Physiological consequences of varying large shark exposure on striped bass (*Morone saxatilis*)

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Abstract: Large marine predators often aggregate seasonally in discrete locations to take advantage of optimal foraging conditions, leading to spatial and temporal variation in their exposure on other species. However, our understanding of the impacts this exposure may have on the behavior and physiology of prey is poor, especially in marine systems. Here, we evaluated the non-consumptive effects of potential exposure to large sharks (white sharks, *Carcharodon carcharias* (Linnaeus, 1758)) on the stress physiology of an economically important teleost, the striped bass (*Morone saxatilis* (Walbaum, 1792)), off Cape Cod, Massachusetts, USA. We sampled fish in habitats that varied significantly in shark exposure across 5 months and over 2 years, evaluating blood physiology stress indicators (i.e., cortisol, glucose, and lactate concentrations) and reflex impairment. None of the blood parameters were influenced by shark exposure, although we did observe subtle temperature and seasonal effects. One of the three reflex tests (the vertical orientation test) was negatively affected by shark exposure, although the mechanistic basis for this finding is unclear. This work supports the notion that predictable sources of predation pressure tend not to manifest in stress-related costs in free-ranging prey, which has implications for shaping our understanding of how large sharks influence ecosystems through non-consumptive effects.

Key words: glucocorticoids, non-consumptive effects, predation, stress, striped bass, *Morone saxatilis*, white shark, *Carcharodon carcharias*.

Résumé : Les grands prédateurs marins se regroupent souvent sur une base saisonnière dans des lieux précis pour profiter de conditions d'approvisionnement optimales, ce qui mène à des variations spatiales et temporelles de l'exposition d'autres espèces à leur présence. La compréhension des impacts de cette exposition sur le comportement et la physiologie des proies demeure toutefois limitée, particulièrement en ce qui concerne les systèmes marins. Nous évaluons les effets non destructeurs de l'exposition potentielle à de grands requins (grands requins blancs, *Carcharodon carcharias* (Linnaeus, 1758)) sur la physiologie du stress d'un téléostéen d'importance commerciale, le bar d'Amérique (*Morone saxatilis* (Walbaum, 1792)), au large de Cape Cod (Massachusetts, États-Unis). Nous avons échantillonné des poissons dans des habitats présentant une diversité d'exposition aux requins sur une durée de cinq mois et sur deux années, pour évaluer des indicateurs sanguins de la physiologie du stress (c.-à-d. concentrations de cortisol, glucose et lactate) et l'altération des réflexes. Aucun des paramètres sanguins n'était influencé par l'exposition aux requins, de subtils effets de la température et de la saison ayant toutefois été observés. Un des trois tests des réflexes (le test d'orientation verticale) a relevé un effet négatif de l'exposition aux requins, bien que le fondement mécaniste de cet effet demeure mal compris. Ces travaux appuient la notion voulant que les sources prévisibles de pression de prédation n'aient pas tendance à se refléter dans les coûts associés au stress chez les proies en liberté, une constatation importante pour la compréhension de l'influence qu'exercent, par l'entremise d'effets non destructeurs, les grands requins sur les écosystèmes. [Traduit par la Rédaction]

Mots-clés : glucocorticoïdes, effets non destructeurs, prédation, stress, bar d'Amérique, *Morone saxatilis*, grand requin blanc, *Carcharodon carcharias*.

Introduction

Predators can affect prey directly, through consumption, and indirectly, through non-consumptive effects, also known as "risk effects" (Lima and Dill 1990; Laundré 2010). These non-consumptive effects can have strong impacts on the physiology and behavior of prey across various contexts and species (Lima and Dill 1990; Peckarsky et al. 2008; Creel et al. 2009). These relationships can be summarized into two hypotheses: (1) the predator-sensitive food hypothesis and (2) the predation-stress hypothesis (Sih 1980; Sinclair and Arcese 1995). The predator-sensitive food hypothesis suggests that predators have a significant effect on the foraging behavior of prey species, thereby limiting their nutritional condition, reproductive output, and overall fitness (Creel et al. 2009). The predation-stress hypothesis predicts that the physiology of prey species will be affected by predator activity, causing a phys-

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iological trigger for glucocorticoids to be expressed (Lima 1998). The predation-stress hypothesis has been supported by studies documenting changes in organismal growth and development following exposure to a predation-linked stressor (Schmitz et al. 2004; Peckarsky et al. 2008). In both of these cases, prey species do not always need to experience direct contact with predators to exhibit observable changes in either behavior or physiology (Gallagher et al. 2016a). Indeed, the presence of higher-order predators can affect the distribution of potential prey at across spatial scales (e.g., Gallagher et al. 2016a, 2016b; Jorgensen et al. 2019). Thus, exposure to predators and their cues can exact changes in prey, and these impacts have the potential to result in chronically stressed conditions, which can have fitness-level impacts (Preisser et al. 2005; Creel and Christianson 2008).

The non-consumptive effects from the exposure of potential encounters with predators are an important component of the overall landscape (Gallagher et al. 2017; Palmer et al. 2017), although the influences of predator exposure on prey physiology remain equivocal. Research on gregarious pumpkinseed fish (*Lepomis gibbosus* (Linnaeus, 1758)) has shown that baseline glucocorticoid hormones were not affected among individuals exposed to large avian predators (Osprey, *Pandion haliaetus* (Linnaeus, 1758; Gallagher et al. 2019). However, Hammerschlag et al. (2017) found that Cape fur seal (*Arctocephalus pusillus pusillus* (Schreber, 1775)) fecal glucocorticoid hormone concentrations varied across seal colonies with differential rates of white shark (*Carcharodon carcharias* (Linnaeus, 1758)) predation activity (exposure), with consistently higher levels of cortisol in colonies exposed to unpredictable white shark exposure. These findings suggest that large aquatic vertebrates may experience changes in baseline physiological stress due to signals related to spatial and temporal encounter rates of predators.

Glucocorticoid hormones in vertebrates, such as cortisol, play diverse roles but are most widely known for their role in facilitating homeostatic recovery from exposure to stressful situations and stimuli (Wendelaar Bonga 1997). Fish exhibit some of the most pronounced stress responses of all vertebrates (Barton 2002). Specifically, cortisol mobilizes stored glycogen to be available as glucose for fueling physical movement to aid in the fight or flight response. As a corollary, lactate may be produced as a metabolic by-product under especially challenging situations such as burst swimming to avoid predation from fast-moving marine predators (Barton and Iwama 1991; Vijayan and Moon 1992). This stress axis allows cortisol, glucose, and lactate to serve as reliable, interconnected biomarkers of physiological stress in fishes (Wendelaar Bonga 1997; Sopinka et al. 2016). All three of these biomarkers are circulating and thus can readily be quantified via non-lethal biopsies of whole blood in wild-caught fishes (Cooke et al. 2008; Sopinka et al. 2016; Lawrence et al. 2018). Along with these biomarkers, reflex impairment can be a useful indicator of elevated stress in fishes as well (Davis 2010). The impairment of reflexes in fishes (orientation correction and startle response in our study) is universally indicative of a stressed state regardless of fish age, size, or cause and is highly relevant to predator–prey interactions in that prey with impaired reflexes are presumably more susceptible to predators than unimpaired individuals (Brownscombe et al. 2013).

The striped bass (*Morone saxatilis* (Walbaum, 1792)) is a large, migratory anadromous teleost species, which is also economically important to fisheries throughout their range (mid-Atlantic to New England). Striped bass have a broad, generalist diet composed of a wide-ranging prey base, including schooling fish such as menhaden (*Brevoortia tyrannus* (Latrobe, 1802)) and Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758), as well as economically valuable invertebrates like the American lobster (*Homarus americanus* H. Milne Edwards, 1837; Nelson et al. 2006). Every summer, striped bass migrate to the northernmost part of their range off Cape Cod, Massachusetts, USA, to take advantage of ephemeral

pulses of clupeid prey (Nelson et al. 2006). In their northern range, they also overlap with two much larger predatory species: grey seals (*Halichoerus grypus* (Fabricius, 1791)) and white sharks. Grey seals have made a dramatic rebound in their population since the establishment of the *Marine Mammal Protection Act*, with Cape Cod populations being estimated at 17 060 individuals in 2015 (Moxley et al 2017). Following the rise in seal populations has been a resurgence of white sharks in the region (Skomal et al. 2012), with seasonal populations of hundreds of white sharks most obviously preying on seals (Skomal et al. 2017). Although marine mammals become an increasingly important prey item as white sharks attain larger size classes (e.g., >3–4 m; Casey and Pratt 1985), finfish and demersal fishes remain an important prey item throughout ontogeny (e.g., Bowman et al. 2000), and white sharks have even been observed switching between mammals and fishes in nearby habitats (Bruce et al. 2006). Anecdotal evidence from the recreational angling community off Cape Cod, coupled with opportunistic white shark stomach content analysis, suggest that white sharks may have begun selecting striped bass as a prey item in the area, likely due to their spatial and temporal overlap throughout most of the region.

Here we describe and evaluate the non-consumptive effects of differential exposure to white sharks on the baseline physiology of striped bass in a variety of habitats off southeastern Cape Cod. Specifically, we evaluated differences in baseline physiological profiles (i.e., cortisol, glucose, and lactate) and reflexes in fish captured and sampled in habitats of differential white shark abundance, a proxy for potential exposure. We hypothesized that individuals captured in habitats exposed to resident white sharks would exhibit elevated baseline glucocorticoid profiles and reflex impairments. We discuss these findings as they relate to predator–prey interactions between large marine species along a dynamic coastal ecosystem and the implications for the striped bass fishery.

Materials and methods

Study sites

Fish were captured in offshore habitats containing known, inter-annual populations of resident, hunting white sharks, as well as among inshore areas where white sharks do not hunt and were thus relatively rare or absent (Fig. 1). Sites considered to have "low shark exposure" were contained entirely within Pleasant Bay, the largest contiguous bay on the Cape Cod National Seashore. A total of three sites within Pleasant Bay, Chatham, Massachusetts, USA, were fished (Crow's Pond Inlet, Strong Island Landing, Scatteree Landing) from shore or from a boat and were composed of shallow sandbars and spits that serve as suitable habitats for striped bass and other fish. Additionally, three protected sites along the Nantucket Sound (Stage Harbor Mouth, Barn Hill Road Landing, Bridge Street) were also included in the study. These sites are commonly fished by recreational anglers and are characterized by dramatic tidal changes. Although Pleasant Bay is accessible to the ocean and allows passage of large animals, white sharks do not appear to exhibit residency inside Pleasant Bay sites. Sites that were considered "high shark exposure" and consisted of two offshore regions: offshore on the ocean side of the Cape and Cape Cod Bay (Fig. 1). These open-water sites were characterized by exposed, edge habitats and were close to white shark hunting grounds (approximately <1 km; Skomal et al. 2012, 2017). The designation of our study regions was validated by cross-checking an open-source, online database of white shark sightings in the region (Sharktivity, Atlantic White Shark Conservancy; available from https://www.atlanticwhiteshark.org/sharktivity-map and accessed 3 March 2019). According to the map, our "low exposure" sites showed a total of one white shark sighting in 2017 and one tagged shark detection in 2018, both of which occurred near the coastal brake connecting Cape Cod Bay to the open ocean, whereas there are hundreds of sightings and detections of

Fig. 1. A map of the sampling locations on Cape Cod, Massachusetts, USA. Habitats with a low potential for encounters with white sharks (*Carcharodon carcharias*) (low exposure) are noted with green circles, whereas habitats with high potential for white shark (high exposure) encounters are noted with red circles with plus signs. Sources: Esri, HERE, Garmin, INCREMENT P, © OpenStreetMap contributors, and the GIS user community. Color version online.
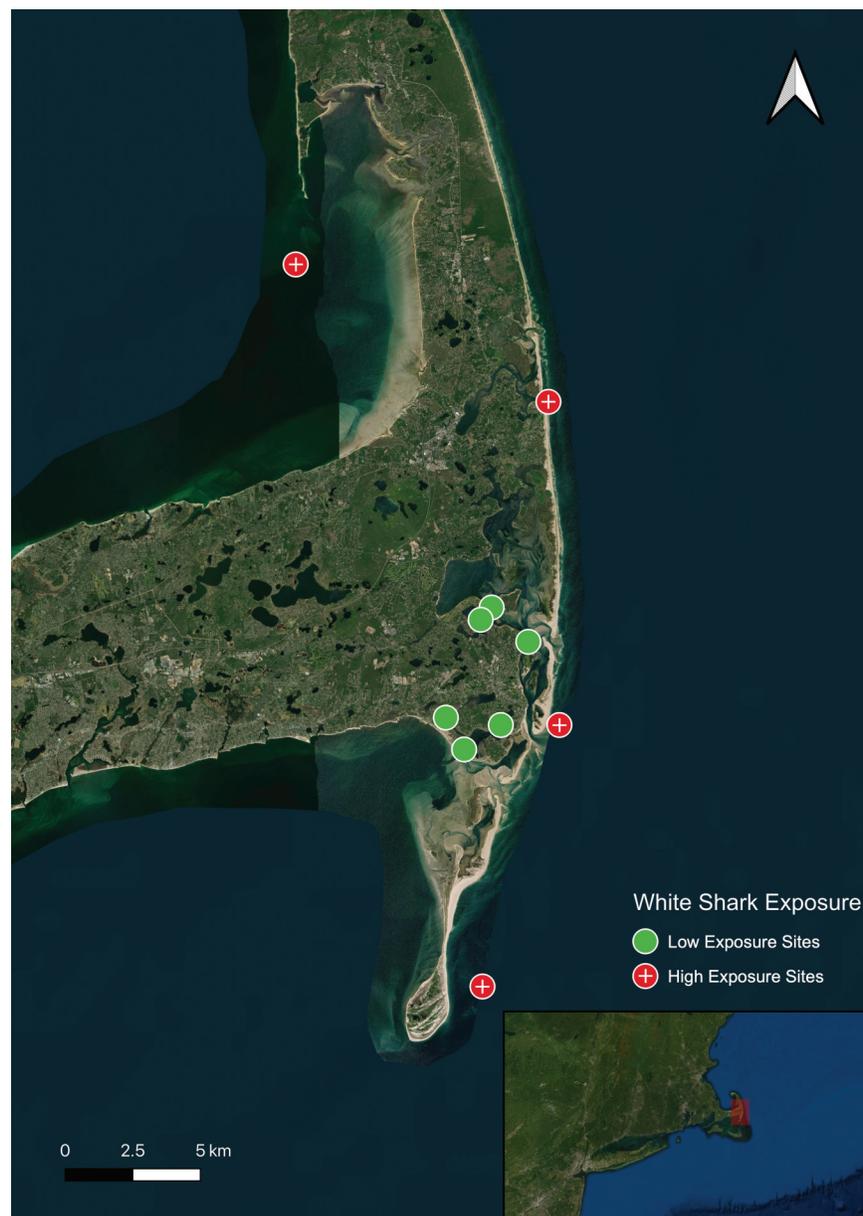
white sharks at the offshore, "high exposure" sites. The Cape Cod Bay site, specifically designated as Billingsgate Shoal, appears to host a subpopulation of resident sharks that are of slightly smaller size (B. Wilson, personal communication).

Fish capture

Fish were caught and sampled through a combination of rod and line fishing from shore using light-weight fishing gear, as well as opportunistic sampling with recreational anglers chartered to capture striped bass. All low shark exposure sites were fished from shore. Fishing methods and gear varied to best optimize chances to capture striped bass, although all methods used rod-and-reel and employed the same overall fishing method for all fish. Fishing strategies included topwater casting using spinning rods, bottom jigging, and trolling. Gear included 30 lb. (13.61 kg) monofilament line for trolling, 30 lb. braided filament for top-

water casting, and 50 lb. (22.68 kg) test wire line for jigging. Lures included weighted jigs, swimming plugs, soft plastic eel baits, and topwaters. Our goal was to obtain a blood sample within 3 min of initial hooking to assess biomarkers indicative of fish physiological state prior to capture. Previous research on a variety of teleost fish species suggests that stress associated with capture and handling alter the biomarkers used in this study beginning at ~4 min (Lawrence et al. 2018). Upon hooking, fish were immediately reeled in and fight times were minimized to be under 2 min. Once landed, we either obtained a blood sample or ran a series of rapid reflex tests; either was done within 1 min of capture per fish. Only jaw-hooked fish were used in this study to control for any potential effects of hooking location (e.g., foul hooking). Given the speed of sampling, the physiological values reported here should be indicative of a baseline state. In support of this, our baseline

Table 1. The total number (N) of striped bass (*Morone saxatilis*) sampled across 2 years in both "high shark exposure" and "low shark exposure" habitat types.

	2017		2018	
	High	Low	High	Low
N	41	126	121	76
Size (cm; mean ± SE)	40.0 ± 0.9	38.2 ± 0.8	47.6 ± 1.0	47.4 ± 0.9
Temperature (°C; mean ± SE)	17.1 ± 0.3	16.0 ± 0.3	18.5 ± 0.2	18.1 ± 0.2

Table 2. The number (N) of striped bass (*Morone saxatilis*) sampled by month across 2 years (2017 and 2018) across both habitat types.

	May	June	July	August	September and October	Total
N (2017)	108	52	7	0	0	167
N (2018)	0	63	40	48	46	197

cortisol values ranged between <0.08 and 54.9 ng/mL, which falls within the range of resting, pre-stress levels found in this species (as well as other species; Barton and Iwama 1991). These values are below post-stress levels, which mostly range from 100 to 300 ng/mL (reviewed in Barton and Iwama 1991).

Blood physiology

We immediately collected ~0.8 mL of whole blood from the caudal vasculature of each fish using 1 mL syringes coated with lithium heparin (to reduce coagulation of samples) and 1.5 inch (38.1 mm), 21 gauge needles. Blood was then immediately analyzed for the secondary stress biomarkers glucose and lactate in situ using an Accuchek glucose meter (Roche Diabetes Care, Inc., USA; Cooke et al. 2008) and a Lactate Plus meter (Nova Biomedical, USA; Hart et al. 2013), respectively. Both of these devices have been validated previously for use on fish and other vertebrates (see Stoot et al. 2014). The remaining whole blood was transported in Vacutainer tubes containing a lithium heparin gel pellet. These were placed on ice during transport to an on-shore laboratory and then spun down ~4 h later using a centrifuge (3000g × 5 min) to isolate plasma. The plasma supernatant was then extracted, frozen, and stored at –20 °C for future analyses of cortisol. Plasma cortisol concentrations were measured using a commercial radioimmunoassay kit (ImmuChem Cortisol Coated Tube RIA Kit; MP Biomedicals, Solon, Ohio, USA) that has been validated for use in teleosts (Gamperl et al. 1994). The vast majority of fish were released immediately after capture. However, a subset of fish sampled opportunistically from recreational anglers were kept by the charter in accordance with fishery-specific size and creel limits.

Reflex assessment

For viable fish that were not blood-sampled, we performed a series of reflex assessments. As above, fish were caught using the same methods, de-hooked, and immediately placed into a customized fish trough padded with foam and filled with fresh seawater. The trough was of sufficient size that fish were able to move and roll as needed. Upon placement into the trough, all fish were tested for their reflex performance (Davis 2010) through two rapid, consecutive tests: (1) equilibrium, where fish were individually placed into the trough upside down and allowed to right themselves, and (2) startle response, where we firmly grasped the caudal peduncle of each fish and recorded their reaction. A startle response was considered present if the individual fish reacted to the grasp with a rapid movement of the caudal fin. Both tests were completed within 2 s. A score of "1" was given when fish responded positively to either test, whereas a "0" was given to any fish that did not react to either test. Each fish was then gently positioned (and righted if necessary) and pinned to one side (to inhibit movement) in the filled water trough, where the fish was fully submerged. We then recorded rates of ventilation as a physical indicator of stress (Barreto and Volpato 2004). Ventilation rates were quantified as the number of opercular beats recorded for a period of 60 s (following a 10 s acclimation period) using a submerged GoPro Hero 4 camera (GoPro, USA) that was fitted to one end of the trough, facing each fish's proximal end. Most fish were released immediately after capture. However, a subset of fish sampled opportunistically from recreational anglers were kept by

the charter in accordance with fishery-specific size and creel limits. All experiments were conducted in accordance with the standards set by the Canadian Council on Animal Care (CCAC) under authorization from Carleton University's Animal Care Committee (AUP B15-12).

Data analysis

To analyze the baseline physiology of individual fish in response to habitat types and environmental variables, we combined univariate analysis of response variables with a multivariate analysis of a fitted model that included the shark exposure level, the month the fish was sampled, the daily temperature of the water measured at each site during fishing, and the fork length of each fish, all as predictors. None of our response variables met the assumptions of normality or heterogeneity. All response variables except ventilation were analyzed using PERMANOVA from the R package *vegan* (Oksanen et al. 2019) to account for bias temporal imbalances in the data. The PERMANOVA assumes that all measurements are taken from independent fish. These results were used as an indicator as to which independent variables could be influential in our models despite the temporal differences in sampling; this was not our primary analysis as PERMANOVA does not account for multiple response variables collected from each animal. Thus, an additional penalized quasi-likelihood (PQL) generalized linear mixed model (GLMM) from the R package MASS (Venables and Ripley 2002) was used, as it accounted for individual variation and the effects of multiple factors on non-normal data (Bolker et al. 2008), as well as the temporal dependence (and thus unbalanced replication) of the fish observations. The effects on each response variable were then further evaluated using an analysis of deviance (type II) of the respective models. The univariate results of the models were then tested using a Holm–Bonferroni method to reduce error from the non-independence of response variables recovered from the same fish (Holm 1979). This resulted in an adjusted p value for use (p'). Ventilation rates were compared between shark exposure levels using a Student's t test and were compared against temperature changes using linear regression. The effects of shark exposure on behavioral tests were analyzed using χ^2 tests. Significance was declared at $p < 0.05$ and all analyses were performed in R Studio (R Core Team 2018).

Results

A total of 364 striped bass were sampled between 2017 and 2018 (Tables 1 and 2). Blood analyses were conducted on 116 fish from high shark exposure environments and 103 from low shark exposure environments, respectively (Tables 2 and 3). Means for each parameter according to month and exposure environment are summarized in Table 3. The PERMANOVA conducted on our physiological biomarkers revealed significant results only for month ($R^2 = 0.1573$, $p = 0.016$) (Table 4). The PQL model for glucose did not reveal a significant effect from shark exposure ($\chi^2 = 1.7562$, $p' = 0.5553$), sampling month ($\chi^2 = 11.2311$, $p' = 0.0939$; Fig. 2a), or fish length ($\chi^2 = 1.3848$, $p' = 0.4786$). However, it did reveal a significant effect on glucose levels from temperature ($\chi^2 = 16.705$, $p' = 0.0001$) (Table 5). The PQL model for lactate revealed significant effects from sampling month ($\chi^2 = 16.3344$, $p' = 0.0179$; Fig. 2b) and fish length ($\chi^2 = 6.4681$, $p' = 0.0329$), but not from temperature ($\chi^2 = 3.0143$, $p' = 0.1651$) or shark exposure ($\chi^2 = 0.0165$, $p' = 1.0000$) (Table 5). The PQL model for cortisol indicated no significant

Table 3. The mean (±SE) measured levels of glucose (mg/dL), lactate (mmol/L), and cortisol (ng/mL) from striped bass (*Morone saxatilis*) in each shark exposure level for the months that sampling occurred.

	May		June		July		August		September and October		Total	
	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low
Glucose (mg/dL)	—	4.18 ± 0.20	4.34 ± 0.17	4.17 ± 0.14	4.48 ± 0.11	3.83 ± 0.15	4.8 ± 0.27	—	3.94 ± 0.27	3.96 ± 0.18	4.47 ± 0.10	4.13 ± 0.11
Lactate (mmol/L)	—	1.41 ± 0.13	1.68 ± 0.19	1.64 ± 0.18	2.77 ± 0.17	—	2.22 ± 0.28	—	1.86 ± 0.34	1.53 ± 0.49	2.14 ± 0.13	1.52 ± 0.12
Cortisol (ng/mL)	—	18.77 ± 3.24	9.33 ± 2.58	7.69 ± 3.35	4.51 ± 1.99	0.21 ± 0.07	5.50 ± 2.84	—	4.57 ± 2.57	2.85 ± 1.05	5.74 ± 0.94	9.40 ± 1.32

Table 4. The permutational multivariate analysis of response variables for physiological tests (glucose, cortisol, and lactate levels) and reflex responses (tail grab and equilibrium test results) of striped bass (*Morone saxatilis*) to shark exposure.

	Source	R^2	df	p
Physiology responses	Shark exposure	0.0329	1	0.073
	Month	0.1573	5	**0.016**
	Temperature	0.0401	1	0.065
	Fork length	0.0077	1	0.542
	Shark exposure × Month	0.0046	1	0.740
Reflex responses	Shark exposure	0.0503	1	**0.009**
	Month	0.0924	5	**0.029**
	Fork length	0.0431	1	**0.013**
	Shark exposure × Month	−0.0071	1	0.974

Note: Values in boldface type indicate statistical significance.

Fig. 2. Monthly means for (*a*) glucose (mg/dL), (*b*) lactate (mmol/L), and (*c*) cortisol (ng/L) for striped bass (*Morone saxatilis*) between each shark exposure level.


effects of month ($\chi^2 = 6.9836$, $p' = 0.2219$; Fig. 2*c*), temperature ($\chi^2 = 2.4056$, $p' = 0.1651$), shark exposure ($\chi^2 = 0.0166$, $p' = 1.0000$), or fish length ($\chi^2 = 0.4823$, $p' = 0.4874$) (Table 5).

Reflex analyses were conducted on 70 separate fish (Fig. 3). The PERMANOVA for reflex tests showed significant effects of shark exposure ($R^2 = 0.0503$, $p < 0.05$), month ($R^2 = 0.0924$, $p < 0.05$), and fork length ($R^2 = 0.0431$, $p < 0.013$) when examining the reflex responses (results from the tail grab test and equilibrium test). These reflex response results also indicated no significant interaction between shark exposure and month ($R^2 = -0.0051$, $p = 0.945$). In high shark exposure sites, approximately 71% and 59% of the fish sampled scored a "1" for the tail grab and body flip tests, respectively. For the low shark exposure, 71% and 89% of fish scored a "1" for the tail grab and body flip tests, respectively. We found that the ability for the fish to right their orientation with the body flip test was significantly affected by shark exposure ($\chi^2 = 7.714$, $p < 0.05$), with fish from low shark exposure sites being able to more right themselves more readily. The tail grab reflex was not affected by shark exposure reflex ($\chi^2 = 6.31 \times 10^{-31}$, $p > 0.05$). Similarly, scores in the body flip were significantly influenced by temperature ($t_{[104]} = 5.43$, $p < 0.001$), whereas tail grab was not ($t_{[106]} = 1.64$, $p = 0.10$). Ventilation rates were recovered from video on 69 of the 70 fish tested in the trough. The mean ventilation rate for fish from high shark exposure was 46.97 ± 2.57 opercular beats/min and 50.17 ± 1.76 opercular beats/min in low shark exposure. Ventilation also decreased significantly with an increase in water temperature, although this relationship is primarily driven by the relationship at low temperatures (Figs. 4A–4D) ($F_{[1,70]} = 12.48$, $R^2 = 0.08$); ventilation was not affected by shark exposure ($t = -1.0327$, $p > 0.05$).

Discussion

We hypothesized that fish sampled in areas of high shark exposure would exhibit elevated baseline glucocorticoid concentrations, as a result of a higher background level of metabolic energy expenditure to cope with predation exposure. However, our results suggest that baseline blood physiology was not different across exposure sites.

Acute exposure to predation has been shown to increase circulating plasma glucocorticoids in teleost fishes (e.g., Barcellos et al.
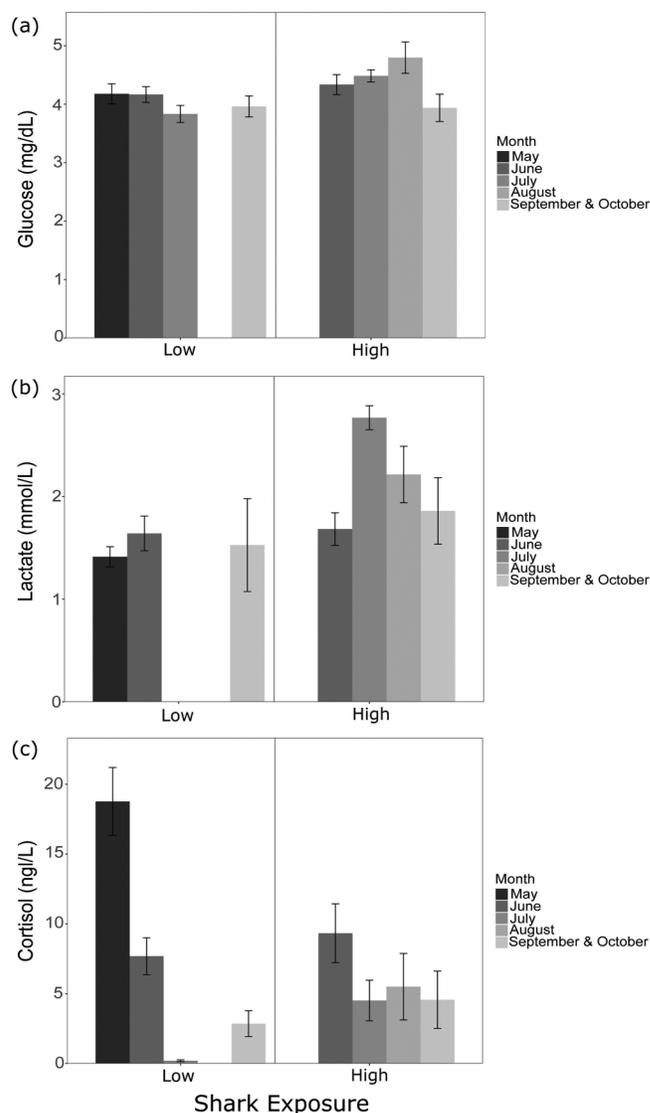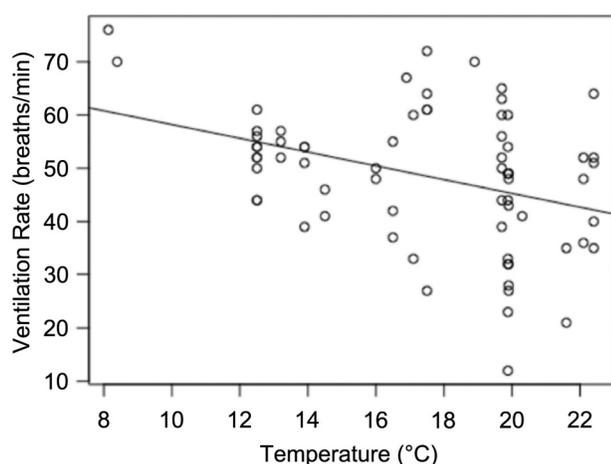
2007; Schreck and Tort 2016). Recent work exposing tethered schoolmaster snapper (*Lutjanus apodus* (Walbaum, 1792)) to a live, swimming shark did elevate individual glucose and lactate concentrations, but had no effect on plasma cortisol concentrations (Lawrence et al. 2018). The lack of an elevated baseline stress profile among bass captured from high shark exposure sites in the present study is consistent with the notion that chronic physiological stress is unlikely in wild prey (Boonstra 2013), although we recognize that we did not control or measure actual exposure rates. Although studies on the predation-stress hypothesis have

Table 5. The type II analysis of variance on penalized quasi-likelihood models fitted to each physiological parameter.

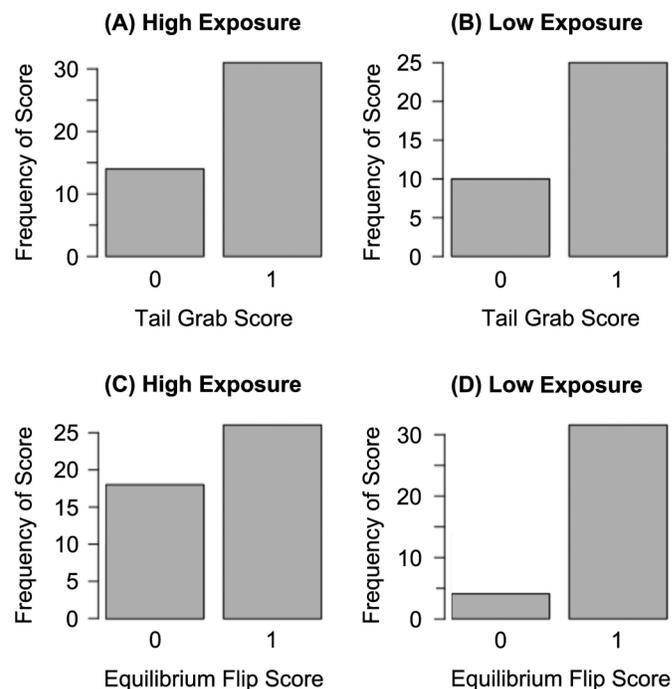|	N	Source	χ^2	df	p	Adjusted p (p')
Glucose	165	Shark exposure	1.7562	1	0.1851	0.5553
		Month	11.2311	5	0.0469	0.0939
		Temperature	16.705	1	0.0000437	**0.0001**
		Fork length	1.3848	1	0.2393	0.4786
Lactate	123	Shark exposure	0.0165	1	0.8978	1.0000
		Month	16.3344	5	0.0059	**0.0179**
		Temperature	3.0143	1	0.0825	0.1651
		Fork length	6.4681	1	0.0109	**0.0329**
Cortisol	102	Shark exposure	0.0166	1	0.8974	1.0000
		Month	6.9836	5	0.2219	0.2219
		Temperature	2.4056	1	0.1209	0.1651
		Fork length	0.4823	1	0.4874	0.4874

Note: Values in boldface type indicate statistical significance.

Fig. 3. The plotted regression of ventilation rates of striped bass (*Morone saxatilis*) in response to water temperature.

Fig. 4. The comparative frequencies for each of the two reflex tests with binary responses for striped bass (*Morone saxatilis*): (A) the tail grab test in habitats with a high shark exposure in which test scores of "1" indicated a response to a physical grabbing of the fish caudal fin by the analyst and a "0" indicated no response; (B) the tail grab test in habitats with a low shark exposure; (C) the equilibrium test in high shark exposure habitats in which test scores of "1" indicated the fish is able to right its orientation when placed upside down in the experimental trough and a "0" indicated the fish remained upside down; (D) the equilibrium test in habitats with low shark exposure.

yielded equivocal results across a variety of ecosystems and species (Peckarsky et al. 2008; Anson et al. 2013; Hing et al 2017), a more recent hypothesis, termed the "control of risk" hypothesis (Creel 2018), may better explain these emerging patterns.

The control of risk hypothesis suggests that predictable sources of predation exposure should not incur stress-related costs, but instead food-related costs (i.e., changes in foraging opportunities or diet; Creel 2018). Our study design yielded sampling sites that were characterized by a regional, stark difference in exposure to predators: our inshore bays experience little to no shark exposure, whereas our offshore sites contained actively patrolling white sharks throughout the warmer months of the study (late June – October; Skomal et al. 2017). Both of these habitat types could thus be considered relatively "predictable" in terms of predation exposure. This theory is also corroborated by similar patterns of predictable sources of potential predation exposure having no effects on prey baseline glucocorticoid concentrations in both freshwater and marine prey (Hammerschlag et al. 2017; Gallagher et al. 2019). Predictable sources of predation exposure may, instead, drive behavioral modifications in prey. Working in Shark Bay, Australia, Wirsing and Heithaus (2012) found that dugongs (*Dugong dugon* (Müller, 1776)) altered their behavior in the presence of tiger sharks (*Galeocerdo cuvier* (Péron and Lesueur, 1822)). The authors described the behavior as foraging (low vigilance of predators), resting (low predator awareness), and traveling (high vigilance towards predators). Dugongs in areas with higher regular presence of tiger sharks exhibited less foraging and resting bouts, limiting their time to feed; these impacts were fear-driven and behavioral modifications were detected. In our

study, we did not detect any stress-related impacts in fish caught in areas with higher potential exposure to white sharks. We did observe a slight effect of shark exposure on fish reflexes, although only one behavior (equilibrium) was affected and could have been instead related to individual-level tank effects on fish mobility.

Temperature is a major controlling factor on fish life histories (Brander 2007; Jonsson and Jonsson 2009; Pankhurst and Munday 2011), and we found that the striped bass baseline glucose response appeared to be higher in the months before white sharks arrive in large numbers (Skomal et al. 2017). This is potentially explained by colder water temperatures and potential food stress (Fig. 2a). Cortisol is known to regulate gluconeogenic pathways (Vijayan et al. 2003), and as such, the two variables are often correlated. Moreover, previous work has shown that sea surface temperature affected cortisol concentrations in juvenile striped bass (Davis and Parker 1990). Our temperature effect on glucose may also suggest mediation via catecholamine hormones, rather than cortisol. Additionally, seasonality affected lactate levels in our fish, which may be explained by differences in migratory behavior during a potentially challenging life-history phase for an anadromous fish species (Wendelaar Bonga 1997; Midwood et al. 2016), such as striped bass (Chapoton and Sykes 1961; Kernehan et al. 1981). Taken together, these results suggest that unpredictable temporal shifts in temperature and life history may have greater effects on striped bass physiology than predictable exposure to large predators.

There are a few potential alternative explanations for the observed lack of a difference in the stress response. First, there may have been infrequent encounter rates with sharks in our offshore

high shark exposure areas. We recognize that we did not explicitly quantify white shark presence or hunting rates in the present study; indeed, this was not an objective of our study. However, long-term monitoring of white shark residency in our study area appears to support the notion that white sharks are resident and actively foraging at virtually all offshore sites in the outer Cape, primarily due to the high abundance of seals and seal haul-out sites (Skomal et al. 2012, 2017). Unsurprisingly, sharks were detected and reported commonly at the offshore sites during both sampling years (Sharktivity, Atlantic White Shark Conservancy; available from https://www.atlanticwhiteshark.org/sharktivity-map and accessed 3 March 2019), whereas only two were reported in Pleasant Bay during our study period, both of which were at the mouth of the harbor. Certainly, these crowd-sourced records are not absolute, but they appear to provide a coarse proxy for abundance and thus exposure. Nevertheless, we realize that our categorization has assumptions without hard quantitative data on shark residency. Previous studies have categorized white shark predation risk to prey using qualitative approaches (e.g., De Vos et al. 2015), and these types of designations have been shown to match with shark movements obtained from tracking data (Hammerschlag et al. 2017). As noted elsewhere, the relative importance of striped bass as a prey item for white sharks has not been quantified, and they may not be naturally heavily depredated or consumed. Yet, there is increasing anecdotal evidence for the white sharks eating line-caught striped bass in the study area year over year, and our team has also observed white sharks naturally breaching on (and presumably consuming) wild striped bass (C.W. Benson, B.D. Shea, and A.J. Gallagher, direct observation). We also realize that because of the free-ranging nature of our study fish, we could not control striped bass daily movements, which can be up to 2–3 km/ day (Graves et al. 2009). Recent work using acoustic tagging and monitoring of striped bass near our study area (southeast coast of Massachusetts) demonstrated that tagged fish showed restricted spatial movements during summer months (June–September; Hollema et al. 2017). Moreover, striped bass in the same study showed relatively small activity spaces (0–8 km²) throughout the span of our sampling period (June – mid-September), and fish did not appear to move in and out of the embayment where they were tagged (Hollema et al. 2017). These data suggest that our fish likely did not move in-between sampling regions and that these fish exhibit seasonal residency across small spatial scales in our study area. Nevertheless, our approach yielded a "snapshot" of the physiological status of sampled fish at the time of capture, which is inclusive of the biotic and abiotic environment and landscape (Gallagher et al. 2017). Although this study attempted to focus on the effects of large sharks as predators, seals and humans present additional predation exposure that could have influenced striped bass during our study. We avoided fishing in areas where there were recreational anglers present, and we monitored for swimming seals and avoided sampling on or near beaches where grey seals were hauled out.

In summary, it appears that areas of high exposure to large sharks did not induce stress-mediated changes in striped bass. Considerations of shark predator effects on striped bass in this system should focus more on behavioral displacement and disruptions in their foraging. The striped bass fishery holds regional socio-economic importance (Richards and Rago 1999), and future studies could consider how recovering populations of apex predators in the region could alter the distribution and condition of this potential prey item. Lastly, this study adds empirical support to the development and further testing of the control of risk hypothesis (Creel 2018), underscoring the notion that context is important when evaluating the impacts of predation exposure in the wild.

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