

The red muscle morphology of the thresher sharks (family Alopiidae)

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Summary

A more medial and anterior position of the red aerobic myotomal muscle (RM) and the presence of a vascular counter-current heat exchange system provide the functional elements that facilitate regional RM endothermy in tunas, lamnid sharks and the common thresher shark (*Alopias vulpinus*). The convergent RM morphology among all species capable of RM endothermy suggests that RM position is a strong predictor of fish endothermic capacity. The present study investigated the comparative RM morphology of the other two thresher shark species (bigeye thresher, *Alopias superciliosus*, and the pelagic thresher, *Alopias pelagicus*), for which there is no information regarding their capacity for RM endothermy, and compared these data with published works on *A. vulpinus*. The digitization of transverse sections along the body of *A. superciliosus* and *A. pelagicus* enabled quantification of the relative amount of RM and the position and placement of the RM along the body. The

RM in both *A. superciliosus* and *A. pelagicus* is positioned subcutaneously, along the lateral edges of the myotomes, and is distributed relatively evenly over the trunk of the body. The position of maximum RM area is at 50% fork length (*FL*) for *A. superciliosus* and at 75% *FL* for *A. pelagicus*. The amount of RM (mean \pm S.E.M.) is $2.31 \pm 0.11\%$ and $3.01 \pm 0.10\%$ in *A. superciliosus* and *A. pelagicus*, respectively. When compared with *A. vulpinus*, all three alopiid sharks have a similar amount of RM. However, *A. superciliosus* and *A. pelagicus* differ from *A. vulpinus* in that they do not possess the medial and anterior RM arrangement that would likely facilitate metabolic heat conservation (RM endothermy).

Key words: *Alopias*, endothermy, red muscle, aerobic, temperature, retina, lamnid.

Introduction

The warming of the red, aerobic myotomal muscle (RM) is a derived character state documented for the tunas (Scombridae), lamnid sharks (Lamnidae) and the common thresher shark, *Alopias vulpinus* (Bonnaterre 1788; Alopiidae) (Carey and Teal, 1966; Carey et al., 1971, 1985; Bernal and Sepulveda, 2005). These groups have converged upon a similar myotomal framework in which the aerobic heat source (i.e. RM) is shifted to a medial and anterior body position and perfused by a vascular counter-current heat exchange system (rete) (Carey et al., 1971; Graham et al., 1983; Bone and Chubb, 1983; Bernal et al., 2001a). Although many studies have examined the physiology of tunas and lamnid sharks and the degree to which they are convergent for RM endothermy (Carey et al., 1971, 1985; Carey, 1973; Block and Finnerty, 1994; Bernal et al., 2001a; Dickson and Graham, 2004; Donley et al., 2004, 2005), few works have focused on the thresher sharks, and several aspects of their comparative anatomy are still unknown.

There are three recognized thresher shark species (the common thresher, *A. vulpinus*; the pelagic thresher, *Alopias*

pelagicus Nakamura 1935; and the bigeye thresher, *Alopias superciliosus* Lowe 1841) that comprise the family Alopiidae. The group is most readily distinguished from other sharks by an unusually elongate upper caudal lobe that is typically as long as the body itself (Compagno, 1984). Despite the many synapomorphic characters of the alopiid sharks (i.e. caudal fin morphology, dermal denticles, chondrocranial similarities, dentition; Gruber and Compagno, 1981; Compagno, 1990), there is little comparative information on the myotomal anatomy of this group, with most of what is known coming from studies of a single species, *A. vulpinus* (Bone and Chubb, 1983; Bernal et al., 2003).

Although *A. vulpinus* has been recognized as having the RM morphology consistent with that of endothermic species (Bone and Chubb, 1983), it was not until recently that *in vivo* body temperatures confirmed RM endothermy in this species (Bernal and Sepulveda, 2005). Because the thresher sharks (Alopiidae) are not considered to be the sister group to the endothermic lamnid sharks (Lamnidae; Compagno, 1990), the RM morphology and endothermic capacity of *A. vulpinus*

marks the third group to have independently evolved the ability to warm its aerobic swimming musculature (anterior and internal RM perfused by retia).

While the RM morphology of *A. vulpinus* has been documented (Bone and Chubb, 1983; Bernal et al., 2003), it is not known whether the myotomal framework that enables RM endothermy is an alopiid synapomorphy (occurring also in *A. superciliosus* and *A. pelagicus*) or an autapomorphic character state of *A. vulpinus*. There are no morphological studies related to RM endothermy for either *A. superciliosus* or *A. pelagicus*, and only two inconclusive muscle temperature measurements exist for *A. superciliosus* (Carey et al., 1971). Because previous works have established a strong correlation between RM position, vascular specialization (i.e. retia) and RM endothermy, the present study quantified the RM morphology of *A. superciliosus* and *A. pelagicus* and compared the findings with those of *A. vulpinus* (Bernal et al., 2003). The objective of this work was to determine whether *A. superciliosus* and *A. pelagicus* possess the aerobic myotomal specializations that are associated with RM endothermy in *A. vulpinus*, lamnid sharks and tunas.

Materials and methods

Sharks used in this study were obtained commercially or captured in accordance with Protocol S00080 of the Animal Care and Use Committee (UCSD) and under the authorization of a California Department of Fish and Game collecting permit (# 803019).

Specimen collection and identification

Due to the difficulty of acquiring whole *A. superciliosus* and *A. pelagicus* (two relatively uncommon species in California waters) and because both sharks are large, slow-growing species for which there is concern over their current status of exploitation, three specimens of each species were used to examine the RM morphology. The three *A. superciliosus* were purchased whole from the California drift-gillnet fishers operating out of San Diego, CA, USA. Two *A. pelagicus* were obtained from Chesapeake Fish Co., San Diego, CA, USA (imported from Guaymas, Mexico), and a third *A. pelagicus* (the largest specimen) was caught by long line during fishing operations aboard the R/V *David Starr Jordan* (National Marine Fisheries Service during an Eastern Tropical Pacific shark census, 2004). Comparative data for *A. vulpinus* were obtained from Bernal et al. (2003).

Because the two *A. pelagicus* that were purchased from commercial fishers were not intact (heads, tails and viscera discarded at sea) their specific identification was verified with DNA sequence analysis of the *16s* and *12s* mitochondrial genes. For all three *A. pelagicus* specimens, DNA extraction and sequencing protocols followed Craig et al. (2004). Total genomic DNA was isolated using the Qiagen DNeasy isolation kit, and polymerase chain reaction (PCR) was used to amplify a 594-bp fragment of the *16s* gene and a 424-bp fragment of the *12s* rDNA gene. Sequences were aligned using ClustalX (

<http://bips.u-strasbg.fr/fr/Documentation/ClustalX/>) and visually optimized using MacClade (<http://macclade.org/>); percent sequence divergence was estimated in PAUP*4b10 (<http://paup.csit.fsu.edu>). Results confirmed the *A. pelagicus* identification for the three specimens and showed no genetic differences among them at the *16s* locus and no appreciable differences (0.2%) at the *12s* locus. Both of these genes in *A. pelagicus* showed a 4.5% and 6.6% difference from *A. superciliosus*, as determined by comparisons with sequences available on GenBank; accession no. AY830718 (Greig et al., 2005).

Body size

For the two processed (i.e. missing the head and tail) pelagic threshers and for the largest bigeye thresher (which was not weighed), morphometric parameters were estimated using established fork length (*FL*) to total length (*TL*) and *TL* vs body mass regressions. Pelagic thresher alternate-length (insertion of first dorsal to insertion of second dorsal) was converted to *TL* using data from the California Drift Gillnet Fishery database (D. Holts, National Marine Fisheries Service, unpublished), and *TL*-body mass relationships were determined using regressions from Liu et al. (1999). The body mass of the *A. superciliosus* specimen was determined using data from Kohler et al. (1995).

Body sectioning, RM quantification and three-dimensional reconstruction

Body sectioning and RM quantification were performed using methods similar to those described in Bernal et al. (2003). Briefly, sharks were frozen whole, in a position that avoided any bending of the body, and transverse sections (~3–4 cm thick) were cut along the entire length of the shark using a large band saw. For all individuals that were intact, observations were made on the presence of RM throughout the length of the entire upper lobe of the caudal fin. The thickness of each slice was measured, and high-resolution digital images (Canon, PowerShot A80) were taken of the anterior surface. For every section, both total (i.e. complete surface) and RM cross-sectional areas (cm²) were measured using the NIH Image J software[®]. The longitudinal distribution of RM was determined following the protocol of Bernal et al. (2003), which adjusted the RM surface area (cm²) at 50% *FL* to a relative value of 1.0, and this relative value was used as a reference point for all other positions along the body. This relative RM surface area (i.e. normalized at 50% *FL*) was estimated for each specimen at 5% *FL* increments, and the mean (\pm S.E.M.) was calculated for each species (i.e. *A. superciliosus*, *N*=3; *A. pelagicus*, *N*=3) in order to build a RM distribution plot along the length of the body. The same procedure was also used for the *A. vulpinus* (*N*=6) data obtained from Bernal et al. (2003). These methods provide a relative RM estimate that enables the comparison of different sized individuals as well as comparison with previously published data on *A. vulpinus* and other species. For each section, RM volume (cm³) was calculated from the product of

RM surface area (cm² averaged from both the anterior and posterior sides) and slice thickness (cm), and the RM mass determined using a density of 1.05 g cm⁻³ (Bernal et al., 2003).

Three-dimensional reconstructions of the muscle morphology were created by using the high-resolution two-dimensional images of the body sections and by building a vector-based outline of the area of interest (e.g. whole body, visceral mass, spine and RM). Outlines were then skinned together using morphometric data for one specimen of each of the three species, and final images rendered using Strata 3D Pro (Strata, St George, UT, USA).

Results

RM arrangement and distribution

Morphometric data for all sharks used in this study and a summary of the findings from the cross-sectional analyses are shown in Table 1. The total mean (\pm S.E.M.) relative RM masses (RM mass as a % of total body mass) for *A. superciliosus* and *A. pelagicus* were 2.31 \pm 0.11% and 3.01 \pm 0.10%, respectively. When compared with *A. vulpinus* (mean relative RM mass, 2.34 \pm 0.21%; data from Bernal et al., 2003), there were no significant differences in the RM quantities among the three thresher shark species (one-way ANOVA, $P > 0.05$).

Both *A. superciliosus* and *A. pelagicus* were found to have their RM located in a lateral/subcutaneous position, which

contrasts the medial arrangement of *A. vulpinus* (Bone and Chubb, 1983; Bernal et al., 2003) (Fig. 1). In addition, *A. superciliosus* and *A. pelagicus* also exhibited similarities in the transverse arrangement of the RM, whereby the RM was predominantly distributed along the edges of the lateral myotomes in both the epaxial and hypaxial musculature (Fig. 1, insets). Although the RM formed a continuous subcutaneous layer around most of the transverse body sections, it was most dense near the region of the horizontal septum, and, in *A. superciliosus*, the RM was almost exclusively positioned along the septum between 20 and 40% FL. The epaxial and hypaxial distribution of the RM around the sides of *A. superciliosus* and *A. pelagicus* differed from that documented for *A. vulpinus*, which, over most of its body, only has RM positioned epaxially (Fig. 1).

The longitudinal distribution of RM in *A. superciliosus* revealed a peak at 50% FL, while *A. pelagicus* exhibited maximum RM at 75% FL (Fig. 2). The contours of the mean RM longitudinal distribution for *A. superciliosus* and *A. pelagicus* were similar, with both species exhibiting gradual, bell-shaped distributions spanning from 30 to 100% FL (Fig. 2A,B). When compared with *A. vulpinus* (peak RM at 45% FL with most of the RM shifted anteriorly, >70% FL; Fig. 2C), both *A. superciliosus* and *A. pelagicus* had RM that was predominantly distributed over the posterior body (60–100% FL).

Although the relative RM amount decreased towards the tail in both *A. superciliosus* and *A. pelagicus*, the ratio of RM to

Table 1. Shark fork length (FL), body mass, red muscle (RM) position, RM cross-sectional area at 50% FL, and relative RM mass

Species (common name)	Specimen #	FL (cm)	Mass (kg)	RM position*	RM cross-sectional area at 50% FL (cm ²)	RM mass (% body mass)
<i>Alopias pelagicus</i> (pelagic thresher)	1	132 [†]	29 [‡]	L	8.79	2.81
	2	144 [†]	38 [‡]	L	10.8	3.11
	3	163 [†]	56 [‡]	L	14.97	3.11
						$\bar{x}=3.01\pm 0.10$
<i>Alopias superciliosus</i> (bigeye thresher)	1	153	49 [§]	L	14.03	2.31
	2	162	58 [§]	L	14	2.12
	3	175	74 [§]	L	15.23	2.51
						$\bar{x}=2.31\pm 0.11$
<i>Alopias vulpinus</i> [¶] (common thresher)	1	85	4.5	M	5.61	2.02
	2	105	20.9	M	8.82	1.98
	3	120	24.9	M	13.4	2.83
	4	123	37.2	M	15.31	2.11
	5	124	34.9	M	12.91	1.96
	6	163	70.4	M	35.13	3.14
						$\bar{x}=2.34\pm 0.21$

*L, lateral, directly under the skin; M, medial, closer to the vertebrae.

[†]Calculated from D. Holts, National Marine Fisheries Service (unpublished).

[‡]Calculated from Liu et al. (1999).

[§]Calculated from Kohler et al. (1995).

[¶]Data taken from Bernal et al. (2003).

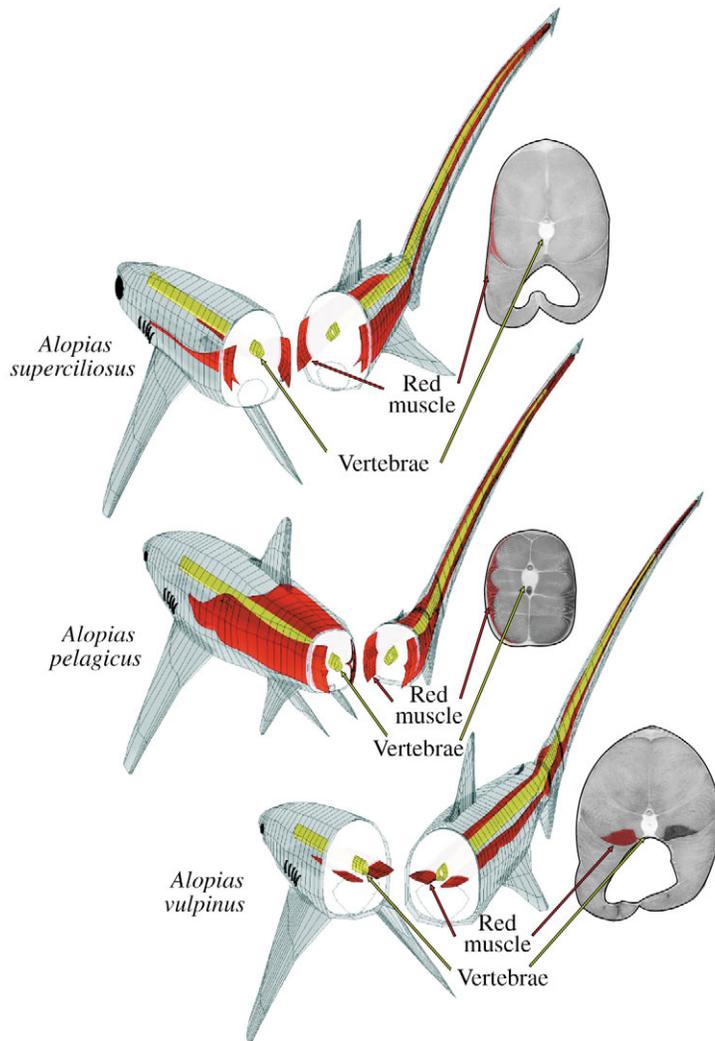


Fig. 1. Whole-body reconstructions of the three thresher shark species, showing the position of the red, aerobic locomotor muscle (RM) (red) and vertebral column (yellow). Top, the bigeye thresher, *A. superciliosus* (58 kg); middle, the pelagic thresher, *A. pelagicus* (56 kg); bottom, the common thresher, *A. vulpinus* (70 kg; modified from Bernal et al., 2003). Location of the transverse section through each species corresponds to the position of maximum RM area (see Fig. 2). Each reconstruction is accompanied by a cross-sectional image taken from the specimen (inset; RM in the left side has been color enhanced for clarity).

WM increased caudally, making RM the dominant fiber type near the caudal peduncle. For all three species, once past the fork of the tail, the RM continued as a thin contiguous section through the upper caudal lobe to the tip of the tail.

Other observations

For both *A. superciliosus* and *A. pelagicus*, the transverse body sections were examined for the presence of vascular structures that would possibly facilitate heat retention (i.e. retia). Detailed observations of both the lateral and central circulation did not reveal the presence of vascular modifications for either species. The observations did,

however, reveal the presence of a dominant central circulation (i.e. large dorsal aorta and post cardinal vein) and a diminished lateral circulation. This contrasts the circulation of *A. vulpinus*, which has a reduced central circulation and dominant lateral blood supply (Bone and Chubb, 1983; Bernal et al., 2003).

Discussion

This study has identified major differences in the aerobic, myotomal RM morphology among the three alopiid sharks. From this work, we have shown that the RM in *A. superciliosus* and *A. pelagicus* is located in a lateral, subcutaneous position with RM myomeres extending above and below the horizontal septum over the entire body. This RM arrangement is similar to that described for ectothermic sharks and distinct from that described for their regionally endothermic sister taxon, *A. vulpinus* (Bone and Chubb, 1983; Bernal et al., 2003; Bernal and Sepulveda, 2005).

RM quantity

Despite differences in RM position among the three thresher species, there were no significant differences in the relative amount of RM present in each (Table 1). This agrees with previous studies that have found no apparent correlation between RM quantity and endothermy in either lamnid sharks or tunas (Graham et al., 1983; Bernal et al., 2003). Further, it appears that among the sharks studied so far (including the three thresher species), they all possess a relatively similar amount of RM (approximately 2–3% of body mass; Bernal et al., 2003; Table 1) despite notable differences in swimming activity level, endothermic status, body size and caudal propeller shape (i.e. lunate, heterocercal). Due to the limited sample size used in this study, it is not possible to discern if there are allometric scaling relationships for the relative amount of RM in both *A. superciliosus* and *A. pelagicus*. However, previous work on *A. vulpinus*, lamnids and other sharks has shown that there is a proportional increase (isometric) in the relative amount of RM and body mass (Bernal et al., 2003), which suggests that the relative RM amount in *A. superciliosus* and *A. pelagicus* may also scale isometrically. This contrasts what has been documented for active bony fishes, which have a somewhat higher and more variable amount of RM (e.g. RM amount ranging from 4 to 13% in scombrids) that scales allometrically (Graham et al., 1983). It is possible that the narrow and consistent range of relative RM amount in sharks may reflect similarities in their physiology and ecology. One common feature among sharks is the widespread use of the liver for buoyancy regulation, a tactic that could decrease the need for additional RM to produce forward thrust in the maintenance of hydrostatic equilibrium. Further, perhaps the narrow range is correlated with a limited scope for aerobic performance. Indeed, swimming tunnel studies on juvenile

mako sharks (*Isurus oxyrinchus*), lemon sharks (*Negaprion brevirostris*), scalloped hammerheads (*Sphyrna lewini*) and leopard sharks (*Triakis semifasciata*) have shown that they only perform over a relatively narrow aerobic range ($0.25\text{--}1.5\text{ L s}^{-1}$; Graham et al., 1990; Lowe, 1996; Bushnell et al., 1989; Bernal et al., 2001b; Donley and Shadwick, 2003; Donley et al., 2004; reviewed by Carlson et al., 2004) when compared with active teleosts (Brett and Glass, 1973; Sepulveda et al., 2000, 2003).

RM position

The transverse distribution of the RM in *A. superciliosus* and *A. pelagicus* (i.e. lateral and above and below the horizontal septum) is similar to that found in the blue shark (*Prionace glauca*) and the leopard shark and parallels the myotomal arrangement of other ectothermic sharks (Bernal et al., 2003; Donley and Shadwick, 2003). This myotomal arrangement is the predominant character state of most bony fishes and elasmobranchs and is, however, distinct from that of their sister taxon *A. vulpinus* and the lamnids (Bone and Chubb, 1983; Carey et al., 1985; Bernal et al., 2003). In *A. vulpinus*, the RM is positioned only in the epaxial musculature until the caudal peduncle, where it also begins to extend into the hypaxial region. This transverse arrangement is also found in the lamnids and may be attributed to several factors, which include the position of the lateral blood supply (which is also above the horizontal septum) or possibly the orientation of the tendon system that transmits force to the caudal propeller (Carey et al., 1985; Bernal et al., 2003; S. Gemballa, P. Konstantinidis, J. M. Donley, C. A. Sepulveda and R. E. Shadwick, submitted). In the present study, we also found the RM to extend to the tip of the upper caudal lobe, a characteristic observed in all three thresher species. This small band of RM may allow thresher sharks to increase the maneuverability of the caudal fin while feeding (Gubanov, 1972; Nakano et al., 2003) or possibly aid in controlling the dorso-ventral angle of the tail as it swings through the water.

RM and regional endothermy

Previous works have speculated about the endothermic status of all three thresher sharks (Carey et al., 1971; Gruber and Compagno, 1981; Bone and Chubb, 1983; Block and Finnerty, 1994; Weng and Block, 2004). Recent field studies have shown that the RM of the common thresher is warmer than ambient seawater temperature (Bernal and Sepulveda, 2005) and that *A. superciliosus* has a large orbital rete, highly suggestive of cranial endothermy (Block and Carey, 1985; Weng and Block, 2004). There are no RM temperature

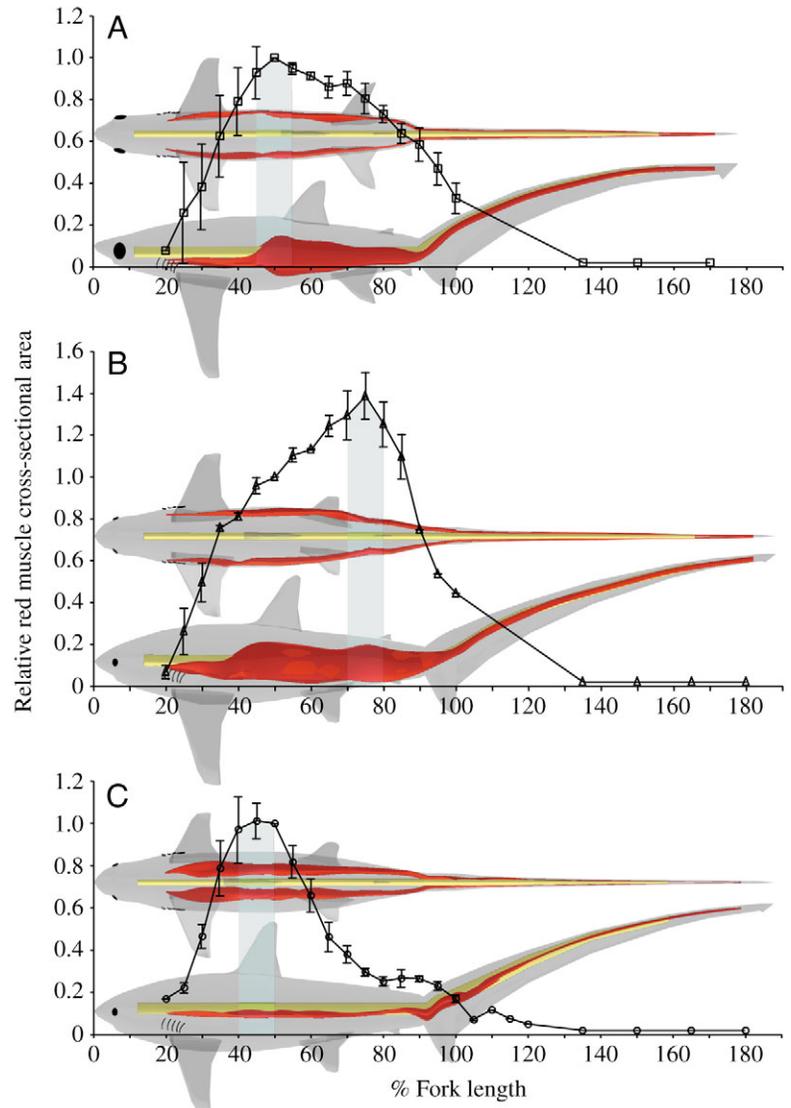


Fig. 2. Longitudinal distribution of the red, aerobic locomotor muscle (RM) for the three thresher shark species. (A) bigeye thresher, *A. superciliosus* ($N=3$), (B) pelagic thresher, *A. pelagicus* ($N=3$), (C) common thresher, *A. vulpinus* ($N=6$; modified from Bernal et al., 2003). Gray-shaded bar indicates the body section where maximum RM (shown in red) is found. Yellow represents the vertebral column. The relative amounts of RM in the different positions along the body are expressed as a proportion of the RM cross-sectional area equal to 1 at 50% fork length (see Table 1 for RM cross-sectional area at 50% FL). Values shown are means \pm S.E.M.

measurements for *A. pelagicus* and only two inconclusive RM temperature measurements for *A. superciliosus* (Carey et al., 1971). Although additional RM temperature data are warranted for both *A. superciliosus* and *A. pelagicus*, it is clear that these species lack a medial RM position, a feature shared by all of the known RM endotherms (i.e. common thresher, lamnids and tunas). In addition, we did not find any vascular heat exchangers in any of the transverse body sections of *A. superciliosus* and *A. pelagicus*. Taken together, the subcutaneous RM position and the lack of a vascular heat

exchange system almost certainly preclude them from maintaining an elevated RM temperature because any heat generated by the RM would be lost to the surrounding water by convection through the skin and *via* diffusion across the gills.

Regional endothermy and thresher shark natural history

While all three thresher species, at times, occupy similar depths and habitats (Hanan et al., 1993); latitudinal and depth-distribution data suggest that *A. vulpinus*, with its warm RM, and *A. superciliosus*, which is probably a cranial endotherm (Weng and Block, 2004), inhabit cooler waters than *A. pelagicus*, a species predominantly found in tropical and subtropical waters (Compagno, 1998; Liu et al., 1999). *A. vulpinus* has been shown to have the greatest overall latitudinal distribution, ranging in the eastern Pacific from 58°N to 55°S (Compagno, 2001). Although the latitudinal distribution of *A. superciliosus* is not as extensive as that of *A. vulpinus* (approximately 35°N to 35°S; Ivanov, 1986; Compagno, 2001), the temperature minima experienced may exceed those of the other threshers when considering the deep waters it has been shown to inhabit. Satellite tagging and acoustic telemetry studies have shown that *A. superciliosus* spends much of the daylight hours at depth in waters between 6 and 12°C (Nakano et al., 2003; Weng and Block, 2004). Similar archival tagging data for *A. vulpinus* also show this species to frequent waters below the thermocline, but the amount of time spent at depth and the range of temperatures encountered (9–17°C; D. Cartamil, unpublished) are less extreme than those of *A. superciliosus*. Future studies that further characterize the vertical and horizontal movements of these two sharks may begin to elucidate which form of regional endothermy (i.e. RM, eye and brain) better enables the threshers to exploit colder environments (i.e. high latitude and greater depth). However, because there are no movement studies on *A. pelagicus*, currently it is not possible to fully assess habitat partitioning and possible niche expansion in this group.

Thresher shark phylogeny

The phylogenetic relationship of the thresher sharks has been examined using both morphological and molecular techniques (Maisey, 1985; Compagno, 1990; Eitner, 1995; Martin and Naylor, 1997; Naylor et al., 1997). Using morphological characters, Compagno (1990) hypothesized that the three thresher species comprise a monophyletic family (Alopiidae) in the Order Lamniformes. This hypothesis is based on several alopiid synapomorphies, which include pectoral fin structure and origin, fin placement, size and morphology, caudal fin morphology and vertebral count, chondrocranial morphology and mouth, teeth and jaw similarities (Compagno, 1990). Compagno (1990) further hypothesized that *A. vulpinus* is the ancestral sister taxon to *A. pelagicus* and *A. superciliosus*. This hypothesis is also supported by the molecular-based analysis of Eitner (1995); however, in the Eitner (1995) study, there was also evidence suggesting a fourth alopiid species. Other hypotheses based on

molecular data fail to provide a monophyletic origin for the threshers; this, however, has been primarily attributed to long branch lengths and short internodes, which can decrease species resolution (Martin and Naylor, 1997; Morrissey et al., 1997; Naylor et al., 1997). Because of the strong morphological hypothesis presented by Compagno (1990), Martin and Naylor (1997) and Naylor et al. (1997) forced monophyly for the alopiids and place the Cetorhinidae (basking shark) as the sister group to the Lamnidae (the lamnids are the only other lamnoid group documented with an internal and anterior RM arrangement). If the Compagno (1990) hypothesis is used in the present study, the presence of an internal and anterior RM arrangement in *A. vulpinus* suggests that this character state is an autapomorphic trait of *A. vulpinus* and cannot be used alone to distinguish the relatedness of the alopiids.

Conclusions

This study compared RM position and quantity in the three species of thresher sharks (family Alopiidae) and has shown that *A. vulpinus* is the only alopiid to possess the aerobic specializations (medial and more anterior RM position) that facilitate RM endothermy. Neither *A. superciliosus* nor *A. pelagicus* have their RM in this body position. Rather, RM in these species occurs along the lateral edges of the myotomes, near the skin, and extends more posteriorly, a pattern typical of species lacking the capacity for RM endothermy.

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