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Behavioural responses to fisheries capture among sharks caught using experimental fishery gear

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Running head: Shark behaviour during capture

Abstract

The response to capture is important in fisheries because it can reveal potential threats to species beyond fishing mortalities resulting from direct harvest. To date, the vast majority of studies assessing shark stress responses have used physiology or biotelemetry to look at sensitivity after capture, leaving a gap in our understanding of the behaviours of sharks during capture. We examined the behavioural responses of sharks to capture by attaching accelerometers to fishing gear and measuring the immediate and prolonged forces they exerted while on the line. We recorded acceleration vectors and derived the rate of intense fighting behaviours of 23 individual sharks comprising three species. Results suggest that blacktip sharks exhibited intense bouts of fighting behaviour at the onset of hooking, while nurse and tiger sharks displayed more subdued acceleration values during capture. We also obtained plasma lactate from a subset of individuals and detected a strong correlation with maximum acceleration. These results align with previously published values and suggest that shark movement during fisheries capture is an important factor during bycatch and catch-and-release interactions.

Introduction

For various reasons (e.g., to comply with harvest regulations, lack of market for a given fish, conservation ethic), some fish captured by fishers are released. Interestingly, fishes exhibit among the most pronounced stress responses to capture among all vertebrates (Barton 2002; Cockrem 2013). Whereas stress responses have evolved to permit animal survival, it is known that they can impair animal survival and vitality when they are prolonged (Sapolsky et al. 2000; but see Boonstra 2013). As such, stress responses are used widely in applied research as valuable biomarkers for understanding vertebrate fitness and conservation needs (Wikelski and Cooke 2006; Dantzer et al. 2014). Moreover, stress responses are useful in improving our understanding of the impacts of catch and release fisheries interactions for many groups of fishes worldwide, especially those which are biologically sensitive to overfishing and of conservation concern (Broadhurst et al. 2006; Donaldson et al. 2011).

Fisheries exploitation of slow-growing and long-lived fishes such as sharks remains an important area of focus for both marine and conservation biology, and in recent years fisheries-based research has expanded to examine the behavioural and physiological consequences of catch and release fisheries interactions on sharks (e.g., Skomal and Bernal 2010, Skomal and Mandelman 2012). To date, physiological analyses (e.g., blood gas, metabolite, and ion analysis) and bio-telemetry (e.g., satellite tagging) of captured sharks have been heavily relied upon to measure the impacts of capture stress acutely and predict survival outcomes at release (e.g., Campana et al. 2006, Skomal 2007; Brill et al. 2008, Gallagher et al. 2014*a*, Marshall et al. 2012, 2015). These types of comparative studies can be used to infer how the sharks' overall 'fighting' intensity affects their physiology, thus allowing us to make predictions about their fate (i.e., survival). However, 'fighting' is rarely characterized, despite the fact that behavioural changes occur directly at the onset of hooking and are intimately connected to a complex suite of

neuroendocrine/hormonal feedbacks and physiological cascades (Barton 2002). Moreover, hooking behaviour may also feedback on the physiological stress response and act as a mediator (e.g., driving differences in stress reactivity), although this link is not well-understood. This knowledge gap is likely due to the logistical challenges of directly observing sharks when they become hooked on a fishing line, particularly since fishing gear is usually left unattended for hours before gear retrieval. Obtaining species-specific data within the context of shark survivability and stress in fisheries may be increasingly valuable to predict the impacts of bycatch and even recreational fisheries, as population trends for many species appear to be variable (e.g., Braccini et al. 2015).

The attachment of accelerometers to wild animals has become a popular approach to studying free-ranging behaviour, energetics, and estimates of metabolism (Wilson et al. 2006); however, they can also provide useful information on how wild animals interact with potentially hazardous stressors and objects (Brownscombe et al. 2013, 2014*a*). The application of bio-logging devices including accelerometers has become increasingly popular for use in shark research in recent years (e.g., Whitney et al. 2007, Papastamatiou et al. 2015); however they are rarely used in an applied fisheries settings. Here we examined the behavioural responses of sharks to capture by attaching accelerometers to fishing gear and measuring the immediate and prolonged forces they exerted while on the line. We focused efforts on five sympatric shark species commonly encountered in the subtropical Atlantic. The study objectives were to: (1) quantify mean and maximum fight intensity using metrics of force measured with accelerometers (Brownscombe et al. 2014*a*) when sharks were captured with an experimental fishery technique; (2) to estimate the frequency (i.e., rate) at which sharks exhibit intense fighting behaviour; and (3) to compare these behavioural measurements with empirical physiological results for the same

group of species. We impart that this information might be used to better understand whether physiological shifts are indeed driven by behavioural changes or more cryptic physiological adaptations, thus allowing the research community to make important eco-physiological and applied evolutionary linkages between the biology of species and fisheries interactions (Horodysky et al. 2015).

Materials and methods

Study site, species, and tools

This work was conducted in four 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 of the Florida Keys (~24.69° N, 80.85° W), in the waters around Key Biscayne and within Biscayne National Park (~25.47° N, 80.19° W), and off the West End of Grand Bahama in the Bahamas (~26.59°N, 79.08° W). Sampling was conducted from March 2013 to May 2014, across the wet and dry seasons (wet = June to November, avg. temp for all locations = 26.5° C; dry = December to April, avg. temp for all locations = 23.0° C).

All sharks were captured using circle hook drumlines, a passive and autonomous fishing technique, following the methods used by Gallagher et al. (2014*a*). Each fishing unit consisted of a weighted base designed to sit on the sea floor, which was tied to a line extending to the surface via inflatable floats. A tuna clip attached a 23-meter monofilament gangion line (~400 kg test) to the weight, terminating at a baited 16/0 non-offset circle hook. The test strength of the final 3 meters of the line leading to the hook was augmented by crimping 4-strands of the monofilament together, and this terminal portion was attached to the main line via a swivel. To quantify shark fighting behaviour and intensity, we mounted tri-axial accelerometers (OpenTag, 12 mA h battery, 10 Hz recording frequency, 13-bit resolution, 69 g in air, Loggerhead Instruments)

firmly to this attachment point on the swivel using three cable ties and duct tape. This experimental fishery technique and data-logging approach enabled us to record undisturbed and relatively unrestricted fighting and capture behaviours in high resolution as sharks swam in a 23-meter radius circle around the base.

Ten baited drumlines were deployed roughly ~500 m apart, allowed to soak for an hour, then sequentially checked for shark presence. Upon gear retrieval, each shark was restrained on a partially submerged platform and was sexed and measured for total length (in cm). For a subset of individuals in the present data set, we obtained whole blood (~7 mL) via caudal venipuncture using chilled 18 gauge needles and 10mL syringes. Approximately 7 mL of the mixed whole blood samples was then centrifuged at 1300g for 5 minutes to separate plasma from whole blood. Samples were frozen on board, then transferred to -20°C freezer on shore where they were stored for future analyses. We then analyzed each plasma sampled for lactate (mmol l^{-1}), by placing a drop (< 0.1 mL) of thawed plasma on the testing strip of a Lactate Plus portable analyzer (Nova Biomedical, Waltham, MA) following standard protocols (Barker et al. 2016). The freezing of plasma has been shown to have negligible effects on plasma lactate concentrations compared to when assayed directly in the field (authors, unpublished data). Accelerometer units from captured sharks were then removed from the fishery gear and all sharks were released. The sharks captured in this study represented ecologically distinct species which are commonly encountered throughout the subtropical Atlantic: blacktip (*Carcharhinus limbatus*), nurse (*Ginglymostoma cirratum*), and tiger (*Galeocerdo cuvier*). We only used jaw-hooked individuals for analysis.

Data Analysis

Tri-axial accelerometers recorded total acceleration (*g*) at 10 Hz in three axes, (*x,y,*and *z*), where *g* (with a maximum of ± 16 g) was defined as the sum of dynamic (the fishing line) and static (gravity) acceleration. Dynamic acceleration is defined as the acceleration due to changes in velocity or movement of the device itself, whereas static acceleration is defined as the inclination of the device with respect to the Earth's gravitational field (Shepard et al. 2008). Each recorded fight scenario comprised two distinctive sections (Figure 1): (1) the initial "burst period" when the animal bites the bait and the hook is set (defined in a 5 minute period); and (2) the resulting "fight scenario" which was broken up into 5 minute periods and ended before the shark was reeled in (in order to increase the resolution of the data and probe temporal differences in the overall capture event). The entire duration of the capture scenario was visually scrutinized for each individual, with each scenario beginning approximately one minute before the animal was hooked, which triggered a significant response in acceleration (Figure 1). We ended each event at the moment before the final, ultimate rise in depth (signaling the researchers reeling the animal in to the boat), thus excluding additional forces from the shark or researcher on the fishing line (Figure 1). From this subset of the entire data recording, total acceleration vectors (*Atotal*), a proxy for overall force (similar to *VeDBA*, see Quasem et al. 2012) and measured in *g*, were calculated as $Atotal = \sqrt{(x^2 + y^2 + z^2)}$ for the entire capture event at 10 Hz. We did not remove static acceleration from the data as we were interested in the total forces following Brownscombe et al. (2014a). We calculated the maximum and mean total acceleration values for the entire duration of the capture scenario, as well as among 5 minute bins. In order to determine and quantify the frequency of intense fighting behaviour, we calculated the number of peaks (*Npeaks)* occurring above the amplitude threshold of 3.5 *g* throughout the capture scenario and calculated a standardized peak rate (*PR)* as $PR = \left(\frac{Npeaks}{capture\ duration\ (mins)}\right) * 60\ min.$ The value of

154 3.5 *g* was chosen after visually scrutinizing acceleration plots for every animal and based on a
155 similar study conducted on largemouth bass (*Micropterus salmoides*, Brownscombe et al.
156 2014*a*). This value was chosen because our goal was to explore and compare amplitudes among
157 and within species with a reference to the only other similar study in the fish literature. The
158 effects of animal size and fight time (using 20 minutes as a minimum cut-off needed to generate
159 sufficient dependent variable data) on peak rate and maximum acceleration were explored via
160 linear regression. We evaluated the impact of season on maximum acceleration using ANOVA.
161 For both these analyses we looked at all individuals combined due to low sample size for two of
162 the species. Both of these dependent variables were log-transformed prior to analysis to meet the
163 assumptions of normality and equal variance. We also evaluated the correlations between plasma
164 lactate and fight time, peak rate, and maximum acceleration using Spearman correlation. All data
165 analyses and data processing were conducted in MatLab (Mathworks, Inc. Natick, MA) and
166 significance was declared at $P < 0.05$.

167
168
169 **Results**
170 By attaching accelerometers to experimental fishing gear, we recorded a total of 1010
171 minutes of time on the hook from 23 individual sharks comprising three species (Table 1):
172 blacktip (n = 7); nurse (n = 9); and tiger (n = 7). Fight times for all sharks ranged from 9 to 88
173 minutes, with a mean of 48.4 ± 25.6 minutes. Measured total lengths suggested that all of the
174 sharks sampled in this study were either subadult or mature (Compagno et al. 2005, Table 1).
175 We detected a range of average and maximum acceleration forces across the entire
176 sample of sharks (Table 2). Average mean acceleration values were similar between blacktip and
177 tiger sharks (1.03 ± 0.27; 1.00 ± 0.22 *g*, respectively; Table 2), whereas nurse sharks exhibited
178 the lowest average mean acceleration values 0.98 ± 0.15 *g* (Table 2). There were no species-

specific differences in maximum acceleration, therefore these data were pooled for all sharks (n = 23). We did not find any significant relationships between maximum acceleration and shark size (total length, $F_{1,22} = 3.43$, $P = 0.08$, $R^2 = 0.14$) or fight time duration (minutes, $F_{1,22} = 0.17$, $P = 0.90$, $R^2 = 0.001$). There was no significant difference in average maximum acceleration values between sampling seasons (one-way ANOVA, $F_{1,22} = 1.147$, $P = 0.23$). Maximum acceleration was a more dynamic measure among species, with blacktip sharks (n = 7) displaying the greatest forces of all species (9.19 ± 4.20, Table 2). Maximum values were lower in tiger sharks (8.35 ± 3.84 *g*) and the lowest among nurse sharks (6.05 ± 2.19 *g*). Approximately 78% of nurse sharks (7 of 9 individuals), 57% of blacktip sharks (4 of 7 individuals), and 57% of tiger sharks (4 of 7) exerted their maximum acceleration values in the initial "burst period."

Peak rates ranged from 0 - 345 peaks/hr for all sharks (Table 1). Blacktip sharks exhibited the highest average peak rates (90.00 ± 119.78 peaks/hr; Figure 2a, although this number is likely driven up by the one individual with 344.95 peaks/hr), followed by tiger sharks (30.96 ± 33.95 peaks/hr, Table 2). Nurse exhibited the lowest peak rates and less variance (17.43 ± 13.06, Table 2, Figure 2b). We did not find species-specific differences in peak rate ($P > 0.05$) and thus pooled all sharks for subsequent analyses. We did find a significant relationship between peak rate and fight time duration ($F_{1,22} = 6.53$, $P < 0.05$, $R^2 = 0.04$), but not with shark size ($F_{1,22} = 0.80$, $P = 0.38$, $R^2 = 0.04$). We did not detect significant differences in mean peak rates between sampling seasons (one-way ANOVA, $F_{1,22} = 3.22$, $P = 0.09$, $R^2 = 0.24$).

We obtained plasma lactate samples from a subset of sharks with accelerometer units attached to their fishing lines (~50%, n = 14). For all species pooled, mean plasma lactate was 3.86 ± 2.99 $mmol^{-1}$, with values ranging from 0.62 – 10.09 $mmol^{-1}$. Blacktip sharks (n = 3) had the highest mean plasma lactate (7.18 ± 3.10 $mmol^{-1}$), followed by tiger sharks (n = 6, 4.35 ±

202 2.27 $mmol^{-1}$). Nurse sharks (n = 5) had the lowest plasma lactate values (1.28 ± 0.86 $mmol^{-1}$). A
203 positive and significant relationship was detected between plasma lactate and maximum
204 acceleration for all sharks combined (r = 0.87, p < 0.01, n = 14, Figure 3). There was a positive
205 but slightly non-significant relationship between plasma lactate and peak rate (r = 0.48, p =
206 0.087, n = 14), and we did not find a relationship between plasma lactate and fight time (r =
207 0.31, p = 0.284, n = 14).

208 **Discussion**
209
210 By exposing sharks to a standardized form of fisheries capture - a physical stressor - we
211 elicited behavioural stress responses that revealed a high degree of inter-individual and among-
212 species variation in fighting behaviour. To date, assessments of shark sensitivity to the process of
213 capture have relied almost entirely on empirical physiological information, with fight time (the
214 duration the shark is on the hook) generally emerging as a good predictor of change for most
215 physiological variables. Previous work has found that the interaction between fight time and
216 animal size was significantly and positively correlated with lactate values obtained via blood
217 samples (Marshall et al. 2012), including from sharks captured on the same fishery gear used
218 here (Gallagher et al. 2014*a*). Lactate is a metabolite produced anaerobically in the white muscle
219 due to exhaustive exercise (Moyes et al. 2006), and continues to be widely regarded as one of the
220 more reliable predictors of capture stress in elasmobranchs as it is produced during burst
221 swimming (Marshall et al. 2012; French et al. 2015). On an individual level, two-thirds of
222 blacktip sharks here displayed their highest acceleration values in the initial "burst" period
223 within five minutes of hooking, and we found that blacktip sharks had consistently high
224 maximum acceleration values. (Table 2). For all sharks for which we were able to pair
225 physiological data with behavioural data (plasma lactate and accelerometer, n = 14), we found a

positive and significant relationship between maximum acceleration and plasma lactate (Figure 2). This is an important finding as it suggests that bouts of intense fighting and high rates of movement, as represented in maximum acceleration herein, are likely to result in physiological stress (Butcher et al. 2015, Guida et al. 2016). However, this relationship was not affected by time on the line, which corroborates the notion that species-specific differences in capture responses may be more likely to drive physiological disruption and survival outcomes than fight time alone, particularly for hard-fighting species (Gallagher et al. 2014*a.b*).

High relative peak rates sharks are defined by the repetition of fighting behaviours over 3.5 *g* (Figure 2). Acceleration bouts over this threshold are nearly three times the mean values for all of the species assessed (Table 1). Blacktip sharks are known to suffer high mortality rates (i.e., up to ~90%) when exposed to longline fishing (e.g., Beerkircher et al. 2002; Gallagher et al. 2014*b*, Butcher et al. 2015), suggesting that intense fighting behaviours when hooked may have negative consequences for survival. Two great hammerheads that were captured opportunistically alongside the main dataset with fishing lines fitted with accelerometers (but not included here due to low sample size) also exhibited high peak rates and are known to be highly vulnerable to capture stress and at-vessel and post-release mortality (Gallagher et al. 2014*a*, Electronic Supplementary Material 1-2). Tiger sharks (the largest species assessed here) exhibited low overall peak rates (~18 peaks/hr, Table 2), a finding that agrees with published information citing this species as resilient to stress induced from the process of capture (e.g., Morgan and Burgess 2007; Butcher et al. 2015). However, one tiger shark in the present study exhibited a peak rate over 100 peaks/hr (Table 2). Clearly more data are needed to decrease the variance in our preliminary findings, but this result may reinforce the tiger shark's ability to increase oxygen delivery to tissues under acidotic conditions – thus permitting recovery - as seen

249 in some teleosts species such as rainbow trout (*Oncorhynchus mykiss*, Rummer et al. 2013).
250 However, since sharks appear unable to exhibit Root effects unlike teleosts, additional
251 physiological research and integration with tools such as accelerometers is needed to better
252 understand these pathways.

253 Whole organismal performance capacities such as maximum locomotor performance are
254 often tied to ecologically-relevant processes such as foraging or avoiding predators (Irschick et
255 al. 2005). The highest maximum acceleration forces in this study were exhibited by blacktip
256 sharks, as 5 of 7 individuals displayed maximum values over 10 *g* (Table 1). Nurse and tiger
257 exhibited, in general, low overall acceleration profiles (including peak rates) and low levels of
258 lactate in the present study. Recent work revealed that that nurse sharks have very low metabolic
259 rates (Whitney et al. 2016*a*), a finding which further explains the empirical agreement between
260 their physiology and behaviour we detected. Whether tiger sharks exhibit similar metabolic and
261 energetic profiles remains unknown, but the consistent trend for this species to exhibit low stress
262 responses provides justification for future work (Mandelman and Skomal 2009, Marshall et al.
263 2012, Gallagher et al. 2014*a*). These data add to the growing realization that a shark species'
264 biology and ecology might be good predictors of stress responses when hooked (in this case,
265 acceleration/behavioural responses), but we do not have enough data yet to confidently support
266 this claim.

267 Although the approach we employed here enabled the detection of consistent trending
268 patterns in the behaviour and physiology of sharks when captured on a specific type of fishery
269 gear, this study should be viewed as an initial step in understanding behavioural stress responses
270 to fishing for sharks. Clearly individuals that fight intensely and for sustained periods of time are
271 likely to be the most vulnerable to negative consequences of fisheries interactions, and more

research is needed to understand performance/mortality thresholds and recovery times. Due to the opportunistic nature of our sampling, we could not control the sample sizes on a species-specific basis. Nevertheless, our data corroborate and add to the general conclusion that catch and release scenarios can threaten the survival of species that mount intense stress responses. This type of information highlights the need for best practices to promote sustainability, such as the use of heavy drag on fishing lines for species which high maximum acceleration values and repeated and intense fighting behaviour when hooked.

In summary, these findings suggest that animal movement during capture may underpin a pivotal mechanism both triggering and maintaining the physiological stress response of sharks when captured in fisheries interactions (Guida et al. 2016). Obtaining physiological data from large and highly mobile apex predators is inherently challenging, and our study highlights the utility in applying bio-logging devices in novel and innovative ways to understand the relationship between animal performance and resilience to human stressors (Whitney et al. 2016*b*). This approach also detected a moderate degree of individual variation in fighting behaviours, which may explain why certain fish suffer mortality or appear to exhibit extreme physiological disturbance when other conspecifics of similar size and shape exposed to the same conditions/stressors do not. Lastly, maximum performance capacities such as those investigated here are often favored by natural selection (Irschick et al. 2008), so continued work in this regard may expose in greater detail how evolutionary theory can be used to predict the vulnerability of threatened fishes (Gallagher et al. 2015). This study supports the growing realization that life-history correlates and ecological traits likely play a larger role in understanding the impacts of fisheries on sharks than previously thought (Young et al. 2006).

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Table 1. Biological (species, sex), length (TL = total length, in cm), and acceleration values (mean and maximum ± SD, in *g*), peak rates (peaks/hr), and fighting durations (minutes) for the 23 sharks assessed in the present study.

Species	Season	Location	TL	Sex	Mean Acc	Max Acc	Peak Rate	Duration
Blacktip	Wet	Outer Reef	170	F	0.99 ± 0.28	12.45	55.71	42
Blacktip	Wet	Key Biscayne	180	F	1.13 ± 0.57	12.2	344.95	12
Blacktip	Dry	Everglades	168	F	1.04 ± 0.39	11.48	147.0	20
Blacktip	Wet	Everglades	133	F	1.06 ± 0.19	11.18	26.59	88
Blacktip	Dry	Everglades	161	F	1.03 ± 0.21	10.34	34.9	55
Blacktip	Dry	Everglades	161	F	0.97 ± 0.11	5.2	2.86	63
Blacktip	Wet	Everglades	103	F	0.99 ± 0.02	1.48	0	37
Nurse	Wet	Outer Reef	240	F	0.97 ± 0.24	10.25	38.2	26
Nurse	Dry	Key Biscayne	230	F	1.01 ± 0.15	8.15	17.9	47
Nurse	Dry	Everglades	200	F	0.96 ± 0.19	7.24	34.0	30
Nurse	Dry	Key Biscayne	249	F	0.95 ± 0.15	7.10	16.2	85
Nurse	Dry	Key Biscayne	247	F	1.00 ± 0.09	6.31	4.73	76
Nurse	Wet	Key Biscayne	161	F	0.96 ± 0.10	5.62	1.40	88
Nurse	Dry	Inner Reef	230	F	0.98 ± 0.13	4.06	5.22	46
Nurse	Dry	Inner Reef	239	M	1.01 ± 0.16	4.06	25.9	37
Nurse	Dry	Inner Reef	212	M	1.00 ± 0.16	3.71	13.3	9
Tiger	Wet	Tiger Beach	378	F	0.97 ± 0.22	13.4	15.5	66
Tiger	Wet	Tiger Beach	373	F	1.07 ± 0.44	11.97	185	13
Tiger	Wet	Tiger Beach	273	F	1.03 ± 0.31	11.53	48.6	37
Tiger	Wet	Outer Reef	289	F	0.90 ± 0.13	7.1	15.0	24
Tiger	Dry	Outer Reef	220	F	1.03 ± 0.21	5.7	27.3	11
Tiger	Dry	Everglades	182	M	1.07 ± 0.11	4.47	5.1	35
Tiger	Wet	Everglades	215	F	0.93 ± 0.14	4.32	5.2	46

Table 2. Species-specific averages ± SD for mean and maximum acceleration (in *g*), as well as peak rate (peaks/hr). Percentage lead maximum (% lead max.) refers to the proportion of individuals exhibiting their highest maximum acceleration value in the first 5 minute period of their entire fight duration/bout.

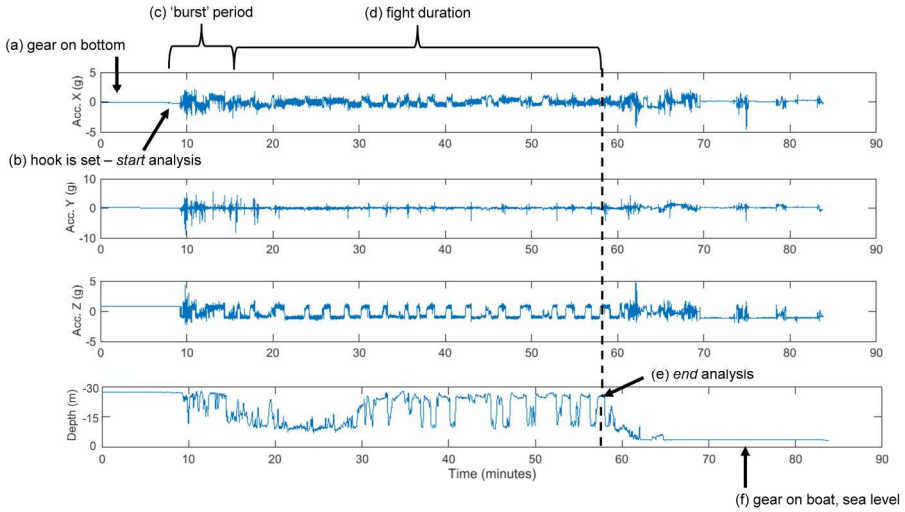
Species	Avg. Mean Acc	Avg. Max Acc	Avg. Peak Rate	% Lead Max
Blacktip (n = 7)	1.03 ± 0.25	9.19 ± 4.20	90.00 ± 119.78	57.00
Nurse (n = 9)	0.98 ± 0.15	6.05 ± 2.19	17.43 ± 13.06	77.80
Tiger (n = 7)	1.00 ± 0.22	8.35 ± 3.84	30.96 ± 33.95	57.00

Figure Captions

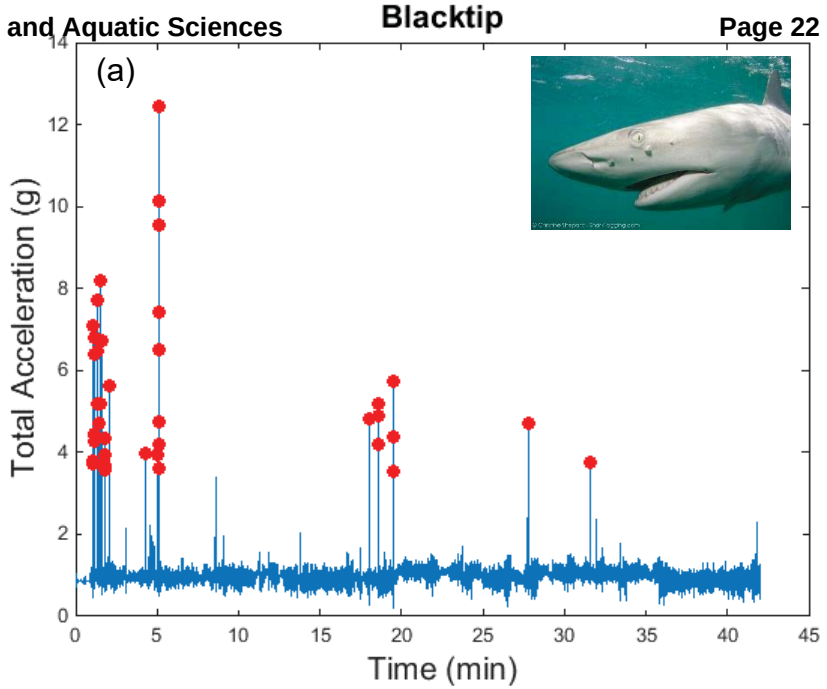
Figure 1. Representative example of time-series analysis conducted on raw tri-axial accelerometer data for a captured great hammerhead shark (no analyses were performed on this species, see Supplementary Material). The four time-series (Acc.X, Axx.Y, Acc.Z, and Depth) present information taken simultaneously at 10 Hz. Pressure (depth) shown due to its role in visually scrutinizing start and end points for analysis: (a) gear on the bottom, (b) the hook is set in the shark serving as a starting point for analysis, (c) the "burst" period, the initial period of 5 minutes from the onset of hooking, (d) fight duration, defined as the remaining portion of data analyzed for each individual, (e) the analysis was ended prior to the subsequent final increase in depth, signifying the shark being landed, and (f) the gear is on the boat at sea level and logger is turned off.

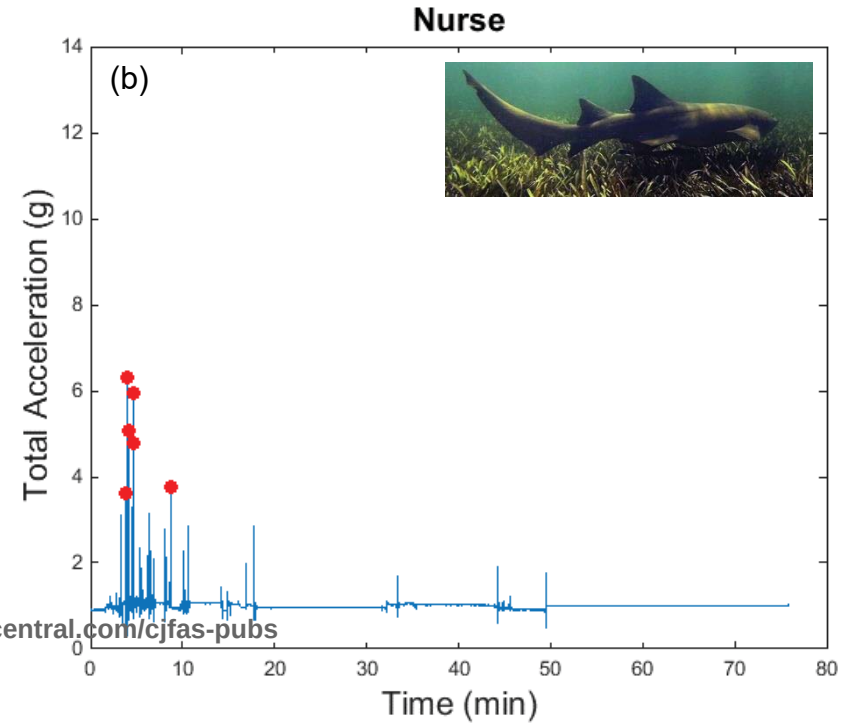
Figure 2. Representative acceleration plots showing the total acceleration vectors among individuals from 2 species of sharks in the present study: (a) blacktip, and (b) nurse. Red dots represent peaks greater than 3.5 *g* (acceleration on the y-axis) along each individual's entire hooking duration (minutes on the x-axis). The number of red dots per entire hooking duration was multiplied by 60 minutes for each species to generate the peak rate in units of peaks/hour. A wave-form with a flat acceleration line at 1 *g* would indicates no animal movement, as seen in (b) suggesting the nurse shark is sitting on the bottom and not moving (this species does not need to swim in order to facilitate respiration). Photos: (a) Christine Shepard and (b) Frank Gibson.

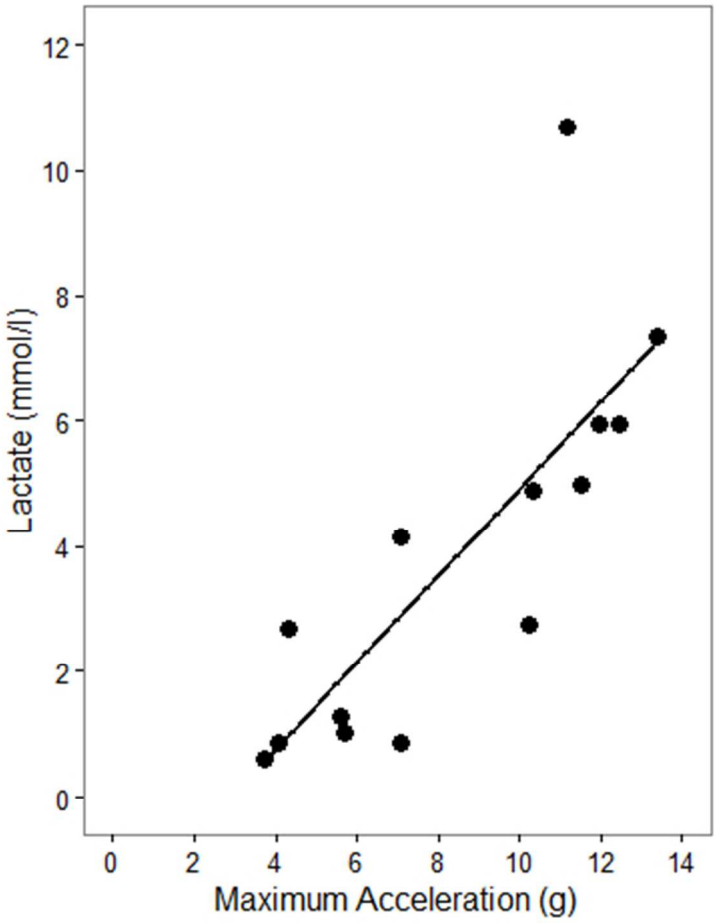
Figure 3. Correlation between maximum acceleration (*g*) obtained via fishing-line-borne accelerometers and plasma lactate (mmol/l) obtained via blood biopsy for a subset of 14 pooled sharks from the present study (blacktip, n = 3; nurse, n = 5; tiger, n = 6).



190x107mm (300 x 300 DPI)


Blacktip
(a)
Total Acceleration (g)
Time (min)
0
2
4
6
8
10
12
14
0
5
10
15
20
25
30
35
40
45


Nurse
(b)
Total Acceleration (g)
Time (min)
0
2
4
6
8
10
12
14
0
10
20
30
40
50
60
70
80



98x124mm (96 x 96 DPI)