Thermal Imaging Reveals Changes in Body Surface Temperatures of Blacktip Sharks (*Carcharhinus limbatus*) during Air Exposure

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ABSTRACT

Fish physiology is significantly affected by temperature variability. During fisheries interactions, fish are often exposed to air and subjected to rapid temperature changes. Fish thermal dynamics during such exposure, and the possible outcomes to their physiology, depend on how heat is distributed across their bodies, the speed at which their body temperatures change, and the size of the individual. Nevertheless, such thermal patterns remain unknown for sharks. This study employed a novel application of thermal imaging to evaluate external body temperature profiles of blacktip sharks (*Carcharhinus limbatus*) above-water exposure after capture. We found that above-water exposure duration, shark total length, and air temperature on the day of capture significantly influenced body surface temperatures of the analyzed sharks ($N = 28$). Body surface temperature significantly increased with increasing exposure; however, thermal profiles of immature sharks (<140 cm) were significantly warmer than those of mature sharks. Moreover, blacktip surface body temperatures were significantly higher during days when air temperatures were at least 2.5°C warmer than water temperatures. We discuss these results as they relate to the ecology of blacktip sharks and their potential vulnerability to fisheries capture due to such changes in peripheral body temperature.

Keywords: conservation physiology, fishing physiology, thermal stress, infrared thermography, elasmobranch.

Introduction

Environmental temperature gradients affect almost all aspects of fish physiology and subsequent behavior (Schlaff et al. 2014). Accordingly, the latitudinal distribution of different fish species reflects optimal temperature zones to sustain efficient physiological function (Crawshaw 1977; DiGirolamo et al. 2012; Schlaff et al. 2014). Since most fish are ectothermic, they generally rely on a behavioral adjustment to regulate their body temperatures, such as undertaking vertical or seasonal migrations (Beitinger and Fitzpatrick 1979; Campana et al. 2011; Speed et al. 2012).

Despite the importance of internal body temperature for thermal dynamics, it is now recognized that the thermoregulation system incorporates both core body and peripheral temperatures (e.g., skin and subcutaneous tissues; Werner 1980, 2010; Romanovsky 2007). Internal and body surface temperatures are intrinsically related, with variations in environmental heat being detected by cutaneous nerves and changes in skin temperature acting as feedback signals in the control of core body temperature (Romanovsky 2014). Conversely, changes in core body temperature can also affect the body surface (Garrick 2008). The thermal relationships between environmental, body surface, and core temperatures have been relatively well studied among teleost fish (Stevens and Fry 1974; Johnston and Dunn 1987; Golovanov 2006). Nevertheless, few studies of this nature have involved sharks (e.g., Hight and Lowe 2007; Speed et al. 2012; Thums et al. 2012), probably because most species are too large to be kept under laboratory-type settings. Among shark studies, behavioral thermoregulation has been pointed out as a strategy adopted by some species to self-regulate to changes in ambient water temperatures; however, it remains unknown whether and how thermal dynamics vary with changes in temperature experienced during air exposure or whether and how these ectothermic animals regulate their body temperature during fisheries capture.

Sharks are often brought above water and subjected to rapid changes in air temperature and solar radiation during fisheries capture (Morgan and Burgess 2007; Cicia et al. 2012; Gallagher et al. 2017), which could influence both surface and core body temperatures. In both commercial and recreational fisheries, captured sharks are often temporarily removed from the water before being released alive to comply with regulations or voluntary conservation ethics. However, when brought above water

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(hereafter "air exposed"), the animals can experience environmental temperatures that surpass body temperature by 10°–20°C (Mitchell et al. 2014), adding to the physiological stress from capture and handling. When sharks are returned to the water, potential thermal alterations may be even greater because of cold shock, contributing to physiological and behavioral impairments (Donaldson et al. 2008). Accordingly, there is a need to better understand the thermal dynamics of sharks when they are air exposed, as frequently occurs during catch and release fishing (Gallagher et al. 2017).

The blacktip shark *Carcharhinus limbatus* (Müller and Henle 1839) is an ectothermic species widespread in warm temperate, subtropical, and tropical waters, with habitat use patterns thought to be driven in large part by temperature variation (Heupel and Hueter 2002; Heupel and Simpfendorfer 2002; Kajiura and Tellman 2016). This species is often caught in commercial fisheries by a variety of fishing gear (Morgan and Burgess 2007; Morgan and Carlson 2010; Serafy et al. 2012). In addition, it is listed as a game fish by the International Game Fish Association, making the species a target of recreational fishing (Shiffman et al. 2014). In the United States, the recreational catch of blacktip sharks has approached or even surpassed the commercial capture (Fowler et al. 2005). Blacktip sharks are also a common target of catch-and-release fishing (Shiffman and Hammerschlag 2014), including land-based fishing in which the species is usually removed completely from the water and landed onshore for photographing (Shiffman et al. 2017). In this study, we used infrared thermography (IRT) as a noninvasive tool to measure external body temperatures of blacktip sharks exposed to air after capture. We used these data to answer the following questions: (1) Do blacktip sharks exhibit increases in body surface temperature when air exposed? (2) If so, what is the rate at which the body surface temperature changes? Moreover, (3) does air temperature at the time of capture influence shark body surface temperatures, and (4) do potential body surface temperature patterns differ in sharks of different size?

Material and Methods

Shark Capture and Sampling

Blacktip sharks were captured with circle-hook drumlines. Briefly, drumlines were deployed to soak in the water for 1 h before being checked for shark presence. Upon capture, sharks were secured with a custom-designed platform at the stern of the boat. Thus, sharks were completely out of the water and exposed to air, permitting thermal imaging. During IRT sampling, shark gills were irrigated with salt water (94.5 L of water/min throughout the procedure) to promote shark health and survivorship, so that our investigation focused on the potential effects of air temperature on body surface temperature without drying the gill lamellae or compromising ventilation. Sharks were also sexed, and their total lengths (TLs) were measured with a standard measuring tape (table 1). Air temperature (27.4° ± 3.6°C) and water temperature (25.2° ± 3.2°C) at the fishing location were also recorded (table 1). Thermal imaging was conducted at the beginning of exposure (1 min landed; T_1), during the exposure (~5 min; T_{int}), and before release (~10 min; T_2) opportunistically as part of ongoing sampling and tagging surveys, and sharks were not subjected to increased air exposure or sampling time for this study. Animals were kept in a dorsal position, and thus no ventral measurements were taken.

IRT and Data Analyses

Thermal images were taken with a FLIR camera (model T420-62101) continuously during shark air exposure (<10 min). Each thermal image was analyzed with the FLIR software tools (FLIR Systems, ver. 5.3.15268.1001, 2016). For each image, temperature measurements were derived from 20 points spread along the animal's entire dorsal surface. The fins and the cephalic region of the thermographed animals were excluded from the analysis, thus allowing standardization of the thermal dynamics of the dorsal surface without possible changes in the readings caused by morphological/functional particularities (e.g., shape and lack of irrigation in the fins). The use of the hose, although common in nonlethal studies, was aimed only at maintaining the ventilatory rate of the animal. In fact, such a volume of water can reduce temperature variation, as observed in the thermal images. That way, the whole cephalic region was also excluded from the analysis to minimize this potential effect. On the basis of average size at maturity described for the southeastern United States (i.e., ~145 cm; Castro 1996), the sharks sampled in this study were categorized as (1) immature ($\mathrm{TL} < 140$ cm) or (2) mature ($\mathrm{TL} > 160$ cm TL).

The potential influences of abiotic and biotic variables on the shark's body surface temperature variation were analyzed with a generalized linear model (GLM) using a Gaussian family of error distribution and an identity link function. Given that sharks were captured in waters of differing temperatures that could potentially confound analyses, body surface temperature measurements were standardized. This was done by subtracting body surface temperature values from the sea surface temperature values at the respective moments and locations of capture. The mean of the 20 standardized body surface temperature measurements from each thermal image at a given exposure time was used as the response variable in the GLM. The candidate predictor variables included air exposure time (min), shark TL (cm), sex (male or female), and standardized air temperature at capture, that is, the corresponding air temperatures subtracted from the corresponding water temperatures at time of capture. This last variable allowed testing for potential effects of varying air temperatures on sharks during the days when air temperatures were warmer than, similar to, or cooler than the water without having to separately test both water and air temperatures as predictor variables.

In the GLMs, a stepwise variable selection procedure was conducted for the inclusion of new predictor variables in the simplest nested model starting from the null model. A new predictor variable was included in the final model only when (1) the variable had statistical support ($P < 0.05$), (2) the Akaike information criterion value was lower than that of the previous

Table 1: Body surface temperature of blacktip sharks

Sex	Total length (cm)	T_1 (°C)	T_{int} (°C)	T_2 (°C)	Air T (°C)	Water T (°C)
Female	105.5	24.7 ± .05	26 ± .02	26.8 ± .03	26.7	24
Female	120	24.6 ± .08	25.3 ± .04	26.4 ± .04	26.7	24
Male	118	23.8 ± .12	24.8 ± .017	25.7 ± .14	23.2	21
Female	118	28.2 ± .04	29 ± .05	29.8 ± .12	30.3	28
Male	159	27.2 ± .02	28.1 ± .06	28.5 ± .18	29	27
Female	160	27.4 ± .14	28 ± .07	28.4 ± .05	29	27
Female	158	26.8 ± .06	27.8 ± .11	28.6 ± .07	29.5	27
Male	146	28.3 ± .02	29.6 ± .05	30.2 ± .02	30	28
Male	157	27.4 ± .07	28.4 ± .03	29.7 ± .02	30	28
Male	151	20.3 ± .11	21.4 ± .13	22.5 ± .14	21	20
Female	132	21.4 ± .06	22.5 ± .17	23.2 ± .07	21	20
Male	151	20.4 ± .07	21.2 ± .05	22.7 ± .06	21	20
Male	130	20.1 ± .15	21.3 ± .03	22.3 ± .04	21	20
Male	152	29.2 ± .13	30.4 ± .04	32.7 ± .18	33	31
Female	134	24.9 ± .09	26.2 ± .06	26.5 ± .05	26.5	24
Female	136	24.7 ± .03	25.8 ± .05	26.7 ± .07	26.5	24
Male	149	25.8 ± .12	26.8 ± .14	27.4 ± .08	28.5	26
Female	176	26.8 ± .02	27.9 ± .05	28.6 ± .06	29	27
Female	162	27.1 ± .14	27.8 ± .12	28.1 ± .09	29	27
Female	165	26.5 ± .06	27.2 ± .08	28.2 ± .12	29.5	27
Female	167	27 ± .08	28.3 ± .03	29.6 ± .06	29.5	27
Female	162	27.2 ± .17	28.5 ± .07	29.2 ± .12	29.5	27
Male	168	28.6 ± .05	29.5 ± .08	29.8 ± .03	30.5	28
Female	171	24.5 ± .05	25.8 ± .04	26.4 ± .08	26.7	24
Male	162	28.8 ± .18	29.8 ± .15	31.5 ± .11	31	28
Female	171	28.5 ± .02	29.8 ± .12	30.2 ± .05	31	28
Male	165	23.8 ± .08	25.4 ± .02	26.2 ± .07	26.7	24
Male	171	20.7 ± .13	21.7 ± .05	22.8 ± .15	21	20

Note. Temperatures (mean ± standard error) were measured just after landing (T_1), after ~5 min of air exposure (T_{int}), and just before release (~10 min; T_2).

nested model, and (3) an ANOVA using the χ^2 test indicated the new model to be significantly different from the previous one. The results of the variable selection procedure are further detailed in the appendix (tables A1, A2). In addition, a predictive function was applied to the final GLM to inspect for the possible trends in shark body surface temperature according to a prolonged exposure period (20 min), which may occur when sharks are removed from the water during land-based recreational fishing.

All analyses were computed with R software, version 3.3.1 (www.R-project.org). Statistical significance was declared at $P < 0.05$.

Results

Twenty-eight blacktip sharks were captured and thermographed (table 1). Thermal images from immature sharks (TL < 140 cm) taken after landing (T_1) and before release (T_2) are presented in figure 1, and thermal images from mature sharks (TL > 160 cm TL) taken after landing (T_1) and before release (T_2) are presented in figure 2.

The final GLM selected the variables exposure time, shark TL, and standardized air temperature as significant influences on shark body surface temperatures during air exposure (table 2). Shark body surface temperatures significantly increased with exposure time, generally resulting in a change of ~2°C over the 10-min handling process (fig. 3*a*; table 2). A negative relationship was found between body surface temperature and shark TL, with immature individuals exhibiting significantly higher body surface temperatures than mature individuals (fig. 3*b*; table 2). Moreover, blacktip sharks sampled on cooler days, when the differences between air and water temperatures was <2.2°C, had significantly lower body surface temperatures than sharks caught on warmer days (fig. 3*c*; table 2). Finally, application of linear models predicted a 4.5°C increase in shark body surface temperature over a 20-min air exposure (fig. 3*a*).

Discussion

Application of thermal imaging revealed that body surface temperature changes in blacktip sharks were significantly affected by above-water exposure time, shark TL, and air temperature on the day of capture. All animals, without exception, showed a gradual increase in surface temperature throughout time of exposure. Some parts of the body, such as fins, showed a

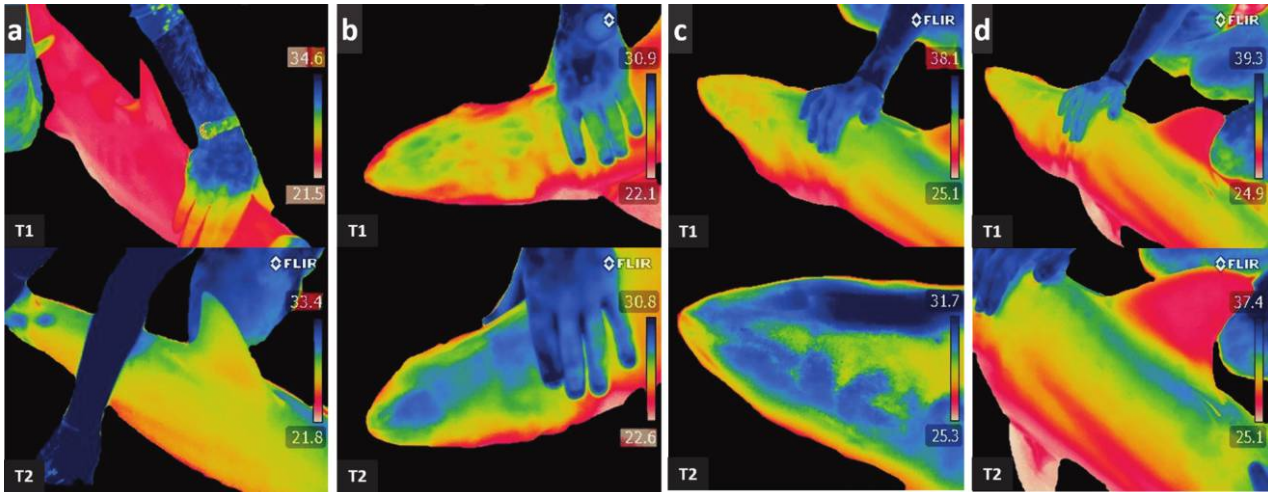

Figure 1. Representative infrared images of immature (<140 cm) blacktip sharks after landing (T1) and before release (T2). Scale for body surface temperature is to the right within each image; note that blue hues represent a relatively warmer spectrum of surface body temperatures, whereas red hues represent a relatively cooler spectrum of surface body temperatures.

slower rate of warming. However, the final body surface increase was homogeneous. The consequences of these results to the thermal dynamics of blacktip sharks are unknown but may have implications for their health and survival after being exposed to air and subjected to changes in temperature and/or solar radiation. For ectothermic species, such as the blacktip shark, the pairing of body temperature with ambient water temperatures can lead to a displacement of the thermal window, which can affect metabolic rates and respiratory dynamics (Di Santo and Benett 2011; Halsey et al. 2015), especially in shark species that are obligate ram ventilators (Bouyoucos et al. 2017).

With two exceptions, all animals had an initial body temperature equal to that of seawater on the day of capture, regardless of time hooked. This result strongly indicates that the exercise done during the time on the line was not sufficient to cause alterations in the thermal dynamics of the animals. This may be because the capture protocol used (i.e., drumlines) allows the animal to swim freely, reducing stress in a very significant way (Gallagher et al. 2014). In fisheries where the animal is exposed to an abrupt stress and strenuous fight, a sufficiently stressful situation may take place.

The effects of thermal shocks in fishes, although still poorly studied, seem to be one of the factors reducing the postrelease recovery (Arlinghaus and Hallermann 2007; Donaldson et al. 2008). In particular, an increase in body temperature of even a few degrees from exposure to slightly warmer air can generate cold shock when animals are returned to the colder water or released from surface lines. Cold-shock stress occurs when a fish

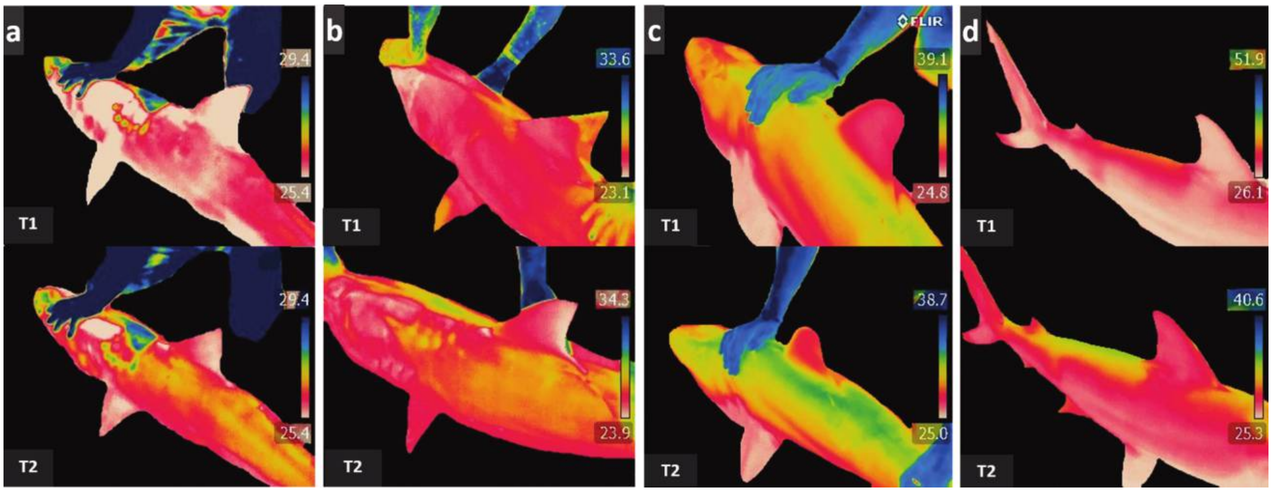

Figure 2. Representative infrared images of mature (>160 cm) blacktip sharks after landing (T1) and before release (T2). Scale for body surface temperature is to the right within each image; note that blue hues represent a relatively warmer spectrum of surface body temperatures, whereas red hues represent a relatively cooler spectrum of surface body temperatures.

Table 2: Generalized linear model of the effects of the abiotic and biotic variables on blacktip shark body surface temperature variation

Variable	Coefficient estimate	Standard error	*t*	*P*
(Intercept)	.44	.72	.61	<.001
Air exposure time	.48	.04	10.42	<.001
Total length	−.02	.01	−4.92	<.001
Standardized air temperature	.77	.20	3.78	<.001

Note. Included for the predictor variables air exposure time, shark total length, and standardized air temperature are the coefficient estimate, standard error, and *t* and *P* values. Model: (body temperature) ~ (exposure time) + (total length) ~ (standardized air temperature).

has been exposed to a specific water temperature and is subsequently exposed to a rapid decrease in temperature (Donaldson et al. 2008). Such rapid change results in a cascade of physiological and behavioral responses and in extreme cases leads to death, depending on the magnitude, duration, and frequency of the change (Donaldson et al. 2008). Traditionally, cold-shock studies have aimed to determine the lethal effects of exposure. However, recently, the number of studies investigating sublethal effects of exposure on fish have been growing, since they can be used as tools in stress studies from a fishery perspective (Gingerich et al. 2007; Donaldson et al. 2008).

Our findings revealed that sharks captured on warmer days, where the difference between water and air temperatures was greater than 3°C, exhibited significantly higher body surface temperatures. This result is consistent with other studies that have demonstrated increased thermal stress in fish captured during warmer periods (Arlinghaus and Hallermann 2007; Gingerich et al. 2007; Donaldson et al. 2008; Di Santo and Benett 2011; Cicia et al. 2012; Danylchuk et al. 2014). Such a thermal response may be especially problematic for blacktip sharks, which mostly inhabit warm waters and thus are captured by recreational anglers in places with generally high air temperatures throughout the year (e.g., Florida; Shiffman et al. 2014, 2017). We did not explicitly test for the effects of cloud cover or solar radiation strength on shark body surface temperatures; however, for all individuals sampled, which likely occurred during days of differing cloud cover and solar radiation, we found significant increase in body temperatures with exposure time.

In our study, immature blacktip sharks showed a higher rate of body surface temperature increase than mature sharks captured in the same area and under the same environmental conditions. It is possible that, in addition to the role shark surface area plays in heat exchange with the environment, shark mass also plays a role in the patterns found, since mass is strictly related to metabolism in ectothermic vertebrates (Stevenson 1985) and might thus influence the thermal dynamics during capture and subsequent air exposure. The lethal and sublethal effects of capture on sharks based on their body size are still poorly understood. Previous studies indicate that smaller fish and sharks are more affected by the stress of capture (Davis and Olla 2002; Halliday and Pinhorn 2002; Davis and Parker 2004). For example, Gallagher et al. (2014) found that in the five species of sharks captured in pelagic longline fisheries as bycatch, at-vessel mortality rates were higher for smaller individuals, perhaps in part because of stress while fighting on the lines. In addition, smaller animals often exhibit higher mortality rates that seem to be linked to hook-related injuries (Arlinghaus et al. 2008). So it is possible that the increases in body surface temperatures we found for immature/smaller blacktip sharks could be an added level of stress to sharks resulting from capture and handling.

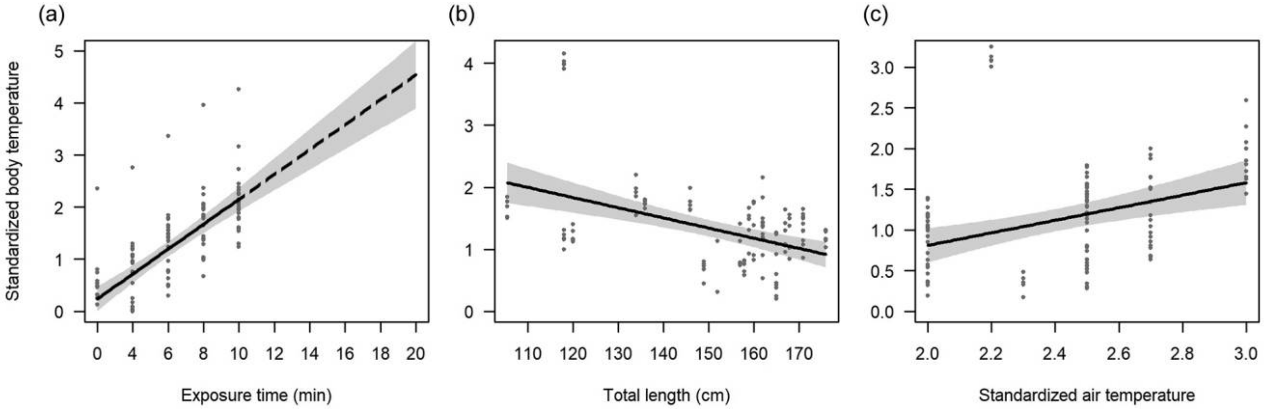

Figure 3. Generalized linear model of blacktip shark body surface temperature variation including the effects of exposure time (*a*; the dashed line is for the predicted function), total length (*b*), and standardized air temperature (*c*). The shaded areas and points, respectively, depict the 95% confidence intervals and the raw data.

Despite a parallel relationship between internal and body surface temperatures in fish (Garrick 2008; Romanovsky 2014), we did not measure core body temperatures of the individuals studied and thus do not know how internal temperatures may have been influenced as a consequence of a warming body surface. Elevated core body temperature in *Carcharhinus limbatus* was reported in the 1970s through measurements of muscle temperature using thermistor probes (Carey et al. 1972), and significant metabolic heat gain (i.e., endothermy) was hypothesized as a potential source, since the animals exhibited a body temperature about 4°C higher than the surrounding environment. Our results revealed a clear increase in body surface temperatures related to air exposure. It is possible that the increase in temperature described here may have contributed, at least in part, to the internal temperatures measured by Carey et al. (1972). Hence, future work of this kind should consider integrating methods for assessing the relationships between air exposure, body surface temperature, internal body temperature, and metabolic, cardiac, and respiratory rates.

In this study, we found that the body surface temperature of the sharks analyzed generally reached that of the ambient air temperature in approximately 9 min of exposure. This finding is relevant in the context of fishing practices, since it determines the threshold at which thermal alterations begin to occur. In our study, we chose a noninvasive and nonlethal approach (Hammerschlag and Sulikowski 2011) that allowed us to opportunistically measure body surface temperatures of sharks during shark-tagging surveys with the goal of minimizing air exposure during sampling and tagging to promote vitality. Thus, exposure times were relatively short (maximum of 10 min) when compared to what is sometimes observed in recreational or commercial fisheries. However, our model suggested that body surface temperature changes exceeding 4°C above ambient water temperature were achievable over 20 min of exposure. This suggests the potential for physiological consequences from ambient air temperatures during fishing activities where sharks are captured and air exposed during handling.

In this study, we did not assess possible postrelease physiological disturbance or behavioral impairment as a consequence of body surface temperature increases from air exposure. We suggest that future studies of this kind should undertake postrelease monitoring to assess potential fitness consequences resulting from changes in shark body temperatures from air exposure. It is also worth considering that the increase in shark body surface temperatures we measured in this study may have been a result of the combined effects of air temperature and solar radiation. Future studies may seek to tease apart the two effects. Doing so would be significant in the case of sharks that are captured and maintained submerged at the surface on lines, where they are exposed for long periods to high solar radiation. This exposure not only could have implications for thermal dynamics but also could cause oxidative stress, at a level still unknown, to these animals.

In summary, this study uses a novel noninvasive approach to investigate aspects of shark thermal dynamics during air exposure. Given that in both recreational and commercial fisheries sharks are often exposed to air and thus vulnerable to temperature changes before release, understanding the potential physiological effects on shark health and survival should be explored, as it may be a form of added stress with potential deleterious effects.

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APPENDIX

Table A1: Stepwise variable selection for the generalized linear model of blacktip shark body surface temperature variation

Model	AIC	ΔAIC	*w*AIC
Null	340.06	91.47	<.0001
Air exposure time (ET)	279.48	30.89	<.0001
Standardized air temperature (SAT)	335.12	86.53	<.0001
Shark total length (TL)	330.38	81.79	<.0001
Sex[a]			
ET + SAT	269.25	20.66	<.0001
ET + TL	260.54	11.95	.0025
ET + TL + SAT[b]	248.59	0	.9974

Note. AIC = Akaike information criterion.

[a] Variable discarded for lack of statistical support ($P > 0.05$).

[b] Final model.

Table A2: Summary of ANOVA between generalized linear models of blacktip shark body surface temperature variation

Model 1	Model 2	Residual df	Residual deviance	df	Deviance	*P*
Null		114	125.13			
Null	ET	113	72.61	1	52.53	<.001
ET	ET + TL	112	60.52	1	12.08	<.001
ET + TL	ET + TL + SAT	111	53.61	1	6.91	<.001

Note. The ANOVA used χ^2 tests to investigate whether the inclusions of new predictors to the model were statistically significant. Included are the models that were analyzed; the residual degrees of freedom (df) and residual deviance; and the df, deviance, and *P*-value. ET = air exposure time; TL = shark total length; SAT = standardized air temperature.

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