SUPPLEMENT • MANATEES

REVISTA DE Biología Tropical

https://doi.org/10.15517/rev.biol.trop..v71iS4.57272

Heat loss or heat uptake? Skin temperature in Antillean manatees (*Trichechus manatus manatus,* Sirenia: Trichechidae) in Belize

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Received 13-VII-2022. Corrected 09-II-2023. Accepted 12-IV-2023.

ABSTRACT

Introduction: The two subspecies of the West Indian manatee (*Trichechus manatus*), Florida manatees (*T. m. latirostris*) and Antillean manatees (*T. m. manatus*), face different environmental challenges. While Florida manatees have to cope with winter water temperatures below their lower critical temperature of ~ 20 °C and air temperatures below freezing, Antillean manatees live in year-round warm Caribbean waters. Sirenians lack effective thermal insulation and have limited capability of controlling peripheral heat loss. Although severe cold related health issues and mortality are primarily known in Florida manatees, it can be assumed that Antillean manatees and other extant sirenians share the cold-sensitivity, but hardly ever experience it. Contrarily, during summer, Antillean manatees may face the opposite form of thermal stress by being exposed to water temperatures close to their body temperature. However, the upper critical temperature of manatees is not known.
Objective: To improve understanding of the impact of high ambient temperatures on manatee physiology.
Methods: We measured skin temperature in six Antillean manatees in two different habitats in Belize, and compared the results to skin temperatures measured in two captive Florida manatees.
Results: We found a similar temperature distribution pattern over the body surface in both subspecies, but significantly higher temperatures and larger temperature ranges among measuring points in Antillean manatees as compared to Florida manatees. In one Antillean manatee, skin temperature was consistently lower than ambient water temperature by up to 2.5 °C. This implies potential heat uptake from the environment, in contrast to the heat loss experienced by Florida manatees at low water temperatures, apparent in skin temperatures above ambient water temperature.
Conclusions: Our findings suggest that heat stress may be a more likely risk for manatees in warm tropical waters. Despite the small sample size, our results present important findings towards understanding thermal tolerance and impact of high ambient temperatures on manatee physiology.

Key words: thermoregulation; peripheral heat loss; heat dissipation; heat retention; blubber lipid composition; thermoregulatory adaptations; surface area to volume ratio SA:V.

RESUMEN

¿Pérdida o absorción de calor? Temperatura de la piel en manatíes antillanos (*Trichechus manatus manatus*, Sirenia: Trichechidae) en Belice

Introducción: Las dos subespecies del manatí antillano (*Trichechus manatus*), los manatíes de Florida (*T. m. latirostris*) y los manatíes antillanos (*T. m. manatus*), enfrentan diferentes desafíos ambientales. Mientras que los manatíes de Florida tienen que hacer frente a temperaturas invernales del agua por debajo de su temperatura crítica ~20 °C y temperaturas del aire por debajo del punto de congelación, los manatíes antillanos viven en aguas cálidas del Caribe durante todo el año. Los sirenios carecen de un aislamiento térmico efectivo y tienen una capacidad limitada para controlar la pérdida de calor periférico. Aunque los problemas de salud y la mortalidad relacionados con el frío se conocen principalmente en los manatíes de Florida, se puede suponer que los manatíes antillanos y otros sirenios existentes comparten la sensibilidad al frío, pero casi nunca la experimentan. Por el contrario, durante el verano, los manatíes antillanos pueden enfrentar la forma opuesta de estrés térmico al estar expuestos a temperaturas del agua cercanas a la temperatura de su cuerpo. Sin embargo, se desconoce la temperatura crítica superior de los manatíes.

Objetivo: Mejorar la comprensión del impacto de las altas temperaturas ambientales en la fisiología del manatí.

Métodos: Medimos la temperatura de la piel en seis manatíes antillanos en dos hábitats diferentes en Belice y comparamos los resultados con las temperaturas de la piel medidas en dos manatíes de Florida en cautiverio.

Resultados: Encontramos un patrón de distribución de temperatura similar sobre la superficie del cuerpo en ambas subespecies, pero temperaturas significativamente más altas y rangos de temperatura más amplios entre los puntos de medición en los manatíes antillanos en comparación con los manatíes de Florida. En un manatí antillano, la temperatura de la piel fue consistentemente más baja que la temperatura ambiente del agua hasta en 2.5 °C. Esto implica una posible absorción de calor del medio ambiente, en contraste con la pérdida de calor que experimentan los manatíes de Florida a bajas temperaturas del agua, lo cual se evidencio con temperaturas de la piel por encima de la temperatura ambiente del agua.

Conclusiones: Nuestros hallazgos sugieren que el estrés por calor puede ser un riesgo más probable para los manatíes en aguas cálidas tropicales. A pesar del pequeño tamaño de la muestra, nuestros resultados presentan hallazgos importantes para comprender la tolerancia térmica y el impacto de las altas temperaturas ambientales en la fisiología de estos mamíferos marinos.

Palabras clave: termorregulación; pérdida de calor periférica; disipación de calor; retención de calor; composición de lípidos de grasa; adaptaciones termorreguladoras; relación superficie-volumen SA:V.

INTRODUCTION

Florida manatees, *Trichechus manatus latirostris* (Harlan, 1824) and Antillean manatees, *Trichechus manatus manatus* (Linnaeus, 1758) are the two subspecies of the West Indian manatee (*T. manatus*). While Antillean manatees are found in the Caribbean and from Mexico down south to the coast of Brazil (Marsh et al., 2011), Florida manatees primarily inhabit Florida coastal and inland waters, with a typical range from Texas to North Carolina in summer with occasional sightings as far north as Massachusetts (Marsh et al., 2011). Although their habitats overlap to a small extent in the Caribbean, each subspecies faces different environmental challenges.

Florida manatees are the northern most Sirenian population and have to face water temperatures (T_{water}) as low as 13 °C in winter over extended periods of time along with air temperatures (T_{air}) below freezing in contrast to summer water temperatures of up to 32 °C and higher (National Oceanic and Atmospheric Administration, 2022). Florida manatees are known to be very sensitive to cold with low metabolic rates (Scholander & Irving, 1941) and a high lower critical temperature of ~ 20 °C (Irvine, 1983) due to poor thermal insulation and limited control of peripheral heat loss. Therefore, they rely on behavioral thermoregulation and migrate to warm water refuges when temperatures drop (Marsh et al., 2011). Still, cold stress is a major threat to Florida manatees, and cold stress syndrome (CSS) affects and kills manatees every winter (Bossart et al., 2002; Hardy et al., 2019). Extant sirenians share low metabolic rates (Gallivan & Best, 1980) and lack of effective thermal insulation (Horgan et al., 2014) and other thermoregulatory adaptations to the aquatic life style (Bryden et al., 1978; Fawcett, 1942; Gallivan et al., 1983), present in other marine mammal species. Therefore, Antillean manatees and other extant sirenians are likely sensitive to cold as well, which is furthermore supported by reports of cold water avoidance behavior (Anderson, 1986; Zeh et al., 2018).

In contrast to Florida manatees, Antillean manatees live in year-round warm Caribbean waters, and knowledge about potential cold sensitivity is only anecdotal. Contrarily, they may experience T_{water} in the range of mammalian body temperature (T_{body}) during summer months (Kaufman & Thompson, 2005), which poses an entirely different thermoregulatory challenge. To investigate and assess the potential risk of heat stress in manatees, knowledge of their upper critical temperature is required. However, manatee upper critical temperature is currently not known.

Due to manatees' poor thermal insulation and limited ability to control peripheral heat loss, their skin temperature (T_{skin}) is ideally suited to indicate the animal's thermal state by assessing heat exchange between body surface and environment (Erdsack et al., 2018; Worthy et al., 2000). Long-term studies of T_{skin} and heat flux in two captive Florida manatees indicated areas of increased heat exchange on the body surface, temperature distribution patterns and potential impact of ambient temperature on manatee T_{skin} (Erdsack et al., 2018; N. Erdsack unpublished).

Besides the unknown upper critical temperature, knowledge about manatee thermoregulation, in particular the impact of high ambient temperature is incomplete. In order to fill some of these gaps, we measured T_{skin} in wild Antillean manatees captured for health assessments in two different habitats in Belize. Here, we present these preliminary data in comparison to T_{skin} measured in captive Florida manatees between 2016 and 2021.

T_{skin} was measured in six adult Antillean manatees captured for health assessments in Belize in May 2019: three females in Southern Lagoon, around Gales Point, and a female and two males in the waters around Placencia. The manatees were captured using a circle net and hefted onto the capture boat for processing. T_{skin} measurements took approximately 10 min and started as soon as the net was removed and the animal was in a safe and stable position on the boat. If necessary, mud was rinsed off with sea water. Animals were shaded by a tarp during processing. T_{skin} was measured using a wireless thermometer with an attached K-Type surface thermocouple (TMD-55W, Amprobe, Everett, WA, USA), which was also used in a long term study of T_{skin} measurements in captive Florida manatees (N. Erdsack unpublished). The 14 defined measuring spots on the manatees' dorsal body surface (Fig. 1A) were selected in accordance with this study (N. Erdsack unpublished). The two trained manatees ("Hugh", "Buffett") are held at Mote Marine Laboratory, Sarasota, FL, U.S. in an outdoor tank at a constant water temperature of 26.3±0.4 °C. For measurements, the manatees were stationing at the water surface and the respective body part was lifted above the water surface. For comparison with Antillean manatees, only measurements at average T_{air} comparable to average T_{air} during measurements in Belize were considered (Hugh: n = 7; Buffett: n = 6). Temperature differences were tested for statistical significance using a two-tailed paired or homoscedastic t-test, respectively, in MS-Excel 2019. Level of significance was $\alpha = 0.5$. Relations between T_{skin} and T_{water}, T_{air} were reported using Pearson correlation coefficient (r).

Average T_{skin} per measuring point in Antillean and Florida manatees are displayed in Fig. 1B. Both subspecies exhibited similar temperature distribution patterns over the body surface. Except for the almost identical temperature on the top of the head, manatees in Southern Lagoon and Placencia exhibited almost congruent temperature distribution patterns. However, average T_{skin} in manatees in Southern Lagoon was significantly higher than in manatees captured around Placencia ($p << 0.0001$), and average T_{skin} in Antillean manatees was significantly higher than in Florida manatees ($p << 0.0001$). Moreover, average temperature range amongst measuring points was significantly larger in Antillean manatees (2.92 ± 1.08 °C, $p = 0.0011$) as compared to Florida manatees (1.28 ± 0.74 °C). One animal captured in Southern Lagoon at T_{water} = 33 °C had average

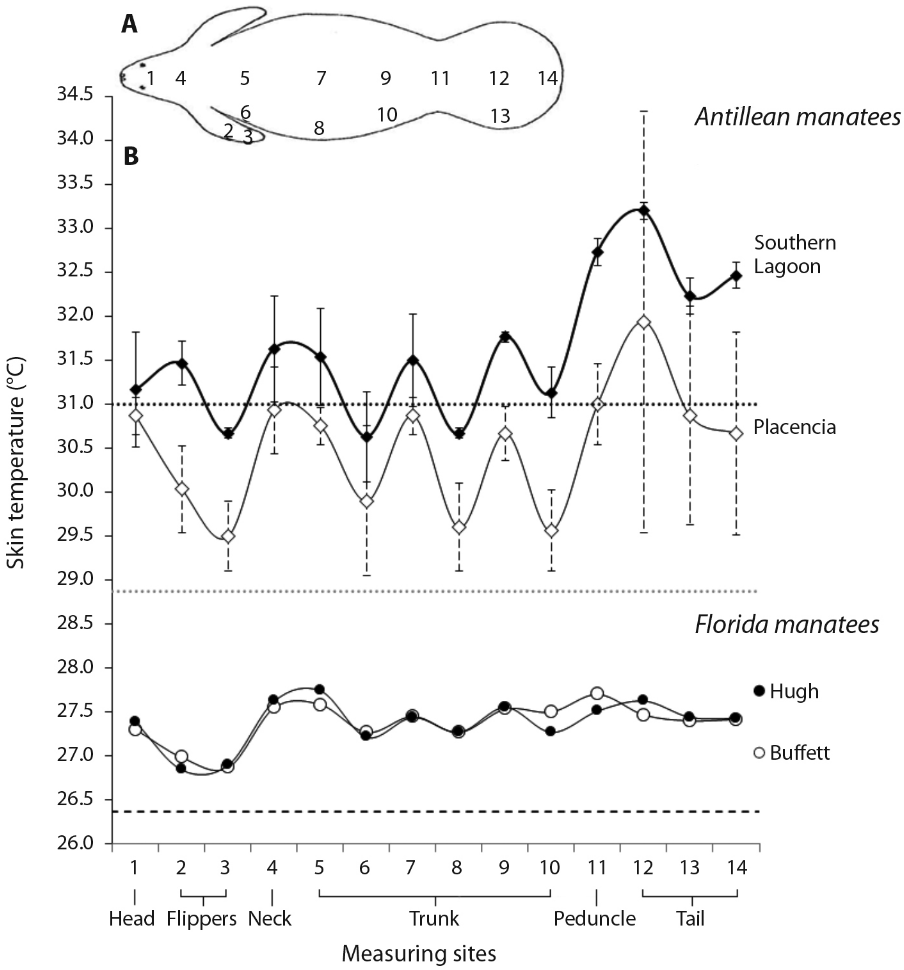

Fig. 1. Location of measuring spots on the manatees' dorsal body surface including ventral (P2) and dorsal (P3) side of the pectoral flipper (A) and average T_{skin}+SD per measuring point (B) in Antillean manatees captured in Southern Lagoon (black diamonds, n = 3), and Placencia (white diamonds, n = 3), and in two captive Florida manatees (Hugh: black dots, n = 7; Buffett: black circles, n = 6). Average T_{water} during measurements was 31±1.7 °C in Southern Lagoon (black dotted line), 28.9±0.6 °C in Placencia (gray dotted line), and 26.3±0.4 °C in the Florida manatee tank (dashed line). Average T_{air} during measurements was 30.2±0.8 °C in Belize, and 30.7±1.3 °C in Florida.

T_{skin} = 31.6 °C and $T_{skin} < T_{water}$ in all but one of the measuring points (center of the tail, P12 = 33.1 °C). In Southern Lagoon, average T_{water} during measurements was 31 ± 1.7 °C, in Placencia 28.9 ± 0.6 °C, and 26.4 ± 0.3 °C in the Florida manatee tank. Average T_{air} during measurements was 30.2 ± 0.8 °C in Belize, and 30.7 ± 1.3 °C in Florida. In Antillean manatees, T_{skin} was weakly correlated to T_{water} (r = 0.60), but no correlation to T_{air} (r = 0.29) was found.

Our measurements revealed similarities but also significant differences in average T_{skin} and T_{skin} distribution between Antillean and Florida manatees. Distribution of T_{skin} over the body surface, indicating body locations with higher and lower heat exchange with the environment, was similar in both subspecies. However, in Antillean manatees, this pattern was much more pronounced, that is, temperature differences between measuring points were significantly larger in Antillean manatees (up to 4.8 °C in individual manatees) than in Florida manatees (up to 2.7 °C). The overall higher T_{skin} in Antillean manatees can likely be attributed to the higher T_{water} in Belizean waters, as indicated by the positive correlation between T_{skin} and T_{water} found in Antillean manatees (r = 0.6). A potential impact of netting and handling on metabolic rate and thermal state of individual manatees cannot be excluded. However, T_{water} cannot explain the significantly larger temperature ranges on the body surfaces of Antillean manatees in comparison to Florida manatees.

The most obvious difference between the two subspecies is their body size. Antillean manatees are on average smaller than their Florida conspecifics (Castelblanco-Martínez et al., 2021; Wong et al., 2012), which are the largest extant Sirenian (sub)species. Since heat exchange with the environment occurs primarily via the body surface, a reduced surface-area-to-volume ratio (SA:V) is favorable in terms of heat retention in the cold (Schmidt-Nielsen, 1997). Florida manatees' larger body size along with the small pectoral flippers found in all sirenians result in a reduced SA:V, constituting an adaptation to the colder climate they inhabit in comparison to other extant Sirenians. This was even more pronounced in the extinct Steller's sea cow, *Hydrodamalis gigas* (Zimmermann, 1780), which inhabited the cold waters of the Bering Sea with estimated body lengths and masses up to 10 m and 10 000 kg (Marsh et al., 2011). In comparison to Florida manatees, Antillean manatees have larger SA:Vs due to their smaller body size (Castelblanco-Martínez et al., 2021). Heat retention is likely not essential in this subspecies, considering that they rarely experience T_{water} < 18 °C. Contrarily, during summer, Antillean manatees may experience T_{water} in the range of mammalian T_{body}. Data on manatee core T_{body} is scarce. Irvine (1983) reported rectal temperatures of 27-32 °C measured in three captive Florida manatees, but simultaneously measured stomach temperatures of 35-36.8 °C, which, moreover, could be significantly impacted by food intake. Recent measurements of pharyngeal temperature in 20 captive Florida manatees resulted in 35.1-35.9 °C (Martony et al., 2020). Average oral temperature measured in wild manatees during health assessments was significantly higher in Antillean (34.6 ± 0.9 °C) than in Florida (32.6 ± 1.8 °C) manatees (Wong et al., 2012). It is likely that during summer months, T_{water} in shallow Caribbean lagoons can reach and exceed these values, regarding that we measured T_{water} up to 33 °C in Southern Lagoon as early as May. Marsh et al. (2011) even mentioned T_{water} as high as 41 °C in an area frequented by Florida manatees in summer. Without a thermal gradient from the body surface to the surrounding water, an animal is not capable of dissipating excess heat, which will eventually result in heat stress. Average T_{skin} measured in one Antillean manatee in Southern Lagoon with $T_{skin} < T_{water}$ did not differ from average T_{skin} measured in the other manatees in Southern Lagoon; however, T_{water} was higher. We did not observe physiological abnormalities in this manatee, suggesting the presence of physiological and/or behavioral adaptations that help them deal with these extreme thermal conditions, at least temporarily. These findings also leave room for speculations about upper critical temperature and thermal tolerance in Antillean manatees, which may be relatively high in the water.

As the differing body sizes, the observed temperature distribution pattern along with the differences in T_{skin} and T_{skin} ranges over the body surface may indicate anatomical adaptations to differing thermal environments. Sirenians lack arteriovenous anastomoses (AVAs) in the skin (Bryden et al., 1978; Fawcett, 1942), which are essential structures for the regulation of peripheral heat dissipation and retention (Hales, 1985). Thus, the observed temperature distribution pattern on the manatees' body surfaces likely displays underlying anatomical structures and conditions, such as distribution of blood vessels, differences in skin thickness, and variations in blubber distribution. Since manatees, in contrast to other marine mammals, do not have thick insulating blubber layers (Reynolds & Lynch, 2017), potential differences in blubber distribution are more likely in lipid composition rather than thickness. Blubber lipid composition varies between species and individuals (Iverson, 2009), as well as intra-individually between body locations and seasons (Neises et al., 2021). Blubber lipid composition in Antillean manatees may have evolved to facilitate higher heat transfer as opposed to thermal insulation and heat retention. Despite the analogous distribution of blood vessels in the subspecies, apparent in the similar temperature distribution pattern, in Antillean manatees, heat dissipation from underlying blood vessels would be more apparent in increased temperatures in the overlying skin. A further possible cause for the higher T_{skin} range measured in Antillean manatees could be increased heat dissipation at the less insulated body parts at high T_{water}. This is indicated by significantly higher T_{skin} at head, flippers and in particular the tail ($p = 0.0001$) than on the trunk, found in Antillean manatees, but not in the Florida manatee data presented here.

The absence of a correlation between T_{air} and T_{skin} in the presented data can likely be attributed to the preliminary state of the data, with small sample sizes and similar T_{air} during measurements. Heat flux measurements in Florida manatees indicated a potential impact of T_{air} on heat flux (Erdsack et al., 2018). In any case, more temperature measurements in Antillean and in particular wild Florida manatees under varying environmental conditions are required. Comparative analyses of blubber lipid composition will help identify potential differences in thermal properties of blubber and their role in manatee thermoregulation. Despite limitations due to small sample size, our findings provide valuable new information and an important step towards a better understanding of thermal tolerance in manatees and the impact of environmental temperature on manatee physiology, thermoregulation and health. This knowledge is essential for the prevention and treatment of thermal stress in the threatened West Indian manatee.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that they followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

Author Contribution: NE was responsible for data collection, data analysis, and preparation of the initial, revised, and final manuscript, JG assisted in data collection, provided background and environmental information, and JP provided supervision, infrastructure, and technical information for this project. Both JG and JP contributed to various versions of the manuscript.

ACKNOWLEDGEMENTS

Manatee research in Belize was conducted under a scientific research permit (#FD/WL/1/19 (20)) issued by the Belize Forest Department and was part of a Clearwater Marine Aquarium Research Institute long-term manatee research and conservation project. We would like to thank Dr. Robert Bonde and Cathy Beck of USGS as well as the Government of Belize and local partners for their expertise and support. Manatee captures were facilitated by our experienced local crew from Gales Point and many volunteers from Belize and abroad. The skin temperature study in Florida manatees was funded by a Research Grant of the German Research Foundation to NE (DFG, ER 800/1-1) and performed under USFWS permits MA837923-8 and MA100361-4.

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