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Original Article

Shark and odontocete depredation on the catch of the tuna longline fishery in New Caledonia (South Pacific Ocean)

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Abstract

Large marine predators feeding on fish caught on fishing gear, referred to as 'depredation', occur in a wide range of fisheries worldwide. Depredation can result in negative ecological and socio-economic impacts, leading to conflict between fishers and depredating species. However, depredation remains understudied in many fisheries, and this hampers the development of effective mitigation solutions. In this study, 21 years of fishing data (2002–2022) were used to assess shark and odontocete depredation in the pelagic tuna longline fishery of New Caledonia. Using generalized linear models, the year, season, effort, soaking time, and vessel were identified as variables significantly influencing the probability of depredation to occur. Results showed that while shark depredation occurred more frequently than odontocete depredation (58.5% vs. 9.2% of the longline sets), they damaged a lower proportion of fish (3.9% vs. 12.3%) over the study period. Unlike sharks, odontocetes selectively depredate tuna, with their highest occurrence during periods of high tuna catch rates, suggesting a co-occurrence with fishing activities. Together, these results indicate that depredation in the New Caledonian fishery is high compared to other regions and provide essential information on the dynamics and impacts of the issue as a basis for considering management and mitigation options.

Keywords: depredation; odontocetes; sharks; fisheries; pelagic longlining; New Caledonia

Introduction

Human–wildlife conflicts result from competition for space and resources (Woodroffe et al. 2005), occurring when actions by humans or wildlife have an adverse effect on the other, such as threaten human property, economy, security, recreation, and safety (Nyhus 2016). They have existed since the dawn of human civilization, but the severity of their socio-economic and ecological impacts has increased with accelerated human population growth, global changes, and the loss of biodiversity (Woodroffe et al. 2005). However, effective and sustainable solutions to the coexistence of humans and animal species, which rely on trade-offs between the viability of socio-economic activities, the food security of human populations, and the conservation of animal species, are still limited and have become a major societal and environmental challenge today (Nyhus 2016).

In the marine environment, the expansion and intensification of large-scale fishing activities over the past 60 years, combined with declining fish stocks, is associated with increased conflicts between humans and marine megafauna (sharks, turtles, seabirds, and marine mammals) (Guerra 2019). These conflicts occur globally, involving all fishing sectors (industrial, artisanal, subsistence, and recreational) and the majority of the world's fisheries (Tixier et al. 2021). They result from a set of indirect and direct (or operational) interactions (Northridge 1991). Indirect interactions include the competition for the targeted resource and other ecosystem effects associated with exploitation (Estes et al. 2011, Lewison et al. 2014, Tixier et al. 2021). Direct interactions include intentional and accidental captures of by-catch species, entanglement of marine fauna in fishing gear, damage to fishing gear, and damage to captured fish due to interactions with non-target predator species. The latter occurs when large marine predators, mainly sharks and toothed whales (odontocetes), feed directly on fish that are captured by fishers on fishing gear, a behaviour termed 'depredation' (Donoghue et al. 2003, Gilman et al. 2006, Hamer et al. 2012).

Depredation on fisheries catches often leads to conflicts between fishers and marine predators that can have negative consequences on the different components of the marine socio-ecological systems involved (Goetz et al. 2011, Werner et al. 2015, Bearzi et al. 2019). For human communities, the costs can be socio-economic through reduced fishing catch, damage to equipment, and additional expenses, including fuel use, and labour incurred by increased fishing effort to either recoup catch losses or to avoid depredating marine predators (Tixier et al. 2021). As the costs of such human–wildlife conflicts can threaten the socio-economic viability of the fishing activities, even the food security of fishing-dependent communities, and the conservation of ecosystems and marine megafauna species, their mitigation often requires integrated approaches accounting for both the human and non-human components to be effective (Madden 2004, Gilman et al. 2008, Nyhus 2016, Guerra 2019). For the depredating species, many of which are vulnerable in terms of conservation, the conflict can directly affect the survival of individuals through increased risks of bycatch and injury (Read et al. 2006, Dalla Rosa and Secchi 2007) or lethal retaliation from fishers when interacting with the fishing gear (Secchi and Vaske 1998, Visser 2000). Bycatch of sharks and, more marginally, odontocetes has been observed in Hawaii-based pelagic longline fisheries (Gilman et al. 2007, Forney et al. 2011). Depredation, by providing marine predators with a facilitated access to their natural prey or access to new prey, may also lead to changes in their foraging behaviour and diet, subsequently altering trophic interactions in ecosystems (Tixier et al. 2015a, 2017, Esteban et al. 2016, Hanselman et al. 2018).

Longline fisheries, whether using pelagic (a main line bearing a series of baited hooks deployed near the surface) or demersal (a main line bearing series of baited hooks deployed on or near the sea bed) longlines, are among the most affected fisheries by shark and odontocete depredation worldwide (Gilman et al. 2006). This is likely because in pelagic drifting longline fisheries, the gear is left soaking for long periods of time and the catch is fully exposed in the water column, with depredation occurring during both the soaking and hauling phases (Wang and Yang 2002, Richard et al. 2020). The first cases of depredation on longline catches were reported from as early as 1952 in the Japanese longline tuna fleet (Nishida and Shiba 2002). In high latitudes, sperm whales (*Physeter macrocephalus*) and killer whales (*Orcinus orca*) are the two species most documented depredating in demersal longline fisheries (Yano and Dalheim 1995, Kock et al. 2006, Sigler et al. 2008, Peterson et al. 2014, Guinet et al. 2015). In tropical and sub-tropical regions, pelagic longlines targeting tuna (*Thunnus* spp.) and swordfish (*Xiphias gladius*) are generally depredated by pelagic sharks such as the oceanic whitetip shark (*Carcharhinus longimanus*) in the Indian, Atlantic, and Pacific oceans (Gilman et al. 2007, Hamer et al. 2015, Madigan et al. 2015, Mitchell et al. 2018), the bull shark (*Carcharhinus leucas*), and the tiger shark (*Galeocerdo cuvier*) in Seychelles and New Caledonia (Clua et al. 2014, Rees et al. 2018), all of which are generalist opportunistic feeders taking advantage of any food source when they happen upon it (Clua et al. 2013, Dicken et al. 2017, Trystram et al. 2017). Depredation is also observed in these regions by odontocetes such as false killer whales (*Pseudorca crassidens*) and short-finned pilot whales (*Globicephala macrorhynchus*) (Nishida and Tanio 2001, Dalla Rosa and Secchi 2007, Hernandez-Milian et al. 2008, Forney et al. 2011, Rabearisoa et al. 2012, Fader et al. 2021). Despite research efforts on the issue increasing after 2000 with the growing awareness of the issue amongst fisheries scientists and stakeholders (Gilman et al. 2007, Gilman et al. 2008, Mitchell et al. 2018, 2023), shark and odontocete depredation remains poorly quantified and understood in many of these pelagic longline fisheries (Nishida and Shiba 2002, Rabearisoa et al. 2018). This often occurs due to a lack of fisheries monitoring programmes, or because the existing programmes do not collect the necessary information to quantify the occurrence of depredation.

Although shark and odontocete depredation on longline fisheries catches is a global issue, mitigation solutions that are effective at minimizing impacts while ensuring both the viability of the fishing activity and the conservation of marine predators, are still limited (Mitchell et al. 2023). This is often due to an insufficient knowledge on the extent to which depredation occurs and on the operational (i.e. behaviour of the fishers, fishing gear, etc.) and ecological (predator species involved, the spatio-temporal distribution, and feeding preferences of individuals, etc.) factors that drive it. Importantly, depredation needs to be understood at local/fishery specific scales, as the context of fishery operations and depredating species are often different among fisheries.

In the case of the pelagic longline commercial fishery targeting tuna in New Caledonian waters (South Pacific Ocean), depredation by sharks and odontocetes is perceived by the industry as a major issue but has not been subject to quantification (SPNMCP 2021a). The fishery was initiated by Japanese longliners in the 1960s and became exclusively operated by New Caledonian vessels in 2001. In 2021, the fleet included 18 licenced longliners (12–29 m in length). The fishery is managed by the government of New Caledonia with data on the catch and fishing operations collected through mandatory logbooks (completed by the crew on 100% of sets) and fishery observers (∼8% of sets). Although the recording of this data is mandatory within the fishery, it is likely that it is not a fully accurate representation of the pelagic tuna longline commercial fishery due to the bias that comes with self-reporting and the poor coverage of fishery observers. These data are provided to the South Pacific Community (SPC), the New Caledonian Government, and the Western and Central Pacific Fisheries Commission (WCPFC) for use in fish stock assessments and informing management recommendations. With over 200 direct jobs and ∼1 billion CFP francs (USD ∼9 086 931) of fish sales for a production of 24 633 metric tonnes of tuna in 2022, the fishery is a major socio-economic component of the development of New Caledonia and supplies a large amount of fish to the New Caledonian population (SPNMCP 2021b). However, shark and odontocete depredation has recently been raised by fishers as an increasing issue impacting the socio-economic performance of the fishery and requiring scientific knowledge to quantify the impacts and underpin consideration of mitigation solutions.

Therefore, the main objectives of this first study on depredation in New Caledonian fisheries were to assess the extent and the drivers of the conflict associated with odontocete and shark depredation in the tuna longline fishery as a baseline assessment that future research could expand upon. Specifically, the aims were (i) to quantify the frequency at which depredation occurs and the amount of fish depredated, and (ii) to identify operational and ecological factors influencing the levels of depredation.

Materials and methods

Study area—and fishery

The New Caledonian pelagic longline fishing fleet operates in the New Caledonian Exclusive Economic Zone (EEZ), which extends over 1.25 million km^2 (Fig. 1). The deep-set gear being used consists of a single monofilament mainline suspended in the water column by a series of floats, along which individual branch lines with a mackerel-type bait on a single hook are regularly spaced. The number of hooks baited varies between 1400 and 2200 per longline, and these hooks are set at depth of ∼400 m (SPNMCP 2021b). Longline sets are dozens of km

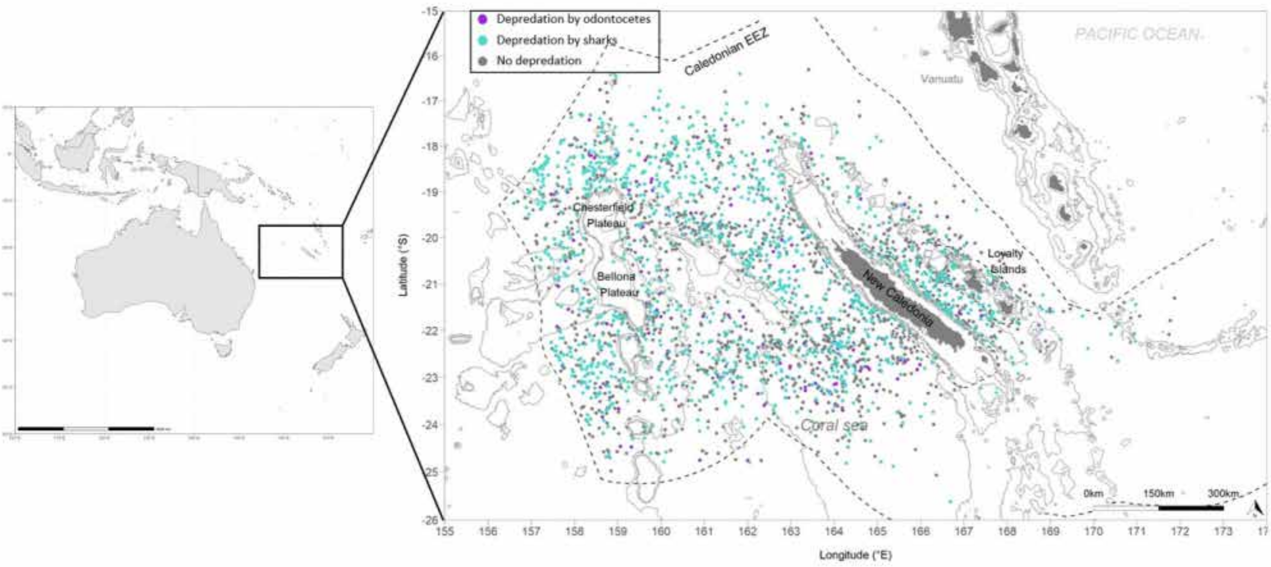

Figure 1. Spatial distribution of longline sets deployed by the tuna longline fishery of New Caledonia monitored by logbooks and observers (SPC and New Caledonian Government) between 2002 and 2022, including sets with and without depredation by sharks or odontocetes.

long and are left soaking for 3–10 h. Vessels haul the longlines starting with the end that was deployed last. The duration of the hauling process ranges from 3 to 10 h (SPNMCP 2021b). In this study, we defined a fishing event as the operation starting at the beginning of the setting of a longline and ending at the end of its hauling.

The main target species are the albacore or longfin tuna (*Thunnus alalunga*), and the yellowfin tuna (*Thunnus albacares*) with smaller catches of bigeye tuna *(Thunnus obesus*). Other species of commercial interest include the opah (*Lampris guttatus*), the common dolphinfish or mahi-mahi (*Coryphaena hippurus*), the wahoo (*Acanthocybium solandri*), the brilliant pomfret (*Eumegistus illustris*), and rostrum fish such as marlins (Istiophoridae) and swordfish (*Xiphias gladius*).

Data collection

Data were used from the onboard observer programme of the New Caledonian longline fishery, as initiated by the 'Fédération des pêcheurs hauturiers (FPH)' and the 'Service du parc naturel de la mer de Corail et de la pêche (SPNMCP)' to monitor fishing activities and catches. These data were collected between 2002 and 2022 by fishers (on 100% of the fishing trips) and fishery observers (on 4.2% of the trips) and were extracted from the SPC database for the study. 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, depredated by sharks or odontocetes and discarded. The fish were assigned a depredated fate when partially consumed by sharks or odontocetes. Although observers sporadically recorded short-finned pilot whales, false killer whales (*Pseudorca crassidens*), and oceanic whitetip sharks (*Carcharhinus longimanus*) as depredating species, this information had not been incorporated into the analysis as it was considered too scarce to produce reliable results. Accordingly, results presented in this study were aggregated at species group level (i.e. sharks and odontocetes) rather than species level. Bite marks were used to differentiate between shark and odontocete depredation. Sharks generally leave crescent-shaped cuts with clean-cut edges and the overall damage to the fish is often represented by few or single bites. Odontocetes leave torn-off pieces of flesh, ragged edges of wounds with traces of conical, widely spaced teeth. Odontocetes also often predate the whole fish leaving only hard parts of the head or up to the position of the hook in the fish mouth (Secchi and Vaske 1998, Chapman et al. 2006). Fishing captains can easily determine if the depredation was from a shark or an odontocete from this distinction.

Data analysis

Assessment of depredation levels

The frequency at which depredation occurred, here defined as the interaction rate (IR) by sharks (IRs) or odontocetes (IRo), was calculated as the number of longline sets hauled with at least one depredated fish (DT) over the total number of longline sets monitored (TS). The depredation rate (DR) was defined as the number of fish damaged by sharks (DRs) or odontocetes (DRo) over the total catch (TC). The catch per unit of effort (CPUE) was calculated as the number of fish caught (TC) per 1000 hooks. The depredation per unit of effort (DPUE) was defined as the number of fish depredated (DC) per 1000 hooks. Unless otherwise stated, means are provided with their standard deviation (±*SD*).

IR, DR, CPUE, and DPUE were calculated over the entire period, per year and per month. The IR, DR, and DPUE were calculated on a 0.5° × 0.5° spatial grid (over the whole study period) to assess spatial variation in these metrics. Differences in the DPUE between sharks and odontocetes were statistically tested using a Wilcoxon–Mann–Whitney test, a non-parametric alternative to the Student's t-test, because of the non-normal distribution of the data and the independence of the samples. Differences in the DPUE across the fish species depredated by sharks or odontocetes, which were considered as independent samples, were statistically tested using the Kruskal–Wallis test.

Selective depredation of fish species

To assess if sharks and odontocetes selectively depredated specific fish species among all species captured on longlines, the resource selectivity index of Ivlev (Krebs 1989) was calculated for each set with depredation, as follows:

$$E_i = \frac{r_i - p_i}{r_i + p_i},$$

where E_i is the Ivlev selectivity index for species '*i*', r_i the proportion of species '*i*' depredated by sharks or odontocetes in the set (DC*i*/DCtotal), and p_i is the proportion of species '*i*', which was captured in the longline during that set (TC*i*/TCprey). Ivlev's index values range between −1 and 1. Values from 0.6 to 1.0 were considered as indicating positive selectivity; values from −0.6 to −1.0 were considered as indicating negative selectivity (i.e. avoidance); and values from −0.6 to 0.6 were considered as indicating neutral selectivity. The relative frequency distribution of positive, negative, and neutral selectivity by sharks and odontocetes was determined for the main commercial fish species only (albacore, dolphinfish, skipjack, wahoo, and yellowfin tuna).

Economic value of depredated fish

The economic value (EL) of the amount of fish lost to shark and odontocete depredation was calculated only considering the depredated fish that were discarded and for the three main commercial species of tuna (albacore, yellowfin, and bigeye tuna), using the mean weight (in kg) of the fish landed per fishing trip times the number of fish depredated and the sale price of the fish per kg. The mean weights of albacore, yellowfin, and bigeye tuna were estimated as 17, 31, and 38 kg, respectively (data provided by the government of New Caledonia for 2020—Gouvernement de la Nouvelle-Calédonie 2021). The mean prices used were 12 USD/kg for albacore, 23 USD/kg for yellowfin, and 29 USD/kg for bigeye tuna (Gouvernement de la Nouvelle-Calédonie 2021). The economic value of the amount of depredated fish per fishing trip (ER) was calculated by dividing the total economic value of the depredated fish by the number of sampled fishing trips.

Influence of temporal, spatial, and operational variables on depredation

Generalized linear models (GLMs; McCullagh and Nelder 1989) were used to assess the influence of spatial, temporal, and operational variables on the probability of shark or odontocete depredation to occur and to examine differences in this probability among vessels. Prior to modelling, collinearity between variables was checked using Spearman's correlation coefficients for categorical variables and Pearson's correlation coefficients for continuous variables. The occurrence of depredation on longline sets was modelled using a binomial distribution with covariates, including 0.5° × 0.5° spatial grid (categorical), year (continuous), month (categorical), latitude and longitude (continuous), vessel (categorical), effort in number of hooks per set (continuous), and duration of the soak, calculated as the difference between the end of setting and the end of hauling, in hours (continuous). The models best explaining the occurrence of depredation, with one model fitted to the occurrence of shark depredation, and one to the occurrence of odontocete depredation, were selected from the full models containing all explanatory variables. A backward stepwise selection was first conducted based on the lowest Akaike Information Criterion (AIC) score using *stepAIC* in R (Hardin and Hilbe 2007, Zuur et al. 2009). Second, the least significant term in models was removed using update. An analysis of variance was used to compare the resulting model with the previous model of the step procedure. Model validation was conducted by examining the dispersion, distribution, and homoscedasticity of residuals through plots and Levene tests.

Results

Depredation levels from the observed data

Data were analysed from a total of 2864 longline sets (5 558 418 hooks) deployed by 31 vessels during 370 trips between 2002 and 2022 within an area encompassing 16°–25°S and 157°–172°E (Fig. 3). The mean fishing effort per set was 1945 ± 307 hooks and ranged from 45 to 2600 hooks. A total of 190 586 fish were caught over the study period [58.3% albacore, 12.3% yellowfin tuna, 6.8% long-snouted lancetfish, 5.3% dolphinfish, 4.1% skipjack tuna (*Katsuwonus pelamis*), 1.5% wahoo, 1.2% bigeye tuna, and 10% other species]. The overall CPUE was 27.9 fish/1000 hooks. CPUE was lower for non-depredated sets (25.3 fish/1000 hooks) compared to those with at least one fish depredated by sharks or odontocetes (39.3 fish/1000 hooks) and sets with shark depredation only and odontocetes depredation only (40.4 and 32.4 fish/1000 hooks, respectively) (Table 1).

On the 2864 sets deployed during the study period, 1803 were subject to shark or odontocete depredation (IR = 63%), including 1676 sets with at least one fish depredated by sharks (IRs = 58.5%) and 264 sets with at least one fish depredated by odontocetes (IRo = 9.2%). One hundred and thirty-six sets were depredated by both sharks and odontocetes ($\text{IR}_{\text{S/O}}$ = 4.7%). Of the 190 586 fish caught during the study period, 7272 fish were reported as depredated (DR = 5.2%), the majority (6523 fish, 89.7% of all depredated fish) being fish from the 3 commercial tuna species. Sharks depredated 5196 fish (DRs = 3.9% of all fish caught on sets with shark depredation), including 4500 tuna (86.6% of all fish depredated by sharks; DRs for tuna = 3.2%). Odontocetes depredated 2076 fish (DRo = 12.3% of all fish caught on sets with odontocete depredation), including 2023 tuna (97.4% of all fish depredated by odontocetes; DRo for tuna = 11.7%) (Table 1). DR per set ranged from 0.5 to 92.6% with a mean of 6.4 ± 9.3% (*n* = 1803 sets). Sharks and odontocetes depredated a mean of 4.3 ± 3.6% (*n* = 1676 sets) and 16.1 ± 18.8% (*n* = 264 sets) of fish per set, respectively. The overall DPUE was 2.0 fish/1000 hooks (1.8 fish/1000 hooks for the three species of tuna). Over the whole time period, sharks depredated 1.6 fish/1000 hooks (1.4 fish/1000 hooks for tuna) and odontocetes depredated 4 fish/1000 hooks (3.9 fish/1000 hooks for tuna) (Table 1). Most of the depredated fish were discarded (91.6% of all fish depredated by sharks; 99.1% of all fish depredated by odontocetes).

Depredation levels by fish species

Albacore tuna and yellowfin tuna were the two most depredated species with 4627 and 1604 individuals depredated, respectively (63.6% and 22.1% of all depredated fish, respec-

Table 1. Summary of the fishing effort, the catch, and the shark/odontocete depredation levels, considering either all fish species captured or the three tuna species only between 2002 and 2022.

		Fishing effort					*Depredation indicators*				
		TT	TS	TH	TC	CPUE	IR	DC	DR	DR per set (mean ± *SD*)	DPUE
No dep	All species	27	1061	1 992 605	50 351	25.3	0	0	0	0	0
	Tuna only					19.0					
Sharks	All species	340	1676	3 319 957	134 227	40.4	58.5	5196	3.9	4.3 ± 3.6	1.6
	Tuna only					30.8			3.2	3.9 ± 3.2	1.4
Odontocetes	All species	168	264	522 923	16 939	32.4	9.2	2076	12.3	13.1 ± 18.8	4.0
	Tuna only					24.5			11.7	15.7 ± 18.4	3.9
Total depredation	All species	343	1803	3 565 813	140 235	39.3	63.0	7272	5.2	6.4 ± 9.3	2.0
	Tuna only					29.9			4.5	6.0 ± 9.2	1.8

TT: total number of fishing trips, TS: total number of longline sets deployed, TH: total number of hooks deployed, TC: total catch (in number of fish), CPUE: the catch per unit effort (in number of fish/1000 hooks), IR: the interaction rate of sharks or odontocetes (in % of all longline sets deployed), DC: the total number of fish depredated, DR: the depredation rate by sharks or odontocetes (in % of the total catch), and DPUE: the depredation per unit effort (in number of fish depredated/1000 hooks).

tively), followed by dolphinfish (4.5%), skipjack tuna (3.2%), and wahoo (2.1%), which represent 95.5% of total depredated fish (Fig. 2).

The mean DPUEo per set (3.9 ± 5.2 fish/1000 hooks, $n = 264$ sets) was significantly higher than the mean DPUEs (1.4 ± 1.3 fish/1000 hooks, $n = 1676$ sets) for sets with depredation (Wilcox test, P-value < .05). Considering the five most frequently depredated fish species, the highest DPUEs were for the wahoo (1.1 ± 1.0 fish/1000 hooks, $n = 1676$ sets) and skipjack tuna (1.1 ± 1.0 fish/1000 hooks, $n = 1676$ sets). The highest DPUEo were for dolphinfish (3.6 ± 4.8 fish/1000 hooks, $n = 264$ sets) and albacore tuna (3.5 ± 4.8 fish/1000 hooks, $n = 264$ sets) (Fig. 2). DPUEs varied significantly between depredated fish species (Kruskal–Wallis; chi-squared = 11.9, P-value = .02), but were not significantly different for DPUEo (Kruskal–Wallis; chi-squared = 3.6, P-value = .5).

For the five overall most frequently depredated fish species, the range of frequencies of negative Ivlev values was larger for odontocetes (2.1% of sets with Ivlev values < −0.6 for albacore tuna and 50% for dolphinfish) than for sharks (3.8% for wahoo and 7.5% for dolphinfish; Fig. 3). For sharks, the frequency of positive values was the highest for albacore tuna (63% of sets with Ivlev values > 0.6, Fig. 3) and the lowest for wahoo (17.6%, Fig. 3). For odontocetes, the percentage of sets with Ivlev values > 0.6 was also highest for albacore tuna (83.6%, Fig. 3) and was neutral for wahoo.

A total fish biomass of 121 805 kg was estimated as depredated, with 85 263 kg by sharks and 36 542 kg by odontocetes from 2002 to 2022, including 74 528 kg of albacore (61%), 45 415 kg of yellowfin tuna (37%), and 1862 kg of bigeye tuna (2%). A mean of 21.20 ± 19.35 (*SD*) depredated fish per fishing vessel per fishing trip was estimated, ranging between 1 and 129 depredated fish per trip, and a mean depredated biomass per trip of 58.9 ± 79.8 kg ($n = 370$ trips). Based on the sale price of fish in 2020, the value of this amount was USD 2 099 016 for the whole fleet for the study period (4.5% of the total value of the landed non-depredated fish) and USD 5719 per fishing trip (Table 2). The total value of the amount of depredated fish was the highest in 2019 with USD 252 174 and the lowest in 2007 with USD 3325.

Factors influencing levels of depredation

The interaction rate (i.e. the proportion of depredated sets over the total number of longline sets) increased from IR < 23.5% of sets to IR > 77.5% in the time period of 2008–2019 (Fig. 4, Supplementary Table S1). It was the highest in 2017 (78.4%) and the lowest in 2005 (17.1%). The shark interaction rate was also the highest in 2017 (IRs = 75.1%) and the lowest in 2007 (17.2%). For odontocetes, it was the highest in 2009 (15.7%) and the lowest in 2007 (1.7%). The depredation rate by sharks and odontocetes (i.e. the proportion of fish damaged over the total catch) was the highest in 2005 (DR = 8.5% of the total catch) and the lowest in 2007 (3.4%). For sharks, it varied from 2% in 2008 to 5.2% in 2005 and for odontocetes, from 4.8% in 2009 to 41.7% in 2007 (Fig. 4). The DPUE, calculated by the ratio between the cumulated number of depredated fish and the cumulated number of hooks over the entire year, ranged from 0.97 fish/1000 hooks in 2003 to 2.6 fish/1000 hooks in 2005–2017. For sharks, it varied from 0.6 fish/1000 hooks in 2008 to 1.9 fish/1000 hooks in 2010, and for odontocetes, from 1.4 fish/1000 hooks in 2003 to 6.7 fish/1000 hooks in 2005 (Fig. 4).

The IR, DR, and DPUE were the highest in December for shark depredation (IRs = 74.3% of all sets; DRs = 5.1% of the total catch; and DPUEs = 2.4 fish/1000 hooks), whereas the IRs and DPUEs were the lowest in September (IRs = 46.5%; DPUEs = 1.2 fish/1000 hooks) and DRs were the lowest in June (DRs = 2.8%) (Fig. 4). For odontocetes, the IRo was the highest in July (IRo = 15.7%) and the DRo and DPUEo in January (DRo = 26.8%; DPUEo = 6.3 fish/1000 hooks), whereas the IRo was the lowest in February (IRo = 3.0%) and the DRo and DPUEo in March (DRo = 4.8%; DPUEo = 1.2 fish/1000 hooks) (Fig. 4). In the absence of depredation, the CPUE varied interannually (minimum: 17.1 fish/1000 hooks in 2003, maximum: 44.1 fish/1000 hooks in 2014) and intra-annually (minimum: 20.5 fish/1000 hooks in March, maximum: 32.5 fish/1000 hooks in July) (Supplementary Table S1).

The model best fitted to the occurrence of shark depredation included year, season, effort, soaking time, and vessel (a unique code for the name of a given vessel) as explanatory terms (AIC = 17 993 against AIC = 18 261 for the null model); and the model best fitted to the occurrence of odon-

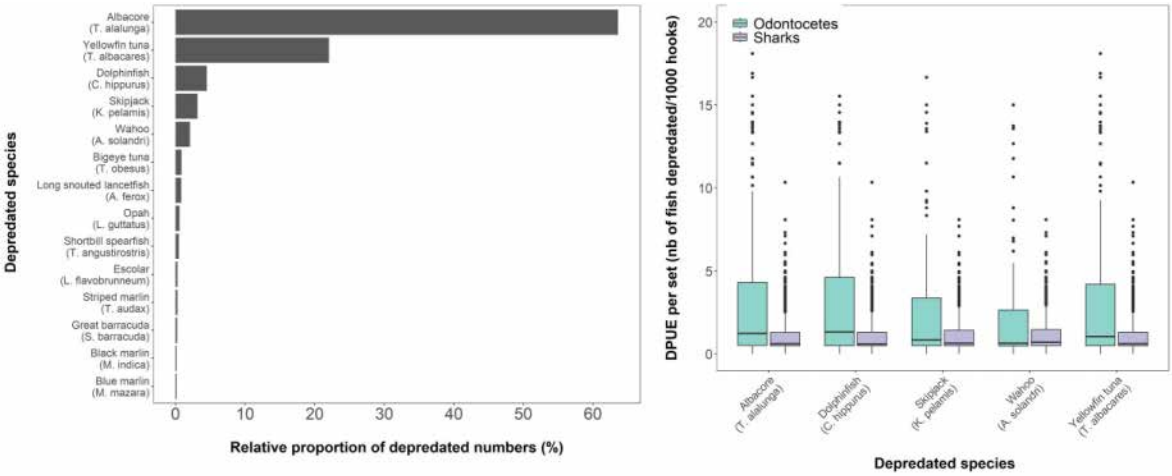

Figure 2. Left: relative proportions of fish species depredated by sharks or odontocetes (% of the species out of all fish depredated) and right: boxplots of the DPUE (number of depredated fish per 1000 hooks, calculated per set using depredated sets only) for main five fish species depredated by sharks (right boxes) and odontocetes (left boxes).

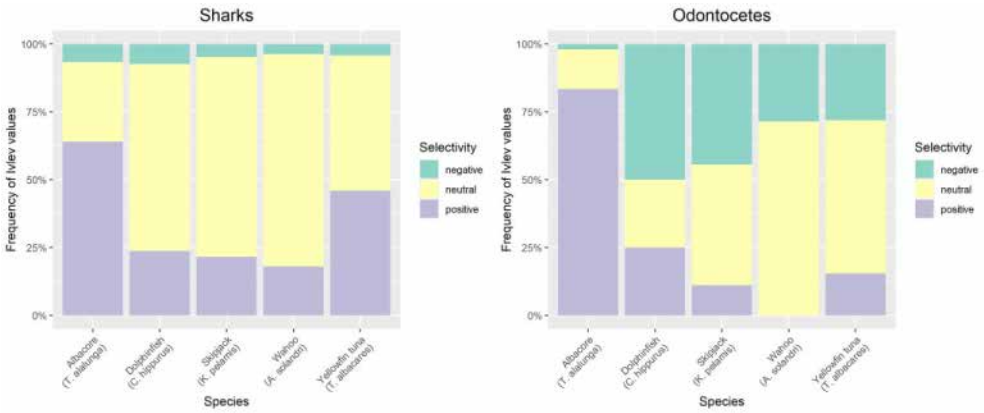

Figure 3. Relative frequency (in % of the depredated longline sets) of the values of Ivlev selectivity index of resources by species that indicate: positive selectivity (Ivlev = 1.0–0.6), neutral (Ivlev = 0.6 to −0.6), and negative selectivity (Ivlev = −0.6 to −1.0). Left panel represents selectivity by sharks and right panel represents selectivity by odontocetes.

Table 2. Estimated depredated fish biomass (in kg) and economic value (in USD) of this biomass for 2002–2022 and per fishing trip, overall (shark and odontocete depredation together), and whether fish was depredated by sharks or odontocetes, for the three commercial species of tuna.

		Economic value	
	Estimated depredated biomass (kg)	Estimated total value of the depredated biomass (USD)	Estimated value of the depredated biomass per trip (USD)
Sharks	85 263	1 555 074	4237
Odontocetes	36 542	543 942	1482
Total depredation	121 805	2 099 016	5719

tocete depredation included effort, soaking time, and season (AIC = 4036 against AIC = 4166 for the null model) but did not include year and vessel as explanatory terms (Table 3). From the model outputs, the probability of depredation to occur significantly increased over the study period only for sharks ($z = 9.117$, P-value $< .005$) (Supplementary Table S2). The months of May and June have a significant and negative effect on the dependent variable compared with other months ($z = -5.620$ and -5.861, respectively, P-value $< .005$). The probability of odontocete depredation was significantly higher in July ($z = 31.88$, P-value $= .001$) and lower in February ($z = -2.251$, P-value $= .024$). (Supplementary Table S2).

None of the best models fitted to the occurrence of shark or odontocete depredation included the grid_id as an explanatory term. However, maps of gridded values from the observed data showed spatial variation in the IR, DR, and DPUE of both sharks and odontocetes (Fig. 5). Areas of high IR (>50% of the sets) and DR (>50% of the catch) were scattered throughout the fishing area for sharks but were spatially localized for odontocetes in the south-western part of

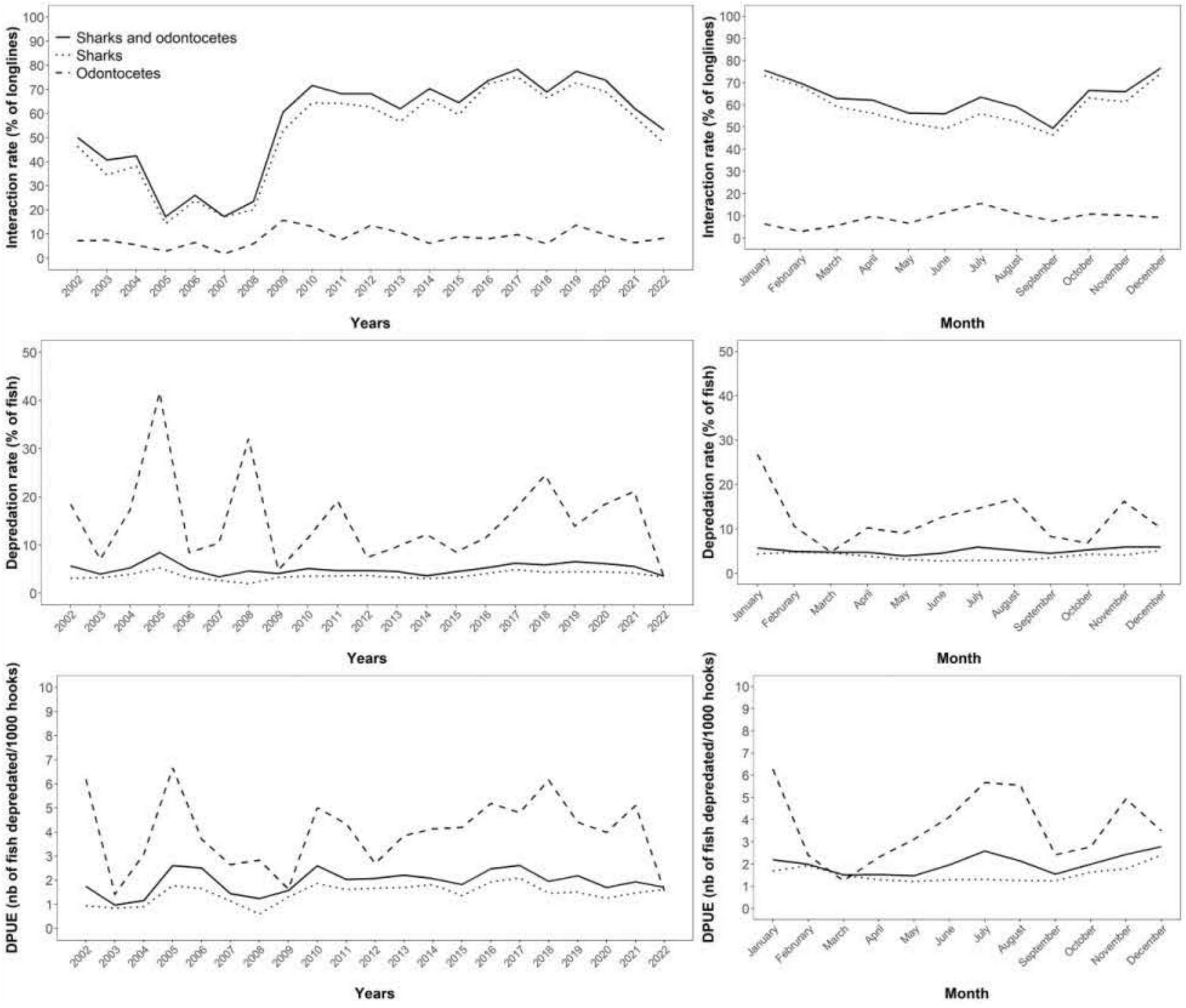

Figure 4. Interaction rate (% of sets with depredation out of all sets), depredation rate (% of fish depredated out of the total catch), and DPUE (number of fish depredated/1000 hooks for sets with depredation) per year (left) and per month (right). Solid lines and circles represent the depredation by sharks or odontocetes; dotted lines and triangles represent depredation by sharks; and dashed lines and squares by odontocetes.

Table 3. Analysis of deviance table for the models best fitted (from an AIC selection) to the occurrence of shark odontocete depredation.

	Sharks					*Odontocetes*				
	Degrees of freedom	Deviance	Residual degrees of freedom	Residual deviance	Pr(>Chi)	Degrees of freedom	Deviance	Residual degrees of freedom	Residual deviance	Pr(>Chi)
NULL			29 544	18 258				29 544	4090	
YEAR	1	102.33	29 543	18 156	<0.005	–	–	–	–	–
MONTH	11	154.03	29 532	18 002	<0.005	11	62.98	29 533	4027	<0.005
EFFORT	1	6.49	29 531	17 995	0.01	1	4.98	29 532	4022	0.03
SOAKING	1	1.88	29 530	17 993	0.17	1	13.97	29 531	4008	<0.005
VESSEL	30	90.21	29 500	17 903	<0.005	–	–	–	–	–

the EEZ, a sector where the fishing effort and the tuna CPUE were high during the study period (Fig. 5).

From the best models, the probability of depredation significantly increased with the number of hooks per set for both sharks and odontocetes ($z = 2.605$, P-value $= .009$; $z = 2.573$, P-value $= .01$) and with the soaking time for sharks ($z = 2.474$, P-value $= .01$) (Supplementary Table S2). However, it significantly decreased with the soaking time for odontocetes ($z = -3.510$, P-value $< .005$). Significant variation in the probability of shark depredation was detected between vessels but not in the probability of odontocete depredation (Supplementary Table S2).

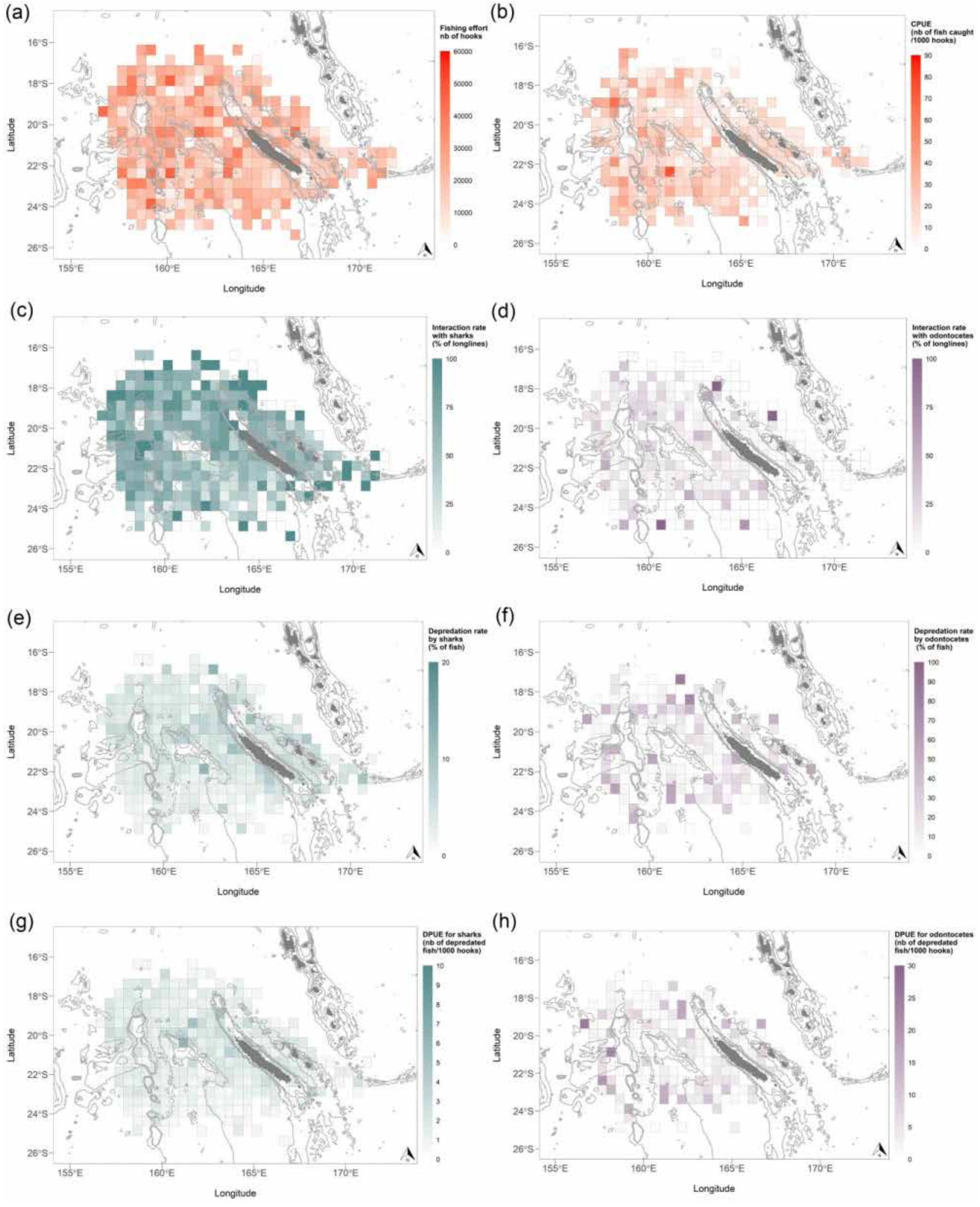

Figure 5. Spatial variation (across a 0.5° × 0.5° grid) of the fishing effort, catch, and shark and odontocete depredation during the period 2002–2022 with (a) the number of hooks deployed; (b) the CPUE of tuna for sets without depredation (number of fish caught/1000 hooks); (c) the shark interaction rate (% of sets with shark depredation); (d) the odontocete interaction rate with odontocetes (% of sets with odontocete depredation); (e) the depredation rate for sets depredated by sharks (% of depredated fish by sharks); (f) the depredation rate for sets depredated by odontocetes (% of depredated fish by odontocetes); (g) the DPUE for sets depredated by sharks (number of depredated fish/1000 hooks); and (h) the DPUE for sets depredated by odontocetes (number of depredated fish/1000 hooks).

Discussion

Depredation levels in New Caledonia in comparison with other regions

This study reports relatively high levels of shark and odontocete depredation on the catch of the pelagic longline fishery of New Caledonia compared to other regions and fisheries facing a similar issue. With 63% of all longline sets with at least one fish depredated by sharks or odontocetes (IR), depredation occurs as frequently or more frequently than in the pelagic tuna longline fisheries of the Seychelles (63% of the sets—Rabearisoa et al. 2018), Reunion Island (41%—Rabearisoa et al. 2018), tropical western Atlantic Ocean (29.7%—Charles et al. 2020), southwestern Atlantic Ocean (6.2%—Passadore et al. 2015b) and in the Azores (3.6%), and the north-eastern region of Brazil (3.3%) (Hernandez-Milian et al. 2008). This is mainly explained by shark depredation occurring on a greater proportion of sets in New Caledonia (58.6%) than in these other cases (ranging from 20 to 45%—Monteiro et al. 2006, Romanov et al. 2007, Rabearisoa et al. 2018), whereas odontocete depredation occurred in similar proportions (9.2% in New Caledonia compared to 1.6–6.2% in other studies—Monteiro et al. 2006, Romanov et al. 2007, Hernandez-Milian et al. 2008, Silva et al. 2011, Passadore et al. 2015a).

The proportion of fish depredated by sharks and odontocetes (DR) in the New Caledonian fishery (2.2% of the total catch between 2002 and 2022) is consistent with depredation rates reported in other longline tuna fisheries (0.2–15%) (Nishida and Shiba 2002, Hernandez-Milian et al. 2008, Ramos-Cartelle and Mejuto 2008, Passadore et al. 2015a, b). Depredation rates for sharks only, were similar to those estimated for the Reunion Island fleet (2%) (Lawson 2001, IOTC Secretariat 2007, Gilman et al. 2008, MacNeil et al. 2009). However, odontocete depredation rates (12.3%) were much higher than those observed in the Reunion Island and Seychelles (0.5%) (Rabearisoa et al. 2018), in Hawaii (3%) (Forney et al. 2011) and in southeast Australia by killer whales (5.2%) (Gimonkar et al. 2022). Most (>90%) of the affected fish were too damaged to be retained, with 58.9 ± 79.8 kg worth of fish per trip being lost. For the entire period, the total volume depredated was 121 805 kg (4.5% of the total catch, equivalent to USD 99 953 per year). While it is difficult to compare among fisheries due to fishery-specific socio-economic characteristics, this could be considered lower than the volume of fish depredated by killer whales and sperm whales in some demersal Patagonian toothfish longline fisheries of the Southern Ocean (e.g. >30% of the catch, equivalent to USD 15 million per year; Tixier et al. 2020). The depredated volume and associated value for the New Caledonian fishery is also smaller than around the Seychelles (130 000 metric tonnes between 2004 and 2010; USD 500 000 per year—Rabearisoa et al. 2018).

Factors influencing depredation levels

The frequency at which shark depredation occurred significantly increased between 2002 and 2022, from <10% of the sets before 2008 to >40% since 2009 and reaching 66% in 2017. Several factors, acting alone or together, might explain such a trend. First, vessels stopped catching/retaining sharks in 2008 within the EEZ, ahead of a ban on shark retention in the EEZ in 2013 (SPNMCP 2021b) and the implementation of a 'Shark sanctuary' in 2013 around New Caledonia covering ~50% of the EEZ (Ward-Paige and Worm 2017). These changes, by reducing the fishing mortality of sharks, may have contributed to increases in the shark population and, thus, to the increased occurrence of depredation by sharks (Ward-Paige and Worm 2017). Similar trends were, e.g. reported in western Australia and around the Maldives, where effective measures for shark conservation were thought to result in an increase of shark population size, which then led to higher probability of shark encounters and thus depredation (Mitchell et al. 2018, Robinson et al. 2022). Second, the probability of sharks encountering fishing vessels may have changed, as a consequence of changes in their natural distribution, feeding patterns, and behaviour, which may include 'learnt' behaviours. This was e.g. observed in the Bahamas, where recurrent seasonal movements of oceanic whitetip sharks are thought to have been influenced by opportunistic feeding on large fish provided by a recreational fishery and dive operators (Madigan et al. 2015). Lastly, an increase in the frequency of shark depredation may be linked to changes in fisher behaviour to catch fish. For example, the choices made with regards to the fishing area, the time of the year, and/or the use of the gear have been shown to strongly influence depredation levels in other studies (Tixier et al. 2015b, Janc et al. 2018, 2021, Richard et al. 2018). Although the interaction rate (IR) of sharks increased after the implementation of shark fishing bans and protected areas, this was not the case for their depredation rate (DR, i.e. the proportion of fish depredated for sets with depredation by sharks). This suggests that sharks interacted more frequently with longlines but there were not necessarily more sharks depredating the same longlines.

Unlike for sharks, no trend in the frequency at which odontocete depredation occurred could be detected but fishers report that the volume of fish they removed from longline sets did increase in recent years. This result suggests that odontocetes may be increasingly effective at removing fish when depredating, and this could explain why fishers feel that odontocete depredation has become more and more problematic over the years (SPNMCP 2021a).

Depredation occurred year-round but was significantly higher in December for sharks and July for odontocetes. For odontocetes, this seasonal variation is consistent with that of the tuna catch rates of the fishery. Similarly, areas of high odontocete depredation overlapped with those areas of high tuna catch rates, as was observed by Fader et al. (2021) with false killer whales in Hawaii. Together, these results suggest that there is a spatio-temporal co-occurrence of fishing vessels and odontocetes in areas and times of the year of high tuna aggregations. One possible explanation for a lower CPUE for non-depredated sets is that fishing vessels and sharks/odontocetes co-occur in areas of high tuna/swordfish densities. While depredation does logically decrease the CPUE, the extent of this decrease (in terms of the proportion of fish depredated out of all fish caught on the longlines) is likely to greatly vary spatio-temporally, and this co-occurrence between fishers and large predators may lead to depredated longlines in areas of high tuna/swordfish densities still producing higher CPUE than non-depredated longlines in areas of low tuna/swordfish densities. For example, such co-occurrence between depredating species and fishing vessels in good fishing areas was highlighted for sperm whales depredating on toothfish in subantarctic waters and was suggested as the main assumption for sperm whale depredation being difficult to detect when examining differences in CPUEs between depredated and non-depredated sets (Roche et al. 2007, Tixier et al. 2010). This hypothesis will be further investigated by a spatial modelling work. In addition, the results showed that when odontocetes found longline sets, they appeared to be selective in the fish species they depredated, with a preference for *T. alalunga*, *C. hippurus*, and *T. albacares*. This may be explained by the natural feeding ecology (in absence of fishing vessels), the level of specialization of the predator species involved in depredation, and the nutritional quality of the fish species caught (Vlieg et al. 1993, Baird et al. 2008, Passadore et al. 2015b, Garagouni and Ganias 2023). This is consistent with what was reported in other cases of depredation, such as killer whales depredating on tuna in the Uruguayan pelagic longline fishery (Passadore et al. 2012, 2015b) or sperm whales depredating on toothfish in subantarctic demersal longline fisheries (Tixier et al. 2019). While the depredating odontocete species have yet to be confirmed, it is likely that they are primarily false killer whales as the species most often documented depredating on catches in other tuna longline fisheries operating in tropical/sub-tropical waters. The results support this assumption since false killer whales were reported also preferentially taking tuna species when depredating in these other fisheries, but also swordfish, mahi-mahi, and wahoo (Baird et al. 2008, Ramos-Cartelle and Mejuto 2008, Passadore et al. 2015b).

Significant differences in the frequency of depredation by sharks were also detected between the fishing vessels of the fleet in the models used in the study and should be further investigated. Such differences have been highlighted in other fisheries faced with shark/odontocete depredation, such as the toothfish longline fisheries in subantarctic waters (Tixier et al. 2010). They can be either attributed to variation in the fishing strategies used by skippers 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. 2015b, Janc et al. 2018, Fader et al. 2021). This study found that increasing the number of hooks on longline sets, and thus their length, as well as leaving these sets soaking for longer periods of time, significantly increased the probability of shark depredation to occur. Longer sets left in the water for longer may increase the probability of sharks to locate fish caught on hooks, as suggested by similar correlations found for sharks (Mitchell et al. 2018), killer whale and sperm whale depredation in demersal longline fisheries (Tixier et al. 2015b). However, other potential drivers of the occurrence of depredation have yet to be investigated in New Caledonia to understand the detected variation of depredation levels between vessels. Among these, environmental factors influencing the distribution of sharks and odontocetes, such as the water temperature or the bathymetry, as well as other operational factors like the depth at which the fishing gear is set, which have been shown to influence depredation in other regions (MacNeil et al. 2009, DiGirolamo et al. 2012, Mitchell et al. 2018). Also, the nature of substrates and habitats (such as reef habitat) can support a greater abundance and diversity of reef sharks, thus leading to higher depredation rates (Chin et al. 2012, Espinoza et al. 2014). High probability of presence of predators can also be influenced by the number of boats fishing in the same area through generating more noise and fish oil/blood, making it easier for sharks and odontocetes to detect and locate fishing activities (Mitchell et al. 2018).

Differences between shark and odontocete depredation

This study showed that there are varying levels and patterns of depredation in the New Caledonian pelagic longline fishery between sharks and odontocetes. While shark depredation occurred more frequently than that of odontocetes, sharks damaged 50% less fish on longlines when depredating compared to odontocetes. When a set was depredated by odontocetes, the proportion of depredated fish was three times higher than that depredated by sharks. These results are consistent with those of Dalla Rosa and Secchi (2007) in Brazil, who showed a higher frequency of interactions with sharks but a lower amount of fish depredated per unit effort compared to killer whale depredation. This difference could be explained by the fact that odontocetes, once they locate a longline set, appear to be taking fish one after the other along the line and, as social species, generally do so in groups unlike sharks such as oceanic whitetip or tiger sharks, which are solitary and non-schooling species (Sivasubramaniam 1964, Forney et al. 2011). Although the models did not show any significant influence of the spatial variable on the occurrence of depredation by sharks and odontocetes, variation in the interaction and depredation rates of odontocetes across the fishing area was suggested by the maps made from the spatial gridding of these two indices. This could be a result of odontocetes actively searching and following fishing vessels, as it was observed with false killer whales in Hawaii (Fader et al. 2021). Unlike odontocetes, shark depredation occurred throughout the fishing area and did not appear to be selective in the fish species they depredated. They depredated a higher proportion of the fish species caught than odontocetes (41% vs. 27% for odontocetes) and even if the Ivlev selectivity index suggested a preference for *T. alalunga*, sharks did not seem to avoid certain species of fish on the line.

The estimates of depredation levels reported here should be considered as minimum estimates due to the nature and the extent of the data available for the study. The use of logbook and observer data can lead to bias that comes with self-reporting and the poor coverage of fishery observers. First, the occurrence of depredation was monitored through records of damaged fish on the line and depredation can be missed if the whole fish are removed from the hooks by predators. This is often reported for odontocetes depredating on fish on demersal longlines (Hucke-Gaete et al. 2004) and, to a lesser extent, on pelagic longlines (Rabearisoa et al. 2018, Fader et al. 2021). Second, the limited information available prevented the use of indicators considering the impacts of depredation associated with damage to fishing gear, depredation of bait or the additional time, bait and fuel spent by fishers to recoup the depredated fish or to avoid depredation. These data limitation issues can be addressed by: (i) implementing additional fields for data to be consistently and systematically collected on depredation in both the skippers' and observers' logbooks, such as the amount of gear damaged, and the observation of sharks and odontocetes (with a clear identification of the species) in the vicinity of the gear; (ii) supplementing surface observations with alternative approaches to detect the occurrence of depredation and to confirm the species involved, such as underwater cameras, accelerometers, acoustic recorders, photo identification, and DNA analyses (Thode et al. 2016, Fotedar et al. 2019, Richard et al. 2020).

In conclusion, this study assessed the extent of the shark and odontocete depredation in the longline fishery of New Caledonia, and this can be used to further understand its impacts on the socio-economic performance of the fishery. Specifically, the amount of fish captured by the fishers but consumed by predators on longlines is an essential information to quantify the costs of depredation for the fishers/fishing companies, the additional mortality it generates on fish stocks not accounted for in stock assessments, and the potential trophic changes that may result from it (Clavareau et al. 2020, Faure et al. 2021, 2023). However, while the study provided initial insights on the potential drivers of depredation in the region, further research is needed to understand the aspects of the fishers' behaviour and/or the marine predators' ecology that can be used to better predict, avoid, and reduce depredation through adjustments in fishing practices. The effectiveness of practices to reduce depredation relies on the characteristics of the species and the habitats involved, the behaviour of the fishers, individually and collectively, as well as their perceptions and attitudes towards sharks and odontocetes (Nishida and Tanio 2001, Gilman 2007, Dickman 2010, Hamer et al. 2012, Pardalou and Tsikliras 2018). These aspects have yet to be understood for shark and odontocete depredation in New Caledonia and adjacent waters of the South Pacific Ocean. We suggest that given the results for New Caledonia, which is a relatively small component of the broader longline fishery in the southern and western Pacific, depredation is likely a major impact on a larger scale and should be further assessed across the Pacific longline fisheries targeting tuna.

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Author contributions

M.M. curated the data, conducted the formal analysis, investigation, and methodology, generated the visualizations, and wrote and edited the manuscript. P.T. supervised the project, including the investigation and methodology, assisted in generating visualizations, and reviewed and edited the manuscript. C.M. supervised the project and reviewed and edited the manuscript. F.P., P.H., and M.H. provided the resources for the project, including the investigation, and reviewed and edited the manuscript. Sam McKechnie provided the resources and software for the project and curated the data.

Supplementary data

Supplementary material is available at *ICES Journal of Marine Science* online.

Conflict of interest : Authors declare that they have no conflict of interests.

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Data availability

All the data are available upon request.

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