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The physiological effects of capture stress, recovery, and post-release survivorship of juvenile sand tigers (*Carcharias taurus*) caught on rod and reel

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ABSTRACT

Current shark fishery management regulations in the US Atlantic, as well as other regions worldwide, mandate the release of sand tigers (*Carcharias taurus*) captured in recreational fisheries. To examine the efficacy of this strategy as a conservation tool, the physical and physiological effects of capture stress and post-release survivorship were examined in juvenile sand tigers angled on conventional rod and reel tackle with offset circle hooks. Analysis of blood samples obtained immediately after capture ($n = 84$) indicated that, relative to minimally stressed captive individuals, juvenile sand tiger blood biochemistry is disturbed after brief (<7 min) angling events. Serial blood sampling of five captive sharks subjected to a 3 min simulated rod and reel angling event revealed rapid and significant disruptions in blood biochemistry with physiological recovery within 12–24 h. Post-release monitoring of 65 sharks surgically implanted with acoustic tags demonstrated high degrees of immediate (99%), short- (82%), and long-term post-release survivorship (75%). Physiological disruptions did not appear to reduce immediate survivorship (5 days post capture), however, sharks hooked internally had lower rates of survival 50–100 days following release. Overall, these results suggest that juvenile sand tigers are able to cope with and survive the physiological stress associated with brief rod and reel capture, but physical trauma associated with hook location can impair post-release survival. Regardless, mandatory release appears to be a viable management strategy for juvenile sand tigers captured in rod and reel fisheries.

1. Introduction

The sand tiger, *Carcharias taurus*, is a large coastal shark that occurs in temperate and subtropical waters of the Atlantic, Indian, western Pacific Ocean and Mediterranean Sea (Compagno, 1984). Historically, the species has been fished directly and/or taken as bycatch throughout its range (Compagno, 1984; Musick et al., 1993), and population declines have been documented in several geographic locations worldwide (US Atlantic – Musick et al., 1993, 2000; Eastern Australia – Otway and Parker, 2000; SW Atlantic – Lucifora et al., 2002). In response, a suite of regional management strategies, including mandated release, have been implemented to reduce fishing mortality in commercial and recreational fisheries (NMFS, 1999, 2006; ASMFC, 2008; Dicken et al., 2006; Bansemer and Bennett, 2008; Lucifora et al., 2009). Although mandatory release policy effectively reduces directed mortality, its true efficacy is contingent on the ability of sand tigers to recover from and survive interactions with fishing gear.

Limited information regarding the physical and physiological effects associated with capture is currently available for sand tigers. Lucifora et al. (2009) reported a high incidence (87.4%) of internal hooking (i.e. in internal organs) in recreational hook-and-line fisheries and suggested that this may result in post-release mortality. Similarly, Bansemer and Bennett (2010) reported that up to 52% of diver-observed sand tigers had retained fishing gear or jaw injuries resulting from capture and suggested that these interactions may ultimately lead to mortality. Such interactions with hook and line fishing gear have been shown to have adverse physical and physiological effects and influence post-release survival in other species (e.g. Skomal et al., 2002; Domeier et al., 2003; Moyes et al., 2006; Skomal, 2007; Campana et al., 2009). However, in the absence of empirical data, the true impact of these factors on sand tiger survivorship remains unknown.

Juvenile sand tigers (<1.5 m) are commonly captured by recreational hook and line anglers in US coastal waters (Bigelow and Schroeder, 1953; Kneebone et al., 2012) as well as other regions

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worldwide (e.g. South Africa-Dicken et al., 2006; Argentina-Lucifora et al., 2009). Given current fishery regulations (i.e. mandatory release) and the importance of juvenile survivorship to sand tiger population growth rates (Cortés, 2002; Goldman, 2002), a comprehensive assessment of the effects of hook and line capture and their influence on post-release survival is warranted. Accordingly, the objectives of this study were: (1) to quantify relative acid–base, electrolyte, and metabolite disturbances in the blood associated with the rod and reel capture of juvenile sand tigers; (2) to assess the magnitude and duration of physiological stress and the recovery of captive juvenile sand tigers subjected to experimental rod and reel capture; and (3) to examine immediate and delayed post-release mortality of these sharks in relation to physical and physiological stressors using passive acoustic monitoring.

2. Materials and methods

2.1. Study site and sampling

Juvenile sand tigers were angled in Plymouth, Kingston, Duxbury (PKD) Bay (August–September, 2008, June–October, 2009, June–October, 2010, and June–October, 2011) using fishing techniques and equipment consistent with current recreational fishing methods for sand tigers in PKD Bay and adjacent coastal waters. All sharks were angled at depths of 1.5–5 m with conventional rod and reel tackle (~15 kg class) rigged with offset circle hooks (size 8/0, model Octopus Circle 4x Strong, Gamakatsu USA Inc., WA, USA) on 36 kg vinyl-coated cable leader baited with cut menhaden (*Brevoortia tyrannus*). Angling events were timed (min) from the hook set to the landing of the shark with a dip net. Upon landing, the sex and fork length (FL; cm) of each shark were recorded. All capture and sampling methods conducted in this study were approved under the University of Massachusetts Dartmouth Institutional Animal Care and Use Committee Protocol Number 10-01.

Ambient bottom seawater temperature (°C) for each angling event was measured using temperature loggers (model HOBO Pendant, Onset Computer Corporation, Onset, MA) deployed at fixed locations throughout PKD Bay (see Kneebone et al., 2012 for details). Temperature data were collected every 30 min with an accuracy of ±0.7 °C (range −20 to 70 °C). Bottom seawater temperature measured by the logger nearest to the capture location (generally within 250 m) was utilized as a proxy for animal temperature (T).

2.2. Physical trauma

Upon capture, all sharks were examined for evidence of external physical trauma and the location of the hook. Each shark was then categorized based on the location and subsequent disposition of the hook: (1) mouth-hooked, hook removed; (2) gut-hooked (i.e. hooked internally), hook removed; or (3) gut-hooked, leader cut (i.e. hook retained). Sharks were considered mouth-hooked if the hook was embedded in the jaw and gut-hooked if the hook was ingested and not visible (i.e. the hook was embedded in the pharynx, esophagus, or stomach). When appropriate, hooks were removed from gut-hooked sharks using a small dehooker (ARC Dehooker, Inc., Bunnell, FL).

2.3. Physiological profiling

Upon landing, a blood sample (2–3 mL) was obtained immediately via caudal puncture and placed on ice. Blood samples were processed following the subsequent handling and release of the animal (usually within ~5 to 15 min) to determine acid–base chemistry at the time of capture. Specifically, pH and pCO_2 (Torr) levels were measured using a portable point-of-care blood gas analyzer (model IRMA Blood Analysis System, International Technidyne Corporation, Edison, NJ) calibrated to 37 °C.

Recent evidence suggests that relationships between blood gas tension and temperature are highly species-specific (Gallagher et al., 2010), but validated conversion factors are not available for sand tigers. Nonetheless, in an attempt to maintain the integrity of relative comparisons, all measured pH and pCO_2 data were subjected to a rough temperature correction (i.e., temperatures at which juvenile sand tigers were captured) using the equations presented in Mandelman and Skomal (2009):

$$pH_{TC} = pH_M - 0.011(T - 37) \quad (1)$$

$$pCO_{2TC} = pCO_{2M}(10^{-0.019(37-T)}) \quad (2)$$

where M and TC refer to the measured and temperature corrected values, respectively. Regardless of this correction, all changes in blood chemistry described by this study are expressed relative to baseline levels and are not intended to represent true *in vivo* conditions.

Blood lactate anion levels (mmol L^{-1}) were measured using a portable analyzer (model Lactate Pro, Arkray, Inc., Kyoto, Japan). In 2010 and 2011, the balance of the blood sample was centrifuged and the plasma was removed and frozen in liquid nitrogen for the subsequent lab-based determination of electrolyte and metabolite levels. In the lab, samples were thawed, diluted 1:1.6 with ultrapure water to fall within the readable range of the instrument, and analyzed with a blood analyzer (model Critical Care Xpress, Nova Biomedical Corporation, Waltham, MA) to determine the concentration of the electrolytes Na^+, Cl^-, K^+, Ca^{2+}, and Mg^{2+} (mmol L^{-1}) and the metabolites glucose (mg dL^{-1}) and lactate (mmol L^{-1}) (Marshall et al., 2012).

Given the minimum detectable blood lactate level of the portable analyzer of 0.8 mmol L^{-1}, we were unable to accurately quantify lactate levels below this threshold for blood samples not analyzed with the lab-based analyzer (2009; $n = 17$). Preliminary regression analysis between blood lactate levels measured by both machines indicated a close linear relationship ($y = 0.95x$, $n = 61$, $R^2 = 0.99$). Therefore, blood samples with lactate levels below the limit of sensitivity of the portable machine were assigned a value of 0.694 mmol L^{-1}, which was the average lactate level determined with the lab-based system for all wild-caught sand tigers with a 'Lo' (i.e. <0.8) Lactate Pro result ($n = 14$). In addition, this close association permitted the combination of data from the portable ($n = 34$) and lab-based ($n = 50$) analyzers for statistical analysis.

Baseline ("unstressed" or "resting") blood biochemistry parameters were obtained via 'grab and stab' at time = 0 h during the captive experiments (discussed in Section 2.4) and analyzed as previously described to establish control values. This method, which relies on the assumption that blood biochemistry is not significantly disrupted during minimal handling, has been widely utilized for obtaining estimates of unstressed baseline conditions in sharks (e.g. Cooper and Morris, 1998; Richards et al., 2003; Brill et al., 2008; Frick et al., 2009; Mandelman and Skomal, 2009; reviewed by Skomal and Bernal, 2010).

Changes in blood biochemistry in response to angling time (min) were assessed with generalized additive models (GAM; Zuur et al., 2009) with a Gaussian error distribution using the 'gamm4' package (Wood, 2011) in R (R Core Development Team, 2011). Control (baseline) data for each measured blood parameter were incorporated into appropriate models; data from a single 7 min angling event were not included in any models. Since previous studies have documented that longer angling times result in greater physiological response to stress (e.g. Skomal, 2007) a Kruskal–Wallis non-parametric analysis of variance was utilized to examine differences in angling times between each hooking treatment (Zar, 1999). Hook location was then incorporated into the model as a main

effect and with an interaction term to assess potential differences in the stress response between mouth- and gut-hooked sharks. To assess the significance of individual explanatory variables (i.e. angling time, hook location), individual terms were dropped and the full and nested models compared using the Akaike Information Criterion (AIC; Akaike, 1973). Zuur et al. (2009) cautioned against assessing statistical significance at p-values close to the 0.05 level in generalized additive models, instead suggesting that 'safe' statistical inference can be made based on p-values of 0.001 or less. Accordingly, significant relationships were identified from models with the lowest AIC value that contained significant terms ($p \leq 0.001$; this significance level was set solely for GAM models). Regression analysis was used to determine whether there was an effect of shark size (FL) on angling time. Significance was accepted at $p < 0.05$.

2.4. Captive experiments

Experimental trials were conducted to simulate 'typical' capture conditions experienced by juvenile sand tigers. Ten individuals were captured on rod and reel within PKD Bay, held in aerated onboard coolers, and transported to a 5700 l outdoor holding tank at the Jones River Landing Environmental Heritage Center; transport time was <30 min. Only sharks hooked in the mouth and free of physical trauma were utilized in experimental trials. All sharks were allowed to acclimate for at least 48 h prior to experimentation. Dissolved oxygen, salinity, and temperature levels were monitored during each experimental trial with a water quality meter (model 85; YSI Inc., Yellow Springs, OH).

Five juvenile sand tigers (two male and three female) ranging in size from 86 to 93 cm FL (90 ± 3 cm; mean ± SD) were subjected to 3 min simulated rod and reel capture event. At the commencement of each experiment, sharks were rapidly dip-netted, restrained at the surface, and a blood sample (2–3 mL) was obtained via caudal venipuncture (time = 0 h); total handling time was <20 s. To simulate the effects of angling, a circle hook (connected to a conventional rod and reel) was inserted through the jaw and the shark released into the tank to be 'angled' for 3 min; this was the maximum angling time observed during the 2009 sampling season. Each shark's activity was noted during the simulated angling event and characterized as either struggling rigorously, moderately, or not at all. The shark was then netted, restrained at the surface, and blood sampled (time = 0.05 h); the hook was removed before the shark was released back into the holding tank. Blood was then serially sampled at times 0.5, 1.0, 3.0, 6.0, 12.0, and 24.0 h post-stress. The behavior of each shark was observed for up to 1 h following each sampling event and characterized as swimming or resting on the bottom of the tank. To act as controls, five sharks (4 male and 1 female) ranging in size from 86 to 97 cm FL (91 ± 4 cm) were transported to the tank and exposed to repeated handling and blood sampling on the same timetable, but without angling. All blood samples were analyzed as previously described; measured pH and pCO_2 levels were temperature corrected using water temperature measured in the tank during each trial. Water quality conditions in the tank, as well as the size of captive sharks were compared between treatments using a two-tailed t-test.

Serial changes in blood acid–base chemistry, electrolytes, and metabolites over the 24 h experimental period were modeled using a generalized additive mixed model (GAMM; Zuur et al., 2009) with Gaussian error distribution in the 'gamm4' package in R. Since observations from each individual shark over time were not independent, 'shark' was incorporated into the model as a random effect to quantify variation of the fixed effects parameters across individuals. Due to the unequal time interval between experimental blood sampling events, time stamp data were square root transformed to improve model fitting. To avoid problems with model comparison, K^+, Ca^{2+}, and Mg^{2+} data were multiplied by a factor of 10. High variability was evident in baseline measurements (time 0) of blood glucose levels. Accordingly, relative changes in this parameter were standardized for each individual and expressed as Δglucose, which was calculated for each sampling event as the absolute difference between the respective glucose concentration and the baseline level. Model selection and significance testing were conducted as previously described for GAM models.

To assess differences in the stress response between experimental treatments (i.e. simulated capture and control), treatment level was incorporated into the model as a main effect and with an interaction term (treatment × time). Individual terms were then dropped and the full and nested models compared using AIC. Sharks were considered physiologically recovered when measured stress parameters returned to levels consistent with measured baseline (time = 0) values.

2.5. Post-release survivorship

Immediately after capture and blood sampling, tonic immobility was induced by restraining sharks ventral side up (Watsky and Gruber, 1990) and individuals were tagged externally with conventional National Marine Fisheries Service (NMFS) shark tags (Kohler and Turner, 2001). A subset of sharks were also tagged internally with individually coded 69 kHz acoustic transmitters (2008 and 2009: model V16-4L, nominal delay 30–90 s, longevity 2779 days; 2010: models V16-4L and V16T-4L, nominal delay 45–135 s, longevity 3650 days; and 2011: model V16T-4L, nominal delay 45–135 s, longevity 3280 days, and model V9AP-2L, nominal delay 60–180 s, longevity 123 days, and model V9AP-2H, nominal delay 60–180 s, longevity 81 days; Vemco Division, AMIRIX Systems Inc., Halifax, Nova Scotia). For tag implantation, a small incision (2–3 cm) was made on the ventral side along the midline, anterior to the pelvic fins, and the tag gently inserted into the body cavity. The incision was then closed by 3–4 interrupted sutures (model 2-0 PDS II, Ethicon Inc., NJ). All surgical implantations were completed within 5–10 min, and sharks were held in the water at the side of the vessel for release immediately following surgery.

Immediate, short-, and long-term post-release survivorship were assessed by passively monitoring acoustically tagged sand tigers for extended periods following release. Within PKD Bay, immediate (defined as ≤5 days) and short-term (defined as 5 to ≤50 days) post-release survivorship were assessed by examining movements of tagged sharks within a fixed acoustic receiver array (model VR2W, Vemco Division, AMIRIX Systems Inc., Halifax, Nova Scotia) deployed during four seasonal monitoring periods from 2008 to 2011 (see Kneebone et al., 2012 for details). Sharks that moved freely throughout the embayment post-release were considered alive, while sharks that displayed no movement (i.e. detected for >24 h at a single receiver) or suddenly ceased to be detected without showing evidence of movement out of PKD Bay were considered dead. Long-term post release-survivorship (defined as 50–100 days) was assessed via the detection of acoustically tagged sand tigers on the growing number of acoustic receivers deployed along the east coast of the United States as part of the Atlantic Cooperative Telemetry (ACT) Network. Confirmation of mortality of tagged sharks outside PKD Bay was impossible, however, any shark detected multiple times on any receiver deployed outside of PKD Bay was considered to be alive. In addition, short- and long-term survivorship was determined from the fishery-dependent recapture of any sharks with conventional external tags.

To examine the relationship between the physiological effects of capture stress on immediate post-release survivorship, all acoustically tagged sharks were classified as 'alive' or 'dead' and associated blood biochemistry data compared between groups. Physiological

stress was not linked to short- and long-term survivorship due to the inability to confirm mortality beyond 50 days and preliminary data that suggested physiological recovery may be achieved rapidly following capture. To assess the protracted effects of physical trauma (i.e. hooking location) on post-release survivorship, the proportion of sharks surviving at each of the aforementioned intervals was calculated for each hooking condition by dividing the total number of sharks that were confirmed to have survived to the end of each time interval (e.g. at least 5, 50, or 100 days following release) by the total number of monitored sharks in each respective time period. Sharks tagged with Vemco V9-AP tags were not included in the assessment of survival at 100 days due to the cessation of battery power by this period (battery life = 81 days; $n = 6$).

For comparative purposes, it was assumed that any reduction in survivorship of mouth-hooked sharks beyond 5 days (i.e. at 50 and 100 days post capture) was not associated with the observed (i.e. initial) capture event and likely the result of natural mortality, fishing mortality (i.e. from a subsequent capture event), or emigration from regions with acoustic receivers. Therefore, assuming these rates remained constant over all sharks (i.e. regardless of hooking condition), relative long-term post-release mortality was assessed by subtracting the percentage of surviving sharks in each gut-hooking category from the percentage of surviving mouth-hooked sharks at 100 days.

3. Results

3.1. Angling events and hooking location

A total of 111 juvenile sand tigers (Goldman et al., 2006) were captured throughout the study, 19 of which were recaptured and re-sampled (130 total angling events; Table 1). All of the latter were recaptured after more than two weeks and assumed to be fully recovered; therefore, data from all capture events were pooled for analysis. Ambient bottom water temperatures for all capture events ranged from 17.8 to 28.9 °C (21.9 ± 2.3 °C). Sharks were observed to be visibly exhausted when angled 3 min or longer (i.e. came to the surface and did not continue to fight aggressively). Linear regression of angling time and shark size (FL) revealed a significant relationship (FL = 0.03, $R^2 = 0.13$, $t = 3.82$, $p < 0.001$). Rates of gut hooking were similar between males (45%) and females (42%). In addition, ten sharks (8%) were observed to have retained hook and line fishing gear at the time of capture, indicative of prior interactions with recreational fishermen.

3.2. Physiological effects of capture

Blood samples were obtained immediately following capture from 72 individuals; details of capture events for these individual are presented in Table 1. There was no significant difference between the angling times experienced by sharks in each of the three hooking conditions (Kruskal–Wallis: $\chi^2 = 1.83$, df = 2, $p = 0.99$). Results of GAM analyses indicated that significant relationships existed between all measured stress parameters and angling time except glucose (Table 2; Fig. 1). There was no significant difference in the stress response between mouth- and gut-hooked sharks for all measured parameters (Table 2).

3.3. Captive experiments

Experimental treatments (simulated capture) were performed in 2010 ($n = 4$) and 2011 ($n = 1$), while the control (repeated sampling) treatments were conducted solely in 2011 ($n = 5$). There was no significant difference between the sizes of sharks used in the simulated capture or control treatments (t-test: $p = 0.43$).

Table 1
Juvenile sand tiger shark capture events observed within each component of the study. Percentages associated with hook location and disposition represent the percent of total sharks analyzed in each study component.

Number of			Fork length (cm)	Sex		Angling time (min)	Hook location (# of sharks)			Hook disposition[b]	
Sharks	Recaptures[a]	Total	Range (mean ± SD)	Male	Female	Range (mean ± SD)	Mouth	Gut	Body	Removed	Retained
All sharks											
111	19	130	78–120 (92 ± 9)	76	54	0.5–7 (1.4 ± 1.1)	72 (56%)	55 (42%)	3 (2%)	35 (27%)	20 (15%)
Blood sampled sharks											
72	12	84	79–120 (92 ± 9)	38	34	0.5–7 (1.5 ± 1.2)	45 (54%)	38 (45%)	1 (0.01%)	24 (29%)	14 (17%)
Post-release monitored											
66	0	66	79–108 (91 ± 8)	34	31	0.5–5 (1.2 ± 0.8)	32 (49%)	34 (51%)	0	21 (32%)	13 (20%)

[a] Sharks were recaptured at least two weeks following their initial capture and assumed to be recovered.
[b] Refers only to gut-hooked sharks. Hooks were removed from all sharks hooked in the mouth or on the body.

Table 2
Summary of AIC model selection results from generalized additive models examining the effects of angling time, hook location (mouth or gut), and their interaction ($T \times$ HL) on blood biochemistry. Models with the lowest AIC values for each parameter are indicated in bold; statistical significance was accepted at $p \leq 0.001$. TC = temperature corrected.

	T[a]	HL[b]	$T \times$ HL	Intercept	F	p
pH_{TC}	**−215.50**	−213.43	−207.97	−152.04	31.44	<0.001
pCO_{2TC}	**418.22**	420.22	425.32	476.61	21.98	<0.001
Lactate	**114.63**	116.29	115.70	155.75	14.75	<0.001
Na^+	**364.41**	366.37	370.62	431.45	29.58	<0.001
Cl^-	**372.89**	374.88	379.11	413.28	14.59	<0.001
Ca^{2+}	**−89.45**	−87.63	−84.58	−67.63	15.52	<0.001
K^+	**59.96**	61.69	65.00	89.08	21.38	<0.001
Mg^{2+}	**−152.75**	−150.85	−146.98	−142.85	7.47	0.001
Glucose	**415.71**	415.13	415.56	418.31	2.43	0.05

[a] Angling time.
[b] Hook location.

Holding tank water temperature (21.6–25.4 °C; 23.6 ± 1.6; range, mean ± SD), salinity (18.7–26.8 ppt; 20.8 ± 2.6), and dissolved oxygen (67.5–95.5%; 81.6 ± 10.2) varied throughout the course of the study. There were no differences in mean dissolved oxygen (t-test: $p = 0.45$) and salinity (t-test: $p = 0.08$) levels between the two treatments, however, water temperatures were significantly higher during the control treatment (23.2–25.4 °C; 24.9 ± 1.0) than the simulated capture treatment (21.6–23.1 °C; 22.3 ± 0.7; t-test: $p = 0.001$).

Sharks exposed to simulated angling trials fought relatively aggressively and swam erratically around the tank, often twisting and shaking their head rapidly in an attempt to throw the hook. All sharks were visibly exhausted near the termination of the simulated angling event and swam slowly at the surface of the tank for the last 10–20 s of the treatment. Upon release back into the tank, all sharks moved directly to the bottom and rested motionlessly while buccal pumping for up to 2 h; on some occasions, brief periods (1–5 min) of slow swimming were observed during this resting period. All sharks resumed normal swimming behavior (as observed in fully acclimated sharks prior to the commencement of the experiment) within 3 h of the simulated angling event and did not return to the bottom for extended periods following any subsequent blood sampling event.

Results of GAMM analyses indicated that all measured blood stress parameters changed significantly throughout the 24 h monitoring period (Table 3). In all sharks, the onset of physiological stress was rapid; the timing of the maximum deviation from baseline levels varied between parameters (Figs. 2–4). Peak disturbances in

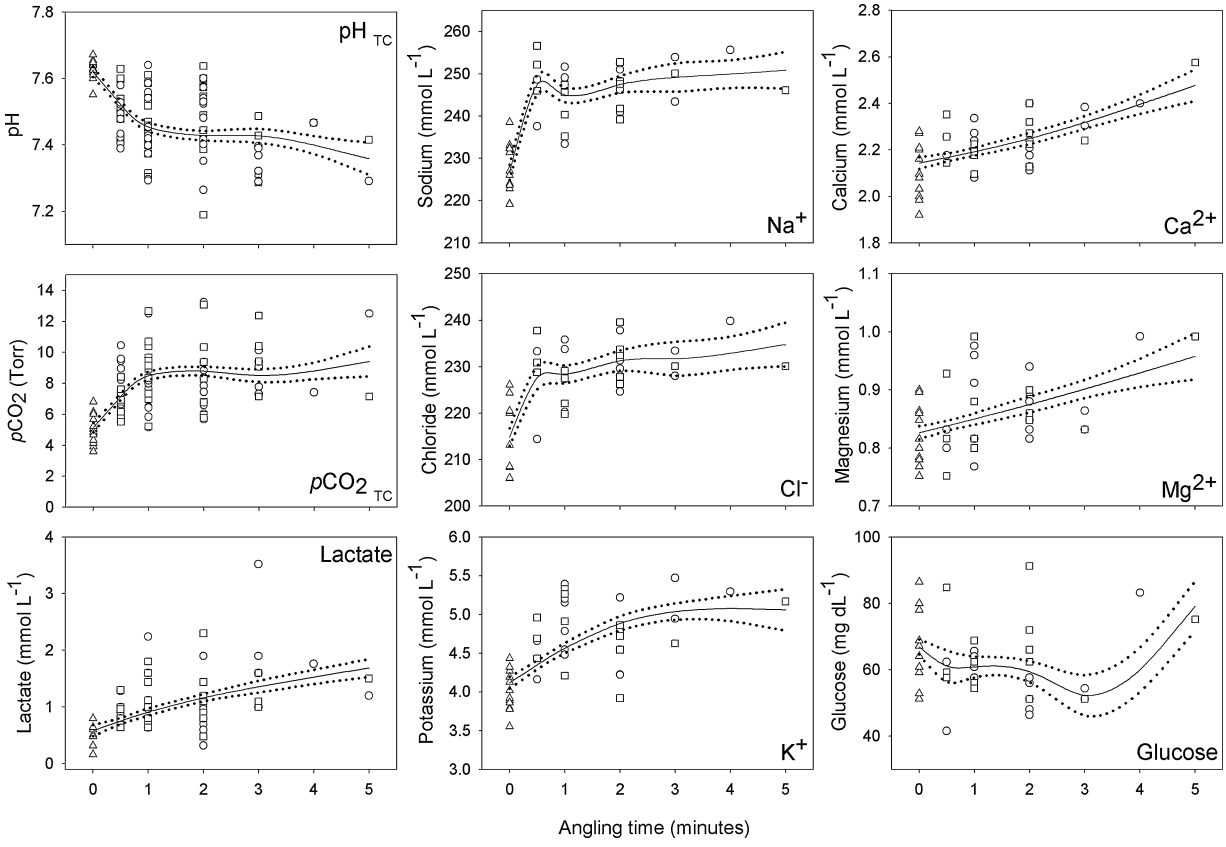

Fig. 1. Changes in blood biochemistry parameters in response to angling time in juvenile sand tigers. Data on baseline levels (triangles) and for mouth (diamonds) and gut (circles) hooked sharks are presented. Smoothers from generalized additive models (solid line) generated from all data combined are plotted with 95% confidence intervals (dotted line). All smoothers represent significant relationships ($p \leq 0.001$) except for glucose. Data from a single 7 min angling event are not presented. Temperature corrected (TC) values of pH and pCO_2 are presented.

Table 3
Summary of results from generalized additive mixed models applied to blood biochemistry data from experimental trials on captive sand tigers. The relationship of each parameter over the 24 h monitoring period (time) was examined via comparison with the intercept only model using the AIC. The model with the lowest AIC is presented in bold; *F* and *p*-values from the optimal model are also presented. Statistical significance was accepted at $p \leq 0.001$. Comparison of the stress response between control (repeated sampling) and treatment (simulated capture) trials using AIC is reported; the model with the lowest AIC is indicated in bold. TC = temperature corrected.

	Simulated capture				Repeated sampling				Treatment comparison		
Parameter	Time	Int[a]	*F*	*p*	Time	Int[a]	*F*	*p*	*Trt[b]	Trt[c]	Time[d]
pH_{TC}	**−58.75**	−12.64	59.36	<0.001	**−60.42**	−52.07	16.18	<0.001	**−118.48**	−114.41	−111.48
pCO_{2TC}	**121.03**	158.98	15.34	<0.001	**110.78**	133.09	9.22	<0.001	**229.25**	238.47	237.09
Lactate	**170.67**	224.44	23.05	<0.001	**84.20**	99.85	11.84	<0.001	**293.66**	352.53	360.64
Na^+	**231.66**	261.85	7.77	<0.001	**195.44**	206.39	1.17	0.16	**434.85**	454.02	465.52
Cl^-	**217.16**	240.36	6.12	<0.001	**207.63**	215.65	1.60	0.23	**418.43**	436.78	443.32
Ca^{2+}	**104.47**	116.17	7.49	0.001	77.45	**76.10**	1.96	0.16	**183.10**	188.38	187.56
K^+	**23.74**	55.06	24.89	<0.001	**176.41**	191.91	3.66	0.007	**363.80**	386.36	388.18
Mg^{2+}	**65.11**	85.49	7.73	<0.001	73.10	**59.02**	1.42	0.24	147.60	142.67	**142.07**
ΔGlucose	**342.97**	362.52	8.12	0.001	**200.38**	221.09	14.27	<0.001	**632.44**	648.99	657.20

[a] Intercept.
[b] Interaction model (treatment × time) – the overall stress response differed over time.
[c] Treatment model – the magnitude of the stress response differed over time.
[d] Control model – no difference between the stress response over time.

acid–base chemistry were evident for pH and pCO_2 at 0.05 and 0.5 h, respectively. Lactate levels were elevated for up to 12 h post-stress; peak disturbance was observed at 3 h. Electrolyte disruptions were evident within 3 h post-stress; peak disturbances were observed at 0.05 (K^+), 0.5 (Na^+, Ca^{2+}, Mg^{2+}), and 1 h (Cl^-). Relative changes in glucose levels were variable between individual sharks; peaking around 12 h post-stress.

Physiological recovery varied for each measured parameter, with recovery of most parameters evident within 3–6 h (Table 4). Collectively, blood acid–base chemistry was fully recovered 12 h

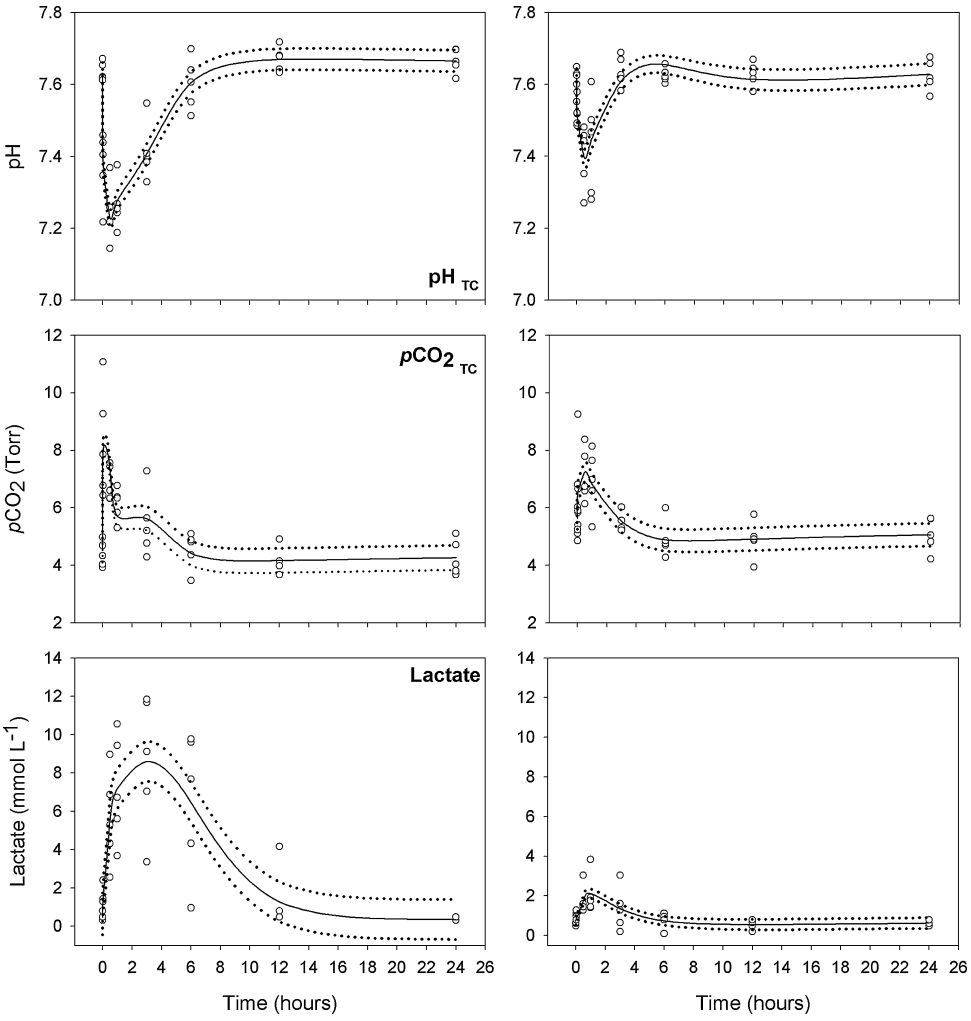

Fig. 2. Changes in pH, pCO_2, and lactate over the 24 h experimental period for treatment (simulated capture, left) and control (repeated sampling, right) groups. Raw data are plotted (circles) in addition to GAMM smoothers (solid line) with 95% confidence intervals (dotted line). Temperature corrected (TC) values of pH and pCO_2 are presented.

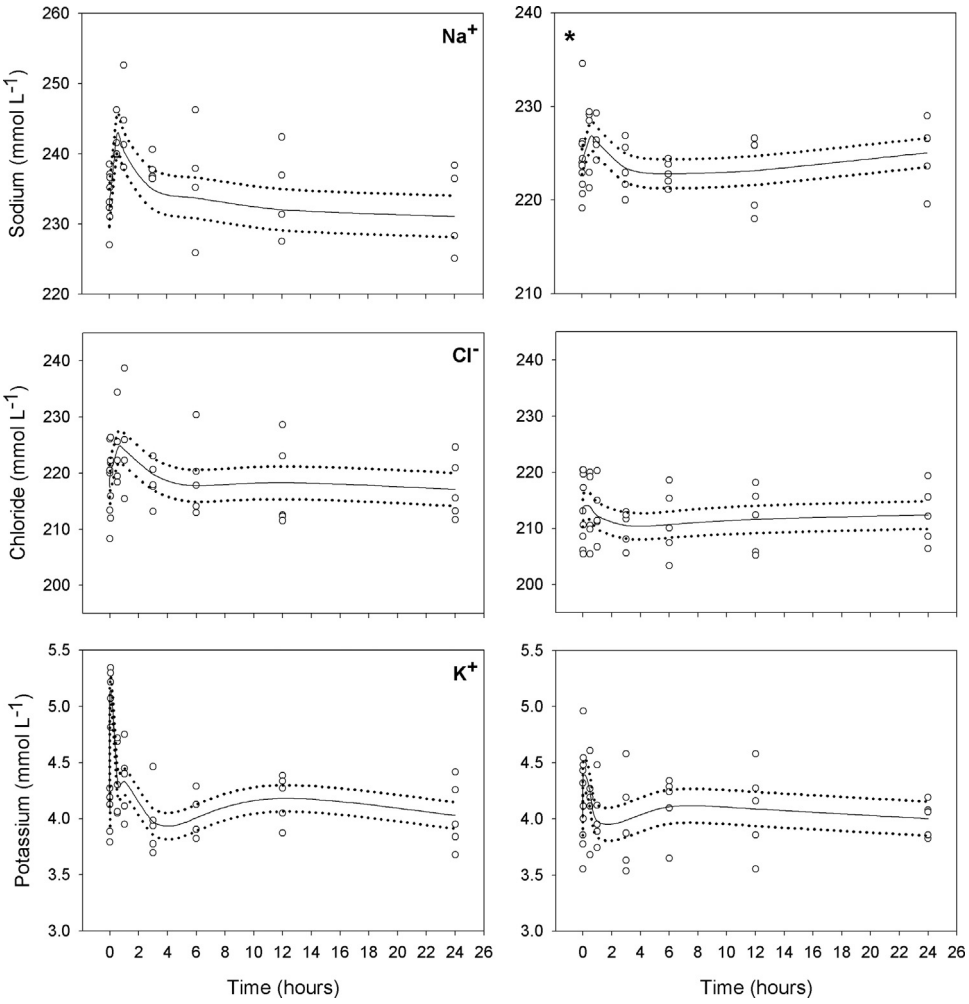

Fig. 3. Changes in Na^+, Cl^-, and K^+ concentrations over the 24 h experimental period for treatment (simulated capture, left) and control (repeated sampling, right) groups. Raw data are plotted (circles) in addition to GAMM smoothers (solid line) with 95% confidence intervals (dotted line). *A difference in axis scale between groups.

post-stress; pH and pCO_2 within 6 h and lactate within 12 h. All measured electrolytes returned to baseline levels within 3 h. Glucose levels returned to baseline levels within 24 h for two of the five individuals; elevated levels were still apparent at 24 h in the remaining sharks.

Sharks subjected to control repeated blood sampling trials exhibited a physiological stress response. After initial blood sampling (i.e. time 0 and +3 min), three of the five sharks swam slowly around the tank; two sharks rested on the bottom for up to 1 h post blood sampling. All sharks resumed normal swimming behavior (as observed in fully acclimated sharks) within 1 h of the initial blood sampling and did not rest for extended periods following any additional blood sampling event.

Statistical comparison of GAMM models indicated that significant relationships existed for pH, pCO_2, lactate, and Δglucose levels and time throughout the 24 h monitoring period (Table 3; Figs. 2–4). No significant relationships were evident for Na^+, K^+, Cl^-, Ca^{2+} or Mg^{2+}; however, relative changes in each parameter were evident over time (Table 3; Figs. 3 and 4). In all sharks, evidence of physiological stress was apparent in the 3 min blood sample; the timing of the maximum deviation from baseline levels varied between parameters (Table 4). Peak disturbances in acid–base chemistry were evident for pH and pCO_2 at 0.5 h, and at 1 h for lactate. In general, electrolyte disruptions were evident within 1 h post stress; peak disturbances were observed at 0.05 h (K^+, Cl^-), 0.5 h (Ca^{2+}, Mg^{2+}), and 1 h (Na^+). Relative changes in glucose levels were variable between individual sharks, though gradual slight elevations were evident throughout the entire sampling period.

Physiological recovery was achieved within the 24 h monitoring period for all measured parameters except for glucose (Table 4). Collectively, recovery of blood acid–base chemistry was variable with pH and pCO_2 fully recovered within 3 h and lactate within 6–12. The recovery of all measured ions was also variable with a return to baseline levels observed at 0.5 h (Cl^-), 1 h (K^+, Ca^{2+}), and 3 h (Na^+, Mg^{2+}). Glucose levels returned to baseline levels within 24 h for three of the five individuals; glucose was still slightly elevated after 24 h in the remaining two sharks.

Comparison of GAMM results indicated that the stress response differed between the simulated capture and repeated sampling treatments (Table 3) with the magnitude of disruptions greater in treatment (simulated angling) groups. There was no statistical difference between treatments for Mg^{2+}, however, closer examination of Mg^{2+} data and resulting plots indicated that there was indeed an absolute difference between treatments; Mg^{2+} levels were greater at 0.5 and 1 h in the simulated angling trials (Fig. 4).

3.4. Post-release survivorship

Sixty-five sharks were surgically implanted with acoustic transmitters and monitored for extended periods of time following release (Table 1). The recapture of a single conventionally tagged

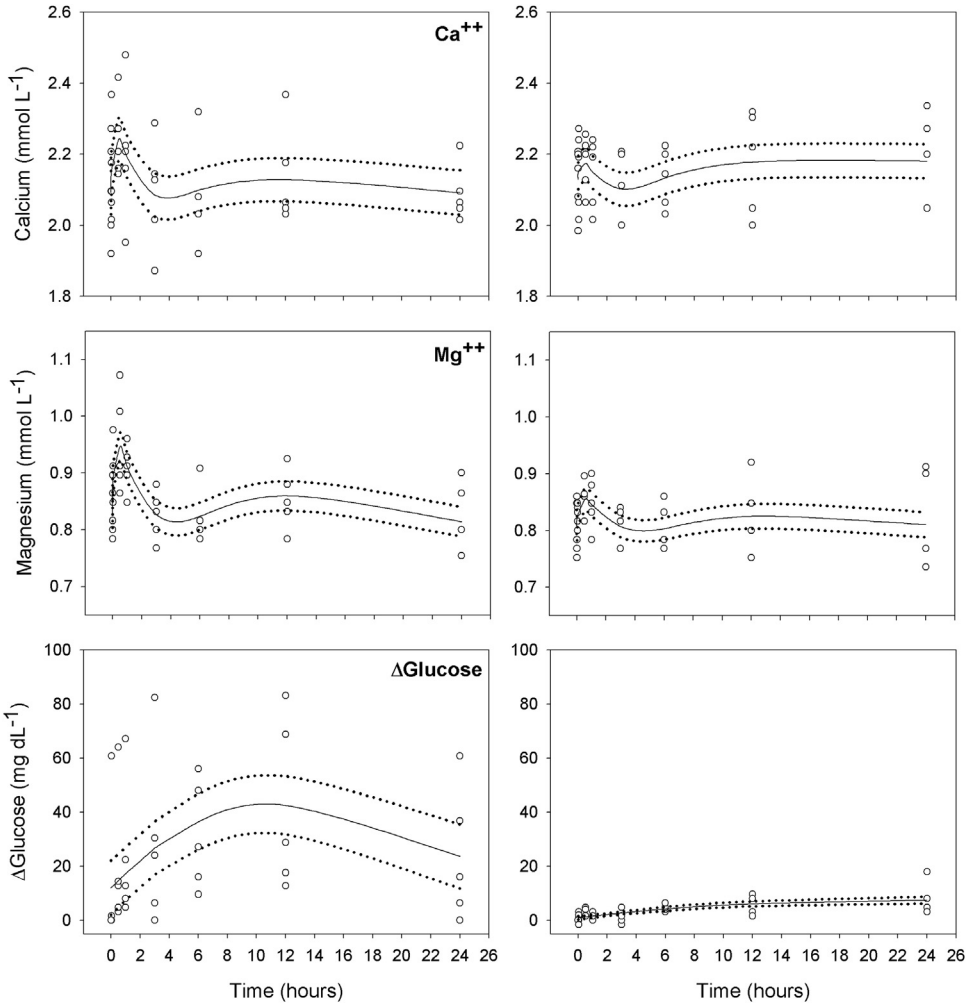

Fig. 4. Changes in Ca^{2+}, Mg^{2+}, and Δglucose concentrations over the 24 h experimental period for treatment (simulated capture, left) and control (repeated sampling, right) groups. Raw data are plotted (circles) in addition to GAMM smoothers (solid line) with 95% confidence intervals (dotted line).

male shark (95 cm FL) 735 days (~24 months) after release was also included in the analysis (total = 66). With the exception of one shark, none of the sharks exhibited immediate mortality, resulting in an overall survival rate of 99% within 5 days post-release (Table 5). The single mortality, a 79 cm FL female, occurred approximately 13 h after release. The angling event for this shark was brief (0.5 min), and all measured blood parameters were minimally disturbed (in relation to control baseline values) following capture. However, the shark was gut-hooked and released with the hook retained. Post-mortem necropsy on this individual (the carcass washed up on shore and was recovered) revealed that the hook had penetrated the pericardial cavity, suggesting that death may have resulted from the physical trauma associated with gut-hooking as opposed to physiological disruption. Overall short- and long-term survivorship was also high (82 and 75%, respectively); survival rates were markedly lower for gut-hooked (both with the hook removed and retained) than mouth-hooked sharks (Table 5). Relative total mortality rates (in comparison to mouth hooked sharks at 100 days) were estimated at 18 and 28% for gut-hooked sharks with the hook removed and retained, respectively.

4. Discussion

The results of this study provide insights into the physical and physiological effects of conventional rod and reel capture on juvenile sand tigers, and their ability to survive catch and release. In general, despite significant physical (i.e. hook damage) and physiological impacts, a large percentage (i.e. at least 75%) of monitored juvenile sand tigers were able to recover from and survive capture related stress. This finding confirms the efficacy of mandatory release policy as a conservation tool for juvenile sand tigers in the US Atlantic and Gulf of Mexico (NMFS, 2006; ASMFC, 2008), Eastern Australia (Environment Australia, 2002) and northern Argentina (Lucifora et al., 2009).

4.1. Hooking location

A high degree of internal (gut) hooking was observed in this study, which is consistent with previously published studies on sand tigers (Otway and Burke, 2004; Lucifora et al., 2009; Bansemer and Bennett, 2010). In spite of this, the use of circle hooks appears to be effective at minimizing internal physical trauma in this species. For example, Lucifora et al. (2009) reported an 87.4% incidence of gut-hooking in an Argentinean recreational fishery that solely utilized 'J-hooks' (L. Lucifora; pers. comm.), whereas 42% of sharks caught on offset circle hooks in this study were gut-hooked; less than half the frequency reported for J-hooks. Thus, though the size of sharks investigated in these studies differed (the majority of the sand tigers sampled in Lucifora et al., 2009 were >150 cm FL), the use of offset circle hooks does appear to reduce gut-hooking, at least in juveniles. Regardless, given the reduced survivorship of internally hooked sharks observed by

Table 4
Sand tiger blood biochemistry at each sampling interval during captive experiments. Measured and temperature corrected (TC) values are presented. All temperature corrections were performed using ambient bottom seawater temperatures measured at the time and location of capture.

Time	pH	pH_{TC}	pCO_2	pCO_{2TC}	Na^+	K^+	Cl^-	Ca^{2+}	Mg^{2+}	Glucose	Lactate	ΔGlucose
Simulated capture (3 min angling event; $n = 5$)												
0	7.47 ± 0.04	7.64 ± 0.03	8.5 ± 1.2	4.4 ± 0.4	232.0 ± 4.4	4.0 ± 0.2	217.6 ± 6.9	2.09 ± 0.14	0.83 ± 0.05	61.1 ± 10.9	0.4 ± 0.2	NA
0.05	7.20 ± 0.09	7.37 ± 0.09	15.9 ± 3.1	8.3 ± 1.9	233.8 ± 3.5	5.1 ± 0.2	219.6 ± 5.7	2.14 ± 0.14	0.88 ± 0.06	73.9 ± 24.5	1.5 ± 0.5	12.8 ± 26.8
0.5	7.07 ± 0.09	7.24 ± 0.08	12.8 ± 2.2	6.8 ± 0.6	241.7 ± 2.6	4.3 ± 0.3	224.0 ± 6.4	2.24 ± 0.11	0.95 ± 0.09	80.9 ± 22.9	5.6 ± 2.4	19.8 ± 25.2
1	7.10 ± 0.07	7.27 ± 0.07	11.8 ± 0.8	6.1 ± 0.6	241.3 ± 8.3	4.3 ± 0.3	224.9 ± 8.6	2.20 ± 0.19	0.90 ± 0.04	84.1 ± 22.2	7.2 ± 2.8	23.0 ± 25.6
3	7.24 ± 0.09	7.41 ± 0.08	10.0 ± 2.3	5.4 ± 1.1	234.3 ± 8.1	3.9 ± 0.3	218.4 ± 3.7	2.08 ± 0.16	0.82 ± 0.04	93.7 ± 39.0	8.6 ± 3.5	32.6 ± 40.9
6	7.43 ± 0.08	7.60 ± 0.07	8.7 ± 1.4	4.5 ± 0.6	234.0 ± 8.8	4.0 ± 0.2	219.1 ± 7.0	2.08 ± 0.15	0.82 ± 0.06	92.4 ± 24.1	6.4 ± 3.8	31.3 ± 20.1
12	7.51 ± 0.04	7.67 ± 0.03	7.6 ± 0.9	4.1 ± 0.5	231.9 ± 8.1	4.1 ± 0.2	217.6 ± 7.8	2.13 ± 0.14	0.87 ± 0.10	103.3 ± 37.7	1.2 ± 1.6	42.2 ± 31.8
24	7.50 ± 0.03	7.67 ± 0.03	8.2 ± 1.4	4.3 ± 0.6	231.0 ± 5.9	4.0 ± 0.3	217.2 ± 5.4	2.08 ± 0.08	0.80 ± 0.11	85.1 ± 32.0	0.3 ± 0.1	24.0 ± 24.8
Control (repeated sampling; $n = 5$)												
0	7.47 ± 0.04	7.61 ± 0.04	9.5 ± 1.8	5.6 ± 0.8	223.1 ± 2.3	4.0 ± 0.4	212.2 ± 4.9	2.12 ± 0.09	0.80 ± 0.05	81.1 ± 21.1	0.6 ± 0.1	NA
0.05	7.38 ± 0.04	7.52 ± 0.04	11.3 ± 3.3	6.6 ± 1.5	225.5 ± 4.9	4.4 ± 0.4	214.6 ± 5.8	2.15 ± 0.11	0.82 ± 0.02	82.1 ± 21.8	1.0 ± 0.2	1.0 ± 1.9
0.5	7.26 ± 0.08	7.40 ± 0.09	12.1 ± 2.1	7.1 ± 0.9	226.2 ± 3.4	4.2 ± 0.3	213.0 ± 5.7	2.17 ± 0.08	0.85 ± 0.03	83.8 ± 22.3	1.7 ± 0.7	2.7 ± 1.6
1	7.29 ± 0.13	7.43 ± 0.14	11.8 ± 1.8	6.9 ± 1.1	226.4 ± 1.6	4.0 ± 0.3	212.9 ± 4.5	2.14 ± 0.10	0.84 ± 0.04	82.7 ± 20.6	2.0 ± 1.0	1.6 ± 1.1
3	7.48 ± 0.08	7.64 ± 0.04	9.3 ± 0.7	5.5 ± 0.3	223.4 ± 2.5	4.0 ± 0.4	210.1 ± 2.8	2.10 ± 0.10	0.80 ± 0.03	82.4 ± 19.8	1.3 ± 1.1	1.2 ± 2.4
6	7.51 ± 0.07	7.63 ± 0.02	8.8 ± 2.4	4.9 ± 0.6	222.8 ± 1.2	4.1 ± 0.3	210.9 ± 5.5	2.13 ± 0.08	0.80 ± 0.04	86.0 ± 20.2	0.7 ± 0.4	4.9 ± 1.4
12	7.49 ± 0.02	7.63 ± 0.03	8.2 ± 1.6	4.9 ± 0.6	223.1 ± 3.7	4.1 ± 0.4	213.4 ± 6.8	2.17 ± 0.15	0.82 ± 0.06	87.2 ± 23.1	0.5 ± 0.2	6.0 ± 3.5
24	7.49 ± 0.04	7.63 ± 0.04	8.6 ± 1.3	5.1 ± 0.6	225.0 ± 3.2	4.0 ± 0.2	214.4 ± 6.1	2.18 ± 0.13	0.81 ± 0.09	88.5 ± 27.3	0.6 ± 0.2	7.4 ± 6.2

this study, further research on ways to further reduce internal hooking (e.g. comparison of straight vs. offset circle hooks) is warranted.

4.2. Blood biochemistry

Despite considerable variation in blood biochemistry data among individuals, significant physiological disruptions were evident in response to angling time. In relation to control (unstressed) conditions, disruptions were apparent even at the shortest angling time (0.5 min) and generally appeared to increase slightly at longer angling times (despite low sample sizes at angling times > 3 min). Trends in acid–base indicators (i.e. pH, pCO_2, lactate) also indicated that rod and reel capture resulted in blood acidosis of both respiratory (i.e. increased pCO_2) and metabolic (increased lactate) origin (e.g. Piiper et al., 1972; Holeton and Heisler, 1978; Cliff and Thurman, 1984; Hoffmayer and Parsons, 2001; Manire et al., 2001; Mandelman and Skomal, 2009). Consequently, juvenile sand tigers experienced impaired respiration during angling (resulting in increased pCO_2) and subsequent proton (H^+) loading in the blood and tissues due to the dissociation of lactic acid generated by anaerobic glycolysis (reviewed by Skomal and Bernal, 2010; Skomal and Mandelman, 2012). Apparent elevations in plasma electrolytes in response to capture stress were also consistent with previous studies (e.g. Cliff and Thurman, 1984; Wells et al., 1986; Skomal, 2006; Moyes et al., 2006) and suggest that juvenile sand tigers may suffer marked homeostatic disruptions during the capture event (Marshall et al., 2012). No significant elevations in plasma glucose levels were observed in response to angling; consistent with previous results on rod and reel captured blue sharks (Skomal, 2006).

Similarities between the physiological stress indicators from mouth- and gut-hooked individuals suggests that, in general, hook location did not significantly influence the physiological stress response in juvenile sand tigers. However, it should be noted that these results only imply that the immediate stress response was not linked to hook location and do not preclude potential differences over a broader time scale. For example, Fobert et al. (2009) reported significant differences in plasma glucose, Na^+, and Cl^- levels between mouth- and gut-hooked bluegill sunfish (*Lepomis macrochirus*) monitored periodically over a 24 h period following capture. Further investigation is warranted to assess the long-term physiological impacts of internal hooking (the extended effects of mouth hooking are discussed herein).

4.3. Captive experiments

Exposure of captive juvenile sand tigers to a 3 min simulated angling event resulted in a rapid and significant physiological stress response. This response was similar to that observed in wild-caught sharks in this study (i.e. metabolic and respiratory acidosis; electrolyte and metabolite disruptions) as well as to those documented for other shark species exposed to experimental stressors (e.g. Cliff and Thurman, 1984; Cooper and Morris, 1998; Brill et al., 2008; Frick et al., 2012; reviewed by Skomal and Mandelman, 2012). The magnitude of disruption of all measured blood parameters was also consistent with previous studies that have monitored the prolonged stress response in sharks following exhaustive exercise (e.g. Brill et al., 2008; Frick et al., 2012). Despite this, all experimental sharks exhibited full physiological recovery within 12–24 h. This recovery period is similar to those reported for other species of sharks when exposed to acute stress, including spotted dogfish (*Scyliorhinus stellaris*; Piiper et al., 1972; Holeton and Heisler, 1978); dusky sharks (*Carcharhinus obscurus*; Cliff and Thurman, 1984); smooth dogfish (*Mustelus canis*; Barham and Schwartz, 1992); spiny dogfish (*Squalus acanthias*; Richards et al., 2003); and gummy sharks (*Mustelus antarcticus*; Frick et al., 2012); yet was markedly

Table 5
Frequency of post-release survival in juvenile sand tigers based on acoustic telemetry detections and fishery dependent tag recaptures. Relative long-term mortality estimates are based on the assumption that all mouth-hooked sharks did not die as a result of rod and reel capture.

Hooking condition	Immediate 5 days	Short-term 50 days	Long-term 100 days	Relative long-term mortality
Mouth-hooked, hook removed	32/32 (100%)	29/32 (91%)	25/29 (86%)	0%[a]
Gut-hooked, hook removed	20/20 (100%)	16/20 (80%)	13/19 (68%)	18%
Gut-hooked, hook retained	13/14 (93%)	10/14 (71%)	7/12 (58%)	28%
Overall survival	65/66 (99%)	54/66 (82%)	45/60 (75%)	

[a] Based on the assumption that 100% of mouth-hooked fish survive the capture event.

longer than the 6 h recovery period observed in juvenile sandbar sharks (*Carcharhinus plumbeus*) exposed to a nearly identical experimental design (Spargo and Skomal, unpublished data).

The initial blood sampling of sharks subjected to simulated angling likely exacerbated the physiological stress response. Sharks exposed to the control repeated blood sampling regime exhibited a marked physiological stress response to the initial (i.e. time 0) blood sampling event, indicating that blood biochemistry was perturbed solely as a result of handling and blood sampling. All experimental sand tigers were observed to struggle most aggressively in response to initial restraint (i.e. time 0 blood sampling), with struggling activity greatly reduced or absent during most subsequent blood sampling events. Concomitantly, relative deviations from baseline conditions were observed in the early stages of the experiment (0–3 h) and not over all blood sampling events. This finding was consistent with that reported for serially sampled sandbar sharks (Spargo and Skomal, unpublished data). Furthermore, most measured blood parameters returned to baseline levels noticeably faster in control sharks (~1 to 3 h) than those subjected to simulated capture (~3 to 12 h), indicating the relative physiological stress imposed by the angling treatment.

Variations in environmental conditions in the outdoor holding tank introduced potential variability into the stress response of captive sand tigers. Due to the inability to control the water temperature in the tank, control trials were conducted in significantly warmer water (22–24; 2.6 °C warmer on average). Temperature is well known to impact the metabolic rate of fish (Schmidt-Nielson, 1997) and exacerbate the stress response in sharks (reviewed by Skomal and Bernal, 2010). However, given that slight, but non-significant, differences in metabolic rates were evident between bonnethead sharks (*Sphyrna tiburo*) acclimated to 20 °C vs. 25 °C (Carlson and Parsons, 1999) the maximum difference in tank temperature observed between the treatments in this study (3.8 °C) potentially had a minimal impact on the stress response. Salinity variation in the Jones River (the water source utilized to fill the holding tank) also influenced plasma concentrations of Na^+ and Cl^- in captive sand tigers during the experimental trial (i.e. sharks held at higher salinities had higher plasma Na^+ and Cl^- concentrations). However, despite these differences, the relative changes in these electrolytes were consistent for each shark over the 24 h experimental period. Furthermore, all water temperatures and salinities recorded during the captive experiments were well within the range recorded in PKD Bay during juvenile sand tigers' seasonal residence (J. Kneebone, unpublished data); thus, variation in these conditions likely did not elicit any additional stress response.

4.4. Post-release survivorship

The high degree of immediate post-release survivorship (99%) indicated that juvenile sand tigers did not experience reduced survivorship as a result of the physiological stress associated with rod and reel capture. In contrast, physical trauma associated with the ingestion of the hook at capture likely resulted in acute and chronic effects that negatively impacted post-release survival. For example, the only immediate (≤5 days) mortality observed in this study occurred in a shark that was gut-hooked; blood biochemistry was minimally disrupted in this individual suggesting that mortality occurred from physical trauma as opposed to physiological disruption. In addition, comparison of short- and long-term survivorship rates between hooking conditions indicated that gut-hooked sharks exhibited markedly lower survivorship than those hooked in the mouth. It should be noted, however, that mortality could not be confirmed for those sharks not detected upon emigration out of the PKD Bay receiver array, precluding a direct assessment of short- and long-term post-release mortality for all monitored fish. As a consequence, the results presented herein are solely indicative of frequency of survival, with reductions in survivorship over time possibly occurring as a result of several factors (e.g. natural mortality, subsequent fishing/bycatch mortality, emigration from regions with acoustic receivers) and not necessarily a result of angling stress. Furthermore, tagged sharks were exposed to additional stress (e.g. air exposure, handling) associated with transmitter implantation that may have impacted survivorship. While it is difficult to take into consideration the effects of these additional stressors, previous studies on other shark species have shown very low or no mortality associated with this procedure (e.g. Heupel and Simpfendorfer, 2002; Conrath and Musick, 2010; Heupel et al., 2010; Murchie et al., 2010). In any event, the results of this study clearly demonstrate the impacts of the physical and physiological effects of rod and reel capture on juvenile sand tiger post-release survivorship.

The high frequency of internal hooking and associated reduction of post-release survivorship suggests that additional measures may be required to minimize detrimental effects of rod and reel capture in juvenile sand tigers. Hooks retained in the viscera have been documented to cause chronic systemic disease in blue sharks (*Prionace glauca*; Borucinska et al., 2002) which has been implicated with long-term delayed mortality. In contrast, previous studies on various species of teleost fish have suggested that mortality rates are higher when ingested hooks are removed rather than left in the animal (e.g. Cooke and Suski, 2004; Butcher et al., 2006, 2007). Ultimately, the available data suggest that internal hooking adversely impacted the post-release survivorship of juvenile sand tigers regardless of whether or not the ingested hook was removed. Taken together, these results suggest that the best practice for maximizing the survival of juvenile sand tigers caught on rod and reel is to minimize angling time (<7 min) and to remove the hook (if possible) from all sharks hooked in the mouth and, in an effort to minimize the risk of injury to the angler and the shark, to cut the leader for all sharks hooked internally.

The results of this study provide detailed insights into the effects of rod and reel capture on juvenile sand tigers and should be of interest to fishery managers. Overall, juvenile sand tigers proved to be capable of enduring, recovering from, and surviving the immediate effects of capture when angled for brief (<7 min) periods on conventional rod and reel tackle. Nonetheless, the high frequency of gut hooking proved to be problematic. Further research is necessary to investigate the stress response and survival of sand tigers

captured with a variety of fishing gears and methods (i.e. 'J-hooks', beach angling, longline gear). However, overall, mandatory catch and release appears to be a viable strategy for minimizing fishing mortality in young individuals of this vulnerable species.

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