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NOTE

Regionally endothermic traits in planktivorous basking sharks *Cetorhinus maximus*

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ABSTRACT: Few fast-swimming apex fishes are classified as 'regional endotherms', having evolved a relatively uncommon suite of traits (e.g. elevated body temperatures, centralised red muscle, and thick-walled hearts) thought to facilitate a fast, predatory lifestyle. Unlike those apex predators, Endangered basking sharks *Cetorhinus maximus* are massive filter-feeding planktivores assumed to have the anatomy and physiology typical of fully ectothermic fishes. We combined dissections of stranded specimens with biologging of free-swimming individuals and found that basking sharks have red muscle located medially at the trunk, almost 50% compact myocardium of the ventricle, and subcutaneous white muscle temperatures consistently 1.0 to 1.5°C above ambient. Collectively, our findings suggest basking sharks are not full ectotherms, instead sharing several traits used to define a regional endotherm, thus deviating from our current understanding of the species and questioning the link between physiology and ecology of regionally endothermic shark species. With successful forecasting of population dynamics and distribution shifts often improved by accurate physiological data, our results may help explain movement patterns of the species, which could ultimately facilitate conservation efforts.

KEY WORDS: Regional endothermy · Ectotherm · Physiology · Anatomy · Biologging

1. INTRODUCTION

Fast swimming is thought to be greatly facilitated in some groups of fish by anatomical and physiological traits that purportedly enhance sustained metabolic and mechanical power (Bernal et al. 2003a). Several lineages of active predatory fishes (e.g. sharks and tunas) have evolved centralisation of the skeletal red muscle at the trunk and other anatomical structures such as the *rete mirabile* heat exchanger, which limit conductive and convective heat loss (Carey et al. 1982). Consequently, these species tend to maintain

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their red muscle at temperatures above ambient and so are often referred to as 'regional endotherms' (Watanabe et al. 2015). Regional endotherms swim faster than similar-sized ectothermic fishes (Harding et al. 2021) and generally have elevated metabolic rates (relative to body mass; Payne et al. 2015), with specialisations such as comparatively large gill surface areas and, often, thick-walled hearts that have a high proportion of compact myocardium (although some exceptions exist; Brill & Bushnell 1991).

Several hypotheses attempt to explain the key ecological advantages of regional endothermy, including expansion of spatial and temporal thermal niches (Weng et al. 2005), faster cruising speeds (Watanabe et al. 2015, Harding et al. 2021), and enhanced environmental perception (Block & Carey 1985). The order Lamniformes contains the only regionally endothermic sharks described in the literature (Lamnidae and Alopiidae) (Carey & Teal 1969, Bernal et al. 2001, Bernal et al. 2003a). All are fast, high-performance, apex predators, so an intuitive link can be drawn between their shared anatomy, physiology, and ecology. The basking shark *Cetorhinus maximus* is a sister taxon to the predatory Lamnidae (Bernal et al. 2001), it is explicitly considered an ectothermic species (Bernal et al. 2001, Watanabe et al. 2015, Ciezarek et al. 2016) and is a low trophic-level filter-feeder that specialises on zooplankton (Sims 1999, 2000). Nevertheless, the basking shark's cruising swim speed (~1.1 m s^{-1}; Sims 1999, 2000) and migration speed (e.g. 9589 km in 82 d; Gore et al. 2008) are more similar to that of regionally endothermic sharks than similarly sized ectothermic fish (Watanabe et al. 2015, Harding et al. 2021). Accordingly, there are both phylogenetic and behavioural reasons to suspect that basking sharks may exhibit anatomical and physiological traits more typical of regional endotherms than full ectotherms.

Basking sharks are globally Endangered (Rigby et al. 2021), and their anatomy and physiology are difficult to study because of the paucity of freshly dead specimens from strandings or accidental capture. Studying the physiology of very large free-swimming sharks is challenging, with no direct internal temperature measurements ever made, to our knowledge, for free-swimming basking sharks. Accurate physiological data can inform robust predictions of population shifts and changes in distribution patterns under climate change (Kearney & Porter 2009), which may help refine future spatial conservation efforts. In this study, we combined opportunistic beach dissections with subcutaneous white muscle temperatures recorded from biologging tags to determine whether red muscle distribution, proportion of compact myocardium, and body temperatures were more similar to those of regionally endothermic shark species or their fully ectothermic counterparts.

2. MATERIALS AND METHODS

2.1. Red muscle distribution and compact myocardium

In 2020, beach dissections were conducted in England on carcasses of 2 stranded male basking sharks measuring 3.8 and 4.5 m total length (Specimens A and B, respectively). Logistical constraints and local government environmental health regulations prevented us from taking full transverse sections through the body of the sharks. Instead, 13 approximate half cross-sections were made from Specimen A and 5 from Specimen B. Images were taken of either the anterior or posterior side of the cross-sections. A 3D reconstruction of skeletal red muscle distribution was created in computer-aided design software (Autodesk 3ds Max 2021, Autodesk Media and Entertainment) using images of whole animals, with red muscle position estimated throughout using images of cross-sections from Specimens A and B.

In 2021, hearts were collected from carcasses of a further 2 basking sharks stranded on the west coast of Ireland, comprising a 6.9 m TL female and a 4.8 m TL male (Specimens C and D, respectively). Hearts were extracted and kept on ice for <24 h before removal of chamber blood and dissection and weighing of the ventricle's compact and spongy components. Because the ventricle's compact and spongy tissue were distinguishable by eye, the 2 tissues were dissected apart and individually weighed using a digital scale.

2.2. Body and ambient water temperature

A new electronic biologging tag package was deployed for body temperature measurements without the need for capture or handling for sensor attachment, reducing potential stress to the animal. Subcutaneous white muscle and ambient water temperature sensors (LAT1810S, accuracy of 0.02°C, Lotek Wireless) were engineered into the package and deployed under license from the Health Products Regulatory Authority of Ireland (AE19136/P127) on 4 free-swimming basking sharks off the coast of Ireland in 2021. Tagged basking sharks measured between 5 and 8 m TL. The internal temperature sensor (200 mm flexible stalk with 70 mm bend relief) was deployed on free-swimming sharks using a custom-designed pole spear to insert the sensor with a titanium M-style dart (Wildlife Computers) no more than 10 cm into the white muscle, with sensor depths estimated between 5 and 7 cm below the subcutaneous layer. A galvanic timed-release link detached from the anchor line approximately 12 h after deployment. Buoyancy and drag of the syntactic foam flotation (surrounding transmitters used to locate the tag post release; VHF transmitter model MM120, Advanced Telemetry Systems and Satellite Position Only Tag model 258, Wildlife Computers) forced the internal temperature sensor from the body upon release. Apart from the titanium dart that pierced the white muscle, sharks were not handled in any other way, and all 4 were seen feeding at the surface within minutes of tag deployment. Calibrated external ambient water temperature and subcutaneous white muscle temperature data were collected at 0.1 Hz and plotted against time in RStudio (RStudio Team 2019).

To check for the contribution of thermal inertia to basking shark body temperature, we adopted an allometric relationship between body mass and heat-transfer coefficients to simulate how body temperature of large basking sharks should vary if they were full ectotherms. We then compared those models to our measured basking shark data to help understand respective roles of body size versus other potential mechanisms in determining body temperature of basking sharks relative to water temperature. We adopted differential equations as described in Nakamura et al. (2020) (see Text S1 in the Supplement at www.int-res.com/articles/suppl/n051p227_supp.pdf).

3. RESULTS

3.1. Red muscle distribution and compact myocardium

Beach dissections of Specimens A and B revealed that basking shark red muscle (Fig. S1 in the Supplement) was not distributed laterally along the trunk, but rather extended from the vertebrae to the edge of a subcutaneous layer of connective tissue (Fig. 1A). Within this connective tissue, and near the lateral extents of red muscle, there appears a paired small artery and large vein (Fig. S2). The red muscle then becomes increasingly lateral towards the caudal fin (Fig. 1A).

Ventricles from Specimens C and D were thick-walled, both having 47% compact myocardium (Fig. 1B).

3.2. Body and ambient water temperature

Biologging data showed that subcutaneous white muscle temperatures of free-swimming basking sharks were consistently 1.0 to 1.5°C higher than ambient water temperature for all 4 individuals across the 6 to 12 h biologging deployments, with gradual

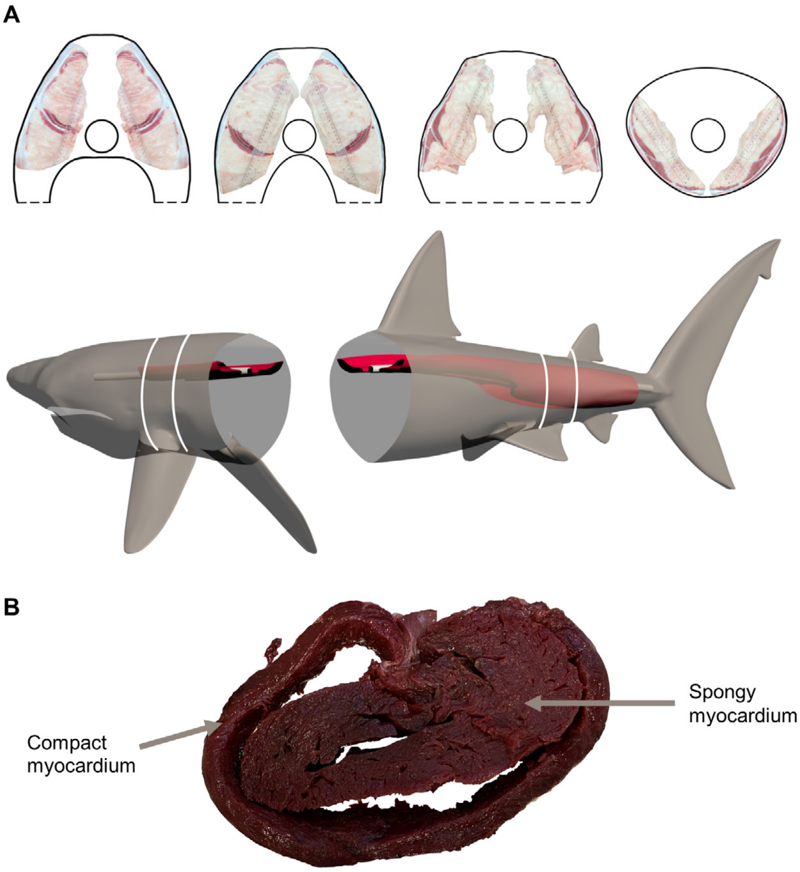

Fig. 1. Anatomical measurements of red muscle distribution and compact myocardium in basking sharks *Cetorhinus maximus*. (A) Anterior to posterior red muscle distribution taken from transverse sections of Specimen A at positions indicated by the white curved vertical lines on the shark. Photographs of transverse sections are incomplete half sections that have been mirrored to aid visual representation (we have not extrapolated distribution anteriorly or posteriorly beyond the extents of our cross-section samples). (B) Ventricular cross-section showing the outer compact myocardium separated by inner spongy myocardium, taken from the atrioventricular junction of Specimen C

declines in body temperature appearing to follow similar general declines in water temperature for 3 sharks (Fig. 2A,B).

Modelled subcutaneous white muscle temperature of a hypothetical fully ectothermic basking shark (Fig. S3) steadily declined toward ambient water temperature over the duration of deployment, whereas our measured subcutaneous white muscle temperature remained consistently elevated above that of ambient for the entire duration of deployment (Fig. 2B).

4. DISCUSSION

While the proportion of red muscle could not be investigated in this study due to logistical constraints at dissections, its location in basking sharks is nonetheless more medial than in typical ectothermic species, such as the blue shark *Prionace glauca* and the leopard shark *Triakis semifasciata* (Bernal et al. 2003a), which have most red muscle immediately beneath the subcutaneous layer. Basking shark red muscle does not form a cylindrical band adjacent to the vertebral column as seen in regionally endothermic salmon shark *Lamna ditropis* and shortfin mako shark *Isurus oxyrinchus* (Bernal et al. 2003a); however, there appears to be a paired small artery and large vein within the connective tissue of the basking shark, near the lateral extents of the red muscle — traits shared with regionally endothermic shortfin mako and white sharks *Carcharodon carcharias*, whose vessels then branch inwards towards the vertebrae to form the heat-exchanging rete (Carey et al. 1982).

Basking shark ventricles had an average 47% outer compact myocardium. The presence of well-developed compact myocardium is thought to facilitate higher blood pressures and blood flows, augmenting the uptake of oxygen across the gills and its offloading at the tissue, particularly the aerobic red muscle. It is often, but not exclusively, found in active, high-performance swimmers that ram ventilate (Brill & Bushnell 1991). Accordingly, highly active regional endotherms tend to have large proportions of compact myocardium, similar to basking sharks. For example, shortfin mako and white sharks have 36 and 42% compact myocardium respectively

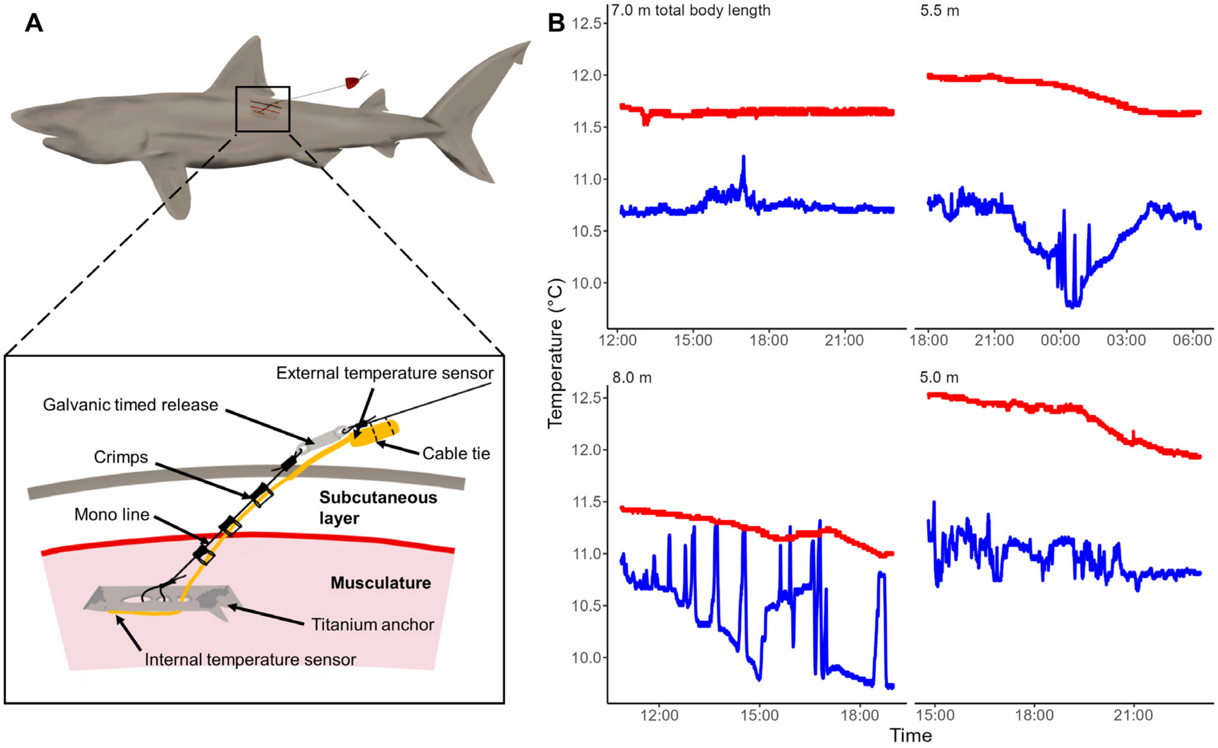

Fig. 2. Biologging tag package and subcutaneous body temperature in free-swimming basking sharks. (A) Titanium anchor deployed into white muscle (between 5 and 7 cm under the subcutanous layer) below the dorsal fin with a biologging device recording temperature (LAT1810S), and a towed float recovery package (shown in red behind the shark's dorsal fin) consisting of a VHF transmitter (model MM120, Advanced Telemetry Systems) and a satellite position only tag (model 258, Wildlife Computers). (B) Subcutaneous white muscle temperature (red lines) compared with ambient water temperature (blue lines) in 4 free-swimming basking sharks across entire deployment periods

(Farrell & Smith 2017), and Pacific mackerel *Scomber japonicus* and Atlantic bluefin tuna *Thunnus thynnus* have approximately 40% (Brill & Bushnell 1991, Farrell & Smith 2017). In contrast, the vast majority of fish species have almost no compact myocardium at all (ca. 80%; Santer & Walker 1980), and those that do generally have less of it. For example, the massive planktivorous and ectothermic whale shark *Rhincodon typus* has only 3% compact myocardium (Hirasaki et al. 2018). Nonetheless, some fully ectothermic and apparently less-active species also have high proportions of compact myocardium (e.g. common carp *Cyprinus carpio*; Brill & Bushnell 1991), so it cannot be used as a clear distinguishing feature, but the regionally endothermic sharks examined to date all have a high percentage of compact myocardium (Emery et al. 1985, Bernal et al. 2003b, Farrell & Smith 2017, Hirasaki et al. 2018).

Biologging data showed that subcutaneous white muscle temperatures of free-swimming basking sharks were consistently 1.0 to 1.5°C higher than ambient water temperature. A temperature elevation of this magnitude in this location is similar to that reported for the regionally endothermic shortfin mako shark (~1.0°C elevation; Carey & Teal 1969), and much greater than that of similarly sized — but fully ectothermic — whale sharks that showed no measurable elevation (Nakamura et al. 2020). Therefore, it is plausible that the deeper white and red muscle of basking sharks will be even warmer closer to the vertebrae, as reported in regionally endothermic sharks; for example, salmon shark subcutaneous white muscle is 1 to 2°C warmer than ambient, whereas its centrally located red muscle can be more than 15°C warmer (Bernal et al. 2005). It is possible that the elevated subcutaneous body temperature of basking sharks arises in part from their large body size and associated thermal inertia; however, the lack of consistent subcutaneous muscle temperature elevation above ambient water of the whale shark (Nakamura et al. 2020), which can reach lengths of 18 to 20 m, suggests this is unlikely the sole explanation for our results. Furthermore, heat-transfer models show that ectothermic sharks exhibit subcutaneous body temperatures that converge toward ambient water temperature, just at slower rates for larger species (Nakamura et al. 2020; also see the Supplement). In contrast, endothermic fishes at constant water temperature have a consistently elevated body temperature (as our basking shark data show) due to the greater contribution and retention of metabolic heat not seen in fully ectothermic species (Malte et al. 2007). Regardless of whether caused by large body size, structures such as the rete mirabile, or other phenomena, our data show that basking sharks have consistent subcutaneous body temperature elevations that are similar to those seen in regional endothermic sharks and quite different to those seen in other large — but ectothermic — shark species.

When viewed collectively, our anatomical and physiological results show that planktivorous basking sharks should at least not be considered fully ectothermic, and arguably should be classed as a regionally endothermic shark based on 3 key traits: (1) red muscle found medially at the trunk, (2) thick-walled ventricle, and (3) elevated subcutaneous body temperatures. This challenges the current understanding that this collection of traits is confined to active, apex predatory fishes at high trophic levels; planktivorous basking sharks are therefore an exception in that respect. Notwithstanding, these findings may help reconcile their close phylogenetic placement to other regionally endothermic shark species (Bernal et al. 2001), along with previous observations that basking sharks cruise at speeds (~1.1 m s^{-1}; Sims 1999, 2000) that are more similar to those of regionally endothermic fishes than their ectothermic counterparts (~0.8 to 1.1 versus ~0.5 to 0.7 m s^{-1}, respectively; Harding et al. 2021) and can undertake rapid, trans-oceanic movements (Gore et al. 2008) apparently at average speeds similar to those of regionally endothermic sharks (Watanabe et al. 2015). The basking shark is additionally unique among sharks in being an obligate ram filter-feeder that can occupy temperate waters (Gore et al. 2008, Johnston et al. 2022). The traits we report here could facilitate, in cooler water, the sustained mechanical power needed to overcome the regular and significant drag arising during ram filter-feeding at speeds averaging ~0.9 m s^{-1} (Sims 1999, 2000), while potentially preserving feeding efficiency (Paig-Tran et al. 2011).

Successful forecasting of population dynamics and distribution shifts is often improved by incorporating accurate physiological information (Kearney & Porter 2009). Endangered basking sharks (Rigby et al. 2021) can undertake long-distance oceanic migrations in relatively short periods of time (82 d; Gore et al. 2008) and can 'overwinter' at high and low latitudes (Sims et al. 2003, Dolton et al. 2020, Johnston et al. 2022). Taken collectively, the new anatomical and physiological insights provided here point toward basking sharks at least not being fully ectothermic and could help explain observed distribution patterns and refine estimates of how they may change in the future.

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