Drivers of at-haulback mortality of sharks caught during pelagic longline fishing experiments

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ABSTRACT

Elasmobranchs (sharks and rays) are a critical part of the bycatch in tropical pelagic fisheries (longline, purse seine, gillnet). The induced mortality can be a major threat to populations especially for vulnerable or endangered pelagic elasmobranchs. Even though retention bans are enforced for some species, it is crucial to reduce the mortality before individuals are released (at-haulback mortality) in longline fisheries. So far, little is known about the drivers of this at-vessel mortality for elasmobranchs. We used data collected during longline fishing experiments (ECOTAP program) in French Polynesia (Central South Pacific Ocean) between 1993 and 1997. Multivariate logistic regression models were used to assess the influence of factors on the survival of the blue shark, oceanic whitetip shark, shortfin mako, and silky shark. Here we found that factors related to fishing techniques, biological and environmental conditions have an impact on at-vessel mortality of several shark species. Epipelagic species (oceanic whitetip and silky shark) are more likely to die when caught at depths deeper than their usual mixed surface layer habitat, and the odds of survival increase with individual's size. Mesopelagic species (blue shark and shortfin mako) survival significantly decreases with time spent being hooked. In regards to the impact of these factors on the at-haulback mortality, mitigation measures aiming to survival at release are discussed.

KEYWORDS

Epipelagic sharks | Mesopelagic sharks | Pelagic longline fishery | Instrumented longline | Hook timers | Central South Pacific Ocean | Mitigation measures

1. Introduction

Bycatch, defined as the unintentional catch of non-target species or sizes, are often considered as one of the greatest threats to marine fish populations, especially for pelagic sharks. The blue shark (*Prionace glauca*) and oceanic whitetip (*Carcharhinus longimanus*) are common bycatch shark species in pelagic longlining (Bromhead et al., 2012). The European Union has adopted a zero discards policy that generally excludes (on scientific advice) threatened species, such as shark species (Ellis et al., 2017). Banning measures such as the retention of sharks on board, finning and trading have been implemented by several Regional Fisheries Management Organizations (RFMOs) concerning different species. The oceanic whitetip shark is the only species concerned by such measures in across oceans. Although beneficial, bans are not the only solution to reduce mortality and contribute significantly to the restoration of shark populations (Tolotti et al., 2015). Further knowledge on bycatch and survival rates of species that are not subject to landing requirements is still needed.

There are three components in fishing mortality: harvest or retained catch (classically defined as fishing mortality), at-haulback mortality (AHM) and post-release mortality (PRM) (Campana et al., 2016). PRM can be consistent depending on the individual status at release related to retention conditions onboard and fishing handling, leading to physiological stress. Discarded individuals that are injured are also more likely to be predated by other predators or sea fleas (Ellis et al., 2017). Capture and release by commercial gears can cause physical damage but it has been suggested that elasmobranchs have a high capacity to heal from physical injuries (Chin et al., 2015) although further studies should be carried out (Ellis et al., 2017).

Bycatch mortality reflects both the vulnerability of the species and fishing practices. Besides, shark size also seems to affect their vulnerability to capture as bigger individuals are more likely to tolerate it thanks to a higher glycogen quantity (Jerome, 2016). Hooking depth and water temperature are significant variables affecting survival for several species that can have respectively a positive and negative effect on capture and survival rates (Diaz and Serafy, 2005). Also, the time spent by a fish on a hook seems to be an important factor impacting on mortality (Diaz and Serafy, 2005). As a result, studies using hook timers deployed on longliners have focused on mortality in relation to hooking time. Time-Depth Recorders (TDR) deployed on longlines also offer an interesting tool to measure shark's behavior while caught on the line and consequently provide information about level of physical exertion and physiological stress experienced (Guida et al., 2016; 2017).

Several studies have tackled the factors affecting mortality rates but none of them could find correlations with fishing methods. The objective of this study is to assess the factors affecting the at-haulback mortality of shark individuals. For this purpose, we used data from scientific cruises carried out on board the R/V "Alis" between 1993 and 1997 in the Central South Pacific Ocean. These cruises aimed to explore the interactions between the pelagic longline gear and the pelagic resources by deploying a monitored longline equipped with hook timers and temperature-depth recorders. The data collected made it possible to estimate whether or not the AHM mortality rate is impacted by, firstly, fishing practices like the time of fishing operations, the hook position on the basket and number of individuals captured on this basket. Indeed, these parameters can influence the tension of the mainline and therefore the animal's freedom of movement and stress conditions. Moreover, the interactions between resource abundance and longline efficiency depend on the vertical distribution of hooks, therefore the selectivity of species for this fishing gear clearly depends on hook depths (Bach et al., 2003) which is hence an important factor to consider. Two environmental factors were studied: the temperature at the depth of capture and the season. The latter could play a role in the physiological response to stress depending on the period in reproduction cycle for instance. Also, factors intrinsic to the animal's biology were studied, such as the size of the individual. Finally, thanks to the deployment of a hook timer on each branchline we were able to estimate the elapsed time since the capture. If the soaking time was already listed as an explanatory variable of the AHM, as far as we know the elapsed time from capture was never been investigated certainly due to the high cost of its collection. All these variables were here investigated for each species individually. The results found will notably enable to come up with responses on how to mitigate the AHM to enhance the effectiveness of the ban retention as a conservation measure aiming to restore the abundance of depleted shark population.

2. Material and methods

Fishing experiments

In the frame of the EOCTAP program, fishing experiments with an instrumented pelagic longline (N = 193) were conducted on IRD R.V. “Alis” in the north eastern part of the French Polynesia EEZ between 20°S and 5°S and 134°W and 155°W around the Society and Marquesas archipelagos between 1993 and 1997 (Figure 1). The fishing gear consisted of a monofilament nylon mainline of 3 mm in diameter to which branchlines were attached using snaps. The nylon monofilament branchlines of 2 mm of diameter were 11 meters long and had a hook at their free end. (Figure 2). Each branchline was equipped with a J-hook 8/0 with no-offset. Hooks were baited with squid, sardine and mackerel used alone or mixed by two.

Longlines are a set of elementary units called baskets composed of a variable number of hooks, generally between 15 and 40 and in the ECOTAP program baskets counted 25 hooks. Baskets are delimited by buoys that maintain the mainline at the surface by buoys fixed at the ends of each basket by means of a 20 meters floatline. At each end of the longline is fixed a transmitting radio buoy which allows to locate the fishing gear through the drifting phase. During setting, the line is launched using a shooter which adjustable speed allows firstly to modulate the distance between hooks on the basket, and secondly to modulate the ratio between the line length per basket between floats (LLBF) and the horizontal distance between floats (DBF), called the sagging rate (SR). In general, the fishing gear was deployed early in the morning around 6 a.m., and retrieved in early afternoon with soaking time varying between 7 and 14 hours.

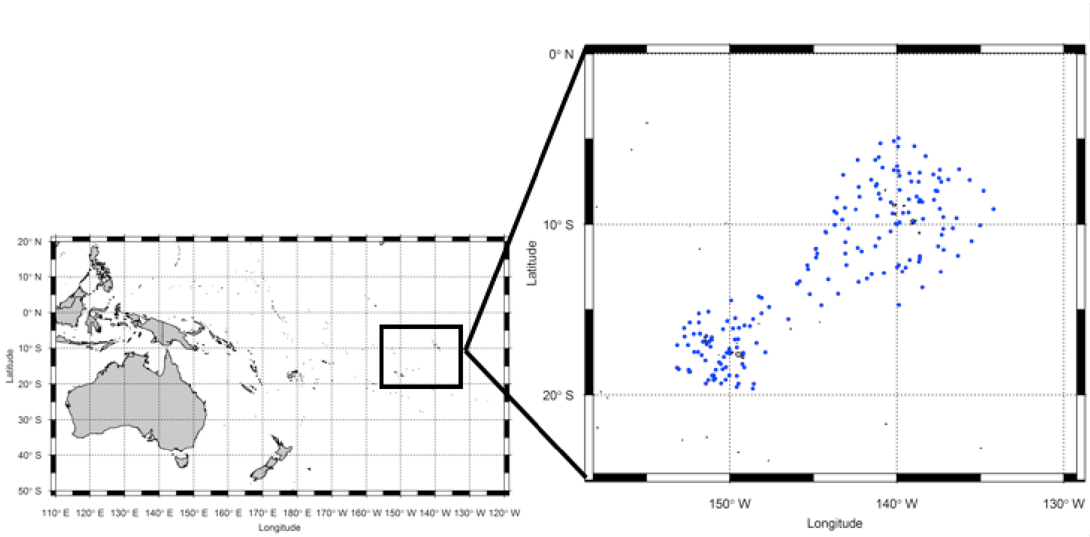

Figure 1. Geographical locations of the monitored longline fishing experiments carried out in the frame of the ECOTAP project.

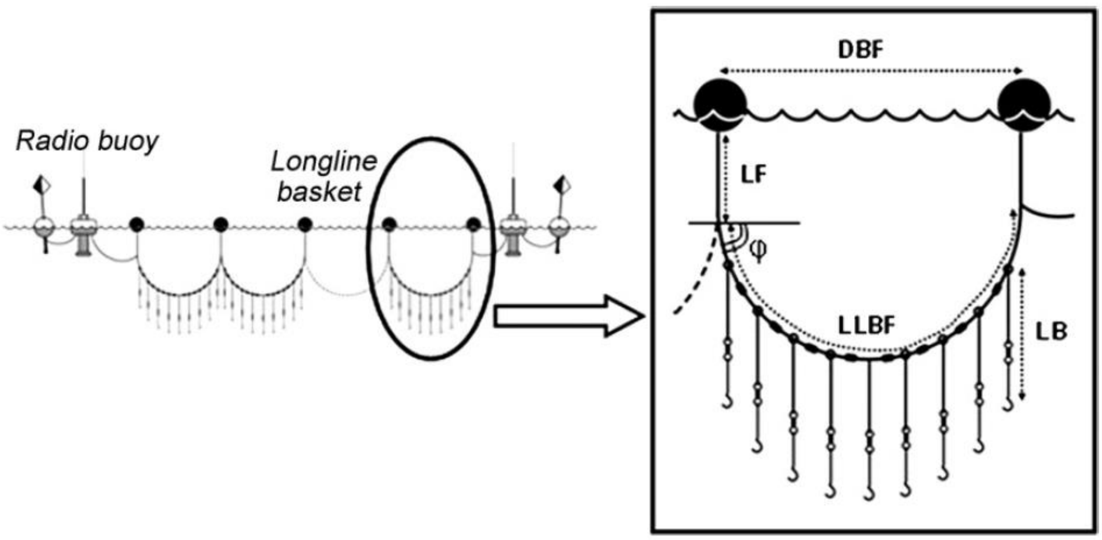

Figure 2. Schematic representation of a longline. DBF: distance between floats, LF: length of the floatline, LLBF: mainline length per basket between floats, LB: length of the branchline, 1: Hook position (from Bach et al., 2009).

Hook depth and time of hooking contacts were monitored through the deployment of two types of instrumentation fitted on the longline: time-depth recorders (TDR, model LL600 from Micrel company) and digital hook timers (Sommerton et al., 1988). TDRs were used to monitor the longline behavior (depth over time) and to determine the depth of capture events. For each set, 40 to 60% of the baskets were equipped with TDRs which were programmed to record fishing depth once per minute. Most of the time, they were placed on the main line at the mid-point of the 25 hook elements, i.e. between the 12th and 13th hooks. This arrangement allowed to obtain the temporal evolution of the longline maximum depth (for one half of each basket equipped). Hook timers (Figure 3) are triggered by individuals when they bite the bait and indicate the elapsed time between the hooking contact and the hauling of the hook (with capture or not) on the vessel's deck. Nearly 89200 hooks were deployed with more than 90% equipped with hook timers

Figure 3. Photo showing hook timers (HT) developed by Somerton et al. (1988). The HT is attached at the top of each branchline and is triggered by the attack of the bait by a predator and therefore indicates the elapsed time between the hooking contact (with success or not) and the hauling of the hook (with capture or not) on the deck.

Fishing experiments that targeted tuna contributed to collect a significant amount of data on non-target species such as elasmobranchs (sharks and rays) which are the subject of the present study. For each of the 1500+ specimen caught, scientists embarked recorded the species, size (fork length-FL for sharks and disk width-DW for rays) and weight. Of these, 250 were elasmobranchs, mainly represented by blue shark (*Prionace glauca*) and oceanic whitetip shark (*Carcharhinus longimanus*). Six other species were also caught to a lesser extent: silky shark (*Carcharhinus falciformis*), bigeye thresher shark (*Alopias superciliosus*), pelagic thresher shark (*Alopias pelagicus*), pelagic stingray (*Dasyatis violacea*), crocodile shark (*Pseudocarcharias* *kamoharai*) and shortfin mako (*Isurus oxyrinchus*). Individuals noted as belonging to the squaliforms family were not identified at the species level.

Description of the at-haulback status

The variable to be explained in this study is the mortality of sharks. The status of each specimen caught was assigned to alive, exhausted (i.e. unlikely to survive) or dead. For each species, the mortality rate was calculated by two different ways: (i) considering individuals which were "exhausted" at hauling as dead and (ii) by considering "exhausted" individuals as alive. Binary coding was used as 0 for dead individuals and 1 for individuals alive.

Candidate variables to consider in the at-haulback mortality modelling

Individual's length. The individual's length is the only variable related to the animal's biology that is considered as a potential driver of at-vessel mortality in our study. It is a continuous variable that corresponds to the FL for sharks and the DW for pelagic stingrays.

Depth at capture. The determination of depth at capture was done for each individual caught. In the best case, the individual was captured on a branchline equipped with a hook timer, the branchline itself positioned on a basket equipped with a TDR. If the capture could be identified on the TDR profile (with significant vertical movements), the depth associated with this event was extracted and noted MeanFD (the TDR being at the deepest point on the basket and assimilated to the maximum fishing depth). This value was then used to calculate the actual depth of the hook on which the individual was captured. The second most relevant case is when the hook that caught the individual was not equipped with a hook timer but its capture can be detected on the depth data series. If this event corresponded to the shark capture and not to another one on the basket, the MeanFD value was then estimated the same way as previously. In the other cases, the MeanFD value was taken as the average of the MeanFD of the surrounding elements, being equipped with a TDR, and not being too affected by capture movements. MeanFD in these cases corresponded to the mean depth during the period generally named the fishing time when the longline was settled at depths between the sinking period after setting and the rising period when hauling.

The theoretical depth of a hook j (Dj) can be estimated by using the catenary geometry by assuming a homogeneous effect of the vertical currents (Yoshihara, 1954; Suzuki et al., 1977; Bach, et al., 2006):

$$Dj = \cos(\alpha) * [LF + LB + (LLBF/2) * \{(1 + \cot^2 \varphi)1/2 - [(1 - (2j / N))^2 + \cot^2 \varphi]1/2\}]$$

with:

$\cos(\alpha) = MeanFD / MFDtheo$

MFDtheo = LF + LB + (LLBF/2) * {(1 + cot² φ)1/2 – (cot² φ)1/2}]

Empirical estimation of φ , φ = βinf*(1- exp(-K* (1-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

βinf = 108,126

K = 1,85

p = 0,57

For each set, temperature, salinity and dissolved oxygen were measured, either after setting or before hauling up, using a Seacat SBE19 multiparameter probe. Hydrological conditions at the time of capture were therefore estimated in relation to the associated catch depth.

Temperature at capture. The temperature was taken at the time of setting the longline or hauling it up using the SBE19 probe that recorded the temperature every one meter up to more than 500 m deep for each set. The capture temperature was estimated as the temperature associated with the depth of capture.

Dissolved oxygen. The dissolved oxygen concentration was recorded by the SBE19 probe every 10 meters when the longline was set or hauled-up. Dissolved oxygen during capture was associated with the depth of capture rounded to the nearest ten meters.

Hook position. The hook position corresponds to the hook number at which the specimen was caught (Figure 2), starting from 1 for the closest of the surface (on both sides of the basket). Each basket has 25 hooks and hook numbers range from 1 for the shallower hook to 13 for the deepest hook. Since depth at-capture potentially has a direct proportional effect on hook position, the variable was studied by removing the effect of depth. To do this, a generalized additive model (GAM) of the hook position as a function of depth was performed. The predictions of this GAM were subtracted from each observation in order to keep the residual variations.

Hooking elapsed time. This variable corresponds to the time elapsed from the time when the fish was hooked to the haulback time. This variable was only recorded for individuals who were captured on a branchline equipped with a hook timer or a basket equipped with a TDR from which a hooking event could be identified on the depth data series.

Time of capture. This variable corresponds to the time at which the fish was hooked. It is calculated using the haulback time and the elapsed time from hooking given by the hook timer.

Statistical analysis

With regard to the study of the factors that could explain the mortality of elasmobranchs, an exploratory analysis of the data was first conducted for each variable to identify outliers which could potentially be removed from the sample. A correlation matrix with all covariables included in the analyses was done to highlight potential collinearity between covariables (Figure 4). A PCA was also performed with the selected variables from the correlation plot in order to highlight possible links between variables but also to identify potential functional groups of species with common catch characteristics (Figure 5). The distribution of each variable was compared between species with boxplots in order to highlight differences or similarities between species, and to identify potential groups of species, for instance, grouped according to their vertical distribution in the water column (Figure 6).

The event of interest to be explained using statistical models was the specimen mortality (coded with 0), while live specimens at haulback were coded with 1. Exhausted specimens were considered as dead as their condition at capture suggested that they were unlikely to survive. Since the main objective of this study was to explore relationships between the mortality and potential explanatory variables (listed above), GAM models were performed during an exploratory phase in order to identify the nature of the potential effects of each variable on mortality, such as bell effects, threshold effects or simply linear effects (results not shown in the document).

Multivariate logistic regressions (that are generalized linear models-GLM; Zuur et al., 2007) were applied to the mortality data for each species and functional groups found in the exploratory phase, using temperature, depth, and dissolved oxygen as the environmental explanatory variables, specimen size (fork length, in cm) as the biological explanatory variable, and finally hook position, hooking elapsed time and hooking time as explanatory variables related to fishing practices. The goal was to model the individual's status at haulback as variable of interest Y, where Ytakes 0 (dead or failure) or 1 (survival or success), with several explanatory variables X. Each specimen caught follows a Bernoulli distribution with p_i (probability of success/surviving at-haulback = π_i), and can be specified as:

$Y_i \sim B(1, \pi_i)$

with the expected value and the variance defined as:

$E(Y_i) = \pi_i$

$Var(Y_i) = \pi_i \times (1 - \pi_i)$

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

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

where x_i are the model covariates and are the coefficients that were estimated by maximum likelihood. All statistical analyses were performed with R software ("R Project for Statistical Computing" version 3.5.3).

The best model was selected according to the lowest AICc (corrected Akaike Information Criterion) after testing all combinations of variables using "dredge" function from the "MuMIn" R library. The AIC criterion is based on a compromise between the quality of fit and the complexity of the model, by penalizing models with a large number of parameters. The AICc makes it possible to increase the penalty on the number of parameters (Bedrick and Tsai, 1994). However, the model was also chosen according to the association of selected variables, they should not be correlated. The significance of the explanatory variables effect is determined with Wald statistics with a significance threshold of 5%, and the pseudo R^2 gives the rate of variability explained by the whole model.

Because the number of alive individuals for blue shark was almost 10 times more than the number of dead individuals, a bootstrap method was used to accommodate the unbalanced sample (Davison and Hinkley, 1997; Manly, 2006). One bootstrap iteration consisted in resampling the same number of dead observations in alive observations and running the model described above 1000 times. Each explanatory variable was considered to be significant when the coefficient β's standard deviation did not overlap zero, which would suggest that the effect is significant.

3. Results

Data exploration

The Spearman correlation plot (Figure 4) allows to visualize which are the potential colinear variables. As expected, temperature-at-capture, depth-at-capture and dissolved oxygen-at-capture are correlated. The depth-at-capture and the hook position variables are also correlated. It therefore seems interesting to keep only one of these four variables for the statistical analyses. Moreover, the capture time and the hooking elapsed time are also correlated.

These results from the Spearman correlation analysis are corroborated by the PCA (Figure 5) which shows a clear negative correlation between capture time and hooking elapsed time on the first axis to which the two variables hooking elapsed time and capture time contribute to almost 80% of first principal component (Table 1). The variables hook position and temperature represent almost 100% of the contribution to second principal component. It is therefore important not to run a model that integrates both the hooking elapsed time and the capture time, or the temperature, hook position and depth.

The relative position of the centroid for each species on the PCA (Figure 5) showed that some species have very similar capture characteristics, firstly blue shark (BSH) and shortfin mako (SMA), and secondly oceanic whitetip (OCS) and silky shark (FAL).

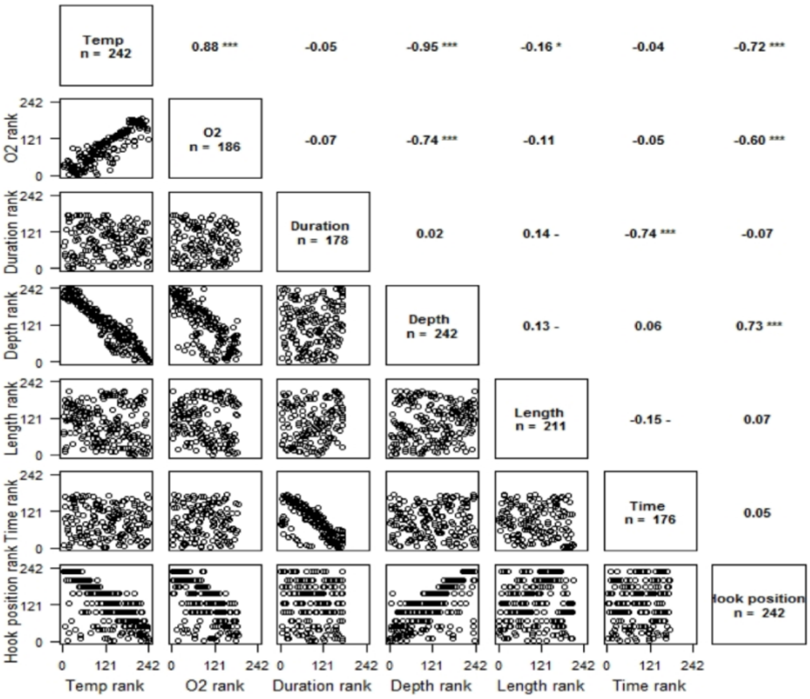

Figure 4. Spearman correlation plot including variables O2 (Dissolved oxygen), Duration (Hooking elapsed time), Depth (Depth-at-capture), Length (Individual length), Time (Capture time), Hook position.

The results from the Spearman correlation analysis are confirmed by the PCA (Figure 5) which shows a clear negative correlation between capture time and hooking elapsed time on the first axis to which two variables, hooking elapsed time and capture time, contribute to almost 80% (Table 1).

The relative position of the centroid for each species on the PCA (Figure 5) shows that some species have very similar capture characteristics, firstly, blue shark (BSH) and shortfin mako (SMA), and secondly, oceanic whitetip (OCS) and silky shark (FAL).

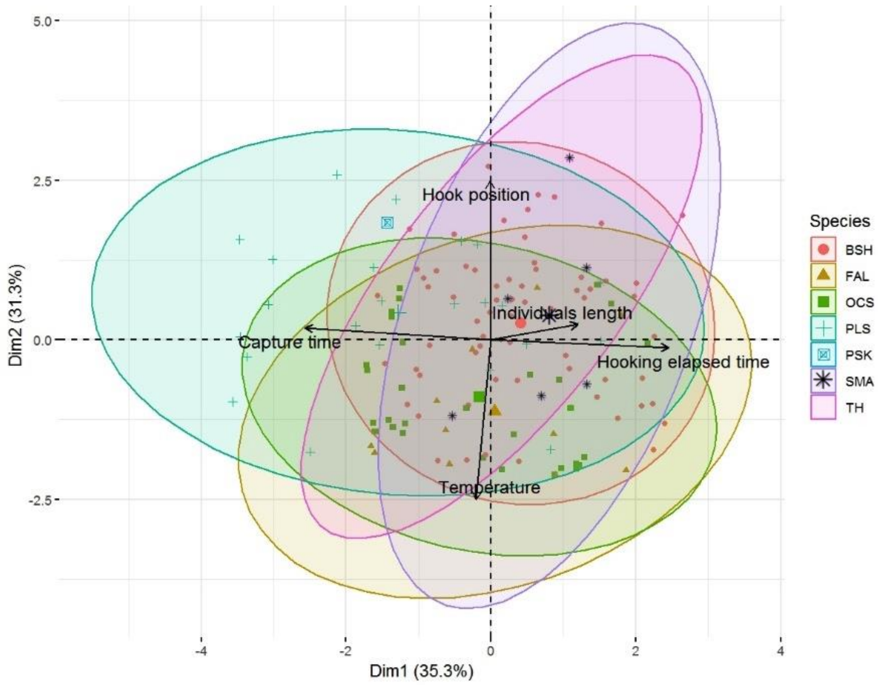

Figure 5. Principal Component Analysis (PCA) plot regarding the first and second components explaining 35.3% and 31.3% of the dataset variability, respectively.

Table 1. Variables contribution to PCA's dimensions 1 and 2

Variables	Contribution to Dim. 1 (%)	Contribution to Dim.2 (%)
Individual length	**10.5**	1
Temperature	1	**49.5**
Hook position	0.5	**48.5**
Capture time	**46**	0.5
Hooking elapsed time	**42**	0.5

The extent of the depth of catches is generally quite large especially for species like the blue shark and the shortfin mako for which mean capture depths are around 200 m (Figure 6). Silky sharks and oceanic whitetip sharks were caught on average at around 125 m. Thresher sharks (PTH and BTH) have the highest catch depth averages without counting crocodile shark that are only represented by two specimens (Figure 6).

Length frequency distributions by species are displayed on the Figure 7. Silky sharks and oceanic whitetip sharks show similar length distributions. On the contrary, blue sharks and shortfin mako sharks have different length ranges with rather large individuals in blue sharks (some individuals reaching almost 250 cm FL) and some rather small individuals (a little more than one meter) in shortfin mako, although their average values are close. Overall, depth individual's length distribution seems quite homogeneous among every species apart from the shortfin mako and the bigeye thresher shark, probably due to the small number of individuals.

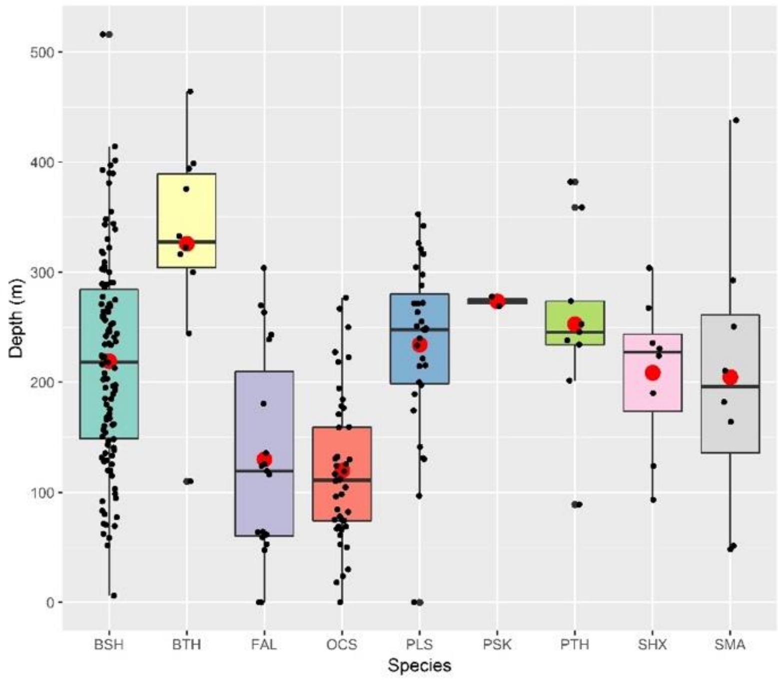

Figure 6. Boxplot of individual depth at capture. BSH: blue shark, BTH: bigeye thresher shark, FAL: silky shark, OCS: oceanic whitetip shark, PLS: pelagic stingray, PSK: crocodile sharks, PTH: pelagic thresher shark, SHX: squaliforms; SMA: shortfin mako.

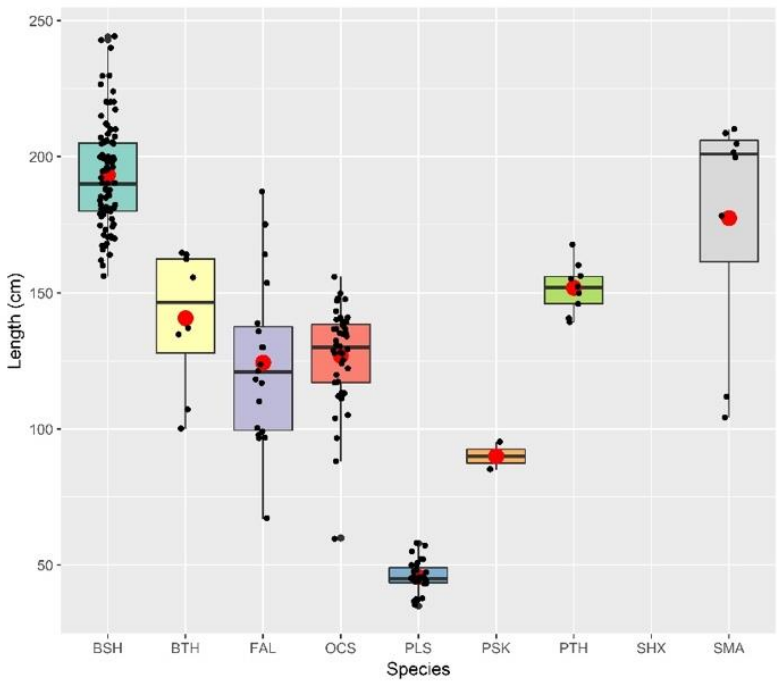

Figure 7. Boxplot of length frequency distribution per species (red dots represent the mean length). BSH: blue shark, BTH: bigeye thresher shark, FAL: silky shark, OCS: oceanic whitetip shark, PLS: pelagic stingray, PSK: crocodile sharks, PTH: pelagic thresher shark, SHX: squaliforms; SMA: shortfin mako.

Drivers of the at-haulback mortality

Epipelagic sharks (oceanic whitetip, OCS and silky shark, FAL)

Including the hooking elapsed time and capture time in the model selection lead to the loss of a third of the data, and considering that these variables did not seem to have an influence on the mortality from preliminary analyses, it was decided not to include them in the model selection. After the selection process, the best available model includes the significant effects of three variables: hook position to which depth effect has been removed, capture depth and individual length (Table 2).

Table 2. Best available models for epipelagic sharks.

Model	Variables	Estimates	Wald statistic p-value	R^2
Model a	Individuals length	0.05	0.006**	*0.26*
	Hook position (HP) without depth effect	-0.30	0.04*	
	Depth	-0.01	0.035*	
Model b	Individuals length	0.05	0.02*	*0.23*
	Hook position without depth effect (HP up to 6 removed)	-0.17	0.37	
	Depth	-0.014	0.02*	

The significant effect of the hook position to which the depth effect was removed in *Model a* can be explained by some capture occurred during the longline setting on hooks normally deep when the longline is stable which were still at the surface (hook number ranged between 7 and 13) before going down at their steady fishing depth.

These observations have been removed from the data set in the *Model b* where the hook position variable no has longer a significant effect on epipelagic shark mortality. The size of the individual has a positive influence on survival, i.e. larger is the individual higher is the odd of survival (Figure 8). On the contrary, the depth at capture has a negative influence on survival, i.e. deeper is the hooking lower will be the survival (Figure 8).

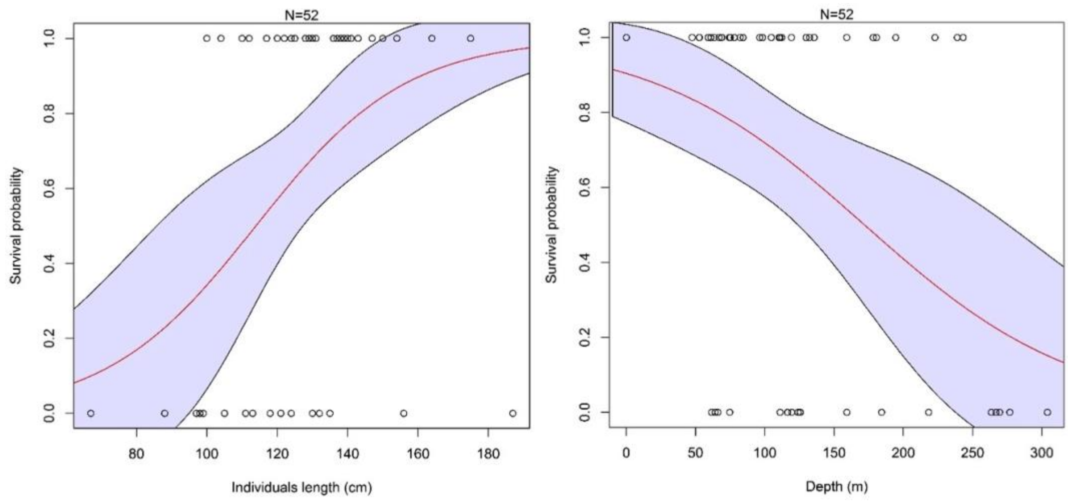

Figure 8. Effects of the individual length (left) and the depth at capture (right) on the survival probability of epipelagic sharks.

<u>Mesopelagic sharks (blue shark, BSH and shortfin mako, SMA)</u>

From the results of univariate GLM for each variable on bootstrapped data, it appears that the only variable influencing mesopelagic shark mortality is the hooking elapsed time which has a significant negative effect on mesopelagic specimen survival (Figure 9) since the 95% confidence interval of the bootstrapped regression parameter does not overlap 0.

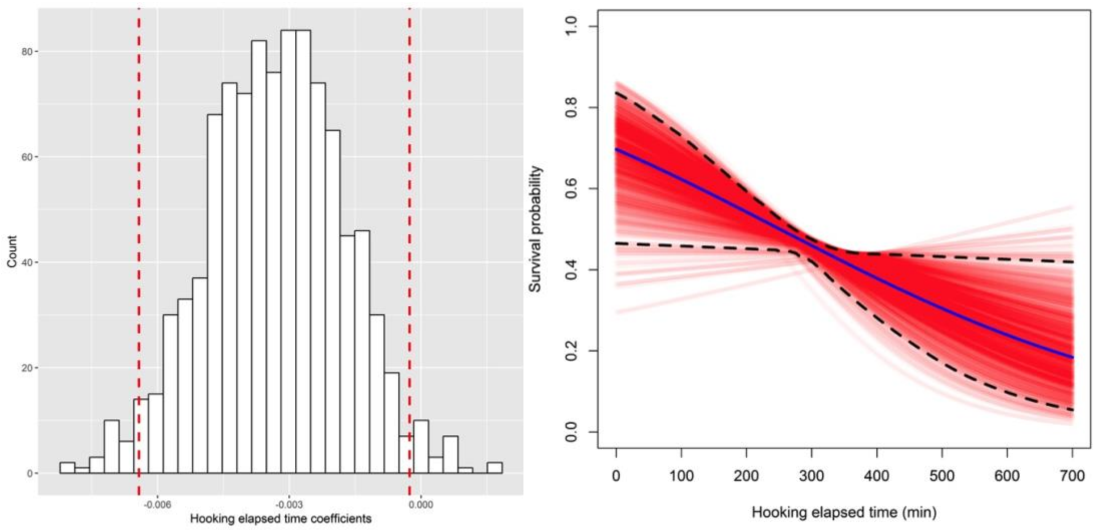

Figure 9. Distribution of hooking elapsed time coefficient values (β1), (left) and effects of the hooking elapsed time on the survival probability of mesopelagic sharks (right). Dashed-lines represent the 95% confidence interval of the bootstrap's predictions.

Survival drivers for the blue shark

The bootstrap method was also applied to the blue shark dataset only. The model retained the hooking elapsed time as unique significant variable (Figure 10) since the 95% confidence interval of the variable's estimates of the thousand models does not overlap 0. The graph of predictions on all the models with bootstrapped sample shows the effect of this variable on the survival of the species, longer is the elapsed hooking time, lower will be the survival of the individual (Figure 10).

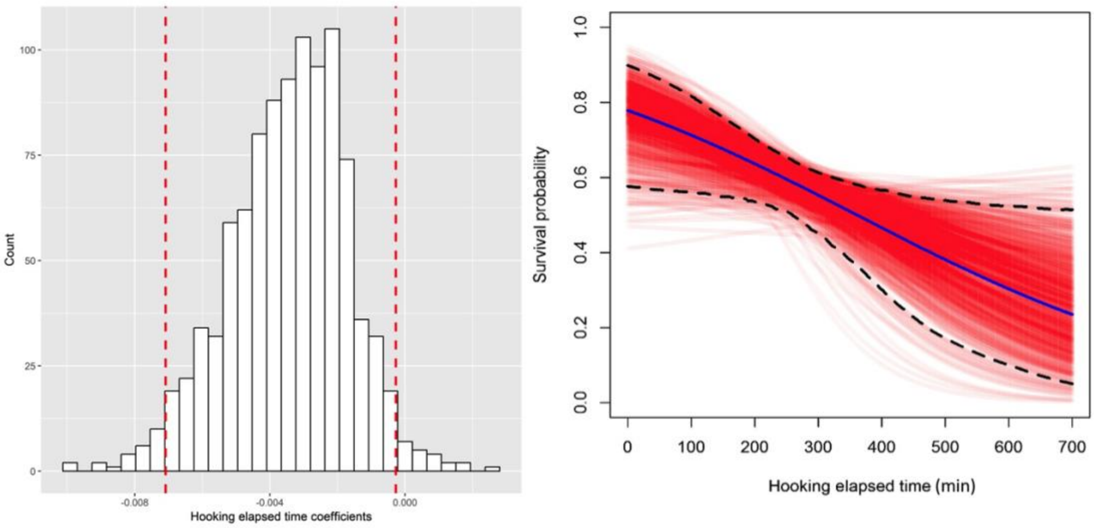

Figure 10. Distribution of hooking elapsed time coefficient values (β1), (left) and effects of the hooking elapsed time on the survival probability of blue sharks (right). Dashed-lines represent the 95% confidence interval of the bootstrap's predictions.

Survival drivers for the oceanic whitetip

The model selection was done by taking all the variables for which data were available, therefore considering only depth, temperature, individual length and hook position without depth effect.

At the end, there is only the effect of the size of the individual for which the significance is valid with a 5% threshold (Table 3). The effect the length of individuals is positive on survival (Figure 11). However, it is interesting to note that temperature has a potential positive effect on survival with a p-value of 7% (Table 3). This model explains 22% of the variability.

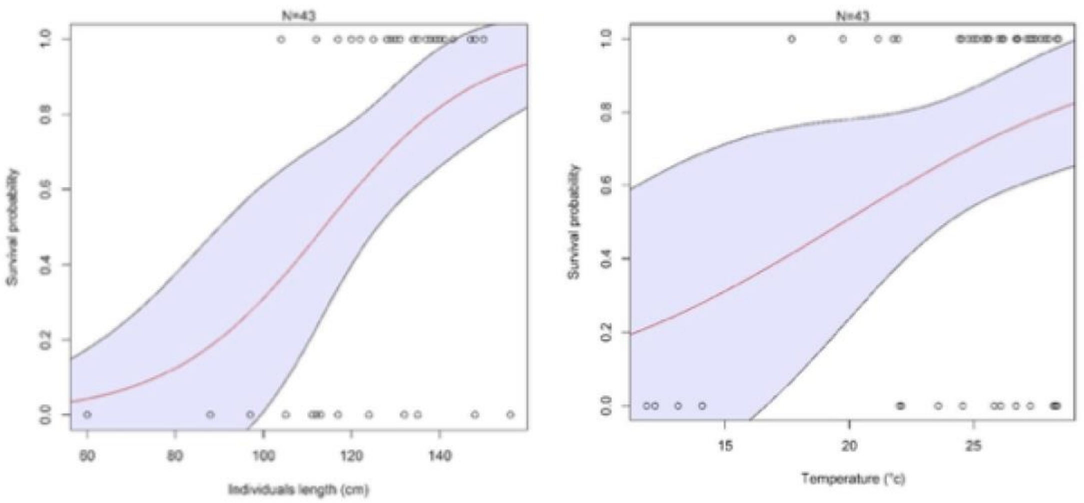

Figure 11. Effects of individual length (left) and temperature art the capture depth (right) on the survival probability of oceanic whitetip individuals.

Table 3. Results of the adjusted model for the oceanic whitetip.

Variables	Estimates	Wald statistic (p-value)	R^2
Individual length	0.06	0.02*	0.22
Temperature	0.17	0.07	

4. Discussion

The survival of epipelagic species that evolve preferentially in the first 100 m of the ocean (Howey-Jordan et al., 2013; Tolotti et al., 2017; Andrzejaczek et al., 2018) appears to be sensitive to the depth at which they are caught. Their odd of survival appears to be reduced as the depth-at-capture increases. Musyl et al. (2011) showed that both species were largely confined to the mixed layer, spending 95% of their daytime at depths below 100 m and thus at temperatures within 2°C of the sea surface temperature. Temperature is a variable that has also emerged as an explanatory factor for the at-haulback mortality of the oceanic whitetip shark, which is part of the epipelagic group. This variable is correlated with the depth and therefore the interpretation is the same for the two variables.

Temperature of the habitat is a key factor that controls physiological processes in ectothermic fish like the oceanic whitetip shark and the silky shark, whose body temperature depend on the external environment. Behavioral thermoregulation for a preferred temperature suggests that fish seek an optimal thermal niche that allows them to maximize growth and reproduction. Sharks select their habitat based on temperature and then food, even at the cost of slower growth in the short term. One reason why the sharks mainly remain in a temperature range is because it implies a lower energy cost (Sims, 2003). The oceanic whitetip shark only ventures momentarily into colder waters

(Howey-Jordan et al., 2013; Tolotti et al., 2017; Andrzejaczek et al, 2018) at higher depths 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). That is why, being held in deep waters during capture, sharks are more likely to die. More observations would be required, particularly with a wider distribution of individual's length and temperature-at-capture, to confirm this interaction between these two variables.

Another hypothesis that explains the effect of temperature on the survival of epipelagic sharks would be that at unusual depths (i.e. greater than 100 m, outside their thermal niche), the shark rushes to a prey more forcefully at depth to somehow have a high chance of catching it and is therefore potentially more likely to swallow deeply the bait with the hook and therefore suffer serious physical injury causing death (Borucinska, 2002; Davis, 2002). Concerning the mesopelagic species group, depth range being wider, it seems logical that the depth of capture would not influence the at-haulback mortality.

Our study is the first showing a potential positive effect of the temperature at capture on the survival of oceanic whitetip sharks and silky sharks. Gallagher et al. (2014a) previously showed the effect of temperature on several species such as the blue shark and the silky shark, but the effect was opposite to our findings, i.e. that as the temperature increased, survival was compromised. However, it should be noted that these environmental variables correspond to the moment of capture, i.e. when the shark has bitten. It would certainly be also interesting to consider the average depth and average temperature that the individual has experienced before hooking.

The size of individuals, in the case of epipelagic sharks, and more specifically oceanic whitetip sharks, can explain part of the at-haulback mortality. Our study is not the first to come up with a relationship between the length of individuals and at-haulback mortality. Diaz & Serafy (2005) and Campana et al. (2009) respectively showed that smaller blue sharks were more likely to die when caught by pelagic longlines. These results are in line with those of Gallagher et al. (2014) that showed a significant negative relationship between individual size and lactate concentration in blood (lactate production decreases with individual's size), the latter also being correlated with mortality. It may be related, according to Carlson et al. (2004) to the ability of larger individuals to recover more easily during capture time by increasing their tail beat amplitude while consuming less energy. It has also been shown that lactate concentration in the blood is correlated with the “fighting time” on the line (Gallagher et al., 2014).

Previous studies on drivers explaining the mortality of sharks caught with pelagic longlines have considered the “soaking time”. According to Diaz & Serafy (2005) and Campana et al. (2009), the increase in set duration also leads to an increase in the number of blue sharks being dead at haulback. Gallagher et al. (2014) also showed a positive effect of longline soaking time on the mortality of blue sharks, but also on silky and porbeagle sharks. However, these results were biased by the time that can elapse between the moment the line is deployed and moment when the individual is caught. Our study shows for the first time that the real time spent on the hook has a significantly positive influence on mesopelagic sharks (shortfin mako and blue shark) and blue shark only mortality. When the oxygen demand in the cells exceeds the rate of supply provided by the cardiovascular system (during intense exercise for example), fish can switch from aerobic to anaerobic metabolism. Two of the products resulting from anaerobic glycolysis are lactate and protons which accumulate in muscles and then in the blood, and can, in high concentrations, encourage acidosis and possible irreversible cell damage. Moyes et al. (2006) found that blue sharks caught with longlines contained 4.8 times more lactate in their blood when they were hauled up considered as moribund than when they were hauled up alive. For shortfin mako lactate levels were measured twice as high in moribund sharks compared to those in good condition (Marshall et al., 2012). These results are consistent with our study that shows an effect of hooking elapsed time on epipelagic species, i.e. the blue shark and shortfin mako. Moreover, the association of lactate accumulation and physiological stress appears to be species-specific. For example, the oceanic whitetip sharks showed very low levels of lactate after capture (Marshall et al., 2012), which could be a potential explanation for the fact that hooking elapsed time does not seem to influence the survival of this species in our study.

Whichever the group of species or the species, the different variables retained amongst the potential drivers of the at-haulback mortality of sharks explained 25% of the observed mortality. Amongst these variables, mitigation measures that might be set up concern only one of them, namely the length of individuals. Therefore, essential fish habitat research on sharks are needed to better define nursery and juveniles habitat for the shark species (Coelho et al., 2018) with the higher susceptibility to pelagic longlining. Other variables like the capture depth and the elapsed time cannot be controlled for a given fishing practice. These results allow to better highlight the importance of the application by fishermen of best practices to increase the survival of discards of individual alive at-haulback.

5. References

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