NRC Research Press

RAPID COMMUNICATION

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

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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 (*Carcharhinus limbatus*) exhibited intense bouts of fighting behaviour at the onset of hooking, while nurse (*Ginglymostoma cirratum*) and tiger sharks (*Galeocerdo cuvier*) 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.

Résumé : La réaction à la capture est importante pour les pêches puisqu'elle peut révéler des menaces potentielles pour les espèces autres que la mortalité par la pêche découlant directement de la prise. À ce jour, la grande majorité des études visant à évaluer les réactions au stress des requins a fait appel à la physiologie ou la biotélémétrie pour examiner la sensibilité après la capture, les comportements des requins durant la capture demeurant donc mal compris. Nous avons examiné les réactions comportementales de requins à la capture en fixant des accéléromètres aux engins de pêche et en mesurant les forces immédiates et soutenues que les requins exercent quand ils sont hameçonnés à la ligne. Nous avons enregistré les vecteurs d'accélération et calculé la fréquence de comportements de lutte intense de 23 individus de trois espèces de requins différentes. Les résultats portent à croire que les requins bordés (*Carcharhinus limbatus*) manifestaient des pointes intenses de comportement de lutte au début de l'hameçonnage, alors que les requins-nourrices (*Ginglymostoma cirratum*) et les requins-tigres (*Galeocerdo cuvier*) présentaient des valeurs d'accélération plus faibles durant la capture. Nous avons également obtenu des concentrations de lactate plasmatique d'un sous-ensemble d'individus et décelé une forte corrélation de ces teneurs avec l'accélération maximum. Ces résultats concordent avec des valeurs déjà publiées et donnent à penser que le mouvement des requins durant la capture pendant la pêche est un important facteur des interactions associées à la prise accessoire et la remise à l'eau. [Traduit par la Rédaction]

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 that 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 biotelemetry (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., Skomal 2007; Brill et al. 2008; Gallagher et al. 2014a;

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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 feed back 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 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). 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 three sympatric species commonly encountered in the subtropical Atlantic. The study objectives were to (*i*) quantify mean and maximum fight intensity using metrics of force measured with accelerometers (Brownscombe et al. 2014) when sharks were captured with an experimental fishery technique; (*ii*) to estimate the frequency (i.e., rate) at which sharks exhibit intense fighting behaviour; and (*iii*) 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 ecophysiological and applied evolutionary linkages between the biology of species and fisheries interactions (Horodysky et al. 2016).

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, mean. temp for all locations = 26.5 °C; dry = December to April, mean 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 m monofilament gangion line (~400 kg test) to the weight, terminating at a baited 16/0 nonoffset circle hook. The test strength of the final 3 m of the line leading to the hook was augmented by crimping four strands of the monofilament to-
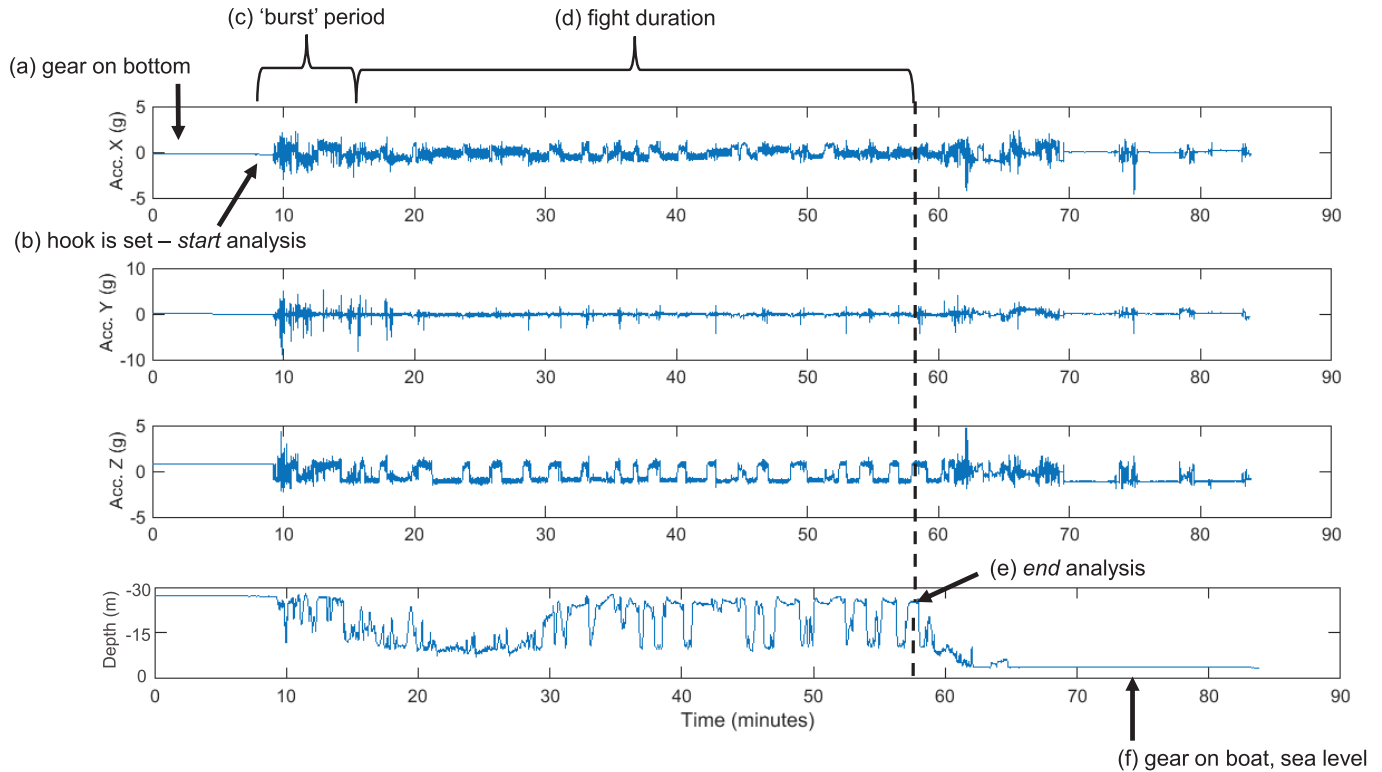
gether, and this terminal portion was attached to the main line via a swivel. To quantify shark fighting behaviour and intensity, we mounted tri-axial accelerometers (OpenTag, Loggerhead Instruments; 12 mA·h battery, 10 Hz recording frequency, 13-bit resolution, 69 g in air) firmly to this attachment 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 m 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 10 mL syringes. Approximately 7 mL of the mixed whole blood samples was then centrifuged at 1300*g* for 5 min to separate plasma from whole blood. Samples were frozen on board, then transferred to a –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, Massachusetts) following standard protocols (Barkley et al. 2016). The freezing of plasma has been shown to have negligible effects on plasma lactate concentrations compared with when assayed directly in the field (A. Gallagher, S. Cooke, and N. Hammerschlag, 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 that 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 (Fig. 1): (*i*) the initial "burst period" when the animal bites the bait and the hook is set (defined in a 5 min period); and (*ii*) the resulting "fight scenario", which was broken up into 5 min periods and ended before the shark was reeled in (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 1 min before the animal was hooked, which triggered a major response in acceleration (Fig. 1). We ended each event at the moment before the final 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 (Fig. 1). From this subset of the entire data recording, total acceleration vectors (**Atotal**), a proxy for overall force (similar to VeDBA; see Qasem 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. (2014). We calculated the maximum and mean total acceleration values for the entire duration of the capture scenario, as well as among 5 min bins. 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*

Fig. 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 online Supplementary Material[1]). The four time series (Acc.X, Axx.Y, Acc.Z, and Depth) present information taken simultaneously at 10 Hz. Accelration and depth are shown due to their 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 min 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.

throughout the capture scenario and calculated a standardized peak rate (PR) as $PR = \left(\dfrac{Npeaks}{capture\ duration\ (mins)}\right) \times 60\ min$. The value of 3.5*g* was chosen after visually scrutinizing acceleration plots for every animal and based on a similar study conducted on largemouth bass (*Micropterus salmoides*; Brownscombe et al. 2014). This value was chosen because our goal was to explore and compare amplitudes among and within species with a reference to the only other similar study in the fish literature. The effects of animal size and fight time (using 20 min as a minimum cutoff needed to generate sufficient dependent variable data) on peak rate and maximum acceleration were explored via linear regression. We evaluated the impact of season on maximum acceleration using ANOVA. For both these analyses we looked at all individuals combined. Both of these dependent variables were log-transformed prior to analysis to meet the assumptions of normality and equal variance. We also evaluated the correlations among plasma lactate and fight time, peak rate, and maximum acceleration using Spearman correlation. All data analyses and data processing were conducted in MatLab (Mathworks, Inc. Natick, Massachusetts), and significance was declared at $P < 0.05$.

Results

By attaching accelerometers to experimental fishing gear, we recorded a total of 1010 min of time on the hook from 23 individual sharks comprising three species (Table 1): blacktip (*n* = 7);

nurse (*n* = 9); and tiger (*n* = 7). Fight times for all sharks ranged from 9 to 88 min, with a mean ± standard deviation of 48.4 ± 25.6 min. Measured total lengths suggested that all of the sharks sampled in this study were either subadult or mature (Compagno et al. 2005; Table 1).

We detected a range of average and maximum acceleration forces across the entire sample of sharks (Table 2). Average mean acceleration values were similar between blacktip and tiger sharks (1.03 ± 0.27*g* and 1.00 ± 0.22*g*, respectively; Table 2), whereas nurse sharks exhibited 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*g*; 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 (seven of nine individuals), 57% of blacktip sharks (four of seven individuals), and 57% of tiger sharks (four of seven) exerted their maximum acceleration values in the initial "burst period".

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Table 1. Biological (species, sex), length (TL = total length, in cm), and acceleration values (mean ± SD and maximum, in g), peak rates (peaks·h⁻¹), 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
	Wet	Key Biscayne	180	F	1.13±0.57	12.20	344.95	12
	Dry	Everglades	168	F	1.04±0.39	11.48	147.00	20
	Wet	Everglades	133	F	1.06±0.19	11.18	26.59	88
	Dry	Everglades	161	F	1.03±0.21	10.34	34.90	55
	Dry	Everglades	161	F	0.97±0.11	5.20	2.86	63
	Wet	Everglades	103	F	0.99±0.02	1.48	0	37
Nurse	Wet	Outer Reef	240	F	0.97±0.24	10.25	38.20	26
	Dry	Key Biscayne	230	F	1.01±0.15	8.15	17.90	47
	Dry	Everglades	200	F	0.96±0.19	7.24	34.00	30
	Dry	Key Biscayne	249	F	0.95±0.15	7.10	16.20	85
	Dry	Key Biscayne	247	F	1.00±0.09	6.31	4.73	76
	Wet	Key Biscayne	161	F	0.96±0.10	5.62	1.40	88
	Dry	Inner Reef	230	F	0.98±0.13	4.06	5.22	46
	Dry	Inner Reef	239	M	1.01±0.16	4.06	25.90	37
	Dry	Inner Reef	212	M	1.00±0.16	3.71	13.30	9
Tiger	Wet	Tiger Beach	378	F	0.97±0.22	13.40	15.50	66
	Wet	Tiger Beach	373	F	1.07±0.44	11.97	185.00	13
	Wet	Tiger Beach	273	F	1.03±0.31	11.53	48.60	37
	Wet	Outer Reef	289	F	0.90±0.13	7.10	15.00	24
	Dry	Outer Reef	220	F	1.03±0.21	5.70	27.30	11
	Dry	Everglades	182	M	1.07±0.11	4.47	5.10	35
	Wet	Everglades	215	F	0.93±0.14	4.32	5.20	46

Table 2. Species-specific averages ± SD for mean and maximum acceleration (in g), as well as peak rate (peaks·h⁻¹).

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

Note: Percentage lead maximum (% lead max.) refers to the percentage of individuals exhibiting their highest maximum acceleration value in the first 5 min period of their entire fight duration.

Peak rates ranged from 0 to 345 peaks·h⁻¹ for all sharks (Table 1). Blacktip sharks exhibited the highest mean peak rates (90.00 ± 119.78 peaks·h⁻¹; Fig. 2a, although this number is likely driven up by the one individual with 344.95 peaks·h⁻¹), followed by tiger sharks (30.96 ± 33.95 peaks·h⁻¹; Table 2). Nurse sharks exhibited the lowest peak rates and less variance (17.43 ± 13.06 peaks·h⁻¹; Table 2; Fig. 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·L⁻¹, with values ranging from 0.62 to 10.09 mmol·L⁻¹. Blacktip sharks ($n = 3$) had the highest mean plasma lactate (7.18 ± 3.10 mmol·L⁻¹), followed by tiger sharks ($n = 6$, 4.35 ± 2.27 mmol·L⁻¹). Nurse sharks ($n = 5$) had the lowest plasma lactate values (1.28 ± 0.86 mmol·L⁻¹). A positive and significant relationship was detected between plasma lactate and maximum acceleration for all sharks combined ($r = 0.87$, $P < 0.01$, $n = 14$; Fig. 3). There was a positive but slightly nonsignificant relationship between plasma lactate and peak rate ($r = 0.48$, $P = 0.087$, $n = 14$), and we did not find a relationship between plasma lactate and fight time ($r = 0.31$, $P = 0.284$, $n = 14$).

Discussion

By exposing sharks to a standardized form of fisheries capture — a physical stressor — we elicited behavioural stress responses that revealed a high degree of interindividual and among-species variation in fighting behaviour. To date, assessments of shark sensitivity to the process of capture have relied almost entirely on empirical physiological information, with fight time (the duration the shark is on the hook) generally emerging as a good predictor of change for most physiological variables. Previous work has found that the interaction between fight time and animal size was significantly and positively correlated with lactate values obtained via blood samples (Marshall et al. 2012), including from sharks captured on the same fishery gear used here (Gallagher et al. 2014a). Lactate is a metabolite produced anaerobically in the white muscle due to exhaustive exercise (Moyes et al. 2006) and continues to be widely regarded as one of the more reliable predictors of capture stress in elasmobranchs, as it is produced during burst swimming (Marshall et al. 2012; French et al. 2015). On an individual level, two-thirds of blacktip sharks here displayed their highest acceleration values in the initial "burst" period within 5 min of hooking, and we found that blacktip sharks had consistently high maximum acceleration values. (Table 2). For all sharks for which we were able to pair physiological data with behavioural data (plasma lactate and accelerometer, $n = 14$), we found a positive and significant relationship between maximum acceleration and plasma lactate (Fig. 2). This is an important finding because 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. 2014a, 2014b).

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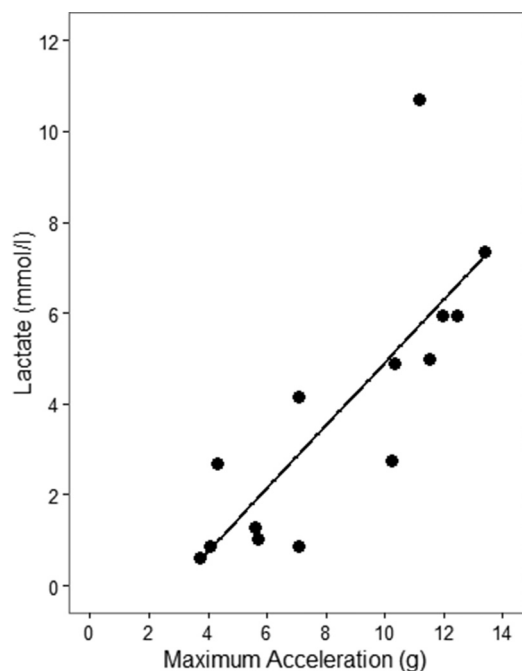
Fig. 2. Representative acceleration plots showing the total acceleration vectors among individuals from two species of sharks in the present study: (*a*) blacktip and (*b*) nurse. Red dots represent peaks greater than 3.5*g* (acceleration on the *y* axis) along each individual's entire hooking duration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

(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 data set with fishing lines fitted with accelerometers (but not included here owing to low sample size) also exhibited high peak rates and are known to be highly vulnerable to capture stress and at-vessel and postrelease mortality (Gallagher et al. 2014*a*; also see online Supplementary Material[1], ESM 1 and ESM 2). Tiger sharks (the largest species assessed here) exhibited low overall peak rates (~18 peaks·h⁻¹; Table 2), a finding that agrees with published information citing this species as resilient to

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