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Drivers of at-vessel mortality of the blue shark (*Prionace glauca*) and oceanic whitetip shark (*Carcharhinus longimanus*) assessed from monitored pelagic longline experiments

Yoluène Massey[a,b], **Philippe S. Sabarros**[a,b], **and Pascal Bach**[a,b]

[a]MARBEC, Univ. Montpellier, CNRS, IFREMER, IRD, Sète, France; [b]Institut de Recherche pour le Développement, Marseille, France

Corresponding author: **Yoluène Massey** (emails: yoluene.massey@gmail.com and yoluene.massey@ird.fr)

Abstract

Elasmobranchs make up a significant part of bycatch in pelagic longline fisheries, whose induced mortality can be a major threat to endangered species. It is therefore crucial to understand the drivers of at-vessel mortality (AVM) for this fishing gear to enhance postrelease survival. To this end, we analysed scientific data collected during monitored longline fishing experiments conducted in French Polynesia to (*i*) estimate AVM for each species based on bootstrapped samples and (*ii*) to assess AVM drivers using multivariate logistic regression models for the blue shark (*Prionace glauca*) and oceanic whitetip shark (*Carcharhinus longimanus*). We found that AVM varies widely between species. Oceanic whitetip sharks are more likely to die when caught in waters outside their comfort temperature range, and their odds of survival increase with body length. For the blue shark, the only driver related to AVM is hooking duration. These results indicate that to reduce the AVM of these two species, the vertical distribution of hooks and soak duration should be considered as mitigation measures related to pelagic longlining.

Résumé

Les élasmobranches représentent une part significative des prises accessoires des pêcheries palangrières pélagiques, dont la mortalité induite peut constituer une menace importante pour des espèces vulnérables ou en danger. La compréhension des facteurs de mortalité au virage (MAV) pour cet engin est donc cruciale pour améliorer la survie après remise à l'eau. Pour cela, nous avons analysé des données recueillies durant des campagnes scientifiques de pêche avec une palangre instrumentée menées en Polynésie française afin (*i*) d'estimer la MAV pour chaque espèce sur la base d'échantillons bootstrappés et (*ii*) d'évaluer les facteurs influençant la MAV à l'aide de modèles de régression logistique multivariée pour le requin peau bleue (*Prionace glauca*) et le requin longimane (*Carcharhinus longimanus*). Nous avons constaté que la MAV diffère grandement entre les espèces. Les requins longimanes sont plus susceptibles de mourir quand ils sont capturés dans des eaux en dehors de leur intervalle de températures de confort et leur probabilité de survie augmente avec la taille des individus. Pour le requin peau bleue, le seul facteur qui influence la MAV est la durée d'hameçonnage. Ces résultats indiquent que, pour réduire la MAV de ces deux espèces, la répartition verticale des hameçons et le temps d'immersion de la palangre devraient être considérées comme mesures d'atténuation dans la pêche palangrière pélagique. [Traduit par la Rédaction]

1. Introduction

Across the globe, fishing activities unintentionally catch nontarget species—i.e., bycatch—and are therefore considered one of the greatest threats to marine populations, especially pelagic sharks (Dulvy et al. 2014). Sharks can account for up to a quarter of pelagic longline catches, making this gear particularly threatening to this group of fish (Gilman et al. 2008; Queiroz et al. 2019). On scientific advice, the European Union's zero-discard policy excludes from landing obligations endangered, threatened, and protected species, including a number of shark species, which are required to be released (Ellis et al. 2017). Several tuna Regional Fisheries Management Organizations (tRFMOs) and international agreements such as the Convention on International Trade in Endangered Species (CITES) have implemented bans on the finning, trading, and retention of sharks on board fishing vessels (e.g., IOTC Res. 17/05, ICCAT Rec. 04-10, and WCPFC CMM 2019-04; IOTC 2017; ICCAT 2004; WCPFC 2019). The oceanic whitetip shark (*Carcharhinus longimanus*) is one of the species protected worldwide by retention bans enforced by each tRFMO (Tolotti et al. 2015). Although this is a step in the right direction, such measures are not enough to reduce fishing-related mortality and to contribute significantly to the recovery of severely depleted shark populations (Tolotti et al. 2015). More knowledge on discarded shark species—including drivers of both at-vessel (AVM) and postrelease mortality (PRM)—is still sorely lacking.

Three main causes are responsible for fishing mortality: AVM, catch dying on board (CDO) (AVM + CDO are traditionally defined as the fishing mortality, *F*), and PRM. The latter can be significant and is related to handling practices that can lead to physiological stress, exhaustion, or injuries (Ellis et al. 2017). AVM depends on both the vulnerability of the species and the impact of fishing practices. Megalofonou (2005) showed different mortality rates for sharks caught on longlines targeting swordfish (*Xiphias gladius*) or albacore (*Thunnus alalunga*) in the Mediterranean Sea. The biology of species strongly affects their respective mortality rates (e.g., their mode of ventilation, skin thickness, physiological status, length, and behavioural reaction to the gear; Ellis et al. 2017). For example, demersal elasmobranchs with buccal pump ventilation (e.g., lesser-spotted dogfish, *Scyliorhinus canicula*) may have better survival rates when hooked than obligate ram-ventilating taxa such as pelagic sharks (Carlson and Parsons 2001; Ellis et al. 2017). Lamnid sharks, for instance (e.g., shortfin mako shark, *Isurus oxyrinchus*), have a high metabolic rate and high oxygen requirements, so they may have more difficulty ventilating while hooked (Campana et al. 2016). In addition, body length may affect survival, as in some species large individuals exhibit higher tolerance to hooking trauma (Campana et al. 2009). Sea temperature can be another significant variable, potentially having a positive or negative effect on capture and (or) survival rates depending on the species (Bromhead et al. 2012; Gallagher et al. 2014*b*). Finally, soak duration (the length of time the longline remains in the water) can be an important factor impacting AVM, as has been shown for the blue shark (*Prionace glauca*) (Diaz and Serafy 2005). In contrast, studies that have analysed oceanic whitetip shark catches on longlines found no effect of fishing practices influencing AVM (e.g., Gallagher et al. 2014*a*; Campana et al. 2016), indicating that the causes of mortality are highly variable depending on species.

To improve knowledge about AVM in sharks, this study aimed to (*i*) estimate the AVM of the main elasmobranch species caught during experiments carried out with a monitored pelagic longline and (*ii*) assess the factors affecting this mortality. We used data from scientific cruises carried out between 1993 and 1997 in the northern part of the French Polynesian EEZ (central South Pacific Ocean). At that time, the domestic French Polynesian pelagic longline fleet was just emerging (Beverly 1998), while today there are more than 60 licensed vessels that mainly target albacore tuna (Gascoigne et al. 2018). Previous to this study, there have been no estimates of the AVM of sharks caught by pelagic longlines in the French Polynesia EEZ. The research cruises carried out in the 1990s aimed to explore the interactions between large pelagic resources and monitored pelagic longlines, which were equipped with hook timers (HTs) and time–depth recorders (TDRs). We used the collected data to consider variables dependent on fishing practices that may explain AVM rates, such as the time of fishing operations, the position of the hook on the basket, and the vertical range of the hooks (Bach et al. 2003; Maunder et al. 2006). The deployment of HTs and TDRs allowed us to analyse for the first time the hooking duration and the hooking depth as drivers of AVM. Two factors related to environmental conditions were also tested: temperature and dissolved oxygen concentration. Additionally, we investigated the relationship between AVM and body length—an intrinsic factor of the animal's biology. These variables were analysed for two species—the blue shark and the oceanic whitetip shark—which were caught in sufficient numbers for viable statistical analysis. The results should contribute to informing fishing guidelines with the aim of improving the conservation of shark species bycaught by pelagic longline fisheries.

2. Materials and methods

2.1. Fishing experiments

The data were collected in the framework of the ECOTAP (Etude du COmportement des Thonidés par l'Acoustique et la Pêche à la palangre en Polynésie Française) programme, which aimed to study the ecology of tuna species through longline fishing and acoustic surveys and was set up to support the development of the local longline fishery. Fishing experiments using monitored pelagic longlines ($n = 193$) were conducted on the French National Research Institute for Sustainable Development (IRD) research vessel *Alis* in the northern part of the French Polynesian EEZ between 20°S and 5°S and 134°W and 155°W around the Society and Marquesas archipelagos between 1993 and 1997 (Fig. 1; Bertrand et al. 2002). The fishing gear consisted of a monofilament nylon mainline (3.6 mm in diameter) to which branchlines were attached using snaps. The 12-m-long nylon monofilament branchlines (2 mm in diameter) were geared with a tuna hook baited with squid (150–200 g), sardine (100 g), or mackerel (150–200 g) used alone or mixed for a fishing set (Fig. 2). Each basket corresponding to a mainline segment between two floats was composed of 25 branchlines. An average of 20 baskets were deployed per set during the surveys, corresponding to a fishing effort of 500 hooks per set. The mainline setting speed was controlled with a tachymeter to ensure a uniform shape between the baskets. Buoys delimiting baskets had 19 m floatlines. During setting, the mainline was launched using a shooter to deploy deep longlines in the pelagic realm from the surface to the 8 °C isotherm (i.e., 450–550 m in depth depending on the latitude; Bertrand et al. 2002). The fishing gear was usually deployed in the morning between 04:00 and 07:00 and retrieved in the afternoon, with a soak duration varying between 7 and 14 h. Setting and hauling mean speeds were respectively 7.5 and 4.3 knots (1 knot = 1.852 $\text{km}\cdot\text{h}^{-1}$).

Capture parameters (hooking depth, hooking duration, and hooking time) were monitored by fitting two types of instruments on the longline: TDRs (model LL600, Micrel) and digital HTs (designed following Somerton et al. 1988). For each set, 40%–60% of the baskets were equipped with TDRs programmed to record the theoretical maximum fish-

Fig. 1. Geographical locations of the monitored longline fishing experiments carried out in the frame of the ECOTAP project (carried out with the oceanmap package; Bauer 2020).

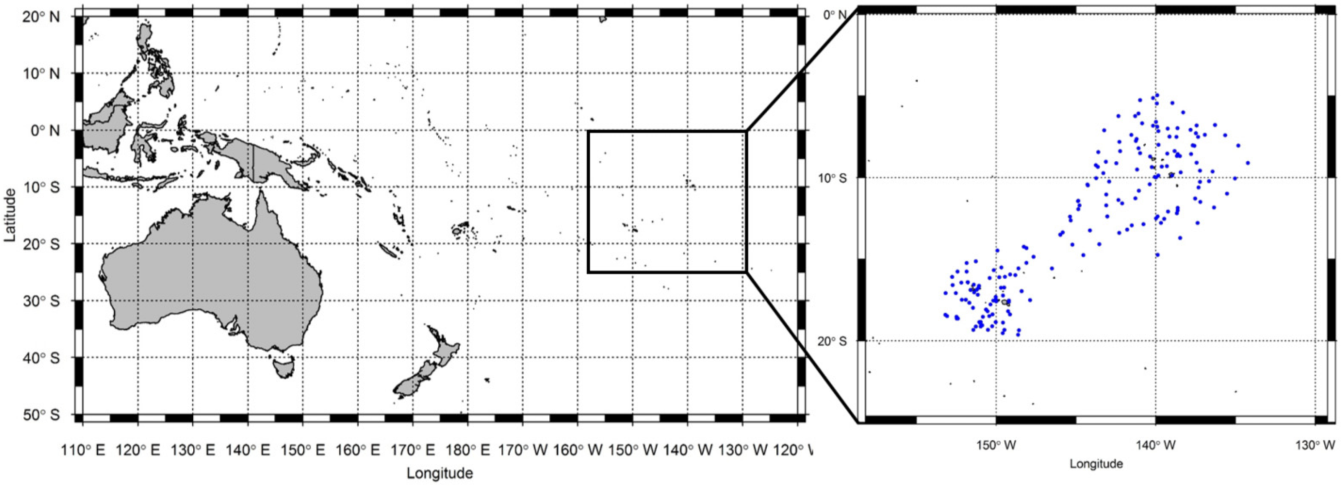
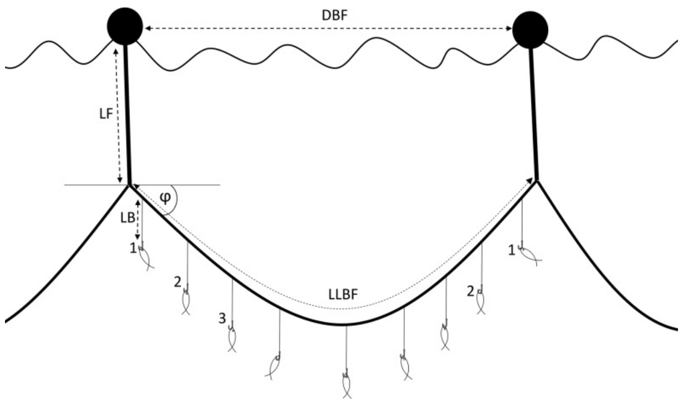


Fig. 2. Schematic representation of a longline. DBF, distance between floats; LF, length of the floatline; LB, length of the branchline; LLBF, mainline length per basket between floats; and 1, hook position.



ing depth once per minute. The TDRs were placed at the midpoint of the basket mainline, i.e., between the 12th and 13th hooks. This setup allowed us to obtain the variation in time of the longline's maximum depth. Almost 89 200 hooks were deployed, with more than 90% equipped with HTs fitted on individual branchlines close to the snap. HTs are triggered when large pelagic fish bite the hook, indicating the elapsed time (hooking duration) between the fish's contact with the hook and its hauling to the vessel's deck. The time at which individuals were caught was calculated from the HT data. Hooking depth was inferred from the hook depth on the TDR profile at capture time estimated from HT data and from a modified catenary equation (Bach et al. 2009).

For each of the 1500+ individuals caught (including both targeted tuna and bycatch species), scientists on board recorded the species, size (e.g., fork length (FL) for sharks and disk width (DW) for rays), weight and sex. Of these individuals, 250 were elasmobranchs, mainly represented by the blue shark (BSH) and oceanic whitetip shark (OCS). Six other species were also caught: the silky shark (*Carcharhinus falciformis*), bigeye thresher shark (*Alopias superciliosus*), pelagic thresher shark (*Alopias pelagicus*), pelagic stingray (*Pteroplatytrygon violacea*), crocodile shark (*Pseudocarcharias kamoharai*), and shortfin mako (*I. oxyrinchus*). Individuals that were caught and hauled to the surface, but broke the line prior to species identification, were grouped as various sharks (SKH) and considered to have escaped alive.

2.2. Description of the at-vessel status

The variable of interest in this study was the AVM of elasmobranch species. The status of each specimen caught was assessed as one of three modalities: alive, exhausted (i.e., motionless with ventilating evidence), or dead. For each species, the mortality rate was calculated in two different ways: considering individuals "exhausted" at haul-back as (*i*) dead or (*ii*) alive. Binary coding was used: 0 for dead individuals and 1 for live individuals.

2.3. Variables considered in AVM modeling

- Body length: the FL (in cm) of the shark.
- Hooking duration: the time elapsed between the fish triggering the timer by biting the bait (whether hooked or not) and the haul-back time (when the individual was brought on board). This variable was only recorded for individuals caught on a branchline equipped with an HT or a basket equipped with a TDR from which no other shark or large pelagic species were caught and a hooking event could be identified from the TDR profile (Bach et al. 2003).
- Time of capture: the time at which the fish was hooked, calculated using the haul-back time and the elapsed time from hooking provided by the HT or a movement signal detected on the TDR profile.
- Hook position: the hook number on which the specimen was caught (Fig. 2), starting at 1 for the closest hook to the surface (on both sides of the basket). Each basket having 25 hooks, by symmetry, hook numbers ranged from 1 for the

shallowest hook to 13 for the expected deepest hook (the depth of the hooks may vary in the water).

- Hooking depth: this was estimated for each individual caught. In the best case, the individual was caught on a basket equipped with a TDR and a branchline equipped with an HT giving the capture time. The TDR depth value recorded at the capture time was noted (InstFD: instrumented fishing depth). This InstFD value was then used to calculate the actual depth of the hook on which the individual was captured (D_j). The second most relevant case was when the triggered hook was not equipped with an HT, but the signal of the hooking could be easily detected in the TDR profile through sharp depth changes with peaks or descents, particularly when the contact occurred near the TDR. If this event corresponded to the capture of interest and not to another capture on the basket, the InstFD value was then estimated in the same way as described previously. In cases where the branchline was not equipped with an HT and no capture signal was noticeable on the TDR profile, the hooking depth was inferred from the MeanFD (this corresponded to the mean TDR value recorded for the period when the longline was considered to be settled at depth, i.e., after sinking and before hauling). When the basket was not equipped with a TDR, MeanFD was defined as the average of the MeanFD of the surrounding instrumented baskets. The TDR profiles with noise from several capture movements were not considered. The theoretical depth of the *j*th hook (D_j) was estimated using catenary geometry by assuming a homogeneous effect of the vertical currents (Yoshihara 1954; Suzuki 1977; Bach et al. 2009) on both the mainline and branchlines:

(1) $D_j = \cos(\alpha) \times [\mathrm{LF} + \mathrm{LB} + (\mathrm{LLBF}/2) \times ((1 + \cot^2\varphi)1/2 - \{[1 - (2j/N)]^2 + \cot^2\varphi\}1/2)]$, with
(2) $\cos(\alpha) = \mathrm{MeanFD}$ (or InstFD)/MFDtheo
(3) $\mathrm{MFDtheo} = \mathrm{LF} + \mathrm{LB} + (\mathrm{LLBF}/2) \times [(1 + \cot^2\varphi)1/2 - (\cot^2\varphi)1/2]$ empirical estimation of φ (Bach et al. 2009)
(4) $\varphi = \beta_{\mathrm{inf}}\,[1 - \exp(-K\,(1 - \mathrm{SR})^p]$

with LF = length of the floatline; LB = length of the branchline; HPB = hooks per basket; N = HPB + 1; SR (sagging rate) = DBF/LLBF; $\beta_{\mathrm{inf}} = 108.126$; $K = 1.85$; and $p = 0.57$.

- Hooking temperature: at the end of each longline set, an SBE19 probe was deployed to collect temperature and oxygen depth profiles. The temperature at capture was the temperature associated with the previously estimated hooking depth.
- Dissolved oxygen at capture: similarly, based on the dissolved oxygen depth profile, this was the dissolved oxygen associated with the previously estimated hooking depth.

2.4. Statistical analyses

A bootstrap method was used to obtain the 95% confidence interval (CI) of the AVM rates for the two cases described in Section 2.2 (exhausted individuals considered either dead or alive). To do so, a random sampling of 50% of the observations for each species with replacement was carried out 500 times (Davison and Hinkley 1997). We compared these AVM estimates by species with values obtained in previous studies.

A principal component analysis (PCA) including all candidate variables (body length, hooking duration, time of capture, hook position, hooking depth, hooking temperature, and dissolved oxygen at capture) was carried out to identify variables explaining the main variance in the data set and to explore potential correlation between the variables to avoid multicollinearity in the final models.

Multivariate logistic regressions (Zuur et al. 2007) were used to test the effect of the potential variables listed above (explanatory variables X) on AVM at the species level. The variable of interest Y to be explained was the individual's status at haul-back, coded "0" for dead individuals (failure) and "1" for live individuals (success). In this analysis, exhausted specimens were considered as dead to obtain more conservative results. Each event i follows a Bernoulli distribution with p_i (probability of success/at-vessel survival = π_i), and is specified as

$$Y_i \sim \mathrm{Bernoulli}\,(1, \pi_i)$$

The link function between the mean value of Y_i and the model covariates considered for this model is the logit:

$$\mathrm{logit}\,(\pi_i) = \log\left(\frac{\pi_i}{1 - \pi_i}\right) = \beta_0 + \beta_1 x_{1,i} + \beta_2 x_{2,i} + \ldots + \beta_k x_{k,i}$$

where x_k is the covariate k and β_k the respective regression coefficient estimated by maximum likelihood. All statistical analyses were performed with R (R Core Team 2019) using the "mgcv" package (Wood 2011).

The best model was selected according to the lowest corrected Akaike information criterion (AIC$_c$) after testing all combinations of variables using the "dredge" function of the "MuMIn" R package (Barton 2019). In the case of collinearity, variables were selected based on the lowest AIC$_c$ value. The pseudo-R^2 provides an indication of the variability explained by the model. Prior to selecting the best model using the AIC$_c$, covariables missing more than 30% of observations/events were excluded if they had no significant effect on the reduced data set.

This modeling approach was performed only for the blue shark and the oceanic whitetip shark due to the sufficient sample size ($n = 110$ and $n = 45$, respectively). The sample size for the other species was too limited to obtain converging models ($n < 20$).

3. Results

3.1. AVM rates

AVM was recorded for most individuals: 242 of the 250 elasmobranchs caught. The AVM rates and bootstrapped AVM rates for each species are presented in Table 1 and

Table 1. Mortality rates for the nine elasmobranch species caught.

FAO code	Scientific name	Common name	Mortality[a] (%)	Mortality[b] (%)	Sample size (*n*)	Alive (*n*)	Exhausted (*n*)	Dead (*n*)
BSH	*Prionace glauca*	Blue shark	12.7	5.5	110	96	6	8
OCS	*Carcharhinus longimanus*	Oceanic whitetip	33.3	25.7	45	30	3	12
PLS	*Pteroplatytrygon violacea*	Pelagic stingray	6.4	3.2	37	29	1	1
FAL	*Carcharhinus falciformis*	Silky shark	47.4	42.1	19	10	1	8
BTH	*Alopias superciliosus*	Bigeye thresher	40.0	40.0	10	6	0	4
PTH	*Alopias pelagicus*	Pelagic thresher	88.9	55.6	9	1	3	5
SMA	*Isurus oxyrinchus*	Short fin mako	75.0	62.5	8	2	1	5
SKH	—	Various sharks	0	0	8	8	0	0
PSK	*Pseudocarcharias kamoharai*	Crocodile shark	0	0	2	2	0	0

[a] Exhausted specimen considered dead.

[b] Exhausted specimen considered alive.

Fig. 3. Mortality rates for the nine elasmobranch species caught. BSH, blue shark; BTH, bigeye thresher shark; FAL, silky shark; OCS, oceanic whitetip shark; PLS, pelagic stingray; PSK, crocodile sharks; PTH, pelagic thresher shark; SKH, various sharks; and SMA, shortfin mako shark.

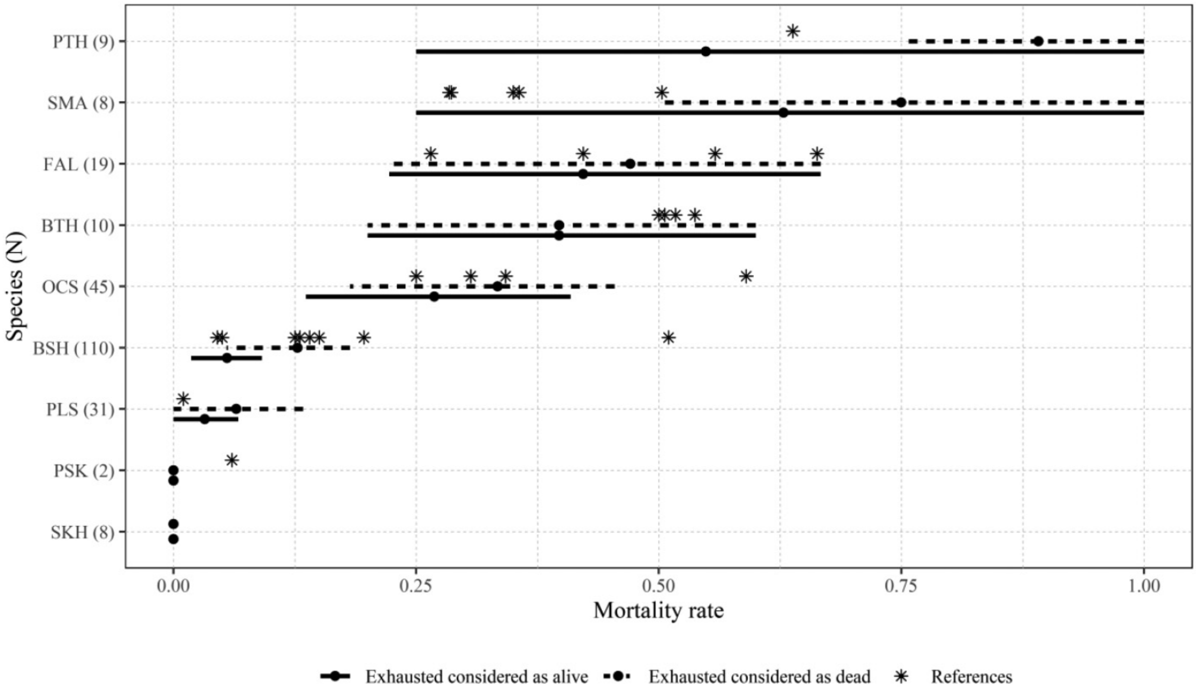
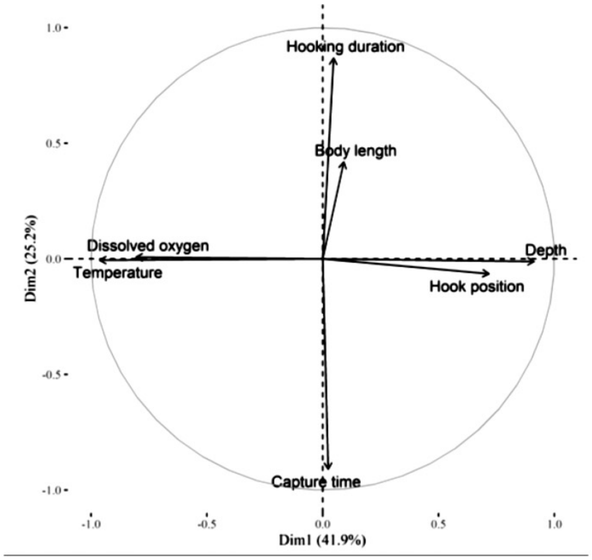


Fig. 3, respectively. When exhausted individuals were considered dead, the highest AVM rates were recorded for the pelagic thresher shark with 88.9% (95% CI: 75–100, $n = 9$) and the shortfin mako with 75% (50–100, $n = 8$). Intermediate AVM rates were observed for the silky shark, bigeye thresher shark, and oceanic whitetip with 47.4% (22.2–66.6, $n = 19$), 40% (20–60, $n = 10$), and 33.3% (18.2–45.5, $n = 45$), respectively. Lower AVM rates were found for the blue shark with 12.7% (5.5–18.2, $n = 110$) and the pelagic stingray with 6.4% (0–13.3, $n = 37$). Unidentified sharks exhibited no AVM ($n = 8$).

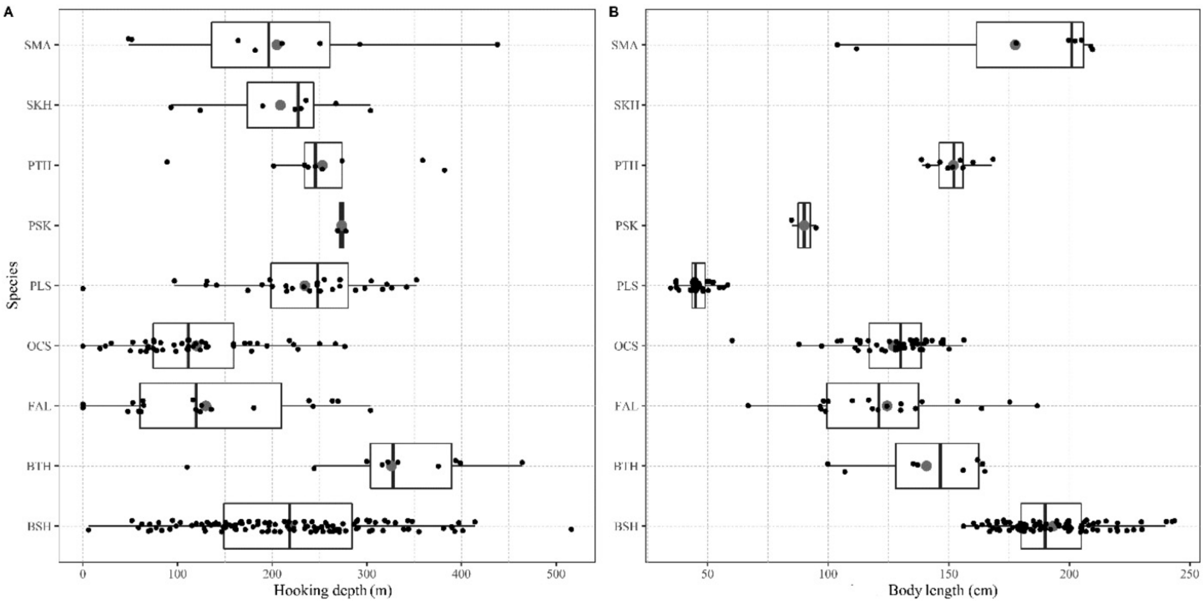
Bootstrapped CIs of AVM varied between 6.7% and 75% between species, with their amplitude somewhat inversely related to the sample size. Except for species with a small sample size ($n < 10$), 95% CIs in the more conservative case (i.e., when exhausted individuals were considered dead) were narrower compared with cases when exhausted individuals were considered alive.

Fig. 4. PCA plot and variables' contribution to the first and second axes of the PCA.



Variables	Contribution to Dim. 1	Contribution to Dim.2
Body length	0.3 %	10 %
Temperature	32 %	< 1%
Depth	28 %	< 1%
Dissolved oxygen	22 %	<1%
Hook position	18 %	0.2 %
Capture time	<1%	47 %
Hooking duration	<1 %	43 %

Fig. 5. Boxplot of hooking depth per species (A) and boxplot of body length frequency distribution per species (B). Grey dots represent the mean values. BSH, blue shark; BTH, bigeye thresher shark; FAL, silky shark; OCS, oceanic whitetip shark; PLS, pelagic stingray; PSK, crocodile sharks; PTH, pelagic thresher shark; SKH, various sharks; and SMA, shortfin mako shark.



3.2. Hooking depth and body length distribution by species

Hooking depth ranges were rather large, especially for species such as the blue shark (6–516 m) and shortfin mako shark (48–438 m); mean hooking depths were 219 and 205 m, respectively (Fig. 5A). Silky sharks and oceanic whitetip sharks were caught on average at 130 m (0–243 m) and 120 m (18–250 m), respectively. Pelagic and bigeye thresher sharks were caught deeper than the other species, at 253 m (89–359 m) and 326 m (110–464 m), respectively.

Silky sharks and oceanic whitetip sharks showed comparable body length distributions with mean sizes of 124 and 127 cm FL, respectively (Fig. 5B). Blue sharks and shortfin mako sharks exhibited different length ranges, with rather large blue shark individuals (some individuals reaching almost 250 cm FL) and some rather small shortfin mako individuals (a little more than 100 cm FL), although their mean size was close (193 and 178 cm, respectively; Fig. 5B). Overall, species length distributions displayed a uniform shape apart from shortfin mako and bigeye thresher sharks, probably due to sample sizes.

3.3. Drivers of AVM

The dispersion parameters of candidate variables for AVM modeling are summarized in Table 2. The first axis of the PCA accounted for 41.9% of the data set variance. Four co-

Table 2. Summary of candidate variables to models.

Variable	Mean	Standard deviation
Hooking temperature	19.3	6.3
Hooking depth	200.9	101.3
Hooking dissolved oxygen	2.80	1.05
Hook duration (min)	256	198
Body length (cm)	146.5	55.2

variables out of seven had a high contribution to this axis (total of 99.6%; Fig. 4). Hook position and hooking depth were strongly positively correlated, as well as hooking dissolved oxygen and hooking temperature, while these two pairs of covariables were negatively correlated (Fig. 4). On the second axis, representing 25.2% of the variance, capture time and hooking duration contributed to almost 90% of this axis and showed a strong negative correlation (Fig. 4). As hooking duration and capture time were strongly correlated, the final logistic regression model integrated only one of them (Table A2). The same process was applied for the following four variables: hooking temperature, hook position, hooking depth, and hooking dissolved oxygen (Table A1).

For the oceanic whitetip shark, the final model retained a significant effect of body length ($p = 0.02$) and a marginal effect of hooking temperature ($p = 0.07$), with this best model having a pseudo-R^2 of 0.22 (Tables 3 and A1). Both variables positively affected the survival of oceanic whitetip sharks. Larger individuals had a better chance of surviving, and the odds of survival also increased with hooking temperature, within the range of hooking temperature values tested (Fig. 6). For the blue shark, the final model retained hooking duration as the only variable affecting at-vessel survival if the significance threshold was set at 10% (pseudo-$R^2 = 0.06$; Tables 3 and A2). The longer the individual spent hooked, the lower was its chance of at-vessel survival (Fig. 7).

4. Discussion

4.1. AVM rates

In Fig. 3, we provide a comparison of our AVM estimates by species with published results (Table A3). We are aware that fishing practices, which partly condition an individual's status at haul-back, are not necessarily identical between the studies. Differences between our results and those of other studies may be due to dissimilar fishing characteristics, particularly hook depth and fishing time (day or night), which affect the target species, as well as hook type. Nonetheless, this comparison allows an estimated range of susceptibility for different species, encompassing the variability of catch conditions between fisheries.

The percentage of dead blue sharks at haul-back in our study was relatively low, which is in line with several published results in which the AVM for this species ranges from 4.5% to 19.6% (Francis et al. 2001; Walsh et al. 2009; Bromhead et al. 2012 (which also focus on this issue in the Pacific Ocean); Megalofonou 2005; Coelho et al. 2012). Those results are applicable to domestic Polynesian longline fisheries, as their fishing strategies were similar to those deployed during the ECOTAP fishing trials (use of a line shooter, 5–6 fathom branchlines (1 fathom = 1.829 m), from 20 to 30 hooks per basket, tuna or circle hooks, sardine, saury, mackerel, and squid baits, soak time of about 6 h (Gascoigne et al. 2018) and a 5 knot mean hauling speed (Moana Nui Développement, personal communication, 2022)). Additional information on CPUE values for albacore, yellowfin, and bigeye tunas for ECOTAP and the French Polynesian pelagic longline fleet targeting tuna is available in the Supplementary Material). However, our results differ from those of the study by Poisson et al. (2010), in which the AVM for the blue shark in the Indian Ocean reached 52%, a value that does not fall within the AVM CI we estimated. Similarly, Poisson et al. (2010) observed an AVM for the oceanic whitetip shark of 60%, which is substantially higher than our result (33.3%) and outside our CI. The data used in Poisson's study were collected from fishing experiments targeting swordfish around Reunion Island in the Indian Ocean. Longlines were deployed in shallower waters at night, which may increase mortality (Poisson et al. 2010). In addition, these fisheries used J-hooks, which are designed for internal hooking and are therefore more likely to injure and kill the animal (Gilman et al. 2016; Reinhardt et al. 2018). These different fishing strategy parameters may explain the difference in our results. In any case, in most studies the AVM for the oceanic whitetip shark generally exceeds 25% (Bromhead et al. 2012; Coelho et al. 2012; Gallagher et al. 2014*a*). These figures confirm the high susceptibility of the oceanic whitetip shark to pelagic longlining, as shown in ecological risk analyses performed for this fishing gear (Cortés et al. 2010; Gallagher et al. 2014*a*).

Concerning the other species investigated with preliminary results, more data on the status at haul-back with similar fishing strategies would be needed to draw meaningful conclusions. However, our results still enable species-specific ranges of AVM to be compared with previous studies. Some species such as the shortfin mako shark and the pelagic thresher shark show relatively high AVM rates (>50%), which is consistent with the findings of Bromhead et al. (2012), who used data based on similar fishing strategies (i.e., targeting tuna with deep hooks). Our AVM result on the pelagic thresher shark confirms the high susceptibility of this species to pelagic longlining shown by Bromhead et al. 2012 (1353 individuals), suggesting the need for particular attention regarding this shark and certainly dedicated measures to mitigate its capture and thereby mortality. This is also the case for the silky shark, for which the published AVM values exceed 26.5% (Bromhead et al. 2012) and may reach up to 66% (Beerkricher et al. 2002). Despite a very low number of bigeye thresher shark bycatch in our study, we determined an AVM confidence interval between 20% and 60%—the previously published values of around 50% fall within this range (Beerkircher et al. 2002; Coelho et al. 2012). In contrast, we found that the pelagic stingray has a very low AVM, which is again consistent with results from previous studies (e.g., Kerstetter and Graves 2006; Bromhead et al. 2012; Ellis et al. 2017).

Table 3. Results of the adjusted model for the oceanic whitetip shark and blue shark.

Species	Variable	Estimates	Odds ratio	Wald statistic (*p*-value)	R^2
Oceanic whitetip	Body length	0.06	1.062	0.02	0.22
	Temperature	0.17	1.185	0.07	
Blue shark	Hooking elapsed time	−0.003	0.997	0.09	0.06

Fig. 6. Effects of body length (left) and hooking temperature (right) on the survival probability of oceanic whitetip individuals. Black circles are collected data.

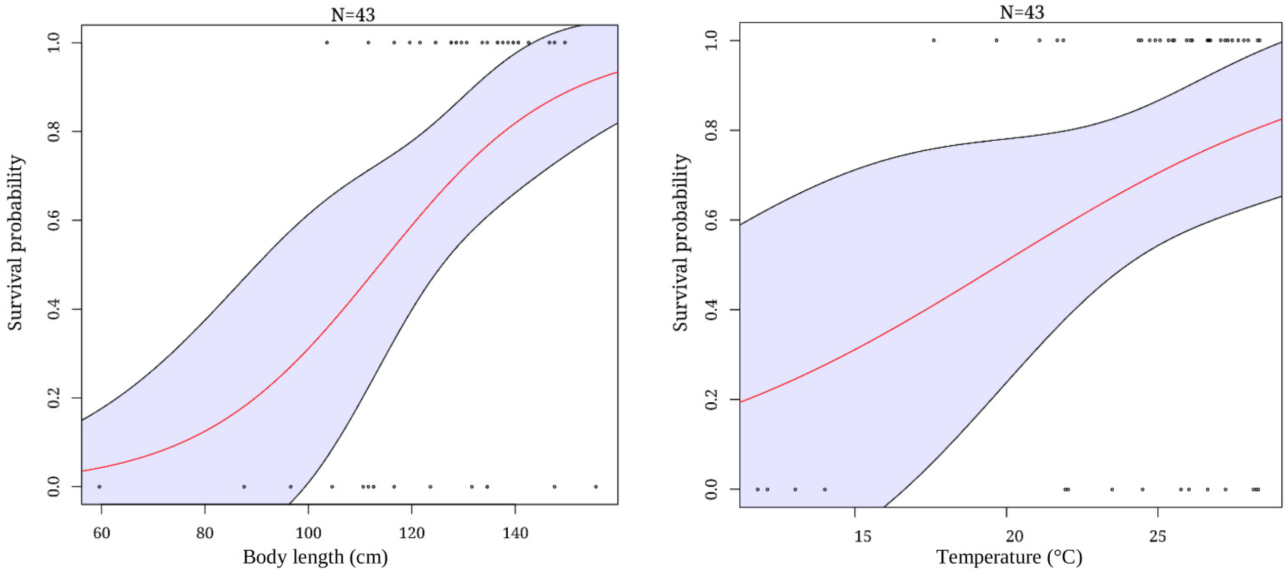
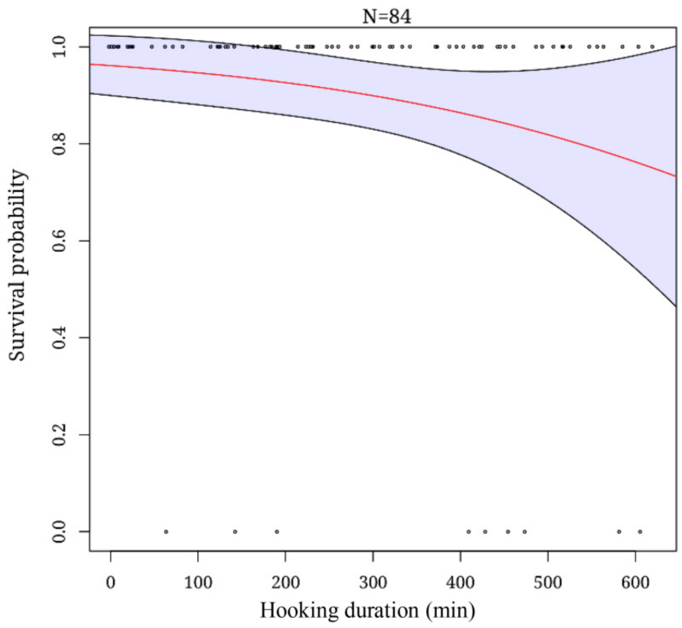


Fig. 7. Effects of hooking duration on the survival probability of blue shark individuals. Black circles are collected data.



Overall, with the qualification that the sample size was small for several species, we found that AVM rates were highly variable between the elasmobranch species caught during our experiments. This is consistent with previous studies showing no phylogenetic predisposition to survive after hooking (Skomal and Bernal 2010). In our study, for instance, even closely related shark species such as the bigeye thresher shark (*A. superciliosus*) and the pelagic thresher shark (*A. pelagicus*) responded differently to capture in terms of AVM. These results suggest the importance of considering management measures for AVM at the species level.

4.2. Drivers of at-vessel survival/mortality

We found a tendency for a positive effect of a habitat-related parameter—temperature—on the survival of oceanic whitetip sharks; our study is the first to show this, although further research is needed to confirm this effect. Gallagher et al. (2014*a*) previously showed the effect of temperature on AVM for several species, such as the blue shark and silky shark; survival was compromised as the temperature increased. Other studies have shown no significant effect of seawater temperature on blue shark survival (Diaz and Serafy 2005; Campana et al. 2009). Yet all these studies considered in situ sea surface temperature (SST) rather than the temperature at the depth of capture, with the former potentially reflecting seasonality or a geographical effect. We found that the survival of the oceanic whitetip shark declines as the hooking temperature decreases. The odds ratio was 1.185, meaning that, assuming a linear relation between water temperature at capture and survival, an individual caught at 25 °C compared with one caught at 15 °C has a $(1.185)^{(25\,^{\circ}\mathrm{C}-15\,^{\circ}\mathrm{C})} = 5.5$ times higher chance of surviving. The oceanic whitetip shark is an epipelagic shark preferentially dwelling in the mixed layer and spending 95% of the daytime within the first 100 m of tropical waters, and thus at temperatures within 2 °C of the SST (Musyl et al. 2011; Howey-Jordan et al. 2013; Tolotti et al. 2017; Andrzejaczek et al. 2018). Temperature is a key factor that controls physiological processes in ectothermic fish such as the oceanic whitetip shark (Angilletta et al. 2002; Sims 2003). Thermoregulatory behaviour suggests that fish seek an optimal thermal niche that allows them to maximize cost-efficient foraging, growth, and reproduction (Reynolds and Casterlin 1979; Meekan et al. 2015). Most shark species remain in a temperature range involving a lower energy cost (Sims 2003). As a consequence, the physiological stress induced by getting hooked at a temperature out of their comfort range significantly increases energy expenditure (Sims 2003; Haesemeyer 2020), which we suggest may damage the physiological condition of the animal and eventually lead to death. Moreover, after making deep dives to forage, ectothermic sharks return to shallower waters to warm their body after heat loss (Peter Klimley et al. 2002), expending a high level of energy to ascend due to their negative buoyancy (Weihs 1973). The oceanic whitetip shark only ventures momentarily into colder waters below the mixed layer (Howey-Jordan et al. 2013; Tolotti et al. 2017; Andrzejaczek et al. 2018) if it is "worth" it; i.e., if the prey is targeted for high-energy efficiency relative to the energy spent to catch it (Sims 2003). This may explain why oceanic whitetip sharks are more likely to die when caught in colder waters below the mixed layer, especially for smaller specimens (see below). In contrast, mesopelagic species (9.7–26.9 °C; Musyl et al. 2011) such as the blue shark, which exhibit wider comfort temperature ranges, are less likely to have temperature at capture affect survival (Musyl et al. 2011), as shown in our study. Whatever the case, in the context of global warming, it would be valuable to investigate the physiological responses of sharks to temperature stress (Pörtner and Peck 2010).

In the case of the oceanic whitetip shark, the size of individuals partly explained the AVM. An odds ratio of 1.062 meant that an individual 10 cm longer was $1.062^{10} = 1.8$ times more likely to survive. Our study is not the first to demonstrate a link between AVM and the body length of sharks; Diaz and Serafy (2005) and Campana et al. (2009) also found that bigger blue sharks were more likely to survive. Tolotti et al. (2017) also showed a positive correlation between body size and vertical movement range for oceanic whitetip sharks, explained by the higher thermal inertia of larger sharks. Our results add to these findings, indicating that hooking temperature and body size have combined effects on the consequences of the stress endured by the individual. Gallagher et al. (2014*b*) showed a significant negative relationship between the size of some shark species and the lactate concentration in the blood, the latter also being correlated with mortality for the blue shark (Moyes et al. 2006). The lactate concentration in the blood can be linked to "fighting time" on the line (Gallagher et al. 2014*b*; Jerome et al. 2018).

Our results also showed a negative effect of the time spent on the hook on blue shark survival; this was shown for the first time in our study, although this trend needs to be confirmed with additional data. Previous studies have investigated soak duration as a potential driver of the AVM of sharks caught by pelagic longlines, showing a positive relationship between this and the number of individuals dead at haulback: for the blue shark (Diaz and Serafy 2005; Campana et al. 2009; Gallagher et al. 2014*b*), the porbeagle, and the silky shark (Gallagher et al. 2014*b*). However, in contrast to our analysis, these studies considered the total set duration rather than the actual time elapsed since capture for each individual caught, and thus were biased by the fact that elapsed soak time and hooking time are not necessarily correlated. The longer an individual is hooked, the longer is the "fighting time" inducing a potentially lethal physiological response (Renshaw et al. 2012). Fighting on the line results in increased cellular oxygen demand that will exceed the rate provided by the cardiovascular system, forcing the shark's metabolism to switch from aerobic to anaerobic (Skomal 2007). Two of the products resulting from anaerobic glycolysis are lactate and protons, which accumulate in muscles and then in the blood (Skomal 2007), and can at high concentrations enhance acidosis and cause possibly irreversible cell damage (Wood 1991). Moyes et al. (2006) found that moribund blue sharks contained 4.8 times more lactate in their blood than live sharks. In shortfin mako sharks, lactate levels in moribund individuals were twice the levels of those in good condition (Marshall et al. 2012).

Other potential drivers not considered in our analysis may also affect AVM. In terms of fishing practices, the type and potentially the size of the hook were shown to impair the survival of several large pelagic species, due to hooking location variation (Afonso et al. 2011; Fernandez-Carvalho et al. 2015; Reinhardt et al. 2018) (data that were not collected in our study). It would also be interesting to consider the length of branchlines, assuming that shorter branchlines restrict the animal's freedom of movement, increasing the stress caused by capture (Gallagher et al. 2014*a*). However, ECOTAP fishing experiments used a single hook design (type and size) and a single length of branchline, preventing us from considering these factors in our analyses. Overall, it is important to consider the terminal gear as a whole, as leader type and length as well as hook type might have cofounding effects on AVM. Finally, of the biological variables that could have an impact on mortality, the sex of the animal (Coelho et al. 2012) was not considered in our study due to the paucity of data available.

4.3. Considerations for mitigation measures

Although pelagic sharks are known to be particularly vulnerable to pelagic longline fishing, numerous studies have shown that vulnerability differs between species. Pelagic shark species have different ranks of conservation status (e.g., IUCN Red List conservation status; IUCN 2020), based on their specific life history traits (e.g., productivity, age at maturity, and size), their exposure to fishing gear (e.g., vertical distribution and gear selectivity), and their postrelease mortality

(Cortés et al. 2010). In regard to pelagic longlining, the bigeye thresher shark, shortfin mako shark, and silky shark are classified as highly vulnerable species, while the oceanic whitetip shark is classified as vulnerable, and the blue shark as the least vulnerable (Gallagher et al. 2014*a*). However, it must be noted that a species' vulnerability ranking for a given fishing gear is defined by a given fishing strategy for a given target species. It is therefore challenging to adapt fishing practices considering the heterogeneous responses to stress and injury of the different shark species caught as bycatch in a given fishery. Yet it is essential to both reduce the capture risk for these species and increase their odds of survival when levels of vulnerable bycatch are deemed high (Poisson et al. 2014).

Hooking temperature appears to be a driver of oceanic whitetip shark AVM (33% in our study), particularly for individuals caught outside their preferential habitat (deeper than 120 m). To enhance the survival of oceanic whitetip sharks interacting with longlines, the deepest hooks could be removed. Although hooking duration, which was a determinant driver of AVM in our study, cannot be controlled for a given fishing practice, the longline soak duration could be reduced to mitigate both interactions and the fighting time on the line for caught individuals (Bach et al. 2012; Auger et al. 2015). In our analysis, the length of individuals was also shown to affect AVM, with small individuals more likely to die on the line. Mitigating the AVM of small sharks by modifying fishing practices (e.g., hook type and size, bait type and size) is an important avenue to explore to improve conservation.

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Author information

Author ORCIDs

Yoluène Massey https://orcid.org/0000-0001-8768-7148

Author contributions

YM: conceptualization, methodology, analysis, visualization, and writing—original draft, review, and editing. PSS: conceptualization, supervision, methodology, analysis, and writing—review and editing. PB: conceptualization, supervision, project administration, data curation, analysis, and writing—review and editing.

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Supplementary material

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References

Afonso, A.S., Hazin, F.H.V., Carvalho, F., Pacheco, J.C., Hazin, H. Kerstetter, D.W., et al. 2011. Fishing gear modifications to reduce elasmobranch mortality in pelagic and bottom longline fisheries off Northeast Brazil. Fish. Res. **108**(2): 336–343. doi:10.1016/j.fishres.2011.01.007.

Andrzejaczek, S., Gleiss, A.C., Jordan, L.K.B., Pattiaratchi, C.B., Howey, L.A., Brooks, E.J., and Meekan, M.G. 2018. Temperature and the vertical movements of oceanic whitetip sharks, *Carcharhinus longimanus*. Sci. Rep. **8**(1): 8351. doi:10.1038/s41598-018-26485-3. PMID: 29844605.

Angilletta, M.J., Niewiarowski, P.H., and Navas, C.A. 2002. The evolution of thermal physiology in ectotherms. J. Therm. Biol. **27**(4): 249–268. doi:10.1016/S0306-4565(01)00094-8.

Auger, L., Trombetta, T., Sabarros, P.S., Rabearisoa, N., Romanov, E.V., and Bach, P. 2015. Optimal fishing time window: an approach to mitigate bycatch in longline fisheries. IOTC–2015–WPEB11–15.

Bach, P., Dagorn, L., Bertrand, A., Josse, E., and Misselis, C. 2003. Acoustic telemetry versus monitored longline fishing for studying the vertical distribution of pelagic fish: bigeye tuna (*Thunnus obesus*) in French Polynesia. Fish. Res. **60**(2): 281–292. doi:10.1016/S0165-7836(02)00180-7.

Bach, P., Gaertner, D., Menkes, C., Romanov, E., and Travassos, P. 2009. Effects of the gear deployment strategy and current shear on pelagic longline shoaling. Fish. Res. **95**(1): 55–64. doi:10.1016/j.fishres.2008.07.009.

Bach, P., Lucas, V., Capello, M., and Romanov, E.V. 2012. Is the fishing time an appropriate bycatch mitigation measure in swordfish-targeting longline fisheries? *In* Symposium EBFM Tuna-2012: Towards ecosystem-based management of tuna fisheries. Mitigating impacts of fishing on pelagic ecosystems, 15–18 October 2012, Montpellier (France). Available from https://ebfmtuna-2012.sciencesconf.org/7416.html.

Barton, K. 2019. MuMIn: multi-model inference. R package version 1.43.6. Available from https://CRAN.R-project.org/package=MuMIn.

Bauer, R.K. 2020. oceanmap: a plotting toolbox for 2D oceanographic data. R package version 0.1.1. Available from https://CRAN.R-project.org/package=oceanmap.

Beerkircher, L.R., Cortés, E., and Shivji, M. 2002. Characteristics of shark bycatch observed on pelagic longlines off the Southeastern United States, 1992–2000. Mar. Fish. Rev. **64**: 40–49.

Bertrand, A., Josse, E., Bach, P., Gros, P., and Dagorn, L. 2002. Hydrological and trophic characteristics of tuna habitat: consequences on tuna distribution and longline catchability. Can. J. Fish. Aquat. Sci. **59**(6): 1002–1013. doi:10.1139/f02-073.

Beverly, S. 1998. Tuna longline fishing takes a different turn in French Polynesia. South Pacific commission fisheries newsletter. Noumea, 85: 36–40.

Bromhead, D., Clarke, S., Hoyle, S., Muller, B., Sharples, P., and Harley, S. 2012. Identification of factors influencing shark catch and mortality in the Marshall Islands tuna longline fishery and management implications. J. Fish Biol. **80**(5): 1870–1894. doi:10.1111/j.1095-8649.2012.03238.x. PMID: 22497410.

Campana, S.E., Joyce, W., and Manning, M.J. 2009. Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. Mar. Ecol.: Prog. Ser. **387**: 241–253. doi:10.3354/meps08109.

Campana, S.E., Joyce, W., Fowler, M., and Showell, M. 2016. Discards, hooking, and post-release mortality of porbeagle (*Lamna nasus*), shortfin mako (*Isurus oxyrinchus*), and blue shark (*Prionace glauca*) in the Canadian pelagic longline fishery. ICES J. Mar. Sci. **73**(2): 520–528. doi:10.1093/icesjms/fsv234.

Carlson, J.K., and Parsons, G.R. 2001. The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. Environ. Biol. Fishes, **61**: 427–433. doi:10.1023/A:1011641302048.

Coelho, R., Fernandez-Carvalho, J., Lino, P.G., and Santos, M.N. 2012. An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. Aquat. Living Resour. **25**(4): 311–319. doi:10.1051/alr/2012030.

Cortés, E., Arocha, F., Beerkircher, L., Carvalho, F., Domingo, A. Heupel, M., et al. 2010. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Aquat. Living Resour. **23**(1): 25–34. doi:10.1051/alr/2009044.

Davison, A.C., and Hinkley, D.V. 1997. Bootstrap methods and their application. Cambridge University Press, Cambridge.

Diaz, G.A., and Serafy, J.E. 2005. Longline-caught blue shark (*Prionace glauca*): factors affecting the numbers available for live release. Fish. Bull. **103**: 720.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M. Harrison, L.R., et al. 2014. Extinction risk and conservation of the world's sharks and rays. eLife, **3**: e00590. doi:10.7554/eLife.00590. PMID: 24448405

Ellis, J.R., Phillips, S.R.M., and Poisson, F. 2017. A review of capture and post-release mortality of elasmobranchs. J. Fish Biol. **90**(3): 653–722. doi:10.1111/jfb.13197. PMID: 27864942

Fernandez-Carvalho, J., Coelho, R., Santos, M.N., and Amorim, S. 2015. Effects of hook and bait in a tropical northeast Atlantic pelagic longline fishery: part II—target, bycatch and discard fishes. Fish. Res. **164**: 312–321. doi:10.1016/j.fishres.2014.11.009.

Francis, M.P., Griggs, L.H., and Baird, S.J. 2001. Pelagic shark bycatch in the New Zealand tuna longline fishery. Mar. Freshwater Res. **52**(2): 165–178. doi:10.1071/mf00086.

Gallagher, A.J., Orbesen, E.S., Hammerschlag, N., and Serafy, J.E. 2014*a*. Vulnerability of oceanic sharks as pelagic longline bycatch. Glob. Ecol. Conserv. **1**: 50–59. doi:10.1016/j.gecco.2014.06.003.

Gallagher, A.J., Serafy, J.E., Cooke, S.J., and Hammerschlag, N. 2014*b*. Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. Mar. Ecol.: Prog. Ser. **496**: 207–218. doi:10.3354/meps10490.

Gascoigne, J., Sieben, C., and Daxboeck, C. 2018. Marine Stewardship Council (MSC) final report French Polynesia albacore and yellowfin longline fishery, on behalf of the Direction des Ressources Marines et Minières prepared by ME Certification Ltd. Available from file:///C:/Users/ymassey/AppData/Local/Temp/2846R05B%20Final%20Report.pdf.

Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J. Mangel, J., et al. 2008. Shark interactions in pelagic longline fisheries. Mar. Policy, **32**(1): 1–18. doi:10.1016/j.marpol.2007.05.001.

Gilman, E., Chaloupka, M., Swimmer, Y., and Piovano, S. 2016. A cross-taxa assessment of pelagic longline by-catch mitigation measures: conflicts and mutual benefits to elasmobranchs. Fish Fish. **17**(3): 748–784. doi:10.1111/faf.12143.

Haesemeyer, M. 2020. Thermoregulation in fish. Mol. Cell. Endocrinol. **518**: 110986. doi:10.1016/j.mce.2020.110986. PMID: 32835783.

Howey-Jordan, L.A., Brooks, E.J., Abercrombie, D.L., Jordan, L.K.B., Brooks, A. Williams, S., et al. 2013. Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. PLoS ONE, **8**(2): e56588. doi:10.1371/journal.pone.0056588. PMID: 23437180.

ICCAT. 2004. Recommendation by ICCAT concerning the conservation of sharks caught in association with fisheries managed by ICCAT. Available from https://www.iccat.int/Documents/Recs/compendiopdf-e/2004-10-e.pdf [accessed 16 September 2020].

IOTC. 2017. Resolution 17/05 on the conservation of sharks caught in association with fisheries managed by IOTC. Available from https://iotc.org/cmm/resolution-1705-%E2%80%A8-conservation-sharks-caught-association-fisheries-managed-iotc [accessed 16 September 2020].

IUCN. 2020. The IUCN Red List of Threatened Species. Version 2020-2. Available from https://www.iucnredlist.org.

Jerome, J.M., Gallagher, A.J., Cooke, S.J., and Hammerschlag, N. 2018. Integrating reflexes with physiological measures to evaluate coastal shark stress response to capture. ICES J. Mar. Sci. **75**(2): 796–804. doi:10.1093/icesjms/fsx191.

Kerstetter, D.W., and Graves, J.E. 2006. Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. Fish. Res. **80**(2): 239–250. doi:10.1016/j.fishres.2006.03.032.

Marshall, H., Field, L., Afiadata, A., Sepulveda, C., Skomal, G., and Bernal, D. 2012. Hematological indicators of stress in longline-captured sharks. Comp. Biochem. Physiol. A, Mol. Integr. Physiol. **162**(2): 121–129. doi:10.1016/j.cbpa.2012.02.008. PMID: 22353217

Maunder, M.N., Hinton, M.G., Bigelow, K.A., and Langley, A.D. 2006. Developing indices of abundance using habitat data in a statistical framework. Bull. Mar. Sci. **79**(3): 15.

Meekan, M., Fuiman, L., Davis, R., Berger, Y., and Thums, M. 2015. Swimming strategy and body plan of the world's largest fish: implications for foraging efficiency and thermoregulation. Front. Mar. Sci. **2**. doi:10.3389/fmars.2015.00064.

Megalofonou, P. 2005. Incidental catch and estimated discards of pelagic sharks from the swordfish and tuna fisheries in the Mediterranean Sea. Fish. Bull. **103**: 620–634.

Moyes, C.D., Fragoso, N., Musyl, M.K., and Brill, R.W. 2006. Predicting postrelease survival in large pelagic fish. Trans. Am. Fish. Soc. **135**(5): 1389–1397. doi:10.1577/T05-224.1.

Musyl, M., Domeier, M., Nasby-Lucas, N., Brill, R., McNaughton, L. Swimmer, J., et al. 2011. Performance of pop-up satellite archival tags. Mar. Ecol. Prog. Ser. **433**: 1–28. doi:10.3354/meps09202.

Peter Klimley, A., Beavers, S.C., Curtis, T.H., and Jorgensen, S.J. 2002. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Env. Biol. Fishes, **63**(2): 117–135. doi:10.1023/A:1014200301213.

Poisson, F., Gaertner, J.-C., Taquet, M., Durbec, J.-P., and Bigelow, K. 2010. Effects of lunar cycle and fishing operations on longline-caught pelagic fish: fishing performance, capture time, and survival of fish. Fish. Bull. **108**: 268–281.

Poisson, F., Séret, B., Vernet, A.-L., Goujon, M., and Dagorn, L. 2014. Collaborative research: development of a manual on elasmobranch handling and release best practices in tropical tuna purse-seine fisheries. Mar. Policy, **44**: 312–320. doi:10.1016/j.marpol.2013.09.025.

Pörtner, H.O., and Peck, M.A. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J. Fish Biol. **77**(8): 1745–1779. doi:10.1111/j.1095-8649.2010.02783.x. PMID: 21078088.

Queiroz, N., Humphries, N.E., Couto, A., Vedor, M., da Costa, I. Sequeira, A.M.M., et al. 2019. Global spatial risk assessment of sharks under the footprint of fisheries. Nature, **572**(7770): 461–466. doi:10.1038/s41586-019-1444-4. PMID: 31340216.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from https://www.R-project.org/.

Reinhardt, J.F., Weaver, J., Latham, P.J., Dell'Apa, A., Serafy, J.E. Browder, J.A., et al. 2018. Catch rate and at-vessel mortality of circle hooks versus J-hooks in pelagic longline fisheries: a global meta-analysis. Fish Fish. **19**(3): 413–430. doi:10.1111/faf.12260.

Renshaw, G.M.C., Kutek, A.K., Grant, G.D., and Anoopkumar-Dukie, S. 2012. Forecasting elasmobranch survival following exposure to severe stressors. Comp. Biochem. Physiol. A, Mol. Integr. Physiol. **162**(2): 101–112. doi:10.1016/j.cbpa.2011.08.001. PMID: 21851860.

Reynolds, W.W., and Casterlin, M.E. 1979. Behavioral thermoregulation and the “final preferendum” paradigm. Am. Zool. **19**(1): 211–224. doi:10.1093/icb/19.1.211.

Sims, D.W. 2003. Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. J. Fish Biol. **63**(S1): 53–73. doi:10.1111/j.1095-8649.2003.00207.x.

Skomal, G.B. 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. Fish. Manag. Ecol., **14**(2): 81–89. doi:10.1111/j.1365-2400.2007.00528.x.

Skomal, G.B., and Bernal, D. 2010. Physiological responses to stress in sharks. *In* Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press. pp. 459–490.

Somerton, D.A., Kikkawa, B.S., and Wilson, C.D. 1988. Hook timers to measure the capture time of individual fish. Mar. Fish. Rev. **50**(2): 1–5.

Suzuki, Z. 1977. The comparison of catches by regular and deep tuna longline gears in the western and central equatorial Pacific. Bull. Far Seas Fish. Res. Lab. **15**: 51–89.

Tolotti, M., Bauer, R., Forget, F., Bach, P., Dagorn, L., and Travassos, P. 2017. Fine-scale vertical movements of oceanic whitetip sharks (*Carcharhinus longimanus*). Fish. Bull. **115**(3): 380–395. doi:10.7755/fb.115.3.8.

Tolotti, M.T., Filmalter, J.D., Bach, P., Travassos, P., Seret, B., and Dagorn, L. 2015. Banning is not enough: the complexities of oceanic shark management by tuna regional fisheries management organizations. Glob. Ecol. Conserv. **4**: 1–7. doi:10.1016/j.gecco.2015.05.003.

Walsh, W.A., Bigelow, K.A., and Sender, K.L. 2009. Decreases in shark catches and mortality in the Hawaii-based longline fishery as documented by fishery observers. Mar. Coast. Fish. **1**(1): 270–282. doi:10.1577/C09-003.1.

WCPFC. 2019. Conservation and management measure for sharks, December 11, 2019, Port Moresby, Papua New Guinea.Available fromhttps://www.wcpfc.int/doc/cmm-2019-04/conservation-and-management-measure-sharks.

Weihs, D. 1973. Mechanically efficient swimming techniques for fish with negative buoyancy. J. Mar. Res. **31**: 194–209.

Wood, C.M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. J. Exp. Biol. **160**(1): 285–308.10.1242/jeb.160.1.285

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. B, **73 (** 1**)**: 3–36.10.1111/j.1467-9868.2010.00749.x

Yoshihara, T. 1954. Distribution of catch of tuna longline. IV. On the relation between K and ψ_0 with a table and diagram. Nippon Suisan Gakkaishi, **19**: 1012–1014.10.2331/suisan.19.1012

Zuur, A., Ieno, E.N., and Smith, G.M. 2007. Analyzing ecological data. Springer.

Appendix A

Table A1. Model selection for the oceanic whitetip shark using AIC$_c$ (after discarding observations of individuals hooked on the surface during the setting and hauling the longline).

Individual’s length	Hooking temperature	AIC$_c$	Delta	Weight	Evidence ratio
+	+	49.8	0	0.66	1
+	NA	51.5	1.7	0.28	2.3
NA	+	55.2	5.4	0.05	14.8
NA	NA	57.7	7.9	0.01	52.3

Note: “+” indicates variables that were considered for a given model; NA indicates not applicable.

Table A2. Model selection for the blue shark using AIC$_c$.

Hooking duration	Individual’s length	Hooking depth	AIC$_c$	Delta	Weight	Evidence ratio
+	NA	NA	54.4	0	0.32	1
NA	NA	NA	55.2	0.8	0.21	1.5
+	NA	NA	55.3	0.9	0.12	2.6
+	NA	+	56.3	1.9	0.11	2.9
NA	NA	NA	56.5	2.1	0.09	3.7
+	+	NA	56.5	2.1	0.08	4.0
NA	NA	+	57.0	2.6	0.04	7.9
NA	+	NA	57.2	2.8	0.03	10.6

Note: “+” indicates variables that were considered for a given model; NA indicates not applicable.

Table A3. AVM rates of shark species caught with pelagic longline fisheries.

Shark species	AVM (%) (*N*)	Targeted species	Reference
Prionace glauca	12–13 (12 404)	Tuna/swordfish	Campana et al. 2009
	15 (19 770)	Tuna/swordfish	Campana et al. 2016
	4.5 (8 295)	Swordfish/albacore	Megalofonou 2005
	4–5.7 (159 922)	Tuna/swordfish	Walsh et al. 2009
	51 (92)	Swordfish	Poisson et al. 2010
	19.6 (3 452)	Tuna	Bromhead et al. 2012
	14 (30 168)	Swordfish	Coelho et al. 2012
	15 (17 780)	Tuna/swordfish	Gallagher et al. 2014*a*
	13 (450 000)	Tuna	Francis et al. 2001
Carcharhinus longimanus	30.6 (917)	Tuna	Bromhead et al. 2012
	34.2 (281)	Swordfish	Coelho et al. 2012
	25 (213)	Tuna/swordfish	Gallagher et al. 2014*a*
	11–28 (152)	Tuna/swordfish	Fernandez-Carvalho et al. 2015
	59 (17)	Swordfish	Poisson et al. 2010
Carcharhinus falciformis	55.8 (310)	Swordfish	Coelho et al. 2012
	66.3 (1 446)	Swordfish	Beerkircher et al. 2002
	26.5 (3 242)	Tuna	Bromhead et al. 2012
	42.2 (1 090)	Tuna/swordfish	Gallagher et al. 2014*a*
Isurus oxyrinchus	35.6 (1 414)	Swordfish	Coelho et al. 2012
	28.4 (25 000)	Tuna	Francis et al. 2001
	35 (80)	Swordfish	Beerkircher et al. 2002
	50.3 (171)	Tuna	Bromhead et al. 2012
	28.6 (2 126)	Tuna/swordfish	Gallagher et al. 2014*a*
Pteroplatytrygon violacea	1 (396)	Swordfish	Coelho et al. 2012
Alopias superciliosus	50.6 (1 061)	Swordfish	Coelho et al. 2012
	53.7 (82)	Swordfish	Beerkircher et al. 2002
	50 (1 636)	Tuna	Bromhead et al. 2012
	51.7 (367)	Tuna/swordfish	Gallagher et al. 2014*a*
Alopias pelagicus	63.8 (1 353)	Tuna	Bromhead et al. 2012
Pseudocarcharias kamoharai	6 (664)	Tuna/swordfish	Fernandez-Carvalho et al. 2015