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Effects of short-term capture on the physiology of white sharks *Carcharodon carcharias*: amino acids and fatty acids

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ABSTRACT: Empirical evaluations of how overexploited marine fishes respond to capture stress (physiologically and behaviourally) have become increasingly important for informed fisheries management. These types of studies are, however, lacking for many protected species. Here, we conducted a novel study on the physiology of juvenile white sharks *Carcharodon carcharias* (139–325 cm fork length), a globally protected and ecologically important predator, in response to a standard fishery interaction using shark-management-alert-in-real-time (SMART) drumlines as part of a bather protection program. Specifically, we assessed the influence of short-term capture duration (average: ~30 min; range: 10–75 min) and other biological (size) and environmental (temperature) variables on blood plasma amino acids and fatty acids, which play essential roles as energy substrates as well as in maintaining physiological functions. None of the assessed amino acids or fatty acids were affected by capture duration, but some were influenced by shark size and water temperature. Our results support the notion that white shark physiology is robust to capture at short capture durations, which has important implications for the fate of released individuals.

KEY WORDS: Amino acid · Capture · Fatty acid · Fishing · Shark · Stress · Biochemistry · Ecophysiology · White shark

1. INTRODUCTION

Understanding the effects of capture on elasmobranchs is important for accurately evaluating the impacts of fisheries interactions, especially for oceanic species which are vulnerable to bycatch and are at high extinction risk (Gallagher et al. 2012, Dulvy et al. 2014). Previous work has demonstrated a range of species- and gear-specific responses to fisheries capture, ranging from physiological disruption to post-release mortality, underscoring the complexity of this issue (e.g. Mandelman & Skomal 2009, Marshall et al. 2012, Butcher et al. 2015, Dapp et al. 2016b). In recent years, studies examining the physiological responses and post-capture behaviour of elasmobranchs, particularly sharks, have expanded from a common set of commercially relevant species subjected to longline fishing (Dapp et al. 2016a) to work on coastal species under recreational and fishery-independent contexts (Danylchuk et al. 2014, Gallagher et al. 2017a, Whitney et al. 2017, Jerome et al. 2018), coral reef-dwelling species (Dapp et al. 2017), polar settings (Barkley et al. 2017), and even the deep sea (Talwar et al. 2017). In addition to advancing our understanding of the comparative physiology of elasmobranchs, this research provides

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managers, fishers, and the general public with relevant information to address targeted conservation problems, should they occur.

Despite growth in this field, certain species of large elasmobranchs which are either critically threatened, globally protected, or tightly regulated remain overlooked. Highly threatened species such as whale sharks *Rhincodon typus* and manta rays *Mobula* spp., which are listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and are incidentally captured in nets, have not been evaluated for their capture stress. The smalltooth sawfish *Pristis pectinata*, which was the world's first elasmobranch species to be listed on the US Endangered Species list in 2003, was only recently evaluated for its physiological response to capture (Prohaska et al. 2018), while a recent study assessed the fate of pygmy devilray, *Mobula kuhlii* cf. *eregoodootenkee* (listed on CITES Appendix II in 2017) caught in the NSW (Australia) shark control program (Broadhurst & Cullis 2019). These data can help the conservation community understand the relative contribution that capture-induced stress and ensuing post-release mortality could have on threatened species when caught and released. Such information is valuable when undertaking ecosystem-based assessments of fisheries catching threatened species as bycatch and during conservation assessments (e.g. IUCN Red List). For example, we now know that capture-induced mortality likely played a role in the population declines of threatened hammerhead shark species *Sphyrna* spp. (Gallagher et al. 2014a,b, Gulak et al. 2015). This information can also help researchers understand how their procedures may affect threatened species.

White sharks *Carcharodon carcharias* are the largest species of predatory shark. They are globally distributed, with hotspots in South Africa, Australia, New Zealand, Mexico, and the United States (Jorgensen et al. 2010, Kock et al. 2013, Skomal et al. 2017, Nazimi et al. 2018). They generate significant public attention and study from researchers (Huveneers et al. 2018), evidenced by a study bias in many areas (Hammerschlag et al. 2011, Ducatez 2019), and they are a primary target of a lucrative global tourism industry (Huveneers et al. 2017, Gallagher & Huveneers 2018). White sharks are protected throughout all of these hotspots and are listed on Appendix II of CITES. However, historical concerns about beach and bather safety in locations such as Australia and South Africa have prompted controversial shark exclusion and removal techniques resulting in decades of white shark captures (Cliff et al. 1989, Cliff & Dudley 1992, Reid et al. 2011). In addition, incidental catches of white sharks still occur in commercial and recreational fisheries (Malcolm et al. 2001, Lowe et al. 2012, Dicken & Booth 2013, Lyons et al. 2013, Curtis et al. 2014). Thus, despite receiving near-global protection from virtually all types of fisheries, the number of white sharks being captured each year may not be trivial — inclusive of fishery-independent research operations. To date, only a single study has evaluated white shark response to capture, using basic blood bio-chemical markers. This study concluded that short-term capture did not affect most of the standard variables indicative of a stress response (Tate et al. 2019). However, it remains unknown whether this conclusion holds true across a broader suite of physiological variables that may signal the transport of energy to tissues. This would provide greater resolution to the paucity of information on white shark responses to fisheries interactions.

In recent years, researchers have begun evaluating novel parameters as potential biomarkers of stress in elasmobranch fishes (e.g. Van Rijn & Reina 2010, Guida et al. 2016a). Biochemical markers such as amino acids and fatty acids (FAs) could give novel insights into the individual-level mechanisms that govern how organisms respond to stress and environmental variation. Under stress, organisms can have additional metabolite requirements due to higher energy demands or secondary stress responses, such as the synthesis of stress-related proteins or hormones. In a number of fish species, repeated acute handling has been shown to affect both the mobilization of amino acids (Aragão et al. 2008, Costas et al. 2011) and plasma free FAs (Mazeaud et al. 1977). Other environmental stressors, such as temperature (e.g. cold acclimation), have also been reported to alter plasma lipid and amino acid concentrations (Hsieh et al. 2003, Ma et al. 2015). Elasmobranch fishes have an unusual lipid metabolism whereby FAs are largely stored in their large livers, which is where most β-oxidation occurs (Ballantyne 1997). Therefore, products such as ketone bodies may be more heavily relied upon as a source of energy than FAs (Gallagher et al. 2017b). In dogfish sharks (Squalidae), plasma concentrations of amino acids and non-esterified FAs have been shown to change in response to feeding and fasting (Wood et al. 2010). Certain FAs (i.e. saturated fatty acids [SFAs] and monounsaturated fatty acids [MUFAs]) are more metabolically active than others (i.e. polyunsaturated fatty acids [PUFAs]; Tocher 2003), and as such we would anticipate a change in the FA profiles associated with capture stress. A few studies

have explored changes in specific FAs with teleost migrations (Bell et al. 1986, Osako et al. 2006), temperature (Gladyshev et al. 2018), and energy expenditure (exercise in Li et al. 2016; swimming velocity in Gladyshev et al. 2018). Thus, it appears that amino acids and FAs could serve as informative indicators of the secondary stress response in sharks. While the capture of sharks and rays has been shown to influence blood glucose, lactate, and pH (Moyes et al. 2006, Brooks et al. 2012, Heard et al. 2014, Jerome et al. 2018), no studies have examined if capture influences amino acid and FA metabolism in sharks despite the growing popularity of these biomarkers in chondrichthyan ecology (Munroe et al. 2018, Meyer et al. 2019), leaving a gap in our understanding of how these analytes may be influenced by external stressors.

Here, we conducted an empirical evaluation of the physiological response of white sharks to capture on shark management alert in real-time (SMART) drumlines, focusing on individuals opportunistically sampled from a shark management program off New South Wales (NSW), Australia. Our study had 2 primary objectives: (1) evaluate and describe an amino acid and FA profile from white shark blood plasma; and (2) evaluate whether these parameters were affected by short-term fisheries capture, and by a set of additional biotic and abiotic variables. We discuss our findings in relation to shark metabolic strategies, provide comparisons to results obtained from other species of large sharks, and make recommendations as to how fisheries interactions might affect this threatened species.

2. MATERIALS AND METHODS

2.1. Fishing gear and animal capture

White sharks were captured, sampled, and released over a 13 mo period between July 2016 and August 2017 onboard research vessels off the mid-north and northern NSW coast, Australia. Sampling was opportunistic, capitalizing on the capture of white sharks on SMART drumlines as a part of a broader research tagging and tracking program associated with a jurisdictional Shark Management Strategy in NSW.

SMART drumlines were configured following Tate et al. (2019). Various semi-barbed and barbed hooks were used as part of other ongoing research with SMART drumlines, but all were baited with ~0.75–1 kg of sea mullet *Mugil cephalus*. A 2.0 m (2 mm ∅) monofilament 'trigger line' was attached between the elasticized cord and the SMART buoy. When an animal bit the hook, the trigger line separated the magnet in the SMART buoy and a signal was transmitted via satellite, alerting researchers via SMS, telephone call, and email. On each fishing day, SMART drumlines were deployed ~500 m from shore in ~4–15 m water depth during daylight hours. Once an alert was received, thus beginning the capture period used to approximate 'hook time', the research vessel would travel to the SMART drumline and monitor the gear and sharks' activity. If multiple alerts came through, the first shark to trigger the system was attended to first. Each shark was approached once it maintained a normal upright swimming position without fighting the 'drumline' buoy. Once the SMART drumline was retrieved, the trace was attached to a longer rope so the shark could be secured to the side of the vessel with that and an additional (1) cross-pectoral fin and (2) tail rope which contained a PVC sleeve to minimize the chance of damaging the shark. Shark sex and size (fork length [FL], to the nearest cm) was recorded.

2.2. Sample extraction and laboratory analyses

Whole blood (~5–8 ml) was sampled via a non-lethal caudal venipuncture biopsy using a 90 mm, 18 gauge needle and a 10 ml syringe according to Butcher et al. (2015), within 1 min of being brought alongside the boat. The timing of the total capture event ended once the blood sample was taken, thereby creating a continuous variable for testing the effects of capture on blood physiology. The blood was transferred to an 8 ml plasma separator tube containing lithium heparin (BD Vacutainer) and was stored on ice temporarily before being centrifuged at 5000 rpm for 4 min. Plasma samples were then separated into three 2 ml vials and immediately frozen at −18°C in the field before being transferred to a −80°C freezer in the laboratory.

Amino acids profiles were quantified by IDEXX Laboratories (Brisbane, Australia) within 7 d to prevent blood chemistry alterations (Barton et al. 2002). Amino acids were divided into 4 groups: (1) ketone body β-hydroxybutyrate; (2) branched-chain essential amino acids: isoleucine, leucine, and valine; (3) other essential amino acids: histidine, lysine, phenylalanine, and threonine; and (4) non-essential amino acids: alanine, aspartic acid, glutamine, glycine, proline, serine, and tyrosine.

Lipids and FAs were extracted from plasma according to the methods detailed by Bligh & Dyer (1959) and Meyer et al. (2017), respectively. This included using various solvent solutions to separate lipids from proteins and carbohydrates (of dichloromethane, methanolde-ionized water) and then to separate individual FAs from the glycerol backbones of polar and non-polar lipids (with methanol, hexane, and hydrochloric acid). Total lipid content was gravimetrically measured and individual FAs were identified and quantified through gas chromatographic analysis using an Agilent Technologies 6890N gas chromatograph fitted with an HP-5 cross-linked methyl silicone fused silica capillary column (50 × 0.32 mm i.d.), a flame ionization detector (FID), a splitless injector, and an Agilent Technologies 7683 Series auto-sampler. Selected samples were further analyzed by GC-MS on a Finnigan Thermoquest system fitted with an on-column injector for peak verification. FA results are expressed as a proportion of the total identified compounds. Only FAs over 0.5% (25 out of 61) were included in statistical analyses.

2.3. Data collected and statistical analysis

We tested the influence of capture duration, shark sex and size, and water temperature on white shark plasma FA and amino acid profiles, using multivariate statistical analyses undertaken in PRIMER7 +PERMANOVA (Clarke & Gorley 2015). Permutational multivariate analysis of variance (PERMANOVA) with Monte Carlo simulations, denoted as p(MC), were run on Bray-Curtis similarity matrices calculated from the square-root-transformed profile data to determine if factors significantly influenced the overall FA and amino acid profiles. Continuous factors (capture duration, shark length, and water temperature) were classified as covariates, and sex as a random categorical variable in the PERMANOVA model containing all 4 factors. Significance was declared at $p(MC) < 0.05$. A canonical analysis of principal coordinates (CAP) (Anderson & ter Braak 2003) of the Bray-Curtis similarity matrix was also run to visualize trends in FA and amino acid profiles across capture time and FL.

We then assessed if individual plasma amino acids and FAs were influenced by capture duration, while accounting for biological (shark sex and size) and environmental (water temperature) variables using a generalized linear model (GLM). We determined the most appropriate statistical family and error distribution (family = gamma; link = log) by examining the distribution of the response variable and visually inspecting the residuals for the saturated models. Statistical significance was declared at $p < 0.05$; these analyses were performed in RStudio (R Core Team 2016).

3. RESULTS

A total of 52 white sharks (47 individuals, 5 recaptures) were sampled for blood during the study period (Table 1). This pool of sharks included 33 females (mean ± SD: 229 ± 45 cm FL) and 19 males (228 ± 45 cm FL). Hook times ranged between 10 and 75 min (29.8 ± 15.2 min; Table 1). The elapsed duration between the time a shark was secured at the boat to completion of blood collection was 3.0 ± 2.0 min (1–13 min). One male and 4 females were recaptured and resampled, with time between capture events being 48, 60, 272, 273, and 244 d, respectively (Table 1).

3.1. Amino acids

A summary of the means and ranges for the 15 amino acids assessed here are presented in Table 2. White shark plasma amino acid profiles were not affected by capture duration (p[MC] = 0.593; Fig. 1A), sex (p[MC] = 0.306) or water temperature (p[MC] = 0.788), but were influenced by shark length (p[MC] = 0.043; Fig. 1B). Modelling of individual amino acids revealed none were affected by capture duration (Table 3), nor were any of the essential amino acids (branched-chain or other) affected by the biological or environmental factors. The only factor that affected several amino acids was shark length (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n040p297_supp.pdf). Specifically, ketone bodies were negatively influenced by shark length ($t_{1,52} = -2.26$, $p < 0.05$; Table 3, Fig. S1). Non-essential amino acids were also influenced by shark length with alanine positively influenced ($t_{1,52} = 2.71$, $p < 0.01$; Table 3, Fig. S1), whereas aspartic acid ($t_{1,52} = 2.06$, $p < 0.05$; Table 3, Fig. S1) and glycine ($t_{1,52} = -2.68$, $p < 0.05$; Table 3, Fig. S1) were negatively affected. Tyrosine was the only amino acid influenced (positively) by water temperature ($t_{1,52} = 2.31$, $p < 0.05$; Table 3, Fig. S1).

3.2. Fatty acids

White shark plasma FA profiles were dominated by PUFAs (40.79 ± 1.45), contributing 1.5 and 1.6 times

Table 1. Summary data of all captured white sharks caught on shark-management-alert-in-real-time (SMART) drumlines from the present study. FA: fatty acid

Date (dd/mm/yyyy)	Location	Sex	Fork length (cm)	Water temp. (°C)	Hook time (min)	FA analysis
28/11/2016	Ballina	F	252	19.4	36	Yes
21/07/2016	Tuncurry	F	192	19	23	Yes
21/07/2016	Tuncurry	M	235	19.2	13	Yes
21/07/2016	Tuncurry	M	179	19.4	19	Yes
22/07/2016	Tuncurry	F	255	19.4	32	Yes
27/07/2016	Crowdy Head	F	201	19	24	Yes
01/08/2016	Coffs Harbour	M	259	19.2	26	Yes
01/08/2016	Coffs Harbour	F	190	19.4	21	No
02/08/2016	Coffs Harbour	M	234	19.3	39	Yes
09/08/2016	Ballina	F	193	20.6	30	No
09/08/2016	Ballina	F	277	20.8	23	Yes
09/08/2016	Ballina	F	223	20.9	27	Yes
06/09/2016	Tuncurry	F	197	18.7	23	No
07/09/2016	Tuncurry	F	230	18.5	25	Yes
07/09/2016	Tuncurry	M	192	18.8	19	Yes
07/09/2016	Tuncurry	M	226	18.9	27	Yes
07/09/2016	Tuncurry	F	139	18.9	16	Yes
08/09/2016	Tuncurry	M	174	19.2	28	Yes
27/09/2016	Ballina	M	252	19.3	24	Yes
28/09/2016	Ballina	M	160	19.3	31	Yes
01/10/2016	Ballina	M	187	18.9	21	Yes
02/10/2016	Ballina	M	240	19.1	18	Yes
02/10/2016	Ballina	M	268	19	75	Yes
02/10/2016	Ballina	M	218	19.2	29	Yes
04/10/2016	Ballina	F	300	18.4	38	Yes
04/10/2016	Ballina	F	202	18.3	10	Yes
06/10/2016	Ballina	M	257	19.4	25	Yes
08/10/2016	Ballina	F	222	19.1	27	Yes
08/10/2016	Ballina	F	192	19.8	28	No
08/10/2016	Ballina	F	187	19.6	22	Yes
15/10/2016	Ballina	F	276	22.3	22	Yes
18/10/2016	Ballina	F	206	21.2	27	Yes
22/11/2016	Ballina	F	255	20.7	53	Yes
29/11/2016	Ballina	F	300	19.5	23	Yes
29/11/2016	Ballina	F	325	19.7	39	Yes
03/12/2016	Tuncurry	F	224	22.3	25	Yes
08/12/2016	Ballina	M	187	20	54	No
10/12/2016	Ballina	M	245	20.4	20	Yes
10/12/2016	Evans Head	F	212	21.3	28	Yes
10/12/2016	Evans Head	F	232	21.3	71	Yes
30/05/2017	Coffs Harbour	M	240	20.8	20	No
06/06/2017	Tuncurry	F	220	19.9	28	No
06/06/2017	Tuncurry	F	290	20	71	No
06/06/2017	Tuncurry	F	251	20.1	20	No
06/06/2017	Tuncurry	F	223	19.6	44	No
06/06/2017	Tuncurry	F	245	20.1	13	No
07/06/2017	Tuncurry	M	221	19.9	16	No

the SFAs (27.18 ± 0.64) and MUFAs (25.12 ± 1.48) to the overall profiles, respectively. PUFA 22:6ω3 (17.47 ± 0.91) was the greatest single FA contributor, followed by SFA 16:0 (14.85 ± 0.38) and MUFA 18:1ω9 (12.14 ± 0.98). PUFAs 20:4ω6 (9.35 ± 0.53) and 20:5ω3 (6.19 ± 0.31) and SFA 18:0 (7.99 ± 0.35) were also substantial contributors, with values >5% (Table 4).

The plasma FA profiles were driven by biological factors, primarily shark length (p[MC] = 0.001; Fig. 2B) and sex (p[MC] = 0.01). Capture duration and water temperature did not measurably affect the FA profiles (p[MC] = 0.989 and 0.127, respectively; Fig. 2). Modelling of individual FAs revealed that none were affected by capture duration, while sev-

Table 2. Plasma amino acid profiles (mmol l^{-1}) from white sharks caught on SMART drumlines in the present study

Amino acid	Mean ± SE	Range
β-hydroxybutyrate	0.32 ± 0.03	0.1–1
Branched-chain essential		
Isoleucine	177.8 ± 8.47	99–368
Leucine	301.8 ± 13.75	158–596
Valine	375.9 ± 17.16	202–809
Other essential		
Histidine	65.34 ± 2.90	33–139
Lysine	407.6 ± 26.18	182–1169
Phenylanaline	83.87 ± 3.81	41–164
Threonine	208.1 ± 12.54	59–431
Non-essential		
Alanine	1004.0 ± 59.45	442–2174
Aspartic acid	40.89 ± 5.17	4–165
Glutamine	260.90 ± 12.65	119–541
Glycine	111.1 ± 10.15	36–435
Proline	111.8 ± 8.12	28–262
Serine	361.0 ± 19.54	189–834
Tyrosine	114.1 ± 4.31	63–211

eral were influenced by abiotic and biotic variables (Table 5, Fig. S2).

4. DISCUSSION

Fish exhibit some of the most pronounced stress responses of all vertebrates (Barton et al. 2002). The extent or magnitude of the acute stress response in fishes can provide essential information on their physiological sensitivity to fisheries interactions while providing insights into the ecological and evolutionary drivers of animal performance and metabolism (Calow & Forbes 1998, Gallagher et al. 2017a). Our results support the notion that white shark physiology is minimally affected by short-term (i.e. <1.5 h) capture durations on SMART drumlines. This conclusion is corroborated by recent work evaluating blood biochemistry and gas tensions under similar contexts (Tate et al. 2019).

Interestingly, none of the amino acids or FAs were affected by capture duration in the present study (Tables 3 & 5). This result is in contrast to work on teleost species, which have demonstrated strong effects of stress on amino acid and FA metabolism (e.g. Aragão et al. 2008, Li et al. 2016, Gladyshev et al. 2018). Exhaustive exercise has been shown to increase and mobilize amino acids into the plasma of various freshwater teleost species, which is thought to be related to the release of glucocorticoid hormones in the primary stress response (Milligan 1997, Vijayan et al. 1997). Similarly, stress-linked hormones have been shown to mobilize FAs which can serve as energy substrates in fish (Wendelaar-Bonga 1997). Branched-chain essential amino acids, which were evaluated in the present study, are important energy substrates in fish, particularly under anaerobic conditions (Li et al. 2009). Ketones are thought to serve as a primary source of metabolic fuel in sharks, largely due to fact that β-oxidation of FAs is confined to the liver (due to the lack of FA bind proteins in the plasma), whereby FAs are oxidized into ketone bodies and transported for energy (Metcalf & Gemmell 2005). However, it is unknown whether amino acids and FAs in elasmobranchs (sharks and rays) are influenced by capture and stress similarly to teleosts. Recent work evaluating the effects of air exposure on Atlantic stingrays *Hypanus sabinus* did not find an effect on ketone bodies, whereas other metrics such

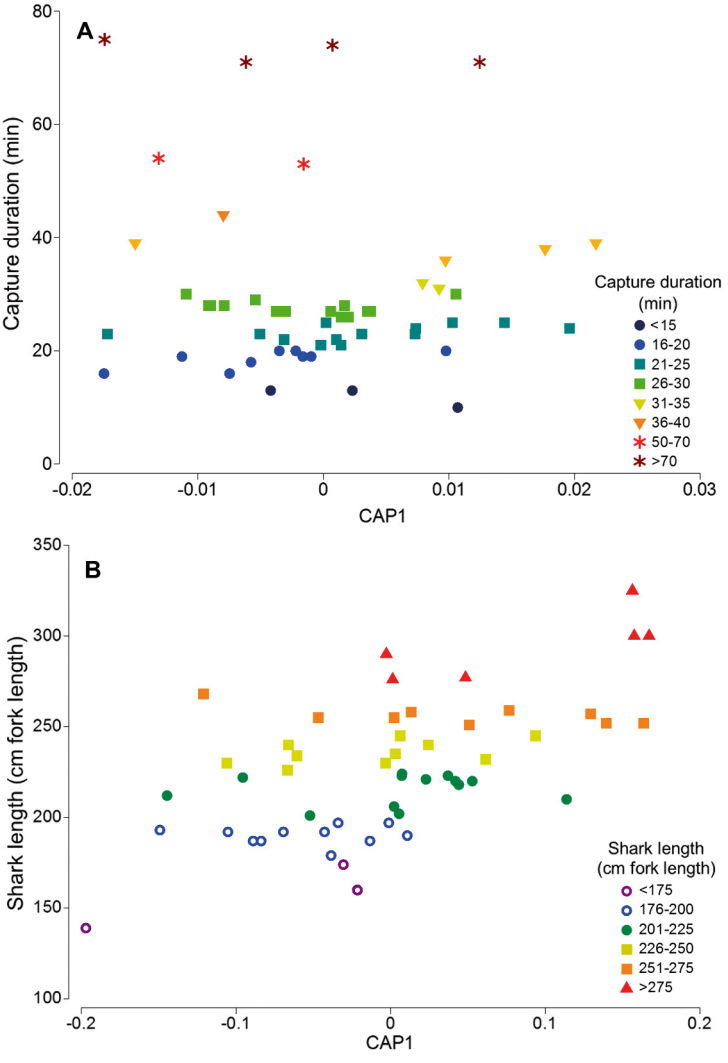

Fig. 1. Canonical analysis of principal coordinates (CAP) of white shark blood plasma amino acid profiles against (A) capture duration and (B) shark length classed as covariates

Table 3. Generalized linear model results testing the effects of biological and operational variables on each of the 15 plasma amino acids from white sharks caught on SMART drumlines in the present study. Significant p-values (<0.05) in **bold**. Est: estimate; Inter: intercept; Time: hook time; FL: fork length; Temp: temperature

Response	Parameter	Est	SE	*t*	p
β-hydroxybutyrate	Inter	1.06	1.94	0.55	0.587
	Time	0.00	0.01	0.01	0.994
	Sex	−0.07	0.18	−0.38	0.704
	FL	−0.01	0.00	−2.59	**0.013**
	Temp	−0.04	0.09	−0.41	0.684
Isoleucine	Inter	5.15	1.23	4.19	0.000
	Time	0.00	0.00	−0.50	0.619
	Sex	0.01	0.11	0.11	0.913
	FL	0.00	0.00	0.65	0.519
	Temp	−0.01	0.60	−0.13	0.890
Leucine	Inter	6.10	1.19	5.14	0.000
	Time	0.00	0.00	−0.50	0.617
	Sex	−0.01	0.11	−0.08	0.935
	FL	0.00	0.00	0.54	0.595
	Temp	−0.02	0.06	−0.43	0.668
Valine	Inter	6.05	1.18	5.11	0.000
	Time	0.00	0.00	−0.47	0.638
	Sex	−0.01	0.11	−0.08	0.940
	FL	0.00	0.00	1.32	0.193
	Temp	−0.02	0.06	−0.43	0.669
Histidine	Inter	3.07	1.14	2.68	0.104
	Time	0.00	0.00	0.55	0.589
	Sex	0.02	0.11	0.16	0.878
	FL	0.00	0.00	0.52	0.609
	Temp	0.04	0.06	0.80	0.431
Lysine	Inter	4.73	1.69	2.87	0.006
	Time	0.01	0.01	0.12	0.907
	Sex	−0.02	0.15	−0.13	0.897
	FL	0.00	0.00	0.24	0.814
	Temp	0.06	0.08	0.75	0.458
Phenylanaline	Inter	3.89	1.12	3.46	0.001
	Time	0.01	0.00	1.46	0.152
	Sex	−0.12	0.10	−1.13	0.266
	FL	0.00	0.00	0.88	0.266
	Temp	0.01	0.05	0.26	0.797
Threonine	Inter	4.91	1.50	3.28	0.002
	Time	0.00	0.00	−0.46	0.645
	Sex	0.10	0.14	0.78	0.459
	FL	0.00	0.00	0.82	0.415
	Temp	0.00	0.07	0.01	0.989
Alanine	Inter	8.39	1.31	6.38	0.000
	Time	0.00	0.00	−0.30	0.765
	Sex	−0.10	0.12	−0.79	0.434
	FL	0.00	0.00	2.71	**0.010**
	Temp	−0.12	0.06	−1.82	0.076
Aspartic acid	Inter	9.98	3.13	3.19	0.003
	Time	0.01	0.01	0.60	0.554
	Sex	−0.18	0.29	−0.61	0.543
	FL	−0.01	0.00	−1.99	0.054
	Temp	−0.23	0.15	−1.52	0.136
Glutamine	Inter	6.02	1.11	5.43	0.000
	Time	0.00	0.00	−0.10	0.920
	Sex	−0.15	0.10	−1.46	0.153
	FL	0.00	0.00	2.06	**0.046**
	Temp	0.00	0.05	−0.82	0.419
Glycine	Inter	6.44	2.00	3.23	0.002
	Time	0.01	0.01	1.27	0.213
	Sex	−0.14	0.18	−0.78	0.440
	FL	−0.01	0.00	−2.75	**0.009**
	Temp	−0.02	0.10	−0.16	0.871
Proline	Inter	5.56	1.92	2.89	0.006
	Time	0.00	0.01	−0.42	0.676
	Sex	−0.06	0.18	−0.34	0.738
	FL	0.00	0.00	0.40	0.692
	Temp	−0.05	0.09	−0.48	0.631
Serine	Inter	5.88	1.29	4.55	0.000
	Time	0.00	0.00	−1.13	0.265
	Sex	0.03	0.12	0.28	0.783
	FL	0.00	0.00	2.34	**0.024**
	Temp	−0.04	0.06	−0.59	0.561
Tyrosine	Inter	3.02	0.85	3.55	0.001
	Time	0.00	0.00	−0.44	0.667
	Sex	0.04	0.08	0.47	0.644
	FL	0.00	0.00	−1.01	0.321
	Temp	0.10	0.04	2.37	**0.023**

Table 4. Fatty acid (FA) profiles (percent contribution, for those that have means above 0.5% of total FA) from white sharks caught on SMART drumlines in the present study. ND: not detectable; FALD: fatty aldehyde; SFA: saturated FA; MUFA: monounsaturated FA; PUFA: polyunsaturated FA

Fatty acid	Mean ± SE	Range
14:0	1.87 ± 0.16	0.81–4.79
i15:0	1.29 ± 0.09	ND–2.54
16:1ω9	0.51 ± 0.11	ND–4.51
16:1ω7	4.21 ± 0.44	1.77–10.87
16:0	14.85 ± 0.38	12.37–24.07
16:0FALD	0.75 ± 0.03	0.34–1.11
17:1ω8+a17:0	0.71 ± 0.03	0.45–1.46
17:0	0.65 ± 0.04	ND–1.00
18:4ω3	0.47 ± 0.09	ND–2.23
18:2ω6	0.80 ± 0.13	ND–3.69
18:3ω3+C20	0.46 ± 0.17	ND–6.35
18:1ω9	12.14 ± 0.98	1.63–26.87
18:1ω7	3.94 ± 0.20	2.29–7.23
18:0	7.99 ± 0.35	0.39–12.61
20:4ω6	9.35 ± 0.53	2.11–15.47
20:5ω3	6.19 ± 0.31	0.10–9.94
20:1ω9	1.08 ± 0.08	ND–2.33
22:5ω6	0.94 ± 0.07	ND–1.91
22:6ω3	17.47 ± 0.91	2.46–27.22
22:4ω6	1.61 ± 0.23	ND–9.08
22:5ω3	3.50 ± 0.17	ND–5.47
22:1ω9	1.04 ± 0.63	0.11–24.08
22:0	0.52 ± 0.03	ND–0.75
24:1ω9	1.47 ± 0.07	0.06–2.79
24:0	0.60 ± 0.04	ND–1.14
Fatty acid groups		
∑SFAs	27.18 ± 0.64	17.91–41.45
∑MUFAs	25.12 ± 1.48	14.85–46.79
∑PUFAs	40.79 ± 1.45	12.71–54.20

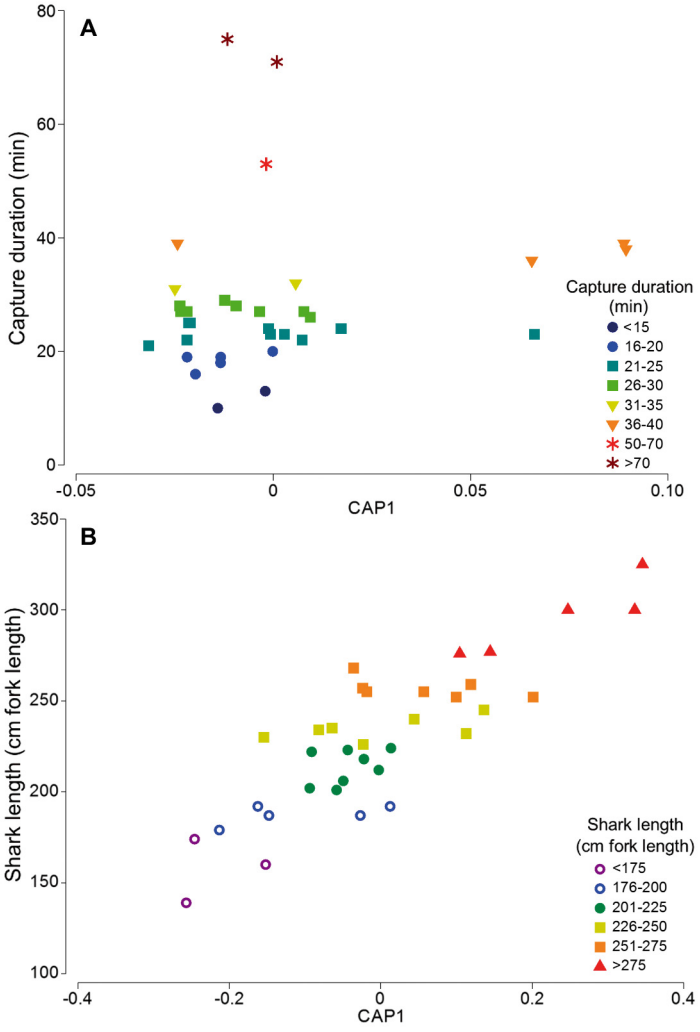

Fig. 2. Canonical analysis of principal coordinates (CAP) of white shark blood plasma fatty acid profiles against (A) capture duration and (B) shark length classed as covariates

as glucose and lactate were affected (Lambert et al. 2018). Our white sharks did not show ketone body sensitivity to capture, suggesting ketone bodies may not be a major source of metabolic fuel under acute stressors. The overall lack of capture duration effect on the indicators in the present study suggests that white sharks do not have an elevated physiological response to short-term capture or that these parameters may not be useful biomarkers for acute capture stress. However, a few non-essential amino acids were affected by shark size, suggesting a relationship between ontogeny and amino acid requirements which may be driven by other growth factors not evaluated here. Alanine, for example, is produced de novo by fish and provides a buffer of skeletal muscle growth in migratory marine fishes (Snyder et al. 2008). Serine, which plays a role in gluconeogenesis (a result of a mobilization of energy from the stress response in fish), is also related to liver function and metabolism; this organ increasingly constitutes a

Table 5. Generalized linear model results testing the effects of biological and operational variables on important fatty acids from white sharks caught on SMART drumlines in the present study. SFA: saturated fatty acid; MUFA: monounsaturated fatty acid; PUFA: polyunsaturated fatty acid. Significant p-values in **bold.** Est: estimate; Inter: intercept; Time: hook time; FL: fork length; Temp: temperature

Response	Parameter	Est	SE	*t*	p
16:0	Inter	2.99	0.44	6.85	0.000
	Time	0.00	0.00	0.27	0.787
	Sex	0.03	0.04	0.61	0.549
	FL	0.00	0.00	−1.23	0.229
	Temp	−0.01	0.02	−0.41	0.683
18:0	Inter	−0.36	0.84	−0.43	0.671
	Time	0.00	0.00	−0.20	0.844
	Sex	0.40	0.09	4.67	**0.000**
	FL	0.00	0.00	−3.54	**0.001**
	Temp	0.16	0.04	3.77	**0.001**
16:1ω7	Inter	4.25	1.40	3.04	0.005
	Time	0.00	0.01	−0.49	0.631
	Sex	−0.58	0.14	−4.04	**0.000**
	FL	0.01	0.00	3.92	**0.000**
	Temp	−0.21	0.07	−3.04	**0.005**
18:1ω9	Inter	4.09	1.19	3.44	0.002
	Time	0.00	0.00	0.04	0.970
	Sex	−0.16	0.12	−1.29	0.206
	FL	0.01	0.00	4.64	**0.000**
	Temp	−0.16	0.06	−2.73	**0.011**
20:4ω6	Inter	1.55	1.15	1.35	0.187
	Time	0.00	0.00	0.10	0.923
	Sex	−0.01	0.00	−5.07	**0.000**
	FL	−0.01	0.00	−5.07	**0.000**
	Temp	0.11	0.06	1.98	0.057
20:5ω3	Inter	0.77	1.08	0.71	0.483
	Time	0.00	0.00	−0.26	0.796
	Sex	−0.01	0.11	−0.13	0.896
	FL	0.00	0.00	0.05	0.964
	Temp	0.06	0.05	1.04	0.307
22:6ω3	Inter	2.42	0.98	2.47	0.019
	Time	0.00	0.00	0.83	0.413
	Sex	0.13	0.01	1.34	0.190
	FL	0.00	0.00	−2.95	**0.006**
	Temp	0.06	0.05	1.18	0.247
SFA	Inter	2.91	0.38	7.69	0.000
	Time	0.00	0.00	0.15	0.882
	Sex	0.11	0.04	2.76	0.10
	FL	0.00	0.00	−2.32	**0.028**
	Temp	0.03	0.02	1.56	0.129
MUFA	Inter	4.27	0.86	4.96	0.000
	Time	0.00	0.00	−0.07	0.942
	Sex	−0.14	0.09	−1.54	0.133
	FL	0.01	0.00	4.70	**0.000**
	Temp	−0.11	0.04	−2.59	**0.015**
PUFA	Inter	3.31	0.61	5.39	0.000
	Time	0.00	0.00	0.35	0.725
	Sex	0.07	0.06	1.05	0.310
	FL	0.00	0.00	−3.31	**0.002**
	Temp	0.05	0.03	1.56	0.128

large portion of a sharks' biomass as they mature (Hussey et al. 2009, Lucifora et al. 2009). White sharks will also rely more on utilizing stored energy as they age, which was supported by our finding that ketone bodies increased with shark length (Fig. S1). The large biomass and low mass-specific metabolic rates of white sharks support this hypothesis (Carlson et al. 2004), such that they may have limited requirements for increasing the bioavailability of non-essential amino acids for energy production. Since all of the white sharks sampled in the present study were below the estimated size at maturity for this species (Bigelow & Schroeder 1948, Bruce 1992), it is unlikely that reproductive activity or status played a role in amino acid or FA levels. While all individuals in the present study were immature, the captured sharks were of a relatively large size range (139–325 cm FL) and included young-of-the-year, small juveniles, and large juveniles.

Numerous studies support the conclusion that shark stress-responses to capture can be highly species-specific (Mandelman & Skomal 2009, Dapp et al. 2016a, Jerome et al. 2018). Although we used a different and novel set of comparative biomarkers for assessing capture stress in sharks than those most commonly used (e.g. blood gas tensions, glucose, and lactate; Marshall et al. 2012), it appears that our results support the notion that shark species can be relatively robust to capture (i.e. tiger sharks; Afonso & Hazin 2014, Gallagher et al. 2014a,b). Lamnid sharks exhibit physiological and metabolic adaptations for heightened aerobic swimming performance (Bernal et al. 2003a,b). This greater aerobic scope could in turn enhance other aerobic physiological processes such as oxygen delivery and the processing of metabolic end-products of anaerobic metabolism (Wood et al. 2007). Yet within this group of sharks, certain species have been shown to exhibit high stress responses (e.g. mako sharks; Wells & Davie 1985) but high survivorship to capture (French et al. 2015), which suggests that there is some degree of within-family variation in the response or that there are context-dependent effects (e.g. we used short hooking durations). Considering the high trophic positions occupied by most lamind sharks, as well as the importance of individual white sharks to overall population health (Cooke et al. 2016, Ward et al. 2016), there are important conservation implications when sharks are captured and released. Although these results are preliminary and additional physiological endpoints should be evaluated, our main result may be an encouraging conclusion for white sharks.

We recognize that the current set of biomarkers used (amino acids, FAs) are novel in their application to studies of shark stress (sensu Van Rijn & Reina 2010, Guida et al. 2016a) and that they may not be as sensitive to capture stress as in other species such as teleosts. A complimentary study recently assessed the physiology of this same sample of white sharks, using more traditional blood biochemistry analytes and found that most parameters did not significantly change with hook time (Tate et al. 2019). Their conclusions align with those from our study using amino acids and FAs; however, we are not able to comment on their true utility as stress indicators on their own, due to the limited sampling window of our study. Thus, amino acids and FAs should be tested under more extreme capture events and used against/correlated with more traditional biomarkers to determine their relative utility. Additionally, the lack of change in biomarker profiles attributed to capture, regardless of whether it is due to their overall suitability as stress biomarkers or the proposed limited stress response, encourages the use of amino acids and FAs in white shark ecology. Both amino acids and FAs were influenced by abiotic (temperature) and biotic (size) factors, mirroring their more traditional use in chondrichthyan ecology (Munroe et al. 2018, Meyer et al. 2019). As such, research teams can confidently apply these biomarkers to questions of white shark diet and habitat use, without the need to incorporate variations in short capture duration, or when precise capture duration may be unknown.

This study represents the first evaluation of white shark response to capture using amino acids and FAs as biomarkers, and one of the first evaluations of white shark physiology in response to capture. Clearly, more work is required to obtain a more comprehensive understanding of this species' physiology and how it changes when exposed to additional fishery settings as well as for more physiological endpoints. This study was limited by the operational aspects of our fishery-independent capture methods (SMART drumlines), which provided short capture durations (averaging ~30 min; ranging 13–75 min) and an ability for white sharks to maintain swimming performance while hooked. The ability to swim while hooked will likely reduce or minimize the magnitude of an individual's physiological response to capture (e.g. Guida et al. 2016b). Nevertheless, hook times below this mean can elicit pronounced stress responses in large sharks, and have been linked to effects ranging from physiological change to mortality, using the same general capture technique (Gallagher et al. 2014a). Moreover, the number of indi-

vidual sharks sampled here greatly exceeds those for most species in other studies. This research suggests that white sharks are likely tolerant of the process of catch and release from SMART drumlines at short to moderate hook times. This result is useful for researchers, managers, and agencies tasked with ensuring high survival rates for this protected species when they are caught and released under research (tagging programs) or management scenarios (bather safety programs), or when they are captured incidentally in non-target fisheries.

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