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ARTICLE

Less Soak Time Saves Those upon the Line: Capture Times and Hooking Mortality of Sharks Caught on Bottom Longlines

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Abstract
The National Marine Fisheries Service is mandated by the Magnuson–Stevens Fishery Conservation and Management Act to implement effective annual catch limits and accountability measures to prevent overfishing. These requirements compel further research into alternative fishing practices that could reduce mortality of sharks (class Chondrichthyes) and allow fishers to release unwanted sharks to the water alive, while still effectively catching targeted species. We used hook timers and temperature–depth recorders aboard contracted vessels and participants in the National Marine Fisheries Service's Shark Research Fishery to collect hooking time and time-on-the-line data for 10 species of sharks that were commonly encountered in the fishery. A subset of standardized fishing sets compared the most popular circle hook and J-hook models. Over 60% of sharks were hooked within 4 h of hook soak time. The fastest to bite the hook was the Atlantic Sharpnose Shark *Rhizoprionodon terraenovae* and the slowest was the Dusky Shark *Carcharhinus obscurus*. Shark resilience to time on the longline varied among species, with Sandbar Shark *C. plumbeus* exhibiting the most resilience and Atlantic Sharpnose Shark the least. Shorter set soak times, approximately 2 h, would still maximize catch, while minimizing at-vessel mortality. The most frequently used circle hook model did not significantly reduce at-vessel mortality over large J-style hooks. The recent circle hook requirement will have little effect for fishers that previously used 12/0 J-hooks, but it may be beneficial by preventing the use of smaller J-hooks that are more likely to cause at-vessel mortality.

The commercial bottom longline fishery for sharks (class Chondrichthyes) is active in the U.S. Atlantic Ocean from the eastern Gulf of Mexico around Florida and northward to North Carolina. This fishery primarily harvests coastal sharks in U.S. Atlantic Ocean waters. It is active year-round but is subject to seasonal closures based on quota limits and participation in other fisheries (i.e., some fishers switch to more profitable species during certain times of the year). Since the initial implementation of the first Federal Management Plan for Sharks in 1993, fishery regulations and the status of sharks have varied considerably overtime (https://www.fisheries.noaa.gov/topic/atlantic-highly-migratory-species). Historically to 2008, fishers targeted primarily Sandbar Shark *Carcharhinus plumbeus*. In 2008, following a stock assessment for this species, Amendment 2 to the 2006 Consolidated Atlantic Highly Migratory Species Fishery Management Plan prohibited the retention of Sandbar Shark and severely reduced trip catch limits for other shark species (NOAA 2008). The stock assessment projections allowed

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for a small quota to be harvested while the stock recovered. The need to continue collecting data on Sandbar Shark in combination with the ability to allow for a small amount of harvest led to the inception of the Shark Research Fishery. This fishery allows a limited number of fishers (5–10) to continue harvesting Sandbar Shark under 100% observer coverage (Hale et al. 2009). Outside of the research fishery, because Sandbar Shark could no longer be harvested, the behavior of the commercial shark fleet changed to target other shark species, such as Blacktip Shark *C. limbatus* and Bull Shark *C. leucas*, and as these species are often found in shallower habitats, the change is observable by a decreasing trend in average fishing depth by year (S. J. B. Gulak and J. K. Carlson, unpublished data).

Stock assessments for populations of Scalloped Hammerhead *Sphyrna lewini*, Blacknose Shark *C. acronotus*, and Dusky Shark *C. obscurus* in U.S. waters have estimated these sharks are currently overfished and experiencing overfishing (Hayes et al. 2009; SEDAR 2011a, 2011b, 2016). As mandated under the Magnuson–Stevens Fishery Conservation and Management Act for stocks experiencing overfishing, the National Marine Fisheries Service must implement effective annual catch limits and accountability measures to prevent overfishing. Alternative fishing measures, such as reducing the soak time of hooks and restrictions on the number of hooks fished or the type of hook used, could reduce mortality of sharks and allow fishers to release unwanted sharks to the water alive, while still effectively catching targeted species. Before such management measures can be considered, data concerning the correlation between a host of environmental and operational fish variables and fishing mortality are needed.

Previous studies have examined the amount of time individual sharks spent caught on a hook and what impact that amount of time had on at-vessel mortality for this fishery. Morgan and Carlson (2010), using hook timers and temperature–depth recorders, assessed the factors affecting the mortality of Sandbar Shark, Blacktip Shark, and Bull Shark and found that mortality rates increased steadily for the three species but appeared to increase the most after 10, 6, and 1 h for these sharks, respectively. For these species, the probability of a hook being bitten increased the most between 5 and 12 h after the longline had been set and the mean amount of time hooks were in the water prior to being bitten was 4, 5, and 9 h, respectively. Gulak et al. (2015) further examined hooking mortality for Scalloped Hammerhead and Great Hammerhead *S. mokarran* for the shark bottom longline fishery and reported at-vessel mortality rates of 62.9% and 56.0%, respectively, with median hooking times of 3.5 and 3.4 h, respectively, and 50% mortality predicted at 3.5 and 3.8 h, respectively. However, mortality rates are highly dependent on the behavior of the fishing fleet, and given that there has been shifts in fishing tactics due to regulations (NMFS 2006 and subsequent amendments, https://www.fisheries.noaa.gov/management-plan/consolidated-atlantic-highly-migratory-species-management-plan) since Morgan and Carlson (2010), a more complete reexamination of the capture times and hooking mortality of sharks caught in this fishery is required.

The objective of this study is to expand upon the initial work of Morgan and Carlson (2010) and Gulak et al. (2015) by exploring and presenting a meta-analysis of a full hook timer data set using time-to-event analysis to predict time at capture and generalized linear mixed models to further assess factors contributing to at-vessel mortality rates.

METHODS

Data collection.— Experimental bottom longline sets ($n = 287$) were conducted on contracted commercial fishing vessels that were participants in the U.S. National Marine Fisheries Service Shark Research Fishery as previously described in Gulak et al. (2015). Hook timers (LP HT-600) were placed on every hook or distributed evenly across the set (every other hook to every 20th hook). When available, temperature–depth recorders (Lotek LAT1100) were also attached at the beginning, middle, and end of the mainline and set to record depth and temperature every 2 min.

Fishery observers or onboard biologists recorded set and haul data (e.g., date, time, and GPS coordinates of gear deployment and retrieval) and catch data. In selected hauls, the hook set time and hook board time for each individual hook was also recorded as it entered and exited the water. The catch data included the time the animal was brought alongside the vessel, hook type, species identity, disposition (alive, dead, alive with damage, dead with damage), fork length (FL; estimated, but measured if brought aboard), sex, and fate (e.g., released alive, released dead). The hook location was recorded as follows: (1) "jaw" if the hook was lodged in the edge of the jaw, the corner of the mouth, or the roof of the mouth; (2) "internal" if the hook was fixed in the throat, gill arches (internally), or swallowed (nonvisible); and (3) "foul" if the fish was entangled in the leader or hooked on the body other than the mouth region.

Hook comparison.— A subset of bottom longline sets ($n = 55$) were standardized to compare two hook types. These sets were comprised of 300 or 600 hooks, and with the exception of hook type and depth, the gear configuration remained constant. Throughout each longline deployment, hooks were alternated between two experimental hook treatments: 10° offset 18/0 circle hooks (model LP-CIR-HK-18-BL; Lindgren-Pitman, Pompano Beach, Florida) and nonoffset 12/0 J-style hooks (model 3407-DT;

Mustad Americas, Doral, Florida). Although the dimensions differ (minimum hook widths of 4.5 and 4.9 cm, respectively [Curran and Bigelow 2011]), these hooks represent the predominant types used in the fishery (Enzenauer et al. 2016) prior to the recent change in regulations effective June 6, 2017 (Amendment 5b to the 2006 Consolidated Highly Migratory Species Fishery Management Plan: Atlantic Shark Management Measures; NOAA 2017). The sites fished were split between two strata by depth (>30.5 m and <30.5 m), which were on either side of an offshore sandbar and located off the coast of Fort Pierce, Florida. Other than the experimental design requirements, the captain was allowed to fish normally and chose the location of fishing. Set soak time, defined as the time from the last hook set into the water to the first hook hauled from the water, was limited to a maximum of 8 h (average set soak time observed for the fishery; Hale et al. 2011).

Data preparation.— Collected data were entered, proofed, and imported into the statistical package R (version 3.5.2, R Core Team 2018) using the RStudio environment (version 1.1.423, RStudio Team 2016). Hook timers recorded time for only 24 h, after which the timer reset to zero. Hauls that had hook soak times of longer than 24 h were excluded ($n = 32$). Small-bodied sharks (such as Atlantic Sharpnose Shark *Rhizoprionodon terraenovae* and Blacknose Shark) often failed to trip the hook timer when captured; instead, the hook timer may have been tripped when tension on the line increased during gear haulback, giving an inaccurate time. To minimize this, sharks that tripped the hook timer during the haulback and had a fork length of less than 100 cm were excluded from the analysis ($n = 116$). Temperature–depth recorders were unavailable for 80 of 287 hauls. The missing temperatures at depth were extracted from the Hybrid Coordinate Ocean Model data set (http://ncss.hycom.org) by modifying parts of the package "HMMoce" (Braun et al. 2018). This ocean model also provides estimates of northward current and eastward current velocity, which likely influences the size of the bait plume. These data were extracted for all set locations at the closest available depth to the set depth. Single vector current velocity (CV) was derived using the Pythagorean theorem.

Hooking times.— Herein, we define hooking time as the time from the hook entering the water to the time a species becomes hooked on the line. We further specify two types of hooking time: actual and estimated, where actual hooking time is derived from the hook set time and the time that the hook was bitten (back-calculated from the board time using the hook timer time). Estimated hooking time refers to hooking times derived from the median set time in absence of the individual hook set time. Neither hooking time should be confused with hook soak time, which is the total time that the hook remains submerged (hook set time to hook board time). Previous analysis (Gulak et al. 2015) included estimated times of hook deployment using the median set time. First, we justified the use of estimated hooking times by testing for differences between actual hooking times and estimated hooking times. After processing, there were 642 actual hooking times from 10 shark species ($n > 30$). Estimated hooking times were generated from median set times. A Wilcoxon's signed rank test was performed to test for significant differences between the two hooking times. We continued to use the actual set time when data were available but included a further 1,595 sharks with estimated set times.

Time-to-event analysis, also known as survival analysis, is commonly used to evaluate the timing of an event (usually mortality). Here, we used this method to predict the hooking time for sharks. It was necessary to test several variables to take into account the disparities in fishing method (bait, depth, and time the gear was deployed) and abiotic variables (temperature, current velocity, and moon phase). We chose the Cox proportional hazard model for analysis of hooking time using the package "survival" (Therneau 2015). This model is considered semiparametric and is more robust than parametric approaches because it is not vulnerable to misspecification of the baseline hazard. The first model compared hooking time among species ($n > 10$). Significant differences in hooking times led to further analysis separately by individual species. Ten species were tested against the following variables: average depth, combined temperature, velocity of the current (m/s), moon phase, hours to or from crepuscular change (dusk or dawn), and bait type (Table 1). The four moon phases were obtained with the package "lunar" (Lazaridis 2014) and "maptools 0.9-4" was used to obtain local dusk and dawns. Bait type (teleost = teleost fish, Scombridae = fish from the family Scombridae, Anguilliformes = eels from the order Anguilliformes, elasmobranch = sharks and rays from the subclass Elasmobranchii, and mixed = bait was a mixture of all other bait types) was defined by the primary bait used in the set (≥90% of total hook count), otherwise it was considered mixed bait. Scombridae and Anguilliformes were separated from the general teleost group due to fishers' preference for exclusively using those baits. All the variables were included in the primary model. Nonsignificant variables were removed in a stepwise fashion. The final model was then tested for model assumption violations using the cox.zph function from the "survival" package. The Cox proportional hazards model assumes that covariates do not vary with time. Such covariates were identified and stratified to satisfy the model assumption. The final model for each species was plotted graphically as cumulative events by strata, and forest plots were created to show the relative importance of significant covariates using the "survminer" package (Kassambara and Kosinski 2018).

TABLE 1. Fixed and random variables used in the generalized linear mixed models by type, showing the range of values and a description of the variable.

Variables	Type	Range	Description
Fixed variable			
Current velocity (CV)	Continuous	0.0–0.8 m/s	Current flow (m/s)
Depth	Continuous	9.1–125.1 m	Average depth of fishing set (m)
Fork length (FL)	Continuous	45–420 cm	Fork length (cm)
Gangion length (GL)	Continuous	1.2–4.6 m	Length of the gangion (m)
Hook location (HL)	Categorical	Jaw, internal, foul	Location of the hook
Hook type (HT)	Categorical	C-16, C-18, C-20, J-9, J-10, J-12, unknown	Hook shape and size (unknown hook types included for Dusky Shark and Great Hammerhead)
Month	Categorical	1–12	Month in which the fishing set was made
Sex	Categorical	Male, female, or unknown	Sex of the shark (unknown sex included for Dusky Shark and Blacknose Shark)
Temperature	Continuous	8.7–30.1°C	Combined temperature–depth recorder and Hybrid Coordinate Ocean Model temperatures (°C)
Time on the line (TOL)	Continuous	0.0–21.4 h	Time elapsed since the shark was hooked (hours)
Weight on the line (WT)	Continuous	10.7–56.3 kg/km	Total amount of weight per kilometer applied to the mainline to keep it on the seafloor. This includes the weight of the mainline (kg/km).
Random variable			
Haul identifier	Categorical	1–287	Haul number in chronological order

Hook comparison.— A subset of fishing sets, with only two alternating hook types, were analyzed for differences in catch per unit effort (CPUE) and at-vessel mortality rates. Mean CPUE by haul was computed as animals per 1,000 hook-hours, where CPUE = (total animals caught/number of hooks set × hours of soak time) × 1,000. If the assumptions of normality (Shapiro test) and homoscedasticity (Bartlett's test) were met, CPUE between hook types was compared, for captures of 10 individuals or greater, by one-factor analysis of variance (ANOVA); otherwise, a Mann–Whitney *U*-test was used. To assess whether at-vessel mortality rates were affected by hook type, mortality rates were compared by species. The at-vessel mortality rate for each species was calculated as the proportion of total dead sharks to total shark catch (total dead sharks at vessel/total sharks caught). At-vessel hooking mortality was compared using a chi-square two-sample test for equality of proportions, with Yates' continuity correction applied for those shark species with a total catch less than 20 individuals (Yates 1934; Pacheco et al. 2011).

At-vessel mortality.— Generalized linear mixed models (GLMMs) were used to predict biological and abiotic factors affecting at-vessel mortality. To include as much hook timer data as possible, it was necessary to test many variables to take into account the variations in fishing gear, month, and location. For those species with sample sizes larger than 100 sharks, incomplete or "unknown" data were removed (e.g., sex unknown, hook type unknown, etc.) and hook types with less than 10 samples were also excluded. Eleven fixed effect variables were investigated (Table 1), and the only random effect variable was the haul identifier (1–287), which was used to account for those animals that were sampled within the same haul (repetitive measures). Models were built with all combinations of factors (global model: at-vessel mortality ~ time on the line + CV + depth + FL + gangion length + hook location + hook type + month + sex + temperature + weight on the line). The final model for each species was chosen by exhaustive search for the lowest Akaike information criterion (AIC; Akaike 1974), with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989) made using the dredge function in the package "MuMin" (Barton 2020). Collinearity in the final model was investigated using the variance inflation factor. Models containing variables with variance inflation factor scores of greater than three resulted in that model being rejected in favor of the next lowest AIC_c. Power analysis (a priori) indicated that data sets with less than 100 sharks would not obtain enough power to include more than two fixed variables. Final models for Blacknose Shark, Dusky Shark, and Great Hammerhead were selected from the lowest AIC_c values from the models that included two fixed variables. Month and sex (only for Great Hammerhead) was excluded from the global models to avoid overparameterization. Individual predictor variables were evaluated for relative importance by estimating the sum of Akaike weights for candidate models in which each predictor was included

(Burnham and Anderson 2002). Variables were considered important with a cumulative weight above 0.95 (95%).

Hook soak time intersection point.— When the proportions of alive to dead sharks for the at-vessel mortality GLMM are reversed and plotted over the hooking-time cumulative event curve, there is an intersection point between the two curves. This point represents an estimate for the maximum proportion of sharks hooked at a minimum at-vessel mortality. Final selected models from hooking-time (survival) analysis and GLMM predictions were plotted together for the seven species that had at-vessel mortality GLMMs. The function curve_intersect from the "reconPlots" package (Heiss 2019) was used to identify the hook soak time intersection point. The proportions of sharks alive and hooked were also calculated at hour intervals for a 2-, 3-, and 4-h hook soak times.

RESULTS

The final data set consisted of 255 hauls. The mean set duration was 0.92 h, the mean set soak duration was 7.73 h, and the mean haul duration was 2.44 h. Hook set time and hook board time were collected for 29,115 hooks from 54 hauls, and mean hook soak time was 9.57 h (range = 4.83–16.17 h). Set, soak, and haul durations for these hauls were similar to the global data set at 1.66, 7.44, and 2.35 h, respectively.

Hooking Times

There were no significant differences found between estimated and actual hooking times for grouped sharks (Wilcoxon's signed rank test: $V = 97{,}311$, $P = 0.322$; Table 2), but when the test was performed for individual species, there were four species that had significant differences between actual and estimated hooking time. Actual mean hooking time varied from 0.75 to 2.74 h, while the same subset with all times estimated varied from 0.71 to 2.56 h. When the actual mean times were combined with the rest of the data set (the remainder estimated), mean hooking time varied from 1.48 to 4.28 h. While actual and estimated mean hooking times were similar, all sharks had longer mean hooking times in the combined data set. Scalloped Hammerhead had the largest deviation from the actual hooking time (0.75 to 2.25 h), while hooking times for the Great Hammerhead did not deviate at all (Table 2).

The Cox proportional hazards model found significant differences in hooking time among shark species, and individual species models were fitted for 10 species (Figures 1, 2). The forest plots indicate which variables had a positive or negative effect to hooking time and their *P*-values (Figures 3, 4). Those factors with a hazard ratio greater than one increased the speed at which a species was hooked. Moon phase and bait type were significant factors in the final models for five species. The full or waning moon resulted in a slower hooking time for Tiger Shark *Galeocerdo cuvier*, Nurse Shark *Ginglymostoma cirratum*, and Scalloped Hammerhead, but Bull Shark and Great Hammerhead bit the hook faster during the waning quarter (Figures 3, 4). Moon phase was the chosen strata for Blacknose Shark, and no test was performed directly on this variable due to violation of the test assumptions. Blacknose Shark appeared to bite the hook slower on the waxing moon (Figure 2). Anguilliformes baits produced the faster hooking times for Tiger and Dusky sharks, but for Atlantic Sharpnose Shark, Bull Shark, and Scalloped Hammerhead catch was quicker on scombrids (Figures 3, 4). The final models for Blacktip, Nurse, and Sandbar sharks were stratified by bait type (Figure 1). Blacktip and Sandbar sharks bit the hook faster on scombrids, but the Nurse Shark cumulative event curves suggested a preference for teleost bait.

Current velocity was influential for four shark species. Dusky Shark and Great Hammerhead bite the line quicker with stronger current, whereas the opposite was found for Nurse Shark and Scalloped Hammerhead (Figures 3, 4). The amount of time from sunrise or sunset was a significant variable for Blacknose Shark and Scalloped Hammerhead, with both species having slower hooking times as time increased from the crepuscular change (Figures 3, 4). The variable was chosen as a stratifying factor for Bull Shark and Great Hammerhead (Figure 2), which appeared to support this relationship as well. The final model for Atlantic Sharpnose Shark was stratified by temperature, and hooking was faster between 25°C and 30°C (Figure 1). The final model for Blacktip Shark was stratified by bait type but did not include any other variables (Figure 1).

Hook Comparison

Fifty-five sets were completed, for a total of 29,441 hooks and 216,932 hook-hours. Soak times averaged 7.4 h (range = 4.8–12.7 h). Sharks were most commonly hooked in the jaw (pooled sharks; 92.7% for circle hooks and 94.3% for J-hooks), and foul hooking occurred more frequently (pooled sharks; 1.4% for circle hooks and 1.6% for J-hooks) than internal hooking (pooled sharks; 0.3% for circle hooks and 0.0% for J-hooks). There were no internally hooked sharks on J-hooks ($n = 672$ J-hooks), and two sharks were internally hooked on circle hooks (one Atlantic Sharpnose Shark and one Blacktip Shark; $n = 611$ circle hooks). There were also sharks caught on both hook types where a hook location was not recorded (pooled sharks; 5.6% for circle hooks and 4.1% for J-hooks).

In most cases, CPUE was lower for sharks caught on circle hooks (Table 3). Higher CPUE for circle hooks was found for Atlantic Sharpnose Shark, Blacktip Shark, Bull Shark, Tiger Shark, and Sand Tiger *Carcharias taurus*. However, despite higher CPUE found for J-type hooks, no significant differences in CPUE between hook types were found (Table 3; Mann–Whitney *U*-test: $P > 0.05$).

Sandbar Shark, Nurse Shark, Bull Shark, Tiger Shark, Lemon Shark *Negaprion brevirostris*, and Sand Tiger were frequently alive when brought alongside the vessel (Table 3; at-vessel mortality ≤ 11.4%). Atlantic Sharpnose Shark, Blacktip Shark, Blacknose Shark, Scalloped Hammerhead, Spinner Shark *Carcharhinus brevipinna*, Dusky Shark, Great Hammerhead, Silky Shark *C. falciformis*, and Finetooth Shark *C. isodon* suffered at-vessel mortality rates of 73.7% or greater on both hook types (Table 3). There were significant differences in at-vessel mortality between hook types for pooled sharks (two-sample test for equality of proportions, $\chi^2 = 10.657$, df = 1, $P < 0.01$); however, this was not the case when shark species were tested individually (Table 3). Lemon Shark, Silky Shark, Finetooth Shark, and Sand Tiger failed to meet the assumptions for the test and were excluded.

At-Vessel Mortality Models

Environmental and abiotic factors influencing at-vessel mortality were modeled for 10 species of sharks using GLMMs. Time on the line was the single most important factor for all species and was included in the final models for all species where models converged, with the exception of the model for Blacknose Shark (Table 4). For this species, we chose to override our selection criteria and selected a model that included time on the line. Sandbar Shark were the most robust to at-vessel mortality over time, with 50% mortality after 19.1 h on the line, and Atlantic Sharpnose Shark were the most sensitive, with over 75% at-vessel mortality after 3 h on the line, regardless of environmental factors (Figures 4, 5). Regression analysis was unsuccessful for Bull Shark, Nurse Shark, and Tiger Shark, likely due to the low rates of at-vessel mortality observed for these species (not enough reported mortality events).

Shark fork length was included in the final models for four species (Table 4). Large sharks handled the stress of capture more readily that smaller sharks. Sex, weight on the mainline (total amount of weight per kilometer applied to the mainline to keep it on the seafloor, including the weight of the mainline itself [kg/km]), and temperature were each important for two species. The final GLMMs for Dusky Shark and Blacknose Shark included sex, and males were more susceptible to at-vessel mortality than females. Weight on the mainline was an influential variable for Scalloped Hammerhead and Atlantic Sharpnose Shark. Both species survived longer when more weight was applied to the mainline. Temperature was important for Blacktip Shark and Sandbar Shark, but the effect was different for each species. Gangion length and hook type were included in the final model for Blacktip Shark. Shorter gangion lengths resulted in a greater survival for this species. Blacktip Shark had higher mortality with smaller hook sizes and survived longest when captured on an 18/0 circle hook versus the other included hook types (16/0 circle hook, 10/0 and 12/0 J-hooks).

Since most model candidates resulted in ΔAIC_c of less than 2, we further evaluated the relative importance of the predictor variables using Akaike importance weights for parameters from candidate models, with Akaike weights above 95% considered important (Table 5). Time on the line was the most important factor for all species except for Blacknose Shark, and fork length was important for Atlantic Sharpnose Shark and Scalloped Hammerhead.

TABLE 2. Mean hooking times (hours from hook set to hooking event) for various shark species, with sample size (*N*), the actual mean hooking time and estimated mean hooking time, the Wilcoxon's signed rank test statistic (*V*) and *P*-value, the combined sample size (*n*), the mean hooking time for the combined data sets, and the mean hooking time from other studies (Morgan and Carlson 2010; Foster et al. 2017). The Wilcoxon's signed rank test results that were significant ($P < 0.05$) are in bold italics.

Species	*N*	Actual	Estimated	*V*	*P*-value	*n*	Combined	Morgan and Carlson 2010	Foster et al. 2017
Atlantic Sharpnose Shark	181	1.14	1.20	6,005	***0.002***	234	1.48		0.59
Sandbar Shark	132	1.32	1.35	4,054	0.537	788	3.03	4	
Nurse Shark	85	1.92	1.94	1,853.5	0.909	283	2.91		0.47
Blacktip Shark	64	2.22	2.10	1,605.5	***>0.001***	230	3.44	5	0.67
Blacknose Shark	54	1.65	1.55	877.5	0.152	75	1.72	4	0.73
Bull Shark	50	2.74	2.80	506	0.400	106	3.14	9	
Tiger Shark	32	2.51	2.56	230	0.536	203	4.28		1.20
Scalloped Hammerhead	25	0.75	0.71	163	0.989	158	2.25		0.69
Dusky Shark	10	2.20	1.87	47	***0.047***	89	4.30		
Great Hammerhead	9	2.23	2.57	5	***0.039***	71	2.23		
Grouped sharks	642	1.64	1.65	97,311	0.322	2,237	2.94		0.64

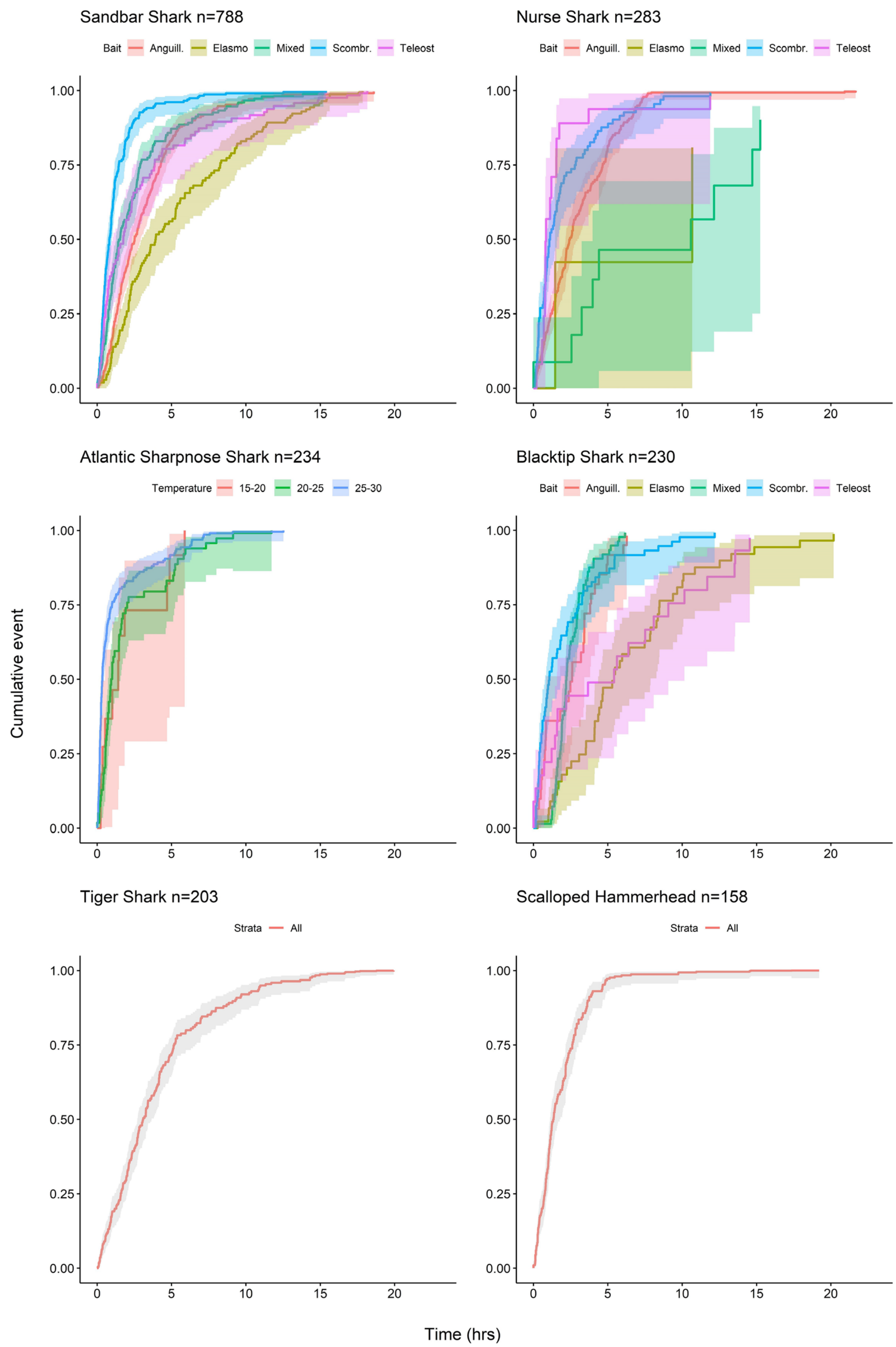

FIGURE 1. Cumulative event plots of hooking times for six shark species. Sandbar, Nurse, and Blacktip sharks are stratified by bait type, and Atlantic Sharpnose Shark is stratified by water temperature (°C). The shaded area represents the 95% confidence interval for the survival function. Bait abbreviations are as follows: Anguill = eels from the order Anguilliformes, Elasmo = sharks and rays from the subclass Elasmobranchii, Mixed = all bait types mixed, Scombr = fish from the family Scombridae, and Teleost = teleost fish. [Color figure can viewed at afsjournals.org.]

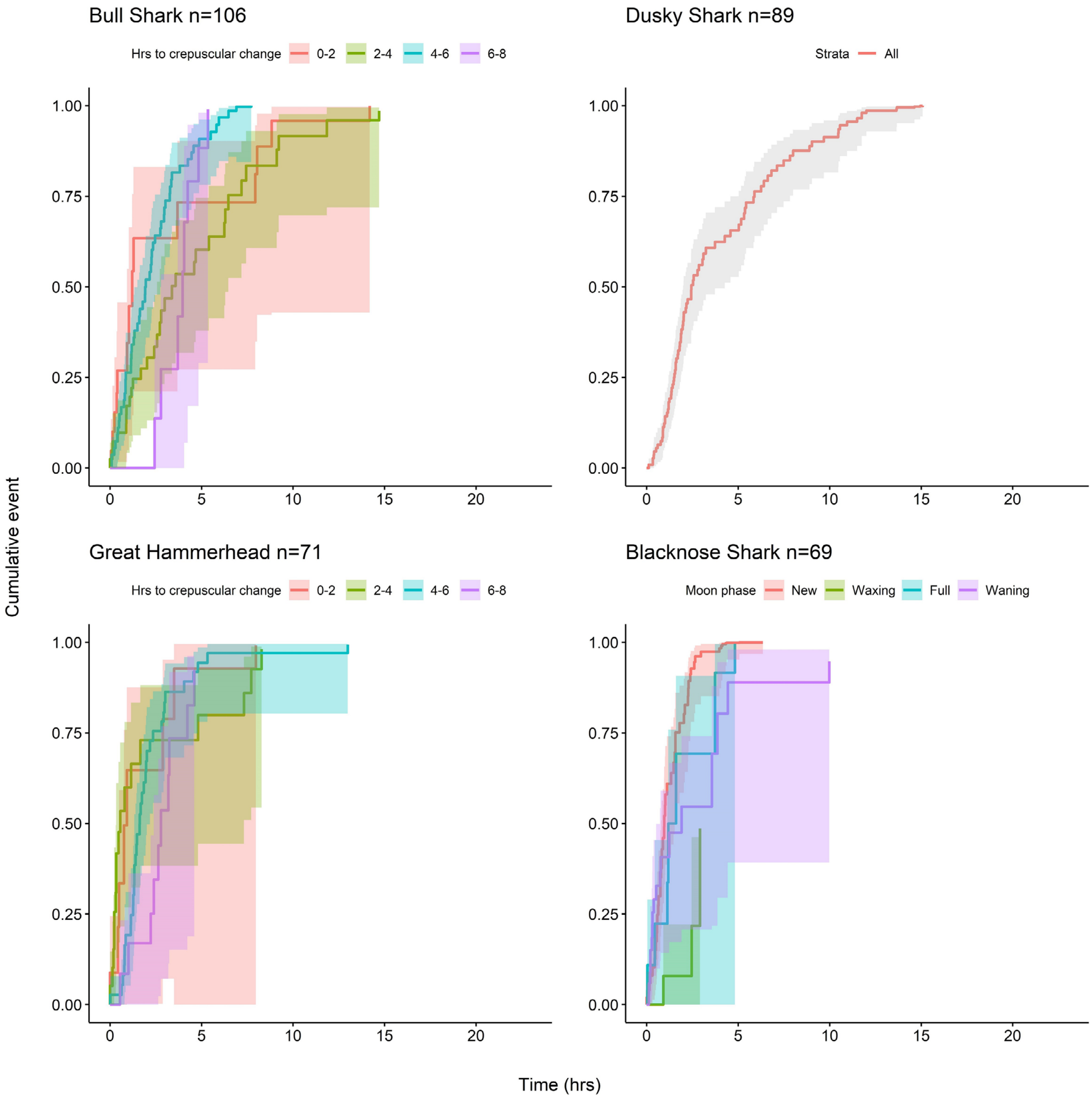

FIGURE 2. Cumulative event plots of hooking times for four shark species. Bull Shark and Great Hammerhead were stratified by hours from crepuscular change, while Blacknose Shark was stratified by moon phase. The shaded area represents the 95% confidence interval for the survival function. [Color figure can viewed at afsjournals.org.]

Hook Soak Time Intersection Point

Over half of all sharks were hooked within 3 h of hook soaking. The intersection point between hooking time and the at-vessel mortality curves varied from 15.6 min (Atlantic Sharpnose Shark) to over 8.6 h (Sandbar Shark; Table 6). The species that suffered high at-vessel mortality (steepest curves) and also bit the line quickly were Atlantic Sharpnose Shark and Blacknose Shark (0.26 and 1.76, respectively). The Great Hammerhead, Scalloped Hammerhead, and Blacktip Shark had moderate intersection times (between 2 to 3 h), and Dusky and Sandbar sharks were much greater (6.22 and 8.60 h, respectively). The

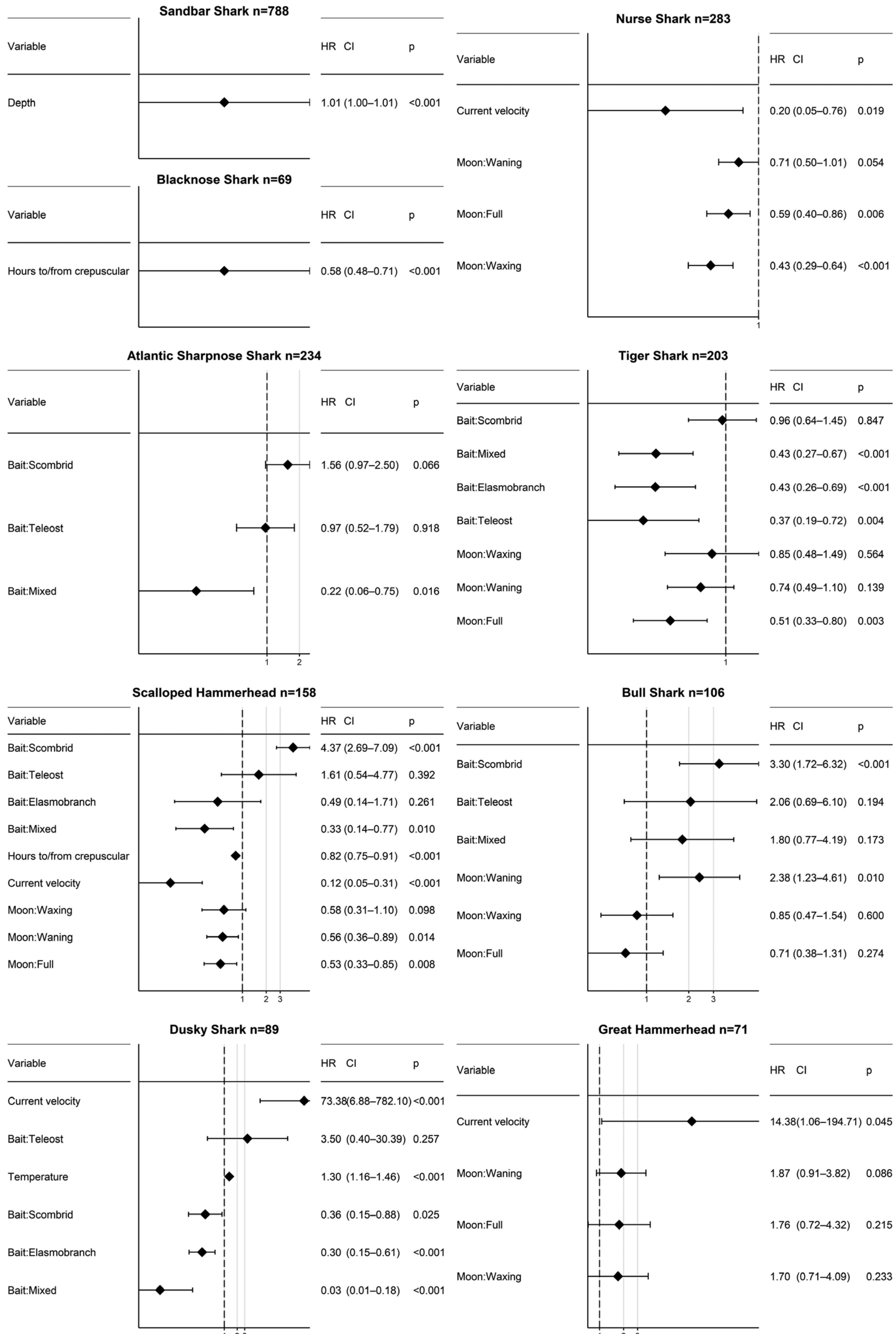

FIGURE 3. Forest plots of nine shark species showing influential variables. A hazard ratio (HR) above 1 indicates a positive correlation with hooking time, while a ratio below 1 indicates a negative correlation. Confidence intervals (CIs) and *P*-values are included.

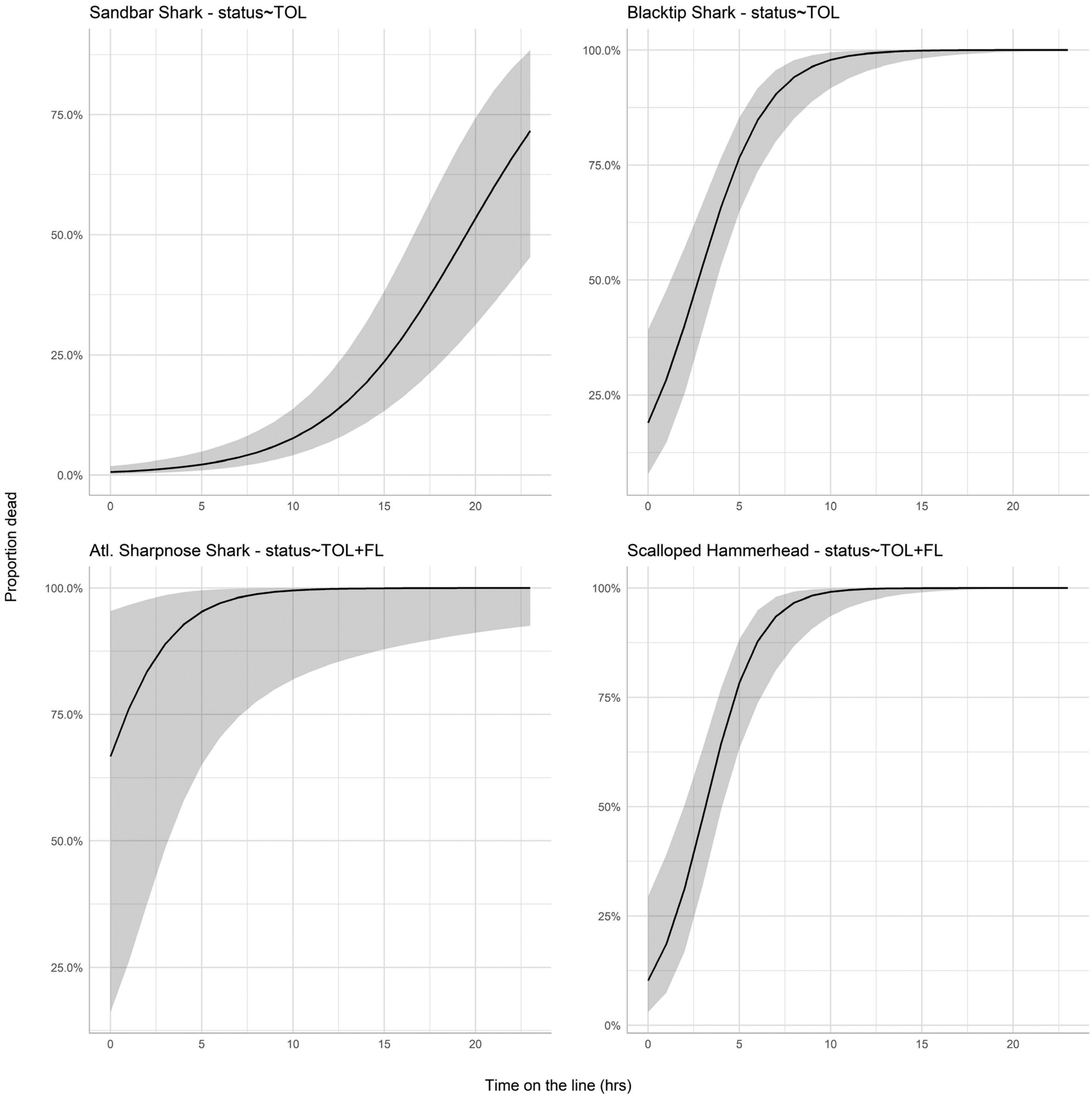

FIGURE 4. Generalized linear mixed models of at-vessel mortality for four shark species, showing the proportion of dead sharks against time on the line (TOL). The final models for Atlantic Sharpnose Shark and Scalloped Hammerhead also include fork length (FL). The shaded areas show 95% confidence intervals.

50% hooking times for Bull Shark, Nurse Shark, and Tiger Shark were 2.43, 1.93, and 3.08 h, respectively. For 2 h of hook soak time, the hooking proportions ranged from 0.40 to 0.82, with at-vessel mortality of sharks between 1% and 83%, and by 4 h of hook soak time 62–97% of sharks were hooked, with 2–93% dead on the line.

DISCUSSION

Hooking Times

Our mean hooking times were different from other studies of shark bottom longlines. Of the data for four species provided in Morgan and Carlson (2010), only the

TABLE 3. Comparisons from 55 sets of total catch (*n*), mean catch per unit effort (CPUE) per 1,000 hook-hours for circle hooks (C) and J-hooks (J), at-vessel mortality rates (%) for circle hooks and J-hooks, and a chi-square (χ^2) two-sample test for equality of proportions between at-vessel mortality rates by species. The abbreviation NT refers to species that were not tested.

		CPUE		At-vessel mortality		
Species	*n*	C	J	C	J	χ^2 (*P*-value)
Atlantic Sharpnose Shark	700	3.05	2.71	96.5	96.0	0.14 (0.71)
Sandbar Shark	185	0.39	0.77	4.8	11.4	2.12 (0.15)
Nurse Shark	92	0.34	0.51	2.4	0.0	1.20 (0.27)
Blacktip Shark	79	0.48	0.46	92.1	85.4	0.89 (0.35)
Bull Shark	71	0.31	0.30	2.9	2.8	0.00 (0.98)
Blacknose Shark	68	0.19	0.24	86.7	73.7	1.73 (0.19)
Tiger Shark	57	0.22	0.21	6.9	0.0	2.00 (0.16)
Scalloped Hammerhead	29	0.06	0.14	100.0	95.0	0.47 (0.49)
Spinner Shark	21	0.05	0.08	87.5	100.0	1.71 (0.19)
Lemon Shark	14	0.07	0.08	0.0	0.0	NT
Dusky Shark	14	0.03	0.04	85.7	28.6	2.63 (0.11)
Great Hammerhead	11	0.04	0.05	75.0	85.7	0.00 (1.00)
Silky Shark	3	0.00	0.02	0.0	100.0	NT
Finetooth Shark	2	0.01	0.01	100.0	100.0	NT
Sand Tiger	1	0.01	0.00	0.0	0.0	NT

Sandbar Shark had a similar mean hooking time. However, the reported mean hooking time was the 50% value from the binomial regression and is not directly comparable. The Cox model found species-specific differences in hooking time, and several factors were identified as influential. Target catch is primarily attracted to longlines by the bait, which produces an odor plume. The initial emission of the attractant is followed by turbulent mixing and then dispersion by current. Bait diffusion varies with the ratio of surface to cross-sectional areas and type, and the release will reduce in strength and thus effectiveness over time (Westerberg and Westerberg 2011). A combination of these factors is the likely cause of the violation of the proportional hazard assumption and the need for stratification by bait type for three species. When bait did not cause this test violation, it was almost always an important factor to hooking time. Bait will affect catches in sharks (Belcher and Jennings 2009; Kumar et al. 2016; Driggers et al. 2017), and the scope of this effect also includes the speed of attraction to the hook as well.

Compared to set soak times historically used in the fishery (13.6 and 8 h; Morgan et al. 2010 and Hale et al. 2011, respectively), sharks did not take much time to be captured, but mean hooking times were greater than reef fish and sharks captured on reef fish bottom longlines (Foster et al. 2017). This should not be surprising as mean set soak times in Foster et al. (2017) were approximately 90 min, whereas shark bottom longline sets were soaked for several hours longer (mean set soak time of 7.7 h). It should be noted that the subset of actual hooking times were more similar with the reef fish longline times for Scalloped Hammerhead. This further supports the position that, while feasible for some species, it may be insufficient to use estimates of hook deployment times for others, even for fishing gear with long soaks.

Moon phase was also frequently selected in the final models and has also been documented to have effects on shark catches (Belcher and Jennings 2009; Wintner and Kerwath 2017). Fishers have often anecdotally expressed that the best catches were on the full moon and new moon. Several final models identified current as an important factor. Currents are directly responsible for the size of the bait plume (Westerberg and Westerberg 2011). Temperature, depth, and time from crepuscular change were all included for at least one species studied. Attractant diffusion may occur faster at higher water temperatures and densities (water pressures). The models for Scalloped Hammerhead and Blacknose Shark indicated that the number of hours from crepuscular change did influence hooking time. Fishers frequently set longline gear for sharks with the intention of soaking for both crepuscular periods (e.g., setting before sunset and hauling after sunrise), and shark activity is often generalized to be higher for these periods and at night. Overall, we found that many factors could assist or delay an individual shark from locating the baited hook, but many of these factors are difficult to control both experimentally and by fishers aiming to minimize at-vessel mortality. As a result, these estimates should be considered preliminary and future studies should attempt to minimize the confounding effects using our findings here.

TABLE 4. Results from generalized linear mixed models for at-vessel mortality of seven shark species, showing the 10 models per species with the lowest Akaike information criterion with the small-sample bias adjustment (AIC_c) scores and ΔAIC_c that had a variance inflation factor of less than three. The variables included the following: current velocity (CV), depth, fork length (FL), gangion length (GL), hook location (HL), hook type (HT), month, sex, temperature, time on the line (TOL), and weight on the line (WT). The last three species were limited to two variables.

Model	AIC_c	ΔAIC_c
Sandbar Shark (*n* = 621)		
TOL + temperature	411.400	0.0
TOL + CV + temperature + WT	411.555	0.155
TOL + temperature + WT	411.858	0.458
TOL + HL + temperature	412.606	1.206
TOL + CV + HL + temperature + WT	412.837	1.437
TOL + sex + temperature	412.997	1.597
TOL + CV + sex + temperature + WT	413.015	1.615
TOL + CV + temperature	413.096	1.696
TOL + depth + temperature	413.108	1.708
TOL + HL + temperature + WT	413.166	1.766
Atlantic Sharpnose Shark (*n* = 218)		
TOL + FL + WT	129.054	0.0
TOL + FL + HT	130.269	1.215
TOL + FL + GL + WT	130.483	1.429
TOL + FL + sex + WT	130.650	1.596
TOL + CV + FL + WT	131.140	2.086
TOL + FL + temperature + WT	131.144	2.09
TOL + depth + FL + WT	131.164	2.11
TOL + FL + HT + WT	131.266	2.212
TOL + FL + HL + WT	131.407	2.353
TOL + FL + GL	131.766	2.712
Blacktip Shark (*n* = 230)		
TOL + FL + GL + HT + temperature	182.506	0.0
TOL + FL + GL + HT + WT	182.945	0.439
TOL + depth + FL + HT	183.622	1.116
TOL + depth + FL + GL + HT	183.817	1.311
TOL + depth + FL + HT + temperature	183.825	1.319
TOL + FL + GL + HT	183.829	1.323
TOL + FL + HT + temperature	183.885	1.379
TOL + CV + FL + GL + HT + temperature	184.489	1.983
TOL + depth + FL + HT + sex + WT	184.677	2.171
TOL + FL + GL + HT + sex + temperature	184.690	2.184
Scalloped Hammerhead (*n* = 111)		
TOL + FL + WT	82.331	0.0
TOL + FL + GL + WT	83.252	0.921
TOL + FL + HT + WT	83.510	1.179
TOL + FL + HT + sex + temperature	83.567	1.236
TOL + FL + HT	83.723	1.392
TOL + FL + temperature + WT	83.854	1.523
TOL + FL + HT + temperature	84.008	1.677
TOL + FL + sex + WT	84.185	1.854
TOL + depth + FL + WT	84.207	1.876
TOL + FL + HT + sex	84.215	1.884
Dusky Shark (*n* = 93)		
TOL + sex	59.660	0.0
TOL + CV	60.322	0.662
TOL + temperature	60.751	1.091
TOL	61.337	1.678
TOL + depth	62.211	2.551
TOL + FL	63.089	3.429
TOL + HL	63.218	3.557
TOL + GL	63.399	3.739
TOL + WT	63.418	3.758
TOL + HT	66.921	7.261
Great Hammerhead (*n* = 70)		
TOL + FL	36.884	0.0
TOL + GL	37.833	0.949
TOL	39.878	2.994
TOL + temperature	39.978	3.094
TOL + HL	40.521	3.637
TOL + WT	41.096	4.212
TOL + CV	41.733	4.850
TOL + depth	41.794	4.911
FL + HL	89.143	52.260
HL	91.319	54.435
Blacknose Shark (*n* = 74)		
Sex + temperature	74.185	0.0
FL + temperature	75.408	1.224
FL + sex	78.274	4.089
TOL + sex	80.246	6.0617
TOL + FL	80.782	6.598
FL + WT	82.613	8.428
FL	82.851	8.666
CV + FL	83.390	9.205
FL + GL	83.614	9.429
GL + temperature	84.288	10.103

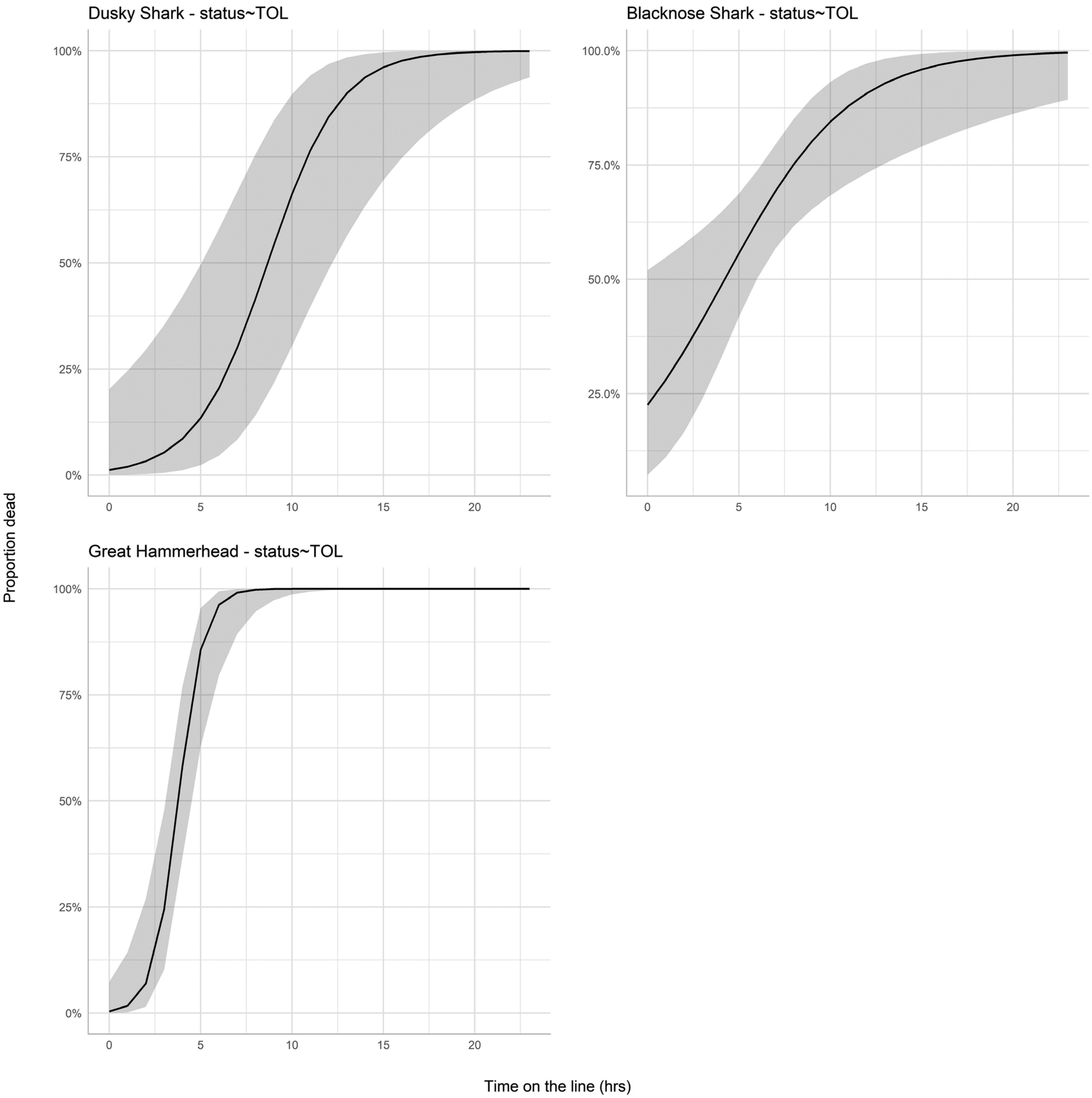

FIGURE 5. Generalized linear mixed models of at-vessel mortality for three shark species, showing the proportion of dead sharks against time on the line (TOL). The shaded areas show 95% confidence intervals.

HOOK COMPARISON

Two commonly used hooks in the shark bottom longline fishery (18/0 circle hook [model LP-CIR-HK-18-BL] and 12/0 J-style hook [model 3407-DT]) were compared in a subset of fishing sets. We found no evidence of differences in CPUE or at-vessel mortality between the hooks types, and the deep ingestion rates were also similar. Longline hook studies often fail to control for varying hook widths when comparing hook shapes, and many studies compared a wider circle hook to a narrower J-hook (Gilman et al. 2016). While our study design also overlooked this, opting for industry standard hooks, the

TABLE 5. Akaike importance weights for parameters from candidate models for at-vessel mortality of seven shark species. The following parameters are included: current velocity (CV), depth, fork length (FL), gangion length (GL), hook location (HL), hook type (HT), month, sex, temperature, time on the line (TOL), and weight on the line (WT). Additional abbreviations are as follows: NA = the parameter was unavailable and EX = the parameter was excluded. Akaike weights above 95% are marked in bold italics.

Species	CV	Depth	FL	GL	HL	HT	Month	Sex	Temperature	TOL	WT
Sandbar Shark	0.424	0.280	0.286	0.281	0.344	0.053	0.237	0.323	0.896	***1.000***	0.599
Blacktip Shark	0.312	0.636	0.787	0.678	NA	0.874	0.002	0.296	0.391	***1.000***	0.688
Atlantic Sharpnose Shark	0.263	0.275	***0.984***	0.340	0.239	0.306	0.135	0.292	0.278	***0.994***	0.570
Scalloped Hammerhead	0.286	0.296	***0.995***	0.385	0.130	0.521	0.013	0.387	0.382	***1.000***	0.596
Dusky Shark	0.194	0.076	0.049	0.042	0.046	0.007	EX	0.274	0.157	***0.995***	0.042
Blacknose Shark	0.007	0.005	0.417	0.009	NA	0.001	EX	0.644	0.851	0.048	0.009
Great Hammerhead	0.035	0.034	0.397	0.247	0.064	0.000	EX	EX	0.085	***1.000***	0.048

TABLE 6. The intersection point of hooking time and at-vessel mortality presented in hours and proportion hooked or alive, and the proportions of hooked and alive sharks for three selected hook soak times by species.

	Intersection point		Hour 2		Hour 3		Hour 4	
Species	Hours	Proportion	Hooked	Alive	Hooked	Alive	Hooked	Alive
Atlantic Sharpnose Shark	0.26	0.31	0.82	0.17	0.85	0.11	0.88	0.07
Blacknose Shark	1.76	0.67	0.63	0.66	0.84	0.59	0.93	0.52
Blacktip Shark	2.15	0.66	0.71	0.69	0.92	0.52	0.97	0.36
Scalloped Hammerhead	2.58	0.52	0.40	0.60	0.58	0.47	0.72	0.34
Great Hammerhead	2.92	0.78	0.65	0.93	0.81	0.76	0.87	0.42
Dusky Shark	6.22	0.78	0.41	0.97	0.58	0.95	0.62	0.91
Sandbar Shark	8.60	0.95	0.53	0.99	0.70	0.99	0.79	0.98

12/0 J-hook and the 18/0 circle hook models have similar narrow hook widths (4.5 and 4.9 cm, respectively) versus the 3.9 cm width of the 9/0 J-hook most commonly used in pelagic longlines (Curran and Bigelow 2011). The larger size of the 12/0 J-hook could account for the lower percentages of deep hooking and the lack of significant differences in at-vessel mortality reported here. Previous shark bottom longline hook studies have indicated higher CPUE on circle hooks (fishery-independent data; Ingram et al. 2005; Godin et al. 2012), higher CPUE on J-hooks (fishery-dependent data; Godin et al. 2012), and no differences (Afonso et al. 2011). Further study of a subset of the data used in Ingram et al. (2005) found differences between catch and fork length between hook types for Blacknose Shark and Atlantic Sharpnose Shark (Hannan et al. 2013), but the authors noted that this could be attributed to hooks with differing minimum hook widths. It is also possible that shark species utilize different feeding strategies when being captured on bottom longlines. Upon encountering hanging (pelagic) bait, a shark can approach at a higher velocity than is possible for a baited hook resting on the seafloor, and thus the probability of swallowing the hook may be greater for sharks captured on suspended fishing gears. Regardless, given the many pelagic longline studies reporting higher rates of deep ingestion on 9/0 J-hooks, we conclude that J-style hooks with the narrowest hook widths of less than 4 cm would likely increase the occurrence of gut-hooking in shark species and significantly increase at-vessel mortality for bottom longlines. Small J-hooks (8/0, 9/0) were commonly used in the shark fishery prior to the recent regulation change (Mathers et al. 2018), and while this study indicates that the recent circle hook requirement had little effect on those fishers using 12/0 J-hooks, it may have been beneficial by preventing the use of those smaller hooks.

At-Vessel Mortality

At-vessel mortality was modeled successfully for 7 of the 10 species with sufficient sample sizes. Regression analysis with time on the line failed for Nurse Shark, Tiger Shark, and Bull Shark. These species exhibited some of the lowest at-vessel mortality (see below in the hook comparison), and there were not enough line mortalities for model convergence. These findings for these species were corroborated by other studies of mortality (Morgan and Burgess 2007; Morgan and Carlson 2010; Lotti et al. 2011) and studies of blood stress levels (Marshall et al. 2012; Gallagher et al. 2014). Nurse Shark can buccal pump and possess spiracles. Tiger Shark buccal pump at birth and later switch to ram ventilation (Tomita et al. 2018). Both Morgan and Burgess (2007) and Lotti et al. (2011) speculated that Tiger Shark and Bull Shark may both be able to buccal pump when necessary. While prolonged time on the hook would eventually result in mortality in these species, it would be far beyond the length of the hook timers (24 h) and not relevant with regards to normal fisher habits. The remaining shark species were affected by time on the line, and this factor described the majority of the variability (highest value of the *z* statistic) and was of highest relative importance. As with static studies of at-vessel mortality, mortality rate varies between species and, in some cases, other variables further influence the result of line capture.

Although not considered a factor of highest importance, bottom temperature was a relevant factor for Sandbar Shark and, unlike Blacktip Shark, Sandbar Shark had faster mortality at lower temperatures. This species has been documented occupying temperatures between 20°C and 26°C (Barnes et al. 2016), and thus temperatures outside of this range (minimum bottom temperature was 10.7°C) may cause additional stress on their metabolism. Blacktip Shark were affected by temperature congruent with other studies, and this species suffered mortality faster at higher temperatures (Lotti et al. 2011). Higher temperatures result in a higher metabolic rate and thus higher oxygen requirements (Carlson et al. 2004). This is exacerbated by the fact that oxygen solubility in seawater reduces with increasing temperature.

At-vessel mortality for Atlantic Sharpnose Shark, Scalloped Hammerhead, Great Hammerhead, and Blacktip Shark was influenced by shark size. In addition, at-vessel mortality was influenced by gangion length for Blacktip Shark and weight (lower amounts) on the longline for Scalloped Hammerhead. The finding that shark size influenced at-vessel mortality is not unusual as larger sharks have been shown to withstand time on the line longer than those of smaller size (e.g., Morgan and Burgess 2007; Morgan and Carlson 2010; Lotti et al. 2011; Gallagher et al. 2014). In regards to gangion length, Gulak et al. (2015) hypothesized that the longer gangions may encourage a stronger fighting response in Great Hammerhead causing increased mortality. Gallagher et al. (2014) also found Blacktip Shark and Great Hammerhead to be the most susceptible to line stress and speculated that it could be due to their burst swimming behaviors, which are energetically expensive. A longer gangion may encourage such behavior. Similarly, less weight on the longline may encourage sharks to struggle harder, thus causing increased stress levels.

Although a variety of factors influenced at-vessel mortality for a number of species, the most important identified for all species by the evaluation of relative importance was time on the line. This is not surprising given that multiple studies have demonstrated evidence for species-specific physiological changes to blood chemistry in response to capture (Marshall et al. 2012; Gallagher et al. 2014; Whitney et al. 2017).

Hook Soak Time Intersection Point

While there may be other methods for evaluating the optimal hook soak time, our analysis has provided useful insight and identified certain species that become captured on bottom longline gear quickly, while also suffering high line mortality as a result of long hook soak times. Atlantic Sharpnose Shark and Blacknose Shark fall into this vulnerable category. Hook soak times of 8 h or more are not necessary to capture sharks, but a long soak time is likely preferred to ensure that the majority of captured sharks will be dead when retrieved. Dead sharks are easier to bring aboard and offer fewer hazards to the fishers while doing so. Dusky Shark had a high intersection point time, but the confidence intervals are large due to poor sample size and model fit (3.47–7.89 h). Taking this into account and using the hammerhead optimum times as a guideline, set soaks could be reduced to benefit vulnerable shark species, while still maintaining sufficient catches. A hook soak time of 3 h is approximately the intersection point for Great Hammerhead and is also the time after which Marshall et al. (2015) observed greater mortality rates for Dusky Shark. With the exception of Blacktip Shark and Dusky Shark, 70% or more of each species were captured on the longline at 3 h. Thus, a hook soak time of 3 h would seem to be a good compromise between line mortality and catch. While the majority of Atlantic Sharpnose Shark and Blacktip Shark would be dead after a 3-h hook soak time, these species are currently caught on longlines with longer set soak times (average set soak duration of 6.2 h and 5.1 h for normal fishery and Shark Research Fishery, respectively; Mathers et al. 2018) and can withstand this level of mortality as stocks are considered healthy (SEDAR 2007, 2012, 2013, 2018). While soak time limitations could benefit some species, they are difficult to enforce on a widely spread fleet. The reef fish bottom longline fishery in the eastern Gulf of Mexico is able to achieve this through a gear restriction of 750 hooks per line. This reduces setting and retrieval times and, ultimately, reduces the total bottom time of the fishing gear so that air-breathing turtles are more likely to survive a fishery interaction. Red Grouper *Epinephelus morio* and Red Snapper *Lutjanus campechanus* are captured on the gangions quickly (mean capture time < 24 min; Foster et al. 2017); thus, the 750-hook limit is economically viable and encourages the fishers to set and haul the fishing gear as fast as possible to increase the number of sets the vessel makes during the daylight hours. In this example, the limitation placed on the amount of fishing gear essentially achieves the regulation of set soak time. However, it is unlikely that this approach could be applied to the shark fishery.

CONCLUSIONS

While factors influencing both hook soak time and at-vessel mortality of shark species captured on bottom longlines requires further study, this work highlights species-specific differences for both hooking times and at-vessel mortality. Sharks were captured on longlines in the following order, fastest to slowest: Atlantic Sharpnose Shark → Blacknose Shark → Great Hammerhead → Scalloped Hammerhead → Nurse Shark → Sandbar Shark → Bull Shark → Blacktip Shark → Tiger Shark → Dusky Shark. Over 60% of sharks were hooked within 4 h. Shark resilience to time on the line varied as follows, from greatest to least: Sandbar Shark → Dusky Shark → Blacknose Shark → Great Hammerhead → Scalloped Hammerhead → Blacktip Shark → Atlantic Sharpnose Shark. Many of the factors affecting at-vessel mortality would be difficult for fishers to control for, but hook soak time is the most likely. Limiting fishing sets to shorter set soak times would maximize live release of prohibited and nontarget catch. This will also have a positive effect on other nontarget, but vulnerable, species. An important distinction when considering set soak times is that individual hook soak times in some cases may be as much as twice the set soak time. Especially when a fishing vessel undertakes a "reverse haul," and the last hook set is the first hook hauled, as this increases the amount of soak time for the first hook set. Our analysis suggests that hook soak times of 3 h should be sufficient to maximize catch, while reducing line mortality. This may require set soak times of 2 h or less, though further study is necessary. Despite some evidence that the use of circle hooks may lead to decreased mortality of sharks in commercial longline fisheries in other studies, we found that circle hooks did not significantly reduce at-vessel mortality for Atlantic Sharpnose Shark, Sandbar Shark, Nurse Shark, Blacknose Shark, Bull Shark, and Tiger Shark over large J-style hooks. Given the potential mitigation benefits to other nontarget protected species (Swimmer et al. 2017) and that target catchability was not decreased when using circle hooks, the requirement of the use of circle hooks throughout the shark bottom longline fishery would likely not reduce the fishery yield for the industry and would close any gap for those fishers that still use smaller J-style hooks.

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