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Stress response and post-release mortality of blacktip sharks (*Carcharhinus limbatus*) captured in shore-based and charter boat-based recreational fisheries

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Summary: In the coastal waters of the southeastern U.S., the blacktip shark (*Carcharhinus limbatus*) is targeted by recreational anglers, and is currently the most commonly captured large coastal shark species. We estimated PRM rates for blacktip sharks captured on rod-and-reel by shore-based and charter boat-based fishermen using acoustic transmitters (n = 81). Additionally, 24 individuals were double-tagged with pop-off satellite archival tags (PSATs) to validate the survivorship results obtained from the acoustic transmitters. The stress response associated with both recreational capture methods was quantified using numerous blood chemistry parameters. Overall, 18.5% of blacktip sharks died post-release (17.1% shore-based; 20.0% charter boat-based). The survivorship results inferred from acoustic transmitters were consistent with results inferred from PSATs, validating our use of acoustic transmitters to assess PRM in blacktip sharks. Fight time (i.e. time on the line) had a significant effect on blood pH, lactate, hematocrit, potassium, and glucose for sharks caught from shore, but only on lactate for sharks caught from charter boats. Fifty percent of foul-hooked sharks (i.e. sharks hooked anywhere but the jaw) died post-release.

Introduction

Given the observed increases in the popularity of recreational shark fishing (Press et al. 2016), coupled with an increasing emphasis on catch-and-release (Bartholomew and Bohnsack 2005), the determination of gear- and species-specific post-release mortality estimates is critical to the effective management of shark species. Through collaboration with recreational anglers, this study assessed PRM rates of blacktip sharks captured and released in both the shore-based and charter boat-based recreational fisheries, and quantified the physiological stress response associated with both recreational capture methods.

2. Materials and methods

2.1 Sampling location and design

Blacktip sharks were caught with rod-and-reel by participating recreational anglers from the shore (i.e. beach) and onboard charter fishing boats. All fishing from charter boats was conducted by the clients who hired the charter, and thus a wide range of angler experience was sampled. Anglers used their personal fishing equipment, which varied in size and strength, and no input was provided by the authors on the fishing equipment (e.g. rod and reel type/size, hook type/size) or capture techniques used. Sampling was conducted from May to October of 2017 and from February to October of 2018, in the coastal waters of South Carolina and Florida, at locations chosen by participating anglers (Fig. 1B, C). During each angling trip, reel type (i.e. conventional level wind versus spinning), hook type (circle versus J), and surface water temperature (°C) were recorded.

Once an angler hooked a shark, the 'fight time,' defined as the time from the initial strike until the time the shark was secured by anglers, was recorded to the nearest second. Once secured, the shark was sampled in the state that the angler handled it (e.g. sharks caught from charter boats were either sampled onboard the boat or in the water, depending on whether or not the charter captain decided to bring the shark onboard for pictures/hook removal). All sharks caught by shore-based anglers were brought out of the water and onto the beach. Sharks were then sampled while the recreational anglers completed their routine (which often included hook removal, measurement, and photographs), to minimize any increased handling time due to the sampling procedure. Blood was drawn via caudal venipuncture immediately after the shark was secured, tag(s) were applied, and sharks were measured to the fork length (cm) and sexed.

Once the sampling procedure was complete, the recreational anglers were responsible for releasing the shark. The 'handling time,' defined as the time from when the shark was initially secured to the release of the shark, was recorded to the nearest second. Upon release, the condition of the shark was assigned to one of five categories, ranging from condition 1 (excellent) to condition 5 (moribund), based on the shark's behavior at release (Table 1). If the anglers decided to revive the shark (i.e. hold the shark in the water until they deemed it strong enough for release), the ‘revival time’ was recorded. Hook status (removed or retained) and hook location were also recorded. The authors provided no input to the anglers regarding hook removal, with some anglers choosing to leave hooks that could not be easily removed.

2.2 Blood chemistry

Blood samples (3 mL) were drawn via caudal venipuncture, using 18-gauge sterilized needles and heparin-rinsed syringes, and samples were immediately injected into 10 mL sodium heparin vacutainers (Becton, Dickinson and Co.). To avoid compromising blood gas accuracy after phlebotomy (Whitney et al. 2017), a subsample of whole blood (90 μL) was immediately (within 30 s) analyzed for pH and lactate using an i-STAT portable blood analyzer (Abaxis Inc., Union City CA) with a CG4+ cartridge. This analyzer has been used in prior field studies on elasmobranch species (e.g. Mandelman and Skomal 2009; Brooks et al. 2012; Gallagher et al. 2014), and measurements of pH and lactate have been validated for relative accuracy in ectothermic sharks (Gallagher et al. 2010; Harter et al. 2015). Measurements of blood pH were temperature corrected to water temperatures at the locations of capture using the following equation:

(1) $pH_{TC} = pH_{M} - 0.011(T - 37)$

where M and TC refer to the measured and temperature corrected values, respectively (Mandelman and Skomal 2009; Gallagher et al. 2010; Brooks et al. 2012; Kneebone et al. 2013; Gallagher et al. 2014; Whitney et al. 2017). All pH values subsequently reported herein have been temperature corrected in this manner.

A separate subsample of whole blood (0.2 mL) was simultaneously placed on ice (within 30 s) for hematocrit analysis, which was completed within 4 h of capture (Manire et al. 2001). At the time of hematocrit analysis, whole blood samples ($n = 3$ per shark) were transferred into microcapillary tubes and centrifuged (Vernitron Medical Products Inc., Carlstadt NJ) for 5 min at 10,000 RPM (10,062 × g). Hematocrit was determined as the percentage of total blood volume comprised of red blood cells, calculated using an EZ Reader Microhematocrit Card (LW Scientific Inc., Lawrenceville GA).

The remaining whole blood was centrifuged (E8 Portafuge, LW Scientific Inc., Lawrenceville GA) for 5 min at 3,500 RPM (1,534 × g), to separate the plasma and the red blood cells. Subsamples of plasma (3 × 0.5 mL) were frozen immediately in liquid nitrogen and, subsequently, stored at –80 °C. At the time of plasma electrolyte analysis, plasma samples were thawed, diluted 2:3 with deionized water (plasma:dH_2O), and approximately 55 µL of the diluted samples were injected into a Critical Care Xpress (CCX, Nova Biomedical, Waltham MA) benchtop analyzer to quantify Na^+, Cl^-, K^+, Ca^{2+}, Mg^{2+}, and glucose. All concentrations were within the detection limits of the instrument.

2.3 Post-release mortality

Blacktip sharks were tagged with external case acoustic transmitters (18.2 × 88 mm; V16-4H, 30 s delay; Vemco Ltd., Bedford, Nova Scotia, Canada) by threading monofilament through a hole drilled into the musculature at the base of the first dorsal fin. This external attachment technique allowed for short handling times and thus minimized any bias introduced by the tagging procedure (Kilfoil et al. 2017). Survivorship was assessed by passively monitoring sharks following release and examining movements of sharks among fixed acoustic receivers deployed along the eastern coast of the U.S. as part of both the Atlantic Cooperative Telemetry (ACT) and the Florida Atlantic Coast Telemetry (FACT) Networks (Fig. 1A). As most mortalities associated with a capture event occur within 12 h of release (Marshall et al.

2015; Whitney et al. 2017; Talwar et al. 2017), sharks that were detected multiple times by an acoustic receiver more than 10 days post-release were considered to have survived the capture event. Moreover, because tags that are ingested during predation events are typically regurgitated within around 5 days of ingestion (Rogers et al. 2017), only assuming survival for individuals detected more than 10 days post-release accounts for possible capture-related predation events.

To validate the survivorship results obtained from the acoustic transmitters, a subset of sharks were also tagged with pop-off satellite archival tags (PSATLife; Lotek Wireless Inc., St. John's, Newfoundland Labrador, Canada). The PSATs (40 × 125 mm) are designed for monitoring post-release survival, and were programmed to record pressure, external temperature, and light intensity every 10 s for a 28-day deployment. If the PSAT was not recovered, summary data were obtained from PSATs via satellite comprised pressure-temperature profiles (5-min means). Recovered PSATs allowed for more detailed analysis of the entire archived dataset, which included pressure, external temperature, and light intensity measured every 10 s. PSATs were programmed to release prematurely if pressure values remained constant (±5 dBar) over a 3-day period, consistent with a dead shark on the ocean floor or a shed tag floating on the surface (Heberer et al. 2010). The PSATs were attached in the same way as the acoustic transmitters, by threading monofilament through a hole drilled into the musculature at the base of the first dorsal fin. Survival of sharks tagged with PSATs was inferred by assessing the pressure, external temperature, and light intensity profiles, following protocols previously used to infer mortality from PSAT data records (Heberer et al. 2010).

2.4 Data analyses

Post-release mortality rates were calculated as the percentage of the total number of tagged individuals that either died after release (as indicated by a PSAT), or were never detected by an acoustic receiver more than 10 days post-release, and were thus assumed to have died as a result of capture. Linear regressions were used to determine if the fight time (i.e. time on the line) had an effect on the blood chemistry parameters. Either analyses of variance (ANOVA) or analyses of covariance (ANCOVA) were used to determine if the blood chemistry parameters differed between the two recreational capture methods.

To predict PRM using the measured blood chemistry parameters, generalized linear models (GLMs) with a binomial probability distribution and a logit link function were fitted to the data for all sharks combined (n = 81) and then separately to sharks caught from shore (n = 41) and sharks caught from charter boats (n = 40) (Schlenker et al. 2016; Talwar et al. 2017). Before constructing the GLMs, principal components analyses (PCA) were performed, in order to examine potential correlations between explanatory variables and to reduce the number of explanatory variables included in the GLMs. The full models for all sharks combined and for sharks caught from shore described the relationships between PRM as a binary response variable and 4 potential explanatory variables, including pH, K^+, Na^+, and glucose. The full model for sharks caught from charter boats included pH, K^+, glucose, and hematocrit. Nonsignificant factors were removed in backwards stepwise fashion, starting with the least significant factor, while evaluating the increases in deviance and Akaike's information criterion (AIC; Akaike 1973) with each removal (Talwar et al. 2017). The model with the fewest number of explanatory variables and lowest AIC was considered the candidate model.

To predict PRM using the observed capture characteristics, GLMs were used to describe the relationship between PRM as a binary response variable and water temperature, fight time, handling time, hook location (not foul-hooked versus foul-hooked), release condition, and capture method (shore-based versus charter boat-based). As above, GLMs were fitted to the data for all sharks combined (n = 81) and then separately to sharks caught from shore (n = 41) and sharks caught from charter boats (n = 40). The candidate model was again selected in a backwards stepwise fashion and had the fewest number of explanatory variables and lowest AIC.

Fisher's exact tests were used to test the null hypothesis that the distribution of survivors and mortalities was equal across both hook locations and release conditions. All analyses were conducted using the R programming language (version 3.5.1; R Core Team 2018), and all graphs were created in RStudio (version 1.1.456). The level of significance for all tests was $\alpha = 0.05$.

3. Results

3.1 Capture Characteristics

A total of 81 blacktip sharks were caught and tagged with acoustic transmitters (n = 41 shore-based; n = 40 charter boat-based). A subset of those individuals (n = 12 shore-based; n = 12 charter boat-based) were also tagged with pop-off satellite archival tags (PSATs). There were no significant differences in fork length, fight time, handling time, or water temperature between recreational capture methods (Table 2). All participating recreational anglers chose to use circle hooks, and hook locations were as follows: jaw, including corner, bottom, and top jaw (n = 75), basihyal (tongue-like structure; n = 3), gut (n = 1), throat (n = 1), and tail (n = 1). Any shark not hooked somewhere in the jaw was considered to be 'foul-hooked' in all subsequent analyses. Anglers chose to remove the hook in all but three instances (corner jaw, n = 1; basihyal, n = 1; gut, n = 1).

3.2 Post-Release Mortality

Fifteen sharks (n = 7 shore-based; n = 8 charter boat-based) died within 10 days of being released by recreational anglers, resulting in post-release mortality rates of 17.1% (shore-based) and 20.0% (charter boat-based). No immediate mortalities were observed, with all individuals swimming away at the time of release. Only 4 of the 81 tagged sharks were revived by anglers before being released, and revival times ranged from 1 to 4 min. Six of the fifteen mortalities were assigned release conditions of 3 ('fair') or 4 ('poor'), due either to signs of physical injury or trauma (e.g. excessive bleeding from the hook location) or a complete lack of movement during the handling procedure and difficulty swimming post-release. Additionally, two of the mortalities were either hooked in the tail (n = 1) or hooked in the jaw but tail-wrapped in the fishing line (n = 1) and were reeled in backwards. The seven remaining mortalities presented no signs of injury or trauma and were assigned release conditions of 1 ('excellent') or 2 ('good').

Five of the fifteen sharks that died were tagged with both PSATs and acoustic transmitters (Table 3), whereas the other ten mortalities were confirmed from acoustic data only. Data obtained from these PSATs indicate that two PSATs were ingested within 6 h of being deployed. Shark #9 was actively swimming when the PSAT was ingested 6 h post-release (Fig. 2A). The PSAT reported fluctuating pressure and light intensity for the 6 h prior to ingestion (pressure min: 0 dBar, pressure max: 9.72 dBar; light min: 93, light max: 384), consistent with vertical movements in the water column during daytime hours. Subsequent to ingestion, the tag reported darkness for 3 days followed by a return to a cyclical day-night pattern (Fig. 2A). Brief increases in light intensity during the ingestion period may indicate partial regurgitation of the foreign object (i.e. PSAT). Shark #43, on the other hand, sank to the bottom immediately after release, where it remained for 5 h before the tag was ingested (Fig. 2B). The PSAT reported very little variation in pressure during the 5 h period prior to ingestion (pressure min: 19.84 dBar, pressure max: 21.59 dBar), and a complete lack of light intensity (light min: 98, light max: 109), consistent with a dead shark lying on the seafloor. Subsequent to ingestion, and similar to shark

#9, the PSAT reported darkness for 4.5 days followed by a return to a cyclical day-night pattern (Fig. 2B).

Of the 24 PSATs deployed, all but 2 PSATs reported data to the Argos satellite system, and 12 PSATs were physically recovered – including one of the two that did not report. Excluding the five mortalities inferred from PSATs, 12 PSATs detached prematurely and 6 PSATs were retained for the entire 28-day deployment. Tag retention periods ranged from 17 min to 28 days (mean = 11.8 ± 10.6 days). PSAT pressure profiles indicated that none of the premature detachments resulted from tags remaining at constant depth, which would have triggered the burning of the release pin. Thus, the two most plausible explanations for the premature detachments are that the anchors were pulled out of the dorsal musculature or the tethers broke. Two of the 12 PSATs that were physically recovered, both of which detached prematurely, presented with numerous bite marks, suggesting that the tags were bitten off.

The data obtained from the acoustic transmitters associated with the five double-tagged mortalities indicate the same survivorship outcomes as the PSATs (Fig. 3). None of the acoustic transmitters from mortalities inferred by PSATs were detected on an acoustic receiver more than 10 days post-release. Both of the acoustic transmitters associated with the PSATs that were ingested were detected on acoustic receivers during the period that the PSAT was ingested. However, the acoustic transmitters were not detected following regurgitation of the PSATs (within 5 days of ingestion), suggesting that both the PSATs and acoustic transmitters were ingested and regurgitated at the same time.

A total of 175,997 acoustic detections were recorded by acoustic receivers along the eastern coast of the United States (Fig. S1), and each acoustic transmitter was detected an average of 2,147 times (sd = 2,300 detections). The greatest movements detected by acoustic telemetry were to waters off the Hudson Shelf, NY to the north and Miami, FL to the south (1,734 km minimum straight-line distance). Seventeen of the 19 double-tagged sharks that survived were detected by acoustic receivers while the PSAT was still attached, and 18 were detected after the PSAT detached. Additionally, for the individual whose PSAT did not report and was not recovered, a total of 6,241 acoustic detections were recorded by 88 different acoustic receivers over 637 days, ranging from Back Sound, NC to Fort Pierce, FL, verifying survivorship.

3.3 Physiological Effects of Capture

Fight time (i.e. time on the line) had a significant effect on blood pH, hematocrit, lactate, potassium, and glucose. Blood pH decreased significantly ($p = 0.0185$; $R^2 = 0.1121$; Fig. 4A), while lactate ($p = 0.0000$; $R^2 = 0.3981$; 4B), hematocrit ($p = 0.0057$; $R^2 = 0.1632$; Fig. 4C), potassium ($p = 0.0241$; $R^2 = 0.1013$; 4D), and glucose ($p = 0.0180$; $R^2 = 0.1131$; Fig. 4E) increased significantly with increasing fight times in sharks caught from shore. Lactate ($p = 0.0000$; $R^2 = 0.4538$; Fig. 4B) increased significantly with increasing fight times for sharks caught from charter boats. There was no change in sodium, chloride, calcium, or magnesium associated with fight time for either capture method ($p > 0.05$). The effect of fight time on any of the blood chemistry parameters did not differ between capture methods (ANOVA or ANCOVA; $p > 0.05$; Fig. 4).

3.4 Predicted Post-Release Mortality

The GLM analysis determined that a model including both pH and glucose provided the best fit to binary PRM data for all sharks combined ($n = 81$; $AIC_{Full\ Model} = 74.96$; $AIC_{Reduced\ Model} = 71.24$) and to sharks caught from shore ($n = 41$; $AIC_{Full\ Model} = 39.65$; $AIC_{Reduced\ Model} = 36.47$), while a model including only potassium provided the best fit for sharks caught from charter boats (n = 40; $AIC_{Full\ Model} = 43.13$; $AIC_{Reduced\ Model} = 38.40$). None of the blood chemistry parameters were a significant predictor of mortality in any of the three candidate models ($p > 0.05$).

With respect to predicting PRM using the observed capture characteristics, a GLM model including only release condition provided the best fit to binary PRM data for all sharks combined (n = 81; $AIC_{Full\ Model} = 72.52$; $AIC_{Reduced\ Model} = 63.24$) and for sharks caught from charter boats (n = 40; $AIC_{Full\ Model} = 39.63$; $AIC_{Reduced\ Model} = 33.39$). A model including water temperature, fight time, and release condition provided the best fit for sharks caught from shore (n = 41; $AIC_{Full\ Model} = 41.33$; $AIC_{Reduced\ Model} = 34.34$). Fight time ($p = 0.0149$) and release condition ($p = 0.0241$) were significant predictors of PRM in the candidate model for sharks caught from shore.

Hook location (not foul-hooked versus foul-hooked) did not have a significant effect on the distribution of survivors and mortalities (Fisher's exact test, $p = 0.0738$). Of the individuals hooked in the jaw (including corner, bottom, or top jaw), 16.0% died, whereas 33.3% of individuals hooked in the basihyal died and 100% of individuals hooked either in the throat or tail died. The release condition assigned did not have a significant effect on the distribution of survivors and mortalities (Fisher's exact test, $p = 0.1280$). Of the individuals assigned a release condition of 'excellent', 18.4% died, whereas a condition of 'good' resulted in 8.3% mortality; 'fair' resulted in 20.0% mortality; and 'poor' resulted in 44.4% mortality (Fig. 5).

4. Discussion

The present study provides insights into both the physical and physiological effects of recreational rod-and-reel capture on the blacktip shark, and how these effects influence post-release mortality (PRM) rates. Furthermore, this study provides data on the physiological stress and mortality experienced by a shark species caught from shore, in a rapidly expanding recreational shore-based fishery. PRM rates were 17.1% (shore-based) and 20.0% (charter boat-based), and the survivorship results inferred from acoustic transmitters were consistent with results inferred from PSATs, validating our use of acoustic transmitters to assess PRM. Significant physiological changes were documented in the blood chemistry, and changes were influenced by the fight time (i.e. time on the line).

4.1 Post-Release Mortality

The PRM rates observed in the present study are higher than PRM rates of many other shark species caught on rod-and-reel, such as 10% for shortfin mako sharks (French et al. 2015), 12.5% for juvenile lemon sharks (*Negaprion brevirostris*) (Danylchuk et al. 2014), and 10% for Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) (Gurshin and Szedlmayer 2004). In addition, the observed PRM rates are approximately twice as high as that reported by Whitney et al. (2017) for blacktip sharks caught in the Florida charter boat-based recreational fishery (9.7%). This difference in PRM rates may be partially attributable to the higher incidence of physical injury or trauma (n = 6), foul-hooking (n = 6), and live predation (n = 1) observed in the present study but not by Whitney et al. (2017). All sharks captured in the present study were caught by recreational anglers using their own personal fishing equipment and thus a wide range of both angler experience and gear types/strengths were sampled. No at-vessel or at-shore mortalities were observed, which were observed to be 88% for blacktip sharks caught on longlines (Morgan and Burgess 2007), and all five of the mortality events inferred from PSATs occurred within 6 h of release. This result suggests that mortalities associated with rod-and-reel capture in the blacktip shark do not occur at landing but can occur up to 6 h post-release. This is consistent with previous research on blacktip sharks demonstrating that behavioral recovery from rod-and-reel capture takes an average of 10.5 h (Whitney et al. 2016). These results are also consistent with other studies that found that most capture-related mortalities in sharks occur within 1 to 4 h after release (Heberer et al. 2010; Marshall et al. 2015; Whitney et al. 2017).

4.2 Predation Post-Release

Post-release mortality rates of blacktip sharks may be influenced by the presence of larger shark species commonly found off the southeastern coast of the United States, such as tiger sharks (*Galeocerdo cuvier*), great hammerheads (*Sphyrna mokarran*), and bull sharks (*Carcharhinus leucas*) (Ulrich et al. 2007; Castro 2011). In the present study, data profiles from PSATs deployed on two blacktip sharks (#9 and #43) indicate that the tags were ingested within 6 h of deployment. Shark #9 was actively swimming at the time of PSAT ingestion, but may have been behaving erratically, as the PSAT was ingested (6 h post-release) within the behavioral recovery window for blacktip sharks caught on rod-and-reel (mean 10.5 h, Whitney et al. 2016). Shark #43 sank to the ocean floor immediately after release, where it remained for 5 h until the PSAT was scavenged. It was impossible to determine with certainty whether only the PSATs were consumed or the PSATs and the blacktip sharks were consumed. However, the acoustic data obtained from both sharks (#9 and #43) suggest that the acoustic transmitters were also ingested and regurgitated at the same time as the PSATs. Thus, it is unlikely that both the PSATs and acoustic transmitters were ingested without predation upon the blacktip shark itself. While this is the first example of live predation on a blacktip shark documented by a PSAT, Lear and Whitney (2016) documented post-release scavenging of a blacktip shark by a larger shark, and live predation events on other species are prevalent in the literature (e.g. white marlin *Tetrapturus albidus* and opah *Lampris guttatus*, Kerstetter et al. 2004; albacore *Thunnus alalonga*, Cosgrove et al. 2015; school sharks *G. galeus*, Rogers et al. 2017; Tolentino et al. 2017). Many shark species have been described to evert their stomachs in response to physical stimuli, such as the ingestion of foreign objects (e.g. shortfin mako sharks *Isurus oxyrinchus*, Brunnschweiler et al. 2011), and the timing between the ingestion and regurgitation events (3.0 and 4.5 days) is similar to that reported in other studies (school sharks *G. galeus*, 4-6 days, Rogers et al. 2017; bull sharks *C. leucas*, 6.8 days, Brunnschweiler 2009). Given that blacktip sharks are known to form large aggregations (Castro 2011), it is possible that conspecifics could have dislodged other PSATs without consuming the sharks, which could explain premature PSAT detachments observed in the present study (Rogers et al. 2017).

4.3 Validation of Acoustic Telemetry to Assess Survival

Through double-tagging individuals with both PSATs and acoustic transmitters, the results of the present study indicate that acoustic transmitters can be effectively used to assess PRM in migratory, coastal shark species (Kneebone et al. 2013; Kilfoil et al. 2017). In the present study, data obtained from the acoustic transmitters suggested the same survivorship outcome as the PSATs for all double-tagged individuals. In particular, none of the five mortalities confirmed from the PSATs were detected on an acoustic receiver more than 10 days post-release, while all 18 of the individuals that were confirmed to have survived from the PSATs were detected from 23 to 557 days post-release (224.8 ± 133.9 days; mean ± sd).

The electronic tags designed for assessing PRM (e.g. PSATs) can be cost prohibitive (Musyl et al. 2011; Rogers et al. 2017; Whitney et al. 2016), forcing many researchers to use relatively small sample sizes and/or to only deploy tags on individuals that they believe have a chance at survival (i.e. so as to not "waste" a tag on an individual that they believe will die), potentially biasing PRM estimates (Rogers et al. 2017). Additionally, the vast majority of PSATs (~ 80%) are shed before their programmed pop-up date (Arnold and Dewar 2001; Gunn and Block 2001), while others often fail to report data to the satellite system altogether (Musyl et al.

2011). In the present study, 67% of PSATs deployed on surviving sharks were shed prematurely, and two PSATs failed to report to the satellite system (8.3% failure rate). Thus, while the cost of such electronic tags already precludes the use of large sample sizes, researchers are also faced with relatively high tag failure rates. The lower cost of acoustic transmitters could allow for the inclusion of much larger sample sizes, and thus more robust assessments of PRM. Additionally, the smaller size of acoustic transmitters, when compared to other electronic tags (e.g. PSATs), could reduce any potential effects of the tag on a shark's behavior post-release and are thus likely more appropriate for the assessment of PRM in smaller fish species. While the effectiveness of using acoustic transmitters to assess PRM depends on the prevalence of acoustic receivers, the applicability of the method will likely increase, as the number of acoustic receivers deployed along the eastern coast of the United States continues to increase (Kneebone et al. 2013).

4.4 Physiological Effects of Capture

The stress experienced by captured sharks has traditionally been quantified through an assessment of the acid-base status of the blood. In the present study, pH decreased with increasing fight time for sharks caught from shore, while lactate increased for both capture methods, suggesting that blacktip sharks experienced proton (H^+) loading in the blood and tissues due to the dissociation of lactic acid generated by anaerobic glycolysis (Skomal and Mandelman 2012; Kneebone et al. 2013). These results suggest that rod-and-reel capture of blacktip sharks results in blood acidosis that is at least partially metabolic in origin, and are consistent with the results reported by Whitney et al. (2017). Mandelman and Skomal (2009) found that increases in pCO_2 explained all of the variation in pH in blacktip sharks captured via longlines, suggesting that acidemia in blacktip sharks caught via longline is driven strictly by a respiratory acidosis. Because measurements of pCO_2 made by the i–STAT system have not been validated, pCO_2 values are not reported in the present study, and thus the potential contribution of CO_2 to the observed acidosis cannot be determined. Regardless, differences in lactate profiles between studies suggest that the origin of the acidosis could be associated with the type of gear used, and support the growing awareness that “fishery-specific” assessments of the stress experienced by captured sharks are necessary (Skomal 2007; Heberer et al. 2010).

In general, exhaustive exercise leads to elevated concentrations of both glucose (Sherwin et al. 1980; Sheridan 1988) and potassium (Medbo and Sejersted 1990). Catecholamines are responsible for stimulating glucose release from the liver during exercise (i.e. glycogenolysis; Sherwin et al. 1980; Sheridan 1988) to meet the energy demands of the muscles, and it has been suggested that the mobilization of glucose may be integral to survival (Marshall et al. 2012). Increases in plasma potassium can be a result of several factors, including a release of potassium from muscle cells due to increased electrical activity (Fenn 1938; Sejersted and Sjogaard 2000) and a decrease in plasma water, due to increased intracellular lactate levels which cause a net fluid shift from extracellular to intracellular compartments (van Dijk and Wood 1988; Wood 1991). In the present study, both glucose and potassium increased with increasing fight times for sharks caught from shore, but not for sharks caught from charter boats. As fight times (i.e. time on the line) did not differ between capture methods, elevated glucose and potassium levels in sharks caught from shore may reflect a higher degree of struggling on the line. Moreover, rhabdomyolysis, a syndrome characterized by muscle necrosis and the release of intracellular electrolytes, often due to muscle trauma associated with intense exercise, can also lead to elevated potassium concentrations (Keltz et al. 2013). The origin of the high glucose and potassium concentrations in sharks caught from shore could simply be a normal response to exercise, but conditions such as rhabdomyolysis cannot be excluded.

The effect of fight time on numerous blood chemistry parameters for sharks caught from shore (i.e. pH, lactate, hematocrit, potassium, and glucose), but not for sharks caught from charter boats (i.e. only lactate), could be a result of the tackle (i.e. fishing gear) used by the participating recreational anglers. In particular, the majority of sharks caught from shore were caught using spinning reels (76%), while the majority of sharks caught from charter boats were caught using conventional level wind reels (85%). Because conventional reels typically have a higher drag capacity than spinning reels, making it more difficult for hooked fish to "run", conventional reels may restrict the movement of captured sharks and thus lessen the degree of muscular exertion and metabolic stress. Additionally, many shore-based fishermen put out far more fishing line initially (e.g. a couple hundred yards, in order to reach deeper water), which may give the shark more room to "run", both vertically and horizontally in the water column. While traditional sportfishing ethics has encouraged the use of light tackle to "give the fish a fighting chance", research has shown that slowly and carefully angling a fish can potentially exacerbate the stress response (Malchoff and MacNeill 1995). The results of the present study support the use of heavy fishing tackle, to minimize the fight time and thus likely reduce the physiological stress experienced by captured sharks. Future research employing the use of repetitive blood sampling (e.g. before and after handling by anglers) could improve our understanding of the effects of capture on shark species, and how those effects are influenced by both gear types and handling techniques.

Overall, blacktip sharks caught on rod-and-reel (the present study; Whitney et al. 2017) exhibit relatively less drastic physiological disruptions than individuals caught on longlines (Mandelman and Skomal 2009; Marshall et al. 2012) and drumlines (Gallagher et al. 2014; Jerome et al. 2018). Mean blood lactate values for blacktip sharks caught on longlines (14.82

mmol l^{-1} Mandelman and Skomal 2009; 36.8 mmol l^{-1}, Marshall et al. 2012) and drumlines (8 mmol l^{-1}, Gallagher et al. 2014; 6.3 mmol l^{-1}, Jerome et al. 2018) are much higher than the mean lactate value reported in the present study (2.48 mmol l^{-1}). The concentrations of plasma electrolytes in blacktip sharks caught on longlines (potassium: 10.2 mmol l^{-1}, sodium: 298 mmol l^{-1}, Marshall et al. 2012), are also higher than the values reported in the present study (potassium: 5.5 mmol l^{-1}, sodium: 273 mmol l^{-1}). Collectively, the more drastic physiological changes observed in blacktip sharks captured via longline or drumline are likely due to the duration of the struggle on the line (e.g. up to 3 hours, Mandelman and Skomal 2009; 2-12 hours, Marshall et al. 2012; mean 46.5 min, Jerome et al. 2018).

4.5 Predicting Post-Release Mortality

Mortality estimates of released fish are critical components of total fishery mortality estimates and are thus of critical importance to fisheries managers. Because the direct estimation of PRM across fisheries is unrealistic, previous studies have aimed to predict PRM through the use of blood chemistry parameters (Moyes et al. 2006; Heberer et al. 2010; Schlenker et al. 2016; Talwar et al. 2017) and various capture characteristics (Manire et al. 2001; Hueter et al. 2006; Musyl and Gilman 2018). In the present study, none of the blood chemistry parameters could be used to predict mortality with any degree of significance. As all blood samples were screened for a suite of blood chemistry parameters (including pH, lactate, hematocrit, sodium, chloride, potassium, calcium, magnesium, and glucose), the lack of ability to use any of the blood parameters to predict mortality suggests that many of the observed mortalities were not a result of the physiological stress associated with rod-and-reel capture. In general, the release condition assigned was the best predictor of PRM, suggesting that many of the mortalities presented with observable signs of injury or trauma. Injuries were often related to the location of the hook and typically involved significant bleeding.

In the present study, 6 of the 81 blacktip sharks tagged were considered to be foul-hooked (i.e. hooked somewhere but the jaw), with hook locations of the basihyal, throat, gut, and tail. Three of the six foul-hooked sharks died within 10 days of release, for a foul-hooked PRM rate of 50%. Hook location has been shown to influence survival in many species (Muoneke and Childress 1994), and mortality is often associated with damage to the gills or visceral tissue caused by deeply embedded hooks (Heberer et al. 2010). In the present study, all recreational anglers chose to use circle hooks – no input was provided by the authors on the type or size of hook used. Thus, while the participating recreational anglers tended to be conservation-minded and were vocal about the importance of using circle hooks, it is likely that instances of foul-hooking would have been much higher if J hooks were used (Prince et al. 2002; Promjinda et al. 2008; Pacheco et al. 2011), although Whitney et al. (2017) found no difference in the incidence of foul-hooking or PRM when comparing the use of J and circle hooks.

The hook location can not only influence PRM through physical trauma (e.g. damage to gills or visceral tissue, Heberer et al. 2010), but it can also impair locomotion and the shark's ability to ventilate properly (Heberer et al. 2010). The blacktip shark is a ram-ventilating species that must be moving forward in order to ventilate its gills, as the orientation and morphology of elasmobranch gill slits preclude water flow over the gills when individuals are pulled backwards (Wegner et al. 2010; Heberer et al. 2010). Therefore, sharks hooked in the tail (i.e. caudal fin) and reeled in backwards experience reduced water flow over the gills and can only ventilate during brief periods of forward swimming. Indeed, in the present study, the only shark hooked in the tail did not survive the capture event. Additionally, the shark that was hooked in the jaw but tail-wrapped in the line and drug in backwards also died post-release. The survival implications for sharks hooked in the tail are well-documented. For instance, Sepulveda et al. (2015) found that 78% of common thresher sharks (*Alopias vulpinus*) hooked in the tail died post-release.

4.6 Conclusions

Overall, PRM rates for blacktip sharks captured in the shore-based and charter boat-based recreational fisheries are similar (17.1% shore-based and 20.0% charter boat-based) and are higher than PRM rates for many other shark species caught on rod-and-reel. The agreement between the results obtained from the acoustic transmitters and the PSATs verifies that acoustic transmitters can be effectively used to assess PRM in migratory, coastal shark species. Significant physiological disruptions were documented in the blood chemistry, and fight time had a significant effect on pH, lactate, hematocrit, potassium, and glucose. Fifty percent of foul-hooked sharks died post-release, with important implications for the use of gear and methods that reduce foul-hooking.

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Table 1. Release condition assigned to each tagged shark (n = 41 shore-based; n = 40 charter boat-based), based on the shark's behavior at the time of release. Values indicate the number of sharks assigned to each condition.

Condition	Issues observed and resulting diagnosis	Capture Method	
		Shore	Charter
1	"*Excellent*" Rapid swimming with no signs of distress	10	28
2	"*Good*" Stressed, swam away but appeared slow or disoriented	14	10
3	"*Fair*" Swam laboriously, or exhibited signs of physical trauma	10	0
4	"*Poor*" Attempted to swim, potential lethal physical trauma (e.g. excessive bleeding, deep hooking)	7	2
5	"*Moribund*" No effort to swim	0	0

Table 2. Capture characteristics, blood chemistry parameter values, and post-release mortality rates for blacktip sharks caught with rod-and-reel by recreational shore-based and charter boat-based anglers. Values are reported as mean ± sd.

Capture Method	**Capture Characteristics**							**Post-Release Mortality (%)**
	No. Tagged	Fight Time (min)	Handling Time (min)	Water Temp (°C)	% Female	Fork Length (cm)	Release Condition	
Charter	40	4.75 ± 2.02	3.55 ± 1.22	26.9 ± 2.5	71	124.2 ± 19.2	1.4 ± 0.7	20.0
Shore	41	5.09 ± 2.82	3.33 ± 1.16	27.7 ± 2.6	77	124.5 ± 24.4	2.4 ± 1.0	17.1

	Acid-Base Status			**Plasma Electrolytes and Metabolites**					
	pH_{TC}	Lactate (mmol l^{-1})	Hematocrit (%)	Na^+ (mmol l^{-1})	Cl^- (mmol l^{-1})	K^+ (mmol l^{-1})	Ca^{2+} (mmol l^{-1})	Mg^{2+} (mmol l^{-1})	Glucose (mg dL^{-1})
Charter	7.34 ± 0.08	2.01 ± 0.87	25.2 ± 2.1	273.1 ± 9.2	267.3 ± 7.3	5.7 ± 0.7	2.8 ± 0.1	1.1 ± 0.2	56.3 ± 5.9
Shore	7.33 ± 0.10	1.74 ± 1.07	24.1 ± 3.0	273.4 ± 7.4	266.5 ± 6.0	5.3 ± 0.7	2.7 ± 0.2	1.1 ± 0.3	58.3 ± 4.9

Table 3. Data records for sharks tagged with both pop-off satellite archival tags (PSATs) and acoustic transmitters. Mortalities are bolded.

Shark ID	Capture Method	Fight Time (min)	Handling Time (min)	Hook Location	Bleeding (Y/N)	Release Condition	Mortality (Y/N)
7	Shore	6.83	2.58	Jaw	N	3	N
9	**Shore**	**4.38**	**3.75**	**Jaw**	**Y**	**3**	**Y**
14	Charter	7.78	4.83	Jaw	N	2	N
17	Charter	4.50	4.10	Jaw	N	1	N
22	Charter	5.12	2.80	Jaw	N	1	N
27	Shore	8.90	6.68	Jaw	N	4	N
28	Shore	9.53	3.78	Jaw	N	3	N
30	**Shore**	**7.00**	**3.07**	**Jaw**	**N**	**1**	**Y**
31	Shore	5.82	2.72	Jaw	N	2	N
34	Shore	14.07	2.83	Jaw	N	4	N
40	Charter	3.13	2.80	Jaw	N	1	N
43	**Charter**	**4.02**	**3.17**	**Throat**	**Y**	**4**	**Y**
44	Charter	6.38	3.48	Jaw	N	2	N
52	Shore	5.62	2.78	Jaw	N	2	N
55	Shore	7.92	4.82	Jaw	N	2	N
58	**Shore**	**6.58**	**4.30**	**Tail**	**N**	**4**	**Y**
59	Shore	3.40	4.05	Jaw	N	2	N
61	Charter	3.92	4.70	Jaw	N	2	N
63	Shore	8.45	3.78	Gut	N	4	N
64	Charter	6.63	3.95	Jaw	N	1	N
67	Charter	6.38	2.73	Jaw	N	1	N
68	Charter	3.37	2.92	Jaw	N	2	N
75	Charter	5.37	5.68	Jaw	N	1	N
77	**Charter**	**8.95**	**4.88**	**Jaw**	**N**	**2**	**Y**

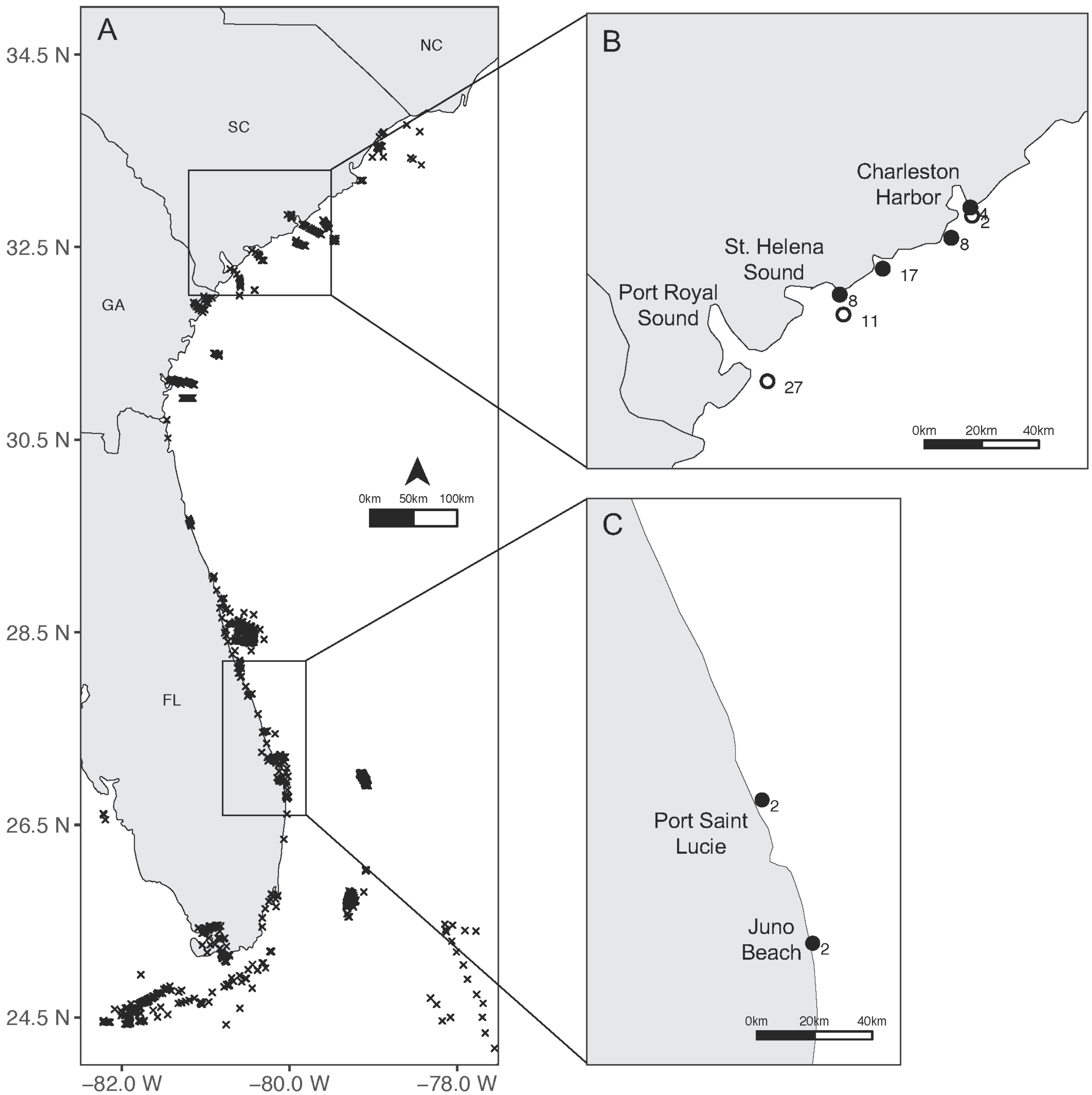

Figure 1. Locations of acoustic receivers along eastern coast of United States and sampling sites. **(A)** All X's denote locations of individual acoustic receivers. Insets show sampling sites off the coasts of **(B)** South Carolina and **(C)** Florida; open circles indicate charter boat-based sampling sites and solid circles indicate shore-based sampling sites. The numbers next to sample sites indicate the number of sharks tagged at each site.

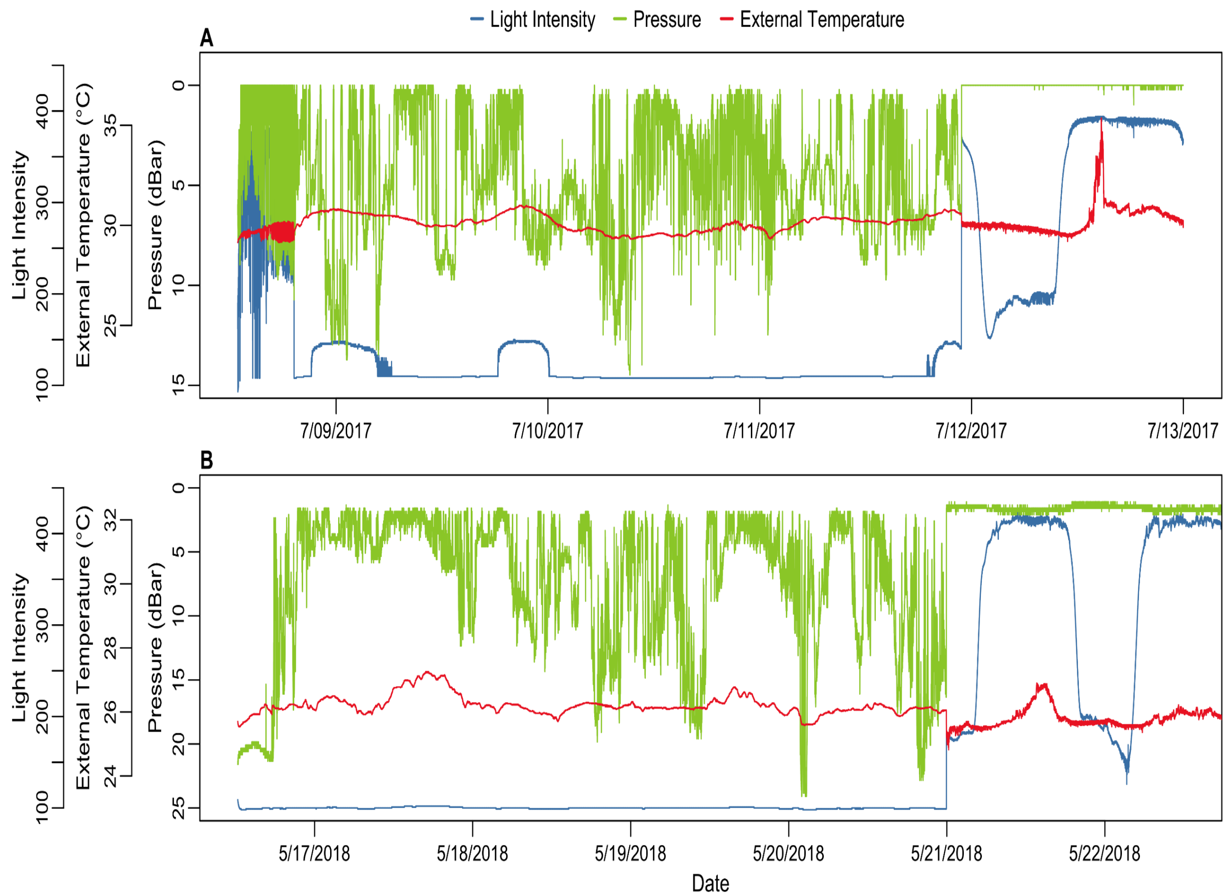

Figure 2. Pressure, external temperature, and light intensity profiles from two pop-off satellite archival tags (PSATs), showing a period of ingestion by another shark. Pressure is indicated by green lines; external temperature by red lines; and light intensity by blue lines. **(A)** Shark #9 was actively swimming at the time of ingestion, 6 h post-release. **(B)** Shark #43 sank to the ocean floor immediately following release, where it remained for 5 h prior to ingestion. Both PSATs were regurgitated within 5 days of ingestion.

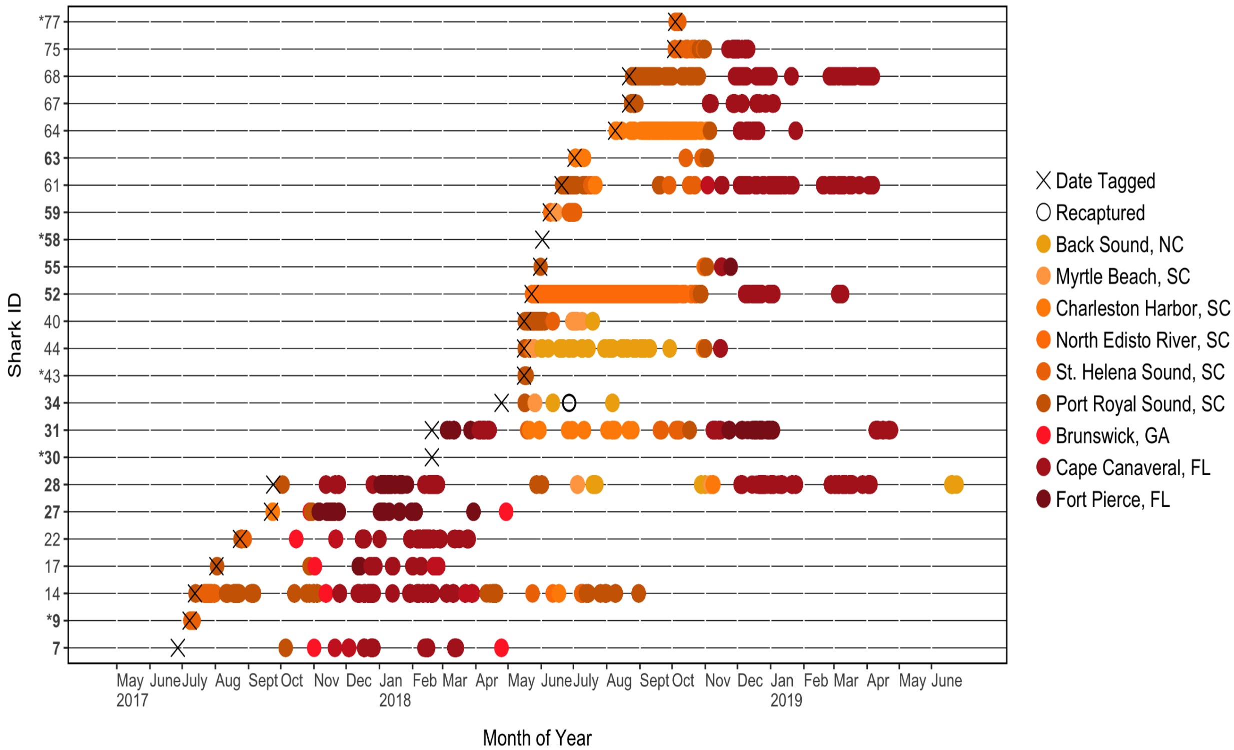

Figure 3. Acoustic detection data for sharks that were also tagged with pop-off satellite archival tags (PSATs; n = 24). Asterisks next to shark IDs indicate the five mortalities inferred from PSAT data. Bold-faced shark ID's indicate sharks caught from shore, while non-bold shark ID's indicate sharks caught from charter boats. None of the 5 known mortalities, as indicated by the PSAT data, were detected on an acoustic receiver more than 10 days post-release.

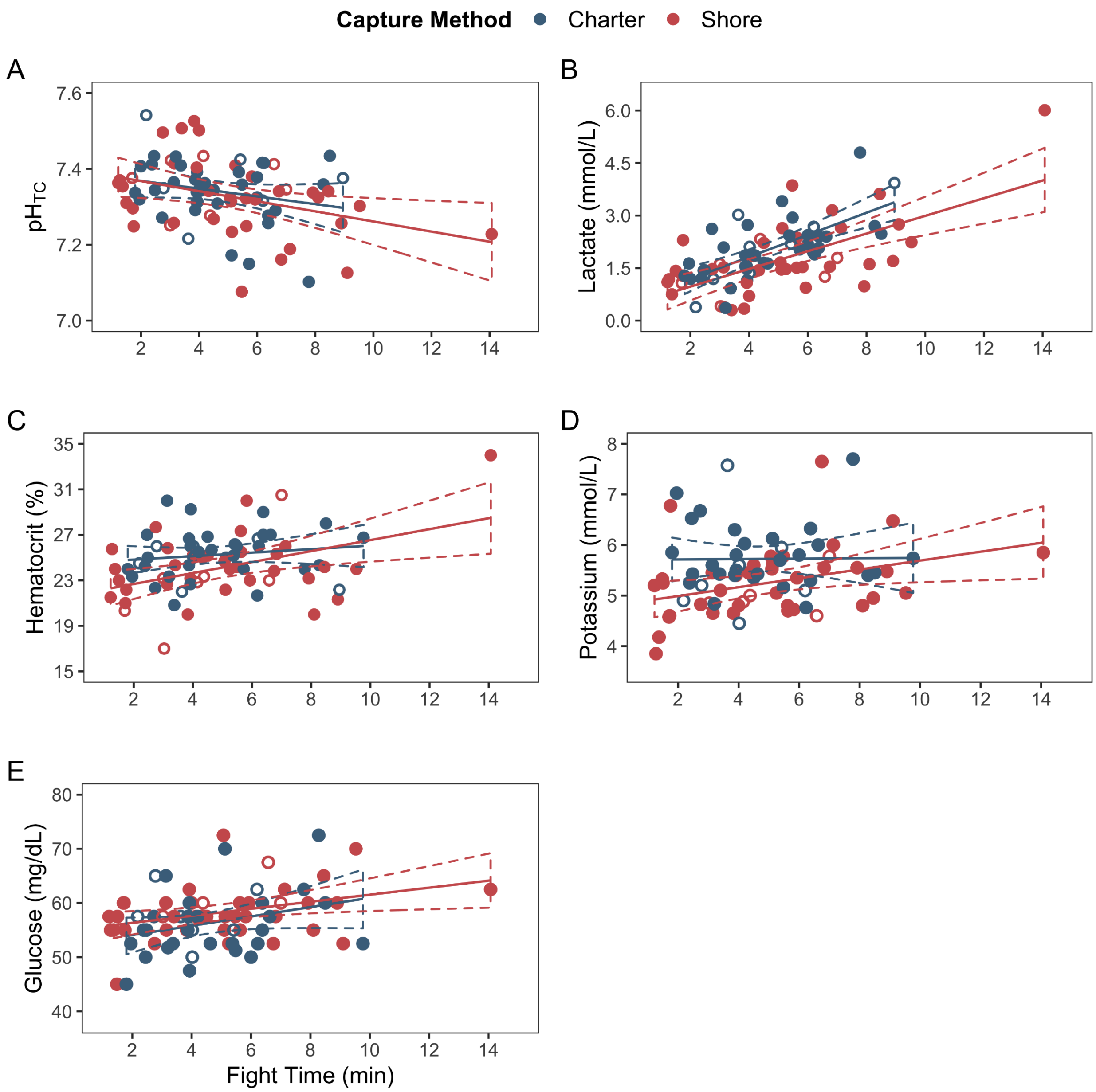

Figure 4. Linear regressions fitted to blood chemistry data from blood samples collected at the time that sharks were secured by recreational anglers, including **(A)** pH$_{TC}$, **(B)** lactate, **(C)** hematocrit, **(D)** potassium, and **(E)** glucose. Fight time refers to the time from the initial strike until the time the shark was secured by anglers. Colors represent the capture method used. Continuous lines indicate regression model predictions and dashed lines indicate 95% confidence intervals. Open circles indicate mortalities.

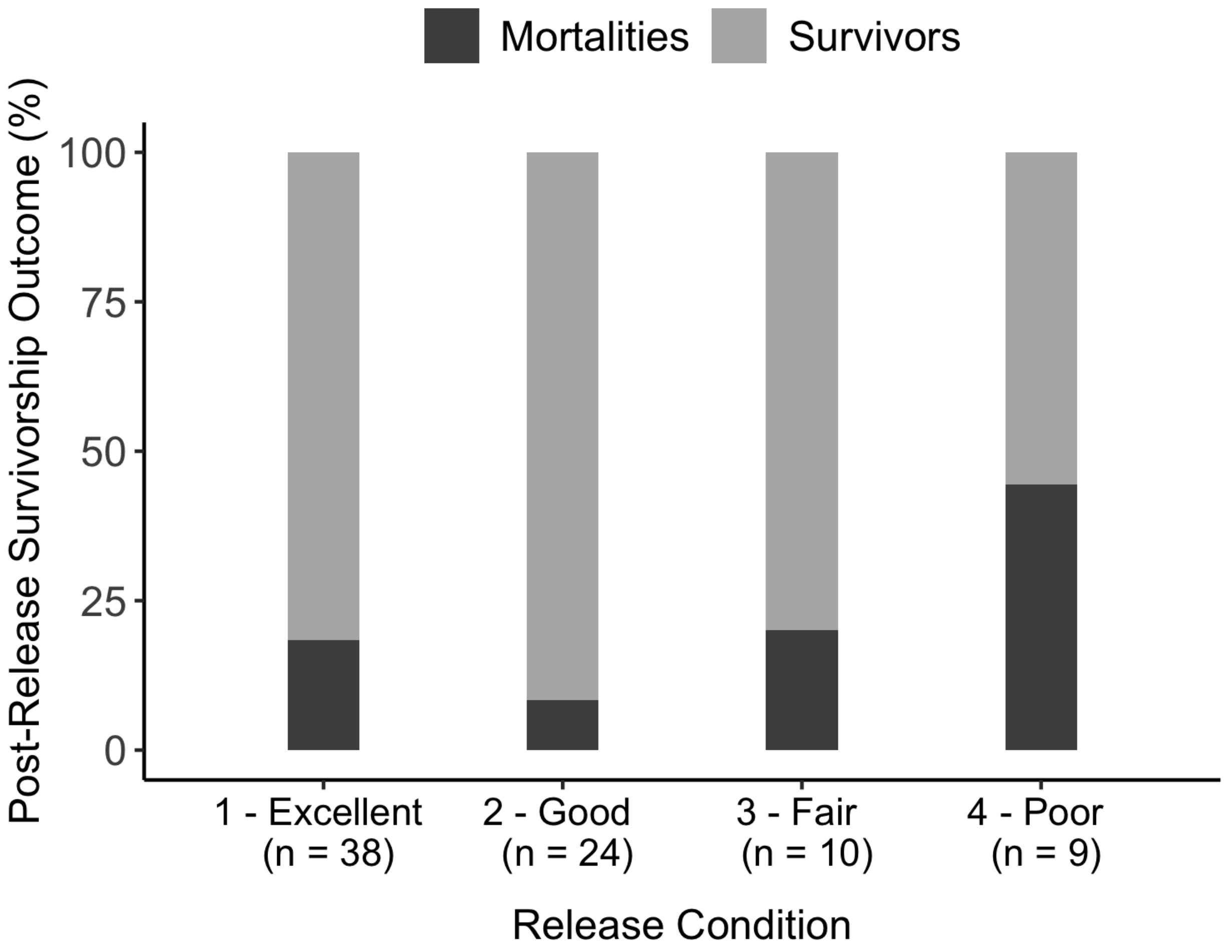

Figure 5. Distribution of survivors and mortalities among release conditions. The dark grey bars represent percent mortalities, while the light grey bars represent percent survivors. Of the individuals assigned a release condition of ‘excellent’, 18.4% died, whereas a condition of ‘good’ resulted in 8.3% mortality; ‘fair’ resulted in 20.0% mortality; and ‘poor’ resulted in 44.4% mortality.

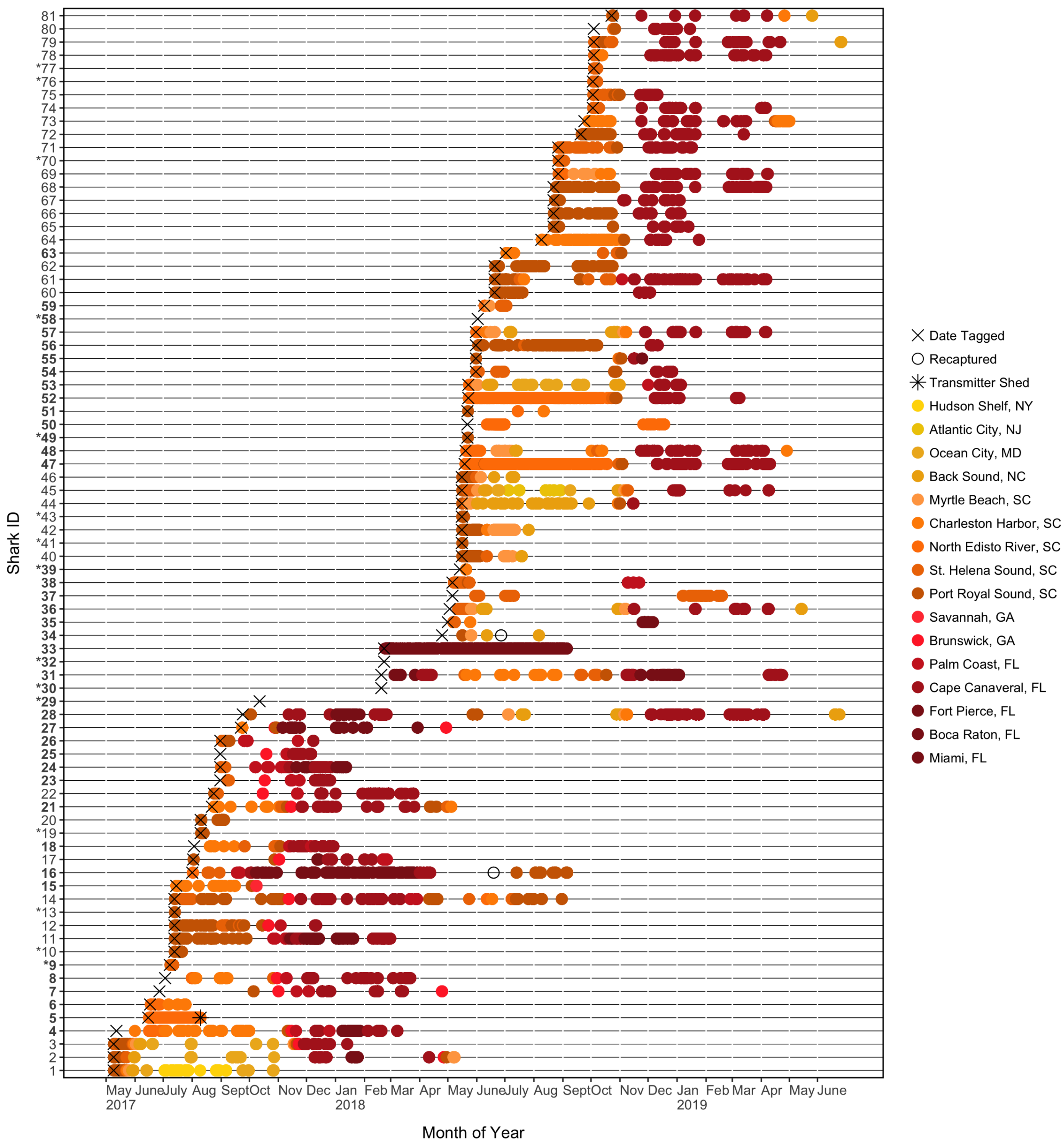

Figure S1. Acoustic detection data for all sharks (n = 81). Asterisks next to shark IDs indicate the fifteen mortalities. Bold-faced shark ID's indicate sharks caught from shore, while non-bold shark ID's indicate sharks caught from charter boats. None of the 15 known mortalities were detected on an acoustic receiver more than 10 days post-release.