that several fishing behaviours (*K-5, C-4, C-5* and *C-6*), which appeared to be mixed fishing behaviours, could be explained by an intra-fishing trip switching of fishing behaviours, and did not accurately define fishers' behaviour (Rogers & Pikitch, 1992; Pelletier & Ferraris, 2000; Palmer et al. 2009). These corresponding trips would be composed of fishing days belonging to several different fishing behaviours due to short-term adaptation and decision-making of fishers toward the fishing success and whale interactions (He et al. 1997; Richard et al. 2018). Conversely, other trips would be entirely composed of fishing days resembling one of the identified fishing behaviours because fishers would have planned their behaviour previously (Salas & Gaertner, 2004). Investigating fishers' decision-making and optimality indicators resulting from that decision at the fishing day level should be studied in the future (Lewy & Vinther, 1994; Pelletier & Ferraris, 2000; Palmer et al. 2009). Moreover, fishers used a passive adaptive strategy by relying on the constantly uploaded information at a finer scale. The fishing day, the hauling session, or the hauled line level may be a useful tool to analyze fishing behaviours in the case of the toothfish demersal fisheries facing depredation by marine predators (Richard et al. 2018; Janc, 2019). Moreover, preliminary visualization of fishing effort localization do not seem to show any significant different between fishing behaviours for fishing trip level at EEZ Crozet and EEZ Kerguelen (Supporting Information document 1, Figures S9 and S10) whereas variations in the spatial distribution of whale-boats interactions have been demonstrated (Gasco, 2013; Tixier et al. 2019b).

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