Discard Mortality of Carcharhinid Sharks in the Florida Commercial Shark Fishery

Nicholas Whitney

SEDAR65- RD06

Received: 11/4/19

Discard Mortality of Carcharhinid Sharks in the Florida Commercial Shark Fishery

Principal Investigator:
Nicholas Whitney, Ph.D.*
Behavioral Ecology and Physiology Program
Mote Marine Laboratory
nwhitney@mote.org

Co-PIs and Collaborators:
Karissa Lear, Murdoch University
Heather Marshall, Ph.D., Atlantic White Shark Conservancy
Jack Morris and Robert Hueter, Ph.D., Mote Marine Laboratory
Gregory Skomal, Ph.D., Massachusetts Division of Marine Fisheries

*Current affiliation: Anderson Cabot Center for Ocean Life
New England Aquarium
1 Central Wharf
Boston, MA 02110

Commercial fishing partners:
Capt. Dave Campo, Madeira Beach, FL
Capt. Jim Bonnell, Madeira Beach, FL
Capt. Luke Hill, Tavernier, FL

National Marine Fisheries Service partner:
John Carlson, Ph.D., Southeast Fishery Science Center

Final Report

Cooperative Research Program Grant No. NA15NMF4540102

November 29, 2017

Table of Contents

Executive Summary

Bycatch mortality is a major factor contributing to declines of shark populations worldwide. In particular, post-release mortality is difficult to quantify, and post-release mortality rates are available for only a few shark species. Here we use acceleration data-loggers (ADLs) to determine acute post-release mortality rates for coastal sharks caught in the Florida commercial shark longline fishery. Post-release outcomes were directly paired with blood stress parameters and other at-vessel metrics collected at the time of capture to determine whether these factors can be used to accurately predict post-release mortality. Accelerometer data were also used to assess recovery periods of surviving sharks after they were released from fishing gear.

Overall, we captured 542 sharks, 435 of which were measured and blood sampled (n=348 alive, n=87 at vessel mortality; AVM). Of the animals landed alive, 332 sharks were tagged with ADLs and 313 of these ADLs were recovered, resulting in a 94.3% tag recovery rate. Tagged sharks ranged in size from 105 to 350 cm total length, with girths ranging from 40 to 172 cm. Post-release mortality rates were 44.2 ± 8.3 (+/- 95% CI, N=95) for blacktip sharks (*Carcharhinus limbatus*), 3.4 ± 2.7 (+/- 95% CI, N=119) for sandbar sharks (*C. plumbeus*), 71.4 ± 19.9 (+/- 95% CI, N=14) for spinner sharks (*C. brevipinna*), 2.0 ± 3.2 (+/- 95% CI, N=51) for tigers sharks (*Galeocerdo cuvier*), and 8.3 ± 13.1 (+/- 95% CI, N=12) for bull sharks (*C. leucas*) respectively.

Post-release outcome was not influenced by time on the line (TOL), but was correlated with water temperature and blood pH, potassium, chloride, and magnesium levels in blacktip sharks, and with blood pH, lactate, and potassium levels in sandbar sharks. Lactate increased significantly with TOL in both blacktip and sandbar sharks, but not in other species. Average species-specific recovery periods were 10.4 ± 1.8 h for tiger sharks, 9.8 ± 2.1 h for sandbar sharks, and 11.1 ± 1.7 h for blacktip sharks.

To our knowledge, this work represents the highest sample size of any post-reelase study to date, and this tagging method has proven highly cost effective, recovering post-release outcomes at approximately $1/8^{th}$ to $1/4^{th}$ the cost of doing so with satellite tagging methods.

Our results indicate that post-release mortality rates vary widely between species, and that no-take regulations may be much more effective for more robust species such as sandbar, tiger, and bull sharks compared to species more susceptible to post-release mortality such as blacktip and spinner sharks.

Introduction

Shark populations are considered more vulnerable to fishing pressure than most teleosts due to their slow growth, late maturity, and low fecundity (Hoenig & Gruber 1990, Cortés 1999, Cortés et al. 2002). In recent years, this concern has led to the modification of techniques to reduce shark bycatch and encourage no-take fishing in commercial and recreational fisheries (NMFS 2006). While these methods undoubtedly reduce mortality, bycatch mortality remains one of the leading factors contributing to shark population declines worldwide (Myers & Worm 2005, Dulvy et al. 2014). At-vessel bycatch mortality can be quantified and reported relatively easily, however, the physical trauma and physiological effects of capture stress can also lead to delayed mortality in an unknown percentage of animals that are discarded alive (Skomal 2007, Skomal & Bernal 2010, Molina & Cooke 2012). Post-release mortality rates vary widely between species, gear types, season and locations (Ellis et al. 2017), and are thus difficult to quantify and often not included in estimates of overall fisheries mortality. This can lead to gross underestimation of the impact of fisheries on shark populations (Worm et al. 2013, James et al. 2015), confounding the benefits of no-take fishing and hindering sustainable management of these species. As such, understanding what happens to sharks after they are released alive from fishing gear is essential to gaining a complete picture of how fisheries impact these important and often vulnerable populations.

Despite the importance of quantifying post-release mortality rates, this information is available for very few shark species, making it difficult to incorporate this central factor into management decisions and regulations. Most recent shark post-release mortality studies have used pop-up satellite archival tags (PSATs) to assess post-release outcomes (e.g., Campana et al. 2009, Stevens et al. 2010, Hoolihan et al. 2011, Musyl et al. 2011, Marshall et al., 2015, Sepulveda et al. 2015, Eddy et al. 2016). These tags can determine post-release outcomes with relative accuracy, however, these studies have been limited in sample size as these tags are expensive, costing around $4K per shark tagged (Lear and Whitney 2016). Alternatively, a few studies have begun using newer survivorship pop-up archival tags (sPATs; e.g., French et al. 2015, Hutchinson et al. 2015). These tags are more economical, at approximately $2K per shark, but are highly specialized tags that strictly provide mortality information without detailed behavioral data.

Another common method of assessing the effects of capture on sharks is by using blood biochemistry parameters to assess capture-induced physiological stress. The reduced ability to respire during capture, high activity levels resulting from the fight-or-flight response, and subsequent cascade of chemical changes resulting from the stress response, can all result in metabolic and respiratory acidosis (Pickering 1981, Adams 1990, Wood 1991, Milligan 1996, Bonga 1997, Kieffer 2000, Skomal 2007, Skomal & Mandelman 2012). These conditions can potentially result in irreversible cellular damage that impacts recovery and may cause delayed mortality (Wood et al. 1983). Although the effects of capture on blood physiology have been studied in various shark species (e.g.,Wells et al. 1986, Hoffmayer & Parsons 2001, Manire et al. 2001, Skomal & Chase 2002, Mandelman & Skomal 2009, Brooks et al. 2011, Hyatt et al. 2011, Marshall et al. 2012, Gallagher et al. 2014), few studies have directly linked blood stress physiology with actual post-release outcomes(Skomal & Chase 2002, Moyes et al. 2006, Skomal et al. 2007, Kneebone et al. 2013, French et al. 2015). This has resulted in a disconnect between at-vessel physiological stress measurements and post-release outcomes, hindering the ability to

use these relatively accessible at-vessel blood parameters to accurately inform causes of mortality, which may allow for prediction of post-release survival estimates in future studies.

Acceleration data loggers (ADLs) have recently shown promise as a reliable technology for quantifying post-release mortality and recovery (Lear and Whitney 2016, Whitney et al. 2016, 2017). ADLs record fine-scale movement data (e.g., tail beat frequency, amplitude, body pitch, etc.), which can be used to assess swimming behavior, and thereby determine acute post-release mortality and recovery behavior (Whitney et al. 2012). Though these tags have to be physically recovered in order to access the data, these tags are much less expensive than satellite tags. For example, including the costs of recovering the tags, this technique costs roughly 1/8th the price of using PSATs (Lear & Whitney 2016), allowing for the formation of robust sample sizes previously unattainable for this type of work, but which are necessary to readily measure accurate post-release mortality (PRM) rates for fisheries management plans (Goodyear 2002).

The present study used ADLs to quantify post-release mortality rates of large coastal shark species caught in the Florida commercial bottom longline fishery, including blacktip (*Carcharhinus limbatus*), sandbar (*C. plumbeus*), spinner (*C. brevipinna*), tiger (*Galeocerdo cuvier*), and bull (*C. leucas*) sharks. Post-release outcomes determined from ADL data are paired with blood stress indicators and other at-vessel metrics collected at the time of capture. This is the first time that these indicators have been paired directly with empirically derived post-release commercial fishing mortality for large numbers of coastal shark species.

Project Objectives

This study integrated novel and conventional methods to document the true impact of bycatch in commercial longline fisheries on large coastal and prohibited shark species. Specifically we:

1. Documented the post-release behavior and mortality of large coastal sharks caught in a commercial longline fishery using shark-borne ADLs.
2. Examined relationships of post-release behavior and mortality to blood biochemistry (e.g. pH, pCO2, and lactate) collected at the time of capture.
3. Examined relationships of both measures of post-release effects (behavior and blood biochemistry) with fish size, hook time, and animal release condition.

Methods

Shark capture, processing, and tagging

Sharks were caught and released near Madeira Beach, FL, and Key West, FL, USA. Sharks were caught on bottom longline gear in sets of 150-250 18/0 circle hooks, with soak times ranging from 2-15 h, specified as time of first hook in the water to the time the first hook was brought up. Hook timers (model HT-600, Lindgren-Pitman, Inc, Pompano Beach, FL) were deployed with each gangion so the actual time-on-the-line (TOL) for each animal was known. At both study sites, specific fishing locations and practices were directed by commercial longline captains to ensure methods were consistent with typical commercial fishing practices. Before each longline set was hauled, oceanographic conditions including water temperature, salinity,

and dissolved oxygen levels were measured using a hand held meter (YSI model Pro Plus, Yellow Springs, OH).

Hooked sharks were brought onboard for processing and tagging, a step that is not typically taken by our commercial fishing partners before releasing large sharks. To mitigate the effects of this step we irrigated the gills with a seawater hose running into the sharks' mouth, and covered their eyes with a wet towel to calm them and control their movements during sampling and tagging. A blood sample (1-3 mL) was taken as soon as the shark was secured via caudal venipuncture with a heparinized syringe and 18-gauge needle. Sex, girth, precaudal (PCL), fork (FL), and total lengths (TL) of each shark were recorded. Hook location and any visible abrasions, bleeding, or other injuries were noted. Live sharks were tagged with an acceleration data logger (ADL) float package. Sharks that were dead at-vessel or too small to carry a tag were also measured and blood sampled.

Depending on location and depth within the sharks' mouth, hooks were either removed or the leaders cut. Prior to release, nictitating membrane, flex, and bite reflexes were tested (Danylchuk et al. 2014). Nictitating membrane reflexes were tested by squirting sea water through a syringe at the eye and noting the presences or absence of a response, bite reflexes were tested by determining whether the shark would bite the irrigation hose, and flex assessed by noting the presence or absence of body flexing as the shark was prepared for release. All reflexes were categorized as a 1 if the reflex was unimpaired, or a 0 if the reflex was impaired or absent (Danylchuk et al. 2014). Upon release, sharks were assigned a condition index score ranging from 1-5 based on their swimming strength and behavior, and their equilibrium reflex was assigned a 1 if they were able to uphold equilibrium when released, and a 0 if they were not.

Accelerometry

Cefas G6a+ ADLs (Cefas Technologies, Lowestoft, UK) were set to record triaxial acceleration at 25 Hz, depth at 1 Hz, and temperature at 0.03 Hz. ADLs were embedded in custom float packages alongside a VHF transmitter (Advanced Telemetry Systems, Isanti, MN, USA). These float packages were hydrodynamic, approximately 3 x 7 x 12 cm in size, and weighed 125 g in air (70 g positively buoyant in seawater; see Whitmore et al. 2016). This amount of positive buoyancy represents less than 0.5% of the body weight of tagged sharks, and is thus well below the 2% of animal body weight typically recommended for tagging studies (Winter, 1983). Float packages were attached to the first dorsal fin of sharks at two points using a tether made from plastic cable ties with a built-in galvanic timed release (GTR; International Fishing Devices Inc., Northland, New Zealand), which corrodes in seawater after a predetermined number of days (Fig. 1; see Whitmore et al. 2016). Once the GTR dissolves, the tether brakes, allowing the package to release from the fin and float to the surface for recovery. Floating packages were detected using a hand-held, multi-channel VHF receiver (R45-20C, Advanced Telemetry Systems, USA), and tracked down and recovered by vessel following methods outlined by Lear and Whitney (2016).

Accelerometer data analysis

Once accelerometers were recovered, they were downloaded and the data analyzed using Igor Pro (Wavemetrics, Inc. Lake Oswego, OR, USA) and Ethographer (Sakamoto et al. 2009). ADL data were used to determine mortality events, easily distinguishable by a constant depth

trace (on the bottom, indicating the negatively buoyant shark has sunk after mortality event), and cessation of movement apparent in the acceleration traces (Fig. 2). Time of death was determined as the point at which the shark settled on the sea floor. Post-release mortality rates were calculated as the percentage of sharks that expired post-release out of the number of tags recovered for each species. Calculations outlined by Goodyear (2002) were used to determine 95% confidence intervals for post-release mortality estimates.

Recovery periods were assessed for sharks that survived longline capture and had deployment periods greater than 12 h using techniques described by Whitney et al. (2016). Multiple metrics to evaluate recovery period were calculated using the acceleration and depth data, as described by Whitney et al. (2016). However, many of these metrics displayed redundant information or showed unclear patterns with time post-release, therefore we chose to use only tailbeat frequency (TBF) to calculate post-release recovery, as this metric showed the clearest representation of a change of behavior post-release.

TBF was calculated by a continuous wavelet transformation of the sway axis, and was averaged into 10 min means for each shark. Several models were built in R (R Core Team 2015) using the nlme (Pinheiro et al. 2014) and mgcv (Wood 2011) packages in order to investigate relationships between time post-release and these metrics, as described in Whitney et al. (2016). Since these models require a relatively large sample size to run accurately, recovery periods were only calculated for species with more than 10 surviving individuals.. Time to recovery was calculated as the amount of time after release it took for TBF to gain 80 percent of the difference between the initial hour post release and the fully recovered value, defined as the upper asymptote in the logistic model (Whitney et al. 2016). This recovery period was calculated for each individual, and the mean of these individual recovery periods for each species was used to calculate species-specific recovery periods.

Blood biochemistry analysis

Whole blood samples were assayed for pH, pCO_2, HCO_3^-, and lactate onboard the fishing vessel within 10 min of the blood draw using an i-STAT hand-held portable blood analyzer with CG4+ cartridges (Abaxis, Union City, CA, USA). Values for pH and pCO_2 were temperature corrected to the water temperature measured mid-depth by the YSI using equations 1B and 2 from Mandelman and Skomal (2009), respectively. A temperature correction for HCO_3^- was calculated based off the temperature corrected pH and pCO_2 values using the Henderson-Hasselbach equation (Mandelman & Skomal 2009). Hematocrit levels were analyzed onboard following the blood draw using microcapillary tubes (n=2-4 per shark), full of whole blood and spun for 5 minutes (x11000rpm) in a hematocrit spinner (ZipOCRIT, LW Scientific, Inc.). Hematocrit levels were calculated after as the percentage of red blood cell volume in total blood volume. Additionally, 1-2 mL of whole blood was injected into 2mL tubes and centrifuged for 5 min at 2000g. Following centrifugation, red blood cell and plasma layers were separated by pipetting, and immediately frozen in a liquid nitrogen shipper (Taylor Wharton, Marathon Products, Inc.). Frozen plasma samples were later analyzed using a bench-top Critical Care Xpress (CCX) blood gas analyzer (Nova Biomedical, Waltham, MA, USA) for glucose, lactate, and ion levels (K^+, Na^+, Cl^-, Mg^{2+}, and Ca^{2+}), following the methods of Marshall et al. (2012).

Integrated analysis

Integrated analyses were conducted in R (R Core Team 2015). Linear regressions were used to determine relationships between blood parameters and TOL, water temperature and fish size (PCL). Linear regressions were also used to assess relationships between acceleration-based recovery periods and measured at-vessel parameters including water temperature, fish size, hook time, and blood biochemistry values.

Lasso logistic regressions were used as a model selection technique to determine which at-vessel metrics were informative for predicting post-release mortality, using the glmnet package (Hastie & Qian 2014). A separate model was run for each species with four or more post-release mortalities and surviving individuals, i.e. blacktip sharks and sandbar sharks. The initial lasso model for each species included fish size, reflex indices, release condition, water temperature, hook time, and all measured blood parameters as predictive variables, with post-release outcome as the response. The optimal logistic model was chosen by selecting the value of λ that minimized the mean squared error in the lasso regression (λ_{min}). Predictor variables that were included in the lasso model at λ_{min} were considered informative predictors of post-release outcome. These predictors were incorporated into a logistic regression model to assess significance, and were used to create a decision tree for each species using the rpart package (Therneau & Atkinson 2015), which determined threshold values of informative parameters that can be used to predict post-release outcomes. A minimum split and bucket size of 10 was used to create the decision tree for blacktip sharks, and a minimum split and bucket size of 2 was used for the sandbar and spinner decision trees.

Unless otherwise noted all mean values are reported ± standard deviation (SD), and significance level set to alpha = 0.05.

Results

Shark capture and tagging

Between December 2013 and May 2017, a total of 58 longline sets were deployed, with 48 near Madeira Beach, FL and 10 near Key West, FL. Longline soak times ranged between 1 and 12 h (mean 3.3 ± 2.7 h). Sets were located between 1 and 38 km offshore (mean 14.8 ± 8.7 km), at depths ranging from 2 to 26 m (mean 11.6 ± 4.9 m). Set water temperatures ranged between 15 and 32°C (mean 25.6 ± 4.7°C).

Of the 542 sharks captured, 435 were measured and blood sampled (n=348 alive, n=87 AVM), with a species composition of blacktip, sandbar, spinner, tiger, and bull sharks. Hook times for all sharks and species ranged from 2 to 956 min (mean 229 ± 233 min). At-vessel mortality (AVM) rates varied substantially by species, ranging from 0% for tiger and bull sharks to 62% for spinner sharks (Table 1). Of the sampled sharks, a total of 332 individuals were tagged with ADLs, (Table 1), and 313 of these ADLs were recovered (94.3% tag recovery rate). Tagged sharks ranged in size from 105 to 350 cm TL, with girths ranging from 40 to 172 cm. Hook times ranged from 2 to 956 min (mean 229 ± 233 min), and handling times ranged from 2 to16 min (averaging 5 ± 2 min).

Post-release mortality and recovery

Accelerometer deployments lasted between 0.7 and 205 h (mean 20.9 ± 18.7 h), in total collecting more than 6,800 h of fine-scale acceleration data. Out of the 313 recovered accelerometers we observed 58 post-release mortalities (PRM; see Table 1). Of the PRM, 91% of mortalities occurred within 5 h of release, and all mortalities occurred within 12 h of release.Sharks that survived post-release typically showed repetitive oscillations, or "yo-yo" diving behavior, between the surface and sea floor for the majority of the deployment (Fig. 2A). Sharks that did not survive post-release typically showed more irregular diving patterns prior to settling on the bottom and struggling for a short time before ceasing all tailbeat movement (Fig. 2B).

Overall PRM rates varied substantially by species, ranging from 1.9% for tiger sharks to 71.4% for spinner sharks (Table 1). Post-release mortality rates were 1.9-10.6% higher than at-vessel mortality rates, averaging 5.6% higher. Considering only sharks with known outcomes, total mortality (at-vessel and post-release, combined) ranged from 2% for tiger sharks to 91.6% for spinner sharks (Fig. 3). Water temperature had a substantial impact on PRM rates for blacktip sharks, the only species experiencing a large number of mortalities and caught in a wide range of water temperatures. Trip-specific blacktip mortality rates ranged from 0% in 18.8°C water (n=3) to 70% in 31°C water (n=10), even though soak times were generally longer during cooler water trips.

Physiological response to capture stress

Summary statistics for species-specific blood parameters are summarized in Table 2. Linear regressions showed significant relationships between all blood parameters and TOL, water temperature, and PCL in sandbar, tiger, blacktip, spinner, and bull sharks (Table 3). Lactate was the blood parameter mostly strongly correlated with hook time in blacktip and sandbar sharks (Fig. 5), though it was not correlated with hook time in any other species.

At-vessel predictors of post-release outcome

Lasso logistic regression analyses determining significant at-vessel predictors of post-release outcomes were run for blacktip and sandbar sharks, the only two species presenting a large enough number of both post-release mortalities and surviving sharks. Parameters included in the lasso models at λ_{min} were water temperature and blood pH, K^+, Cl^-, and Mg^+ for blacktip sharks, and blood pH, K^+, Cl^-, and lactate for sandbar sharks.

The logistic regression models using these indicated parameters determined that pH was the only significant predictor of PRM in blacktip sharks ($p<0.01$), and no parameters were significantly correlated with post-release outcome in sandbar sharks. The decision tree analyses determined pH, K^+ and Cl^- as informative predictors of PRM in blacktip sharks, and pH and K^+ as informative predictors of PRM in sandbar sharks (Fig. 4).

Recovery period

Recovery from capture was assessed for blacktip, sandbar, and tiger sharks. Individual recovery periods for sharks ranged from 6.3 to 15.8 h. Average species-specific recovery periods

were 10.4 ± 1.8 h for tiger sharks, 9.8 ± 2.1 h for sandbar sharks, and 11.1 ± 1.7 h for blacktip sharks.

Conclusions

Our findings indicate relatively low mortality for commercially caught and released sandbar, tiger, and bull sharks, and high mortality for caught and released blacktip and spinner sharks. Total mortality rates range from 91.7% for spinner sharks to 2% for tiger sharks, although AVM rates may have been lower than normal because soak times were frequently shortened in order to target live animals.

Post-release mortality rates were 44.2 ± 8.3 (+/- 95% CI, N=95) for blacktip sharks (*Carcharhinus limbatus*), 3.4 ± 2.7 (+/- 95% CI, N=119) for sandbar shark (*C. plumbeus*), 71.4 ± 19.9 (+/- 95% CI, N=14) for spinner shark (*C. brevipinna*), 2.0 ± 3.2 (+/- 95% CI, N=51) for tigers sharks (*Galeocerdo cuvier*), and 8.3 ± 13.1 (+/- 95% CI, N=12) for bull sharks (*C. leucas*).

Post-release outcome was not influenced by time on the line (TOL), but was correlated with water temperature and blood pH, potassium, chloride, and magnesium levels in blacktip sharks, and with blood pH, lactate, and potassium levels in sandbar sharks. Lactate increased significantly with TOL in both blacktip and sandbar sharks, but not in other species. These results indicate that post-release mortality rates vary widely between species, and that no-take regulations may be much more effective for more robust species such as sandbar, tiger, and bull sharks compared to species more susceptible to post-release mortality such as blacktip and spinner sharks.

Acknowledgements

We would like to thank our commercial fishing captains, Dave Campo, Randy Lauser, Jim Bonnell, and Luke Hill, for their expertise, help, and support throughout this work. Captains Ryan Kane, Dean Dougherty, Greg Byrd, Chuck Jelicks, and Pete Hull, and pilots Gary Roam, Fernando Casey, and Buddy Powell were essential to successful tag recovery. Alyssa Andres was integral to the success of the fieldwork in this study. Connor White, Gail Schwieterman, and Alex Ontkos provided assistance with fieldwork and logistics. John Tyminski assisted with editing the manuscript. Diego Bernal provided bench time for blood analysis. We also thank numerous Mote Marine Laboratory interns and volunteers who helped with this work.

Publications and Presentations

Lear, K., and Whitney, N. (2016) Bringing data to the surface: recovering data loggers for large sample sizes from marine vertebrates. *Animal Biotelemetry*, 4: DOI 10.1186/s40317-016-0105-8.

Schwieterman, G., Lear, K., Marshall, H., Morris, J., White, C., Hueter, R., Skomal, G., Whitney, N. "Post-release mortality of coastal sharks in a commercial longline fishery." Poster presentation. American Elasmobranch Society, New Orleans, LA. July 2016.

Whitney, N., White, C. Gleiss, A., Schwieterman, G., Anderson, P., Hueter, R., Skomal, G. (2016). A novel method for determining post-release mortality, behavior and recovery period using acceleration data loggers. *Fisheries Research*, 183: 210-221.

Literature Cited

Adams SM (1990) Biological Indicators of Stress in Fish. Am Fish Soc Symp 8:191

Afonso AS, Hazin FHV (2014) Post-release survival and behavior and exposure to fisheries in juvenile tiger sharks, *Galeocerdo cuvier*, from the South Atlantic. J Exp Mar Biol Ecol 454:55-62

Barnes CJ, Butcher PA, Macbeth WG, Mandelman JW, Smith SDA, Peddemors VM (2016) Movements and mortality of two commercially exploited carcharhinid sharks following longline capture and release off eastern Australia. Endanger Species Res 30:193-208

Bonga W (1997) The stress response in fish. Physiol Rev 77:591-625

Bouyoucos IA, Suski CD, Mandelman JW, Brooks EJ (2017) The energetic, physiological, and behavioral response of lemon sharks (Negaprion brevirostris) to simulated longline capture. Comp Biochem Physiol A Mol Integr Physiol 207:65-72

Brooks EJ, Mandelman JW, Slowman KA, Liss S and others (2011) The physiological response of the Caribbean reef shark (*Carcharhinus perezi*) to longline capture. Comp Biochem Physiol, A: Mol Integr Physiol 162:94-100

Butcher PA, Peddemors VM, Mandelman JW, McGrath SP, Cullis BR (2015) At-vessel mortality and blood biochemical status of elasmobranchs caught in an Australian commercial longline fishery. Global Ecology and Conservation 3:878-889

Campana SE, Joyce W, Manning MJ (2009) Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. Mar Ecol Prog Ser 387:241-253

Campana SE, Joyce W, Fowler M, Showell M (2016) Discards, hooking, and post-release mortality of porbeagle (Lamna nasus), shortfin mako (Isurus oxyrinchus), and blue shark (Prionace glauca) in the Canadian pelagic longline fishery. ICES Journal of Marine Science: Journal du Conseil 73:520-528

Cicia AM, Schlenker LS, Sulikowski JA, Mandelman JW (2012) Seasonal variations in the physiological stress response to discrete bouts of aerial exposure in the little skate, Leucoraja erinacea. Comp Biochem Physiol A Mol Integr Physiol 162:130-138

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science: Journal du Conseil 56:707-717

Cortés E, Brooks L, Scott G (2002) Stock assessment of large coastal sharks in the US Atlantic and Gulf of Mexico, Vol. National Marine Fisheries Service, Southeast Fisheries Science Center Contribution SFD-2/03-177

Danylchuk AJ, Suski CD, Mandelman JW, Murchie KJ, Haak CR, Brooks AM, Cooke SJ (2014) Hooking injury, physiological status and short-term mortality of juvenile lemon sharks

(Negaprion bevirostris) following catch-and-release recreational angling. Conserv Physiol 2:cot036
Dapp DR, Huveneers C, Walker TI, Drew M, Reina RD (2016) Moving from Measuring to Predicting Bycatch Mortality: Predicting the Capture Condition of a Longline-Caught Pelagic Shark. Frontiers in Marine Science 2
Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. eLife 2014:e00590
Eddy C, Brill R, Bernal D (2016) Rates of at-vessel mortality and post-release survival of pelagic sharks captured with tuna purse seines around drifting fish aggregating devices (FADs) in the equatorial eastern Pacific Ocean. Fish Res 174:109-117
Ellis JR, McCully Phillips SR, Poisson F (2017) A review of capture and post-release mortality of elasmobranchs. J Fish Biol 90:653-722
French RP, Lyle J, Tracey S, Currie S, Semmens JM (2015) High survivorship after catch-and-release fishing suggests physiological resilience in the endothermic shortfin mako shark (Isurus oxyrinchus). Conserv Physiol 3:cov044
Gallagher AJ, Serafy JE, Cooke SJ, Hammerschlag N (2014) Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. Mar Ecol Prog Ser 496:207-218
Goodyear CP (2002) Factors affecting robust estimates of the catch-and-release mortality using pop-off tag technology. Trans Am Fish Soc 30:172-179
Gulak SJB, de Ron Santiago AJ, Carlson JK (2015) Hooking mortality of scalloped hammerheadSphyrna lewiniand great hammerheadSphyrna mokarransharks caught on bottom longlines. Afr J Mar Sci 37:267-273
Hastie T, Qian J (2014) Glmnet vignette. Technical report, Stanford
Heard M, Van Rijn JA, Reina RD, Huveneers C (2014) Impacts of crowding, trawl duration and air exposure on the physiology of stingarees (family: Urolophidae). Conserv Physiol 2:cou040
Heberer C, Aalbers SA, Bernal D, Kohin S, DiFiore B, Sepulveda CA (2010) Insights into catch-and-release survivorship and stress-induced blood biochemistry of common thresher sharks (*Alopias vulpinus*) captured in the southern California regreationl fishery. Fish Res 106:495-500
Hoenig JM, Gruber SH (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. In: H.L. Pratt J, Gruber SH, Taniuchi T (eds) Elasmobranchs as Living Resources NOAA Technical Report NMFS 90: 1-16
Hoffmayer ER, Parsons GR (2001) The physiological response to capture and handling stress in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Fish Physiol Biochem 25:277-285
Hoolihan JP, Luo J, Abascal FJ, Campana SE and others (2011) Evaluating post-release behavior modification in large pelagic fish deployed with pop-up satellite archival tags. ICES J Mar Sci 68:880-889
Hutchinson MR, Itano DG, Muir JA, Holland KN (2015) Post-release survival of juvenile silky sharks captured in a tropical tuna purse seine fishery. Mar Ecol Prog Ser 521:143-154
Hyatt MW, Anderson PA, O'Donnell PM, Berzins IK (2011) Assessment of acid-base derangements among bonnethead (*Sphyrna tiburo*), bull (*Carcharhinus leucas*), and lemon (*Negaprion brevirostris*) sharks from gillnet and longline capture and handling methods. Comp Biochem Physiol, A: Mol Integr Physiol 162:113-120

James KC, Lewison RL, Dillingham PW, Curtis KA, Moore JE (2015) Drivers of retention and discards of elasmobranch non-target catch. Environ Conserv 43:3-12
Kieffer JD (2000) Limits to exhaustive exercise in fish. Comparative Biochemistry and Physiology 126:161-179
Kneebone J, Chisholm J, Bernal D, Skomal G (2013) The physiological effects of capture stress, recovery, and post-release survivorship of juvenile sand tigers (Carcharias taurus) caught on rod and reel. Fish Res 147:103-114
Lear KO, Whitney NM (2016) Bringing data to the surface: recovering data loggers for large sample sizes from marine vertebrates. Animal Biotelemetry 4
Mandelman JW, Skomal GB (2009) Differential sensitivity to capture stress assessed by blood acid–base status in five carcharhinid sharks. J Comp Physiol B 179:267-277
Manire C, Hueter R, Hull E, Spieler R (2001) Serological changes associated with gill-net capture and restraint in three species of sharks. Trans Am Fish Soc 130:1038-1048
Marshall H, Field L, Afiadata A, Sepulveda C, Skomal G, Bernal D (2012) Hematological indicators of stress in longline-captured sharks. Comp Biochem Physiol, A: Mol Integr Physiol 162:121-129
Marshall H, Skomal G, Ross PG, Bernal D (2015) At-vessel and post-release mortality of the dusky (Carcharhinus obscurus) and sandbar (C. plumbeus) sharks after longline capture. Fish Res 172:373-384
Milligan CL (1996) Metabolic recovery from exhaustive exercise in rainbow trout. Comparative Biochemistry and Physiology 113:51-60
Molina JM, Cooke SJ (2012) Trends in shark bycatch research: current status and reasearch needs. Rev Fish Biol Fish 22:719-737
Morgan A, Burgess GH (2007) At-Vessel Fishing Mortality for Six Species of Sharks Caught in the Northwest Atlantic and Gulf of Mexico. Gulf Caribb Res 19
Morgan A, Carlson JK (2010) Capture time, size and hooking mortality of bottom longline-caught sharks. Fish Res 101:32-37
Moyes CD, Fragoso N, Musyl MK, Brill RW (2006) Predicting Postrelease Survival in Large Pelagic Fish. Trans Am Fish Soc 135:1389-1397
Musyl MK, Brill RW, Curran DS, Fragoso NM and others (2011) Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. Fish Bull 109:341-368
Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. Philos Trans R Soc Lond B Biol Sci 360:13-20
NMFS (2006) FInal Consolodated Atlantic Highly Migratory Fishery Management Plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Springs, MD, Public Document, pp 1600
NMFS (2011) SEDAR 21 Stock Assessement Report. HMS Dusky Shark. SEDAR, 4055 Faber Place Drive, Suite 20, North Charleston, SC 29405
Pickering AD (1981) Stress and fish, Vol. Academic Pr, New York, USA
Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2014) nlme: Linear and Nonlinear Mixed Effects Models. R package version 31-117
Rodríguez-Cabello C, Sánchez F (2017) Catch and post-release mortalities of deep-water sharks caught by bottom longlines in the Cantabrian Sea (NE Atlantic). J Sea Res

Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? PLoS ONE 4:e5379. doi:5310:1371/journal.pone.005379
Sepulveda CA, Heberer C, Aalbers SA, Spear N, Kinney M, Bernal D, Kohin S (2015) Post-release survivorship studies on common thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery. Fish Res 161:102-108
Shepard ELC, Wilson RP, Liebsch N, Quintana F, GÃ³mez Laich A, Lucke K (2008) Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals. Endanger Species Res 4:157-164
Skomal G, Lobel PS, Marshall G (2007) The use of animal-borne imaging to assess post-release behavior as it relates to capture stress in grey reef sharks, Carcharhinus amblyrhynchos. Mar Technol Soc J 41:44-48
Skomal G, Bernal D (2010) Physiological responses to stress in sharks. In: Carrier JC, Heithaus LI, Musick JA (eds) Sharks and Their Relatives II. CRC Press, Boca Raton, FL, p 713
Skomal GB, Chase BC (2002) The physiological effects of angling on post-release survivorship in tunas, sharks, and marlin. Am Fish Soc Symp 30:135-138
Skomal GB (2007) Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. Fish Manage Ecol 14:81-89
Skomal GB, Mandelman JW (2012) The physiological response to anthropogenic stressors in marine elasmobranch fishes: a review with a focus on the secondary response. Comp Biochem Physiol A Mol Integr Physiol 162:146-155
Stevens JD, Bardford RW, West GJ (2010) Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: depth behavior, temperature experience and movements. Mar Biol 157:575-591
Team RC (2015) R: A language and environment for statistical computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2014
Therneau T, Atkinson E (2015) Foundation, M., 2015: An Introduction to Recursive Partitioning Using the RPART Routines. CRAN R Project
Wells RMG, McIntyre RH, Morgan AK, Davie PS (1986) Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. Comp Biochem Physiol, A: Mol Integr Physiol 84:565-571
Whitmore BM, White CF, Gleiss AC, Whitney NM (2016) A float-release package for recovering data-loggers from wild sharks. J Exp Mar Biol Ecol 475:49-53
Whitney NM, White CF, Gleiss AC, Schwieterman GD, Anderson P, Hueter RE, Skomal GB (2016) A novel method for determining post-release mortality, behavior, and recovery period using acceleration data loggers. Fish Res 183:210-221
Wood CM, Turner JD, Graham MS (1983) Why do fish die after severe exercise? J Fish Biol 22:189-201
Wood CM (1991) Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. J Exp Biol 160:285
Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J Roy Stat Soc Ser B (Stat Method) 73:3-36
Worm B, Davis B, Kettemer L, Ward-Paige CA and others (2013) Global catches, exploitation rates, and rebuilding options for sharks. Mar Policy 40:194-204

Tables

Table 1: Species-specific catch numbers, at-vessel mortality (AVM), and post-release mortality (PRM) rates. Other than indicated rates, all numbers reported represent sample size (n). Number of individuals blood sampled (BS) are shown in parenthesis. PRM rates are listed ± 95% confidence intervals, calculated using equations outlined by Goodyear (2002). Unrecovered ADL floats and floats that were attached to sharks for less than 6 h post-release were not included in post-release mortality rate calculations.

Species	Caught	Alive at vessel (BS)	AVM (BS)	Tagged	Used in PRM estimate	PRM	AVM rate (%)	PRM rate (± 95% CI)
Blacktip	221	121 (101)	100 (59)	107	95	42	45.2	44.2 ± 8.3
Sandbar	153	152 (140)	1 (1)	140	119	4	0.7	3.4 ± 2.7
Spinner	54	20 (19)	34 (27)	17	14	10	63.0	71.4 ± 19.9
Tiger	95	95 (75)	0 (0)	55	51	1	0.0	2.0 ± 3.2
Bull	19	19 (13)	0 (0)	13	12	1	0.0	8.3 ± 13.1
All Species	542	407 (348)	135 (87)	332	291	58	24.9	19.9

Table 2. Species- and condition (i.e., at-vessel and post-release outcome) specific blood parameter means (±standard deviation) for sharks blood samples in this project. AVM=at-vessel mortality; PRM=post-release mortality; Hct=hematocrit; TC=temperature corrected; Glu=glucose; Lac=lactate.

Species	At-vessel	Outcome	n	Hct (%)	pH_{TC}	pCO_{2TC}	HCO_{3TC}	Na (mM)	K (mM)	Cl (mM)	Ca (mM)	Mg (mM)	Glu (mM)	Lac (mM)
Blacktip	Alive	Survived	54	25.7±4.0	7.30±0.2	8.8±2.8	8.3±2.2	299.6±12.4	5.6±0.7	291.6±7.9	3.0±0.1	1.1±0.1	6.1±1.5	18.2±11.8
	Alive	PRM	42	25.3±4.4	7.07±0.2	10.9±3.1	6.2±2.7	299.7±14.9	7.0±1.4	284.9±12.0	3.0±0.2	1.2±0.1	6.3±1.5	30.2±13.7
	AVM		67	23.6±8.6	6.68±0.1	23.7±10.2	4.1±1.3	293.4±10.7	11.0±3.5	275.5±35.5	3.1±0.2	1.4±0.2	5.1±1.3	35.8±9.5
Bull	Alive	Survived	12	24.2±3.2	7.29±0.2	7.9±2.4	7.6±2.6	297.5±9.5	6.0±0.5	297.9±6.4	2.9±0.2	1.2±0.2	4.8±1.4	8.3±6.3
	Alive	PRM	1	19.0	6.74	12.9	3.0	286.8	7.23	291.9	3.21	1.35	5.6	20.4
	AVM		-	-	-	-	-	-	-	-	-	-	-	-
Sandbar	Alive	Survived	113	25.4±2.9	7.43±0.1	6.6±1.6	8.8±2.0	283.8±9.4	4.3±0.5	284.2±7.1	2.6±0.1	0.97±0.1	4.4±1.0	9.0±7.6
	Alive	PRM	3	29.1±1.5	7.23±0.2	8.3±0.3	7.2±3.6	287.1±4.9	6.9±1.5	270.3±10.7	2.7±0.1	1.2±0.2	5.9±2.7	26.6±7.1
	AVM		1	-	7.10	6.1	3.47	291.9	9.6	262.8	2.6	1.4	6.7	38.1
Spinner	Alive	Survived	4	30.6±3.3	7.42±0.1	7.1±0.7	9.5±2.1	296.4±12.9	6.2±0.9	285.5±7.3	2.8±0.1	1.2±0.2	7.1±1.2	13.5±9.8
	Alive	PRM	10	32.6±3.9	7.31±0.2	6.9±1.0	7.4±3.4	301.9±16.9	6.9±1.5	282.6±16.3	2.9±0.2	1.2±0.1	6.5±2.9	30.6±13.8
	AVM		31	32.6±11.3	6.81±0.2	17.1±6.1	4.7±1.6	283.4±9.5	12.5±4.2	266.9±9.7	2.9±0.2	1.4±0.2	5.6±2.7	40.6±12.5
Tiger	Alive	Survived	49	26.7±4.7	7.51±0.1	5.7±1.8	9.0±1.9	276.4±8.5	5.2±0.6	281.4±7.7	2.7±0.1	1.0±0.1	7.2±0.9	4.3±5.0
	Alive	PRM	1	28.2	7.56	5.8	10.6	258.9	5.0	264.3	2.6	0.9	6.8	1.5
	AVM		-	-	-	-	-	-	-	-	-	-	-	-

Table 3: Blood parameters showing significant correlations ($p<0.05$) with hook time, water temperature, and fish size (PCL) in the study species.

Species	***n***	**Hook time**	**Water temperature**	**PCL**
Blacktip	92	Lactate, K^+, Mg^{2+}, Na^+	pH, pCO_2, Mg^{2+}	Ca^{2+}, lactate, Mg^{2+}, Na^+
Sandbar	127	Lactate, pH, glucose, pCO_2, Cl^-, K^+, Mg^{2+}, Na^+	pH, HCO_3^-, pCO_2, lactate, Mg^{2+}, Na^+	pH, HCO_3^-
Tiger	54	K^+, Cl^-	pH, pCO_2, Ca^{2+}, Na^+	Ca^{2+}
Bull	9	-	pCO_2, Mg^{2+}	pH, HCO_3^-
Spinner	13	K^+, Mg^{2+}	Mg^{2+}	Mg^{2+}

Figures

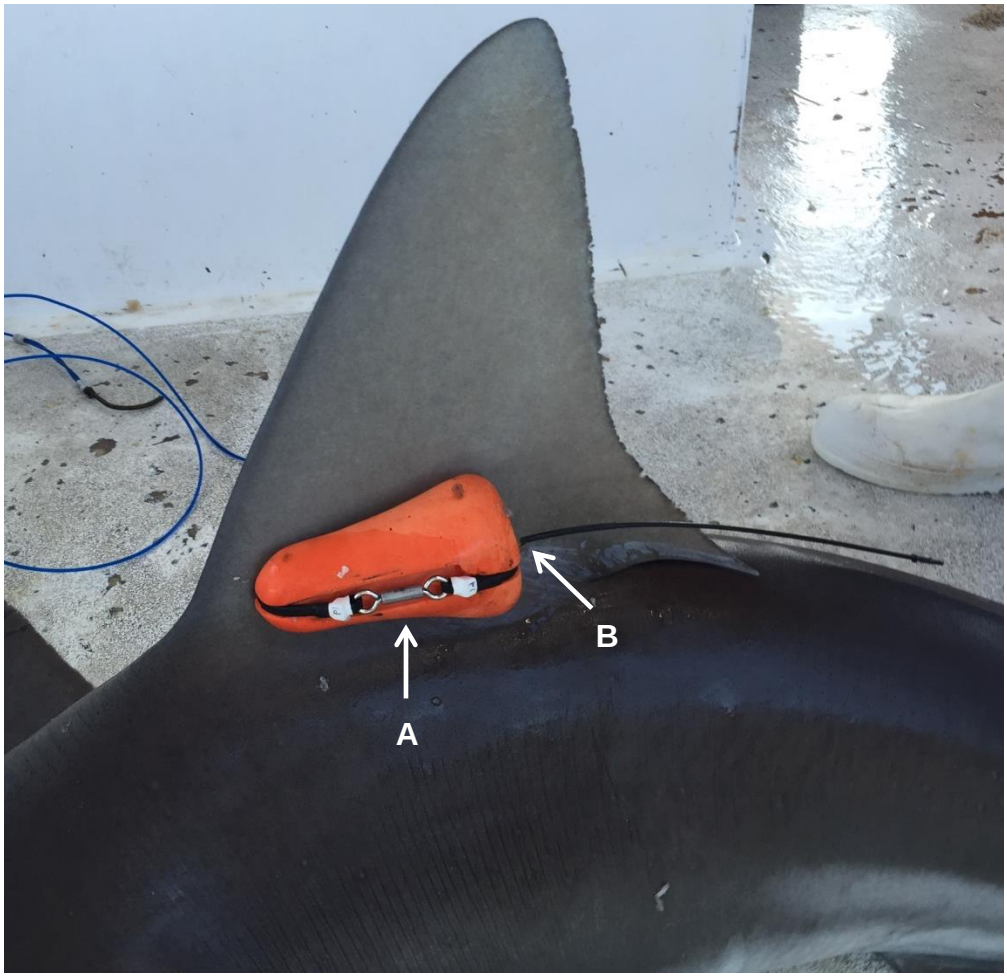

Figure 1: An ADL float package attached to the first dorsal fin of a sandbar shark (also see Whitmore et al., 2016). ADL packages were attached to the fin at two points using a cable tie with a built in galvanic timed release (GTR; A). Once the GTR corrodes, the float packages release from the fin and rise to the surface where the VHF (B) could be detected and the package recovered (see Lear and Whitney, 2016).

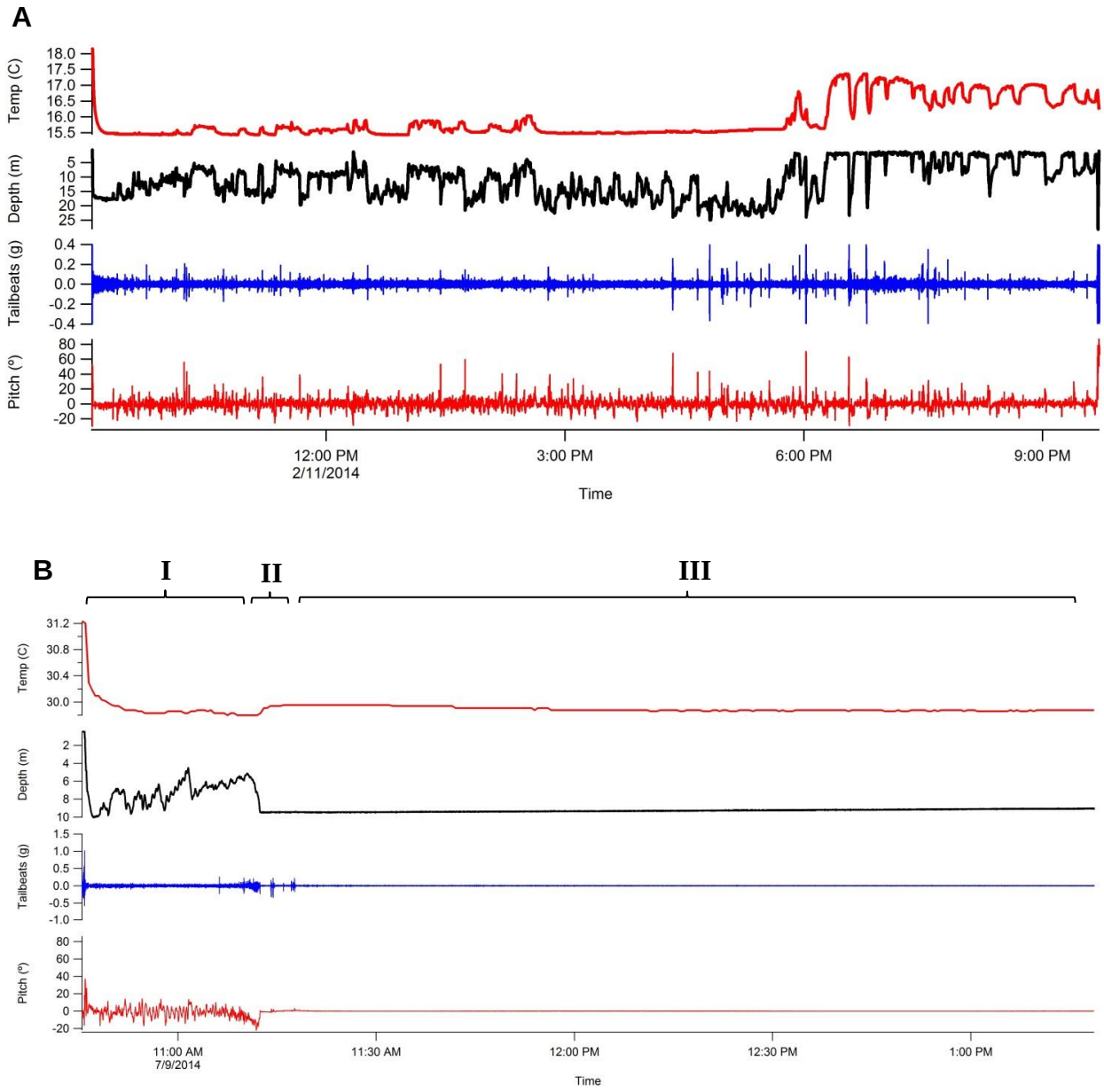

Figure 2: Temperature, depth, pitch, and tailbeat movements for (A) a sandbar shark that survived capture and release showing typical "yo-yo" diving behavior, and (B) a blacktip shark that died around 30 min after release. This shark swam for 30 min (I) before settling on the bottom and struggling a few times, seen on the tailbeat axis (II), before all movement ceased (III).

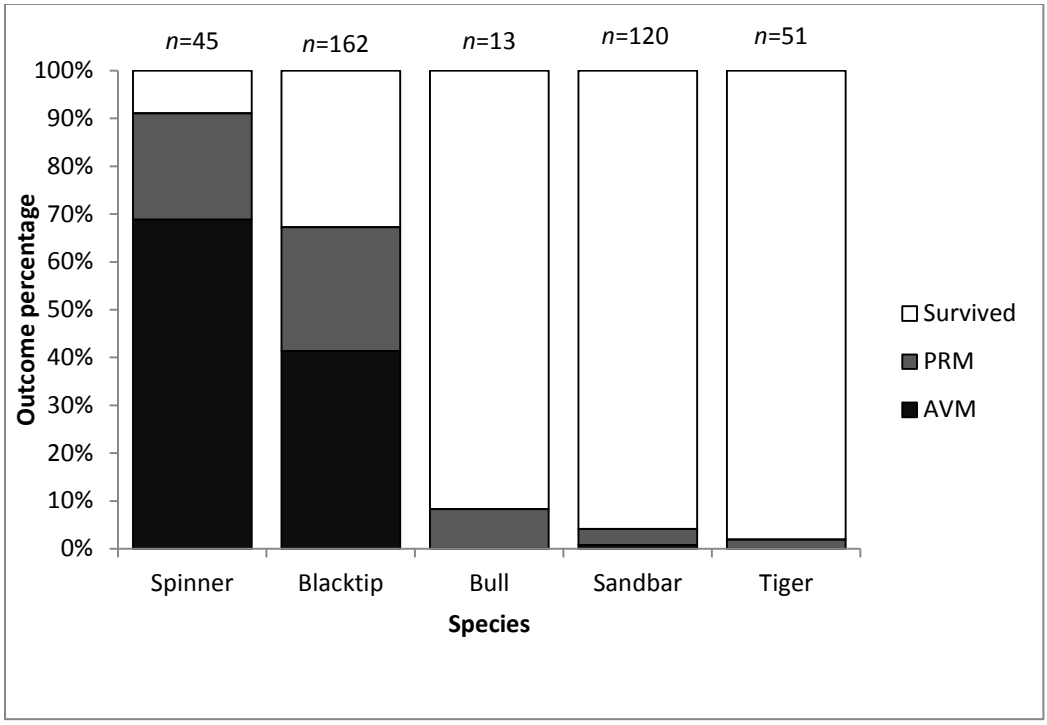

Figure 3: At-vessel and post-release outcome percentages of the total catch by species (animals with known outcomes only). Total mortality rates range from 91.7% for spinner sharks to 2% for tiger sharks. AVM rates may have been lower than normal because soak times were frequently shortened to target live animals.

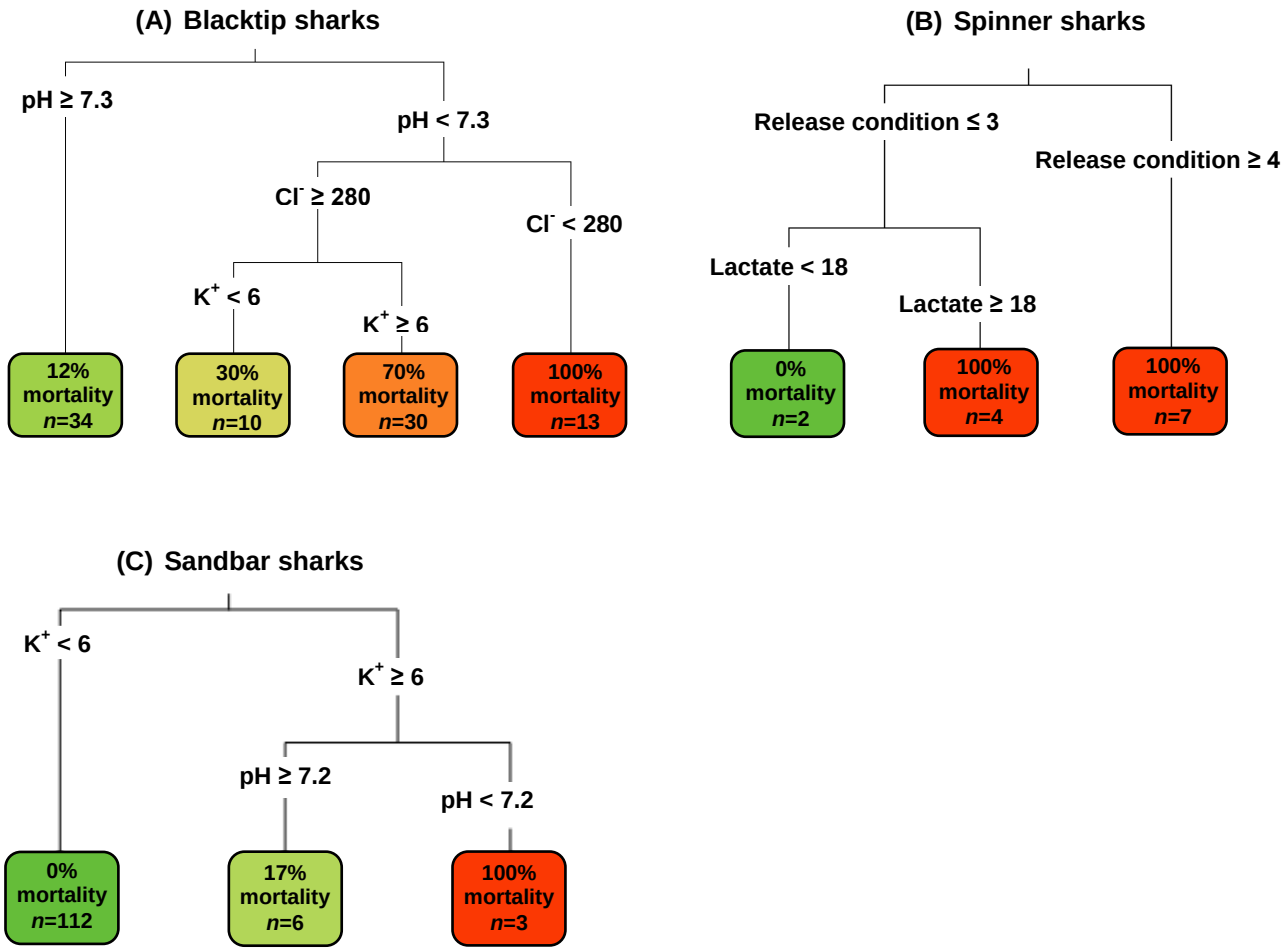

Figure 4: Decision trees for (A) blacktip, (B) spinner, and (C) sandbar sharks using at-vessel metrics to predict post-release outcomes.

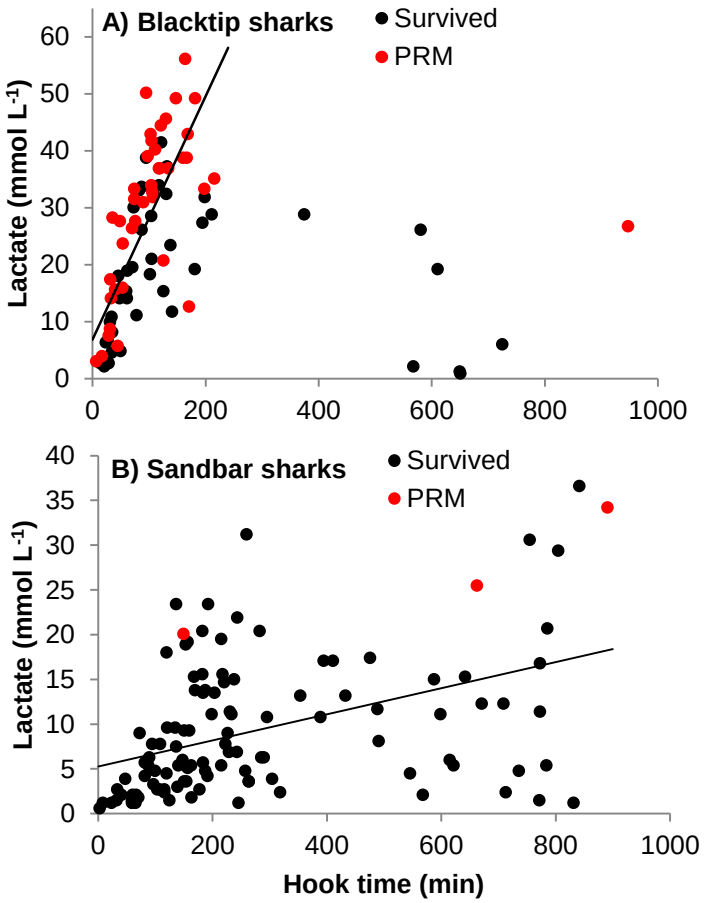

Figure 5: Blood lactate versus hook time for (A) blacktip sharks, and (B) sandbar sharks.