ICES Journal of
Marine Science

ICES Journal of Marine Science (2020), 77(7-8), 2763–2775. doi:10.1093/icesjms/fsaa146

Original Article

Variation in behavioural responses of sub-tropical marine fishes to experimental longline capture

Brendan S. Talwar [1,2,3]*, Ian A. Bouyoucos[1], Edward J. Brooks[1], Jacob W. Brownscombe [4], Cory D. Suski[5], Steven J. Cooke[4], R. Dean Grubbs[3], and John W. Mandelman[6]

[1]*Shark Research and Conservation Program, Cape Eleuthera Institute, Rock Sound, The Bahamas*
[2]*Department of Biological Sciences, Florida International University, North Miami, FL, USA*
[3]*Florida State University Coastal and Marine Laboratory, St. Teresa, FL, 32358, USA*
[4]*Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, ON K1S5B6, Canada*
[5]*Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL, 61801, USA*
[6]*Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA, 02110, USA*

**Corresponding author: tel: (242) 334-8552; e-mail: talwar.brendan@gmail.com.*

Talwar, B. S., Bouyoucos, I. A., Brooks, E. J., Brownscombe, J. W., Suski, C. D., Cooke, S. J., Grubbs, R. D., and Mandelman, J. W. Variation in behavioural responses of sub-tropical marine fishes to experimental longline capture. – ICES Journal of Marine Science, 77: 2763–2775.

Received 26 February 2020; revised 18 July 2020; accepted 20 July 2020; advance access publication 16 October 2020.

Fishes are often caught as bycatch on longlines and subsequently discarded. The behavioural response of fishes to longline capture is poorly understood, although it may be linked to the magnitude of the physiological stress response, and, ultimately, contribute to stress-induced mortality. We used accelerometers, video cameras, and hook timers to analyse the behavioural response of 13 subtropical teleost and elasmobranch species to experimental longline capture in The Bahamas. We found that, across all species and species groups, fight intensity during a capture event was best described by a negative linear and positive quadratic response. Nurse sharks and tiger sharks had lower fight intensity values and exhibited less steepness in their quadratic response during the first 10 min of capture than other species, particularly blacktip and Caribbean reef sharks. Nurse sharks also exhibited the most consistent fight intensity during the entire capture event compared to other shark species, particularly the blacknose shark. Generally, obligate ram ventilators and mixed ventilators exhibited higher steepness in fight intensity trajectories than buccal/spiracular pumpers, which had more consistent, lower fight intensity values. Behavioural responses to longline capture are species specific but may be linked to distinct evolutionary traits such as respiratory mode.

Keywords: accelerometer, bycatch, capture behaviour, fisheries capture, longline, shark, stress physiology, ventilation mode

Introduction

The accidental capture and subsequent discarding of fishes can lead to population declines and ecosystem-level effects (Lewison *et al.*, 2004; Harrington *et al.*, 2005) as a result of sub-lethal impairment, reduced fitness, and mortality in discarded individuals (Harrington *et al.*, 2005; Raby *et al.*, 2014; Wilson *et al.*, 2014). These interactions represent a serious challenge to the sustainable management of commercial fish stocks (Davies *et al.*, 2009) and likely involve a greater diversity of fishes than ever before because commercial fleets have expanded into pelagic (Swartz *et al.*, 2010) and deepwater habitats (Watson and Morato, 2013).

Longline fishing is a common capture method for sharks and teleosts (Beerkircher *et al.*, 2002; Lewison *et al.*, 2004; Mandelman *et al.*, 2008; Oliver *et al.*, 2015); yet, despite its prevalence, the response of fishes to longline capture is poorly understood compared to other gear types (Skomal and Mandelman, 2012; Cook *et al.*, 2019). Recent studies have provided insights into the physiological stress response of marine fishes during and after longline capture and the link between physiological disruption and post-release mortality (Moyes *et al.*, 2006; Skomal, 2007; Frick *et al.*, 2010; Danylchuk *et al.*, 2014; Gallagher *et al.*, 2014a; Marshall *et al.*, 2012; Roth and Rotabakk, 2012; Humborstad *et al.*, 2016; Talwar *et al.*, 2017; Bouyoucos *et al.* 2018). Generally, the magnitude of the species-specific stress response is proportional to the magnitude of the stressor (Skomal and Mandelman, 2012), driven by the gear type, respiratory mode, and metabolic capacity of the species in question (Davis, 2002; Mandelman and Skomal, 2009; Dapp *et al.*, 2016b; Ellis *et al.*, 2017). Longer fight times are also correlated with increased physiological disturbance (Danylchuk *et al.*, 2014; Brownscombe *et al.*, 2015; Dapp *et al.*, 2016a) as fish deplete energy reserves and shift from aerobic to anaerobic respiration (Kieffer, 2000; Richards *et al.*, 2003; Brownscombe *et al.*, 2014).

The behavioural component of the stress response during capture has been poorly studied despite its possible role in mediating or amplifying physiological disruption or being a manifestation of the stressor (Schreck *et al.*, 1997; Guida *et al.* 2016; Gallagher *et al.*, 2017). Past research has suggested that behaviour may vary during a hooking event, shifting from an initial high-intensity escape response to a period of reduced activity (Brooks *et al.*, 2012; Gallagher *et al.*, 2017). This shift may facilitate the physiological recovery of Caribbean reef sharks (*Carcharhinus perezi*) during extended longline capture durations (Brooks *et al.*, 2012). Similarly, limited movement and stationary respiration may mitigate the physiological stress response of gummy sharks (*Mustelus antarcticus*) to longline capture (Guida *et al.*, 2016).

Quantifying capture behaviour and the links between behaviour and physiological disruption has been a challenge (Frick *et al.*, 2010), but the recent application of accelerometers (Brown *et al.*, 2013) to captured animals and capture gear has been helpful. Accelerometer-derived data have documented variability in intra- and inter-specific fight behaviours during capture as well as behaviours after release (Brownscombe *et al.*, 2014; Whitney *et al.*, 2016b; Bouyoucos *et al.*, 2017; Gallagher *et al.*, 2017; Guida *et al.*, 2017; Bouyoucos *et al.*, 2018). Brownscombe *et al.* (2014), for instance, used accelerometers to describe the fight behaviour of largemouth bass (*Micropterus salmoides*) during angling events and suggested that fight intensity had little effect on their physiological impairment, behavioural impairment, or survival after short (<2 min) capture durations on recreational gear. However, fight intensity may have more of an influence in commercial capture scenarios, particularly those associated with longer capture durations. Gallagher *et al.* (2017), for example, found a correlation between fight intensity and the magnitude of the stress response in sharks caught on drumlines for up to 88 min. The role of on-hook fight behaviour had yet to be thoroughly examined for most fishes caught on commercial gear types (Guida *et al.*, 2017), although this understanding could be helpful when developing gear modifications to reduce mortality (Barton, 2002; Guida *et al.*, 2016; Gallagher *et al.*, 2017).

The goal of this study was to quantify the on-hook behavioural responses of a diversity of subtropical marine elasmobranch and teleost fishes to longline capture. We were particularly interested in differences in shark capture behaviour between ventilation modes (obligate ram, mixed, and buccal/spiracular pumpers) because the ability to efficiently respire while on the line may be closely tied to swimming impairment and physiological disturbance through positive feedback loops (Dapp *et al.*, 2016a).

Material and methods

Study site

This study took place between January 2012 and December 2013 in waters adjacent to the Cape Eleuthera Institute (CEI) in Eleuthera, The Bahamas (24.54°N, 76.12°W). Research was conducted under research permits MAF/FIS/17 and MAF/FIS/34 issued by the Department of Marine Resources of the Government of The Bahamas. Permission to capture sharks within The Bahamas Shark Sanctuary was established in accordance with Department of Marine Resources Form 20A, Regulation 36D(3), permitting the fishing of sharks. Research followed CEI animal care protocols based on guidelines from the Association for the Study of Animal Behavior and the Animal Behavior Society (Rollin and Kessel, 1998), as well as the Florida State University Animal Care and Use Committee Protocol Number 1412.

Animal collection

We targeted seven elasmobranchs (*Carcharhinus acronotus*, *Carcharhinus limbatus*, *C. perezi*, *Galeocerdo cuvier*, *Ginglymostoma cirratum*, *Negaprion brevirostris*, and *Squalus cubensis*) and six teleosts (*Caranx latus*, *Epinephelus striatus*, *Lutjanus analis*, *Mycteroperca bonaci*, *Ocyurus chrysurus*, and *Sphyraena barracuda*). We caught fishes opportunistically in shallow water (2–20 m deep) on stationary mid-water longlines or in deep water (400–700 m deep) on demersal longlines. Mid-water longlines were ∼125 m long and included six experimental gangions spaced 5 m apart separated by surface floats every two gangions. Each gangion was 1.3 m long and consisted of a longline snap crimped to 0.15 m of monofilament attached to 1.0 m of braided polyester line, which we crimped to 0.15 m of steel leader terminating in a 16/0 circle hook. We placed swivels (size 8/0) at each attachment point. We mounted GoPro cameras (Hero 1 and Hero 3 Silver, San Mateo, CA, USA) on 10 cm × 2.5 cm polyvinylchloride (PVC) pipes with roll bar mounts directly adjacent to the longline snap. We rigged a hook timer (LP Hook Timer HT 600; Lindgren Pittman, Pompano Beach, FL, USA) between the monofilament and braided polyester sections of the gangion, which allowed us to back-calculate the initial time of capture for video and accelerometer reference. Lastly, we set a tri-axial data-logging accelerometer (Hobo Pendant G Logger; Onset Computer Corporation, Bourne, MA, USA; measurement range of ±3 g, 29.4 m/s^2; accuracy of ±0.075 g, 0.735 m/s^2 at 25°C) in a 7.6 cm × 3.8 cm PVC capsule ∼15 cm above the circle hook (Figure 1; Grace *et al.*, 2010). Accelerometers logged acceleration every second and were secured in uniform orientation in the PVC capsule using foam pool noodle fragments (Figure 1). We baited hooks with 100 g sections of little tunny (*Euthynnus alleteratus*).

We checked mid-water lines every 30 min to assess the condition of captured fishes. We limited capture duration to <4.5 hr (Brooks *et al.*, 2012) and attempted to experimentally bin capture durations into 0–0.5, 2–2.5, and 4–4.5 hr categories, although fishes that were observed in poor condition were immediately released (including those with a hooking location other than the jaw or mouth and teleosts with overinflated swim bladders). In

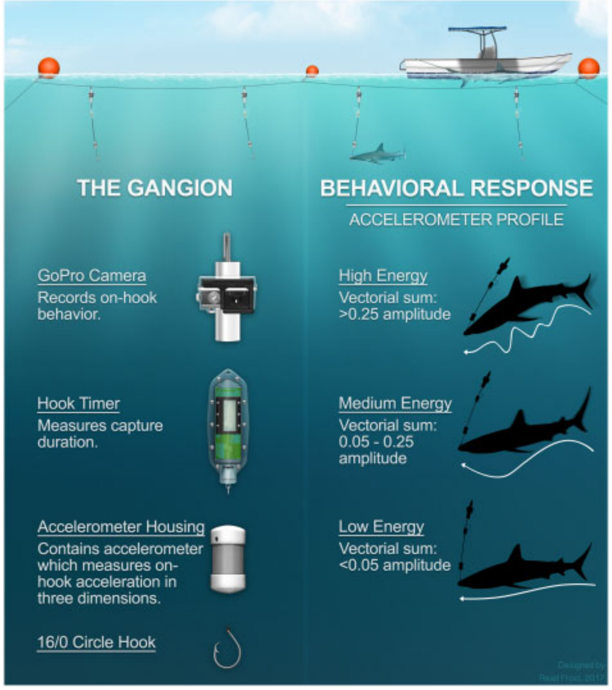

Figure 1. Graphical representation of the experimental gangions on mid-water longlines and accelerometer profiles.

the field, we defined capture duration as the time between hooking (back-calculated from the hook timer) and gangion removal from the longline and then cross-referenced that with video footage in case the hook timer mechanism was delayed (see Supplementary material—nurse shark capture). We secured fishes alongside the boat to collect length measurements, sample blood and tissue for other studies, and tag before release. We held sharks in tonic immobility as much as possible during sampling.

Deepwater demersal longlines were a minimum of 1.5 times the water depth and consisted of a tarred, polyester mainline held to the seafloor by a grapnel anchor or cinderblock with eight gangions attached via longline snaps. Each gangion consisted of 0.70 m of steel leader with a deep-sea capsule made of black delrin (5.08 cm in diameter, 10.16 cm in length; Blue Turtle Engineering, FL, USA) containing the same data-logging accelerometers described previously crimped in place 15 cm above a 12/0 circle hook baited with miscellaneous fish scraps. We spaced gangions 5–10 m apart and placed an archival temperature and depth recorder (Lotek LAT-1400, Newfoundland, Canada) 5 m from the last hook to record depth and temperature every 4 s. We determined capture duration by careful examination of accelerometer profiles and defined it as the first major spike in acceleration to the time of longline retrieval. We recorded longline depths and temperatures as the deepest and coldest points of a longline set, which in some instances may have been above the seafloor. Soak times were roughly 3.5 hr. We hauled longlines using an electric pot hauler (Waterman Industries of Florida, Inc., Odessa, FL, USA) at a rate of 0.3 m/s and worked up animals as described previously. We used demersal longlines to catch only one species examined in this study (*S. cubensis*).

Accelerometer and video data analysis

We summarized tri-axial acceleration data by calculating the vectorial sum, VS = $\sqrt{(x^2 + y^2 + z^2)}$, for each second during capture. We used *k*-means clustering (as per Sakamoto *et al.*, 2009) on the spectral characteristics of VS, which identified three unique acceleration signals that were consistent amongst all captured animals, including high (>0.25 g signal amplitude), medium (0.05–0.25 g amplitude), and low (<0.05 g amplitude) intensity categories. We used video footage of capture events to validate accelerometer measurements, which indicated that the high-intensity cluster represented burst swimming behaviour. The medium intensity cluster represented more routine swimming behaviours, while the low-intensity cluster represented the fish resting, hanging from the longline, or floating at the surface (Table 1 and Figure 1). We used these data to qualitatively describe the response to capture and provide context for the acceleration measurements that we analysed in detail. We also calculated the sum and mean acceleration values per minute (VS per minute), with the "fight intensity" variable measured in sum *g*'s per minute. We analysed acceleration data with Igor Pro 6.0 software (WaveMetrics) and Ethographer (see Sakamoto *et al.*, 2009).

Statistical analysis

Prior to running multi-level, random effects linear models (Raudenbush and Bryk, 2002), we explored the dataset to identify possible trends between and within variables to inform our selection of model predictors. We examined the normality and skewness of our response variable (fight intensity) using the Shapiro–Wilk test and calculated descriptive statistics for variables of interest (fork length, water temperature, capture duration, species, ventilation mode—determined based on *in situ* observations). We then ran bivariate analyses using each animal as the unit of analysis, including Spearman's correlations to look for relationships between fight intensity and predictors as well as Mann–Whitney tests to identify differences in fight intensity between species groups. We further used the non-parametric Kruskal–Wallis *H* test to determine if there were differences in fight intensity between species. Lastly, we ran a Wilcoxon signed-rank test to assess whether there were significant differences in fight intensity during capture. Fight intensity was split into two bins for this analysis (the first 5 min of capture, referred to as the "initial capture event", and the remainder of the capture event) based on the hypothesis that the highest fight intensity values would be recorded during this initial period (Gallagher *et al.*, 2017). In preliminary analyses, capture duration was examined as a continuous variable and a categorical variable (split into the 25, 50, and 75 percentiles) using pairwise comparisons of marginal linear predictions to identify any possible inflection points prior to running full models that included covariates.

We transformed the fight intensity variable based on the results of a Tukey ladder of powers in an attempt to reduce its heavy skewness (Tukey, 1977). The final multi-level models that we used to describe fight intensity included some combination of fork length, capture duration, species (or species group), ventilation mode, linear and quadratic terms for capture duration, and interaction terms for capture duration (both linear and quadratic terms) by species. These models used the GLS estimator and included a random intercept for "animal ID" to account for the dependency among repeated measures taken over time from the same individual. Only species captured five or more times were

Table 1. Coded behavioural categories of on-hook behaviours defined by movement patterns, orientation, and relative activity levels.

Behaviour	Definition	Relative activity
High-energy escape response	Burst swimming and/or strong muscular contortions	High energy
Low-energy escape response	Brief aggravated movement (e.g. head shaking)	High energy
Directional swimming	Slowly swimming uniformly in one direction	Medium energy
Circling	Circular swimming with gangion outstretched	Medium energy
Low-energy circling	Slow circling, inability to maintain upright orientation	Low energy
Resting on bottom	Unmoving, voluntary resting on bottom	Low energy
Exhaustion-induced immobility	Momentary exhaustion-induced immobility	Low energy
Vertical immobility	Hanging vertically on the gangion	Low energy

included in these analyses. We examined fight intensity for a maximum of 175 min for sharks and 48 min for teleosts to avoid inaccurate estimates due to the loss of observations over time (as not all animals were hooked for long capture durations). Since the median capture duration for each group was very different (sharks: 71 min, teleosts: 20 min), we split the data into "shark" and "teleost" groups to examine fight intensity across the whole capture event, whereas for the first 10 min of capture we examined the effects of species and time for all fishes together because there were sufficient observations for most species sampled. We included fork length as a covariate in the analysis of fight intensity for the first 10 min of capture (which excluded serranids because fork length was measured for fewer than five animals) and across the capture event for sharks. We did not include fork length as a covariate in our final model for teleost fight intensity across the entire capture event due to a lack of observations. We did not include ventilation mode in the model for teleosts and did not include water temperature in any models because it had no significant effects in our preliminary bivariate analyses. Furthermore, our sample size would have been greatly reduced due to missing temperature values, and variability in temperatures was too low to detect effects (26.8 ± 2.23°C, mean ± *SD*).

Reference categories for each multi-level model were as follows: *C. perezi* in the model describing fight intensity during the first 10 min of capture and the model describing fight intensity across shark species, buccal pumping (which includes spiracular pumping) for the model describing fight intensity across ventilation modes, and *S. barracuda* for the model describing fight intensity across teleost species. We used *post hoc* tests (i.e. pairwise comparisons) to test for species-specific differences that were adjusted by Sidak multiple-comparisons corrections using the Stata command xtreg.

Results

Qualitative behavioural response to capture

The most common behavioural response to capture involved an immediate escape response, whereby an animal rapidly and repeatedly swam the length of the gangion, followed by a lower energy response characterized by brief periods of intermittent burst swimming separated by longer periods of circling, directional swimming (often angled into the current), and resting (if possible). Exhaustion-induced behaviours were apparent when individuals slowed to the point of vertical immobility on the line, particularly in *C. limbatus* and *C. acronotus* (see Supplementary material for video footage of *C. perezi* and *G. cirratum*).

Descriptive statistics

We collected 11 302 animal-minute observations from 148 unique animals hooked on longlines for an average of 76.4 full, 1-min periods (Table 2). Of these observations, 10 629 were from shark species and 673 from teleosts. Fight intensity, our primary response variable, exhibited strong positive asymmetry with skewness coefficients >10 for both shark and teleost groups prior to power transformation. Measured variables included fork length (mean: 169 cm, range: 58–257 cm), capture duration (mean: 75 min, range: 3–274 min), and water temperature at the time of capture (mean: 27°C, range: 22-31°C). We summarized these variables by species and species group (Table 2).

Preliminary analyses

When we conducted preliminary bivariate analyses (Table 3), we found a moderate negative correlation between mean fight intensity and capture duration (Spearman's rho −0.478, $p < 0.001$) as well as fork length (Spearman's rho −0.295, $p < 0.001$), while we found no association between fight intensity and capture temperature. We detected no differences between fight intensity levels exhibited by sharks and teleosts ($z = -0.60$, $p = 0.55$). There were also no differences in fight intensities across species when including species with three or more individuals ($\chi^2(11) = 12.98$, $p = 0.295$). We did find significant differences between fight intensity values observed during the initial capture event and the remainder of capture when all minute observations were pooled together ($z = 10.18$, $p < 0.001$). These results were consistent within sharks ($z = 9.563$, $p < 0.001$) and teleosts ($z = 3.46$, $p < 0.001$).

A power transformation of $\lambda = -5.46$ (Tukey ladder of powers) was optimal in reducing the asymmetry of the fight intensity variable's distribution. This resulted in skewness of almost zero (−0.002). When exploring the fight intensity variable for all shark observations in the absence of covariates, we found that (i) when capture duration was analysed as a continuous variable, there was a significant negative linear term and a significant positive quadratic term for fight intensity over time, and (ii) when capture duration was organized as a categorical variable (group 1: minute 0 to minute 25, group 2: 26 to 70, group 3: 71 to 120, group 4: 121 to last minute of capture), we identified significant differences between all periods ($p \leq 0.001$) except when comparing group 4 with group 3 ($p = 0.51$). These results demonstrate that there was a decrease in fight intensity during the first 120 min of capture followed by a period of increasing fight intensity thereafter.

When exploring the fight intensity variable for all teleost observations in the absence of covariates, we found the following: (i) when capture duration was analysed as a continuous variable, there was a significant negative linear term and a significant

Table 2. Capture characteristics of longline-caught fishes in waters adjacent to Cape Eleuthera, The Bahamas.

Species	Common name	Ventilation mode	*N*	Mean fork length ± *SD* (cm)	Mean capture duration ± *SD* (min)
C. limbatus	Blacktip shark	Obligate ram	10	166.6 ± 22.9	91.4 ± 65
C. acronotus	Blacknose shark	Obligate ram	5	104 ± 6.9	102.3 ± 106.7
C. perezi	Caribbean reef shark	Mixed	41	151.1 ± 32.5	84.6 ± 57.7
G. cuvier	Tiger shark	Mixed	8	183.6 ± 45.2	24.7 ± 17.8
N. brevirostris	Lemon shark	Mixed	2	243.5 ± 19.1	9.5 ± 5.8
G. cirratum	Nurse shark	Buccal pumping	59	207.2 ± 31.0	95.6 ± 98.3
S. cubensis	Cuban dogfish	Buccal/spiracular pumping	4	40.1 ± 6.8	85.8 ± 35.1
S. barracuda	Great barracuda		10	97.6 ± 10.1	62.9 ± 55.5
E. striatus	Nassau grouper		4	80 ± 14	19.5 ± 13.1
C. latus	Horse-eye jack		3	71 ± 3	76.1 ± 43.3
L. analis	Mutton snapper		3	62.8 ± 5.3	17.7 ± 5.1
M. bonaci	Black grouper		2	104	90.3
O. chrysurus	Yellowtail snapper		1	–	19.7

Table 3. Mean (± *SD*) and median untransformed values of fight intensity for various predictor variables, as well as results from the preliminary bivariate analyses used to inform final modelling procedures.

	Fight intensity				
Predictor (n)	**Mean (± *SD*)**	**Median**	**Test statistic**	**df**	***p*-Value**
Species group			z = −0.60		0.55
Sharks (125)	1.06 ± 0.07	1.05			
Teleosts (23)	1.10 ± 0.14	1.04			
Species			$\chi^2 = 12.98$	11	0.30
C. limbatus (10)	1.09 ± 0.12	1.05			
C. acronotus (5)	1.05 ± 0.04	1.05			
C. perezi (41)	1.08 ± 0.08	1.07			
G. cuvier (8)	1.07 ± 0.04	1.07			
N. brevirostris (2)	1.01 ± 0.01	1.01			
G, cirratum (59)	1.04 ± 0.04	1.04			
S. cubensis (4)	1.02 ± 0.05	1.02			
S. barracuda (10)	1.10 ± 0.13	1.05			
E. striatus (4)	1.09 ± 0.13	1.07			
C. latus (3)	1.05 ± 0.12	0.99			
L. analis (3)	1.06 ± 0.05	1.08			
M. bonaci (2)	1.27 ± 0.37	1.27			
O. chrysurus (1)	1.04	1.04	[a]		
Time—all			z = 10.18		***
Initial capture event (148)	1.25 ± 0.19	1.20			
Remainder of capture event (146)	1.03 ± 0.04	1.02			
Time—sharks			z = 9.563		***
Initial capture event (125)	1.26 ± 0.19	1.2			
Remainder of capture event (124)	1.03 ± 0.03	1.02			
Time—teleosts			z = 3.46		***
Initial capture event (23)	1.19 ± 0.19	1.12			
Remainder of capture event (23)	1.04 ± 0.08	1.02			

p-Values indicate the level of significance for the following statistical tests: Mann–Whitney (between species groups), Kruskal–Wallis (between species comparisons), and Wilcoxon signed-rank (across time of capture). *$p<0.05$, **$p<0.01$, ***$p\leq0.001$

[a] *Ocyurus chrysurus* excluded from a Kruskal–Wallis test for differences in fight intensity between species.

positive quadratic term for fight intensity over time, and (ii) when capture duration was analysed as a categorical variable (group 1: minute 0 to minute 12, group 2: 13 to 20, group 3: 21 to 42, group 4: 42 to last minute of capture), there was a significant decrease in fight intensity between group 2 and group 1 ($B = -0.077$, $p = 0.002$). Group 3 also showed a significant decrease in fight intensity compared with group 1 (B= -0.079, $p = 0.001$), while group 4 was not significantly different than group 1 ($p = 0.16$). These results agree that the relationship between fight intensity and capture duration is best described by a quadratic relationship for teleosts.

Multi-level models: variability in fight intensity during a capture event

In the multi-level model that examined fight intensity during the first 10 min of capture, we found a significant negative slope for

Table 4. Results of final multi-level regression model describing fight intensity for all species during the first 10 min of capture, as well as contrasts of marginal linear predictions (joint hypothesis test) for differences between species and interaction terms.

	GLS regression outputs					**Joint hypothesis test**		
Variables	**Coef.**	**s.e.**	***z***	***p***	**95% *CI***	**df**	χ^2	***p***
Time (linear)	−0.26	0.02	−14.21	***	−0.29, −0.22			
Species or species group						6	28.25	***
C. perezi	Ref	Ref	Ref	Ref	Ref			
C. acronotus	−0.05	0.14	−0.37		−0.31, 0.21			
C. limbatus	0.19	0.11	1.72		−0.03, 0.40			
G. cuvier	−0.32	0.11	−2.87	**	−0.54, −0.10			
G. cirratum	−0.24	0.064	−3.74	***	−0.37, −0.11			
S. barracuda	−0.12	0.11	−1.03		−0.34, 0.10			
Lutjanidae and Carangidae	−0.16	0.13	−1.24		−0.41, 0.09			
Time (linear) × species or species group						6	20.38	**
C. acronotus	0.01	0.05	0.18		−0.10, 0.11			
C. limbatus	−0.02	0.04	−0.43		−0.10, 0.06			
G. cuvier	0.13	0.04	3.07	**	0.05, 0.21			
G. cirratum	0.08	0.02	3.25	***	0.03, 0.12			
S. barracuda	0.005	0.04	0.11		−0.08, 0.09			
Lutjanidae and Carangidae	0.01	0.05	0.22		−0.08, 0.10			
Time (quadratic)	0.02	0.002	10.53	***	0.01, 0.02			
Time (quadratic) × species or species group						6	14.88	*
C. acronotus	−0.002	0.005	−0.39		−0.01, 0.007			
C. limbatus	0.00005	0.004	0.01		−0.007, 0.007			
G. cuvier	−0.01	0.004	−2.66	**	−0.02, −0.003			
G. cirratum	−0.005	0.002	−2.66	**	−0.009, −0.001			
S. barracuda	0.002	0.004	0.4		−0.006, 0.009			
Lutjanidae and Carangidae	0.001	0.004	0.13		−0.008, 0.009			
Covariates								
Fork length	0.0002	0.0004	0.52		−0.0006, 0.001			
Capture duration	−0.0001	0.0002	−0.52		−0.0005, 0.0002			
Constant	0.02	0.08	0.21		−0.13, 0.17			
Overall R^2			0.44					
Rho			0.21					
Animal level (Σu)			0.11					
Occasion level (Σe)			0.22					

Unstandardized coefficients are presented. "Ref" refers to reference category for the model.
$^*p < 0.05$,
$^{**}p < 0.01$,
$^{***}p \leq 0.001$.

time (linear). We also found significant differences in fight intensities between species ($\chi^2(6) = 28.3$, $p < 0.001$; Table 4). We recorded the highest fight intensity values for *C. limbatus* followed by *C. perezi*, *C. acronotus*, *S. barracuda*, the lutjanid/carangid group, *G. cirratum*, and *G. cuvier* (Figure 2). Significant differences from pairwise comparisons included the following: (i) *C. limbatus* exhibited greater fight intensity than *G. cuvier* ($z = -3.6$, $p = 0.007$) and *G. cirratum* ($z = -4.0$, $p = 0.001$) and (ii) *C. perezi* exhibited greater fight intensity than *G. cirratum* ($z = -3.7$, $p = 0.004$). We also found a significant interaction between fight intensity over time (linear) and species ($\chi^2(6) = 20.4$, $p = 0.002$) and between fight intensity over time (quadratic) and species ($\chi^2(6) = 14.9$, $p = 0.02$). Fight intensity decreased sharply after capture followed by an increase towards the end of this 10-min period as suggested by the estimates for the linear slope (negative) and quadratic slope (positive, Table 4). Compared to *C. perezi*, *G. cuvier* and *G. cirratum* exhibited significant positive slopes for time (linear) and significant negative slopes for time (quadratic). Fork length had no effect on fight intensity in this model.

In the multi-level model that investigated differences in fight intensity between shark species across an entire capture event, we found no significant differences in fight intensity values ($\chi^2(4) = 3.31$, $p = 0.508$). We did find a negative slope for time (linear) and significant differences in the linear slopes of fight intensity over time between species as indicated by a significant interaction term ($\chi^2(4) = 65.68$, $p < 0.001$). Compared to *C. perezi* (the reference species), *C. acronotus* exhibited a negative relationship between fight intensity and time and *G. cirratum* exhibited a positive relationship between fight intensity and time. There was also a positive slope for time (quadratic) and a significant difference in the quadratic term for fight intensity over time between species ($\chi^2(4) = 133.71$, $p < 0.001$; Figure 3 and Table 5), with *C. acronotus* displaying a positive quadratic relationship and *G. cirratum* displaying a negative quadratic relationship compared to *C. perezi.* Sharks in the genus *Carcharhinus* exhibited the most dramatic changes in fight intensity over time (Figure 3). Fork length had a negative relationship with fight intensity in this model. *S. cubensis*, the only deepwater shark that we sampled, exhibited some of the lowest fight intensity values of any in this study but was not included in this model.

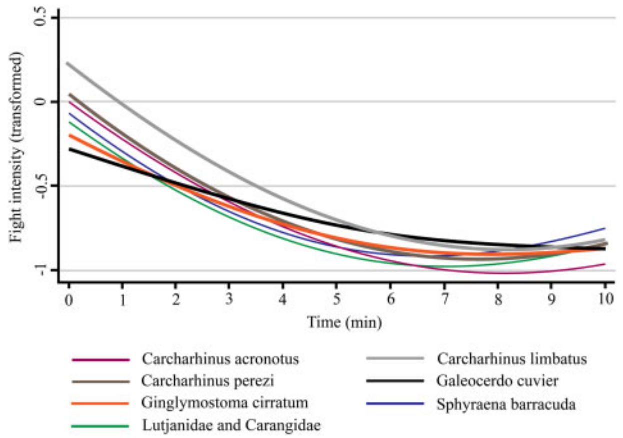

Figure 2. Model outputs showing fight intensity (transformed) measured by on-hook accelerometers during the first 10 min of capture for seven species and species groups of fishes caught on longlines. Species of interest are highlighted by bold colours and represent those species with significant differences in fight intensity: *C. limbatus* exhibited greater fight intensity than *G. cuvier* and *G. cirratum,* and *C. perezi* exhibited greater fight intensity than *G. cirratum.*

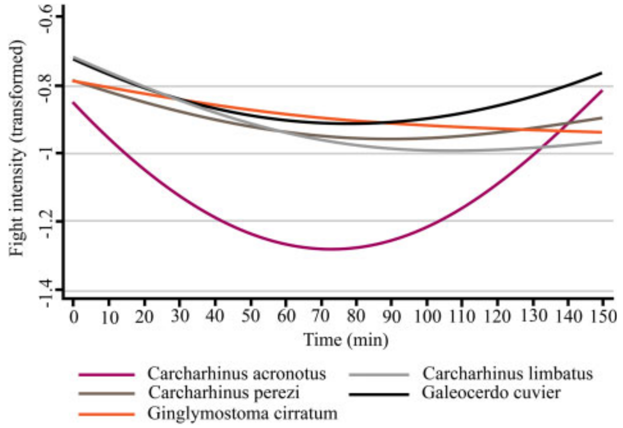

Figure 3. Model outputs showing fight intensity (transformed) measured by on-hook accelerometers for five shark species during longline capture.

In the multi-level model that investigated differences in fight intensity between shark ventilation modes (which were assigned based on video footage and *in situ* observations, Table 1) across an entire capture event, we found a negative slope for time (linear) and a positive slope for time (quadratic). There were no significant differences in fight intensities between groups ($\chi^2(2) = 0.09$, $p = 0.96$; Table 6). We did find significant differences in the linear ($\chi^2(2) = 62.84$, $p < 0.001$) and quadratic slopes ($\chi^2(2) = 140.35$, $p < 0.001$) for the interaction between fight intensity over time and ventilation mode. This suggests that there were significant differences in fight intensity trajectories between ventilation modes (Figure 4), with mixed and ram ventilators exhibiting significant negative slopes for time (linear) and significant positive slopes for time (quadratic) compared to buccal pumpers. Fork length had a negative relationship with fight intensity in this model.

In the multi-level model that investigated differences in fight intensity between teleost species groups across an entire capture event, there was a significant negative slope for time (linear) and a significant positive slope for time (quadratic). There were no significant differences in fight intensity between groups ($\chi^2(2) = 1.54$, $p = 0.463$), but there were significant differences in the linear slopes of fight intensity over time (linear; $\chi^2(2) = 14.8$, $p < 0.001$) and time (quadratic; $\chi^2(2) = 16.01$, $p < 0.001$). The lutjanid/carangid group exhibited a significant negative slope for time (linear) and a significant positive slope for time (quadratic) compared to *S. barracuda* (Figure 5 and Table 7).

Discussion

The goal of this study was to quantify the behavioural response of 13 species of subtropical marine fishes to longline capture. We found that the relationship between fight intensity and time hooked on a longline was best described by a non-linear, quadratic response that was suggested by multiple statistical approaches. Specific model outputs, however, should be interpreted carefully because r^2 values were low. The model describing fight intensity for the first 10 min of capture displayed the best fit ($r^2 = 0.44$), and others exhibited poor fits, although this is not uncommon for field-based studies examining the stress response in fishes (Brooks *et al.*, 2012). Furthermore, we collected fight intensity data from fishes captured on experimental gear that was designed to limit mortality. Our longline gear was not identical to commercial pelagic or coastal longlines (Beerkircher *et al.*, 2002; Hale *et al.*, 2011), and the capture durations that we manipulated also represent a fraction of commercial longline hooking durations that can reach >10 hr (Morgan and Carlson, 2010). Still, our results provide an understanding of one possible mechanism tied to differences in sub-lethal physiological stress and mortality (Bouyoucos *et al.*, 2017, 2018).

For all species, the highest fight intensity values (e.g. burst swimming) were recorded during the first 5 min of the capture event. High-intensity, burst swimming is supported by anaerobic metabolic pathways that initiate the secondary stress response (e.g. increased blood lactate, French *et al.*, 2015; Gallagher *et al.*, 2017) and can lead to physiological exhaustion within minutes (Wood, 1991; Kieffer, 2000). The intensity of these behaviours can influence the magnitude of changes in concentrations of electrolytes, metabolites, and physicochemical properties of the blood (Gallagher *et al.*, 2017; Bouyoucos *et al.*, 2018) that can contribute to mortality (Hutchinson *et al.*, 2015; Talwar *et al.*, 2017). We previously demonstrated associations between markers of the secondary stress response (blood pH and lactate concentration and plasma chloride concentration) and capture duration, which was negatively correlated with mean fight intensity per minute in *C. perezi* and *G. cirratum* caught on the same experimental longlines as those used in this study (Bouyoucos *et al.*, 2018). Therefore, the intensity of a fish's behavioural response during the initial capture event could play a role in determining the status of a fish after longline capture. Despite these associations, all behavioural traces in this study showed evidence of stabilization or recovery late in the capture event (but, again, capture durations were short). Additional research is warranted to understand how fight intensity during the initial capture response influences recovery or mortality.

We found that smaller sharks exhibited higher fight intensity values than larger sharks. Previous studies have shown that size is negatively correlated with physiological disturbance and mortality

Table 5. Results of final multi-level regression model describing fight intensity for shark species during the entire capture event, as well as contrasts of marginal linear predictions (joint hypothesis test) for differences between species and interaction terms.

	GLS regression outputs					Joint hypothesis test		
Variables	**Coef.**	**s.e.**	***Z***	***p***	**95% *CI***	**df**	χ^2	***p***
Time (linear)	−0.004	0.0002	−17.4	***	−0.004, −0.003			
Species or species group						4	3.31	0.51
C. perezi	Ref	Ref	Ref	Ref	Ref			
C. acronotus	−0.06	0.07	−0.77		−0.20, 0.09			
C. limbatus	0.07	0.06	1.17		−0.05, 0.18			
G. cuvier	0.06	0.06	1.03		−0.05, 0.18			
G. cirratum	0.004	0.04	0.10		−0.07, 0.07			
Time (linear) × species or species group						4	65.68	***
C. acronotus	−0.009	0.002	−3.81	***	−0.01, −0.004			
C. limbatus	−0.001	0.001	−1.74		−0.003, 0.0002			
G. cuvier	−0.001	0.001	−1.21		−0.003, 0.0007			
G. cirratum	0.002	0.0003	5.84	***	0.001, 0.002			
Time (quadratic)	0.00002	0.00	20.13	***	0.00001, 0.00002			
Time (quadratic) × species or species group						4	133.71	***
C. acronotus	0.0001	0.00002	2.79	**	0.00002, 0.0001			
C. limbatus	0.00	0.00	0.46		−6.48e−06, 0.00001			
G. cuvier	0.00001	0.00	1.53		−3.14e−06, 0.00003			
G. cirratum	−0.00001	0.00	−10.56	***	−0.00001, −1e−05			
Covariates								
Fork length	−0.0009	0.0003	−2.91	**	−0.002, −0.0003			
Capture duration	−0.0001	0.0002	−0.32		−0.0004, 0.0003			
Constant	−0.60	0.05	−11.07	***	−0.71, −0.50			
Overall R^2			0.08					
Rho			0.31					
Animal level (Σu)			0.134					
Occasion level (Σe)			0.199					

Unstandardized coefficients are presented. "Ref" refers to reference category for the model.

*$p < 0.05$,

**$p < 0.01$,

***$p \leq 0.001$.

for fishes caught on longlines and drumlines (Neilson *et al.*, 1989; Milliken *et al.*, 1999; Diaz and Serafy, 2005; Morgan and Burgess, 2007; Gallagher *et al.*, 2014b; Talwar *et al.*, 2017). This relationship can be species-specific, parameter-specific (Bouyoucos *et al.*, 2018), or even positive. After finding that size was positively correlated with mortality in sandbar sharks *Carcharhinus plumbeus*, Morgan and Carlson (2010) hypothesized that larger sandbar sharks may struggle more during capture and ultimately suffer greater physiological disturbance leading to mortality. While sandbar sharks were not included in our study, the effect of size was consistent in our models for five other shark species, suggesting that an alternative hypothesis may better explain the trend for sandbar sharks (e.g. hooking location, as discussed in Morgan and Carlson, 2010).

Among sharks, certain species groups exhibited pronounced responses to capture. Sharks in the genus *Carcharhinus*, particularly obligate ram and mixed ventilators with active benthopelagic lifestyles (e.g. *C. limbatus*, *C. acronotus*, *C. perezi*), exhibited higher fight intensity values, larger negative linear trajectories, and larger positive quadratic trajectories in fight intensity over time compared to *G. cuvier* and *G. cirratum*. Ram ventilation is an energy efficient ventilation mode that requires forward momentum to force oxygenated water over the gills (Roberts, 1978; Steffensen, 1985; Carlson *et al.*, 2004). The associated active lifestyle is linked to higher metabolic rates than those that are more stationary or benthic-associated (Carlson *et al.*, 2004; Killen *et al.*, 2016). During a hooking event, swimming ability is limited by the gangion. This restraint may prevent ram ventilators from reaching the swimming speeds (Morgan and Burgess, 2007) necessary to uptake enough oxygen to meet the demanding requirements of increased muscle activity (Morgan and Carlson, 2010; Skomal and Mandelman, 2012). Ram ventilators may become exhausted and swim at speeds below the minimum velocity required for hydrostatic equilibirum (Sepulveda *et al.*, 2007), thus reducing oxygen uptake even further. This can lead to a positive feedback loop that results in tissue hypoxia and, eventually, asphyxiation (Dapp *et al.*, 2016b). Ram-ventilating species exhibit significantly higher mortality rates compared to species that can respire when stationary (Dapp *et al.*, 2016b; Ellis *et al.*, 2017). Short gangion lengths may exacerbate this problem by further reducing freedom of movement and increasing the likelihood of gear entanglement, particularly with increased soak and/or hooking times (Morgan and Burgess, 2007; Gallagher *et al.*, 2014b; Dapp *et al.*, 2016b; Guida *et al.*, 2016). How gangion length influences the sub-lethal and lethal outcomes of a capture event warrants further study and has direct management implications (Dapp *et al.*, 2016a).

Carcharhinus limbatus and *C. acronotus*, both obligate ram ventilators, exhibited behavioural patterns characteristic of the feedback loops described above. Both species were observed in

Table 6. Results of final multi-level regression model describing fight intensity for shark ventilation modes for the entire capture event, as well as contrasts of marginal linear predictions (joint hypothesis test) for differences between ventilation modes and interaction terms.

	GLS regression outputs					Joint hypothesis test		
Variables	**Coef.**	**s.e.**	***Z***	***p***	**95% *CI***	**df**	χ^2	***p***
Time (linear)	−0.002	0.0002	−12.19	***	−0.002, −0.002			
Species or species group						2	0.09	0.96
Sharks: buccal pumping	Ref	Ref	Ref	Ref	Ref			
Sharks: mixed ventilation	0.009	0.03	0.3		−0.05, 0.07			
Sharks: obligate ram	0.005	0.05	0.09		−0.09, 0.10			
Time (linear) × species or species group						2	62.84	***
Sharks: mixed ventilation	−0.002	0.00	−6.56	***	−0.002, −0.001			
Sharks: obligate ram	−0.003	0.0006	−5.51	***	−0.005, −0.002			
Time (quadratic)	0.00	0.00	9.8	***	5.36e−06, 8.04e−06			
Time (quadratic) × species or species group						2	140.35	***
Sharks: mixed ventilation	0.00001	0.00	11.34	***	0.00001, 0.00002			
Sharks: obligate ram	0.00002	0.00	4.56	***	0.00001, 0.00003			
Covariates								
Fork length	−0.001	0.0003	−2.71	**	−0.001, −0.0002			
Capture duration	−0.0001	0.0002	−0.26		−0.0004, 0.0003			
Constant	−0.63	0.06	−9.73	***	−0.75, −0.50			
Overall R^2			0.07					
Rho			0.32					
Animal level (Σu)			0.136					
Occasion level (Σe)			0.199					

Unstandardized coefficients are presented. "Ref" refers to reference category for the model.
*$p < 0.05$,
**$p < 0.01$,
***$p \leq 0.001$.

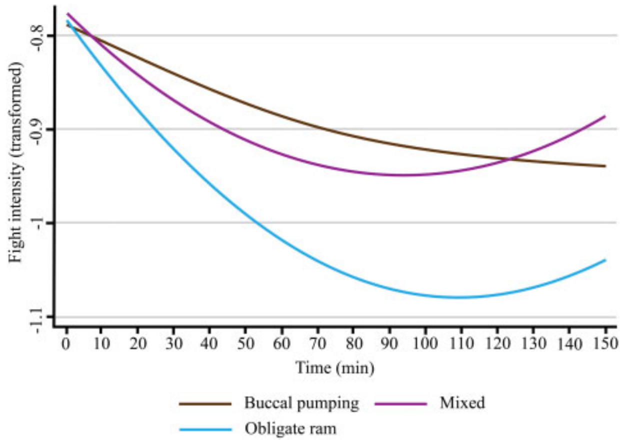

Figure 4. Model outputs showing fight intensity (transformed) measured by on-hook accelerometers during longline capture for sharks that exhibit buccal (and spiracular) pumping, mixed, and obligate ram ventilation modes.

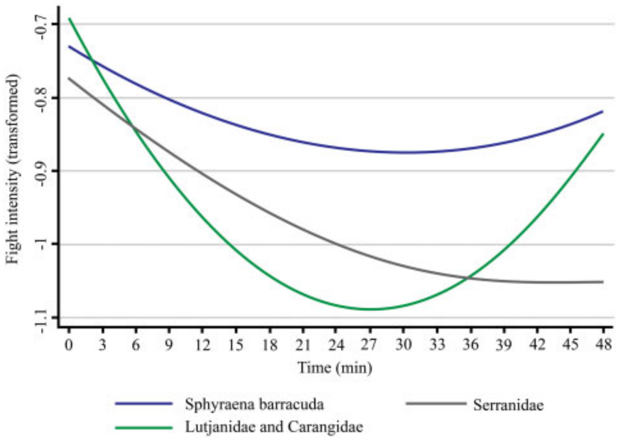

Figure 5. Model outputs showing fight intensity (transformed) measured by on-hook accelerometers during longline capture for teleost species and species groups.

vertical immobility after exhibiting dramatic burst swimming responses during the initial capture event. *Carcharhinus limbatus* exhibits a similar response when captured on drumlines (Gallagher *et al.*, 2017). Our model predictions for *C. limbatus* ($n = 10$) suggest high initial fight intensity values (Figure 2) followed by low fight intensity values and limited recovery at greater capture durations (Figure 3). The model for *C. acronotus* predicts a steep quadratic response in fight intensity ($n = 5$; Figure 3), but the predicted recovery is based on data from just one individual hooked past the 107th minute and should be interpreted with caution. Past studies have documented high mortality rates associated with longline capture for *C. acronotus* (Morgan and Carlson, 2010) and *C. limbatus* (up to 90%; Beerkircher *et al.*, 2002; Gallagher *et al.*, 2014a; Butcher *et al.*, 2015; Gallagher *et al.*, 2017), although mortality for *C. limbatus* is low after rod-and-reel capture (Whitney *et al.*, 2016b). Other obligate ram ventilators such as hammerhead sharks also exhibit high levels of stress and mortality after longline capture (Morgan and Burgess, 2007;

Table 7. Results of final multi-level regression model describing fight intensity for teleosts across the entire capture event, as well as contrasts of marginal linear predictions (joint hypothesis test) for differences between species and interaction terms.

	GLS regression outputs					Joint hypothesis test		
Variables	**Coef.**	**s.e.**	***z***	***p***	**95% *CI***	**df**	χ^2	***p***
Time (linear)	−0.01	0.0030	−3.33	**	−0.02, −0.004			
Species or species group						2	1.54	
S. barracuda	Ref	Ref	Ref	Ref	Ref			
Serranidae	−0.04	0.06	−0.73		−0.15, 0.07			
Lutjanidae and Carangidae	0.04	0.06	0.63		−0.08, 0.15			
Time (linear) × species or species group						2	14.83	**
Serranidae	−0.003	0.004	−0.83		−0.01, 0.005			
Lutjanidae and Carangidae	−0.02	0.005	−3.79	***	−0.03, −0.01			
Time (quadratic)	0.0002	0.0001	3.31	**	0.00007, 0.0003			
Time (quadratic) × species or species group						2	16.01	**
Serranidae	−0.00001	0.0001	−0.20		−0.0001, 0.0001			
Lutjanidae and Carangidae	0.0004	0.0001	3.63	***	0.0002, 0.0006			
Covariates								
Capture duration	−0.002	0.0009	−1.90		−0.003, 0.00005			
Constant	−0.66	0.04	−15.26	***	−0.74, −0.57			
Overall R^2			0.21					
Rho			0.07					
Animal level (Σu)			0.06					
Occasion level (Σe)			0.21					

Unstandardized coefficients are presented. "Ref" refers to reference category for the model.
*$p < 0.05$,
**$p < 0.01$,
***$p \leq 0.001$.

Gallagher *et al.*, 2014b; Gallagher *et al.*, 2017), which could be related to their propensity for burst swimming behaviour during prey capture that may translate to on-hook behaviour (Gallagher *et al.*, 2014c, 2017).

Species that can switch between modes of ventilation, including many teleosts, *C. perezi*, *G. cuvier*, and *N. brevirostris*, may be able to compensate for limited movement during a hooking event by increasing mouth gape or forcefully pumping water through the mouth (Morgan and Burgess, 2007). During the first 10 min of capture, *G. cuvier* had lower fight intensity values and a negative quadratic slope compared to *Carcharhinus* spp. (i.e. its fight intensity trajectory exhibited less steepness/less upward concavity). *Galeocerdo cuvier* is very resilient to the stress of longline capture (Gallagher *et al.*, 2014a) based on roughly 97% at-vessel survivorship in swordfish and tuna longline fisheries and low mortality in other studies (Morgan and Burgess, 2007; Morgan and Carlson, 2010). *Carcharhinus perezi* is similarly ranked as one of the more resilient carcharhinids studied to date behind *G. cuvier* and *C. plumbeus* (Mandelman and Skomal, 2009; Brooks *et al.*, 2012) and experiences low at-vessel mortality rates (Brooks *et al.*, 2012; Bouyoucos *et al.*, 2018). Both *C. perezi* and *G. cuvier* showed similar positive quadratic fight intensity trajectories (i.e. increases in fight intensity towards the later minutes of capture), suggesting behavioural recovery consistent with the physiological recovery documented for *C. perezi* in Brooks *et al.* (2012).

Benthic-associated sharks exhibited the most subdued response to capture. Generally, these species are characterized by large spiracles, heterocercal caudal fins, and a dorso-ventrally flattened form, and are able to buccal pump, pull in water through the first gill slit (Grigg, 1970), or utilize spiracles to respire. These species, such as *S. cubensis* (which uses both spiracles and buccal pumping) and *G. cirratum* (which relies largely on buccal pumping), are capable of stationary respiration and show lower fishing-related mortality rates than many carcharhinid species (Morgan and Carlson, 2010; Talwar *et al.*, 2017). We hypothesize that the low fight intensity values exhibited by *S. cubensis* were due to (i) cold capture temperatures (∼13°C) that are associated with low metabolic rate and activity at depth (Koslow, 1996), (ii) the ability to respire through spiracles and buccal mechanisms as discussed previously, and (iii) the ability to rest on the seafloor during the capture event (made possible by being captured on a demersal longline). Similarly, hooked *G. cirratum* were often obseved resting on the bottom after dragging the mid-water longline to the seafloor. As would be expected, they had some of the most subdued fighting behaviours of any shark, in agreement with the results of Gallagher *et al.* (2017), which suggested that low metabolic rates (Whitney *et al.*, 2016a) may explain this behaviour. This propensity for resting and exhibiting low fight intensity while on the line has been linked to higher blood pH (i.e. less stress) after capture (Bouyoucos *et al.*, 2018).

Teleosts exhibited a similar negative linear and positive quadratic relationship between fight intensity and time on the hook to that seen in sharks. Teleost fish can be physiologically resilient to the exhaustive exercise associated with hook-and-line capture (Roth and Rotabakk, 2012), but the relationship between their on-hook behaviour and physiological status has not been demonstrated (Brownscombe *et al.*, 2014). Overall, the status of captured teleost fishes is impacted by hooking injury (mediated by hook and lure type; Cooke and Suski, 2004; Reinhardt *et al.*, 2018), barotrauma (Rummer and Bennett, 2005), air exposure during handling (Cook *et al.*, 2015), capture duration (Skomal, 2007), and depredation (Mitchell *et al.*, 2018) among other factors. In this study, limited sample size precluded us from drawing robust species-specific conclusions. We did observe overinflated swim bladders in some hooked teleosts during longline checks, which suggests an immediate deleterious outcome of the initial capture event that could increase the risk of depredation. Immobility in fish with overinflated swim bladders would have likely resulted in low fight intensity values, but this factor was not recorded in the field or examined in our analyses (and was often off-camera because of the lack of tension on the gangion). The effects of catch and release are still relatively unknown for longline-captured teleosts (Cook *et al.*, 2019) and warrant further study.

Conclusions

This study provides insights into the variation in behavioural responses of elasmobranch and teleost fishes captured on a commercially relevant gear type. Our data support past studies in showing that inter- and intra-specific fighting behaviour is variable among longline-captured fishes (Guida *et al.*, 2017), with some ram-ventilating carcharhinids demonstrating a pronounced escape response that could be related to their high levels of physiological disturbance and mortality shown in other studies. These data also highlight the significance of the initial capture event as a possible point of influence on the fate of a captured fish because the most concentrated burst swimming and thus most energetically costly behaviours occured during this period (Bouyoucos *et al.*, 2017). Responses of teleost fishes to longline capture warrant further investigation, especially in the contexts of bycatch and food quality.

These findings have implications for researchers and fisheries managers. Waiting until an animal has recovered from its initial escape response before adding the compounding stress of a workup procedure may reduce handling risk to researchers and sensitive or endangered fishes. The behavioural response to longline capture may partially explain relative vulnerability to mortality, thus our findings can inform predictive risk assessments. Furthermore, quantifying and mitigating the behavioural component of a fish's stress response may be more practical than mitigating physiological stress. Research that aims to reduce fish stress and mortality could explore links between longline configurations (e.g. gangion length, hook-associated drag, set depth) and reductions in detrimental behaviours (e.g. burst swimming) that lead to physiological disturbance (Guida *et al.*, 2016; Guida *et al.*, 2017; Bouyoucos *et al.*, 2018).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

The authors thank numerous hard-working staff and volunteers in the CEI Shark Research & Conservation Program including A. Carey, R. Fry, G. Hunt, R. Labella, E. Liddell, M. Piersiak, C. Morgan, T. Sanford, A. Schreiber, O. Shipley, D. Swift, C. Treyz, M. Violich, J. Wilchcombe, P. Wilson, and many others. The authors also thank L. Madden and R. Frost for their contributions to graphic design. The authors are grateful for the field support and enthusiasm of The Island School students of the fall 2012, spring 2013, and fall 2013 semesters, including G. Andres, J. Boyce, R. Frost, L. Gould, I. Jamerson, S. Johnson, C. Jones, M. Malpani, J. Martin, L. Merison, M. Montgomery, J. Norfleet, T. Nugent, P. Shaw, L. Silverstein, I. Swearingen, and N. Teter. BST thanks R. Andres for statistical consultation and M. Heithaus and three anonymous reviewers for their feedback on the manuscript.

Funding

This work was supported by the Cape Eleuthera Foundation, the New England Aquarium, Anderson Cabot Center for Ocean Life, Florida State University Coastal and Marine Laboratory, and an anonymous grant to JWM and EJB.

References

Barton, B. A. 2002. Stress in Fishes: A Diversity of Responses with Particular Reference to Changes in Circulating Corticosteroids. Integrative and Comparative Biology, 42: 517–525.

Beerkircher, L., Cortés, E., and Shivji, M. 2002. Characteristics of shark bycatch observed on pelagic longlines off the southeastern United States, 1992–2000. Marine Fisheries Review, 64: 40–49.

Bouyoucos, I. A., Suski, C. D., Mandelman, J. W., and Brooks, E. J. 2017. The energetic, physiological, and behavioral response of lemon sharks (*Negaprion brevirostris*) to simulated longline capture. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 207: 65–72.

Bouyoucos, I. A., Talwar, B. S., Brooks, E. J., Brownscombe, J. W., Cooke, S. J., Suski, C. D., and Mandelman, J. W. 2018. Exercise intensity while hooked is associated with physiological status of longline-captured sharks. Conservation Physiology, 6: coy074.https://academic.oup.com/conphys/article/doi/10.1093/conphys/coy074/5255023.

Brooks, E. J., Mandelman, J. W., Sloman, K. A., Liss, S., Danylchuk, A. J., Cooke, S. J., Skomal, G. B., *et al.* 2012. The physiological response of the Caribbean reef shark (*Carcharhinus perezi*) to longline capture. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 162: 94–100.

Brown, D. D., Kays, R., Wikelski, M., Wilson, R., and Klimley, A. P. 2013. Observing the unwatchable through acceleration logging of animal behavior. Animal Biotelemetry, 1: 20.

Brownscombe, J. W., Griffin, L. P., Gagne, T., Haak, C. R., Cooke, S. J., and Danylchuk, A. J. 2015. Physiological stress and reflex impairment of recreationally angled bonefish in Puerto Rico. Environmental Biology of Fishes, 98: 2287–2295.

Brownscombe, J. W., Marchand, K., Tisshaw, K., Fewster, V., Groff, O., Pichette, M., Seed, M., *et al.* 2014. The influence of water temperature and accelerometer-determined fight intensity on physiological stress and reflex impairment of angled largemouth bass. Conservation Physiology, 2: cou057.

Butcher, P. A., Peddemors, V. M., Mandelman, J. W., McGrath, S. P., and Cullis, B. R. 2015. At-vessel mortality and blood biochemical status of elasmobranchs caught in an Australian commercial longline fishery. Global Ecology and Conservation, 3: 878–889.

Carlson, J. K., Goldman, K. J., and Lowe, C. G. 2004. Metabolism, energetic demand, and endothermy. In: Biology of Sharks and Their Relatives, 1st edn, pp. 203–225. Ed. by J. C. Carrier, J. A. Musick and M. R. Heithaus. CRC Press, Boca Raton.

Cook, K. V., Lennox, R. J., Hinch, S. G., and Cooke, S. J. 2015. Fish out of water: how much air is too much? Fisheries, 40: 452–461.

Cook, K. V., Reid, A. J., Patterson, D. A., Robinson, K. A., Chapman, J. M., Hinch, S. G., and Cooke, S. J. 2019. A synthesis to understand responses to capture stressors among fish discarded from commercial fisheries and options for mitigating their severity. Fish and Fisheries, 20: 25–43.

Cooke, S. J., and Suski, C. D. 2004. Are circle hooks an effective tool for conserving marine and freshwater recreational catch-and-release fisheries? Aquatic Conservation: Marine and Freshwater Ecosystems, 14: 299–326.

Danylchuk, A. J., Suski, C. D., Mandelman, J. W., Murchie, K. J., Haak, C. R., Brooks, A. M., and Cooke, S. J. 2014. Hooking injury, physiological status and short-term mortality of juvenile lemon sharks (*Negaprion bevirostris*) following catch-and-release recreational angling. Conservation Physiology, 2: cot036–cot036.

Dapp, D. R., Huveneers, C., Walker, T. I., Drew, M., and Reina, R. D. 2016a. Moving from measuring to predicting bycatch mortality: predicting the capture condition of a longline-caught pelagic shark. Frontiers in Marine Science, 2: 126.

Dapp, D. R., Walker, T. I., Huveneers, C., and Reina, R. D. 2016b. Respiratory mode and gear type are important determinants of elasmobranch immediate and post-release mortality. Fish and Fisheries, 17: 507–524.

Davies, R. W. D., Cripps, S. J., Nickson, A., and Porter, G. 2009. Defining and estimating global marine fisheries bycatch. Marine Policy, 33: 661–672.

Davis, M. W. 2002. Key principles for understanding fish bycatch discard mortality. Canadian Journal of Fisheries and Aquatic Science, 59: 1834–1843.

Diaz, G. A., and Serafy, J. E. 2005. Longline-caught blue shark (*Prionace glauca*): factors affecting the numbers available for live release. Fisheries Bulletin, 103: 720.

Ellis, J. R., McCully Phillips, S. R., and Poisson, F. 2017. A review of capture and post-release mortality of elasmobranchs. Journal of Fish Biology, 90: 653–722.

French, R. P., Lyle, J., Tracey, S., Currie, S., and Semmens, J. M. 2015. High survivorship after catch-and-release fishing suggests physiological resilience in the endothermic shortfin mako shark (*Isurus oxyrinchus*). Conservation Physiology, 3: cov044.

Frick, L. H., Reina, R. D., and Walker, T. I. 2010. Stress related physiological changes and post-release survival of Port Jackson sharks (*Heterodontus portusjacksoni*) and gummy sharks (*Mustelus antarcticus*) following gill-net and longline capture in captivity. Journal of Experimental Biology and Ecology, 385: 29–37.

Gallagher, A. J., Hammerschlag, N., Shiffman, D. S., and Giery, S. T. 2014c. Evolved for extinction: the cost and conservation implications of specialization in hammerhead sharks. Bioscience, 64: 619–624.

Gallagher, A. J., Orbesen, E. S., Hammerschlag, N., and Serafy, J. E. 2014a. Vulnerability of oceanic sharks as pelagic longline bycatch. Global Ecology and Conservation, 1: 50–59.

Gallagher, A. J., Serafy, J. E., Cooke, S. J., and Hammerschlag, N. 2014b. Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. Marine Ecology Progress Series, 496: 207–218.

Gallagher, A. J., Staaterman, E. R., Cooke, S. J., and Hammerschlag, N. 2017. Behavioral responses to fisheries capture among sharks caught using experimental fishery gear. Canadian Journal of Fisheries and Aquatic Science, 74: 1–7.

Grace, M. A., Watson, J., and Foster, D. 2010. Time, temperature and depth profiles for a Loggerhead sea turtle (*Caretta caretta*) captured with a pelagic longline. Southeastern Naturalist, 9: 191–200.

Grigg, G. C. 1970. Use of the first gill slits for water intake in a shark. Journal of Experimental Biology, 52: 569–574.

Guida, L., Dapp, D. R., Huveneers, C. P., Walker, T. I., and Reina, R. D. 2017. Evaluating time-depth recorders as a tool to measure the behaviour of sharks captured on longlines. Journal of Experimental Marine Biology and Ecology, 497: 120–126.

Guida, L., Walker, T. I., and Reina, R. D. 2016. Temperature insensitivity and behavioural reduction of the physiological stress response to longline capture by the gummy shark, *Mustelus antarcticus*. PLoS One, 11: e0148829.

Hale, L. F., Gulak, S. J. B., Napier, A. M. and Carlson, J. K. 2011. Characterization of the shark bottom longline fishery, 2010. NOAA Technical Memorandum NMFS-SEFSC611, 35 p.

Harrington, J. M., Myers, R. A., and Rosenberg, A. A. 2005. Wasted fishery resources: discarded by-catch in the USA. Fish and Fisheries, 6: 350–361.

Humborstad, O.-B., Breen, M., Davis, M. W., Løkkeborg, S., Mangor-Jensen, A., Midling, K. Ø., and Olsen, R. E. 2016. Survival and recovery of longline- and pot-caught cod (*Gadus morhua*) for use in capture-based aquaculture (CBA). Fisheries Research, 174: 103–108.

Hutchinson, M. R., Itano, D. G., Muir, J. A., and Holland, K. N. 2015. Post-release survival of juvenile silky sharks captured in a tropical tuna purse seine fishery. Marine Ecology Progress Series, 521: 143–154.

Kieffer, J. D. 2000. Limits to exhaustive exercise in fish. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 126: 161–179.

Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S. T., and Halsey, L. G. 2016. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. The American Naturalist, 187: 592–606.

Koslow, J. A. 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. Journal of Fish Biology, 49: 54–74.

Lewison, R. L., Crowder, L. B., Read, A. J., and Freeman, S. A. 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends in Ecology and Evolution, 19: 598–604.

Mandelman, J. W., Cooper, P. W., Werner, T. B., and Lagueux, K. M. 2008. Shark bycatch and depredation in the US Atlantic pelagic longline fishery. Reviews in Fish Biology and Fisheries, 18: 427–442.

Mandelman, J. W., and Skomal, G. B. 2009. Differential sensitivity to capture stress assessed by blood acid–base status in five carcharhinid sharks. Comparative Biochemistry and Physiology Part B: Biochemistry & Molecular Biology, 179: 267–277.

Marshall, H., Field, L., Afiadata, A., Sepulveda, C., Skomal, G., and Bernal, D. 2012. Hematological indicators of stress in longline-captured sharks. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 162: 121–129.

Milliken, H. O., Farrington, M., Carr, H. A., and Lent, E. 1999. Survival of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic longline fishery. Marine Technology Society Journal, 33: 19–24.

Mitchell, J. D., McLean, D. L., Collin, S. P., and Langlois, T. J. 2018. Shark depredation in commercial and recreational fisheries. Reviews in Fish Biology and Fisheries, 28: 715–748.

Morgan, A., and Burgess, G. H. 2007. At-vessel fishing mortality for six species of sharks caught in the Northwest Atlantic and Gulf of Mexico. Gulf and Caribbean Research, 19: 123–129.

Morgan, A., and Carlson, J. K. 2010. Capture time, size and hooking mortality of bottom longline-caught sharks. Fisheries Research, 101: 32–37.

Moyes, C. D., Fragoso, N., Musyl, M. K., and Brill, R. W. 2006. Predicting postrelease survival in large pelagic fish. Transactions of the American Fisheries Society, 135: 1389–1397.

Neilson, J. D., Waiwood, K. G., and Smith, S. J. 1989. Survival of Atlantic halibut (*Hippoglossus hippoglossus*) caught by longline and otter trawl gear. Canadian Journal of Fisheries and Aquatic Science, 46: 887–897.

Oliver, S., Braccini, M., Newman, S. J., and Harvey, E. S. 2015. Global patterns in the bycatch of sharks and rays. Marine Policy, 54: 86–97.

Raby, G. D., Packer, J. R., Danylchuk, A. J., and Cooke, S. J. 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. Fish and Fisheries, 15: 489–505.

Raudenbush, S. W., and Bryk, A. S. 2002. Hierarchical Linear Models: Applications and Data Analysis Methods, 2nd edn. Sage, Thousand Oaks, CA.

Reinhardt, J. F., Weaver, J., Latham, P. J., Dell'Apa, A., Serafy, J. E., Browder, J. A., Christman, M., *et al.* 2018. Catch rate and at-vessel mortality of circle hooks versus J-hooks in pelagic longline fisheries: a global meta-analysis. Fish and Fisheries, 19: 413–430.

Richards, J. G., Heigenhauser, G. J. F., and Wood, C. M. 2003. Exercise and recovery metabolism in the pacific spiny dogfish (*Squalus acanthias*). Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology, 173: 463–474.

Roberts, J. L. 1978. Ram gill ventilation in fish. *In* The Physiological Ecology of Tunas, pp. 83–87. Ed. by G. D. Sharp, and A. E. Dizon. Academic Press, New York.

Rollin, B. E., and Kessel, M. L. 1998. Guidelines for the treatment of animals in behavioural research and teaching. Animal Behaviour, 55: 251–257.

Roth, B., and Rotabakk, B. T. 2012. Stress associated with commercial longlining and recreational fishing of saithe (Pollachius virens) and the subsequent effect on blood gases and chemistry. Fisheries Research, 115-116: 110–114.

Rummer, J. L., and Bennett, W. A. 2005. Physiological effects of swim bladder overexpansion and catastrophic decompression on red snapper. Transactions of the American Fisheries Society, 134: 1457–1470.

Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., and Wanless, S. 2009. Can ethograms be automatically generated using body acceleration data from free- ranging birds? PLoS One, 4: e5379.

Schreck, C. B., Olla, B. L., and Davis, M. W. 1997. Behavioural responses to stress. In Fish Stress and Health in Aquaculture, pp. 145–170. Ed. by G. K. Iwama, A. D. Pickering, J. P. Sumpter, and C. B. Schreck. Cambridge University Press, Cambridge.

Sepulveda, C. A., Graham, J. B., and Bernal, D. 2007. Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*. Marine Biology, 152: 1087–1094.

Skomal, G. B. 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. Fisheries Management and Ecology, 14: 81–89.

Skomal, G. B., and Mandelman, J. W. 2012. The physiological response to anthropogenic stressors in marine elasmobranch fishes: a review with a focus on the secondary response. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 162: 146–155.

Steffensen, J. F. 1985. The transition between branchial pumping and ram ventilation in fishes: energetic consequences and dependence on water oxygen tension. Journal of Evolutionary Biology, 150: 141–150.

Swartz, W., Sala, E., Tracey, S., Watson, R., and Pauly, D. 2010. The Spatial Expansion and Ecological Footprint of Fisheries (1950 to Present). PLoS ONE, 5: e15143.

Talwar, B., Brooks, E. J., Mandelman, J. W., and Grubbs, D. G. 2017. Stress, post-release mortality, and recovery of commonly discarded deep-sea sharks caught on longlines. Marine Ecology Progress Series, 582: 147–161.

Tukey, J. W. 1977. Exploratory Data Analysis. Addison-Wesley, Boston, MA, USA.

Watson, R. A., and Morato, T. 2013. Fishing down the deep: accounting for within-species changes in depth of fishing. Fisheries Research, 140: 63–65.

Whitney, N. M., Lear, K. O., Gaskins, L. C., and Gleiss, A. C. 2016a. The effects of temperature and swimming speed on the metabolic rate of the nurse shark (*Ginglymostoma cirratum*, Bonaterre). Journal of Experimental Marine Biology and Ecology, 477: 40–46.

Whitney, N. M., White, C. F., Gleiss, A. C., Schwieterman, G. D., Anderson, P., Hueter, R. E., and Skomal, G. B. 2016b. A novel method for determining post-release mortality, behavior, and recovery period using acceleration data loggers. Fisheries Research, 183: 210–221.

Wilson, S. M., Raby, G. D., Burnett, N. J., Hinch, S. G., and Cooke, S. J. 2014. Looking beyond the mortality of bycatch: sublethal effects of incidental capture on marine animals. Biological Conservation, 171: 61–72.

Wood, C. M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. Journal of Experimental Biology, 160: 285–308.

Handling editor: Michael Pol