



Multispecies thermal dynamics of air-exposed ectothermic sharks and its implications for fisheries conservation

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ABSTRACT

Body temperature is a crucial component of thermoregulation, being strongly linked to variables such as energy flow, metabolic rates, activity patterns and resilience. With exception of lamnid sharks, elasmobranchs are classified as ectothermic, depending on ambient temperature for heat modulation. Despite often being removed from the water during fisheries interactions, the known effects of air exposure on sharks are limited to the hypoxia experienced. Comparatively little is known about the potential effects of changing ambient temperatures and solar radiation experienced by sharks during air exposure, and if such scenarios may compromise their thermal dynamics and survival. Here we used infrared thermography (IRT) to measure external body temperature of 10 different shark species ($N = 62$), ranging in size from 106 to 340 cm total length, experimentally exposed to air. We tested the hypothesis that all individuals would exhibit body surface temperature increases when air-exposed, with temperature uniformly distributed across the body surface regardless of species. Our results did not support this hypothesis. Although ectothermic, sharks exhibited significant species-specific variations in heat distribution and warming along the body surface. Moreover, these thermal patterns were significantly impacted by both environmental factors (water temperature at capture) as well as biological traits (shark size and body region). Multivariate analyses separated the 10-shark species into five groups according to the influences of shark body size, body region and water temperature on variations in the thermal profiles detected. We discuss the potential physiological, ecological and conservation implications of these findings.

1. Introduction

Ambient temperature has a profound effect on fish physiology and is considered as the main abiotic factor determining geographic range and individual vulnerability to temperature changes (Brett, 1971). Accordingly, fishes generally remain within a narrow thermal window that is optimal to support relevant physiological traits, such as metabolism and cardio-ventilatory dynamics during swimming (Lowe and Goldman, 2001; Ballantyne and Robinson, 2011; Bernal et al., 2012). The above considerations have practical implications, such as the need to determine maximum air exposure times, considering not only hypoxia but also direct exposure to solar radiation for sharks in a fisheries conservation context,

where sharks are captured and released due to fishing regulations (e.g., size limits, species restrictions) or as a result of voluntary conservational ethics, with the goal of promoting post-release survival. However, during these capture events, sharks are often exposed to changes in ambient temperatures when they are brought up from deeper colder waters to shallower warmer waters, and especially when animals are removed from the water and exposed to air and direct solar radiation during handling, and then once again when released back into the water (Wosnick et al., 2018). It seems reasonable to postulate that, under this context, shark survival depends on the interrelationships between anthropogenic and environmental factors, such as physiological capture stress from both handling and ambient temperature changes.

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Although several studies have elucidated the combined effects of water temperature and air exposure on fish survival (Chopin and Arimoto, 1995; Ross and Hokenson, 1997; Davis et al., 2001; Davis, 2002; Poisson et al., 2014), little is known about how air temperature or direct solar radiation influence the external body temperature of captured sharks and its potential consequences for post-release recovery or mortality (Cicia et al., 2012; Wosnick et al., 2018). The assessment of thermal dynamics upon air exposure permits not only a better comprehension of warm-shock associated to the transition from water to air but can also raise important points regarding the effects of the reciprocal cold-shock when returned to their natural environment. However, such dynamics would likely depend on how heat is distributed across the body, the speed at which body temperatures change, the duration of exposure, and on the size or life-stage of the individual (Wosnick et al., 2018).

While elasmobranch body temperatures have been determined with temperature-recording devices inserted into the epaxial muscle shortly after capture (Carey and Teal, 1969; Carey et al., 1971), infrared thermography (IRT) provides a relatively non-invasive technology for assessment of external body temperatures and heat distribution patterns (Tattersall and Cadena, 2010; Tattersall et al., 2016; Wosnick et al., 2018). This is particularly relevant for sharks, because it has been hypothesized that cutaneous nerves detect environmental temperature and respond so that they change skin temperature in a feedforward signal mechanism (e.g., reflex vasoconstriction) that controls body temperature (Romanovsky, 2014). This is different from a typical physiological feedback control, which is directly modulated by changes in a controlled variable (e.g., body core temperature). Instead, the feedforward mechanism responds to disturbances before onset of changes in the controlled variable (e.g., changes in the surrounding temperature before it affects the internal temperature of an individual) (Romanovsky, 2014).

In the present study we used IRT to measure external body temperature of 10 different ectothermic shark species during experimental air exposure to evaluate the potential extrinsic and intrinsic factors influencing body surface temperature variation. These data were used to answer the following questions: (1) Do body surface temperatures vary by species, sex, body-shape and/or size of shark? (2) Do ambient water or air temperatures at capture influence body surface temperatures of shark when air exposed? (3) Do body surface temperatures change with increasing duration of air exposure, and if so, do these changes occur uniformly across body-regions, and across different species? Based on previous IRT research on air-exposed blacktip sharks (*Carcharhinus limbatus*, Wosnick et al., 2018), we hypothesized that regardless of species, all individuals would exhibit body surface temperature increases with increasing air-exposure, with temperature uniformly distributed across the body surface.

2. Materials and methods

2.1. Study site and thermal analysis

Sampling was conducted from 25 October 2015 to 17 April 2016 within Florida state waters (between latitudes 25.791 N and 25.597 N) across the wet and dry seasons (wet – June to November; dry – December to May). Sharks were captured using circle hook drumlines as described in Gallagher et al. (2014a), as part of ongoing research surveys off the coast of Miami, Florida (USA) by the Shark Research and Conservation Program at the University of Miami (UM SRC). Briefly, drumlines were deployed (between 10 and 40 m deep) to soak for 1 h before being checked for shark presence. Upon capture, sharks were secured using a custom-designed platform at the stern of the boat. Thus, animals were completely removed from the water and exposed to air, permitting thermal imaging. To promote welfare and vitality of sharks during sampling, a water pump was inserted into the shark's mouth and remained pumping 94.5 l of water per minute throughout the handling

procedure (total of 5 min) to enable ventilation of the gills and to ensure survival. It is important to mention that the water used to ventilate the gills was taken from the sea surface. So, to avoid interferences of the pumped water temperature, the thermal analyzes excluded readings near the gill slits. Sharks were also sexed, and total lengths measured using a standard measuring tape.

Thermal imaging was conducted, during normal shark surveys conducted by the UM SRC, following the procedure described below. The animals were not subjected to increased air exposure or sampling time for the current study. Experimental procedures and animal husbandry were approved by the University of Miami Institutional Animal Care and Use Committee (Protocol 15–238) and research permits from Florida Fish and Wildlife Conservation Commission, Biscayne National Park and National Marine Fisheries Service.

Thermal images were taken using a FLIR camera (model T420–62101 Wilsonville, Oregon, EUA) immediately upon shark landing (hereafter referred as initial time) and again after a 5-min exposure period (considered here final time) (Fig. 1). The water temperature was measured with a regular thermometer placed at the sea surface. The relative humidity, air temperature and distance to the animal were measured by the camera and then calibrated according to the daily conditions, as established by thermal measurement protocols (Kastberger and Stachl, 2003). Emissivity coefficient was set at 0.98–0.99 units of energy according to the value established for skin in animal research (Kastberger and Stachl, 2003). Each thermal image was analyzed using the FLIR software tools (FLIR® Systems, Inc. version 5.3.15268.1001, 2016).

2.2. Detailed patterns of body heat distribution

To evaluate if surface temperatures vary across the shark's body, thermal imaging analyses was focused on three main body regions: (i) head: region comprised between the snout tip and the last branchial arch; (ii) dorsal: upper region horizontally comprised between the last branchial arch and the end of the caudal fin and vertically limited by the end of the dorsal fin and insertion line of the pectoral fin; and (iii) ventral: region composed by the flanks (lateral of the body) and ventral portion of the animal, excluding the ventral region of the head which is already included in the first category.

Using the thermal images, 30 points were randomly selected within the three body regions described above (90 in total for each animal) and the average of each body region was used to estimate the corresponding initial (i.e. at landing) and final (i.e. after a 5-min exposure and prior to release) individual body surface temperatures (hereafter referred as the exposure period). Given that sharks were captured across a range of waters temperatures and similarly exposed to a range of air temperatures during sampling, a centering procedure was adopted to account for variability in the environmental influence upon the shark surface body temperatures following the approach of Wosnick et al. (2018). Specifically, both shark body surface temperatures values (response variable) and the respective air temperature values during sampling (predictor variable) were subtracted from the corresponding water temperatures at capture prior to statistical analysis. These generated standardized body surface temperature values and air temperature values (Wosnick et al., 2018).

2.3. Species-specific and across-species multivariate patterns

To investigate for possible species-specific patterns in body surface temperature changes during air exposure, analysis of covariance (ANCOVA) were independently performed for each shark species. For this purpose, the measured body surface temperature variations were quantified as an interactive effect between the categorical variables' exposure period (i.e. initial and final) and body region. In addition, a complementary approach was conducted to assess how shark body surface temperatures varied in relation to the corresponding water

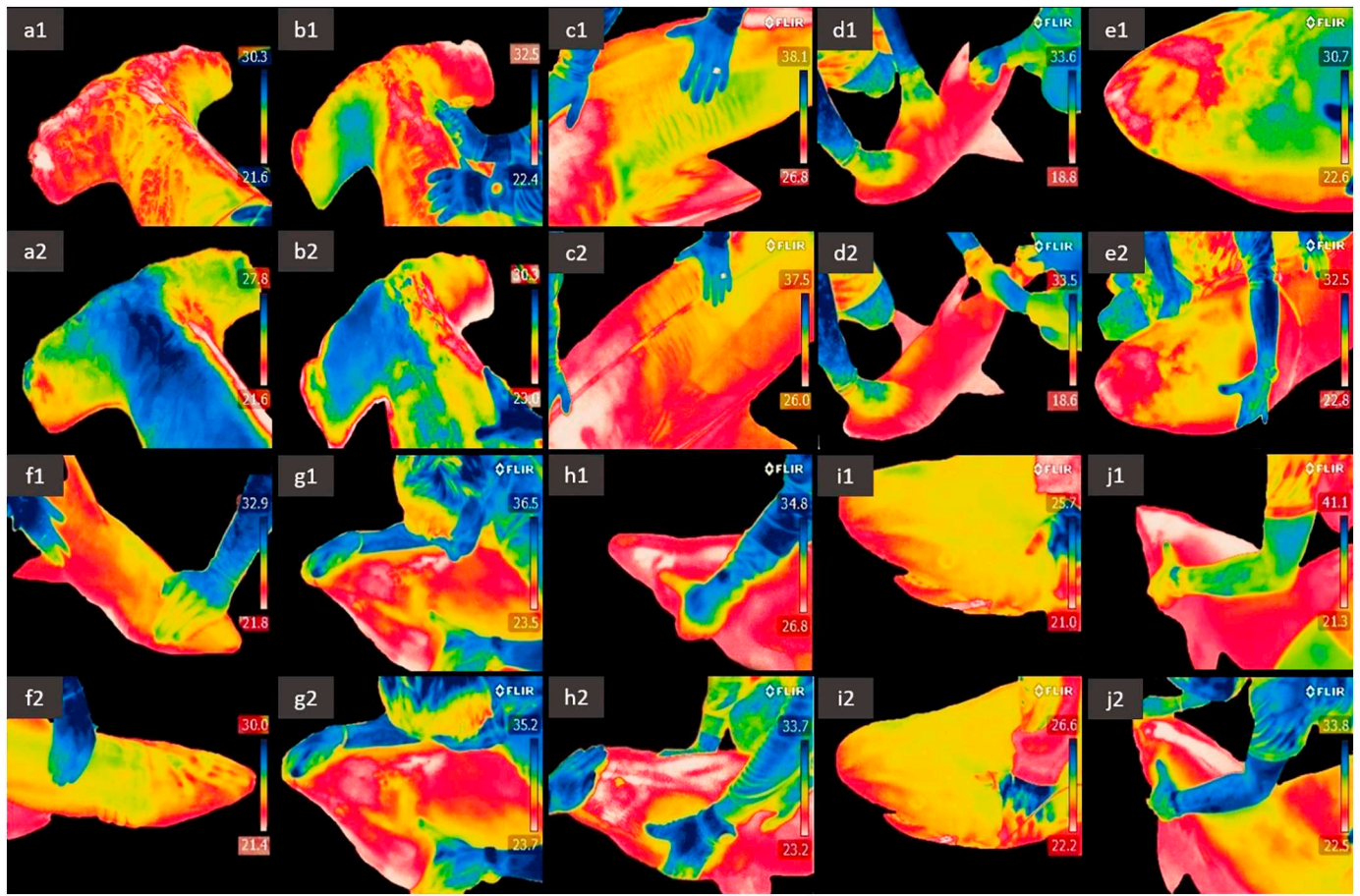


Fig. 1. Thermal images of shark species sampled in the present study. (a) great hammerhead (*Sphyrna mokarran*); (b) scalloped hammerhead (*S. lewini*); (c) nurse shark (*Ginglymostoma cirratum*); (d) blacknose shark (*Carcharhinus acronotus*); (e) bull shark (*C. leucas*); (f) blacktip shark (*C. limbatus*); (g) dusky shark (*C. obscurus*); (h) sandbar shark (*C. plumbeus*); (i) tiger shark (*Galeocerdo cuvier*); (j) lemon shark (*Negaprion brevirostris*). Number one (1) represent time at landing and number two (2) represents 5 min after air exposure.

temperatures during the thermal readings, using generalized linear models (GLM) with Gaussian families of error distribution. The GLMs were individually run for each body region and exposure period, including the standardized body temperatures as response variable and the categorical variable shark species as candidate predictor. A new artificial level called “water”, i.e. a zero value for each specimen and for all body regions sampled, was included as a predictor variable and set as the intercept in the modeling approach. This was performed not only to avoid arbitrarily selecting any of the shark species sampled as the comparison base level for the analysis, but also to investigate the significance level of the corresponding shark temperatures registered in relation to their environment, i.e. whether cooler, warmer or not different. The less representative species, i.e. with a reduced number of individuals sampled (≤ 2); where not included in the species-specific statistical approach, however, a descriptive analysis was performed to simply investigate how body temperature varied for these sharks during air exposure.

All shark species sampled during the thermal readings were pooled together for a multivariate approach, which aimed at identifying possible multi-specific groups with similar trends in body surface temperature variations during air exposure. A redundancy analysis (RDA) was performed with the *vegan* package (Oksanen et al., 2013) using the corresponding body surface temperature variations for each body region per specimen as the response variable. Candidate environmental variables comprised the corresponding water and standardized air temperatures at capture, and the biological candidate predictors included sex, body part region and total length (TL). New variables were

progressively added to the initial null model following a significant effect and according to their lower Akaike Information Criterion (AIC) values. The total variance explained by the final RDA model was partitioned to verify the respective amount of contribution from each group of variables, i.e. environmental and biological. The level of similarity among the multi-specific shark groups identified by the RDA were inspected using analysis of similarities (ANOSIM). For this analysis, the total matrix of species-specific body surface temperature variations was subdivided according to each multi-specific group and Bray-Curtis dissimilarity indices were calculated for each one of them. The ANOSIM were performed individually for each new matrix considering only the significant variables identified in the RDA, as proposed by Niella et al. (2017). Significant strong similarities were identified when the ANOSIM statistic (R) was inferior to 0.1. All the statistical analyses were performed in the R software (version 3.4.2).

3. Results

3.1. Sharks sampled and total body surface temperature variations

A total of 62 sharks were thermo-imaged in the present study, comprising 3 families, 5 genera and 10 species (Table 1). The smallest specimen analyzed was a 105.5 cm TL female blacktip shark (*Carcharhinus limbatus*) and the largest was a 340 cm TL male great hammerhead shark (*Sphyrna mokarran*) (Table 1). Sharks were captured across water temperatures ranging from 20 to 32 °C, and air temperatures spanning between 21 and 34 °C (Table 1). Across all body regions,

Table 1

Summary of the shark species sampled during the thermal experiment, including the corresponding sex, number of specimens (N), total length amplitudes (TL) and corresponding water (Water), air (Air) and body surface temperature variation (ΔBtemp) amplitudes.

Family	Species	Sex	N	TL (cm)	Water (°C)	Air (°C)	ΔBtemp (°)
Sphyrnidae	<i>Sphyrna mokarran</i>	Male	6	259.0–340.0	20.0–26.0	21.0–28.5	0.2–5.0
		Female	5	200.0–238.0	24.0–32.0	26.7–34.0	0.4–7.0
	<i>S. lewini</i>	Male	1	289.0	25.0	26.8	0.6–3.6
		Female	1	306.0	24.5	26.0	0.6–3.1
Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	Male	7	145.0–267.0	24.0–28.0	26.4–30.8	1.4–1.5
		Female	9	167.0–264.0	24.0–28.0	26.5–30.2	1.6–1.8
Carcharhinidae	<i>Carcharhinus acronotus</i>	Male	1	115.0	24.0	26.7	0.3–0.6
		Female	1	125.0	27.0	28.0	0.1–0.3
	<i>C. leucas</i>	Male	1	189.0	27.0	28.3	0.1
		Female	5	240.0–270.0	24.0–27.0	26.5–29.0	0.1–0.9
	<i>C. limbatus</i>	Male	8	118.0–171.0	20.0–31.0	21.0–33.0	0.6–2.1
		Female	7	105.5–171.0	20.0–28.0	21.0–31.0	0.4–1.8
	<i>C. obscurus</i>	Male	1	265.0	24.5	26.0	0.2–0.5
		Female					
	<i>C. plumbeus</i>	Male	2	193.0–201.0	28.0	30.0–30.3	0.1–0.6
		Female	4	187.0–210.0	25.0–32.0	27.3–34.0	0.2–0.6
	<i>Galeocerdo cuvier</i>	Male	1	120.0	28.0	30.0	0.1–0.4
		Female	1	202.0	25.0	27.4	0.2–0.6
<i>Negaprion brevirostris</i>	Male	1	266.0	24.0	26.2	0.3–2.7	
	Female						

shark body surface temperature variations ranged from 0.1 to 7 °C with the highest values observed among the great hammerheads, followed by the scalloped hammerheads (*S. lewini*), the lemon (*Negaprion brevirostris*) and the blacktip sharks (Table 1).

3.2. Species-specific patterns of shark body warming

The ANCOVA revealed that body surface temperatures of nurse sharks (*Ginglymostoma cirratum*) varied significantly with increased exposure and between body parts according to exposure period (Table 2). Upon capture, the ventral regions of nurse sharks exhibited the highest temperature values compared to the rest of their bodies and tended to cool with increased exposure, while the other body regions contrastingly warmed (Fig. 2a). The body surface temperatures of blacktip (*C. limbatus*) and great hammerhead (*S. mokarran*) sharks also significantly varied with air exposure (Table 2), with the whole bodies of the sharks tending to warm (Fig. 2b–2c). No significant variations

Table 2

Species-specific analysis of covariance (ANCOVA) of body temperature change considering an interaction between the variables exposure period (Period), i.e. initial at landing and final after air exposure, and shark body region (Region), i.e. head, dorsal and ventral. (*) Significant effects.

Species	Main effects	Sum Sq.	Mean Sq.	F-value	p-value	R ²
<i>G. cirratum</i>	Period	0.40	0.35	0.87	.353	0.938
	Region*	579.10	289.54	719.55	< .001	
	Period: Region*	10.30	5.13	12.74	< .001	
	Residuals	36.20	0.40			
<i>C. limbatus</i>	Period*	18.77	18.76	13.27	< .001	0.097
	Region	0.33	0.16	0.11	.891	
	Period: Region	1.57	0.79	0.56	.576	
	Residuals	38.82	1.41			
<i>S. mokarran</i>	Period*	36.50	36.53	5.44	.023	0.115
	Region	26.20	13.11	1.95	.151	
	Period: Region	27.60	13.82	2.06	.137	
	Residuals	40.31	6.72			
<i>C. leucas</i>	Period	0.08	0.08	0.02	.895	–0.027
	Region	18.06	9.03	2.00	.152	
	Period: Region	0.16	0.08	0.02	.982	
	Residuals	135.12	4.50			
<i>C. plumbeus</i>	Period	0.40	0.40	0.22	.641	–0.134
	Region	0.93	0.46	0.26	.774	
	Period: Region	0.21	0.10	0.06	.943	
	Residuals	54.07	1.80			

were observed for the body surface temperatures of bull sharks (*C. leucas*) or sandbar sharks (*C. plumbeus*) during air exposure (Table 2). However, the head temperatures of bull sharks were warmer as compared to the rest of the body upon landing, a trend which was kept constant during air exposure (Fig. 2d). On the other hand, the sandbar sharks showed a uniform heat distribution on their whole body and warmed at a slow rate (Fig. 2e).

The GLMs suggested significant species-specific patterns of body surface temperatures relative to ambient seawater temperatures (Table 3). The entire surface of great hammerhead sharks was significantly cooler (by ~2 °C) than ambient water temperatures at landing, whereas after 5-min of air exposure, their head temperatures generally became > 1 °C hotter than seawater while the rest of their body remained fairly constant, warming at a slow rate (Fig. 3a). Upon landing, nurse sharks were > 5 °C warmer than ambient water temperatures, with only the ventral region cooling during increased air exposure, while their dorsal regions warmed to about ~1 °C above ambient water temperatures (Fig. 3b). For blacktip sharks, their heads were slightly warmer than ambient water temperatures at landing, but their entire body became uniformly > 1 °C hotter than ambient seawater with increased exposure period (Fig. 3c). Upon landing, the heads of bull sharks were > 1 °C warmer than ambient water temperatures, with the rest of the body remaining similar to the ambient water temperature; a pattern that was maintained with increased exposure (Fig. 3d). In contrast, body surface temperatures of sandbar sharks showed no significant changes relative to ambient seawater temperatures during air exposure (Fig. 3e).

The single dusky (*C. obscurus*) and lemon shark sampled exhibited contrasting patterns of body surface temperature variations. A considerably greater warming was observed on the head of the dusky shark in comparison with the rest of its body (Fig. 4a). On the other hand, despite the lemon shark was sampled on a considerably hotter day (air temperature 2.2 °C > water temperature) than the dusky shark (air temperature 1.5 °C > water temperature), its highest body surface temperature variation consisted on a 2.7 °C cooling on its ventral region (Fig. 4b). The two blacknose sharks (*C. acronotus*) analyzed (TL = 115 cm; TL = 125 cm) were captured on days where the air temperatures were 1.0 °C and 2.7 °C higher than the ambient water, with a comparatively ~2-fold increase in the magnitude of body surface heating exhibited by the shark sampled on the warmer day (Fig. 4c). For the two scalloped hammerhead sharks (*Sphyrna lewini*) (TL = 289 cm; TL = 306 cm) which were caught at very similar

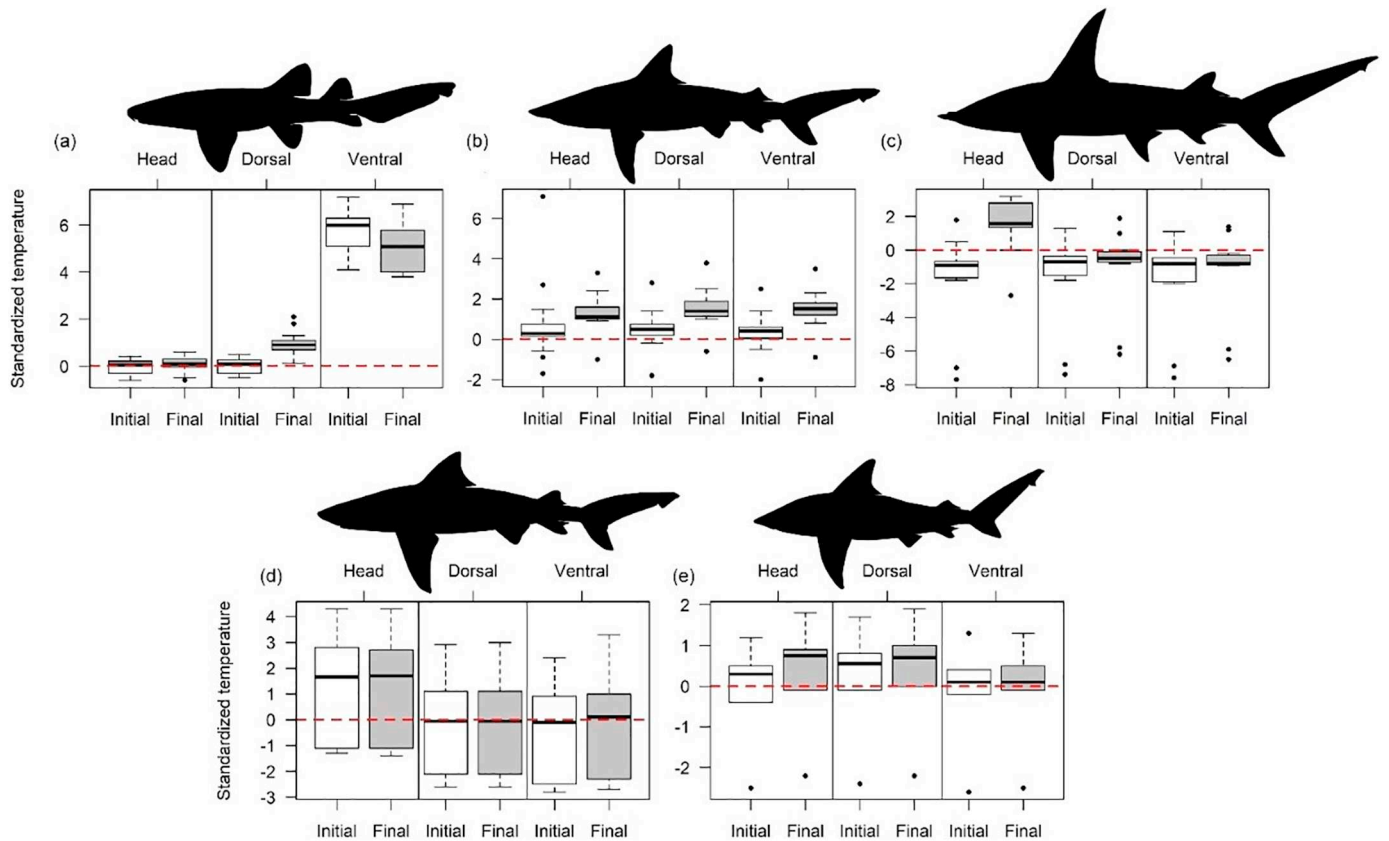


Fig. 2. Standardized body surface temperature variations during air exposure per body region for the (a) nurse (*Ginglymostoma cirratum*; $n = 16$), (b) blacktip (*Carcharhinus limbatus*; $n = 15$), (c) great hammerhead (*Sphyrna mokarran*; $n = 11$), (d) bull (*C. leucas*; $n = 6$) and (e) sandbar (*C. plumbeus*; $n = 6$) sharks. The dashed red lines represent the water temperature threshold. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

environmental conditions, i.e. air temperatures 1.5 and 1.8 °C warmer than the seawater, both exhibited a ~3-fold greater warming on their heads as compared with the rest of their bodies (Fig. 4d). The two tiger sharks (*Galeocerdo cuvier*) sampled were also caught at comparable environmental conditions, i.e. air temperatures 2 and 2.4 °C warmer than the seawater, however, although most of their bodies seemed to warm at similar rates, the dorsal region of the specimen caught on a slightly hotter day showed a 2-fold higher warming than the other specimen (Fig. 5e).

3.3. Multi-specific trends in shark body surface temperature variations

The final RDA model respectively selected the variables TL (p -value = .005; F-value = 11.01), body region (p -value = .005; F-value = 3.47) and water temperature (p -value = .015; F-value = 1.91) to significantly influence variations in shark body surface temperature during air exposure. The final model was confirmed after a significant ANOVA (residual variance = 8.94; F-value = 5.07; p -value = .001) and exhibited a total variance of 10.5%, which was mostly influenced by

Table 3

Generalized linear models of centralized shark body surface temperatures in relation to ambient water temperature (intercept) for each body part analyzed, including the significant effects of exposure period per species.

Body part	Species	Initial exposure					Final exposure				
		Estimate	Std error	T-value	p-value	R ²	Estimate	Std error	T-value	p-value	R ²
Head	<i>S. mokarran</i>	-1.82	0.43	-4.19	< .001	0.206	1.50	0.29	5.24	< .001	0.353
	<i>G. cirratum</i>	-0.02	0.37	-0.05	.960		0.07	0.25	0.28	.780	
	<i>C. limbatus</i>	0.79	0.38	2.05	.042		1.33	0.25	5.28	< .001	
	<i>C. leucas</i>	1.33	0.56	2.36	.020		1.32	0.37	3.53	< .001	
	<i>C. plumbeus</i>	-0.10	0.56	-0.18	.859		0.31	0.37	0.85	.396	
Dorsal	<i>S. mokarran</i>	-1.65	0.36	-4.51	< .001	0.172	-1.08	0.35	-3.11	.002	0.305
	<i>G. cirratum</i>	0.03	0.31	0.09	.921		0.97	0.30	3.24	.001	
	<i>C. limbatus</i>	0.51	0.32	1.59	.115		1.55	0.31	5.05	< .001	
	<i>C. leucas</i>	-0.13	0.47	-0.28	.780		-0.12	0.45	-0.26	.796	
	<i>C. plumbeus</i>	0.18	0.47	0.38	.701		0.35	0.45	0.77	.440	
Ventral	<i>S. mokarran</i>	-1.88	0.38	-4.99	< .001	0.789	-1.31	0.37	-3.56	< .001	0.749
	<i>G. cirratum</i>	5.78	0.32	17.85	< .001		5.12	0.32	16.22	< .001	
	<i>C. limbatus</i>	0.34	0.33	1.02	.309		1.50	0.32	4.63	< .001	
	<i>C. leucas</i>	-0.36	0.49	-0.75	.456		-0.08	0.47	-0.17	.862	
	<i>C. plumbeus</i>	-0.15	0.49	-0.31	.760		-0.10	0.47	-0.21	.834	

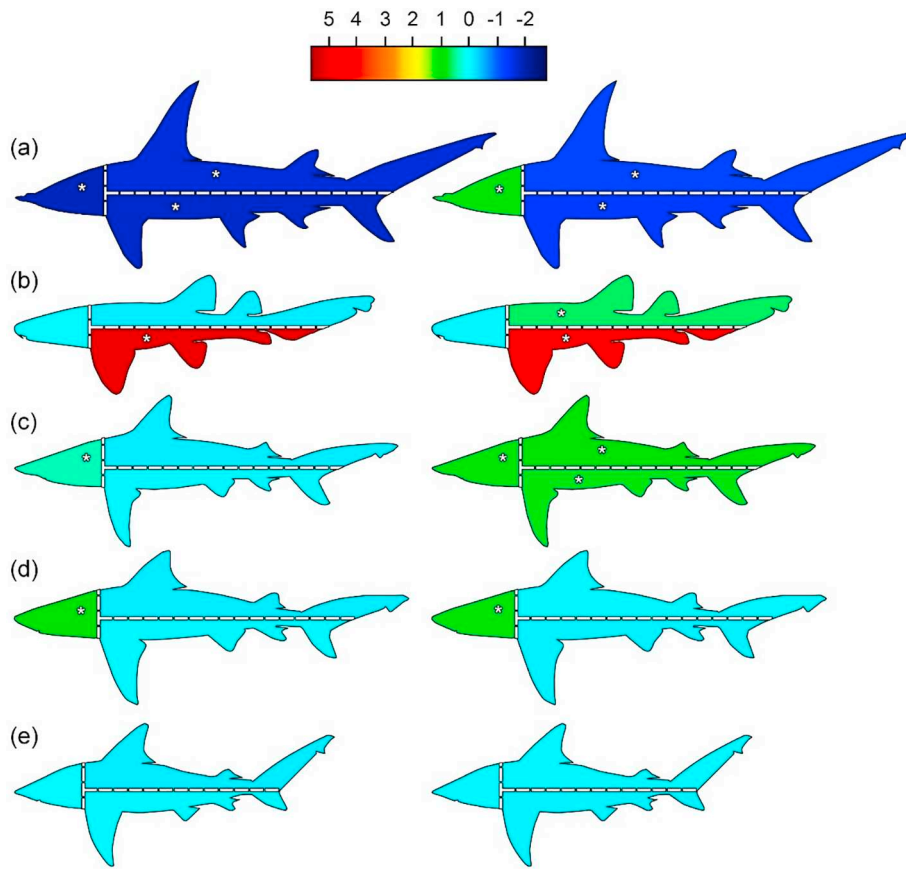


Fig. 3. Conceptual models built from the Generalized Linear Model outputs of shark body temperatures in relation to the sea water, at landing (left panel) and after a 5-min air exposure (right panel) for each body part of (a) hammerhead sharks (*Sphyrna mokarran*, *S. lewini*); (b) nurse sharks (*Ginglymostoma cirratum*); (c) blacktip sharks (*Carcharhinus limbatus*); (d) bull sharks (*C. leucas*) and (e) sandbar (*C. plumbeus*), lemon (*Negaprion brevirostris*), blacknose (*C. acronotus*), tiger (*Galeocerdo cuvier*) and dusky sharks (*C. obscurus*). The color scale depicts the corresponding coefficient estimates for each shark body part separated by the dashed lines. (*) Significant levels (p -value < .05).

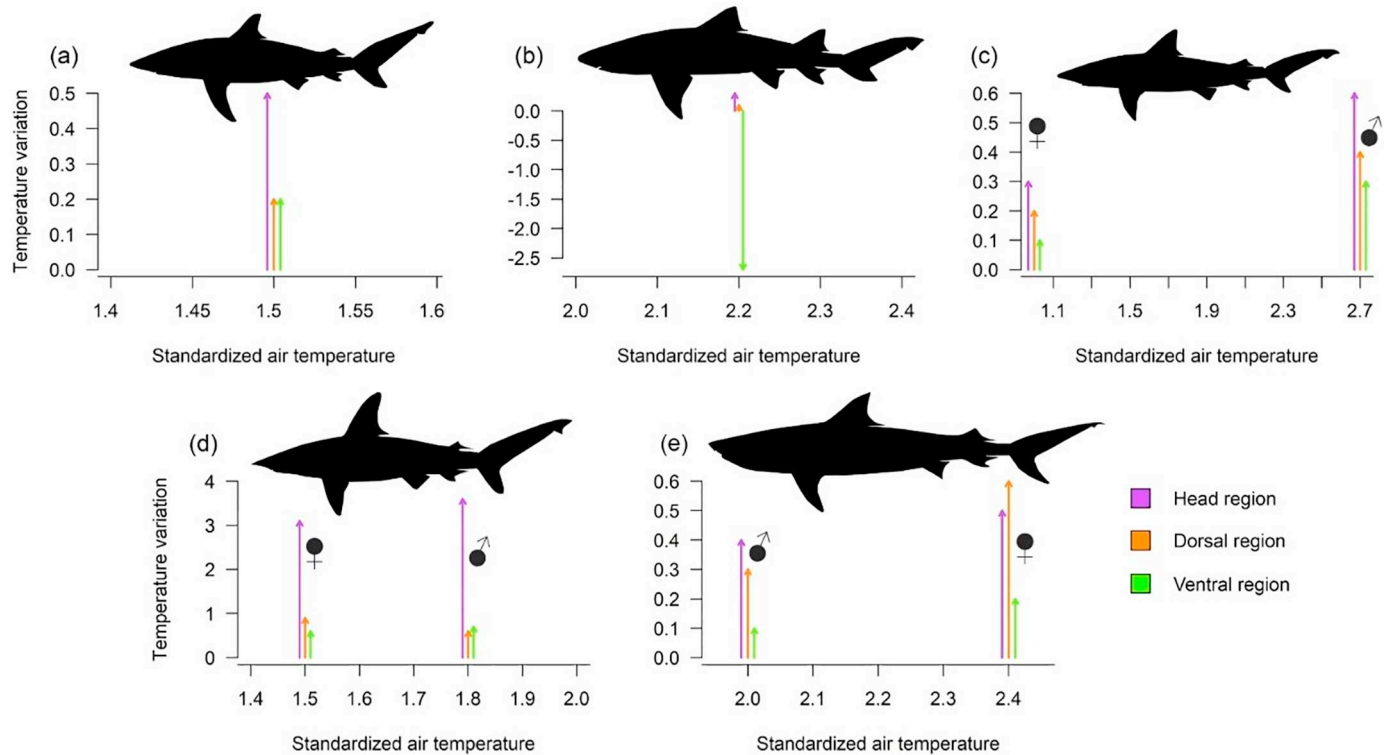


Fig. 4. Magnitude of body surface temperature variations per body region in relation to the corresponding standardized air temperatures at sampling for each specimen of (a) dusky (*Carcharhinus obscurus*), (b) lemon (*Negaprion brevirostris*), (c) blacknose (*C. acronotus*), (d) tiger (*Galeocerdo cuvier*) and (e) scalloped hammerhead shark (*Sphyrna lewini*).

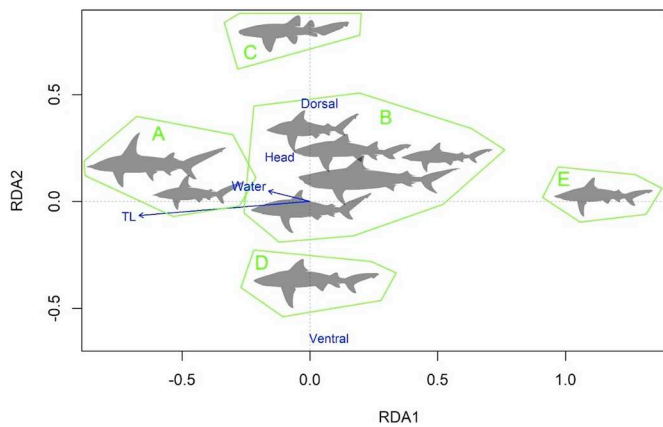


Fig. 5. RDA triplots of the shark body surface temperature variations constrained by the significant variables total length (TL), body region, i.e. head, dorsal and ventral, and water temperature (Water). The most similar groups of species comprised (A) the hammerhead sharks (*Sphyrna mokarran*; *S. lewini*); (B) the sandbar (*Carcharhinus plumbeus*), lemon (*Negaprion brevirostris*), blacknose (*C. acronotus*), tiger (*Galeocerdo cuvier*) and dusky sharks (*C. obscurus*); (C) the nurse sharks (*Ginglymostoma cirratum*); (D) the bull sharks (*C. leucas*) and (E) the blacktip sharks (*C. limbatus*).

biological (9.56%), versus environmental (0.94%), variables. This multivariate approach separated all shark species sampled during the present study into five functional groups according to their patterns of body surface temperature variation: A) the hammerhead sharks; B) most of the carcharhinid species, i.e. the sandbar, lemon, blacknose, tiger and dusky sharks; C) the nurse shark; D) the bull shark; and E) the blacktip shark (Fig. 5). The hammerhead sharks were grouped according to similar higher body surface temperature variations according to higher TL and warmer water temperatures, especially in their heads (Fig. 5). Contrarily, the greater body surface temperature variations among the remainder shark species were usually associated with smaller TL and days with cooler seawater temperatures, especially for the blacktip sharks (Fig. 5). In addition, the nurse sharks differed due to a characteristic pattern of ventral cooling associated with a dorsal warming, whereas the generally warm heads of the bull sharks and their ventral warming separated them from the carcharhinid group B (Fig. 5).

Only two multi-specific groups were identified by the RDA modeling, i.e. groups A and B (Fig. 5). The ANOSIM indicated the group A as the one including the most similar shark species, i.e. the great and scalloped hammerhead sharks, due to strong significant similarities for all biological and environmental variables, especially body region (Table 4). On the other hand, the carcharhinid sharks included in group B only showed significant similarities regarding their body surface temperature variations in relation to the water temperatures at capture, whereas dissimilarities were observed for the biological variables analyzed (Table 5).

Table 4
Region-specific analysis of variance (ANOVA) of total body surface temperature variation of great hammerhead sharks. (*) Significant effects.

Region	Variable	Sum sq.	Mean sq.	F-value	p-value	R ²
Head	TL*	15.408	15.408	9.608	.017	0.486
	Sex	0.073	0.073	0.045	.837	
	Stand.air	4.489	4.489	2.799	.138	
	Residuals	11.226	1.604			
Dorsal	TL*	0.543	0.543	11.534	.011	0.723
	Sex	0.005	0.005	0.121	.738	
	Stand.air*	0.823	0.823	17.492	.004	
	Residuals	0.329	0.047			

Table 5
Analysis of similarity performed between the multi-specific shark groups identified by the RDA (Group A = Sphyrnid sharks; Group B = most of the Carcharhinid sharks), and the significant variables responsible to influence their body surface temperature variations per category (biological and environmental).

Group	Category	Variable	R	p-value
A	Biological	TL	0.017	.018
		Body region	0.020	.001
	Environmental	Water	0.021	.010
B	Biological	TL	0.597	.001
		Body region	0.210	.228
	Environmental	Water	0.018	.006

4. Discussion

Here we used infrared thermography to examine potential body surface temperature changes during air exposure for 10 species of ectothermic sharks, spanning 5 genera and 3 families. Our results failed to support our initial hypothesis that regardless of species, all individuals would exhibit surface body temperature increases uniformly distributed across the body surface with increased exposure time. We found significant species-specific changes in shark body surface temperatures following 5 min of air exposure, ranging from 0.1 to 7 °C, with the most significant changes being found in hammerhead sharks. Interestingly, we also found that temperatures were not uniformly distributed across the body surface in several species. For example, the cephalic region (i.e., cephalofoil) of hammerhead sharks were significantly warmer than the rest of the body. Among the variables analyzed, body size, body region and water temperature influenced the thermal patterns observed across all specimens, separating shark species into five groups. We summarize and discuss the potential implications of these groupings below:

4.1. Hammerhead sharks

For both great and scalloped hammerhead sharks, the magnitude of body surface temperature change was influenced by individual size, body region, and water temperature. Our data suggest that hammerhead sharks may be particularly susceptible to thermal effects when larger individuals are removed from the water during warmer days. This is relevant since this species is often the target of land-based fishing activities, where animals are dragged on land, particularly during summer fishing tournaments (Shiffman et al., 2017). The high rates of body surface warming found for hammerheads, and the potential physiological consequences, could contribute, at least in part, to the high rates of at-vessel and post-release mortality known for this species (Gallagher et al. 2014 a,b,c).

Hammerhead sharks displayed a significant increase in surface temperatures of the cephalofoil. This may be explained by the high surface area to volume ratio and vascular specialization of the cephalofoil (Muñoz-Chápuli and De Andrés, 1995; Nakaya, 1995; Kajiura, 2001). It is possible that associated changes in blood flow dynamics in peripheral tissues may serve as de facto heat exchangers in a pattern similar to gigantothermy (Paladino et al., 1990; Meekan, 2016). Their tropical distribution on warm coastal habitats, hunting tactics in shallow waters (Roemer et al., 2016) and morphostructural adaptations, i.e. UV protection in the eyes and skin (Lowe and Goodman-Lowe, 1996; Nelson et al., 2003), add some rationale to this hypothesis. It is plausible that such a physiological system possibly enhances the exploration of shallow environments with rapid transitions across temperatures, reducing thermal shock during diel vertical migrations.

4.2. The carcharhinid sharks

This shark grouping (i.e., sandbar, lemon, blacknose, tiger and dusky sharks) is ecologically diverse, but are similar in gross morphology (Irschick et al., 2017). The effect of water temperatures at capture on body surface temperatures influenced most of the similarities observed among this group. In particular, these data suggested smaller (younger) individuals may be more susceptible to greater body warming during air exposure. This result is consistent with data from shark bycatch in pelagic longline fisheries (Gallagher et al., 2014b), where at-vessel mortality rates of several carcharhinid species, including sandbar and dusky sharks, were affected by both sea surface temperature and shark length (i.e., higher surface temperatures and smaller individuals = higher mortality). Although our results suggest that future management and conservation plans focused on any of the sharks combined in this group might possibly also benefit the remaining species, similarly as proposed by Niella et al. (2017), such an assumption might be considered with caution due to the low number of sampled specimens from some of these species.

4.3. Nurse sharks

Nurse sharks exhibited characteristic heat dissipation restricted to the ventral region of the body, where most of the red musculature is inserted (SupFig 1). While the mechanism for this ventral heat dissipation is unknown, studies have shown that humans exposed to severe exercise exhibit similar heat dissipation on the ventral surface (Krustrup et al., 2001), whereby a portion of the energy generated through metabolism is dissipated as heat (Gnaiger, 1983). In the present study, temperature measured on the ventral region of nurse sharks was highest at landing and lowest at release. It is plausible this pattern of heat dissipation may be linked to initial increased red muscle activity within the ventral region upon capture, when nurse shark exhibits an initial explosive capture response, followed by a characteristic significant attenuation in capture response, and likely decreased muscular contraction, with increasing hooking duration (Gallagher et al., 2016) followed by restricted movement during sampling.

4.4. Bull sharks

Thermal imaging revealed the head region of bull sharks were warmer than the surrounding water at capture and remained warmer with increasing exposure, a pattern not found for the rest of the body. These results are suggestive of a possible unknown form of endothermy in the cranial region for this species. Indeed, some fish species possess cranial endothermy related to the presence of orbital rete and differentiated anatomy of the cephalic veins that irrigate the red musculature of this region (Tubbesing and Block, 2000; Runcie et al., 2009; Thorrold et al., 2014). Such adaptations are necessary to maintain body temperatures and minimize heat loss through branchial ventilation (Carey et al., 1971). While thermal studies confirm that billfishes, tunas, and lamnid sharks are able maintain higher body temperatures, it is plausible that the presence of counter-current heat exchangers could be present in other species (Tubbesing and Block, 2000), such as the bull shark. However, this requires detailed anatomic and physiological study, for example, following the approach of Tubbesing and Block (2000).

4.5. Blacktip sharks

Blacktip sharks showed a unique full body increase in surface temperatures with increasing air exposure, a result consistent with Wosnick et al. (2018). By including the blacktips in the present analyzes it was possible to assess how unique their patterns of body warming are, not only in relation to other shark families, but even within the carcharhinid group. Across all species analyzed, the blacktip shark

exhibited the most uniform variation in body surface temperatures when removed from the water, i.e. a full body significant heating after 5 min of air exposure. That is probably the reason why the species was included in a separate group by the multivariate approach, especially because of the effect posed by TL. This result may be responsible, at least in part, for the documented vulnerability of immature blacktips to fisheries capture when removed from the water (Heupel and Simpfendorfer, 2002).

It is worth considering some important study limitations that could be accounted for in future research of this kind. First, we chose an approach based on less-invasive and non-lethal sampling (Hammerschlag and Sulikowski, 2011), whereby thermal imaging was conducted opportunistically during normal shark surveys with all the efforts to reduce time out the water for the animals. Thus, the time of exposure to air investigated here was relatively short (5 min of exposure during which saltwater was pumped over the gills) when compared to what is commonly observed in recreational (tens of minutes) or commercial fisheries (hours). However, our data points to rapid body surface temperatures increases during exposure, especially for great hammerhead sharks, for which increases of up to 7 °C were documented within just 5 min of air exposure. This suggests the potential for physiological consequences in animals exposed to the time commonly practiced in some fisheries. Another limitation of this study is that the evaluation of possible sub-lethal impairment or post-release mortality in relation to body surface temperature was not performed. Therefore, we were unable to link our results with fitness consequences. Future studies of this kind may consider post-release monitoring or tracking to assess potential fitness consequences resulting from changes in body temperature resulting from capture. Also, worth noting is that our use of thermal imaging only provided information on surface body temperatures. While increases in surface temperature influence internal body temperature (Romanovsky, 2007, 2014) the rate and magnitude of this change is unknown. Hence, future work of this kind should consider integrating methods for assessing the relationships between air exposure, body surface temperature, internal body temperature, metabolic, cardiac and respiratory rates. Finally, in the current study, sharks were subjected to changes in temperatures resulting from the combined effects of air temperature and solar radiation. We were unable to tease apart the potential effects of each independently, but future studies may seek to investigate this, especially for the animals that are held on lines in surface waters for hours being exposed to higher solar radiation.

5. Conclusion

In summary, we found differences among species and similarities within species groups with respect to body surface temperature responses to air exposure. We hypothesize these patterns are related to both biological and behavioral traits exhibited by these species. Importantly, we also found that ambient water temperatures on the day of capture significantly impacted shark body surface temperature variation during air exposure. If these associated changes in body surface temperatures have consequences for post-release fitness and/or survival, then both ambient water temperatures and duration of air exposure should be considered in decisions whereby sharks are captured and released to promote conservation efforts. The results and hypotheses presented in this paper provide an avenue for future study of shark thermal dynamics.

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Supplementary data

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