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 by fishers 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 Caledonia 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.

Keywords: Depredation, sharks, odontocetes, modelling, hotspots, fisheries, New Caledonia

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 (Herrero et al., 2005; Swenson et al., 1999). 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 also leads to human-wildlife conflicts. The severity of these conflicts has increased substantially globally over the past 60 years as a result of the expansion of fisheries (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), 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) technological, aimed at developing fishing gears or devices placed on fishing gears, that can prevent or deter marine predators from accessing the catch, and ii) operational, aimed at modifying the way fishers use their gear and the fishing areas and times to avoid or minimise depredation (Hamer et al., 2012; Peterson & 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., 2019). 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., 2019). In some cases, however, certain species, especially toothed whales (odontocetes), have been observed actively searching for and following fishing vessels, which offers them opportunities to depredate on fishing catch, thereby potentially altering their natural distribution range (Janc et al., 2018; Towers et al., 2019).

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 fleet of 14 vessels is now locally managed by the government of New Caledonia, which can benefit from the South Pacific Community (SPC) scientific support and, as a participating territory, complies 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*) and short-finned pilot whales (*Globicephala macrorhynchus*) for odontocetes and blue sharks (*Prionace glauca*), oceanic whitetip sharks (*Carcharhinus longimanus*), tiger sharks (*Galeocerdo cuvier*), mako sharks (*Isurus oxyrinchus*), or silky sharks (*Carcharhinus falciformis*) for sharks, 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 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 9M of fish sales for a production of approximately 2,500 tonnes of tuna per year (WCPFC, 2023). 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 km²; Martin & 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 Caledonia 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 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. This improved understanding of environmental and operational drivers of depredation explicitly projected in space and time will provide helpful knowledge for fishery managers to mitigate this important socio-economic and conservation issue.

2. Materials and methods

2.1. Study area and data collection

The study area encompassed the entire New Caledonia EEZ (from 154 to 175°E, and from 26 to 14°N) (Figure 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 Caledonia 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). Floats are regularly placed along the mainline, such that around 15-30 branch lines/hooks are deployed between two floats, with the early and later deployed hooks being in shallower depths due to the branch line catenary between the floats. Longline sets, as described above, are on average 50 kilometres long and are left soaking for 4 to 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 3h30, to the end of the retrieval phase (i.e., the hauling phase), which lasts around 7h30.

The data used for the analysis were collected by fishers (on 100% of the fishing trips) and fishery observers (on 4.2% of the trips) 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 assigned a depredated fate when partially consumed by sharks or odontocetes, and 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) were used to differentiate depredation between the two taxa (Mollier et al., 2024). When depredation occurred, 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".

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, salinity, and pelagic fish abundance) variables that were extracted for a study area covering the New Caledonia EEZ. 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 & van Etten, 2012). The distance to the nearest seamount was derived from the seamount database described in Allain et al. (2008). Water temperature, current velocity, sea surface height, mixing layer depth, salinity, and chlorophyll-a concentration were extracted from Copernicus (https://data.marine.copernicus.eu/products). The eddy kinetic energy was calculated from the current velocity as follows: $EKE = 0.5*(U^2 + V^2)$, 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. Density of vessels operating simultaneously was calculated as the number of vessels that hauled longline sets within 200 km and ± 3 days of the observed longline set. 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° and for fish abundance at 0.5°), but for the analyses, all variables were re-scaled to a resolution of 0.1° (i.e., spatial cells of about 10 x 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	15 arcsecond	Static	GEBCO
Slope	slope	°	15 arcsecond	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_0.200m Temps_mean_200.500m	°C	1/12°	Monthly (2010 – 2019)	COPERNICUS
Currents	Current_mean_surf Current_mean_0.200m Current_mean_200.500m	$m^2.s^{-2}$	1/12°	Monthly (2010 – 2019)	COPERNICUS
EKE – Eddy Kinetic Energy	Eke_mean_surf Eke_mean_0.200m Eke_mean_200.500m	$m^2.s^{-2}$	1/12°	Monthly (2010 – 2019)	COPERNICUS
Chlorophyll-a concentration	CHL_mean_surf CHL_mean_0.200m CHL_mean_200.500m	$mg.m^{-3}$	1/4°	Monthly (2010 – 2019)	COPERNICUS
Sea surface height	SSH_mean	m	1/12°	Monthly (2010 – 2019)	COPERNICUS
Depth of mixed layer	MLD_mean	m	1/12°	Monthly (2010 – 2019)	COPERNICUS
Salinity	Sal_mean_surf Sal_mean_0.200m Sal_mean_200.500m		1/12°	Monthly (2010 – 2019)	COPERNICUS
Vessel identity	vessel_id				Logbooks
Vessel density (number of all vessels within 200km ±3 days)	density				Logbooks
Soaking time	soak	Hours			Logbooks

Number of hooks set	hook_set				Logbooks
Presence of depredation on previous set of same vessel	presence_prev_shark presence_prev_odont				Logbooks

2.3. Model selection

Generalised additive models (GAMs; Hastie & 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 Caledonia 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. 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), Pearson coefficients were calculated between each pair of variables and variables with coefficients >0.7 were removed. 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 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 and discrimination power were respectively assessed by calculating the root of mean square error (RMSE) and the Spearman correlation coefficient (rho) 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 to 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 Caledonia 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 S1) 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 S2). 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 S3) were also averaged by season: austral summer (December-February), austral autumn (March-May), austral winter (June-August), and austral spring (September-November).

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%) and 89 sets were subject to depredation by odontocetes (8.3%).

3.1. Models selection

After correlation checks between variables (Figure S4), the variables used in the models included: bathymetry, slope, temp_mean_surf and temp_mean_200.500m, current_mean_surf and current_mean_200.500m, SSH_mean, CHL_mean_surf, soak, hook_set, vessel density, min_distance_to_seamounts, presence_prev_odont, presence_prev_shark and vessel_id. From the model selection based on AIC and REML, the variables selected to best explain the occurrence of shark depredation were vessel_id, temp_mean_surf, current_mean_surf, soak, hook_set, and vessel density, and those selected to best explain the occurrence of odontocete depredation were vessel_id, bathymetry, temp_mean_surf, current_mean_200.500m, SSH_mean, CHL_mean_surf, and soak (Table 2).

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 discrimination score was significant (0.30, $p < 0.001$), 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 discrimination score was also significant (0.19, $p = 0.02$), the AUC was high (0.71), but the overall accuracy was low (0.27) despite a high true negative rate (100%; Table 3).

3.2. Environmental and operational drivers of depredation

From the final model's outputs and predictions, the probability of shark depredation to occur increased with the soaking time and the number of hooks, with the highest probability (P(depredation) > 0.73) for soaking times >15h and numbers of hooks >1,750 (P(depredation) > 0.36; Figure 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) = 0.45) and for surface current velocities of 0.10-0.15 $m^2.s^{-2}$ (P(depredation) = 0.40).

The probability of odontocete depredation to occur was the highest 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 0.60-0.70m. It also decreased from 0.40 to 0.08 between 4,000 and 2,000 m of depth (Figure 2B). Operational variables such as hook_set, vessel density, and presence_prev_odont were not significant and were not retained in the final odontocete depredation model.

The vessel_id term was significant in both the shark depredation and odontocete depredation models, with predicted probabilities of depredation to occur per vessel ranging from 0.12 to 0.88 for sharks, and from 0 to 0.53 for odontocetes (Figure 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 S5).

Table 2: Outputs of the GAM models that best fitted the occurrence of odontocete and shark depredation in the New Caledonia longline fishery from 2010 to 2019. SE: standard error, edf: estimated degrees of freedom in GAM fitting, χ2: Chi-square statistic, P: p-value.

	Sharks					Odontocetes				
Term	**Estimate**	**SE**	**edf**	**χ2**	**P**	**Estimate**	**SE**	**edf**	**χ2**	**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			1.79	12.77	<0.001			2.10	25.03	<0.001
Current surface			1.57	5.73	0.03					
Current 200-500m								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	84.79	<0.001			1.54	4.97	0.04
Number of hooks set			1.72	17.60	<0.001					
Vessel density			2.38	12.04	0.003					

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, Discrimination: Spearman correlation coefficient, 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**	**Discrimination**	**True negative rate**	**AUC**

Odontocetes	24.8%	0.270	0.19 p = 0.018	100%	0.71
Sharks	19.6%	0.474	0.30 p < 0.001	100%	0.68

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 = 13h) 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 (Figure 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 S2). 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 (Figure 4B). The standard error of predictions ranged from 0.5 to 2.1 throughout the prediction area (Figure S6), 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 summer (P(depredation) = 0.30) and the lowest in winter (P(depredation) = 0.20) with low variation between seasons. Higher probabilities were observed in the south of the EEZ in austral summer and autumn than in austral winter and spring (Figure S8).

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 (Figure 5A). These areas were characterised by greater depths (>2,000m), lower sea surface temperatures and low to moderate sea surface heights (Figures 1, S1). 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 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 (Figure 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 S7). Seasonal predictions showed that high probabilities of odontocete depredation to occur were spread out across the entire EEZ in austral winter and austral spring where the mean predicted probability was the highest (P(depredation) = 0.37), and were restricted to the south of the EEZ in austral summer (P(depredation) = 0.17) and austral autumn (P(depredation) = 0.15) with lower values (Figure S9).

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, uncertainty was detected in both model outputs, with relatively 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). 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 (whole fish may be removed from hooks by the predators, leaving no evidence of depredation, especially for odontocetes; Hucke-Gaete et al., 2004; Rabearisoa et al., 2018; Fader et al., 2021) and from the limited proportion of fishing operations monitored by observers (<10% of all operations). 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., 2019). 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 as 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 Caledonia 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 to occur was higher in cold to temperate waters and during the coldest months. This seasonal change is consistent with the pattern observed for false killer whale depredation in Hawaii (Bradford et al. 2020; Fader et al., 2021). Our study found the highest probability of depredation occurrence in water with sea surface temperatures of 21-22°C, while predicted densities of Globicephalinae (including false killer whale and short-finned pilot whale) have been observed 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 without fishing activity, such as the shallow waters of the Chesterfield and Bellona lagoons or above the Landsdowne Bank, appeared to be potential shark depredation hotspots based on the environmental conditions. Except for current velocity, for which the relationship was found to be inversely correlated with the probability of depredation to occur 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 Caledonia tuna fishery may reduce the probability of depredation to occur 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). For sharks, increased opportunities to depredate in the New Caledonia 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). 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 to occur across the vessels of the New Caledonia 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, 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).

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. On the one hand, except for some specific zones of low shark depredation despite high fishing effort (e.g., northwest of Chesterfield), shark depredation was highly likely to occur across the entire fishing area. This 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 shark fishing 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 appears much lower compared to that of odontocete depredation, and fishers are generally able to cope with it (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 (Mollier et al. 2024; Receveur et al., 2022), 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 Chesterfields, and where fishing success is high. Similarly, favouring the areas of low probabilities of depredation to occur 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. 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.

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.

Data availability

Data will be made available on request.

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Figure captions

Figure 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.

Figure 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.

Figure 3: Predicted probability of the occurrence of shark (A) and odontocete (B) depredation per vessel in the New Caledonia 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.

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

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

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	15 arcsecond	Static	GEBCO
Slope	slope	°	15 arcsecond	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_0.200m Temps_mean_200.500m	°C	1/12°	Monthly (2010 – 2019)	COPERNICUS
Currents	Current_mean_surf Current_mean_0.200m Current_mean_200.500m	$m^2.s^{-2}$	1/12°	Monthly (2010 – 2019)	COPERNICUS
EKE – Eddy Kinetic Energy	Eke_mean_surf Eke_mean_0.200m Eke_mean_200.500m	$m^2.s^{-2}$	1/12°	Monthly (2010 – 2019)	COPERNICUS
Chlorophyll-a concentration	CHL_mean_surf CHL_mean_0.200m CHL_mean_200.500m	$mg.m^{-3}$	1/4°	Monthly (2010 – 2019)	COPERNICUS
Sea surface height	SSH_mean	m	1/12°	Monthly (2010 – 2019)	COPERNICUS
Depth of mixed layer	MLD_mean	m	1/12°	Monthly (2010 – 2019)	COPERNICUS
Salinity	Sal_mean_surf Sal_mean_0.200m Sal_mean_200.500m		1/12°	Monthly (2010 – 2019)	COPERNICUS
Vessel identity	vessel_id				Logbooks
Vessel density (number of all vessels within 200km ±3 days)	density				Logbooks
Soaking time	soak	Hours			Logbooks

Number of hooks set	hook_set				Logbooks
Presence of depredation on previous set of same vessel	presence_prev_shark presence_prev_odont				Logbooks

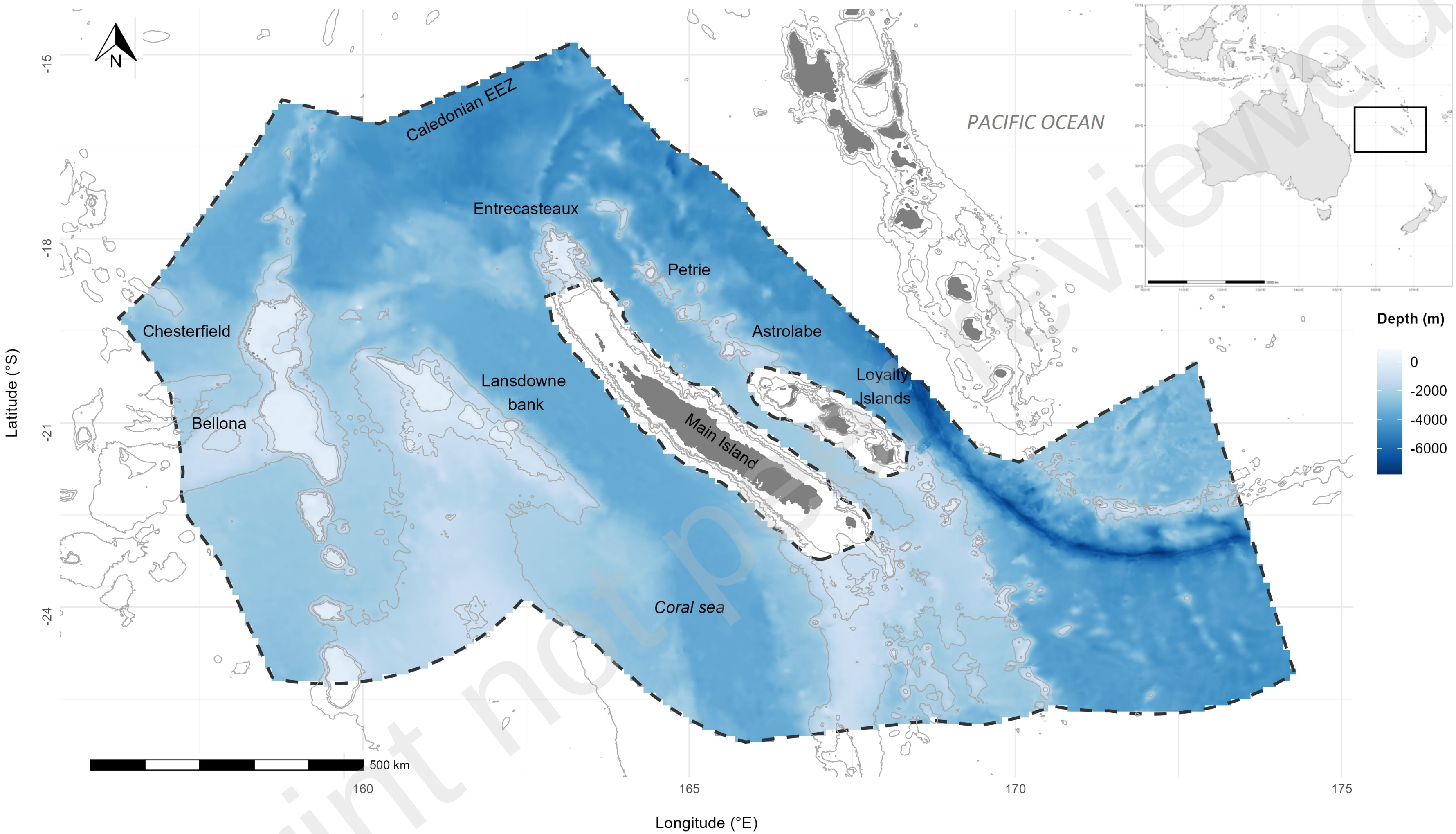
Table 2: Outputs of the GAM models that best fitted the occurrence of odontocete and shark depredation in the New Caledonia longline fishery from 2010 to 2019. SE: standard error, edf: estimated degrees of freedom in GAM fitting, χ2: Chi-square statistic, P: p-value.

	Sharks					Odontocetes				
Term	**Estimate**	**SE**	**edf**	**χ2**	**P**	**Estimate**	**SE**	**edf**	**χ2**	**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			1.79	12.77	<0.001			2.10	25.03	<0.001

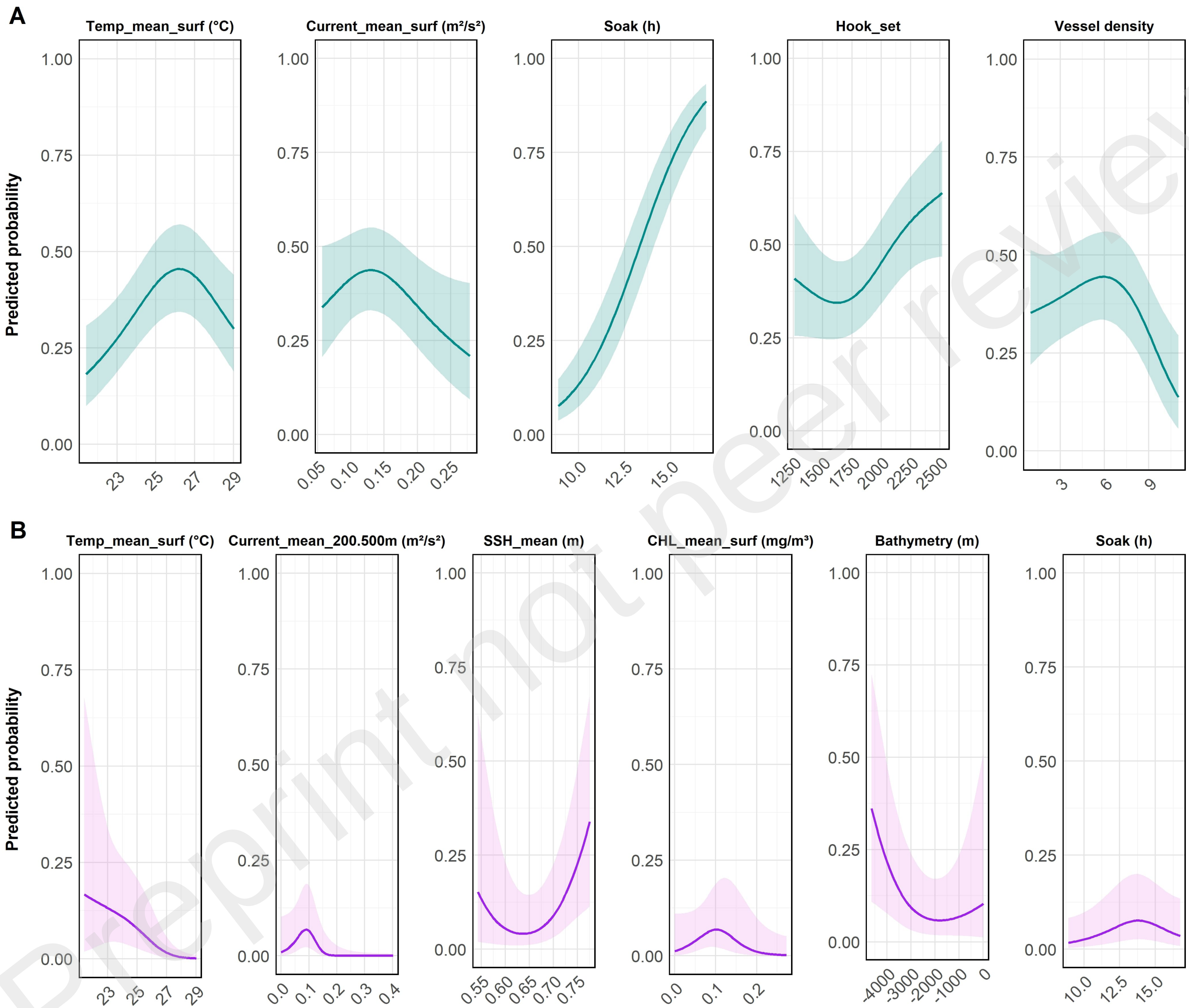
Current surface	1.57	5.73	0.03			
Current 200-500m				1.75	5.88	0.03
Sea surface height				1.69	13.24	<0.001
Chl-a				1.58	4.66	0.04
Soaking time	0.99	84.79	<0.001	1.54	4.97	0.04
Number of hooks set	1.72	17.60	<0.001			
Vessel density	2.38	12.04	0.003			

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, Discrimination: Spearman correlation coefficient, 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.

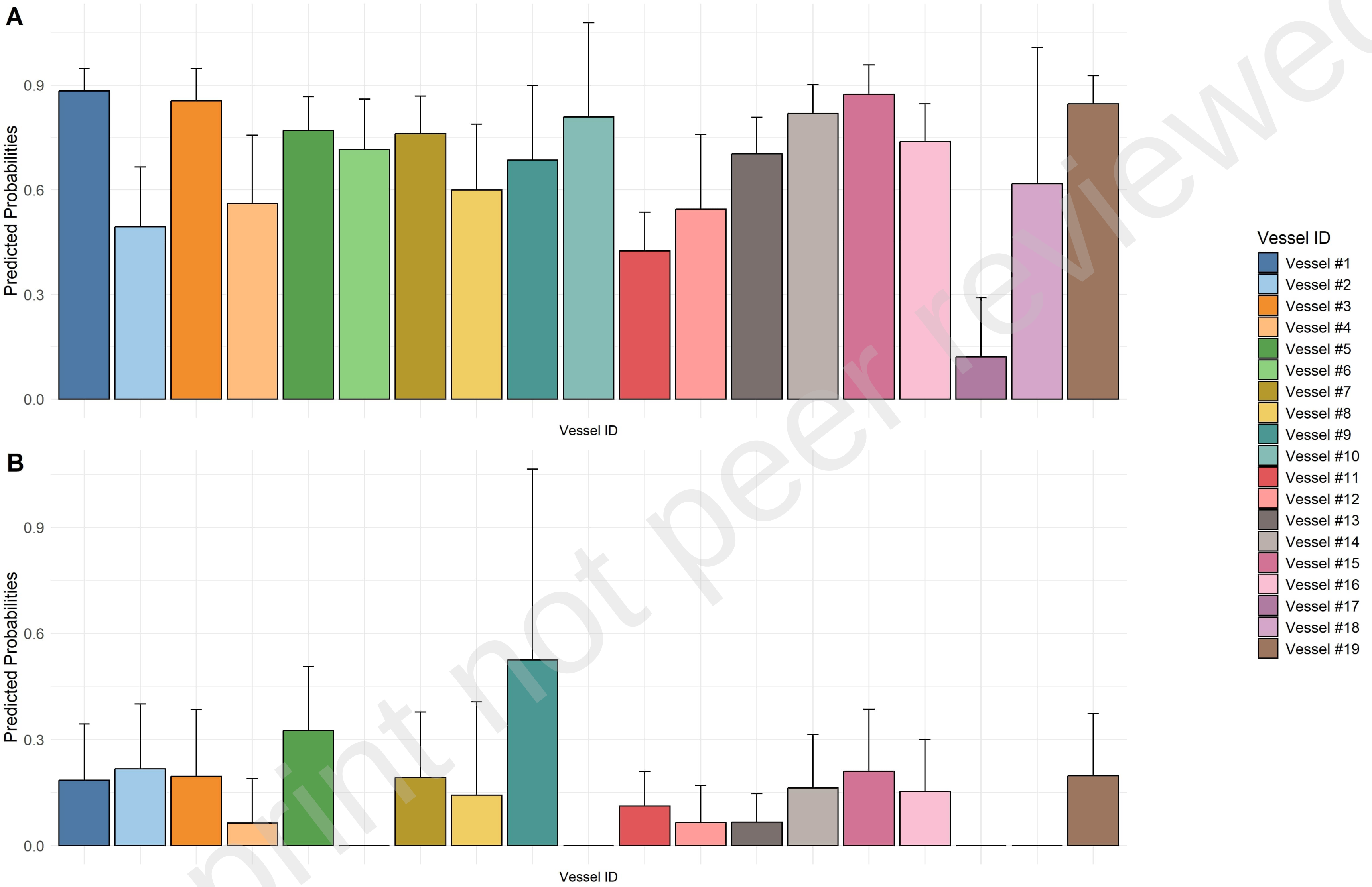
Model training	**Evaluation on test fold**				
Model	**Dev.exp.**	**Accuracy**	**Discrimination**	**True negative rate**	**AUC**
Odontocetes	24.8%	0.270	0.19 $p = 0.018$	100%	0.71
Sharks	19.6%	0.474	0.30 $p < 0.001$	100%	0.68



N
Caledonian EEZ
Entrecasteaux
Petrie
Astrolabe
Chesterfield
Loyalty
Islands
Lansdowne
bank
Bellona
Main Island
Coral sea
PACIFIC OCEAN
Depth (m)
0
-2000
-4000
-6000
500 km
Latitude (°S)
-15
-18
-21
-24
Longitude (°E)
160
165
170
175



A
Temp_mean_surf (°C)
Current_mean_surf (m²/s²)
Soak (h)
Hook_set
Vessel density
Predicted probability
0.00
0.25
0.50
0.75
1.00
23
25
27
29
0.05
0.10
0.15
0.20
0.25
10.0
12.5
15.0
1250
1500
1750
2000
2250
2500
3
6
9
B
Temp_mean_surf (°C)
Current_mean_200.500m (m²/s²)
SSH_mean (m)
CHL_mean_surf (mg/m³)
Bathymetry (m)
Soak (h)
Predicted probability
0.0
0.1
0.2
0.3
0.4
0.55
0.60
0.65
0.70
0.75
-4000
-3000
-2000
-1000
0


A
B
Predicted Probabilities
0.0
0.3
0.6
0.9
Vessel ID
Vessel ID
Vessel #1
Vessel #2
Vessel #3
Vessel #4
Vessel #5
Vessel #6
Vessel #7
Vessel #8
Vessel #9
Vessel #10
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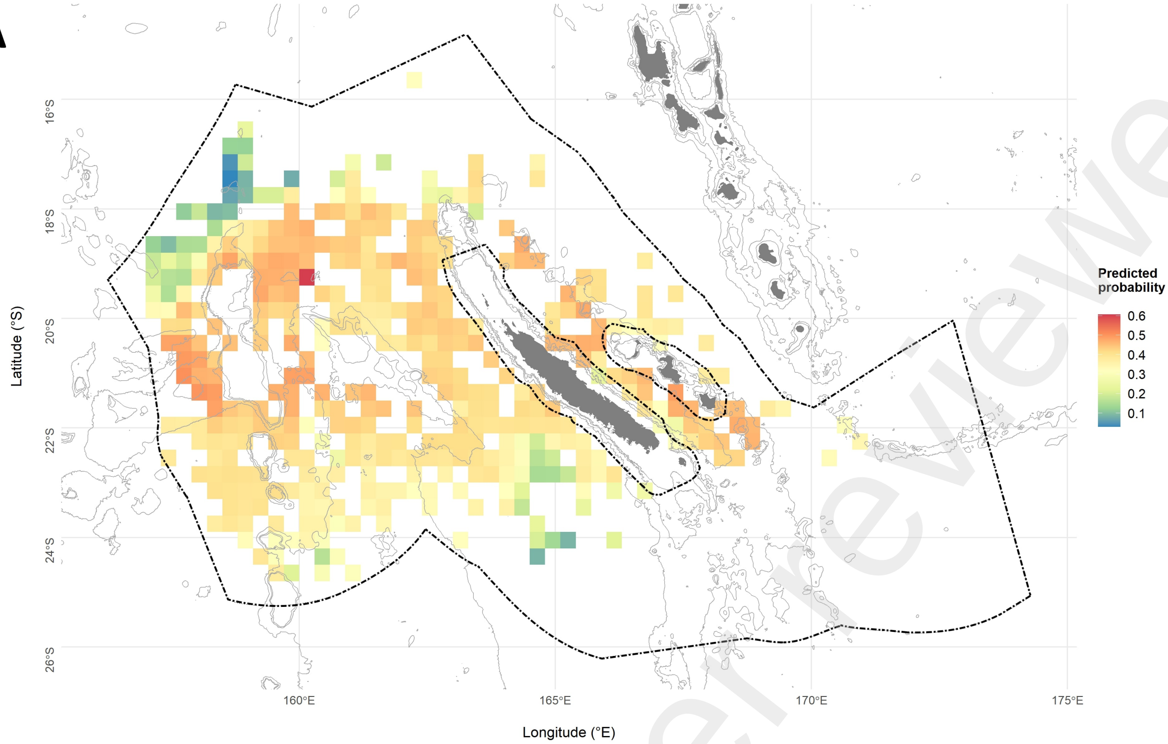
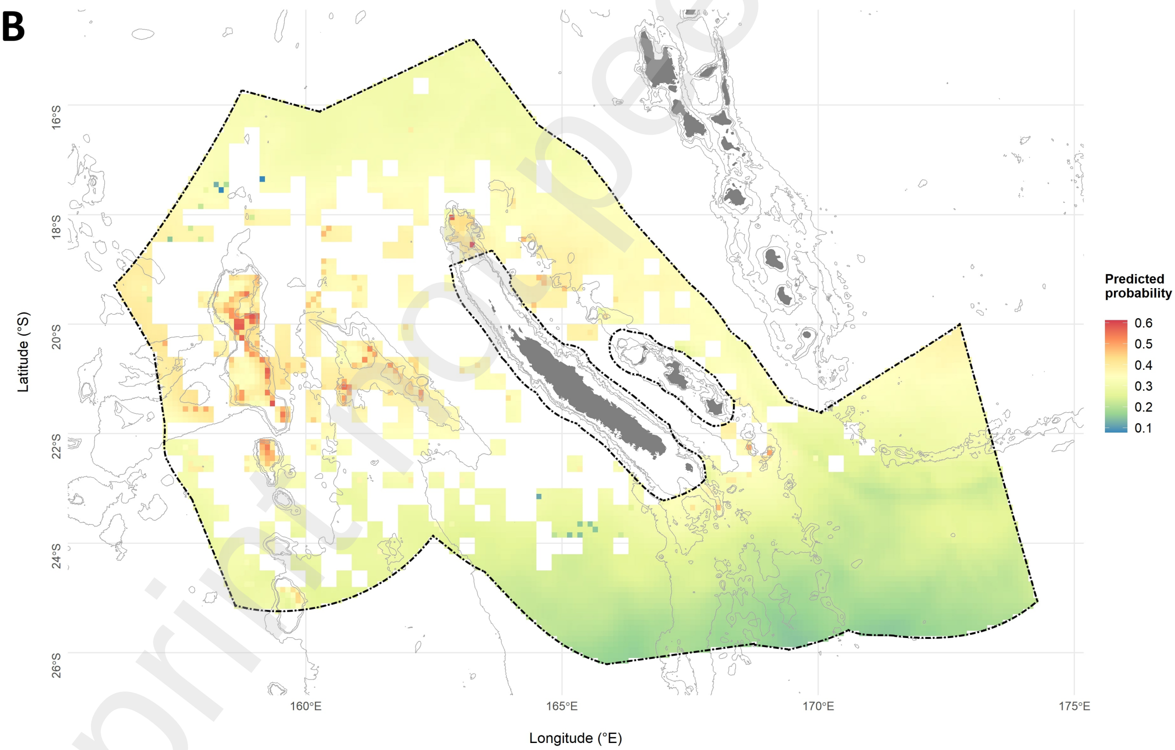
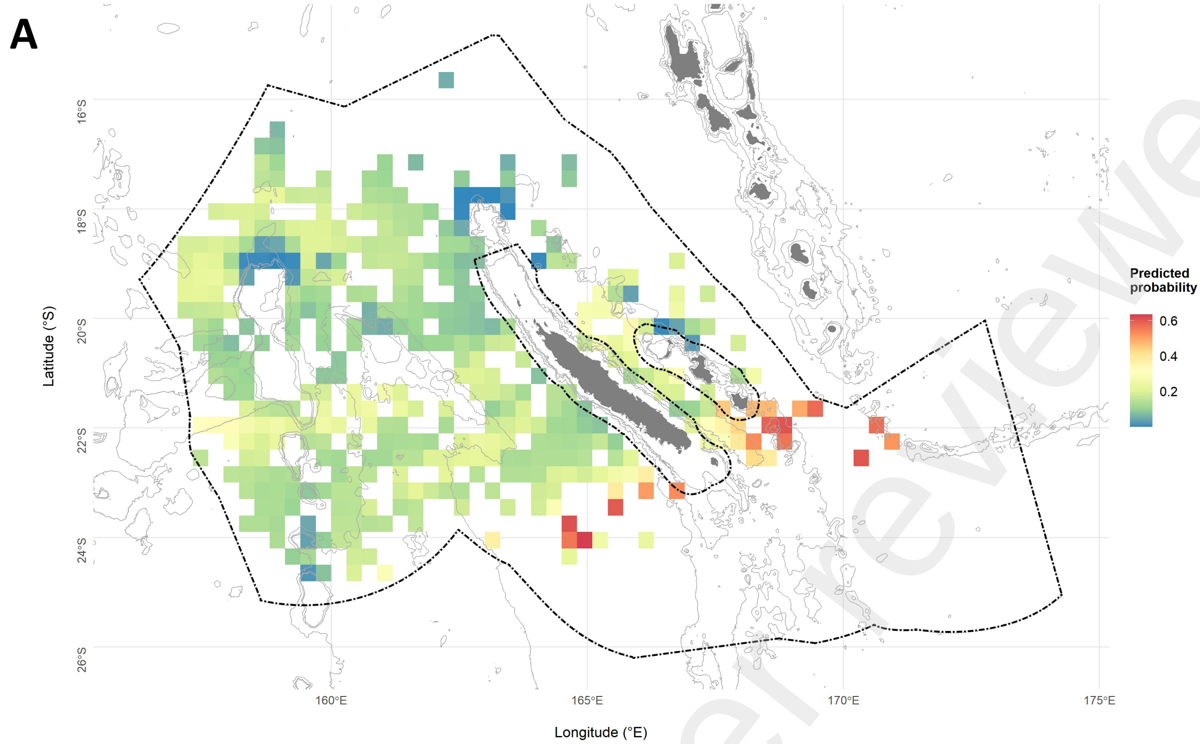
Vessel #13
Vessel #14
Vessel #15
Vessel #16
Vessel #17
Vessel #18
Vessel #19

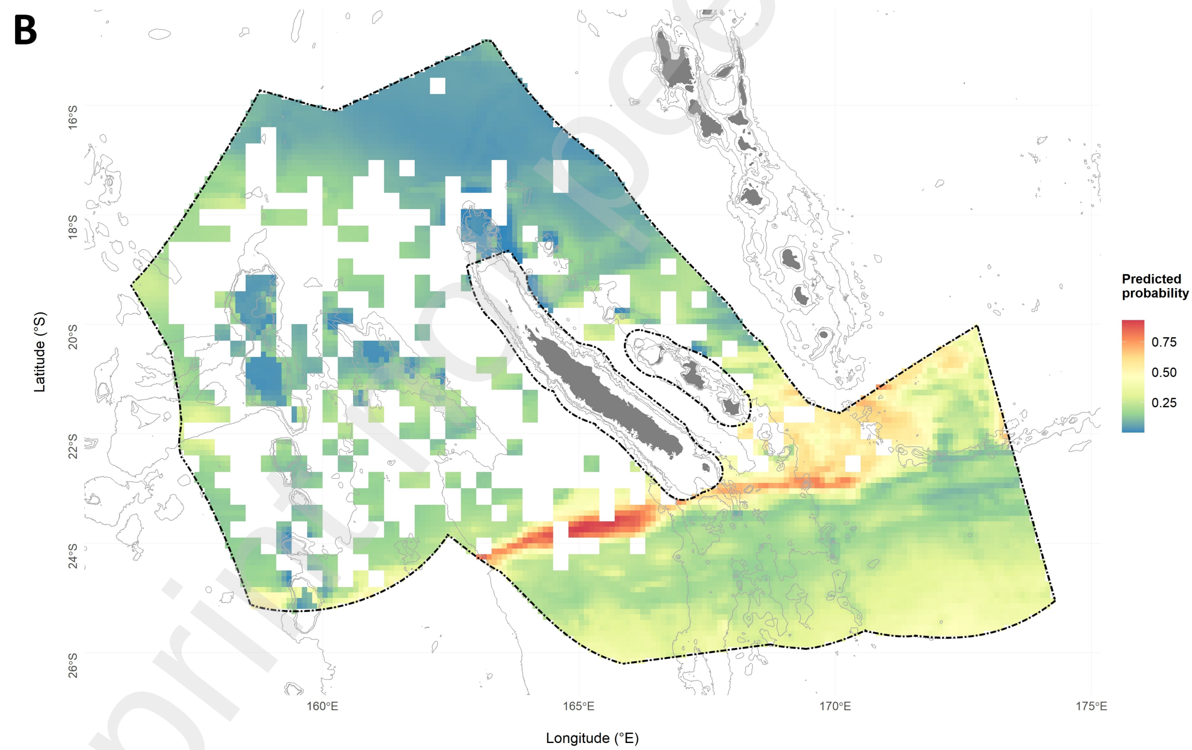
A


16°S
18°S
20°S
22°S
24°S
26°S
Latitude (°S)
160°E
165°E
170°E
175°E
Longitude (°E)
Predicted probability
0.6
0.5
0.4
0.3
0.2
0.1

B


16°S
18°S
20°S
22°S
24°S
26°S
Latitude (°S)
160°E
165°E
170°E
175°E
Longitude (°E)
Predicted probability
0.6
0.5
0.4
0.3
0.2
0.1


A
16°S
18°S
20°S
22°S
24°S
26°S
Latitude (°S)
160°E
165°E
170°E
175°E
Longitude (°E)
Predicted probability
0.6
0.4
0.2


B
16°S
18°S
20°S
22°S
24°S
26°S
Latitude (°S)
160°E
165°E
170°E
175°E
Longitude (°E)
Predicted probability
0.75
0.50
0.25