

Analysis of the at-haulback mortality of striped marlin (*Tetrapturus audax*) in the western Indian Ocean by Chinese longline fishing using a GLM

LI Xiuzhen (✉), WANG Xuefang, GUO Yingcong, WU Feng, ZHU Jiangfeng

✉ m210210752@st.shou.edu.cn

College of Marine Sciences, Shanghai Ocean University, Shanghai 201306, China

Abstract

Striped marlin (*Tetrapturus audax*) is an oceanic pelagic migratory fish. The stock status of striped marlin in the Indian Ocean is now considered to be overfished and subject to overfishing. Quantifying the level of at-haulback mortality caused by tuna longline fishing is critical to reducing fishing pressure and protecting the fate of billfish stocks. This study was based on data from 2,482 longline fishing operations carried out by Chinese observers in the western Indian Ocean from 2012 to 2019. The dataset includes information on the survival status of 774 striped marlin and their corresponding details. We used a generalized linear model (GLM) to analyze the level of at-haulback mortality and its potential influencing factors. The results indicate that the distribution of 774 striped marlin had a lower jaw-fork length range from 130 to 220 cm, and 51.5% of the samples died at the time of haul-back. The observed at-haulback mortality rates showed significant differences among quarters, hook type, bait type, longitude, and environmental variables; the GLM model revealed that quarter, sea-surface temperature (SST), hook type, lower jaw-fork length (LJFL), chlorophyll (CHL), and longitude had significant effects on at-haulback condition when the fish were retrieved on board, with the quarter and sea surface temperature having the most significant effects. The interaction term between hook type and lower jaw-fork length also had a significant effect on at-haulback mortality, with the model predictions showing that mortality increased with LJFL when using circle hooks, but decreased when using Japanese tuna hooks. There has been limited observational analysis of hooking mortality rates for striped marlin, and the present study may provide an important reference for the conservation and management of striped marlin stocks in the Indian Ocean.

Keywords: at-haulback mortality, generalized linear models, striped marlin (*Tetrapturus audax*), tuna longline fishery, western Indian Ocean

1. Introduction

The striped marlin (*Tetrapturus audax*), a species of fish belonging to the family Istiophoridae and the genus *Tetrapturus*, is widely distributed in tropical and temperate waters of the Indo-Pacific oceans (Rohner et al., 2020). This species, a large oceanic apex predator, is highly migratory (Shimose et al., 2010; Rohner et al., 2020). In the Indian Ocean, striped marlin is a commercially valuable incidental catch in tuna longline fisheries (Rohner et al., 2020). The 2021 stock assessment of striped marlin by the Indian Ocean Tuna Commission (IOTC) Working Party on Billfish (WPB) determined that the striped marlin had been overfished and was currently subject to overfishing (Parker et al., 2018; Wang et al., 2021). It is therefore important to reduce the harm caused to striped marlin populations by fishing pressure, and quantifying mortality rates is critical for understanding the fate of marlin released from commercial fisheries (Ellis et al., 2008). The relevant information obtained from this study can be utilized to develop informed conservation and management measures.

Mortality is one of the key parameters required for modeling species population dynamics, and in fisheries biology, fishing mortality includes two components: at-haulback mortality and post-release mortality (Musyl et al., 2015). Among these, at-haulback mortality refers to the percentage of deaths in the total number of catches when the fishing tackle is retrieved on board (Orbesen et al., 2019). With the development of tuna longline fisheries, various marine species such as seabirds, sea turtles, marine mammals, and elasmobranchs are harmed as bycatch (Gilman, 2011). Reducing the mortality of associated species is a high priority for management and conservation (Musyl et al., 2015), and observations focusing on levels of at-haulback mortality in tuna longline catches have been conducted globally (Watson et al., 2005; Morgan and Burgess, 2007; Campana et al., 2009; Afonso et al., 2012; Santos et al., 2012).

Many studies have focused on specific factors affecting the level of at-haulback mortality. These factors include sea surface temperature (Epperly et al., 2012; Kadagi et al., 2022), salinity (May 1990), water depth (Faccin, 1983; Childress, 1989; Hubbard and Miranda, 1991), and dissolved oxygen (Plumb et al., 1988). Additionally, researchers have explored fish biological characteristics such as lower jaw-fork length (Coelho et al., 2012; Rui et al., 2014) and gender (Morgan and Burgess, 2007). Temporal and spatial factors such as capture quarter (Kadagi et al., 2022), latitude,

and longitude (Coelho et al., 2012; Kadagi et al., 2022) are also considered in these investigations. Furthermore, operational and fishing gear characteristics such as hook type (Watson et al., 2005; Afonso et al., 2012; Coelho et al., 2012; Epperly et al., 2012) and bait type (Watson et al., 2005; Epperly et al., 2012), are also considered as potential factors. It is widely acknowledged that these factors may have varying impacts on at-haulback mortality rates for different species, necessitating specialized studies targeting specific fish species.

Compared to research on other catches in longline fisheries, research on the mortality of striped marlin is currently limited and has focused on post-release mortality analyses. For example, Domeier conducted a study on the post-release mortality of striped marlin off the Pacific coast of Mexico using pop-up satellite archival tags (Domeier et al., 2003). Similar studies have been carried out for other billfish species such as blue marlin (*Makaira nigricans*) and white marlin (*Kajikia albida*) (Horodysky and Graves, 2005; Serafy et al., 2009; Musyl et al., 2015; Schlenker et al., 2016). Therefore, it is essential to investigate the level of at-haulback mortality and analyze the associated influencing factors for billfish species, as this can provide more comprehensive information that can be used to enhance fishing techniques and implement effective resource conservation management measures (Musyl et al., 2009).

This study addresses the state of striped marlin resources in the Indian Ocean region and the lack of information on at-haulback mortality. To achieve this, the research utilized a dataset from the Chinese tuna longline observer program and acquired oceanographic environmental data. A generalized linear model (GLM) was employed to analyze the at-haulback mortality levels of striped marlin in this area. The primary objective was to assess the impacts of various factors, including environmental conditions, temporal and spatial factors, biological characteristics, and fishing gear characteristics, on at-haulback mortality rates. The study aimed to predict how the mortality rates vary under different levels of these factors. Ultimately, the research sought to provide essential support for the conservation and sustainable development of striped marlin resources in the Indian Ocean region.

2. Materials and methods

2.1 Data collection

The data used in this study were obtained from the Chinese Tuna Longline

Fisheries Observer Program, specifically the fishery dataset for the western Indian Ocean region. The study period spanned the years from 2012 to 2019, encompassing a total of 22 fishing voyages, during which 2,482 longline fishing operations were observed. The location distribution of the recorded survey sites is shown in Figure 1, and the main area is from 34°N–30°S, 40°E–83°E.

The Chinese tuna longline fleet consists of ultra-low-temperature longline vessels and ice-fresh longline vessels, and the target species are mainly bigeye tuna (*Thunnus obesus*) and albacore tuna (*Thunnus alalunga*). The main line used by the fleet consists of nylon braid or glass filament monofilament, with a length of 70,000–249,570 m. The length of the main line between the two floats is 726–1,102 m; the length of the floating line is 20–40 m; the length of the branch line is 18–52 m, and the spacing of the branch line is 30–57 m. The fleet normally uses Japanese tuna hooks, but it also includes some circle hooks and other hook types.

Observers recorded basic information such as the date, time, location (latitude and longitude), hook type, and bait type for each fishing trip and recorded individual biological information of the caught species, including lower jaw-fork length and at-haulback condition. The at-haulback condition refers to the condition of the marlin when they are retrieved on board and was classified into four levels: alive and healthy (A 1), slightly injured (A 2), seriously injured to near death (A 3), and dead (D). A total of 814 striped marlins were caught on all voyages; excluding samples with incompletely recorded information, a total of 774 striped marlin recordings were used in this study for the at-haulback mortality analysis.

2.2 Acquisition of response and explanatory variables

The at-haulback condition of striped marlin was used as the response variable for modeling, and in this study was a binary variable following a binomial distribution distinguishing only between alive (comprising A 1, A 2, and A 3) and dead. In terms of selecting potential explanatory variables, apart from considering biological characteristics, gear characteristics, and temporal-spatial information, marine environmental factors have also been suggested to influence at-haulback mortality rates for different fish species. For example, Coelho and Muñoz-Lechuga (2019)

found that at-haulback mortality of swordfish (*Xiphias gladius*) increased with sea surface temperature; Plumb et al. (1988) found that an environment with a high concentration of dissolved oxygen significantly reduced at-haulback mortality. Additionally, Sippel et al. (2007) found that chlorophyll concentration affected the foraging condition of striped marlin; May (1990) found that at-haulback mortality of striped bass (*Morone saxatilis*) increased with decreasing salinity. Therefore, this study selected sea surface temperature, sea surface salinity, chlorophyll, and dissolved oxygen as potential environmental explanatory variables for analyzing the at-haulback mortality rate. Environmental data were downloaded from the Copernicus Marine Service website (CMEMS, <https://marine.copernicus.eu/>). The names, types, and ranges of all explanatory variables selected for this study are shown in Table 1.

2.3 Establishment of a GLM

Prior to model construction, the Variance Inflation Factor (VIF) was calculated for all continuous variables to address the issue of correlations among explanatory variables. Variables with VIF values below 5 were considered to have no significant problem of multicollinearity, while those with VIF values exceeding 5 were removed to ensure model accuracy and avoid the impact of collinearity (Ghani and Ahmad, 2010). A Pearson correlation analysis was conducted to assess the associations between continuous variables. the closer the absolute value of the correlation coefficient is to 1, the stronger the correlation between the variables, while the closer the absolute value of the correlation coefficient is to 0, the weaker the correlation between the variables (Gogtay and Thatte, 2017). By integrating these two criteria, ten candidate explanatory variables were selected for the GLM modeling in this study.

The response variables followed a binomial distribution with a 0-1 response, and thus the relationship between the at-haulback condition of the striped marlin and the influencing factors was expressed using a GLM wherein the link function was a logarithmic function in the binomial distribution family. The expression formula for this model is:

$$\text{logit}(P) = \log\left(\frac{P}{1-P}\right) = \beta_0 + \beta_1\text{Quarter} + \beta_2\text{HT} + \beta_3\text{LJFL} + \beta_4\text{Lon} +$$

$$\beta_5 Lat + \beta_6 SST + \beta_7 DO + \beta_8 SSS + \beta_9 CHL + \beta_{10} BT + \varepsilon_i, \quad (1)$$

where P is the probability of a striped marlin dying after being retrieved onboard; β_0 is the intercept of the model; β_i ($i = 1, 2, 3, \dots, 10$) are coefficients estimated by the maximum likelihood method. "Quarter" represents the quarter when the striped marlin was caught; "HT" represents the type of hook when the striped marlin was caught; "LJFL" represents the lower jaw-fork length of the striped marlin; "Lon, Lat" represent the longitude and latitude, respectively, when the striped marlin was caught; "SST, SSS, DO, and CHL" represent sea surface temperature, sea surface salinity, dissolved oxygen, and chlorophyll, respectively, at the locations where the striped marlin were captured; "BT" represents the type of bait used when the striped marlin was caught, and ε_i is the error term of the model.

The names, types and ranges of all explanatory variables selected for this study are shown in Table 1. For model building, all of the explanatory variables were employed initially, and a backward stepwise regression approach based on the Akaike Information Criterion (AIC) was applied. The goal was to select the model with the lowest AIC as the initial best-fitting model for subsequent analysis (Akaike, 1998). After establishing the initial model, possible interaction terms were taken into consideration and added to the model. The same stepwise screening process described earlier was then used to determine the final model.

For model validation, the Hosmer–Lemeshow test is commonly used to assess the goodness of fit for binary logistic regression models (Hosmer et al., 2013). Additionally, the Area Under The Curve (AUC) of the Receiver Operating Characteristic Curve (ROC) is a widely used evaluation metric to measure the performance of binary classification models and is employed in K-fold cross-validation (Fushiki, 2011). The level of model fit for at-haulback mortality was estimated by K-fold cross-validation. Since a binary classification model was used in this study, cross-validation was conducted by randomly dividing the original dataset into K subsets. One subset was used as the validation dataset, while the remaining K-1 subsets were used as the training dataset to build the model (Fushiki, 2011). The cross-validation process was repeated K times until each subset was used as the

validation dataset; in this study $K=10$. Finally, the area under the ROC curve was calculated as well as the 95% confidence interval of the model. The AUC should be in the range 0.5–1.0, with higher AUC values indicating a better predictive ability of the model, and lower AUC values suggesting a poorer predictive ability (Bradley, 1997).

All statistical analyses were performed using RStudio (version 4.1.3). The package "car" was used to perform VIF screening of continuous variables; the package "GGally" was used to present the results of correlation analyses; the packages "visreg" and "ggplog2" were used to show the relationship between explanatory and response variables; the software package "cvAUC" was used for cross-validation, and site maps were drawn using the software ArcMap (10.8).

3. Results

3.1 Description of the sample

The LJFL distribution of 774 samples ranged from 130 to 220 cm (mean LJFL = 188.4 ± 18.2 cm), with the dominant group falling within the range of 190–200 cm that accounted for 40% of the total sample (Figure 2 A). For quarter, the highest number of striped marlin were captured during the second quarter, accounting for 32%, while the catches in the first and fourth quarters were both approximately 24%, and the third quarter was the least, accounting for only 20% (Figure 2 B). For hook type, the majority of striped marlin were caught using Japanese tuna hooks, comprising 49% of the total. Circle hooks were the second most common, accounting for 41%. Other hook types represented only 10% of the total (Figure 2 C).

3.2 Screening of explanatory variables

The VIF test indicated that after removing the latitude of capture and dissolved oxygen ($VIF > 5$), all other continuous variables had VIF values below 5. The Pearson analysis for continuous variables showed that the correlation coefficients between latitude and DO, latitude and SST, and DO and SST were all greater than 0.8. High correlations suggested strong linear relationships between the variables (Figure 3). Based on the results of the VIF test and Pearson correlation analysis, the latitude and DO were finally removed from the analysis. The preliminary model was constructed using variables such as LJFL, longitude, SST, SSS, and CHL.

3.3 Proportions of at-haulback mortality

Of the 774 marlin samples, 399 were dead when the fish were retrieved on board, while the remaining 375 were alive, representing an overall at-haulback mortality rate of 51.5%. Regarding the variables such as quarter, hook type, and bait type, the observed at-haulback mortality rates were significantly different between categories. The at-haulback mortality rate was notably lower during the third season and when using sardine as bait, whereas it was higher when using circle hooks, which differed significantly from the other categories (X-squared = 89.613, df = 3, $p < 2.2e-16$; X-squared = 17.053, df = 2, $p = 0.0001981$; X-squared = 79.339, df = 2, p-value $< 2.2e-16$) (Figure 4 A–C).

In this study, continuous variables such as longitude, LJFL, and environmental variables were grouped by quartiles to analyze the trends in observed mortality rates. The results revealed that the mortality rate of striped marlin caught in the region east of 60°E was significantly lower than in the region west of 60°E. Additionally, smaller striped marlin exhibited a notably higher survival rate, particularly under low-temperature conditions. Furthermore, the mortality rate showed a declining trend with increasing SSS and CHL (Figure 4 D–H).

3.4 Prediction of the probabilities of at-haulback mortality

The deviance effects of each explanatory variable on the model are shown in Table 2. Among the variables used to explain at-haulback mortality of striped marlin, Quarter and SST exhibited the most significant impacts on the model deviance, followed by hook type and LJFL. Lastly, the effects of longitude and CHL had relatively smaller effects on the at-haulback mortality of striped marlin, although they remained statistically significant variables in the model. Furthermore, the interaction between hook type and LJFL also had a significant effect, and the deviance effect value was high.

Regression diagnosis and comparison were performed on the model before and after adding the interaction term, and the final model included the interaction term. There was no overfitting or over-spreading of the two models. In terms of

goodness-of-fit, the simple model had an R^2 of 0.2037, whereas after incorporating the interaction terms, the model fit improved significantly, resulting in an R^2 of 0.2535. Furthermore, the average AUC of 100 cross-validation for the simple model was 0.712, with a 95% confidence interval of (0.663, 0.758). After adding the interaction term, the mean AUC for 100 cross-validation of the model was 0.759, with a 95% confidence interval of (0.694, 0.805). This enhancement indicates that the model has become more accurate and reliable with the inclusion of interaction terms.

For the best-fitting GLM model, the effects of explanatory variables on the at-haulback mortality rate are shown in Figure 5. Quarter (Figure 5 A) remained the most influential factor affecting the mortality rate, even after incorporating the interaction terms. There were significant differences in mortality rates among different quarters. The highest mortality rate was observed in the fourth quarter, reaching 77.8%. The first and second quarters had lesser rates, while the third quarter showed significantly lower mortality at only 51.5%. This was followed by SST (Figure 5 B), where we observed that the mortality rate increased with higher SST, ranging from 0.5% to 85.4%. In terms of hook type (Figure 5 C), the mortality rate of striped marlin caught with Japanese tuna hooks was higher (67.4%), followed by circle hooks (47.9%), and the lowest mortality rate of striped marlin was recorded when using other hook shapes (38.3%). For LJFL (Figure 5 D), mortality rates increased with sample size, ranging from 37.0% to 78.4%. Finally, the factors that had the least effect on at-haulback mortality of striped marlin were CHL (Figure 5 E) and longitude (Figure 5 F). The mortality rate increased with higher CHL, ranging from 64.4% to 95.4%. Moreover, the mortality rate was higher when the capture location was further east, with a range of 55.5–88.0%.

The interaction between hook type and LJFL was also an important explanatory variable. The effect of LJFL on the at-haulback mortality of striped marlin was affected by hook type. When using circle hooks, the mortality rate increased with LJFL (Figure 6 A), whereas the opposite trend occurred when using Japanese tuna hooks and other hooks, declining with larger LJFL (Figure 6 B–C). In addition, for the smaller striped marlin, mortality was significantly less with circle hooks, while

Japanese tuna hooks consistently exhibit higher mortality rates (Figure 6 A–B).

4. Discussion

According to the IOTC's 20th Working Party on Billfish (WPB), the average annual catch of striped marlin in the Indian Ocean from 2017 to 2021 was 2,946 tons (IOTC, 2022), and the stock is chronically highly depleted (Parker et al., 2018; Wang et al., 2021). Among the various fishing methods used for striped marlin, gillnetting and longline fishing are the most prominent, contributing to 59.5% and 27.0% of the total catch, respectively (IOTC, 2022). There is a notable lack of information and research regarding the mortality rates of striped marlin resulting from these fishing practices in the Indian Ocean region, a situation that will affect the development of conservation management measures such as control of fishing mortality and promoting the practice of live release. Therefore, conducting dedicated research and gathering relevant data are of paramount importance to ensure the conservation and protection of marlin in the region.

4.1 Comparison of at-haulback mortality for striped marlin

In this study, 51.5% of the total fish sampled died when the striped marlin were retrieved on board. Although no specific studies on the mortality rate of the same species were found, we were able to compare our results with the at-haulback mortality rates of other billfish or swordfish species. For example, Kerstetter and Graves (2006) found that mid-Atlantic longline white marlin had an at-haulback mortality rate of 34.4%, while at-haulback mortality rates were even higher near the Caribbean Sea and the Gulf of Mexico, reaching 50%. In the Venezuelan longline fishery, Jackson and Farber (1998) found an at-haulback mortality rate of 51.4% for blue marlin. In the Indian Ocean, at-haulback mortality of longline swordfish was 64% (Guo et al., 2022), which was similar to the average rate of 67.5% observed in north Atlantic longline swordfish fisheries (Epperly et al., 2012). In general, we observed that the at-haulback mortality rate of striped marlin in the western Indian Ocean was comparable to the highest rates observed in other regions for billfish species but significantly lower than that of swordfish (Table 3). This difference may be due to the fact that billfish inhabit shallower water layers than swordfish (Brill et

al., 1993; Pepperell and Davis, 1999; Horodysky et al., 2007; Dewar et al., 2011). Additionally, the result could be influenced by species-specific physiological characteristics, operating area, fishing techniques, hook types, and habitat preferences.

4.2 Factors affecting at-haulback mortality of striped marlin

In this study, quarter was the most important factor influencing the mortality of striped marlin in the western Indian Ocean. The seasonal variation in mortality may be related to the physiological characteristics of the species. According to the findings of Pillai and Ueyanagi (1978), the spawning of striped marlin occurs from November to January, based on the distribution of juveniles. During the spawning period, the broodstock are in a less favorable physiological condition, making them more vulnerable to fatal injuries caused by fishing activities (Kopf et al., 2012). As a result, the mortality rates were notably higher in the fourth and first quarters.

SST was a secondary factor. At-haulback mortality of striped marlin increased with SST (Figure 5 B), a trend that was consistent with the findings from mortality studies on swordfish conducted by Portuguese longline fleets in the Atlantic and on tuna and swordfish by U.S. longline fleets in the same region. These studies consistently demonstrate that the survival rates of swordfish and elasmobranch species tend to decrease with increasing temperature (Gallagher et al., 2014; Coelho et al., 2019). Water temperature may be directly related to the physiological limitations of fish (Muoneke and Childress, 1994). As the water temperature increases and the dissolved oxygen concentration decreases, resulting in increased respiratory demand for fish, the insufficient supply of dissolved oxygen limits metabolic activity (Bartholomew and Bohnsack, 2005; Rubalcaba et al., 2020), thereby reducing the recovery capacity of captured individuals (Guida et al., 2016). In addition, injured individuals are more susceptible to infection in warmer water (Muoneke, 1992). In conclusion, rising sea surface temperatures intensify the decline in the survival probability of the caught fish. Implementing fishing operations in times/zones with lower water temperatures can significantly mitigate the mortality rate of these magnificent fish.

The effect of hook type on at-haulback mortality was also significant, a result

that has been repeatedly confirmed in studies of many other species (Carruthers et al., 2009; Gilman et al., 2016). Specifically, the health status of sharks, swordfish, tuna, and other fish caught with circle hooks was better than their counterparts using Japanese tuna hooks, and thus circle hooks were effective in reducing at-haulback mortality. This result may be due to the fact that the tips of circle hooks curve inwards perpendicular to the shank and usually hook into the mouth or jaw of the catch (Ward et al., 2009), reducing the risk of fatal injury. In contrast, Japanese tuna hooks with tips parallel to the shank are more likely to become embedded in deeper locations (e.g., in the stomach and throat), resulting in severe bleeding (Cooke and Suski, 2004; Kerstetter and Graves, 2006) that damages internal organs and leads to a higher mortality rate. This phenomenon is supported by the present study, as the at-haulback mortality of striped marlin caught on circle hooks was significantly lower than with Japanese tuna hooks (Figure 5 C). Therefore, encouraging the use of circle hooks may be a beneficial management measure to reduce at-haulback mortality (Bowlby et al., 2021; Knotek et al., 2022). However, it is essential to acknowledge that some studies have concluded that hook type does not have a significant differential effect on at-haulback mortality (Kerstetter and Graves, 2006; Coelho et al., 2012), and the effectiveness of hook type may vary according to species.

There are species-specific differences in the factors affecting hooking mortality, including fish size (Diaz and Serafy, 2005; Morgan and Burgess, 2007; Morgan and Carlson, 2010). For example, Morgan and Carlson (2010) found that the mortality of sandbar sharks (*Carcharhinus plumbeus*) increased with LJFL, contradicting the results of Diaz and Serafy (2005) and Morgan and Burgess (2007), who found that the mortality of blue sharks (*Prionace glauca*), sandbar and blacktip sharks (*Carcharhinus plumbeus*), and blacktip sharks (*Carcharhinus plumbeus*) decreased with increasing LJFL. In our study, we observed a positive correlation between at-haulback mortality and LJFL in striped marlin from the western Indian Ocean (Figure 5 D). This may be because larger individuals require greater tension when captured by longline equipment, and excessive struggle increases blood lactate levels and is more likely to allow

the hook to penetrate the tissue completely, thereby increasing mortality (Morgan and Carlson, 2010; Gilman and Huang, 2017). At the same time, larger individuals are more prone to swallow the hook, causing significant internal injuries (Yokota et al., 2006). In addition, the captured large striped marlin were concentrated in areas with high temperatures (Figure 3). These individuals are more thermally sensitive (Pörtner et al., 2007; see the section on the effects of SST) and are thus more likely to die. Therefore, the relationship between at-haulback mortality and LJFL variation among different species may not be a universal pattern; rather, it is influenced by various interacting factors, necessitating specialized studies for specific species. The interaction between hook type and LJFL further confirmed this hypothesis, and the relationship between predicted mortality and LJFL differed across different hook types (Figure 6), similar to the differences observed in at-haulback mortality rates of swordfish in this region (Guo et al., 2022).

Finally, CHL and longitude contributed very little to the deviation explanation of at-haulback mortality in striped marlin but were still significant variables in the model. The specific mechanism by which at-haulback mortality of striped marlin increases with increasing CHL is unknown. However, according to Sippel et al. (2007), striped marlin are visual predators and prefer to hunt in sufficiently clear waters. For billfish species, including striped marlin, adequate food availability is crucial to meet their metabolic demands (Hyde et al., 2006). Therefore, waters with higher CHL are less conducive to foraging by striped marlin, a factor that may account for the relatively poor physical condition of individuals in these waters. For longitude, we found that the farther east the capture location, the higher the mortality rate. Mortality rates affected by capture location have been found in other studies, for example, blue sharks and crocodile sharks (*Pseudocarcharias kamoharai*) have higher mortality rates in the equator and south Atlantic than in the northeast Atlantic, while the trend in shortfin mako (*Isurus oxyrinchus*) was opposite (Coelho et al., 2012). In the western Indian Ocean, Guo et al. (2022) also observed that at-haulback mortality in swordfish decreased with capture locations oriented towards the east.

4.3 Research Outlook

This study conducted an analysis of the factors affecting the at-haulback mortality of striped marlin in the western Indian Ocean, using data collected from fisheries observers along with matched environmental information. However, there remain other potential factors that are thought to affect at-haulback mortality in longline catches (Broadhurst et al., 2005; Campana et al., 2009; Braccini and Waltrick, 2019). For example, previous research has indicated that the mortality of blue sharks increases with soak time, and reducing the soak time of longline gear can effectively lower the mortality of caught species (Diaz and Serafy, 2005; Campana et al., 2009). Additionally, Broadhurst et al. (2005) made a significant observation, highlighting the importance of the location where the fish is hooked in determining the mortality rate. Hooking deep into the fish (e.g., the esophagus, stomach, and gills) tended to result in high mortality rates. Similarly, Braccini and Waltrick (2019) found that hook depth significantly affected at-haulback mortality in western Australian elasmobranch species, potentially due to trauma resulting from rapid decompression in deep waters (Aló s et al., 2008). It is essential to acknowledge that these factors were not included in the current analysis due to limitations in available data. However, encouraging future research to incorporate these factors through specialized experimental designs and advanced instrumentation can provide valuable insights into their impact on at-haulback mortality.

5. Acknowledgments

We thank the Tuna Technical Group of the China Ocean Fisheries Association for providing the fishery scientific observer data of the Chinese fleet for this study. We are also deeply grateful for the collaboration of observers and tuna longline fishing vessels.

6. References

- Rohner, C. A., Bealey, R., Fulanda, B. M., & Pierce, S. J. (2020). Movement and habitat use of striped marlin *Kajikia audax* in the Western Indian Ocean. *Journal of Fish Biology*, 97(5), 1415-1427. <https://doi.org/10.1111/jfb.14508>
- Shimose, T., Yokawa, K., & Saito, H. (2010). Habitat and food partitioning of

- billfishes (*Xiphoidei*). *Journal of Fish Biology*, 76(10), 2418-2433.
<https://doi.org/10.1111/j.1095-8649.2010.02628.x>
- IOTC, 2022. Report of the 20th Session of the IOTC Working Party on Billfish. IOTC-2022-WPB20-R[E].
- Parker, D., Winker, H., da Silva, C., & Kerwath, S. (2018). Bayesian state-space surplus production model JABBA assessment of Indian Ocean striped marlin (*Tetrapturus audax*) stock. iOTC, WPB16-16, 1-21. <http://dx.doi.org/10.13140/RG.2.2.22315.90400>
- Wang, S., Xu, W., Lin, C. Stock assessment of Striped marlin (*Tetrapturus audax*) in the Indian Ocean using the Stock Synthesis. In Proceedings of the 19th Session of the IOTC Working Party on Billfish, Virtual, 13-16 September 2021. IOTC-2021- WPB19-14-Rev1.
- Ellis, J. R., Clarke, M. W., Cortés, E., Heessen, H. J., Apostolaki, P., Carlson, J. K., & Kulka, D. W. (2008). Management of elasmobranch fisheries in the North Atlantic. in *Advances in Fisheries Science. 50 years on from Beverton and Holt* (pp. 184-228). Blackwell Publishing Oxford.
- Musyl, M. K., Moyes, C. D., Brill, R. W., Mourato, B. L., West, A., McNaughton, L. M., ... & Sun, C. L. (2015). Postrelease mortality in istiophorid billfish. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(4), 538-556.
<https://doi.org/10.1139/cjfas-2014-0323>
- Orbesen, E. S., Brown, C. A., Snodgrass, D., Serafy, J. E., & Walter III, J. F. (2019). At-vessel and postrelease mortality rates of bluefin tuna (*Thunnus thynnus*) associated with pelagic longline gear in the northern Gulf of Mexico. *Fishery Bulletin*, 117(1-2), 15-23.
- Gilman, E. L. (2011). Bycatch governance and best practice mitigation technology in global tuna fisheries. *Marine Policy*, 35(5), 590-609. <https://doi.org/10.1016/j.marpol.2011.01.021>
- Morgan, A., & Burgess, G. H. (2007). At-vessel fishing mortality for six species of sharks caught in the Northwest Atlantic and Gulf of Mexico, 19(2), 123-129.
<http://hdl.handle.net/1834/29440>

- Campana, S. E., Joyce, W., & Manning, M. J. (2009). Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine Ecology Progress Series*, 387, 241-253. <https://doi.org/10.3354/meps08109>
- Afonso, A. S., Santiago, R., Hazin, H., & Hazin, F. H. (2012). Shark bycatch and mortality and hook bite-offs in pelagic longlines: interactions between hook types and leader materials. *fisheries Research*, 131, 9- 14. <https://doi.org/10.1016/j.fishres.2012.07.001>
- Watson, J. W., Epperly, S. P., Shah, A. K., & Foster, D. G. (2005). Fishing methods to reduce sea turtle mortality associated with pelagic longlines. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(5), 965-981. <https://doi.org/10.1139/f05-004>
- Santos, M. N., Coelho, R., Fernandez-Carvalho, J., & Amorim, S. (2012). Effects of hook and bait on sea turtle catches in an equatorial Atlantic pelagic longline fishery. *Bulletin of Marine Science*, 88(3), 683-701. <https://doi.org/10.5343/bms.2011.1065>
- Epperly, S. P., Watson, J. W., Foster, D. G., & Shah, A. K. (2012). Anatomical hooking location and condition of animals captured with pelagic longlines: the grand banks experiments 2002-2003. *Bulletin of Marine Science*, 88(3), 513-527. <https://doi.org/10.5343/bms.2011.1083>
- Kadagi, N. I., Wambiji, N., Mann, B., Parker, D., Daly, R., Thoya, P., ... & Sumaila, U. R. (2022). Status and challenges for sustainable billfish fisheries in the Western Indian Ocean. *Reviews in Fish Biology and Fisheries*, 32(4), 1035-1061. <https://doi.org/10.1007/s11160-022-09725-8>
- May, E. (1990). An evaluation of angler induced mortality of striped bass in Maryland. MD Dept. DNR, Federal Aid in Sport Fish Restoration, Project AFC-I, Annapolis.
- Facchin, A. (1983). Hooking mortality of fly-caught Duncan River rainbow trout (*Salmo gairdneri*) in Harper Lake, British Columbia. Province of British Columbia, Ministry of Environment.
- Hubbard, W. D., & Miranda, L. E. (1991). Mortality of white crappie after catch and

- release. In Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies, 43(1989), 49-55.
- Childress, W. M. (1989). Catch-and-release mortality of white and black crappie. Catch-and-release fishing: a decade of experience. Humbolt State University, California Cooperative Fisheries Research Unit, Arcata, California, 175-186.
- Plumb, J. A., Grizzle, J. M., & Rogers, W. A. (1988). Survival of caught and released largemouth bass after containment in live wells. *North American Journal of Fisheries Management*, 8(3), 325-328. [https://doi.org/10.1577/1548-8675\(1988\)008%3C0325:SOCARL%3E2.3.CO;2](https://doi.org/10.1577/1548-8675(1988)008%3C0325:SOCARL%3E2.3.CO;2)
- Coelho, R., Santos, M. N., & Amorim, S. (2012). Effects of hook and bait on targeted and bycatch fishes in an equatorial Atlantic pelagic longline fishery. *Bulletin of Marine Science*, 88(3), 449-467. <https://doi.org/10.5343/bms.2011.1064>
- Coelho, R., Lino, P. G., & Santos, M. N. (2011). At-haulback mortality of elasmobranchs caught on the Portuguese longline swordfish fishery in the Indian Ocean (pp. 1-9). IOTC-2011-WPEB07-31.
- Domeier, M. L., Dewar, H., & Nasby-Lucas, N. (2003). Mortality rate of striped marlin (*Tetrapturus audax*) caught with recreational tackle. *Marine and Freshwater Research*, 54(4), 435-445. <https://doi.org/10.1071/MF01270>
- Serafy, J. E., Kerstetter, D. W., & Rice, P. H. (2009). Can circle hook use benefit billfishes? *Fish and Fisheries*, 10(2), 132-142. <https://doi.org/10.1111/j.1467-2979.2008.00298.x>
- Schlenker, L. S., Latour, R. J., Brill, R. W., & Graves, J. E. (2016). Physiological stress and post-release mortality of white marlin (*Kajikia albida*) caught in the United States recreational fishery. *Conservation Physiology*, 4(1), cov066. <https://doi.org/10.1093/conphys/cov066>
- Horodysky, A. Z., & Graves, J. (2005). Application of pop-up satellite archival tag technology to estimate postrelease survival of white marlin (*Tetrapturus albidus*) caught on circle and straight-shank ("J") hooks in the western North Atlantic recreational fishery. *Fishery Bulletin*, 103(1), 84-96.
- Musyl, M. K., Moyes, C. D., Brill, R. W., & Fragoso, N. M. (2009). Factors

- influencing mortality estimates in post-release survival studies. *Marine Ecology Progress Series*, 396, 157-159. <https://doi.org/10.3354/meps08432>
- Coelho, R., & Muñoz-Lechuga, R. (2019). Hooking mortality of swordfish in pelagic longlines: comments on the efficiency of minimum retention sizes. *reviews in Fish Biology and Fisheries*, 29(2), 453-463.
- Sippel, T. J., Davie, P. S., Holdsworth, J. C., & Block, B. A. (2007). Striped marlin (*Tetrapturus audax*) movements and habitat utilisation during a summer and autumn in the Southwest Pacific Ocean. *Fisheries Oceanography*, 16(5), 459-472. <https://doi.org/10.1111/j.1365-2419.2007.00446.x>
- Ghani, I. M. M., & Ahmad, S. (2010). Stepwise multiple regression method to forecast fish landing. *Procedia-Social and Behavioral Sciences*, 8, 549-554. <https://doi.org/10.1016/j.sbspro.2010.12.076>
- Gogtay, N. J., & Thatte, U. M. (2017). Principles of correlation analysis. *Journal of the Association of Physicians of India*, 65(3), 78-81.
- Akaike, H. (1998). Information theory and an extension of the maximum likelihood principle. In *Selected papers of hirotugu akaike* (pp. 199-213). New York, NY: Springer New York.
- Hosmer Jr, D. W., Lemeshow, S., & Sturdivant, R. X. (2013). *Applied logistic regression*, 398. John Wiley & Sons.
- Fushiki, T. (2011). Estimation of prediction error by using K-fold cross-validation. *Statistics and Computing*, 21, 137-146. <https://doi.org/10.1007/s11222-009-9153-8>
- Bradley, A. P. (1997). The use of the area under the ROC curve in the evaluation of machine learning algorithms. *Pattern recognition*, 30(7), 1145-1159. [https://doi.org/10.1016/s0031-3203\(96\)00142-2](https://doi.org/10.1016/s0031-3203(96)00142-2)
- Kerstetter, D. W., & Graves, J. E. (2006). Survival of white marlin (*Tetrapturus albidus*) released from commercial pelagic longline gear in the western North Atlantic. *Fishery Bulletin*, 104(3) *Fishery Bulletin*, 104(3) , 434-444.
- Jackson, T. L., & Farber, M. I. (1998). Summary of at-sea sampling of the western Atlantic Ocean, 1987-1995, by industrial longline vessels fishing out of the port

- of Cumana, Venezuela. Venezuela. ICCAT (International Commission for the Conservation of Atlantic Tunas) Collective Volume of Scientific Papers, 47, 203-228.
- Guo, Y., Wang, X., Li, X., Wu, F., & Zhu, J. (2022). Analysis of at-haulback mortality and influencing factors of Indian ocean swordfish (*Xiphias gladius*). *Fishes*, 7(5), 256. <https://doi.org/10.3390/fishes7050256>
- Dewar, H., Prince, E. D., Musyl, M. K., Brill, R. W., Sepulveda, C., Luo, J., ... & McNaughton, L. M. (2011). Movements and behaviours of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *fisheries Oceanography*, 20(3), 219-241. <https://doi.org/10.1111/j.1365-2419.2011.00581.x>
- Pepperell, J. G., & Davis, T. L. O. (1999). Post-release behaviour of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. *Marine Biology*, 135(2), 369-380. <https://doi.org/10.1007/s002270050636>
- Brill, R. W., Holts, D. B., Chang, R. K. C., Sullivan, S., Dewar, H., & Carey, F. G. (1993). Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents. *Marine Biology*, 117, 567-574. <https://doi.org/10.1007/BF00349767>
- Horodysky, A. Z., Kerstetter, D. W., Latour, R. J., & Graves, J. E. (2007). Habitat utilisation and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: inferences from short duration pop-up archival satellite tags. *Fisheries Oceanography*, 16(3), 240-256. <https://doi.org/10.1111/j.1365-2419.2007.00419.x>
- Pillai, P. P., & Ueyanagi, S. (1978). Distribution and biology of the striped marlin, *Tetrapturus audax* (Philippi) taken by the longline fishery in the Indian Ocean. *Bulletin of Far Seas Fisheries Research Laboratory*, 16, 9-32. <http://eprints.cmfri.org.in/id/eprint/8233>
- Gallagher, A. J., Orbesen, E. S., Hammerschlag, N., & Serafy, J. E. (2014).

- Vulnerability of oceanic sharks as pelagic longline bycatch. *Global Ecology and Conservation*, 1, 50-59. <https://doi.org/10.1016/j.gecco.2014.06.003>
- Muoneke, M. I., & Childress, W. M. (1994). Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Science*, 2(2), 123-156. <https://doi.org/10.1080/10641269409388555>
- Rubalcaba, J. G., Verberk, W. C., Hendriks, A. J., Saris, B., & Woods, H. A. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences*. 117(50), 31963-31968. <https://doi.org/10.1073/pnas.2003292117>
- Bartholomew, A., & Bohnsack, J. A. (2005). A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries*, 15, 129-154. <https://doi.org/10.1007/s11160-005-2175-1>
- Guida, L., Walker, T. I., & Reina, R. D. (2016). Temperature insensitivity and behavioural reduction of the physiological stress response to longline capture by the gummy shark, *Mustelus antarcticus*. *PLoS One*, 11(2), e0148829. <https://doi.org/10.1371/journal.pone.0148829>
- Muoneke, M. I. (1992). Seasonal hooking mortality of bluegills caught on natural baits. *North American Journal of Fisheries Management*, 12(3), 645-649. [https://doi.org/10.1577/1548-8675\(1992\)012%3C0645:SHMOBC%3E2.3.CO;2](https://doi.org/10.1577/1548-8675(1992)012%3C0645:SHMOBC%3E2.3.CO;2)
- Carruthers, E. H., Schneider, D. C., & Neilson, J. D. (2009). Estimating the odds of survival and identifying mitigation opportunities for common bycatch in pelagic longline fisheries. *Biological Conservation*, 142(11), 2620-2630. <https://doi.org/10.1016/j.biocon.2009.06.010>
- Gilman, E., & Huang, H. W. (2017). Review of effects of pelagic longline hook and bait type on sea turtle catch rate, anatomical hooking position and at-vessel mortality rate. *reviews in Fish Biology and Fisheries*, 27, 43-52. <https://doi.org/10.1007/s11160-016-9447-9>
- Ward, P., Epe, S., Kreutz, D., Lawrence, E., Robins, C., & Sands, A. (2009). The effects of circle hooks on bycatch and target catches in Australia's pelagic longline fishery. *Fisheries Research*, 97(3), 253-262. <https://doi.org/10.1016/j.fishres.2009.06.003>

org/10.1016/j.fishres.2009.02.009

- Cooke, S. J., & Suski, C. D. (2004). Are circle hooks an effective tool for conserving marine and freshwater recreational catch-and-release fisheries? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 14(3), 299-326. <https://doi.org/10.1002/aqc.614>
- Kerstetter, D. W., & Graves, J. E. (2006). Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. *Fisheries Research*, 80(2-3), 239-250. <https://doi.org/10.1016/j.fishres.2006.03.032>
- Bowlby, H. D., Benoît, H. P., Joyce, W., Sulikowski, J., Coelho, R., Domingo, A., ... & Anderson, B. (2021). Beyond post-release mortality: inferences on recovery periods and natural mortality from electronic tagging data for discarded lamnid sharks. *Frontiers in Marine Science*, 8, 619190. <https://doi.org/10.3389/fmars.2021.619190>
- Knotek, R. J., Frazier, B. S., Daly-Engel, T. S., White, C. F., Barry, S. N., Cave, E. J., & Whitney, N. M. (2022). Post-release mortality, recovery, and stress physiology of blacknose sharks, *Carcharhinus acronotus*, in the Southeast US recreational shark fishery. *Fisheries Research*, 254, 106406. <https://doi.org/10.1016/j.fishres.2022.106406>
- Morgan, A., & Carlson, J. K. (2010). Capture time, size and hooking mortality of bottom longline-caught sharks. *Fisheries Research*, 101(1-2), 32-37. <https://doi.org/10.1016/j.fishres.2009.09.004>
- Diaz, G. A., & Serafy, J. E. (2005). Longline-caught blue shark (*Prionace glauca*): factors affecting the numbers available for live release, 103(4), 720-724. <http://hdl.handle.net/1834/26208>
- Yokota, K., Kiyota, M., & Minami, H. (2006). Shark catch in a pelagic longline fishery: comparison of circle and tuna hooks. *Fisheries Research*, 81(2-3), 337-341. <https://doi.org/10.1016/j.fishres.2006.08.006>
- Pörtner, H. O., & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *science*, 315(5808), 95-97. <https://doi.org/10.1126/science.1135471>

Hyde, J. R., Humphreys, R., Musyl, M., Lynn, E., & Vetter, R. (2006). A central North Pacific spawning ground for striped marlin, *Tetrapturus audax*. *Bulletin of Marine Science*, 79(3), 683-690.

Kopf, R. K., Davie, P. S., Bromhead, D. B., & Young, J. W. (2012). Reproductive biology and spatiotemporal patterns of spawning in striped marlin *Kajikia audax*. *Journal of Fish Biology*, 81(6), 1834-1858.
<https://doi.org/10.1111/j.1095-8649.2012.03394.x>

Table 1 Scope of each continuous explanatory variable and the classification of each categorical explanatory variable evaluated for importance in at-haulback mortality of striped marlin.

Explanatory Variable	Name	Type	Scope/Classification
Biological Characteristics	Lower Jaw-Fork Length	Continuous	130 cm – 220 cm
	Sea Surface Temperature	Continuous	15.90°C – 30.70°C
Environmental Factors	Sea Surface Salinity	Continuous	34.34‰ – 36.28‰
	Chlorophyll Dissolved Oxygen	Continuous	0.06 mg·m ⁻³ – 0.84 mg·m ⁻³ 196.06 mmol·m ⁻³ – 251.74 mmol·m ⁻³
Temporal-Spatial Elements	Quarter	Categorical	First (Jan, Feb, Mar)/Second (Apr, May, Jun)/Third (Jul, Aug, Sept)/Forth (Oct, Nov, Dec)
	Longitude	Continuous	40°E – 83°E
	Latitude	Continuous	34°N – 30°S
Fishing Gear Characteristics	Hook type	Categorical	Japanese Tuna Hook/Cirle Hook/Others
	Bait type	Categorical	Mackerel/Sardine/Others

Table 2 Analysis of deviance in the GLM model for at-haulback mortality of striped marlin after adding the interaction term.

	Df	Deviance	Resid.	Resid.	Pr(> z)
NULL			773	1072.25	
Quarter	3	94.727	770	977.52	<0.05
SST	1	66.852	769	910.67	<0.05
Hook type	2	12.848	767	897.82	<0.05
LJFL	1	9.763	766	888.06	<0.05
CHL	1	7.259	765	880.80	<0.05
Lon	1	4.827	764	875.97	<0.05
Hooktype : LJFL	2	56.598	762	819.37	<0.05

Note: "Df" is the degrees of freedom. "Deviance" is the interpretation deviation. "Resid.Df" is the residual degrees of freedom. "Resid.Dev" is the residual deviance. The definitions of the abbreviations are listed in the notes for equation 1.

Table 3 Comparison of at-haulback mortality for billfish and swordfish in longline fisheries in various oceans.

Reference	Oceans	Species	At-haulback mortality
Kerstetter and Graves (2006)	Mid-Atlantic	White marlin/ <i>Kajikia albida</i>	34.4%
Kerstetter and Graves (2006)	Caribbean Sea and Gulf of Mexico	White marlin/ <i>Kajikia albida</i>	50%
Jackson and Farber (1998)	Atlantic	Blue marlin/ <i>Makaira nigricans</i>	51.4%
Guo et al., 2022	Indian Ocean	Swordfish/ <i>Xiphias gladius</i>	64%
Epperly et al., 2012	North Atlantic	Swordfish/ <i>Xiphias gladius</i>	67.5%

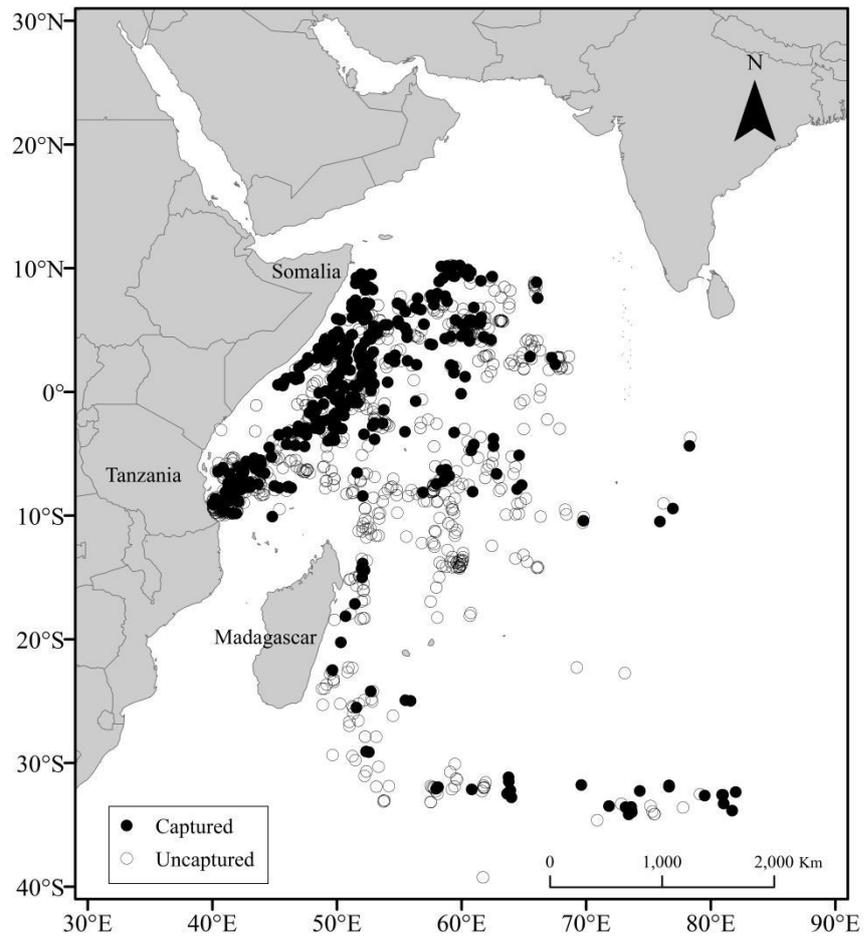


Figure 1. Distribution of tuna longline survey sites recorded by fisheries observers, 2012-2019.

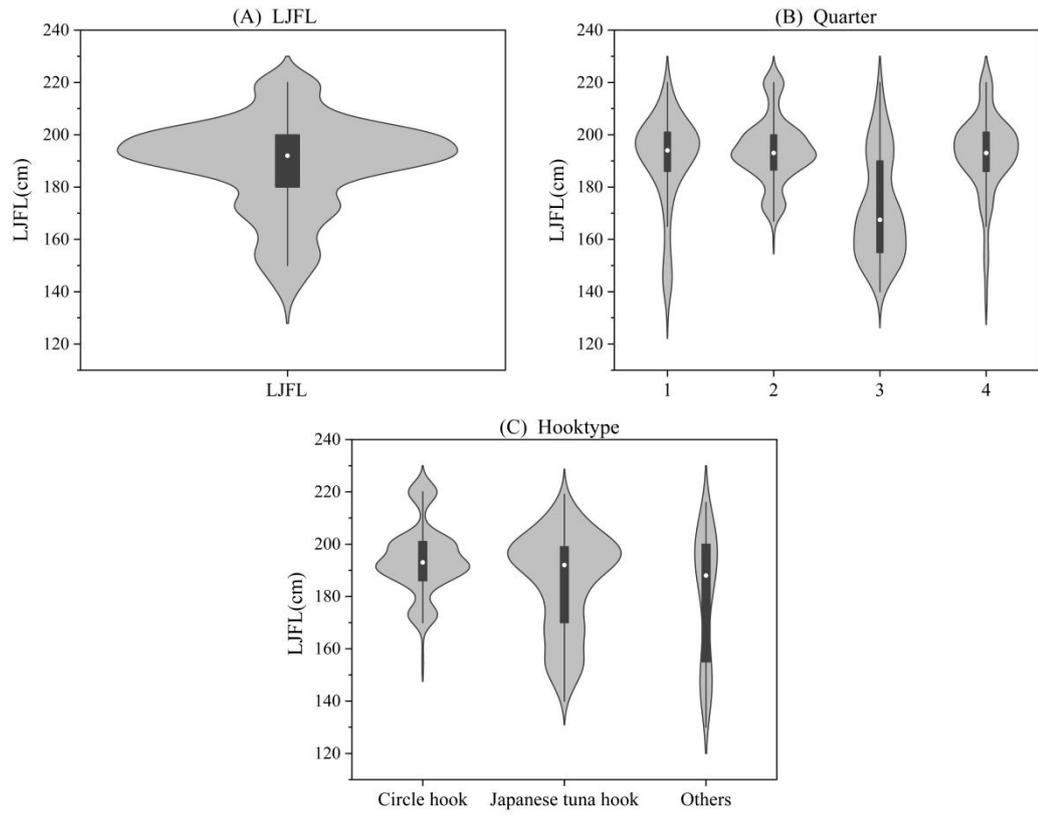


Figure 2. Distribution of lower jaw-fork length of striped marlin in the western Indian Ocean from 2012 to 2019. The definitions of the abbreviations are listed in the notes for equation 1.

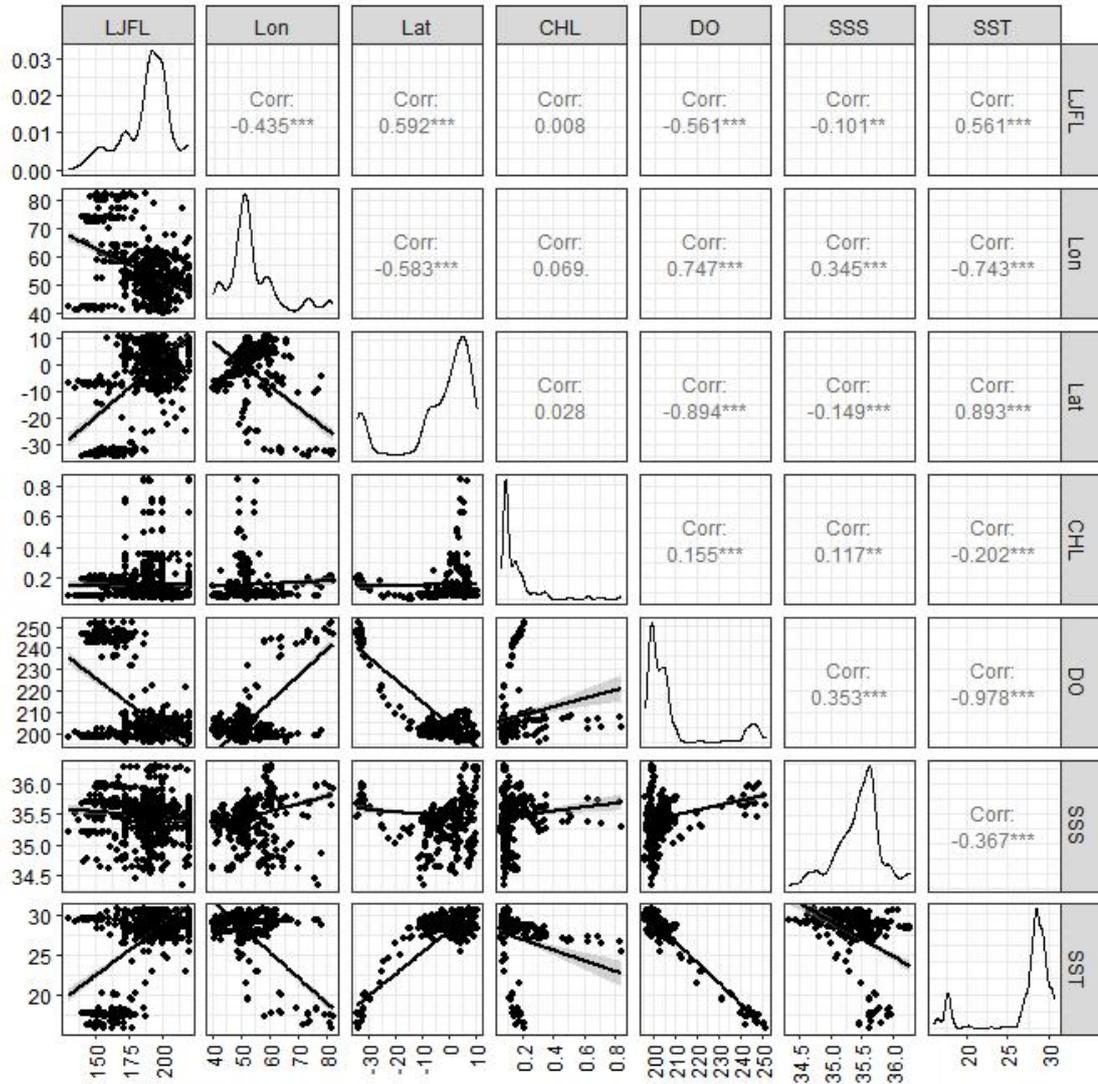


Figure 3. Visualization of Pearson's correlation analysis for continuous explanatory variables. The definitions of the abbreviations are listed in the notes for equation 1.

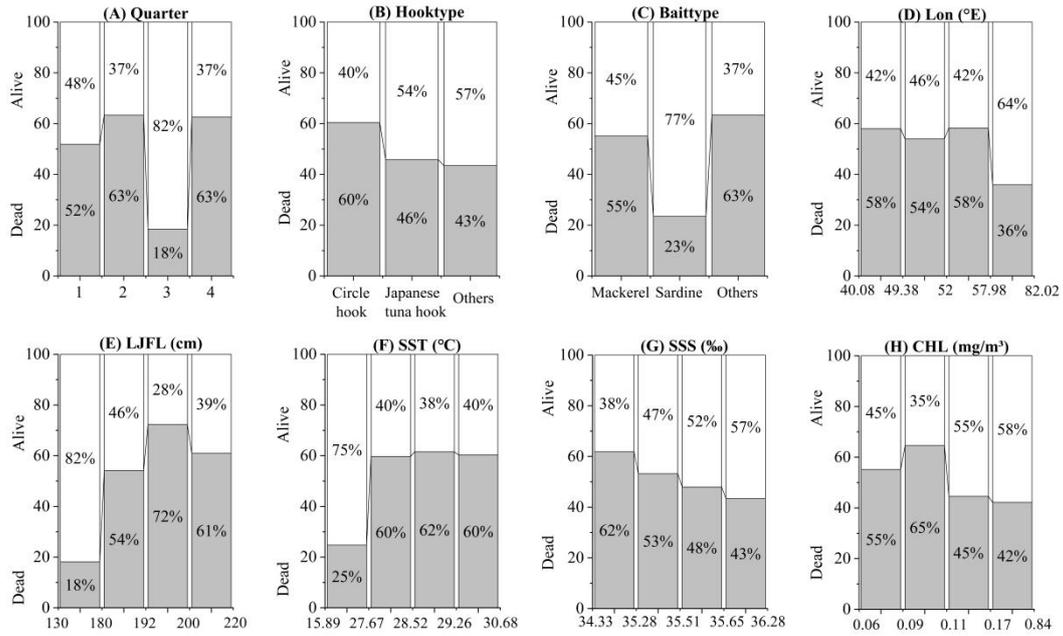


Figure 4. Proportions of striped marlin at-haulback conditions (dead vs. alive) with the various categorical and continuous explanatory variables considered in this study. The continuous variables are categorized by quartiles. The definitions of the abbreviations are listed in the notes for equation 1.

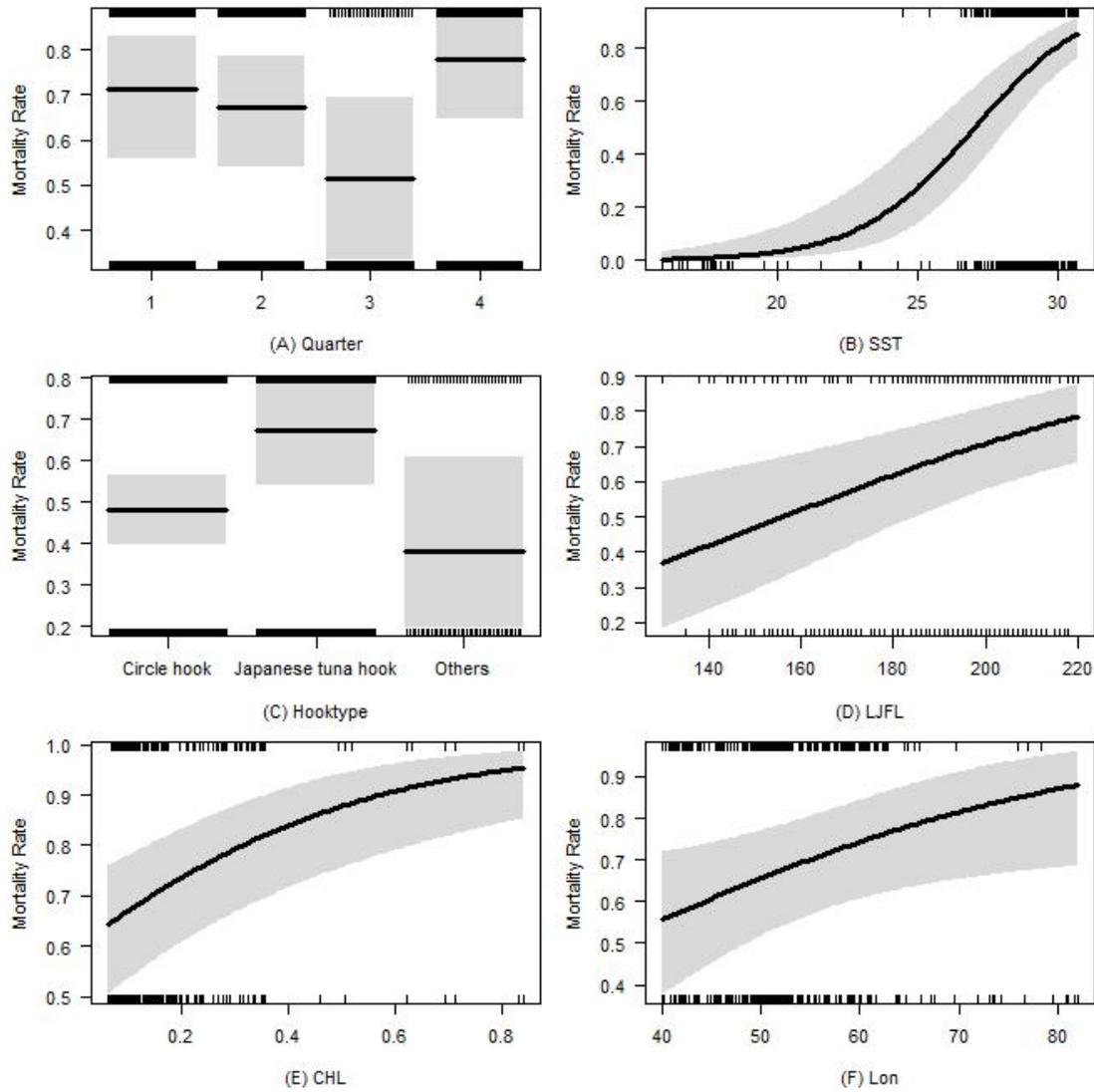


Figure 5. Effects of different explanatory variables on at-haulback mortality of striped marlin in the Indian Ocean. (The solid black line indicates the predicted probability of mortality as a function of the explanatory variable, and the grey shaded area indicates the 95% confidence interval of the variable. Short lines at the top and bottom of the figure indicate the numbers of fish that died and survived under that explanatory variable. The definition of the abbreviation is described in the notes for equation 1.

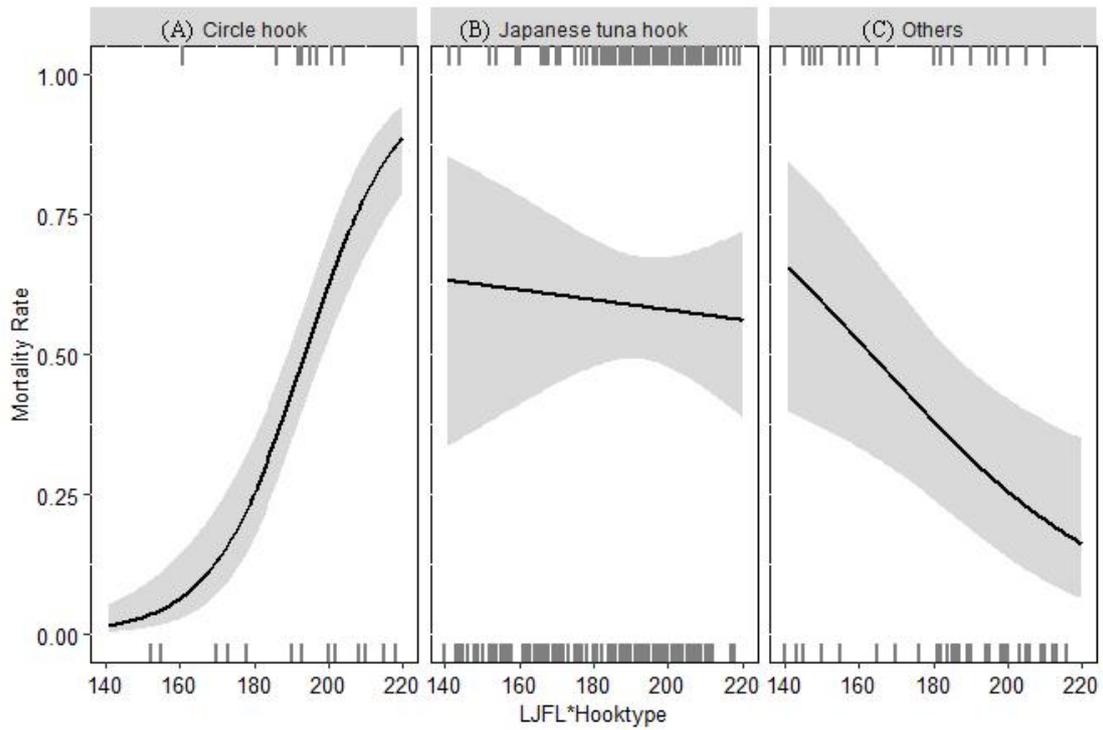


Figure 6. Interaction between lower jaw-fork length (LJFL) and hook type on at-haulback mortality of Indian Ocean striped marlin. (The different boxes indicate the change in at-haulback mortality of Indian Ocean striped marlin with LJFL when using the hook type (circle hook, Japanese tuna hook, others). Short lines at the top and bottom of the figure indicate the respective numbers of fish that died and survived under the LJFL.