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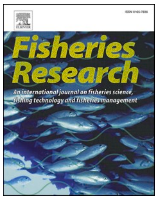

Both environmental conditions and fisher behaviour influence the occurrence of shark and odontocete depredation on the longline catch in New Caledonia

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ABSTRACT

Large marine predators feeding on fish caught on fishing gear, a behaviour termed “depredation”, frequently results in conflicts with significant ecological and socio-economic impacts. While adjusting fishing practices through spatio-temporal avoidance of depredation may offer an expedient and cost-effective mean of mitigating the conflict, its effectiveness is often limited by a poor understanding of the underlying drivers. Using 10 years of logbook data and generalised additive models, our study identified the environmental and operational factors influencing shark and odontocete (toothed whales) depredation on tuna catches of the New Caledonian longline fishery. Odontocete depredation was primarily driven by environmental factors such as sea surface temperature, bathymetry and sea surface height, whereas shark depredation was primarily driven by operational factors like the number of hooks set and soaking time. The findings suggest that depredation is more likely to occur in areas where predator natural distribution overlaps with fishing activities, and when fishers increase opportunities for predators to locate their gear. Targeted strategies, such as reducing soaking time to under 12 hours or limiting hooks per set to fewer than 1,750, could halve the likelihood of depredation, offering practical solutions to mitigate these interactions. Modelled predictions of the spatio-temporal patterns of depredation show well-delineated hotspots of odontocete depredation that can inform avoidance strategies developed by fishers. However, large variations in depredation probabilities among vessels suggest that additional factors related to individual fishers' behaviours, or with intrinsic features of vessels influencing their detectability, need further investigation to fully understand depredation mechanisms.

1. Introduction

The competition for resources and space often leads to conflicts between humans and wildlife. These conflicts can threaten the socio-economic viability of human activities and the conservation of wildlife species (Woodroffe et al., 2005). In the terrestrial environment, crop damage by large herbivores and attacks on humans or livestock by large carnivores are among the main sources of human-wildlife conflicts (Woodroffe et al., 2005; Chapron et al., 2014; Carter and Linnell, 2016; Nyhus, 2016; Støen et al., 2018). Their mitigation, which often requires changes in human practices, has been subject to extensive research efforts (Swenson et al., 1999; Herrero et al., 2005; Clavareau et al., 2024). In the marine environment, large marine predators such as sharks and marine mammals feeding directly on fish that are captured by fishers on fishing gear is a behaviour termed “depredation” that has been documented worldwide and that also leads to human-wildlife conflicts

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(Atlantic, Pacific and Indian Oceans, Northridge, 1991; Read, 2008; Hamer et al., 2012; Mitchell et al., 2018). The severity of these conflicts has increased substantially globally over the past 60 years as a result of the expansion of fisheries and changes in fisheries management (Donoghue et al., 2003; Gilman et al., 2006; Read, 2008; Hamer et al., 2012; Tixier et al., 2020). Depredation can result in lost catch, which means lost revenue, but also results in unaccounted fish mortality of target species, which can have implications for fish stock assessments. Further, the species responsible for depredation are at risk of becoming bycaught or suffering physical retaliation from fishers. Thus, depredation has negative consequences on multiple components of the marine socio-ecological systems involved (Werner et al., 2015; Bearzi et al., 2019; Tixier et al., 2021). Yet, and unlike for most terrestrial cases of human-wildlife conflicts, the knowledge needed to identify changes in fishing practices that could effectively mitigate depredation is often limited by a lack of data on both fishing operations and the associated behaviour of large marine predators.

While lethal control of predators was the primary approach used to reduce depredation in the early decades of large-scale fisheries (Gilman et al., 2008; Werner et al., 2015; Bearzi et al., 2019), for example in response to grey and harbour seal depredation between the 1970s and 1990s (USA, Morris, 1996; Scotland, Quick et al., 2004; UK, Butler et al., 2008; Baltic Sea, Westerberg et al., 2008) or Icelandic killer whales in the 1950s (Mitchell, 1975), efforts are now directed towards finding effective, non-invasive and cost-effective mitigation approaches. These are designed to ensure the socio-economic viability of fishing activities and the conservation of the large marine predator species involved. These approaches can be classified into two types: i) limiting (or preventing) access to catch by large marine predators through the use of deterrents or gear modifications, and ii) avoidance of large marine predators by vessels to eliminate the spatiotemporal overlap necessary for depredation to occur (Hamer et al., 2012; Peterson and Carothers, 2013; Tixier et al., 2015; Janc et al., 2018). The latter approach, and specifically the set of strategies through which fishers can anticipate and avoid areas and time periods of high risk of depredation, often offer immediate, easy-to-implement and cost-limited mitigation solutions for depredation (Stepanuk et al., 2018; Tixier et al., 2015, 2019a), except if relocating causes a decrease in the overall net catch rate. However, to be effective and adaptive, these solutions require a better understanding of the drivers of the spatio-temporal occurrence of depredation that can be used to accurately identify or predict likely “conflict hotspots” (Abade et al., 2014; Gastineau et al., 2019).

The occurrence and level of depredation are likely to be mostly driven by the spatio-temporal overlap between fishing activities and marine predators. This assumes that marine predators switch from foraging on free-ranging prey to depredation when opportunities to feed at low foraging costs emerge from fishing activities in their environment (Hamer et al., 2012). This switch occurs either because predators and fisheries compete for the same species or because fishing operations expose predators to new species that are typically outside their natural range or capabilities (Tixier et al., 2019b). Depredation acquired as a new foraging behaviour when the fish targeted by fishers is a natural prey of local predator populations, was evidenced in some fish-eating killer whale populations (Strait of Gibraltar, Esteban et al., 1984; Norway, Similä, 2005; Alaska, Peterson et al., 2013). Generalist species or populations may also be more inclined to develop depredation on prey that are not part of their natural diet, such as common bottlenose dolphins, grey seals, harbour seals, or generalist killer whale populations (Tollit et al., 1998; Austin et al., 2004; Rossman et al., 2015; Tixier et al., 2019b). In some cases, certain species, especially toothed whales (odontocetes) and sharks, have been observed actively searching for and following fishing vessels providing them with opportunities to depredate on fishing catch, thereby potentially altering their natural distribution range (Janc et al., 2018; Towers et al., 2019; Mitchell et al., 2020; 2024).

The spatio-temporal occurrence of depredation can therefore be determined by factors related to both the ecology/behaviour of marine predators (hereafter “environmental” factors), and the behaviour of fishing vessels (hereafter “operational” factors). For sharks or marine mammals, environmental factors often include biophysical variables that are used as proxies for the distribution of their prey (Redfern et al., 2017), with both static (e.g., bathymetry, slope; Thorne et al., 2017) and dynamic variables (e.g., chlorophyll-a concentration, net primary production, sea surface temperature, sea surface height; Woodworth et al., 2011; Hazen et al., 2017; Brodie et al., 2018). Operational factors may include fisher’s decisions about where to fish (Stepanuk et al., 2018) and how they use their gear when fishing, for example, the amount of gear they deploy or the time they leave it soaking, which can influence the extent of depredation opportunities for marine predators (Tixier et al., 2015; Janc et al., 2018; Fader et al., 2021).

In New Caledonia, the pelagic longline commercial fishery targeting tuna is subject to high depredation by both sharks and odontocetes with 63% of longline sets (i.e., a mainline bearing thousands of baited hooks) and 5% of the total catch depredated (Mollier et al., 2024). The fishery was initiated by Japanese longliners in the 1960s and became exclusively operated by New Caledonian vessels in 2001. The number of vessels varied between 14 and 19 per year since 2010, with a total of 19 different vessels that have operated at least once between 2001 and 2019. In 2019, 14 vessels were part of the fleet being locally managed by the government of New Caledonia, with scientific support from the South Pacific Community (SPC) and complying with the Western and Central Pacific Fisheries Commission (WCPFC) recommendations. The key tuna species targeted by the fishery (south Pacific albacore *Thunnus alalunga* and yellowfin tuna *Thunnus albacares*, with small amounts of bigeye tuna *Thunnus obesus*) are part of larger migratory stocks in the western and central Pacific that are regionally managed under the jurisdiction of the WCPFC. The main depredating species remain uncertain, but likely involve false killer whales (*Pseudorca crassidens*), short-finned pilot whales (*Globicephala macrorhynchus*), blue sharks (*Prionace glauca*), oceanic whitetip sharks (*Carcharhinus longimanus*), tiger sharks (*Galeocerdo cuvier*), mako sharks (*Isurus oxyrinchus*), or silky sharks (*Carcharhinus falciformis*), among others (Mollier et al., 2024; P. Hamer & F. Prioul, pers. comm.).

Depredation has recently emerged as a growing concern, significantly impacting the socio-economic performance of the fishery, a key driver of New Caledonia’s development. Indeed, this small-scale industry supplies a large amount of fish for consumption to the New Caledonian population and generates over 200 direct jobs and approximately USD 9 M of fish sales for a production of approximately 2,500 tonnes of tuna per year (WCPFC, 2023). Despite the absence of a vessel-based quota system in this fishery, the high frequency of depredation events and the associated removal of catches by sharks and odontocetes result in non-negligible direct and indirect costs for fishers, in the form of catch losses and additional fishing effort to compensate for these losses and/or to avoid depredation (Secchi and Vaske, 1998; Peterson et al., 2014; Gimonkar et al., 2022). Moreover, depredation, and the negative impacts it can have on predators and their ecosystem, involves high conservation stakes since the fishery operates in a designated Marine Protected Area: the Natural Park of the Coral Sea (i.e., “Parc Naturel Marin de la Mer de Corail”). The park encompasses the entire Exclusive Economic Zone (EEZ) of New Caledonia (1.3 million km^2; Martin and Lecren, 2014) and is characterised by a high richness and diversity of prey and predators (Allain et al., 2012; Ceccarelli et al., 2013; Laran et al., 2024; Receveur et al., 2022). Together, these high socio-economic and conservation stakes make the mitigation of shark and odontocete depredation in the New Caledonian tuna longline fishery a priority management action through the implementation of avoidance strategies. However, to be effective, these avoidance strategies require a better understanding of the drivers of depredation occurrence in the area in order to provide reliable predictions for fishers and managers.

Using ten years of fishing data collected on all fishing operations between 2010 and 2019, this study aimed to identify the environmental and operational factors influencing shark and odontocete depredation on the catch of the New Caledonian tuna longline fishery. Specifically, the study aimed to i) model the occurrence of shark and odontocete depredation as a function of both static and dynamic environmental and operational variables, and ii) generate spatio-temporal predictions of the probability of depredation in both space and time.

2. Materials and methods

2.1. Study area and data collection

The study area encompassed the entire New Caledonian EEZ (from 154 to 175°E, and from 26 to 14°N) (Fig. 1) where the longline fishery operates. This area is characterized by rich continental shelves, protected coral reefs, deep-sea slopes, and the influence of ocean currents such as the south equatorial current and upwelling, fostering high biological productivity (Andréfouët et al., 2009; Gasparin et al., 2011). The New Caledonian tuna longline fishery uses horizontal pelagic longlining. The standard longline is a monofilament mainline deployed in the water column typically at depths between 30 and 350 m, with between 1,400 and 2,200 regularly spaced individual branch lines, each equipped with a hook (predominantly circle hooks) that is mostly baited with mackerel (SPNMCP, 2021b). Longline sets, as described above, are on average 50 kilometres long and are left soaking for 4–15 hours, typically deployed early in the morning around dawn and retrieved by late afternoon. A fishing event is defined from the beginning of the deployment phase (i.e., the setting phase) of a longline set, which lasts around 3.5 hours, to the end of the retrieval phase (i.e., the hauling phase), which lasts around 7.5 hours.

The data used for the analysis were collected by fishers (on 100% of the fishing trips) and combined with fishery observers (on 4.2% of the trips) data to supplement the fishers reports and provide additional details, as part of the onboard observer programme of the New Caledonian longline fishery, and were extracted from the SPC database for the study (SPNMCP, 2021a). For each longline set, the following data were recorded: vessel ID, longline set ID, time at the start and end of setting, time at the start and end of hauling, geographic position (latitude and longitude) of the start and end of the longline set, the number of hooks per set, the catch by species (in number of individuals), and its fate, including the number of fish per species, that were non-depredated and retained, depredated by sharks or odontocetes and retained, and depredated by sharks or odontocetes and discarded. Fish were considered depredated when partially consumed by sharks or odontocetes, meaning that depredated fish remains retrieved on the hooks were identified by fishing crews with extensive knowledge of depredation and experience in determining the depredating taxa based on bite marks. As in most other studies on depredation by these two types of predators in pelagic longline fisheries, the type of bite marks (sharks leave bites with clear crescent-shaped cuts, while odontocetes often predate the whole fish leaving only hard parts of the head (Figure S1), Secchi and Vaske, 1998; Chapman et al., 2006; Gilman et al., 2006; Romanov et al., 2009; Rabearisoa et al., 2018) were used to differentiate depredation between the two taxa (Mollier et al., 2024). The species of odontocetes involved in depredation, which are mainly false killer whales in pelagic longline fisheries, including in the New Caledonian fishery we studied here, rarely remove the fish entirely from the hook (Secchi and Vaske, 1998). When depredation occurred, fishers and observers were only occasionally able to confirm the depredating species, so subsequent analyses on the occurrence of depredation were conducted at the shark/odontocete taxa level. Longline sets in which none of the fish were partially consumed were considered as “non-depredated”, sets in which at least one fish was partially consumed by sharks were considered as “depredated by sharks” and sets in which at least one fish was partially consumed by odontocetes were considered as “depredated by odontocetes”.

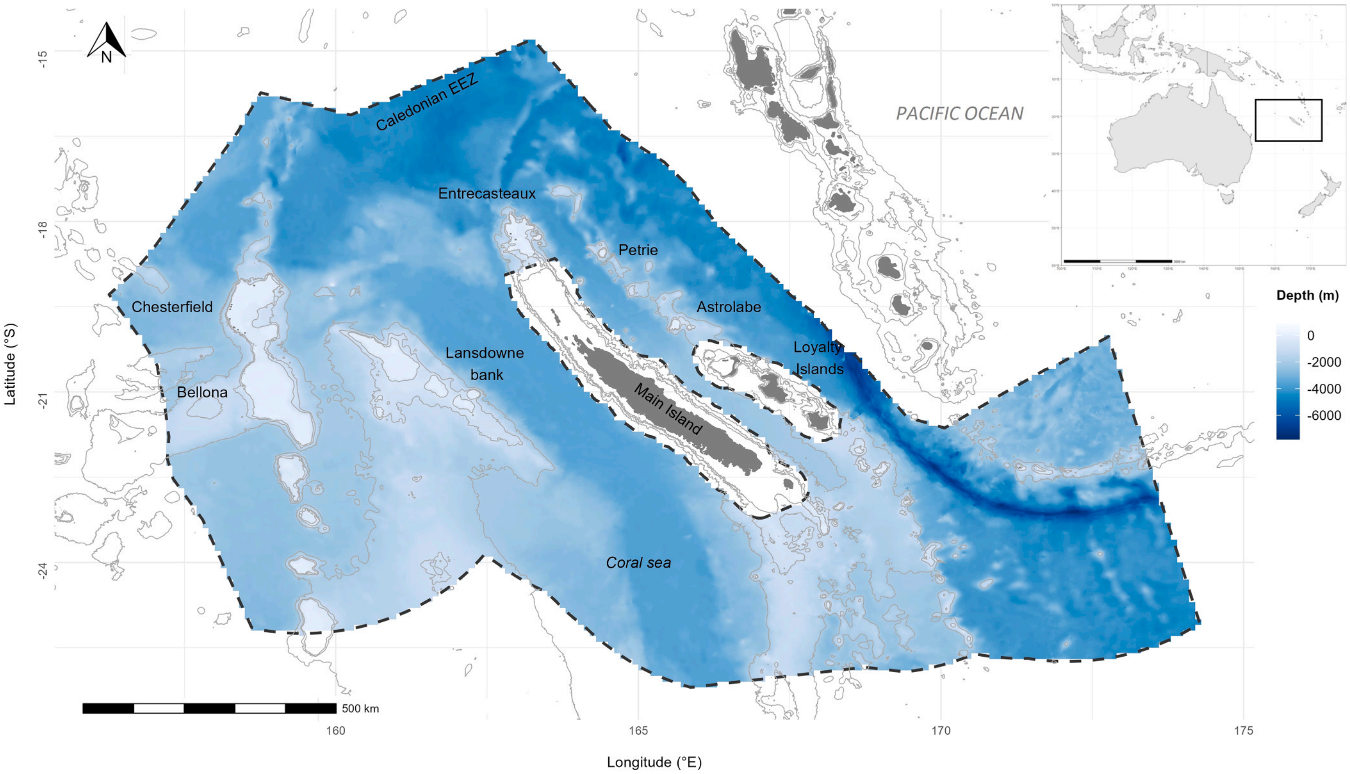

Fig. 1. Map of the study area with depth (in meters) and 500, 1,000 and 2,000-m isobaths. The dashed line represents the EEZ delimitations. Note that the coastal waters of the main island and Loyalty islands shown with a white background are not exploited by the longline fishery.

2.2. Environmental and operational variables

The influence of environmental factors on the occurrence of depredation was examined using 11 variables known to influence the distribution of large marine predators by mediating prey availability (Table 1; Praca et al., 2009; Virgili et al., 2024; Lerebourg et al., 2023). They included both static (bathymetry, slope, and distance to the nearest seamount) and dynamic (temperature, currents, eddy kinetic energy, chlorophyll-a concentration, sea surface height, depth of mixed layer and salinity) variables that were extracted for a study area covering the New Caledonian EEZ. Month was also included to reflect temporal variability, as a circular cubic splines term in the models. Bathymetry was extracted from the GEBCO database (https://download.gebco.net/), and was used to calculate the slope (in degrees) using the "terrain" function from the "raster" package in R (Hijmans and van Etten, 2012). The distance to the nearest seamount was derived from the seamount database described in Allain et al. (2008). Due to the relatively deep-diving capacities of the species involved in depredation, and the fact that depredation on fishing sets of the New Caledonian fishery mainly occurs at depth, we extracted dynamic ocean variables at various depths from numerical modelled oceanographic products: GLOBAL_ANALYSISFORECAST_PHY_001_024 for water temperature, current velocity, sea surface height, mixing layer depth and salinity; and GLOBAL_ANALYSISFORECAST_BGC_001_028 for chlorophyll-a concentration, provided by Copernicus (https://data.marine.copernicus.eu/products). The eddy kinetic energy was calculated from the current velocity as follows: $\mathrm{EKE} = 0.5*(U^2 + V^2)$, where U and V are the two current components.

The influence of operational factors on the occurrence of depredation was examined using five variables that have been shown to affect depredation on longline catches in other regions: the vessel identity, the spatial density of vessels operating simultaneously, the soaking time, the number of hooks on longline sets and the occurrence of depredation on the longline sets previously hauled by the same vessel during the same trip (Table 1; Tixier et al., 2015; Janc et al., 2018; Fader et al., 2021). These variables were all extracted from the logbook data for specific positions and dates. As a way to assess the potential effect of multiple vessels operating in the same area and time window, vessel density was calculated as the number of vessels that hauled longline sets within 200 km and ± 3 days of the observed longline set. These values were chosen based on the values used for assessing the effect of the density of vessels on depredation in the tuna longline fishery of Hawaii (Fader et al., 2021) as a trade-off between having a gradient large enough for that covariate (vessels may simultaneously operate tens / hundreds of km away from each other) and encompassing the travelling distance / time sharks and odontocetes are able to travel. The number of hooks on longline sets was the total number of hooks hauled. Soaking time was calculated as the time (in hours) between the time the last hook of a longline set was deployed and the time the last hook was hauled.

For the dynamic environmental variables, data were extracted for the period spanning from January 1st 2010 to December 31st 2019 with a monthly temporal resolution, and for three depth layers: the surface, between 0 and 200 m, and between 200 m and 500 m. For each depth layer and each variable, monthly climatological averages and standard deviations over the 9 years of extracted data were calculated to assess the inter-annual variability of these variables. This means that for each month of the year (Jan-Dec), the mean and standard deviation of the months over ten years (2010–2019) were calculated. Static variables were extracted at a resolution of 0.004°, and dynamic variables at a resolution of 0.08° (except for chlorophyll-a at 0.25°), but for the analyses, all variables were re-scaled to a resolution of 0.1° (i.e., spatial cells of about 10 ×10 km). The values of these variables were assigned to each longline set based on the date and position at which it was hauled.

Table 1

Environmental and operational variables used for modelling the occurrence of shark or odontocete depredation on the catch of the longline tuna fishery in the New Caledonian EEZ.

Variable	Name	Units	Spatial resolution	Temporal resolution	Source
Bathymetry	bathymetry	m	0.004°	Static	GEBCO
Slope	slope	°	0.004°	Static	Derived from bathymetry
Distance to the nearest seamount	min_distance_to_seamounts	km		Static	Derived from seamounts position database (Allain et al. 2008)
Temperature	Temp_mean_surf Temp_mean_0.200 m Temps_mean_200.500 m	°C	0.08°	Monthly (2010 – 2019)	COPERNICUS
Currents	Current_mean_surf Current_mean_0.200 m Current_mean_200.500 m	m^{2}.s^{-2}	0.08°	Monthly (2010 – 2019)	COPERNICUS
EKE – Eddy Kinetic Energy	Eke_mean_surf Eke_mean_0.200 m Eke_mean_200.500 m	m^{2}.s^{-2}	0.08°	Monthly (2010 – 2019)	COPERNICUS
Chlorophyll-a concentration	CHL_mean_surf CHL_mean_0.200 m CHL_mean_200.500 m	mg.m^{-3}	0.25°	Monthly (2010 – 2019)	COPERNICUS
Sea surface height	SSH_mean	m	0.08°	Monthly (2010 – 2019)	COPERNICUS
Depth of mixed layer	MLD_mean	m	0.08°	Monthly (2010 – 2019)	COPERNICUS
Salinity	Sal_mean_surf Sal_mean_0.200 m Sal_mean_200.500 m		0.08°	Monthly (2010 – 2019)	COPERNICUS
Vessel identity	vessel_id				Logbooks
Vessel density (number of all vessels within 200 km ±3 days)	density		Point data		Logbooks
Soaking time	soak	hours	Point data		Logbooks
Number of hooks set	hook_set		Point data		Logbooks
Presence of depredation on previous set of same vessel	presence_prev_shark presence_prev_odont		Point data		Logbooks
Month	month			Monthly (2010–2019)	Logbooks

2.3. Model selection

Generalised additive models (GAMs; Hastie and Tibshirani, 1990) were used to model the occurrence of shark and odontocete depredation on the catch of the tuna longline fishery as a function of environmental and operational variables in the New Caledonian EEZ. GAMs are flexible regression techniques that rely on smooth functions to estimate non-linear and non-monotonic relationships between a response variable and covariates (Wood, 2017). Here, GAMs were fitted using the "gam" function of the "mgcv" package (Wood, 2017), with a binomial distribution and logit link function. One model was developed for shark depredation (longline sets not depredated by sharks vs. depredated by sharks) and one model for odontocete depredation (longline sets not depredated by odontocetes vs. depredated by odontocetes), with covariates including the eleven environmental and five operational variables described above. GAMs were also fitted to the number of fish depredated per set using a Tweedie distribution because of the large number of zeros and the overdispersed data. The variable vessel_id was included as a fixed effect in the models.

As collinearity between explanatory variables is known to affect the stability of a model (Dormann et al., 2013), Spearman coefficients were calculated between each pair of variables and variables with coefficients >0.7 were removed to avoid excessive multicollinearity and to retain ecologically relevant variables in the model (Zuur et al., 2010; Dormann et al., 2013; Braunisch et al., 2013). The Variance Inflation Factor (VIF) of the variables included in the final models was also checked to assess the stability of the model's coefficients, using a threshold of 3 as advised by Zuur et al. (2010) (Table S1). GAMs were applied using the Restricted Maximum Likelihood method and the smoothed explanatory variables were modelled with penalised thin-plate regression splines with a limited basis size of 5 to prevent overfitting (Wood, 2017). For each taxon (sharks or odontocetes), binomial GAMs were ranked based on Akaike's information criterion (AIC) scores (Akaike, 1974; Burnham and Anderson, 2004; Symonds and Moussalli, 2011) and a backward stepwise procedure was used for variable selection, considering a p-value of 0.05 as the threshold for excluding non-significant covariates.

2.4. Evaluation and predictions

Models were run with a 10-fold cross-validation, blocked by year (rather than systematically excluding a given year) to account for temporal structure (Roberts et al., 2017). Test–train splits were generated, where each split selected 20% of the data for model evaluation (testing data), and 80% of the data for model fitting (training data). The percentage of deviance explained by each model was calculated over the training dataset. The external evaluation of the models was computed over the testing dataset. Model accuracy was assessed by calculating the root of mean square error (RMSE) between observed and predicted probabilities in the testing dataset (Brodie et al., 2021). The ability of the models to accurately predict areas with no occurrence of depredation was assessed using true negative rates. Predictive performance was assessed by calculating AUC (Area Under the ROC curve) over the testing dataset, as AUC is a metric of the capacity of models to discriminate between presence and absence points over a range of 0–1 (Swets, 1988). Functional response plots were produced for all significant variables in the shark and odontocete models (approximate smooth term significance with p-value <0.05).

The selected models were used to predict the spatial probability of occurrence of shark and odontocete depredation, within the New Caledonian EEZ on a 10-km resolution grid, using the "predict" function of the "mgcv" R package (Wood, 2017). Prediction maps were produced using the monthly grids of environmental variables (Figure S2) and a new grid was built for the vessel density calculated over a 0.1° spatial grid with a value of 1 for areas without fishing data (Figure S3). The other operational variables were set to their mean value in the predict function. In the prediction maps, areas where fishing data were available were distinguished from those with no data. These no-data areas represent either unexploited areas or areas where fishing occurred but the data were not included in the subsample of the total fishing effort used for this study. Monthly predictions were averaged over the entire study period (2010–2019) and the mean standard error of predictions was reported as a metric of the uncertainty. Predictions and vessel density (Figure S4) were also averaged over three-month periods: December-February (Dec-Feb), March-May (Mar-May), June-August (Jun-Aug), and September-November (Sep-Nov).

3. Results

Data were analysed from a total of 1,066 longline sets deployed by 19 vessels between 2010 and 2019. Out of the 1,066 sets, 654 sets were subject to depredation by sharks (61.4%), 89 sets were subject to depredation by odontocetes (8.3%) and 50 sets were subject to depredation by both sharks and odontocetes (4.69%). When depredation occurs, sharks removed a mean of 3.2 ± 2.7 of fish per set while odontocetes depredated a mean of 11.9 ± 15.2 of fish per set.

3.1. Models selection

After correlation checks between variables (Figure S5), model selection based on AIC and REML showed that the variables selected to best explain the occurrence of shark depredation were vessel identity, sea surface temperature, surface currents, soaking time, number of hooks set, vessel density, and month, while the variables selected to best explain the occurrence of odontocete depredation were vessel identity, bathymetry, surface temperature, currents at 200–500 m, sea surface height, chlorophyll-a concentration, and soaking time (Table 2). From the model's with Tweedie distribution outputs, the number of fish depredated by sharks was influenced by vessel identity, sea surface temperature, chlorophyll-a concentration, soaking time, number of hooks set and vessel density. The number of fish depredated by odontocetes was influenced by vessel identity, bathymetry, slope, sea surface temperature and surface currents (Table S2, Figure S7).

The average percentage of deviance explained by these final models, calculated across the 10-fold runs, were 19.6% for the shark depredation model and 24.8% for the odontocete depredation model. For the shark depredation model, the AUC was high (0.68), the overall accuracy was 0.47 and the true negative rate was 100% (Table 3). For the odontocete depredation model, the AUC was high (0.71), but the overall accuracy was low (0.27) despite a high true negative rate (100%; Table 3). Interestingly, the percentage of deviance explained was higher for the model fitted to the number of fish depredated by sharks (21.5%) than for the shark depredation occurrence model (19.6%), whereas the opposite pattern was observed for odontocetes, with a higher deviance explained for the occurrence model (24.8%) than for the model predicting the number of fish depredated. However, the predictive power of these models was not substantially improved compared to that of models fitted to the occurrence of depredation (Table S3).

3.2. Environmental and operational drivers of depredation

From the final model's outputs and predictions, the probability of shark depredation occurring increased with the soaking time and the number of hooks, with the highest probability (P(depredation) > 0.73) for soaking times >15 h and numbers of hooks >1,750 (P(depredation) > 0.36; Fig. 2A). It also increased with the vessel density up to 6 vessels and decreased with vessel density from 6 to 9 vessels. It was the highest for surface temperatures of 26°C (P(depredation) = 0.35) and for surface current velocities of 0.10–0.15 $m^2.s^{-2}$ (P(depredation) = 0.37). Finally, the probability of shark depredation occurring was higher between December and January (P(depredation) = 0.54) than between June and August (P(depredation) = 0.36).

The probability of odontocete depredation occurring was the highest

Table 2

Outputs of the GAM models that best fitted the occurrence of odontocete and shark depredation in the New Caledonian longline fishery from 2010 to 2019. SE: standard error, edf: estimated degrees of freedom in GAM fitting, $\chi2$: Chi-square statistic, P: p-value.

	Sharks					Odontocetes				
Term	**Estimate**	**SE**	**edf**	**$\chi2$**	**P**	**Estimate**	**SE**	**edf**	**$\chi2$**	**P**
Parametric terms										
Vessel ID										
Vessel #1	1.66	0.30			<0.001	-2.73	0.51			<0.001
Vessel #2						-2.53	0.56			<0.001
Vessel #3	1.42	0.36			<0.001	-2.82	0.62			<0.001
Vessel #4						-4.19	1.09			<0.001
Vessel #5	0.86	0.25			<0.001	-1.99	0.42			<0.001
Vessel #7	0.80	0.28			0.005	-2.61	0.60			<0.001
Vessel #8						-3.67	1.10			<0.001
Vessel #11	-0.65	0.19			<0.001	-3.72	0.50			<0.001
Vessel #12						-3.97	0.86			<0.001
Vessel #13	0.51	0.23			0.03	-4.03	0.65			<0.001
Vessel #14	1.16	0.26			<0.001	-3.29	0.59			<0.001
Vessel #15	1.58	0.37			<0.001	-2.59	0.52			<0.001
Vessel #16	0.69	0.26			0.007	-4.34	0.79			<0.001
Vessel #17	-2.34	0.81			0.004					
Vessel #19	1.36	0.29			<0.001	-2.92	0.60			<0.001
Smoothed terms										
Bathymetry								1.70	11.06	0.001
Sea surface temperature			1.20	3.10	0.02			2.10	25.03	<0.001
Current surface			1.68	8.49	0.006					
Current 200–500 m								1.75	5.88	0.03
Sea surface height								1.69	13.24	<0.001
Chl-a								1.58	4.66	0.04
Soaking time			0.99	82.20	<0.001			1.54	4.97	0.04
Number of hooks set			1.71	16.89	<0.001					
Vessel density			2.32	11.20	0.004					
Month			2.52	7.74	0.006					

Table 3

Summary of the GAM models that best fitted the occurrence of odontocete and shark depredation, with Dev.exp: the percentage of explained deviance, Accuracy: RMSE, True negative rate: proportion of actual negative cases that are correctly identified by the model as negative, and AUC: area under the ROC curve. All metrics are averaged across the 10-fold cross validation runs.

Model training	Evaluation on test fold			
Model	**Dev.exp.**	**Accuracy**	**True negative rate**	**AUC**
Odontocetes	24.8%	0.270	100%	0.71
Sharks	19.6%	0.474	100%	0.68

for cooler sea surface temperatures of 21.4°C (P(depredation) = 0.17) and decreased when temperature was >22°C, was the highest (P (depredation) = 0.09) for current velocities of 0.1 $m^2.s^{-2}$, chlorophyll-a concentrations of 0.1 $mg.m^{-3}$ and for soaking times >10 h, and was the lowest (P(depredation) = 0.06) for sea surface heights of 0.60–0.70 m. It also decreased from 0.40 to 0.08 between 4,000 and 2,000 m of depth (Fig. 2B).

The vessel_id term was significant in both the shark depredation and odontocete depredation models, with predicted probabilities of depredation occurring per vessel ranging from 0.12 to 0.88 for sharks, and from 0 to 0.53 for odontocetes (Fig. 3). Vessels with zero or low probability of depredation were those with low fishing effort, except for Vessel 6 and Vessel 9, which, despite a low fishing effort, showed a high probability of depredation (Figure S6).

3.3. Predictions of shark and odontocete depredation hotspots

For spatial predictions, the operational variables of the final model were fixed at a mean value (hook_set = 2,000, soak = 13 h) and a vessel with an average predicted probability of depredation was selected (vessel #1). The mean predicted probability of shark depredation occurrence was high (P(depredation) = 0.38) throughout the part of the EEZ where fishing data were available. Maximum probabilities (P (depredation) = 0.61) were found to the west of the main island, especially around Chesterfield and Bellona, as well as west of d'Entrecasteaux, near Petrie and Astrolabe, and between the main island and the Loyalty Islands (Fig. 4A). These areas were associated with sea surface temperatures between 25 and 27°C, low surface current velocities and a mean vessel density of 6 (Figures S1, S2). On the contrary, areas of low predicted probability of depredation (P(depredation) < 0.2) were located to the north-west of Chesterfield and the south-west of the main island where simultaneous vessel density was high on average (Figure S3). The predicted number of fish depredated by sharks was high in areas such as north of Chesterfield and low in areas such as north-west of the core fishing zone (Figure S8). Results in areas where no fishing data were available showed high predicted probability of depredation (P (depredation) > 0.45) in the shallow waters of the Chesterfield and Bellona lagoons and on the summit of neighbouring seamounts and banks (Fig. 4B). The standard error of predictions ranged from 0.5 to 2.1 throughout the prediction area (Figure S10), and was high (SE > 1.5) in areas where no fishing data were available except for the area between the main island and the Lansdowne bank. Seasonal predictions showed that the mean probability of shark depredation to occur was the highest in Dec-Feb (P(depredation) = 0.30) and the lowest in Jun-Aug (P (depredation) = 0.20) with low variation between seasons. Higher probabilities were observed in the south of the EEZ in Dec-Feb and Mar-May than in Jun-Aug and Sep-Nov (Figure S12).

Areas of high probability (P(depredation) > 0.5) of odontocete depredation where fishing data were available were predicted to occur in the south of the main island, from the west to the east of the EEZ, and to the east of the Loyalty Islands with the highest probability of 0.63 (Fig. 5A). These areas were characterised by greater depths (>2,000 m), lower sea surface temperatures and low to moderate sea surface heights (Fig. 1, S1). The predicted number of fish depredated by odontocetes was high to the south-east of the fishing zone (Figure S9). Areas with low probability (P(depredation) < 0.5) of odontocete depredation to occur were predicted in areas with shallower depths, high sea surface heights, warmer waters and areas with higher current velocities. For the areas

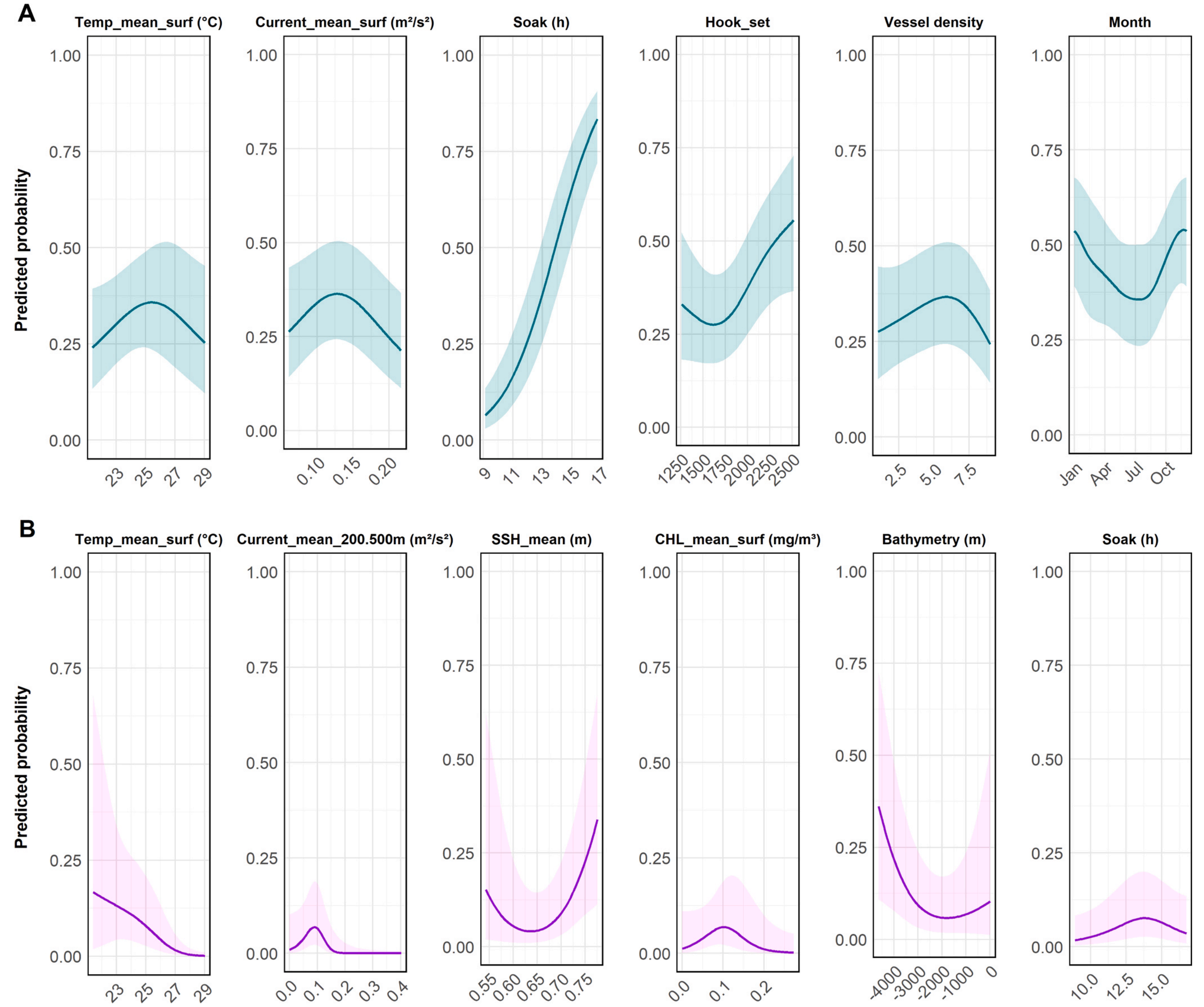

Fig. 2. Relationships between the probability of shark (A) and odontocete (B) depredation to occur and the variables selected in the final GAMs. Solid lines represent the estimated smooth functions and shaded regions show the approximate 95% confidence intervals, both averaged over the 10-folds cross-validation.

where no fishing data were available, the mean predicted probability of depredation was 0.2, with the highest probability (P(depredation) = 0.9) to the south of the main island (Fig. 5B). The standard error of predictions was lower than for sharks and varied between 5.10^{-7} and 0.81 throughout the prediction area, with larger uncertainty occurring in the south-eastern area of the EEZ in the New Hebrides Trench (Figure S11). Seasonal predictions showed that high probabilities of odontocete depredation occurring were spread out across the entire EEZ in Jun-Aug and Sep-Nov where the mean predicted probability was the highest (P(depredation) = 0.37), and were restricted to the south of the EEZ in Dec-Feb (P(depredation) = 0.17) and Mar-May (P(depredation) = 0.15) with lower values (Figure S13).

4. Discussion

This study suggests that multiple factors including both environmental and operational variables influence the occurrence of depredation by sharks and odontocetes on the catch of the pelagic longline fishery in New Caledonia. While limitations associated with the data or knowledge of the species involved are discussed, the findings suggest that both the natural distribution of predators and the way fishers use their gear may contribute to high probabilities of depredation to occur.

Despite the large amount of data used in the study and our attempt to build a robust modelling approach, we must highlight some caveats and limitations. Firstly, fitting models to the occurrence of depredation as a binary response variable was useful for estimating the probability of fishers to experience shark or odontocete depredation, but did not assess the extent of depredation on fishing sets. Secondly, while GAMs fitted to the number of depredated fish on fishing sets did allow for predicted estimates of the severity of depredation to be produced, these were likely underestimated by the fact that depredated fish may have been missed given that depredation in New Caledonia was monitored using partially eaten fish only. GAMs provide a flexible framework for capturing nonlinear effects, however their power for spatial extrapolation may be limited, especially in areas where the data is sparse. To mitigate this, we ensured that our models were carefully validated and we only interpreted their predictions in data rich areas. We also provided maps of the uncertainty associated with model predictions, such as the standard deviation of predicted probabilities of the occurrence of depredation, which should be considered when interpreting the results on the spatial variation of shark and odontocete depredation. In addition, uncertainty was detected in both model outputs, with relatively

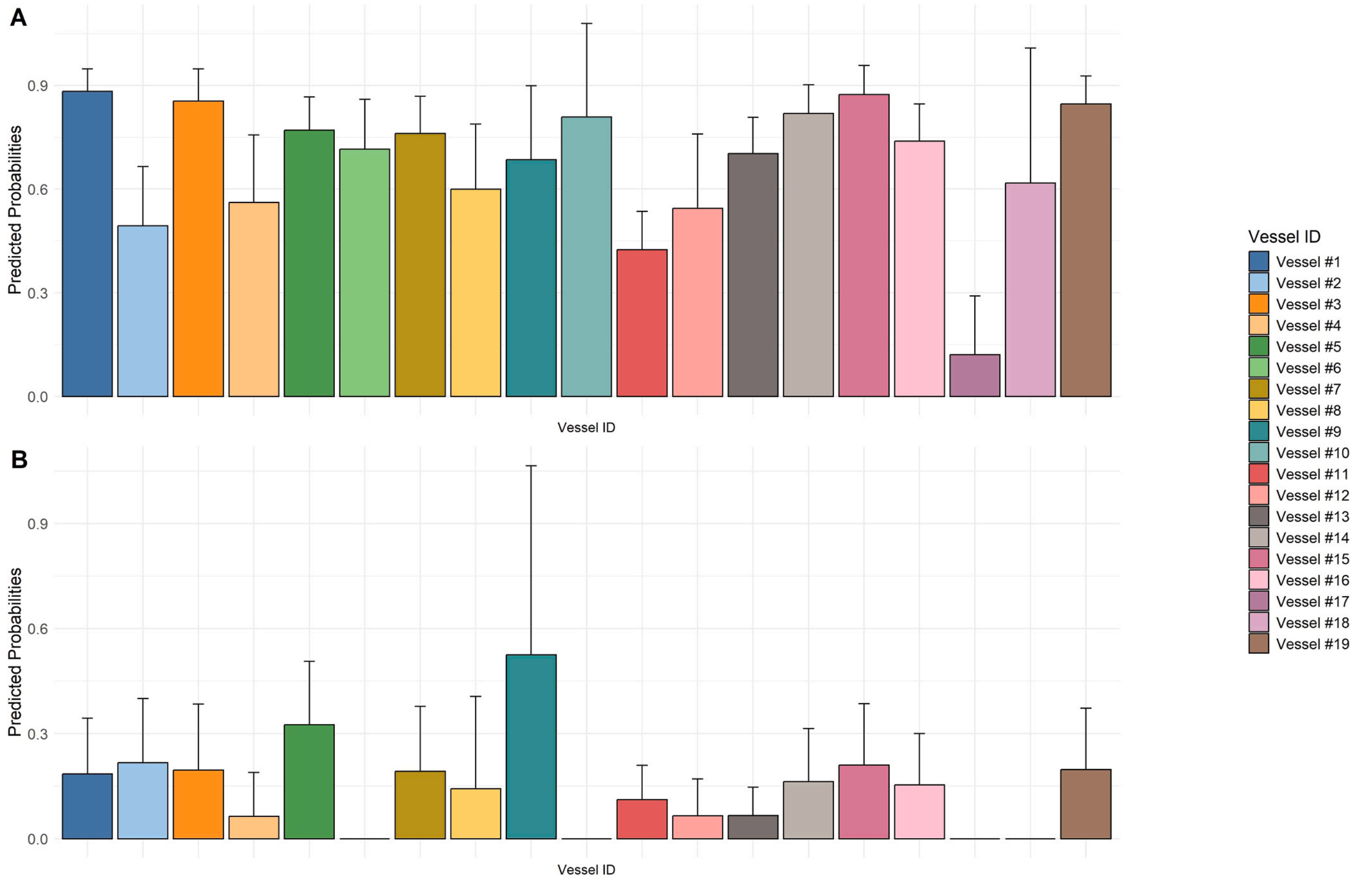

Fig. 3. Predicted probability of the occurrence of shark (A) and odontocete (B) depredation per vessel in the New Caledonian tuna longline fishery between 2010 and 2019. The bars are the predicted probabilities for each vessel and the error bars show the upper confidence bounds for the predictions.

low rates of deviance explained by the models, as well as in model predictions. The rates of deviance explained are rarely high for models fitted to explain the distribution of predators. This is due to the difficulty of using causal predictors, such as the distribution and concentration of potential prey (Pendleton et al., 2020; Virgili et al., 2021), but also the wide range of complex, interacting environmental variables that influence predator ecology (Receveur et al., 2022), as well as fishing behaviour. Therefore, studies often examine indirect predictors such as environmental conditions instead (Austin, 2002). Typically, here, the influence of the distribution and concentration of the prey of the predators involved in depredation could not be examined since: i) the specific depredating shark and odontocete species are uncertain, and ii) the prey preferences and diet composition of the species most likely to be involved in depredation, such as false killer whales, short-finned pilot whales and oceanic species of sharks, have not been documented in the study region. The low rate of deviance explained by the models may also be due to uncertainty in the data resulting from depredation events potentially being missed by observers and from the limited proportion of fishing operations monitored by observers (<10% of all operations).

Depredation was monitored through records of damaged fish on the lines, and we cannot exclude the possibility that depredation was missed if whole fish were removed from the hooks by predators (Hucke-Gaete et al., 2004; Rabearisoa et al., 2018; Fader et al., 2021). However, based on what we know about the species involved and their depredation behaviour in other tuna pelagic longline fisheries similar to the New Caledonian fishery, it is rare for them to take the fish entirely, leaving the hooks empty (Secchi and Vaske, 1998; Chapman et al., 2006; Gilman et al., 2006; Romanov et al., 2009; Rabearisoa et al., 2018). As such, the depredation estimates we provided here should be considered as minimum estimates. Missed depredation events due to whole fish having been depredated, along with inaccurate assignments of the depredating taxa to depredated fish by the fishers, may also have introduced bias to our data and led to underestimated depredation levels. Although the impact of these biases on the spatio-temporal predictions from models is believed to be negligible given the usually clear distinction between fish depredated by sharks and fish depredated by odontocetes based on bite marks, the large amount of data available for the study, and the large experience of fishers in assessing depredation, the study highlights the need to improve the monitoring of depredation in the New Caledonian fishery. This could be achieved, for instance, through increasing photo documentation of depredated fish by captains and through the implementation of alternative monitoring approaches of depredation using electronic monitoring, line acceleration signals and/or acoustics (Thode et al., 2016; Emery et al., 2019; Gilman et al., 2019; Stahl et al., 2023). In addition, the occurrence of depredation may not reflect the natural distribution of predators due to the attraction effect that fishing activities may have on predators, which may be stronger for some vessels than for others (Gilman et al., 2008; Rabearisoa et al., 2012; Hamer et al., 2012; Clua et al., 2013; Tixier et al., 2019a). However, despite these limitations, and despite the spatio-temporal heterogeneity in the observed data, the predictive power of the models (AUC = 0.7) was considered to be sufficiently high to produce reliable predictions of the probability of depredation to occur, even in areas with low or no data available.

The environmental drivers of the occurrence of depredation in the New Caledonian tuna longline fishery were, in order of importance, sea surface temperature, current velocity, bathymetry, sea surface height and chlorophyll-a concentration. For odontocetes, the probability of depredation occurring was higher in cold to temperate waters and during the coldest months. This seasonal change is consistent with the

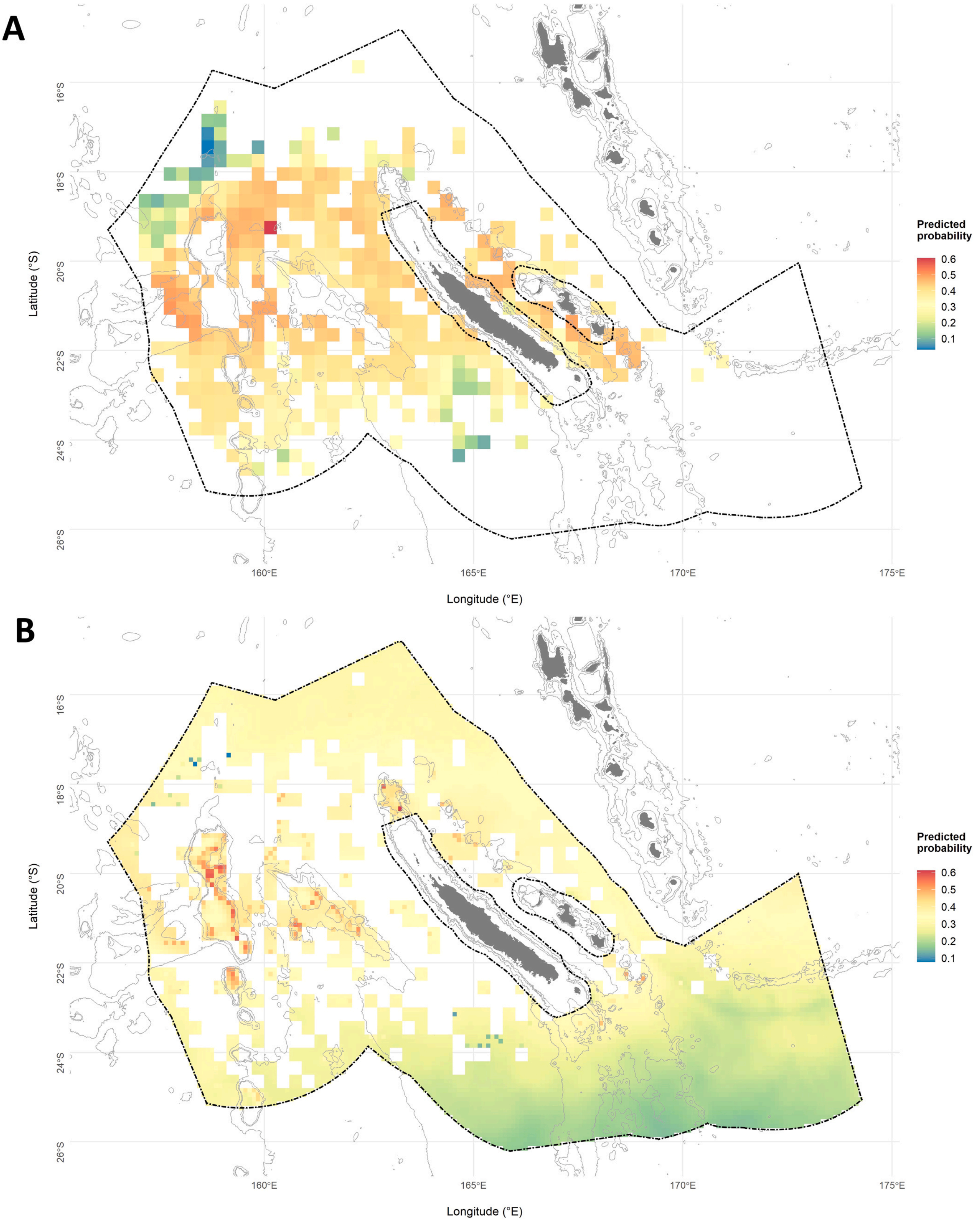

Fig. 4. Mean predicted probabilities of shark depredation to occur in the tuna longline fishery over the 2010–2019 period across the New Caledonian EEZ where fishing data were available (A) and the mean predicted probabilities of shark depredation to occur where no fishing data were available (B).

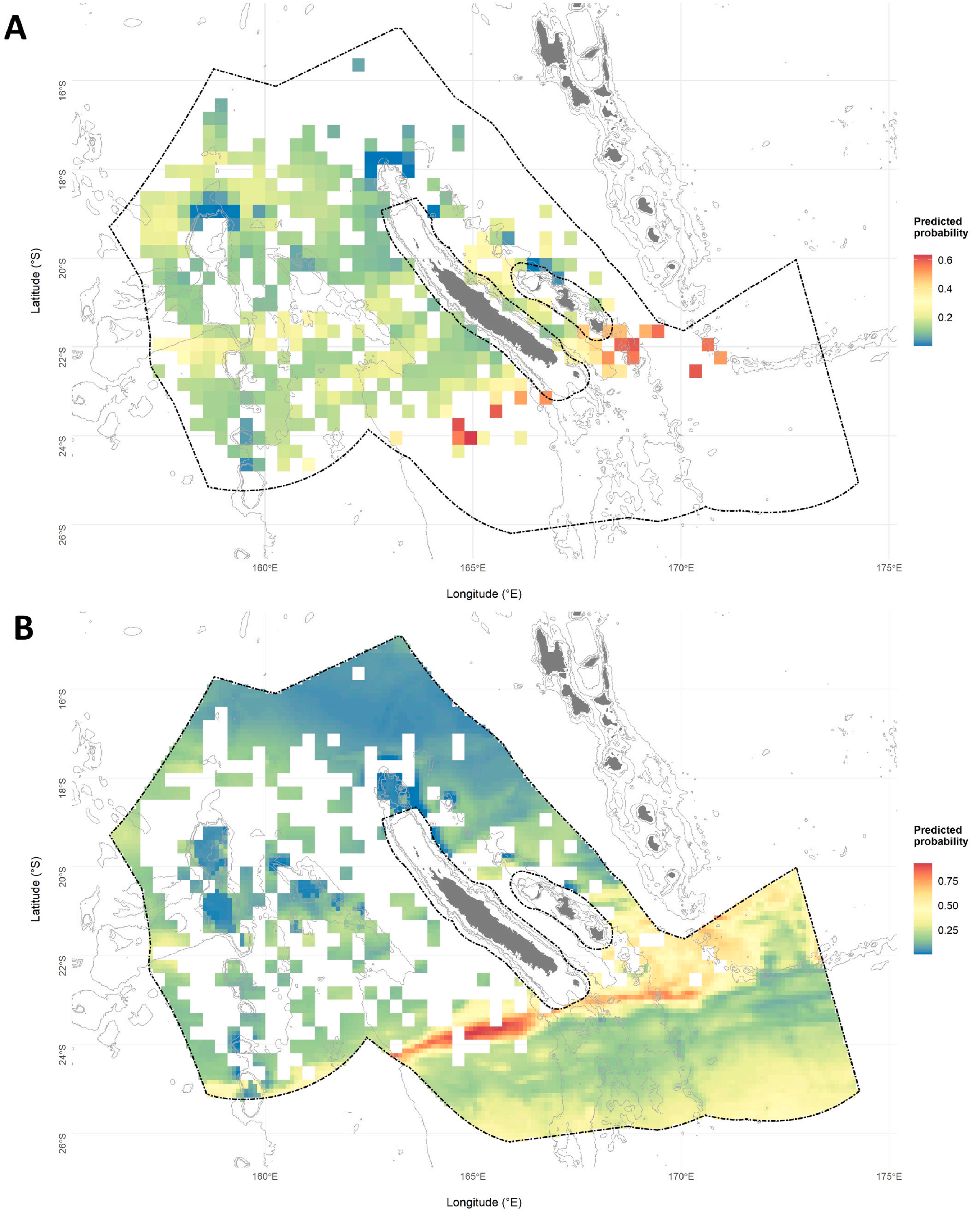

Fig. 5. Mean predicted probabilities of odontocete depredation to occur in the tuna longline fishery over the 2010–2019 period across the New Caledonian EEZ where fishing data were available (A) and the mean predicted probabilities of odontocete depredation to occur where no fishing data were available (B).

pattern observed for false killer whale depredation in Hawaii (Bradford et al., 2020; Fader et al., 2021). Our study suggests that the highest probability of depredation was in water with sea surface temperatures of 21–22°C, but Globicephalinae species (including false killer whale and short-finned pilot whale) have been reported to occur with the highest densities in sea surface temperatures between 26 and 27.5°C in French Polynesia (Mannocci et al., 2014) and above 27°C in New Caledonia (Receveur et al., 2022). For sharks, depredation was more likely to occur in warmer waters and at warmer times of the year, which is consistent with what has been reported for oceanic shark species like silky sharks *Carcharhinus falciformis,* oceanic whitetip sharks, or *Sphyrna spp*. in the eastern Pacific Ocean (Díaz-Delgado et al., 2021). Areas such as the shallow waters of the Chesterfield and Bellona lagoons or near the Landsdowne Bank, were predicted as hotspots of shark presence based on environmental conditions but uncertainty associated with predictions in these areas where no fishing data were available was high. Except for current velocity, for which the relationship was found to be inversely correlated with the probability of depredation occurring for both sharks and odontocetes, the relationships found with bathymetry, sea surface height and chlorophyll-a concentration all suggested that depredation was most likely to occur in areas of higher productivity and, therefore, potentially higher prey availability for these species (Hernandez-Milian et al., 2008; Di Tullio et al., 2016; Thorne et al., 2017; Correia et al., 2021). For example, the probability of odontocete depredation to occur increased with the sea surface height, which is indicative of mesoscale features such as eddies and fronts that concentrate prey (Chelton et al., 2011), as observed with false killer whales depredating on tuna catch in the Hawaiian longline fisheries (Fader et al., 2021). It is therefore crucial to determine whether the fish species targeted by the fishery are also part of the predators' diet, as this has implications both for the management of the fishery, due to potential ecosystem consequences, and for the management of depredation, particularly in terms of predator-prey co-occurrence.

The occurrence of depredation was influenced by operational factors related to fishers' behaviour, and more specifically, to the extent to which fishers provided predators with opportunities to depredate. Indeed, the probability of depredation to occur increased with the soaking time for both sharks and odontocetes, and with the number of hooks set for sharks, suggesting that the more gear fishers deploy, and the longer they leave it in the water, the more likely depredation is to occur. In fact, the model estimated that fishers of the New Caledonian tuna fishery may reduce the probability of depredation occurrence by 50% by using sets of less than 1,750 hooks or by shortening the soaking time to less than 12 hours. Similar effects have been reported for sperm whales and killer whales depredating catch on demersal longlines in the Southern Ocean (Tixier et al., 2015), for false killer whales depredating catch on pelagic longlines in Hawaii, and for oceanic whitetip sharks, blue sharks and silky sharks depredating catch on pelagic longlines in the north-western Atlantic Ocean (Mandelman et al., 2008; Mitchell et al., 2018; Fader et al., 2021). These effects were attributed to longer sets and soaking time, giving predators more time to locate the fishing gear and access the catch (Tixier et al., 2015). Nevertheless, further analysis is needed to investigate changes in the overall net catch landed in response to reducing soak time and the number of hooks set, in order to propose realistic scenarios that take into account the trade-off between losses and benefits. For sharks, increased opportunities to depredate in the New Caledonian longline fishery may also be reflected in the increased probability of depredation predicted to occur with increasing density of fishing vessels operating simultaneously within a 200 km radius and over ±3 days. However, this increase was only detected for up to six vessels in the area, and the probability of shark depredation to occur decreased when more than six vessels were operating simultaneously. This may be explained by the fact that with a finite number of shark individuals present in fishing areas, increasing the number of fishing vessels operating simultaneously may induce a dilution effect of depredation (Tixier et al., 2015), while also potentially leading to a higher number of sharks being hooked as bycatch. Although specific operational factors were identified as influencing depredation, the vessel effect was still strong in the models for both sharks and odontocetes, with a large variability in probabilities of depredation occurrence across the vessels of the New Caledonian longline fleet. As reported in other fisheries subject to similar depredation, this variability may be attributed to variation in the fishing strategies used by captains on vessels, including the spatio-temporal distribution of their effort and the way they use their fishing gear (for example the speed at which they haul the lines or the way they use the engine during maneuvers generating varying levels of noise), or to intrinsic features of the vessels (i.e. the nature and the level of noise they make), making them more or less likely to be detected and subject to depredation by sharks/odontocetes (Tixier et al., 2015; Janc et al., 2018; Fader et al., 2021). It may also reflect differences in how fishers report depredation events.

The results from the spatial predictions suggest that while avoiding shark depredation hotspots in New Caledonia is challenging, fishers of the tuna longline fishery may be able to implement odontocete depredation avoidance strategies at limited socio-economic costs. Conversely, except for some specific zones of low shark depredation despite high fishing effort (e.g., north-west of Chesterfield), shark depredation was highly likely to occur across the entire fishing area. The results from alternative models using the number of fish depredated per set as the response variable helped identify areas where depredation was particularly severe when it occurred. For instance, while the north-west of Chesterfield showed a lower probability of shark depredation to occur, the number of fish depredated by sharks on longline sets was high, suggesting that, on average, there were fewer depredation events, but during those events, more fish were taken by sharks in this area. However, predictions of the number of depredated fish, although informative in complement to probabilities of depredation to occur, should be interpreted with caution, and as minimum estimates, because of the possibility that the number of depredated fish may not have been reliably recorded on lines with multiple depredated fish in the New Caledonian fishery. The high likelihood of shark depredation across the entire area is possibly due to the presence of multiple shark species with distinct fundamental niches, which can thrive in a wide range of environmental conditions (Queiroz et al., 2016; Díaz-Delgado et al., 2021). Additionally, the high abundance of sharks in the region is likely influenced by the overlap of the fishing area with the Natural Park of the Coral Sea MPA, where targeting, landing and selling sharks has been prohibited since 2008, and a 'Shark Sanctuary' was established in 2013 (Ward-Paige and Worm, 2017; SPNMCP, 2021b). However, the impact of shark depredation on the longline catch in New Caledonia is significantly lower than that of odontocete depredation, which removes more fish per affected set. Fishers are therefore generally able to cope better with shark depredation (Mollier et al., 2024). On the other hand, this study identified clear hotspots of odontocete depredation with areas of high probability of depredation to occur, located in the south-east of the main island and the Loyalty Islands, that could be avoided by fishers without severely reducing their fishing success or having to travel longer distances and spend more time at sea, which are the commonly reported indirect costs of avoidance strategies of depredation (Gilman et al., 2006; Peterson et al., 2014; Tixier et al., 2021). Indeed, most of these hotspots of depredation are not located in areas of high tuna or dolphinfish CPUE (Receveur et al., 2022; Mollier et al., 2024), providing fishers with the opportunity to find areas where the probability of depredation is lower, or even null in the case of d'Entrecasteaux and the north of the Chesterfield, and where fishing success is high. Similarly, favouring the areas of low probabilities of depredation occurrence identified here may not incur additional fishing time or fuel consumption costs to the fishers as these are not located further from the main island and ports (mostly Nouméa). Finally, the variable indicating whether depredation occurred on the previous set of the same trip was not included in the final models, suggesting that depredation may not necessarily occur in the same area over time, allowing fishers the possibility of avoiding it by moving over relatively short distances.

5. Conclusion

In conclusion, by identifying key environmental and operational drivers of shark and odontocete depredation, this study provides knowledge that can help improve the effectiveness of mitigation strategies of the issue through avoidance and evolving practices, not only in New Caledonia but also in other regions faced with similar fisheries – large marine predators conflicts. However, as sharks and odontocetes may respond and adapt to new fishing practices implemented to mitigate these conflicts, the monitoring of depredation and the research on solutions should be continued (Mitchell et al., 2024). While the findings can guide fishers in their practices, and more specifically, in their choices of the fishing areas and in the way they use their gear, the spatio-temporal variability of depredation remains largely unexplained. This suggests that other factors, such as those related to the ecology of the predators involved, factors related to the decisions fishers make, or intrinsic features of the vessels, have yet to be identified. However, the study still demonstrates the relevance of using species distribution models as a tool to enhance our understanding and predictive potential of human-wildlife conflicts arising from depredation.

CRediT authorship contribution statement

Tixier Paul: Writing – review & editing, Validation, Supervision, Methodology, Formal analysis. **McKechnie Sam:** Writing – review & editing, Data curation. **Hosken Malo:** Writing – review & editing, Data curation. **Hamer Paul:** Writing – review & editing, Data curation. **Mazé Camille:** Writing – review & editing, Supervision. **Derville Solène:** Writing – review & editing, Validation, Methodology. **Mollier Margaux:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Virgili Auriane:** Writing – review & editing, Methodology, Formal analysis. **Prioul François:** Writing – review & editing, Validation, Data curation. **Lerebourg Clara:** Validation, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2025.107378.

Data availability

Data will be made available on request.

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