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Assessment of acid–base derangements among bonnethead *(Sphyrna tiburo)*, bull *(Carcharhinus leucas)*, and lemon (*Negaprion brevirostris*) sharks from gillnet and longline capture and handling methods ☆

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ABSTRACT

Blood gasses of wild bonnethead, bull, and lemon sharks were measured with the i-STAT clinical analyzer with the CG4+ cartridge immediately after capture; and again immediately prior to release after tagging, handling and morphometric measurements were taken. Relative reference ranges of post-capture status were established. Among species, stress response to capture was similar for all parameters; however, pH declined and lactate concentrations rose over time, indicating continued insult from capture and/or response to additional handling stress. pCO_2 rose faster for *S. tiburo* than for *C. leucas*, and lactate concentrations rose faster for *S. tiburo* than for *N. brevirostris*. All species caught in gillnets experienced lower pH and higher lactate concentrations than on longlines. Discriminant analysis justified the use of blood gas analysis to assess physiological stress induced by different capture methods. From these results, we recommend 1) that gear be monitored closely and sharks be removed immediately, or suboptimally, that gear is deployed for the shortest soak time possible; 2) longline over gillnet gear; and 3) extra caution with sensitive species (e.g., *S. tiburo*), which may include the administration of blood buffers and other therapeutics if a shark is beyond the limits of relative reference ranges reported here.

1. Introduction

Carcharhinid sharks have become important ambassadors for threatened species in conservation research, sport and commercial fisheries, and public display in aquaria. Working with carcharhinid sharks, however, presents challenges due to their extreme sensitivity to capture and handling stresses, especially affecting acid–base physiology. In general, sharks have a low capacity for aerobic metabolism and quickly shift to anaerobic metabolism when caught or handled (Cliff and Thurman, 1984; Hoffmayer and Parsons, 2001; Manire et al., 2001; Brill et al., 2008; Mandelman and Skomal, 2008). Sharks will use anaerobic muscle activity for short bursts of speed, but response to prolonged capture and handling stress can exacerbate anaerobic metabolism, often to exhaustion. This leads to a metabolic acidosis as lactate and hydrogen ions (H^+) move from muscle cells to the extracellular space and bloodstream. The resultant acidemia lowers blood pH and increases blood lactate concentrations (Holeton and Heisler, 1983; Cliff and Thurman, 1984; Hoffmayer and Parsons, 2001; Manire et al., 2001; Mandelman and Skomal, 2008).

In addition, many sharks are obligate ram ventilators; they need to continually swim to provide oxygenated water to their gills for respiration. In times of capture stress, their ventilation is depressed or even stopped, leading to an increase in carbon dioxide in the blood (pCO_2), which can deleteriously lower the blood pH further due to conversion of CO_2 to carbonic acid, thus producing a respiratory acidosis (Mandelman and Skomal, 2008). Sharks that struggle and are unable to swim are more severely affected with a mixed metabolic and respiratory acidosis (Manire et al., 2001; Mandelman and Farrington, 2007a,b; Mandelman and Skomal, 2008). This is a major reason that sharks experience a high rate of morbidity and mortality associated with capture and handling.

Sharks are more often exploited as by-catch in commercial fisheries than they are the primary target, but even as by-catch, sharks suffer high mortality rates (Hueter and Manire, 1994; Skomal, 2007; Mandelman et al., 2008; Frick et al., 2009, 2010; Walsh et al., 2009). These rates vary greatly among shark species in commercial and recreational fisheries. In the U.S. Atlantic pelagic longline fishery, mortality rates ranged from 12% in blue sharks (*Prionace glauca*), 35% in shortfin mako (*Isurus oxyrinchus*), to 80% in night sharks

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(*Carcharhinus signatus*) (Mandelman et al., 2008). Gillnet fisheries in the Gulf Coast region also reported varying mortality rates; from 0% in *Negaprion brevirostris*, 2% in *Carcharhinus leucas*, to 31% in *Sphyrna tiburo* (Hueter and Manire, 1994). Manire et al. (2001) found that when gillnets were deployed up to 1 h, *S. tiburo* suffered a 31% mortality rate whereas *C. leucas* were lost at 19%. Extensive research is underway to develop mitigating strategies to reduce fisheries-related shark mortality (Mandelman et al., 2008). However, a thorough understanding of the pathophysiology of capture-related mortality should be established in order to develop methods to reduce capture and handling stress, and resultant mortalities.

Research has shown that there is wide species variability among carcharhinid sharks in response to acid–base derangements (Manire et al., 2001; Mandelman and Skomal, 2008). Some species like *C. leucas* seem to have a higher capacity for capture stress and have lower morbidity rates, whereas other species, such as *S. tiburo* and blacktip sharks (*Carcharhinus limbatus*) appear to be very sensitive to stress, resulting in more severe blood gas changes and resultant higher morbidity rates (Hoffmayer and Parsons, 2001; Manire et al., 2001; Mandelman and Skomal, 2008). These differences underscore the necessity for developing blood gas reference limits representing expected responses to capture and handling stress for individual species.

Two common methods of shark capture include gillnetting and longline fishing. Severity of blood gas changes are affected by duration of entrapment, whether entangled in the net or hooked on the line, and force of struggle. Some studies have evaluated sharks for capture stress, but after captured in a net or on a line for an unknown and often extended period of time (Manire et al., 2001; Mandelman and Skomal, 2008).

This study was designed to quantify acute stress due to metabolic and respiratory acidosis associated with capture and handling of wild sharks. Results will provide information to scientists that can enhance the health and welfare of sharks in conservation research, and improve veterinary care of captive sharks. Specific aims of this study were (1) to provide relative reference ranges of blood gas analysis in a minimally stressed state for *S. tiburo*, *C. leucas,* and *N. brevirostris*; (2) to evaluate and compare acute changes in blood gas parameters among these species of sharks associated with capture and handling stress; and (3) to compare effects of two capture techniques, gillnet or longline, on blood gas physiology.

2. Materials and methods

2.1. Capture

We conducted sampling in the Ten Thousand Islands of southwest Florida within three bays (Faka Union, Fakahatchee, and Pumpkin Bays, Fig. 1). Each bay was sampled one evening per month, from two hours before until two hours after sunset. One gillnet and two longlines were utilized at the same location, with the two longlines running parallel to the gillnet, approximately 15 m off each flank. Longlines consisted of two 10 hook 100 m floating mainlines of 8 mm braided nylon rope anchored at both ends. Each gangion contained one float while the mainlines, anchored at both ends, had four floats, one at each end and two in the middle. Gangions were constructed of 1 m of 500 lb test monofilament with 20/0 Mustad circle hooks or 15/0 Mustad circle hooks baited with frozen or fresh mullet (*Mugil* spp.). The gillnet was 91.4 m of 12.7 cm stretch mesh 0.57 mm (30 pound test) monofilament anchored at both ends. The float line had floats every 1.5 m and the lead line had lead weights every 20 cm. Surface buoys were used at both ends to mark the location of the net. Gillnets and longlines were monitored continuously atop a nearby anchored houseboat to allow rapid removal of animals after capture.

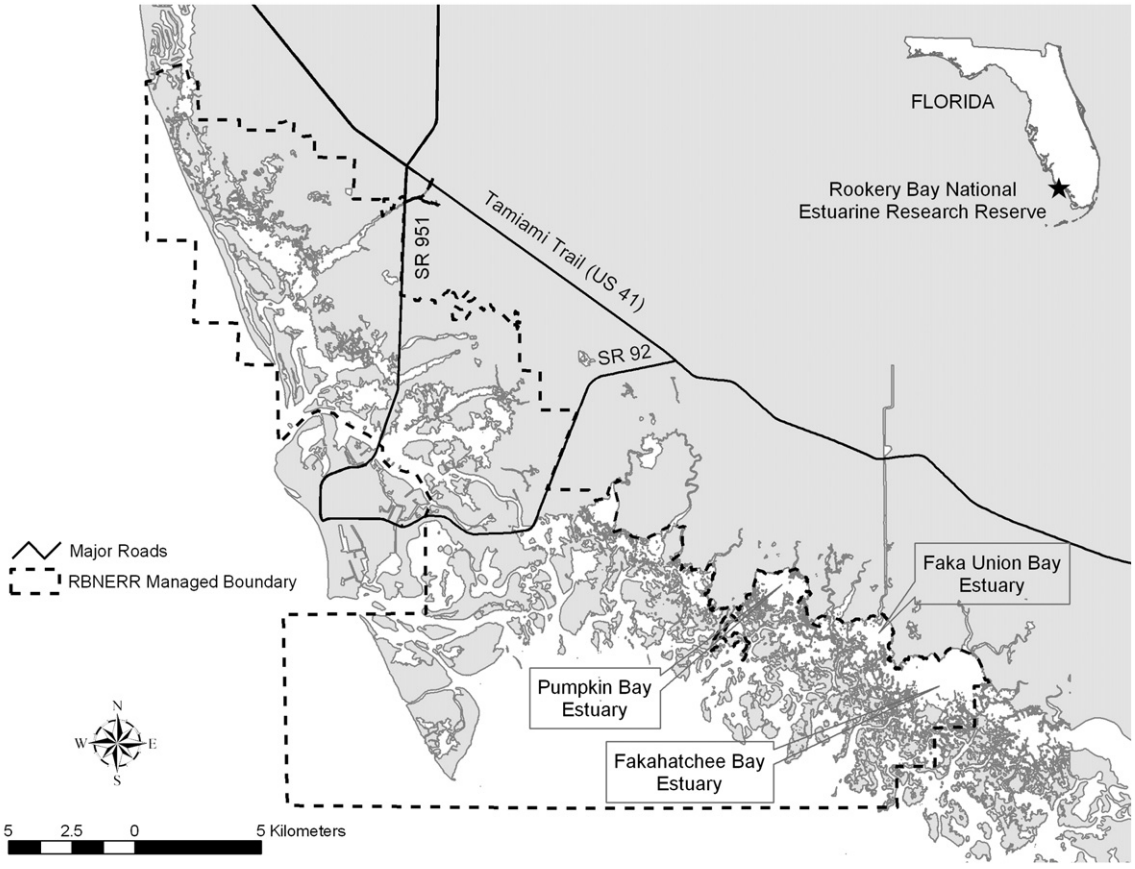

Fig. 1. Map of the study areas of Faka Union Bay, Pumpkin Bay and Fakahatchee Bay within the Rookery Bay National Estuarine Research Reserve in the 10,000 Islands Chain of Florida.

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2.2. Blood sampling and data collection

Once a shark was captured, it was approached with a 7.6 m outboard motorized mullet skiff. The shark was brought on to the skiff and placed in a 1.5 m diameter plastic pool for monitoring and assisted swimming, if needed. Within 5 min of the shark being caught and brought on to the skiff, the first blood sample (approximately 1 ml) was obtained via caudal venipuncture using a heparin washed 3 ml syringe and 22 g 19 mm (0.75 in) or 38 mm (1.5 in) needle (depending on shark size). Blood gas analysis was obtained through the use of the i-STAT portable clinical analyzer (Abaxis, Union City, CA) and an i-STAT CG4+ disposable cartridge measuring pH, lactate (mmol/L), and partial pressure of carbon dioxide (pCO_2, mm Hg) and oxygen (pO_2, mm Hg); and calculating bicarbonate (HCO_3, mmol/L), total carbon dioxide (TCO_2, mmol/L), base excess (BE, mmol/L) and percent oxygen saturation (sO_2,%). pH, pCO_2 and pO_2 were temperature corrected automatically by the i-STAT based on recorded water temperature (see below) as the body temperature recorded into the analyzer. After blood draw, all sharks were tagged, and the following additional measurements were taken: body weight (kg), and total length (cm, measured as the straight length from the snout to the tip of dorsal caudal lobe). Life stage was classified as young-of-the-year (yoy, umbilical scar open or healed but still visible), immature (male, soft, not calcified claspers, rhipidion cannot be opened; female, estimated according to TL) or mature (male, hardened, calcified claspers, rhipidion opens freely; female, estimated according to TL). Sharks were tagged with yellow plastic dart tags (Hallprint Inc, Victor Harbor, South Australia). Prior to release, a second blood draw was obtained as described previously. A second blood gas analysis was also performed as before. If not active at the time of release, the shark was ram ventilated over the side of the boat while at an idle speed. Once released away from the study site so as not to be recaptured, a release condition classification, similar to schemes described by Hueter and Manire (1994) and Manire et al. (2001), were assigned; as good (swim off with vigor), fair (slowly swim away), poor (no swimming and sank) or moribund (dead in boat).

2.3. Statistical analysis

Statistical procedures were executed using Minitab (v. 15, Minitab, Inc., State College, PA). Descriptive statistics were computed for each blood gas parameter from the first blood samples of each species and presented to describe parameters of freshly caught wild sharks. Relative reference ranges of selected blood gas parameters from the first blood samples were constructed with interquartile ranges.

To assess effects of species and capture method in blood gas parameters of freshly caught sharks, two-factor analyses of variance (ANOVAs) were run for pH, pCO_2, HCO_3, and lactate concentrations of the first blood sample. Linear and quadratic discriminant analyses (DA) with cross-validation were also employed to assess the ability of pH, pCO_2, HCO_3 and lactate to predict capture method for *C. leucas* (only this species was selected for this analysis because of its adequate sample size).

To assess the effects of the continued stress response and additional handling, pH, pCO_2, HCO_3 and lactate were compared between the first and second blood samples using a paired *t*-test. Also, to compare the stress response during handling among species and to standardize handling effect due to varied times on the boat, the rates of change of these analytes were assessed. The rate of change was calculated as:

$$\Delta X / \Delta T = \frac{X_2 - X_1}{T_2 - T_1} \quad (1)$$

where X_1 and X_2 refer to a blood gas parameter from the 1st and 2nd blood sample, respectively, and T_1 and T_2 refer to the time of the 1st and 2nd blood sample, respectively. The rate of change was compared among species using the above-mentioned two-factor ANOVA model, followed by Tukey's test comparisons of means.

3. Results

3.1. Blood gas analysis relative reference ranges

Data were collected from 105 sharks captured between April 2007 and June 2010, including 43 *C. leucas*, 43 *S. tiburo*, and 19 *N. brevirostris*.

Table 1
Comparison of post-capture blood gas parameters as measured by the i-STAT CG4+ among *Carcharhinus leucas*, *Sphyrna tiburo*, and *Negaprion brevirostris*. Values are mean ± SD in the first row, interquartile range within parenthesis in the second row. ANOVA statistics are reported as numerator *df*, denominator *df*, F-value.

	Carcharhinus leucas (n = 41)	*Sphyrna Tiburo* (n = 42)	*Negaprion brevirostris* (n = 17)	ANOVA	*p*
pH	7.036 ± 0.132 (6.918–7.136)	7.122 ± 0.171 (7.088–7.230)	7.100 ± 0.117 (7.011–7.202)		DNT[a]
pH_{tc}[b]	7.115 ± 0.164 (6.981–7.215)	7.221 ± 0.188 (7.184–7.346)	7.186 ± 0.124 (7.086–7.332)	2, 94, 1.61	0.205
pO_2 (mm Hg)	36 ± 33 (16–49)	56 ± 24 (36–70)	42 ± 25 (26–60)		DNT
pO_{2tc} (mm Hg)	23 ± 21 (11–26)	33 ± 15 (22–43)	21 ± 19 (17–34)		DNT
pCO_2 (mm Hg)	13.5 ± 4.4 (9.6–16.8)	12.0 ± 4.3 (9.2–13.4)	10.9 ± 3.1 (9.0–12.2)		DNT
pCO_{2tc} (mm Hg)	10.4 ± 3.7 (7.4–13.2)	8.6 ± 3.0 (6.5–9.5)	8.2 ± 2.6 (6.3–9.8)	2, 94, 0.52	0.596
HCO_3 (mmol/L)	3.6 ± 1.0 (2.8–4.3)	3.9 ± 1.2 (3.1–4.5)	3.5 ± 1.1 (2.5–4.5)	2, 94, 1.84	0.165
sO_2 (%)	38 ± 31 (13–69)	70 ± 25 (57–88)	52 ± 28 (31–79)		DNT
Lactate (mmol/L)	5.44 ± 2.67 (3.60–7.18)	4.27 ± 2.84 (2.01–5.61)	5.58 ± 4.14 (2.52–7.96)	2, 94, 2.04	0.136

[a] DNT = did not test.
[b] tc = temperature corrected.

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Since the 3 study sites are known shark nursery grounds (Steiner et al., 2007), *C. leucas* and *N. brevirostris* specimens sampled were almost all juveniles (neonate, young-of-the-year and immature classes), except for 1 mature *N. brevirostris*; but *S. tiburo* specimens were comprised mainly of mature individuals ($n=38$). Average weights and lengths (mean ± SD) of the species were as follows: *S. tiburo*, 2.1 ± 1.0 kg, 80.7 ± 12.2 cm; *C. leucas*, 5.7 ± 3.9 kg, 89.5 ± 18.1 cm; and *N. brevirostris*, 7.1 ± 5.2 kg, 108.5 ± 27.7 cm. Once sharks were retrieved from the gillnet or longline and brought onboard, the first blood sample was taken 5.2 ± 2.8 min (mean ± SD) from the time of capture. The time between the first and second blood samplings, during which sharks were handled, was 8.1 ± 3.9 min (mean ± SD). Total time sharks were subjected to capture and handling stress through the second blood draw and subsequently released was 13.4 ± 4.8 min (mean ± SD).

Descriptive statistics of blood gas analytes are presented in Table 1. Initially, both raw and temperature corrected values of the analytes (e.g., pH and pH_{tc}) are presented in Table 1 for comparison for other work not using temperature corrections; but only the temperature corrected values were used in statistical analysis, and herein, all values for pH and pCO_2 are assumed to be temperature corrected. Because TCO_2 and BE were often too low for detection, these parameters are neither presented nor analyzed. Also, BE is an analyte only used in mammals since it is calculated in part based on a body temperature of 37 °C and standardized to blood pH of 7.4 and pCO_2 kept at a constant 40 mm Hg (DiBartola, 2006); all of which are inaccurate conditions in elasmobranchs. pO_2 and sO_2 were highly variable as blood samples collected via caudal venipuncture are considered mixed arterial and venous samples based on anatomically close approximation of both artery and vein. These parameters were expected to demonstrate bimodal distributions; thus, they violated assumptions of normality and were also excluded from further analysis. On the other hand, Cooper and Morris (1998) found no significant difference from arterial and venous pH and pCO_2 levels in elasmobranchs, justifying the pooling of data from mixed arterial and venous samples for these measures. Blood gas analysis relative reference ranges were developed for each species based on the first blood sample collected (Table 1).

3.2. Species comparison

Post-capture acid–base status was not significantly different among species for pH, pCO_2, HCO_3, or lactate (Table 1). Comparing blood gas changes from the second to the first blood draw via paired *t*-tests showed significant changes in parameters in all species (Fig. 2). Among the rates of change examined ($\Delta pH/\Delta t$, $\Delta pCO_2/\Delta t$, $\Delta HCO_3/\Delta t$, and $\Delta lactate/\Delta t$, Table 2), pCO_2 rose more precipitously for *S. tiburo* than for *C. leucas*, with *N. brevirostris* demonstrating an intermediate rate of change. Lactate concentrations rose more precipitously for *S. tiburo* than for *N. brevirostris*, with *C. leucas* demonstrating an intermediate rate of change.

3.3. Comparison of capture methods

Sharks caught in gillnets suffered a greater degree of acidosis (mean pH ± SD for pooled species: gillnet, 7.155 ± 0.178; longline, 7.255 ± 0.132; $F_{1,94}=6.38$, $p=0.013$) accompanied by a higher lactate concentration, indicative of metabolic acidosis (mean lactate ± SD for pooled species: gillnet, 5.16 ± 2.84 mmol/L; longline, 4.04 ± 3.94 mmol/L; $F_{1,94}=4.27$, $p=0.041$, Table 3). Other parameters were not significantly different between the two capture methods. Overall, blood gas analytes predicted capture method in *C. leucas* with 78.0% accuracy using linear DA and 73.2% accuracy using quadratic DA (Table 4).

4. Discussion

The i-STAT portable clinical analyzer is used routinely for blood gas analysis and other blood chemistry parameters in veterinary medicine and research to evaluate metabolic and respiratory status during anesthesia, animal capture and handling, emergency and critical care, and post-operative recovery. The i-STAT's accuracy has been validated in humans (Erickson and Wilding, 1993; Jacobs et al., 1993; Dascombe et al., 2007) and domestic animals (Grosenbaugh et al., 1998; Looney et al., 1998; Verwaerde et al., 2002). It has also been evaluated in teleosts for accuracy of blood chemistry and hematological parameters (Wells and Pankhurst, 1999; Harrenstien et al., 2005; Cooke et al., 2008; DiMaggio et al., 2010), but has rarely been used in teleosts for blood gas analysis (Hanley et al., 2010). As there are currently no commercially available assays for the primary stress hormone in elasmobranchs (1α-hydroxycorticosterone, Nunez and Trant, 1999), blood gas analysis has become standard practice to assess stress response in elasmobranchs (Hadfield et al., 2007; Gallagher et al., 2010). Because of elasmobranchs' unique sensitivity to stress-induced

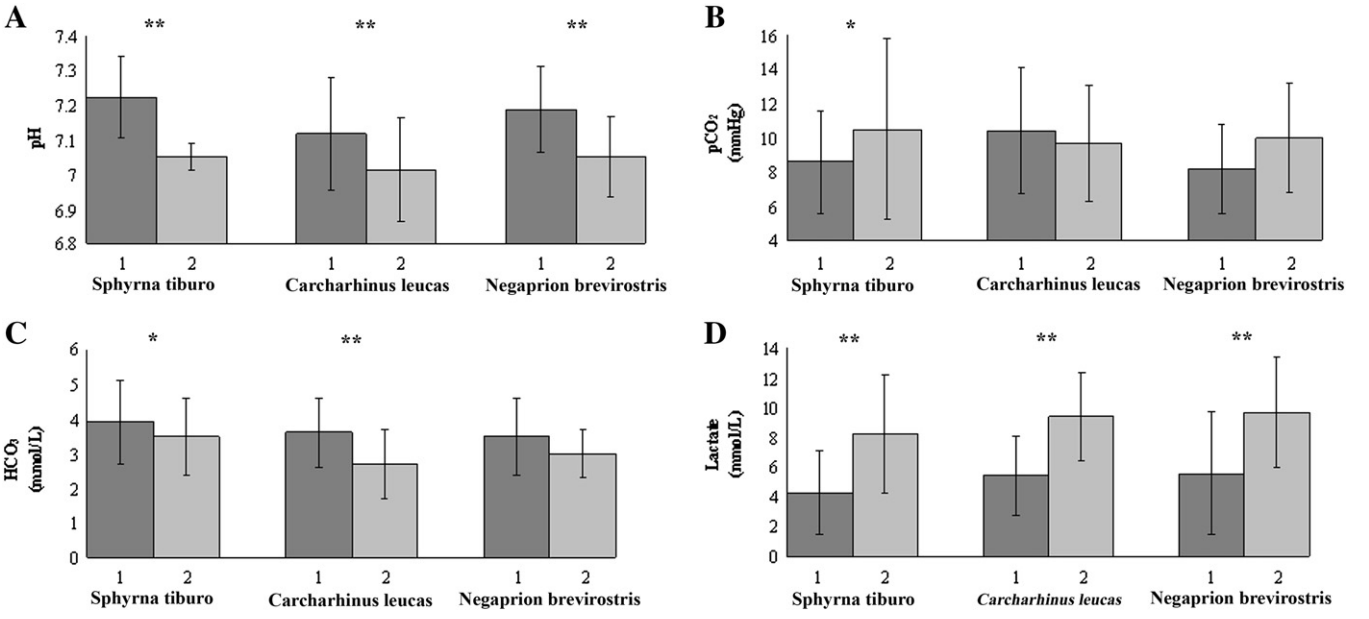

Fig. 2. Comparison of blood gas parameters of *Sphyrna tiburo*, *Carcharhinus leucas*, and *Negaprion brevirostris*, immediately post-capture (1) and immediately pre-release (2) using paired t-tests. A) pH, B) pCO_2, C) HCO_3, D) Lactate. Bars represent means ± SD. * $p<0.05$, ** $p<0.001$.

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Table 2
Interspecific comparison of rates of change of pH, pCO_2, HCO_3 and lactate among *Carcharhinus leucas*, *Sphyrna tiburo*, and *Negaprion brevirostris* during post-capture handling. Values are means ± SD. ANOVA statistics are reported as numerator *df*, denominator *df*, F-value. Significant *p*-values are in bold. For Tukey's test, species in column A have significantly ($p<0.05$) higher values than species in column B. Species in column AB have intermediate values.

	Carcharhinus leucas (n = 39)	*Sphyrna tiburo* (n = 34)	*Negaprion brevirostris* (n = 16)	ANOVA	*p*	Tukey's Test		
						A	AB	B
ΔpH/Δt	−0.015 ± 0.016	−0.023 ± 0.029	−0.017 ± 0.012	2, 87, 1.36	0.262			
$\Delta pCO_2/\Delta t$ (mm Hg/min)	−0.1 ± 0.7	0.4 ± 1.1	0.3 ± 0.5	2, 87, 3.86	**0.025**	*St*[a]	*Nb*[b]	*Cl*[c]
$\Delta HCO_3/\Delta t$ (mmol/L/min)	−0.1 ± 0.1	−0.1 ± 0.1	0.0 ± 0.2	2, 87, 2.79	0.067			
ΔLac/Δt (mmol/L/min)	0.55 ± 0.29	0.65 ± 0.37	0.37 ± 0.31	2, 87, 3.98	**0.017**	*St*	*Cl*	*Nb*

[a] *St* = *S. tiburo*.
[b] *Nb* = *N. brevirostris*.
[c] *Cl* = *C. leucas*.

acidosis, the i-STAT CG4+ panel is now routinely used to quickly evaluate acid–base physiology in anesthetic procedures, exams, and field research. However, in the literature, most work evaluating acid–base physiology in elasmobranchs has been performed using a variety of standard benchtop laboratory instruments (Holeton and Heisler, 1983; Cliff and Thurman, 1984; Lai et al., 1990; Cooper and Morris, 1998; Wise et al., 1998; Hoffmayer and Parsons, 2001; Cooper and Morris, 2004), while other research that has used the i-STAT has been comparable to our results (Mandelman and Farrington, 2007a,b; Mandelman and Skomal, 2008). Recently, work has been done to validate the i-STAT for blood gas analysis in elasmobranchs (Gallagher et al., 2010).

Because the physiological stress response begins as soon as a shark is captured (Cliff and Thurman, 1984; Hoffmayer and Parsons, 2001; Manire et al., 2001; Mandelman and Skomal, 2008), it is impossible to gather unstressed baseline blood gas values from sharks in a field environment. Therefore, the baseline data we have provided and coined "relative reference ranges" are used to describe parameters expected with acute capture stress within five to ten minutes of the initial capture event. Most controlled laboratory studies evaluating changes in acid–base status in elasmobranchs relied on dogfish as the model (Butler and Taylor, 1975; Heisler et al., 1980; Holeton and Heisler, 1983; Wells and Weber, 1983; Richards et al., 2003). The dogfish has a different metabolic demand as it is a bottom dweller, lives in cold water and does not require ram ventilation as most carcharhinid sharks; thus making comparisons between dogfish and carcharhinids inappropriate. In addition, these laboratory studies employed catheterized vascular access rather than caudal venipuncture. Our results were obtained in an uncontrolled field environment, which is more comparable to natural scenarios. These reference data provide a more practical application for assessing post-capture acid–base physiology, and aids in the management of acidosis, such as in the use of blood buffers like sodium acetate (Stamper et al., 2004; Hadfield et al., 2007).

All three species of sharks studied demonstrated wide intraspecific variability in their blood gas analytes. Because of this finding, an interquartile range was chosen to produce reference ranges to avoid extreme outliers. However, when comparing species, there was no significant difference for any analyte for the immediate post-capture timeframe. This was surprising, as *S. tiburo* individuals appeared at times to be more stressed with signs of lethargy and resting on the bottom, requiring forced water ventilation over the side of the boat; both *C. leucas* and *N. brevirostris* appeared more resilient to capture and handling. One explanation for differences in observed shark behavior and physiological response could be that *S. tiburo* are simply less resilient compared to the other species at the same physiological acid–base characteristics. Any possible true differences in post-capture stress parameters among the species we studied may have been masked by high intraspecific variability, which may be due to true variation among individuals and/or differences in intensity, duration, and severity of entrapment.

Our study is different from most other post-capture acid–base studies in terms of duration of animal entrapment in gear (5 min compared to 1 to 3 h). However, our data are similar to Cliff and

Table 3
Comparison of selected blood gas parameters from the first blood sample in response to capture by either gillnet or longline among *Carcharhinus leucas*, *Sphyrna tiburo*, and *Negaprion brevirostris*. ANOVA statistics are reported as numerator *df*, denominator *df*, F-value. Significant *p*- values are in bold.

	Gillnet		Longline		ANOVA	*p*
	n	Mean ± SD	*n*	Mean ± SD		
pH					1, 94, 6.38	**0.013**
Carcharhinus leucas	34	7.086 ± 0.155	7	7.259 ± 0.140		
Sphyrna tiburo	40	7.213 ± 0.189	2	7.374 ± 0.042		
Negaprion brevirostris	9	7.154 ± 0.116	8	7.221 ± 0.131		
pCO_2 (mm Hg)					1, 94, 0.80	0.373
Carcharhinus leucas	34	11.0 ± 3.6	7	7.5 ± 2.8		
Sphyrna tiburo	40	8.6 ± 3.0	2	8.1 ± 1.5		
Negaprion brevirostris	9	7.6 ± 2.6	8	8.9 ± 2.7		
HCO_3 (mmol/L)					1, 94, 2.74	0.101
Carcharhinus leucas	34	3.6 ± 1.1	7	3.6 ± 0.8		
Sphyrna tiburo	40	3.8 ± 1.2	2	5.0 ± 0.9		
Negaprion brevirostris	9	3.2 ± 1.3	8	3.9 ± 0.8		
Lactate (mmol/L)					1, 94, 4.27	**0.041**
Carcharhinus leucas	34	5.89 ± 2.67	7	3.25 ± 1.25		
Sphyrna tiburo	40	4.41 ± 2.84	2	1.52 ± 0.00		
Negaprion brevirostris	9	5.78 ± 2.87	8	5.36 ± 5.45		

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Table 4
Discriminant analysis with cross-validation: linear and quadratic predictions of capture method in *Carcharhinus leucas* from post-capture pH, HCO_3 and lactate.

	True method			
	Linear		Quadratic	
Predicted method	GN[a]	LL[b]	GN	LL
GN	27	2	26	3
LL	7	5	8	4
Total *n*	34	7	34	7
n correct	27	5	26	4
Proportion	0.794	0.714	0.765	0.571
Total proportion	0.780		0.732	

[a] GN = gillnet.
[b] LL = longline.

Thurman (1984) and Hoffmayer and Parsons (2001) because of their hook-and-line capture strategies obtaining initial results within 5–10 min; our blood gas reference limits fall within the ranges of *Carcharhinus obscurus* (pH: 7.12–7.29, pCO_2: 16–18 mm Hg, HCO_3: 3.6–4.6 mmol/L, lactate: 1–3 mmol/L) and *R. terraenovae* (pH: 6.78–6.86, lactate: 2–13 mmol/L). Manire et al. (2001) found no species differences in serum lactate among *S. tiburo*, *C. leucas* and *C. limbatus* caught in gillnets, yet there were species differences in other serum biochemistries that are not part of the blood gas panel. pH, pCO_2, and HCO_3, to our knowledge, have not been published for these species in a minimally stressed environment. In contrast, Mandelman and Skomal (2008) reported species differences in blood gasses of sharks caught on demersal longlines, with tiger (*Galeocerdo cuvier*) and sandbar (*Carcharhinus plumbeus*) sharks showing minimal impairment (*Gc*, pH: 7.30–7.57, pCO_2: 3.8–7.6 mm Hg, HCO_3: 5.5–10.5 mmol/L, lactate: 1.4–8.1 mmol/L; *Cp*, pH: 6.98–7.54, pCO_2: 4.6–9.3 mm Hg, HCO_3: 3.5–10.4 mmol/L, lactate: 2.7–22.4 mmol/L); and dusky (*C. obscurus*), Atlantic sharpnose (*Rhizoprionodon terraenovae*), and *C. limbatus* demonstrating the largest perturbations (*Co*, pH: 6.61–7.41, pCO_2: 5.9–12.1 mm Hg, HCO_3: 1.7–8.7 mmol/L, lactate: 6.6–7.4 mmol/L; *Rt*, pH: 6.78–7.40, pCO_2: 5.4–14.8 mm Hg, HCO_3: 2.6–9.1 mmol/L, lactate: 4.0–20.0 mmol/L; *Cl*, pH: 6.60–7.22, pCO_2: 8.3–20.9 mm Hg, HCO_3: 2.7–6.6 mmol/L, and lactate: 7.3–23.3 mmol/L).

All three species showed significant decreases in blood pH, developing acidosis within the average 8 min of handling (13 min from capture). Only *S. tiburo* showed respiratory compromise with a significant increase in pCO_2. *C. leucas* actually showed a decrease in pCO_2, although not significant, which may indicate the species' ability to adapt under stress by maintaining efficient gas exchange. This would concur with Manire et al.'s (2001) observations of *C. leucas* resting on the bottom, not requiring ram ventilation. Only *N. brevirostris* did not have a significant drop in HCO_3. The decrease in HCO_3 is likely indicative of the shark's compensatory buffering response to the acidosis, albeit not a large response as compared to mammals (DiBartola, 2006). This may indicate that sharks use different compounds to help buffer their blood, such as urea, trimethylamine oxide (TMAO), amino acids or other protein structures (Cliff and Thurman, 1984). *N. brevirostris* may have a slower response, or may rely even less on HCO_3 as a buffering agent. Lactate significantly increased in all three species with concentrations almost doubling after just 8 min. This metabolic compromise appears to be a main causative factor for acidosis in this study, and provides evidence that these three species all have low anaerobic thresholds.

The changes in acid–base physiology witnessed in this study from the first blood sample to the second blood sample may be due to a continued response from the initial capture insult, and/or the additional handling on the boat may have exacerbated the stress response. Cliff and Thurman (1984) showed that pH and HCO_3 in *C. obscurus* continued to decline for 3 h after capture before signs of recovery were observed. They also observed that pCO_2 continued to rise for at least 70 min after capture, and lactate did not begin to decrease until 6 h post-capture. Hoffmayer and Parsons (2001) found that pH in *R. terraenovae* continued to decline and lactate continued to increase after 1 h, although these sharks remained on hook-and-line. However, in spiny dogfish (*Squalus acanthias*), pH and HCO_3 declined only for 1 h before beginning to recover; pCO_2 increased initially, but then decreased within 1 h; yet lactate increased for 4 h before decreasing (Richards et al., 2003). Differentiating the effects of handling after capture from the initial capture stress on acid–base physiology is beyond the scope of this study, but emphasizes the need for research to evaluate the effects on handling after capture to determine if it significantly alters acid–base physiology in addition to the initial capture stress.

The calculated rates of change of pH, pCO_2, HCO_3 and lactate to further evaluate acid–base physiology changes in response to capture and handling stress in elasmobranchs, have not been utilized before to our knowledge. Because handling times varied among individuals these rates of change were calculated in order to evaluate the parameters for comparison that standardized for differences in handling times. $\Delta pCO_2/\Delta t$ increased more rapidly in *S. tiburo* than in *C. leucas* (*N. brevirostris* demonstrated an intermediate rate of increase). Thus, *S. tiburo*'s respiration becomes compromised more rapidly; i.e., respiratory acidosis sets in quickly for this species. $\Delta Lac/\Delta t$ also increased more rapidly in *S. tiburo* than in *N. brevirostris* (*C. leucas* demonstrated an intermediate rate of increase). Thus, *S. tiburo* also develops metabolic acidosis more rapidly. There was no difference in $\Delta HCO_3/\Delta t$ among the three species during the initial post-capture time frame. This could change if evaluated during a longer post-capture time frame allowing more time for compensatory blood buffering to occur, as this process can occur over hours to days (DiBartola, 2006). Conversely, this may indicate the HCO_3 function is preserved across these shark species.

The increased sensitivity of *S. tiburo* to capture and handling stress as evidenced through more rapid development of respiratory and metabolic acidosis as compared to *C. leucas* and *N. brevirostris* may be explained by evaluating differences in metabolic rate. *S. tiburo* has a higher metabolic rate than either *C. leucas* or *N. brevirostris* (Nixon and Gruber, 1988; Parsons, 1990; Schmid and Murru, 1994; Sundstrom and Gruber, 1998). Teleosts and elasmobranchs with higher metabolic rates have been shown to have lower anaerobic thresholds (Dickson et al., 1993), and thus would likely become acidotic quicker. Lactate dehydrogenase (LDH), an index of anaerobic capacity, will be lower in species with a higher metabolism and lower anaerobic threshold (Dickson, et al., 1993; Bernal et al., 2003). Manire et al. (2001) discovered that *S. tiburo* had an LDH interquartile range of 1.0–3.0, while the more resilient *C. leucas* had an LDH interquartile range of 10.5–42.0. Furthermore, as *S. tiburo* is an obligate ram ventilator, this species will increase swim speed and mouth gape in the face of hypoxic conditions to maintain oxygenation (Parsons and Carlson, 1998; Carlson and Parsons, 2003). Being entrapped in a gillnet preventing swimming and mouth gape would lead to a quicker respiratory compromise.

All three shark species experienced a greater degree of acidosis when caught in gillnets vs. longlines, demonstrating lower pH values and higher lactate concentrations. The higher degree of acidosis/capture stress is likely due to more extensive exhaustive fighting and gill entrapment within the gillnet; in contrast, those caught on longline were able to continually swim. Discriminant analysis, although subjective, corroborates the utility of blood gas analysis to assess physiological stress induced by different capture methods.

Frick et al. (2010) compared gillnet and longline capture methods in a controlled environment using Port Jackson sharks (*Heterodontus portusjacksoni*) and gummy sharks (*Mustelus antarcticus*). Their data conflicted with our results as *H. portusjacksoni* appeared more stressed with higher plasma lactate concentrations in those caught

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on longline than gillnet. But, *M. antarticus* was considered a more sensitive species with higher plasma lactate concentrations found in those caught in gillnet than on longline. This species also suffered far greater immediate and post-capture mortality in gillnet than *H. portusjacksoni*. Due to the quick response to shark captures, our study had a very low mortality rate. Three out of 108 sharks (2.8%), all *S. tiburo*, that died in our study were all caught on gillnet.

Other studies have shown that shark species sensitive to capture and handling stress with higher mortality rates also had more pronounced changes in blood gas analysis indicating mixed respiratory and metabolic acidosis (Cliff and Thurman, 1984; Manire et al., 2001; Mandelman and Farrington, 2007a,b; Skomal, 2007; Mandelman and Skomal, 2008). Our findings suggest that *S. tiburo* may be more sensitive to handling stress than *C. leucas* or *N. brevirostris*, while developing a mixed respiratory and metabolic acidosis more rapidly, with the potential of a higher post-capture mortality rate.

These findings lend us to recommend that gear be monitored closely and sharks be removed from gear as soon as the capture is made. If longlines cannot be monitored, we advise the shortest duration of soak times as possible to limit the stress imposed on sharks by the capture and subsequent mortality. We advise using longline over gillnet as gear of choice, if there is an option. Otherwise, gillnet soak times should be shorter than longline soak times. Extra caution should be exercised if working with a sensitive species, such as *S. tiburo*; being mindful of the amount of stress imposed through the extent of fight during capture and duration of handling. We recommend veterinary monitoring when possible; anesthesia may be necessary to prevent or slow further acid–base derangements. We highly recommend using the blood gas analysis relative reference ranges to assess the degree of capture stress and acidosis. There should be cause for concern if blood gas parameters are at the ends of the reference ranges. Veterinary recommended treatments for acidosis may include blood buffers, such as sodium acetate at 1 mg/kg added to fluid therapy, or given intramuscularly (IM), intravascularly (IV) or intrasinusly (IS); shark ringers solution (Stamper et al., 2004) fluid therapy delivered at 5–10 ml/kg IV, IS, or intracoelomically (ICe); and corticosteroids, such as prednisilone sodium succinate at 2.5–5 mg/kg IM, IV, or IS; and should be considered in captive animals if blood pH is below the relative reference limit. These treatments are general guidelines, and treatment should be directed on a case-by-case basis under the guidance of a veterinarian. Treatment is prohibited in released wild elasmobranchs in Florida waters under the Florida Fish and Wildlife Conservation Commission Marine Fisheries Special Activity License Program, Chapter 68b-8.003, section 7 (FWCC, 2009). Work in other states should be directed to that state's fisheries laws.

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