

Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release

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ABSTRACT: In many fisheries, some component of the catch is usually released. Quantifying the effects of capture and release on fish survival is critical for determining which practices are sustainable, particularly for threatened species. Using a standardized fishing technique, we studied sublethal (blood physiology and reflex impairment assessment) and lethal (post-release mortality with satellite tags) outcomes of fishing stress on 5 species of coastal sharks (great hammerhead, bull, blacktip, lemon, and tiger). Species-specific differences were detected in whole blood lactate, partial pressure of carbon dioxide, and pH values, with lactate emerging as the sole parameter to be significantly affected by increasing hooking duration and shark size. Species-specific differences in reflex impairment were also found; however, we did not detect any significant relationships between reflex impairment and hooking duration. Taken together, we ranked each species according to degree of stress response, from most to least disturbed, as follows: hammerhead shark > blacktip shark > bull shark > lemon shark > tiger shark. Satellite tagging data revealed that nearly 100% of all tracked tiger sharks reported for at least 4 wk after release, which was significantly higher than bull (74.1%) and great hammerhead (53.6%) sharks. We discuss which mechanisms may lead to species-specific differences in sensitivity to fishing and suggest that observed variation in responses may be influenced by ecological and evolutionary phenomena. Moreover, our results show that certain species (i.e. hammerhead sharks in this study) are inherently vulnerable to capture stress and mortality resulting from fisheries interactions and should receive additional attention in future conservation strategies.

KEY WORDS: Stress · Physiology · Vulnerability · Fishing · Angling · Fisheries · Reflex impairment

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INTRODUCTION

The life history, behavior, and fitness of organisms are dictated by their physiology (Ricklefs & Wikelski 2002, Wikelski & Cooke 2006). Many populations of marine fishes are threatened globally, primarily by heavy fishing pressure. Therefore, understanding

how fishes respond, from a physiological perspective, to fisheries interactions in their natural environment may elucidate patterns of vulnerability and resilience to fishing (Cooke et al. 2013a,b). These patterns may be especially important for threatened species, because management largely depends on our ability to identify how major stressors shape their populations,

either directly (e.g. mortality) or indirectly (e.g. growth and/or fitness impairments; Donaldson et al. 2011, Koehn et al. 2011).

In commercial, recreational, and some subsistence fisheries, a component of the catch is released, usually because of harvest regulations, conservation ethics or because the captured organism was not the target (Hall et al. 2000, Cooke & Cowx 2006, Arlinghaus et al. 2007). Although it was once assumed that fishes released alive with no obvious signs of injury will survive capture and release with minimal fitness impacts (Wydoski 1977), they often succumb to post-release mortality, even days after release. Information on delayed mortality is needed by wildlife fishery managers and scientists to estimate fishing mortality levels conducive to sustainable fishing practices (Bartholomew & Bohnsack 2005, Lewin et al. 2006). Therefore, there is wide interest in understanding the timing of, and conditions that bring about, post-release mortality, as well as how to minimize mortality of discarded or released individuals (Cooke & Cowx 2004).

Numerous studies have focused on the lethal (initial, short-term, and delayed mortality) and sublethal (e.g. physiological disturbances, injury, changes in post-release behavior) endpoints of teleost fishes that are hooked and released in both commercial and recreational fisheries (Chopin & Arimoto 1995, Cooke & Suski 2005, Serafy et al. 2009). Such studies now number more than 300 for recreational fisheries alone (Arlinghaus et al. 2007). Until recently, research directed toward understanding the physiological consequences of hook and line capture on sharks has been relatively rare (e.g. Moyes et al. 2006, Mandelman & Skomal 2009). However, given declines in certain shark populations, there is an increasing trend toward management regulations that require release of threatened or protected species that are captured (i.e. shark sanctuaries), and many recreational fishers are now adopting voluntary release procedures in the name of conservation (Babcock 2008, Skomal et al. 2008). Thus, there is a need to understand the consequences of hook and line capture and release on sharks to both increase post-release survival and to determine if these activities are compatible with regulations and voluntary conservation practices where sharks are released.

Biotelemetry (Cooke et al. 2004) and biologging (Block 2005, Ropert-Coudert & Wilson 2005) devices are commonly used to study fish post-release survival (Donaldson et al. 2008), and post-release mortality estimates have been inferred from satellite telemetric data in some sharks (Moyes et al. 2006, Campana et

al. 2009, Heberer et al. 2010, Musyl et al. 2011a). Concurrently, there have also been advances in the development and validation of non-lethal blood biopsy procedures with portable diagnostic tools that can be used *in situ* to characterize physiological stress responses (Suski et al. 2007, Gallagher et al. 2010).

Another measure of fish condition and vitality after fishery interactions is the index of reflex impairment (Davis 2007). Reflexes are involuntary movements that are elicited by external stimuli, representing components of more complex behaviors that have direct relevance to a species' ecology and fitness (Mesa et al. 1994). Impairment of certain reflexes (e.g. orientation, startle response, visual-ocular response) have been documented as useful predictors of post-release survivorship in salmon *Oncorhynchus* spp., rockfish *Sebastes* spp., and halibut *Hippoglossus* spp. (Davis 2007, Raby et al. 2012). Use of reflex activity as a metric for experimentally evaluating fishing stress has not been applied to sharks (but see Braccini et al. 2012, using 'activity and stimuli'). A shark's nictitating membrane is a thin, opaque sheet of connective tissue that serves as a protective mechanism for guarding against mechanical damage (Bell & Satchell 1963). Generally, this membrane can be seen activating (unilaterally) or 'firing' during predation events or in response to a pressure change around the eye or body (Gruber & Schneiderman 1975). It is plausible that this reflex could be a suitable stress indicator because it is not mediated by visual stimuli and does not fire once a shark is dead (Bell & Satchell 1963).

In this study, we used blood chemistry assessment, reflex tests, and telemetry to study the sublethal consequences and delayed mortality associated with 5 coastal shark species. Study objectives were to (1) characterize species-specific changes in physiological disturbance (measured using selected blood chemistry parameters) in sharks exposed to a standardized experimental fishing interaction as well as to identify factors that influence these outcomes, including shark size, species, and hooking duration (hereafter termed 'fight time'); (2) assess the utility of nictitating membrane reflex impairment as a measure of capture stress; (3) infer differences in post-release survival for a subset of species from satellite tag reporting rates; and (4) estimate and rank overall species vulnerability to fishing via integration of the above metrics. We tested the hypotheses that the magnitude of physiological disturbance and reflex impairment would be correlated with fight time and that physiological disturbance and reflex impairment

would be further modulated by biological characteristics including shark size and species. Further, we predicted that satellite telemetry reporting rates would be lowest for species exhibiting higher physiological disturbance and reflex impairment.

MATERIALS AND METHODS

Study sites and species

This study was conducted in 3 subtropical locations: inside Florida state waters within Everglades National Park (~25.0°N, 81.0°W), in US federal waters off the reef edge in the middle Florida Keys (~24.7°N, 80.9°W), and off the west end of Grand Bahama Island, Bahamas (~26.6°N, 79.1°W). Sampling was conducted from June 2010 to December 2012, across the wet and dry seasons (wet = June to November, average temperature for all locations = 26.5°C; dry = December to April, average temperature for all locations = 23.0°C). We evaluated individuals of the following 5 species: blacktip shark *Carcharhinus limbatus*, bull shark *Carcharhinus leucas*, great hammerhead shark *Sphyrna mokarran*, lemon shark *Negaprion brevirostris*, and tiger shark *Galeocerdo cuvier*.

All sharks were captured using standardized circle-hook drumlines, a passive, autonomous fishing technique (following Hammerschlag et al. 2011a). The gear consisted of a submerged weight base tied to a line running to the surface by means of an attached, inflatable buoy float (diameter/length = 37/49.5 cm). A 23 m monofilament gangion line (~400 kg

test) was attached to the submerged weight by a swivel, which terminated at a baited 16/0 5°-offset circle hook (Fig. 1). This method permitted sharks to swim in a 23 m radius circle around the base when captured. The proximal end of the monofilament line was connected to the weight via a hook timer (Lindgren Pitman HT600, recorded in minutes). Ten baited drumlines were deployed roughly ~500 m apart and allowed to soak for an hour. After an hour from the first deployment, each drumline was sequentially checked for shark presence. If a shark was captured, the force on the line triggered the hook timer (~3.6 kg release pressure) to start measuring fight time (to the nearest minute), which was recorded at drumline retrieval. Only jaw-hooked individuals that triggered their hook timers were considered in analyses.

Reflexes

Upon gear retrieval, sharks were brought alongside the boat and rapidly restrained on a partially submerged platform, after which individuals were sexed and measured for total length (TL; Table 1). Next, a reflex activity test on the nictitating membrane of each shark was performed. Each reflex test consisted of a small (3 ml) burst of seawater at a distance of 4 cm to the eye from a 10 ml plastic needleless syringe. After the burst of water, we checked for reflex activity of the nictitating membrane, which was tallied as either 'present' (membrane fired fully or partially) or 'absent' (membrane did not fire). Our reflex tests targeted the center portion of the right eye of each shark.

Blood chemistry

After administering the reflex test, whole blood was drawn from each individual through caudal venipuncture using 18 gauge needles and plastic non-heparinized syringes. The time between landing the fish and blood sampling was ≤ 3 min. Blood was immediately analyzed using an i-STAT 1 portable clinical analyzer (Abbott Laboratories) using the CG4+ cartridge for the following parameters: pH, pCO₂ (mm Hg), and lactate (mmol⁻¹). This tool has become popular for field physiology studies on teleost and elasmobranch fishes (e.g. Suski et al. 2007, Mandelman & Skomal 2009, Brooks et al. 2012) and has been validated for relative accuracy in select blood gas properties in ectothermic sharks (Gallagher et al. 2010).

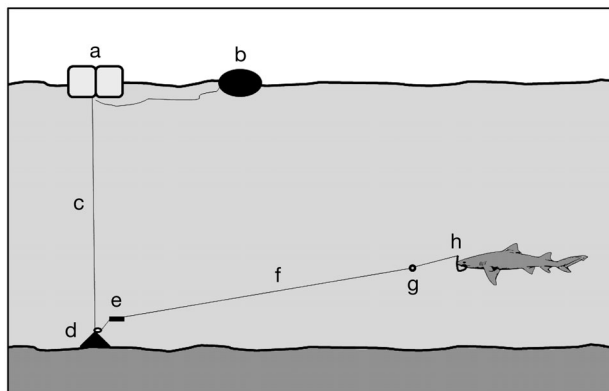


Fig. 1. Drumline fishing apparatus: (a) bullet floats; (b) large floating poly-ball; (c) rope attaching float to submerged weight; (d) ~18 kg cement weight; (e) hook timer; (f) main line of ~410 kg test monofilament; (g) 4 m double-stranded leader of ~410 kg test monofilament; (h) 16/0 5°-offset circle hook. The distance between (e) and (h) was 23 m, and the length between (a) and (d) ranged from 30 to 60 m

Table 1. Summary of physiological samples (blood panel includes pH, partial pressure of carbon dioxide, lactate, and reflex test), mean shark size and range, fight time range, and number of Smart Position or Temperature Transmitting satellite tags (SPOT5) deployed for each of the 5 species surveyed (na = species not assessed)

Shark species	Blood panel	Total length (cm)		Fight time (min)	No. of tag replicates
		Mean \pm SD	Range		
Blacktip	32	140.7 \pm 25.7	90–195	13–132	na
Bull	17	185.2 \pm 18.3	170–245	9–138	27
Great hammer-head	8	289.8 \pm 30.6	101–345	17–131	28
Lemon	23	195.0 \pm 24.1	780–153	24–124	na
Tiger	22	271.3 \pm 69.2	157–403	10–185	28

Post-release survival

In conjunction with a concurrent study on shark spatial ecology, we placed Smart Position or Temperature Transmitting (SPOT) satellite tags (SPOT5, Wildlife Computers) on bull ($n = 27$), great hammerhead ($n = 28$), and tiger ($n = 28$) sharks to investigate their potential post-release survival (Table 1). These are coastal species that spend considerable time at or near the water surface (Compagno et al. 2005), making them suitable for SPOT tags, which require the animal to surface for location transmission by the tags. This subset of sharks was tagged on separate surveys from 2010 to 2012 (see methods in Hammerschlag et al. 2011a, 2012a,b). All sharks selected for satellite tagging were alive and responsive (i.e. swimming away) upon release. Total time needed to affix a satellite tag averaged 4 min (following basic measurements). Satellite-tagged animals were not reflex tested nor blood sampled, and because specific fight time data were not available for all individuals, only the range of fight times (2 to 180 min) is represented in the data. All satellite-tagged animals swam away in good condition (strong tail beat and swimming behavior).

Statistical analyses

All pH and pCO₂ data were temperature adjusted to daily water temperature measurements (following Mandelman & Skomal 2009, Gallagher et al. 2010), and the pCO₂ and raw lactate data were log transformed to meet assumptions of normality and homogeneity of variances. Generalized linear models were used to explore relationships among blood parameters and the independent variables fight time, shark species, and shark length. A stepwise, backwards elimination approach was taken, starting with fully saturated models

that included all second- and third-order interactions. Beginning with the highest order terms, factors were removed sequentially if their p-values were >0.05 . Once final models were attained, least squares means were generated to examine for mean species-specific differences (if any) after controlling for fight time and/or size effects. Three-dimensional plots were constructed using predicted values obtained from regression coefficients using MATLAB (The Mathworks). Logistic regression was used to examine relations between nictitating mem-

brane reflex (binary response variable) and each of the following: pH, pCO₂, lactate, and fight time. Chi-square analysis was employed to examine for species-specific differences in overall reflex impairment.

Using species-specific least squares means for each of the 3 physiological and 1 reflex indicators, we ranked species according to their overall vulnerability to the fishing stressor. Vulnerability to each parameter ($V_{\text{parameter}}$) was used as a proxy for physiological and reflex disturbance (1 = least disturbed, 5 = most disturbed), as follows: vulnerability increased as lactate, pCO₂, and reflex impairment increased and as pH decreased (Mandelman & Skomal 2009). Cumulative vulnerability rankings were generated to estimate an overall relative 'risk of fishing' ($R = V_{\text{pH}} + V_{\text{CO}_2} + V_{\text{lactate}} + V_{\text{reflex}}$). All statistical analyses were performed using SAS (1990), and statistical significance was declared at $p < 0.05$.

Nominal estimates of tag reporting rates were determined for each species by calculating the total percentage of animals with reporting tags after 2, 3, and up to 4 wk following release; chi-square analysis was used to examine if these rates differed significantly (Sauer & Williams 1989). A reporting tag was indicated by any successful transmission (following Hammerschlag et al. 2012a). Previous work on large gamefishes and sharks has shown that mortality can occur from days to weeks after release (e.g. Moyes et al. 2006, Campana et al. 2009, Stokesbury et al. 2011); we increased the time allocated for detecting individuals when they remained at depth for extended periods following release.

RESULTS

Fight times for all 102 blood- and reflex-sampled individuals ranged from 9 to 185 min (mean \pm SD =

61.4 ± 41.7; Table 1), representing a range of capture stress. Based on measured TL and species life history (Compagno et al. 2005), all sharks sampled in this study were either subadult or mature (Table 1). Mean sizes were similar for the 3 medium-bodied sharks in our survey, represented by blacktip, bull, and lemon sharks. Our survey also assessed large apex predatory species, which included great hammerhead and tiger sharks.

Species effects were significant in the final models for all 3 parameters ($p < 0.05$; Table 2). Furthermore, the final model for lactate indicated that fight time and shark size had significant effects; however, no such relationships emerged for $p\text{CO}_2$ or pH values (Table 2). Further, lactate values were positively correlated with fight time, with no indication of a species-specific difference in the rate of lactate increase

Table 2. Results from the most parsimonious generalized linear models. * $p < 0.05$; ns = non-significant; $p\text{CO}_2$ = partial pressure of carbon dioxide

Model parameter	pH	$p\text{CO}_2$ (mm Hg)	Lactate (mmol l ⁻¹)
Fight time	ns	ns	*
Species	*	*	*
Size	ns	ns	ns
Fight time × Size	ns	ns	*

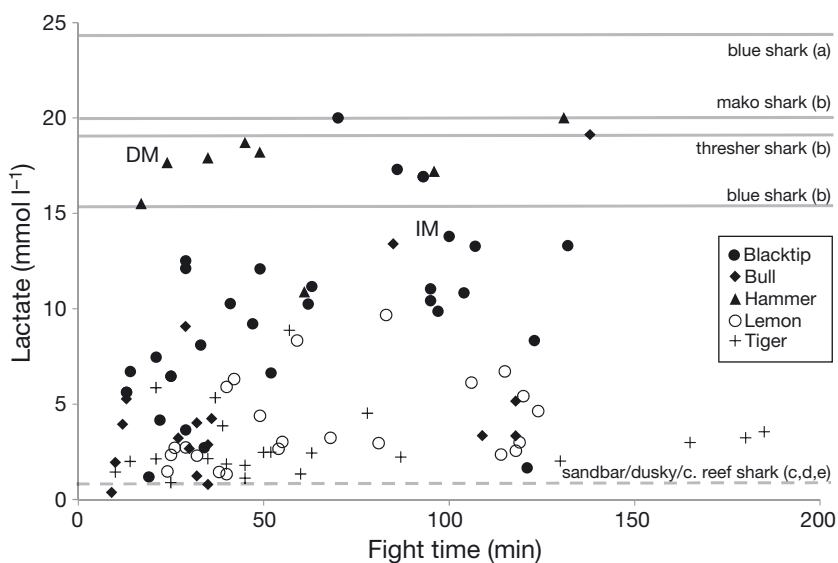


Fig. 2. Lactate (mmol l⁻¹) values from all sharks ($n = 102$) as a function of fight time (min). DM = delayed mortality; IM = immediate mortality. Solid lines: mean lactate values obtained from moribund sharks in previous studies. Dashed line: 'baseline' lactate values less than or equal to 1 mmol l⁻¹ from various carcharhinid sharks. (a) Moyes et al. 2006, (b) Hight et al. 2007, (c) Spargo 2001, (d) Cliff & Thurman 1984, (e) Brooks et al. 2012

(Table 2, Fig. 2). The emergence of a significant Size × Fight time interaction (and lack of a significant Species × Fight time interaction) suggested that Size was a better predictor than Species for lactate levels during exertion. It also suggested that the rate of lactate accumulation tended to decline with increasing Size ($p < 0.01$).

Post-hoc examination of least squares means for each of the 3 blood parameters indicated that great hammerhead sharks had higher values for both lactate and $p\text{CO}_2$ than the other 4 species (Fig. 3a,b). Blacktip sharks also displayed higher lactate levels (Fig. 3a). Lastly, blood pH values of great hammerhead, blacktip, and bull sharks were lower than those of lemon and tiger sharks (Fig. 3c). Delayed post-release mortality (~30 min) was observed (via animal-borne imaging) for 1 individual in this study, a 345 cm great hammerhead shark with a lactate value of 18.76 mmol l⁻¹ (DM in Fig. 2).

A wide range in reflex impairment among species was evident and generally agreed with the magnitude of differences in blood values on a species-specific basis. The reflex in great hammerhead shark individuals ($n = 8$) was 87.5% impaired and significantly different from the 0% rate of impairment in lemon and tiger sharks ($\chi^2 = 26.00$, $p < 0.0001$ and $\chi^2 = 25.10$, $p < 0.0001$, respectively). Blacktip and bull sharks both exhibited 53% impairment and were significantly different from both lemon ($\chi^2 = 17.69$, $p < 0.0001$ and $\chi^2 = 15.37$, $p < 0.0001$, respectively) and tiger ($\chi^2 = 17.96$, $p < 0.0001$ and $\chi^2 = 14.80$, $p < 0.0001$, respectively) sharks. However, we did not detect any significant effects of fight time, species, or any of the 3 blood parameters on the nictitating membrane reflex.

Ranking of vulnerability across each of the blood and reflex measures created a range of apparent risk to fishing stress (Table 3). Tiger sharks were consistently ranked low for each of the blood measures (low vulnerability to physiological disturbance), followed closely by lemon sharks. Conversely, blacktip and great hammerhead sharks generally ranked higher in their overall blood physiological disturbance, with hammerhead rankings the highest for all 3 measures. Bull sharks showed the greatest degree of heterogeneity in their rankings. Species' reflex rankings were

generally consistent with patterns evident in the blood. By summing each of the rankings for each species, a spectrum of overall relative 'risk' was generated, from low to high: tiger, lemon, bull, blacktip, and great hammerhead sharks (Table 3).

We deployed a total of 83 SPOT tags between January 2010 and December 2012 and analyzed species-specific differences in tag reporting rates over 2, 3, and 4 wk (Table 4). Tiger sharks displayed the highest reporting rates, with 100% of tagged individuals ($n = 28$) communicating after 4 wk except for a single individual that was killed (Table 4). Significant differences in tag reporting rates after 2 wk were detected between tiger and great hammerhead sharks ($\chi^2 = 15.27$, $p < 0.0001$) and between tiger and

bull sharks ($\chi^2 = 8.32$, $p < 0.01$). Significant differences in reporting rates between both sets of species were maintained after 3 and 4 wk ($p < 0.01$ in all cases).

DISCUSSION

Capture and restraint elicit profound physiological and biochemical responses among various taxa, as they are perceived as a threat to an animal's immediate survival (Kock et al. 1987, Romero 2004). In these situations, organisms mount stress responses, which affect short- and long-term fitness of individuals once they are released (Mazeaud et al. 1977, Wendelaar Bonga 1997). By using a standardized fishing technique and 3 approaches (blood chemistry, reflex impairment, and telemetry), we documented differences in the stress response to fishing and post-release alterations in survival among multiple coastal shark species.

Of the 3 blood parameters used in the current study, whole blood lactate emerged as the most informative endpoint because it was the only parameter to be significantly affected (positively) by increasing fight time ($R^2 = 0.54$; Table 2). When the rate of demand for oxygen in cells exceeds the rate of supply by the cardiovascular system (during exercise, for example), animals undergo a shift from aerobic to anaerobic metabolism, and lactate is generated as a by-product of the anaerobic glycolysis (Wood 1991). Lactate is gradually diffused from the white muscle into the blood, and Marshall et al. (2012) documented a significant positive relationship between empirical lactate levels of longline-captured sharks with at-vessel mortality rates. In a study of longline capture on blue sharks *Prionace glauca*, lactate emerged as

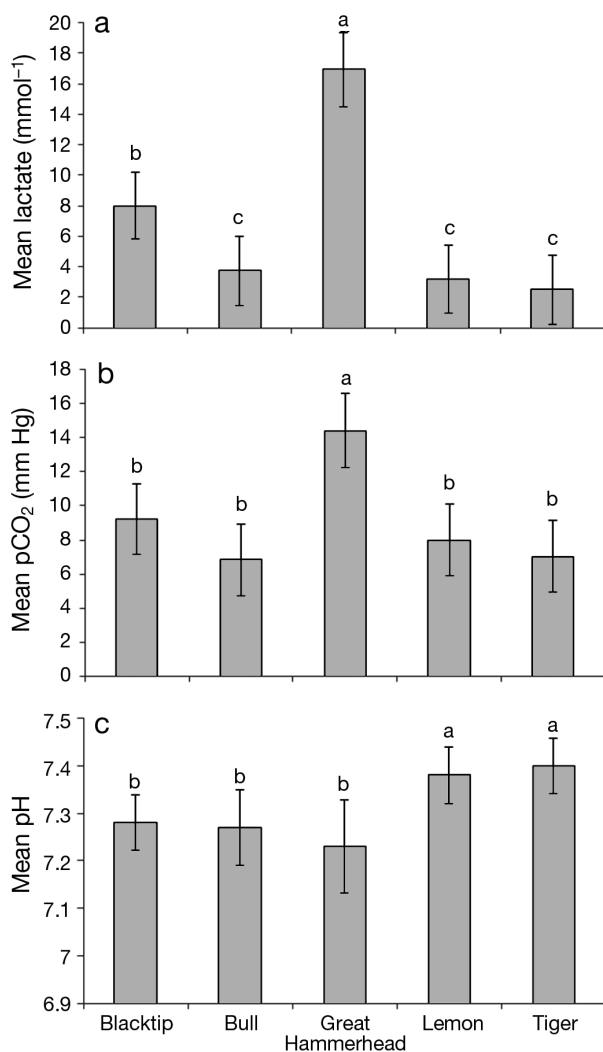


Fig. 3. Least squares means for (a) lactate, (b) partial pressure of carbon dioxide (pCO_2), and (c) pH for each species of shark. Error bars represent 95% CI. Lower-case letters indicate significant differences ($p < 0.05$)

Table 3. Relative rankings of vulnerability (V) and overall cumulative rank (R) for each of the 5 species (1 = least disturbed, 5 = most disturbed); vulnerability increased as lactate, partial pressure of carbon dioxide (pCO_2), and percent reflex impairment (Reflex) increased but as pH decreased. Cumulative ranks were calculated by adding each of the vulnerability ranks for each species

Shark species	V_{pH}	V_{pCO_2}	$V_{lactate}$	V_{reflex}	R
Blacktip	3	4	4	2	13
Bull	4	1	3	3	11
Great hammer-head	5	5	5	4	19
Lemon	2	3	2	1	8
Tiger	1	2	1	1	5

Table 4. Smart Position or Temperature Transmitting satellite tag reporting rates (calculated as the percentage of remaining reporting individuals from the total number originally tagged) after 2, 3, and 4 wk

Shark species	n	After 2 wk (%)	After 3 wk (%)	After 4 wk (%)
Bull	27	74.1	74.1	74.1
Great hammerhead	28	57.1	53.6	53.6
Tiger	28	100	100	96.4 ^a

^aOne tiger shark transmitted up to 26 d, after which it was caught and killed by a fisherman

one of the best predictors of post-release mortality, with moribund sharks exhibiting lactate values of ~ 20 mmol l⁻¹ (Moyes et al. 2006). Similar work on large sharks has also correlated mortality with mean lactate values at ~ 16 mmol l⁻¹ for blue sharks, 19 mmol l⁻¹ for pelagic thresher sharks *Alopias pelagicus*, and 20 mmol l⁻¹ for shortfin mako sharks *Isurus oxyrinchus*, while the range of observed values was 1 to 40 mmol l⁻¹ (Hight et al. 2007). In the present study, lactate levels were lowest in tiger sharks, yet significantly higher levels were evident in blacktip sharks (9.56 ± 4.65 mmol l⁻¹) and, to a greater extent, great hammerhead sharks (17.00 ± 2.78). By releasing a great hammerhead shark alive with an animal-borne video camera in the present study, we observed the individual begin swimming in a tilted position, lasting <10 min, then sink and die, after only a 24 min fight time (individual had a lactate level of ~ 19 mmol l⁻¹). While we do not have baseline, non-stressed values in the present study, previous work has reported lactate values between 0 and 1 mmol l⁻¹ for closely related shark species that were either held under laboratory conditions or sampled immediately after capture (Cliff & Thurman 1984, Spargo 2001, Skomal et al. 2007, Brooks et al. 2012).

We also detected a significant interaction between fight time and shark size for lactate, which revealed that rate of lactate production generally decreased as sharks increased in size (Fig. 4). This result may be related to the ability of larger individuals to more readily recover over time by increasing the amplitude of their tail beat despite a lower energetic cost of swimming (Carlson et al. 2004). Among fishes, propulsion is primarily generated from the caudal fin, whereby larger fin spans for a given body length generate enhanced lift performance (Daniel et al. 1992, Lingham-Soliar 2005). However, the greater the aspect ratio (fin span relative to fin area), the less energy is required to move the fish (Alexander 1990,

Lingham-Soliar 2005). It is plausible that this could be reflected in the metabolic consequences of anaerobic exercise or that smaller individuals may exhibit more exaggerated or repeated escape attempts.

Unlike other studies (e.g. Brooks et al. 2012), we did not observe significant changes in pCO₂ and pH values with increasing fight times (Table 2). One possible explanation for this result could be the differential (lower) aerobic potential afforded to sharks when fighting on shorter gangions, as used in previous work (gangion length = 2.5 m in Brooks et al. 2012), versus our experimental drumlines (23 m gangions; Fig. 1), which permitted the captured sharks to swim in circles around the base. It is plausible that the higher potential for ram-ventilating sharks hooked on the drumlines used in our study is driving the lack of a fight time effect on blood pH and pCO₂ values.

Our investigation of the nictitating membrane reflex response as a proxy of vitality in sharks did not yield any significant patterns between reflex impairment and blood parameters. However, values of reflex inhibition mirrored the general patterns of physiological disturbance, as indicated in our risk rankings, and these values significantly differed among species (Table 3, Fig. 3). We recognize the potential limitations of using just 1 reflex indicator, and future work on sharks should include multiple reflexes (orientation, ventilation, muscle tension, jaw tension) and calculate the total proportion of reflexes impaired (reflex action mortality predictor; sensu Davis 2010), upon which correlation with fishery-operational or biological variables is possible (Davis 2007, Raby et al. 2012).

We used SPOT tags to generate tag reporting rates, upon which we inferred post-release survival, and found that tiger sharks displayed the highest tag reporting rate (100%) in the first 2 wk of our study, followed by bull (74.1%) and great hammerhead sharks (57.1%; Table 4). Because of the requirement of sharks to surface to transmit data via SPOT tags, we realize the limitations and assumptions in generating estimates of mortality using this technology. Although we used a different tagging approach than the more commonly used pop-off archival tags for assessing survival (Musyl et al. 2011b), SPOT tags track sharks for longer durations because of a reduced probability of tag shedding (see review by Hammerschlag et al. 2011b). Moreover, because of the attachment methods and use of anti-fouling paint on our tags (Hammerschlag et al. 2011a, 2012a), it is likely that individuals that never transmitted over a 4 wk period (while conspecifics did report) died

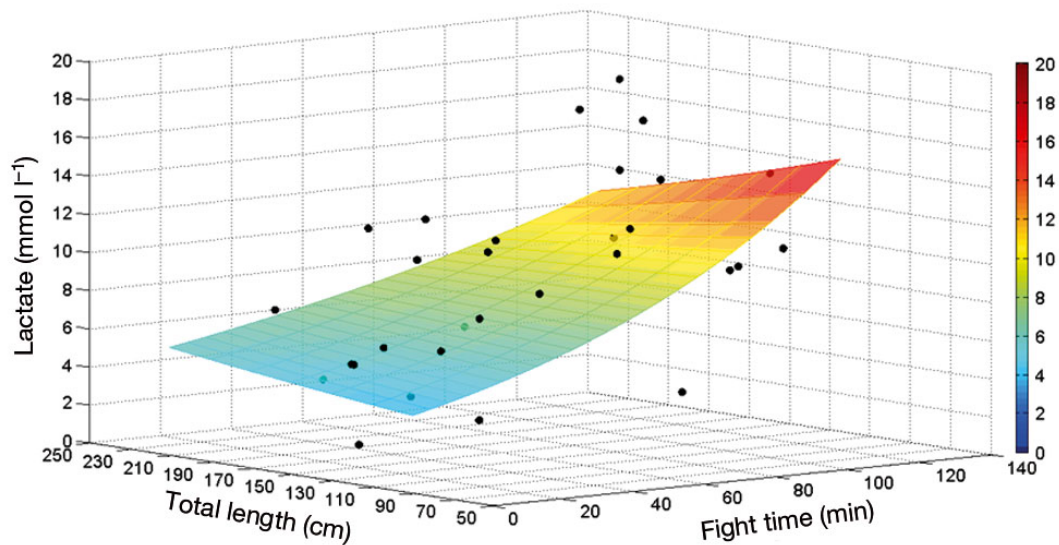


Fig. 4. *Carcharhinus limbatus*. Lactate as a function of shark size and fight time. Predicted values were generated according to the slope and intercept outputs from the most parsimonious generalized linear models. Fight time inputs ranged from 0 to 120 min at 20 min intervals; length inputs were generated according to the observed minimum and maximum sizes, with each step interval occurring at 20 cm increments. Observed lactate values are shown with black dots

(either from exhaustion or predation) without tag failure or shedding. This prediction is further supported by the fact that the entire random subset of 28 satellite-tagged tiger sharks reported up to the 4 wk mark (with the exception of the fished individual; Table 4), and some of them transmitted for periods of up to 297 d post-release with total distances traveled spanning up to 3500 km from the tagging location (Hammerschlag et al. 2012a). Individual variation in the surface behavior of species may have contributed to the differences in reporting rates. Regardless of the specific drivers of tag failure (i.e. shedding, mortality), our data suggest that almost all tags that stopped transmitting did so almost entirely within the first 2 wk for bull and great hammerhead sharks, a pattern which was not evident for tiger sharks.

These patterns of sensitivity resemble data published on at-vessel mortality rates of sharks captured as bycatch during longline fishing. In these studies, tiger sharks are consistently ranked as the most tolerant species, generally exhibiting less than 5% at-vessel mortality (Beerkircher et al. 2002, Morgan & Burgess 2007, Gallagher et al. unpubl.). Conversely, large hammerhead shark species exhibit at-vessel mortality rates ranging from 60 to 90% (Morgan & Burgess 2007, Morgan & Carlson 2010, Gallagher et al. unpubl.). Although we did not empirically derive post-release survival estimates for blacktip sharks, estimated at-vessel mortality rates for this species are relatively high (88%; Beerkircher et al. 2002). Here, we found this species ranked second only to great

hammerhead sharks in terms of vulnerability (in the blood parameters), although future empirical measurements of post-capture fitness and survival are needed.

Interspecific rankings and comparisons

Physiological variation directly affects the fitness of individuals, and differences among species may provide clues into patterns of resilience to stressors (Feder et al. 1987). Stress responses can be used as biomarkers of the combined effects of physiological challenge, energy budgets, and anthropogenic disturbance (Romero 2004), and the functional traits of species may be useful in understanding how species are affected by fishery interactions (Conrad et al. 2011, Gallagher et al. 2012, O'Connell et al. 2012). We attribute the range of stress responses to the performance/equilibrium differences of closely related species and variation in the operation of species' physiological machinery.

Burst activity using white muscle is fueled by anaerobic pathways and is energetically costly, and this type of metabolic strategy in vertebrates is linked to prey capture and escape from predators (Bennett 1982, Videler & Weihs 1982). Great hammerhead sharks are large apex predators that feed on a variety of prey including other elasmobranchs (e.g. Cliff 1995) and have been observed hunting seasonal migrations of blacktip and spinner *C. brevipinna*

sharks at high speeds in the surf zone off Florida (filmed by J. Abernethy). We speculate that similar metabolic pathways are enacted during the 'fight or flight' response to fishing capture for this species. We have documented intense and sustained fighting behavior immediately post-hooking for hammerhead sharks by placing underwater cameras on fishing gear (authors' unpubl. data). When hooked, this species has also 'towed' our submerged drumlines large distances from the deployment location (up to ~2 km). The blacktip shark, however, is a smaller sympatric species (Drymon et al. 2010) and may rely on burst swimming to escape predation from larger sharks (flight). Indeed, the burst/stamina continuum of prey capture or predator escape has been widely documented in other closely related taxonomic groups of vertebrates, as demonstrated by the intense metabolic acidosis and exhaustion when amphibians (frogs vs. toads) and large reptiles are faced with capture stress (Feder 1987). Crocodiles, for example, are largely sit-and-wait predators that rely on burst activity to capture mobile prey ('death roll'); however, these species are known to exhibit intense metabolic acidosis (large spikes in lactate production), exhaustion, and higher risk of mortality when faced with the stressors of capture (Bennett et al. 1985, Seymour et al. 1985; resting lactate values were $<1 \text{ mmol l}^{-1}$).

Evidence of burst swimming seems less obvious for species with lower risk rankings such as tiger and lemon sharks, whose swimming and fighting behavior may be more stamina-based. Captured tiger sharks were often observed with non-triggered hook timers (not included in analysis), also documented by Morgan & Carlson (2010), suggesting that the on-line stress response is more subdued than in other species examined. Whereas research on smaller teleost fishes has shown that endurance-trained fishes exhibited fatigue resistance and enhanced anaerobic capacity (Hammond & Hickman 1966), further work is needed to better understand if/how physiological (hematological anomalies) and morphological (gill surface area, gape size) properties of large elasmobranchs function to attenuate their stress response. While post-release survival was not investigated for lemon sharks, recreational fishers in the Florida Keys regularly capture, fight, and release the same individuals over successive years in the same location (C. Johnson pers. comm.). Whether these lifestyle traits (i.e. burst/stamina, morphology) may be reflected in the stress responses of sharks requires further validation (i.e. video analysis, placement of accelerometers on terminal fishing gear); however, the variation evident in our risk assessment suggests that the historical

selection of biological and physiological traits in shark species may have differential fitness consequences when individuals are exposed to fishing.

CONCLUSIONS

Although the approach applied here enables the evaluation of physiological alterations relative to a range of fight times, the absence of control data makes it difficult to infer the extent to which alterations deviate from resting levels (i.e. 'true' metabolic or respiratory acidosis). Furthermore, it remains unknown whether species exhibiting high to extreme physiological disturbance at low fight times (0 to 20 min for great hammerhead and blacktip sharks; Fig. 2) is a consequence of a rapid manifestation of lactate in the bloodstream missed by the present study or whether those species are regularly swimming at higher levels. Other assumptions in the present study are reflected in the potential variance in time needed to land, restrain, and blood sample each shark when captured, but aspects of the capture event including the hooking, fight/struggle, and handling are inherent with any gear types that use hook and line to capture fish (Cooke & Cowx 2006). The use of the standardized experimental fishing technique revealed species-specific patterns that may be translatable to other fishing gears, yet we caution extrapolating the results obtained herein beyond the study's general parameters. Nonetheless, we believe the combination of blood, reflex, and telemetry data revealed patterns among species that are useful in determining their relative vulnerabilities to fishing, and future application of video imaging and accelerometer devices to both fishing gear and the animals at release may provide additional information on the stress response and post-release impacts (e.g. Brownscombe et al. 2013 for accelerometer example).

This study may also suggest that relying on visual observations of post-release vitality could underestimate mortality and that these events could still occur in conservation zones that wholly restrict shark harvest (e.g. shark sanctuaries) and/or require release of threatened or protected species (e.g. regional/national prohibited species, endangered species list). For example, in January 2012, the state of Florida added 3 species of hammerhead sharks (great, scalloped [*Sphyrna lowini*], and smooth [*S. zygaena*]) to their prohibited species list, requiring individuals caught in state waters to be released. However, our results suggest that great hammerhead sharks are particularly vulnerable to fighting on a

line with short fight times, even when sharks are observed swimming away vigorously post-release. Thus, potential conservation strategies to address these issues in great hammerhead sharks (in addition to restricting harvest) could include having fishers avoid peak or aggregation areas/times, use weak fishing line or hooks, or simply cut the line nearest the hook (without having to 'fight' the animal; Stokesbury et al. 2011).

In summary, there is clearly the need for additional research on the levels of mortality and factors that contribute to capture and release mortality and for information on the population-level consequences of fishing mortality for many elasmobranch species. Although the concept of shark no-harvest zones is laudable, without information on fishing effort and capture and release mortality, it is difficult to know whether that regulatory approach is sufficient to enable depleted shark populations to recover. The approach used here demonstrates the value of tracking fitness in wild animals and reveals how such information can be used to inform management and conservation.

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