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Allometric Growth of the Enigmatic Deep-Sea Megamouth Shark *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983 (Lamniformes, Megachasmidae)

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Abstract: Megamouth sharks *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983, are a large-bodied, planktivorous, deep-sea species with peculiar morphology. Since their initial description in the late 20th century, many individuals of different sizes have been reported, but few studies examined ontogenetic changes in body shapes. Here, we assess the growth changes in their heads and fins based on length measurements from nine different-sized individuals (177–544 cm in total length). Bivariate analyses showed that the head becomes larger relative to body length with increasing body size (i.e., positive allometry), whereas the relative size of the caudal fin remains constant (i.e., isometric growth). This trend differs from basking sharks and apparently resembles whale sharks and some baleen whales, although they are all large-bodied filter feeders. Given that relative mouth size is linked to feeding modes, our results suggest that megamouth sharks have different feeding modes from ram-feeding basking sharks and may have some similarity with suction-feeding whale sharks and engulfment-feeding baleen whales.

Keywords: ichthyology; chondrichthyes; elasmobranch; lamniformes; megachasmidae; ontogeny

Key Contribution: As megamouth sharks grow, their head proportions become larger, but there seems to be no significant change in parts such as the caudal fin. This trend is similar to that of whale sharks and baleen whales rather than basking sharks, suggesting that megamouth sharks may differ in their feeding methods from those of basking sharks.

1. Introduction

On 19 November 1976, a large adult male shark about 4.5 m long was captured by a US research vessel, AFB-14, about 42 km Northeast of Oahu, Hawaii. At that time, it was obvious that the shark was a new species that was previously unknown to science, as it exhibited a highly unusual tadpole-like bauplan with very large and long head, a short but broad and rounded snout, a huge mouth with numerous small, hooked teeth, and a cylindrical trunk that tapered rearward from the head. Thus, it was described and designated as the holotype of a new species, the megamouth shark *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983, and classified as a sole surviving member of the family Megachasmidae within the order Lamniformes [1]. While it was initially suggested that megamouth sharks are closely related to another large, filter-feeding species, basking sharks, *Cetorhinus maximus* (Gunnerus, 1765), in the family Cetorhinidae [2], the subsequent molecular and paleontological analyses did not support the suggestion but instead support the distinctiveness of Megachasmidae from other clades [3–6]. Currently, Megachasmidae is considered to be an early-diverging lineage located outside the Lamnidae + Cetorhinidae clade within the Lamniformes [6]. After description and naming by Taylor et al. [1], more than 200 individuals of megamouth sharks have been reported to date [7]. Increasing

evidence suggests that megamouth sharks are a filter-feeding, deep-sea species and primarily feed on epipelagic and mesopelagic invertebrates such as krill. Despite their rare status, they have cosmopolitan distributions, occurring widely in the Atlantic, Indian, and Pacific Oceans [5,8–12]. Currently, megamouth sharks are listed as "Least Concern" on the IUCN Red List. They can reach 7 m in body length [10,11] and are found at various depths, ranging from the surface to 1500 m [7,10,13]. A possible segregation among different ontogenetic stages or between sexes as well as seasonal migrations are also recognized [9,12]. However, much remains unknown about the ecology and biology of this enigmatic shark species [11,12].

Ontogenetic changes in body shape have long been examined for many taxa as they provide insights into how animals may or may not shift their ecology as they increase in size [14–17]. In sharks, relatively small-bodied species (e.g., spiny dogfish *Squalus acanthias* Linnaeus, 1758) have isometric growth, conserving overall proportions throughout ontogeny [14,15,18–20]. In contrast, while still having isometric scaling in various parts of the body [14,20,21], large carcharhiniform and lamniform sharks undergo allometric scaling during ontogeny in some body regions [14,15,19–22]. For example, basking sharks show a negative allometry in the head and caudal fin (i.e., head and fins become smaller relative to the body as they grow) in the manner of large carnivorous sharks such as white sharks *Carcharodon carcharias* Linnaeus, 1758, and tiger sharks *Galeocerdo cuvier* Peron and Lesueur, 1822 [15]. Given that megamouth sharks share many constraints regarding swimming and feeding with basking sharks [5], it would be important to examine whether they exhibit similar negative allometric growth. Amorim et al. [23] noted that despite some minor differences, the body proportion of a juvenile megamouth shark "agrees well" with that of adults, indicating an isometric growth; however, this has yet to be confirmed through morphometric analyses. Nakaya [8], Watanabe and Papastamatiou [11], and Yu et al. [7] investigated the allometric relationships among multiple variables of different-sized megamouth sharks, but these studies only examined several basic variables (e.g., total length, body mass) and did not compare results to other species.

In this study, we examine growth changes in various body parts of megamouth sharks based on the measurements from nine different-sized individuals reported in the literature. Specifically, we determine whether the variables scale isometrically or allometrically as the animals increase in size. The results are compared with other sharks, especially basking sharks, to provide insights into the ecology of this enigmatic species. Our results open the possibility that the feeding method of megamouth sharks is different from basking sharks.

2. Materials and Methods

Data from a total of 26 morphometric, straight-line measurements (Figure 1 and Table S1) of the various parts of the body of megamouth sharks were collected from the literature. Twenty-three of them are the same as in Ahnelt et al. [15], who examined the ontogenetic growth of basking sharks. We included three additional measurements from pectoral fins, which are considered important for controlling body posture during slow-speed swimming [24] in megamouth sharks. A total of nine individuals were included in the analyses (Table 1 and Table S1), although a few measurements were unavailable for some specimens [1,23,25–30]. Preoral length provided by Lee and Shao [28] (NMMBP8950 and ASIZP0071582) were considered as errors and excluded from the analyses.
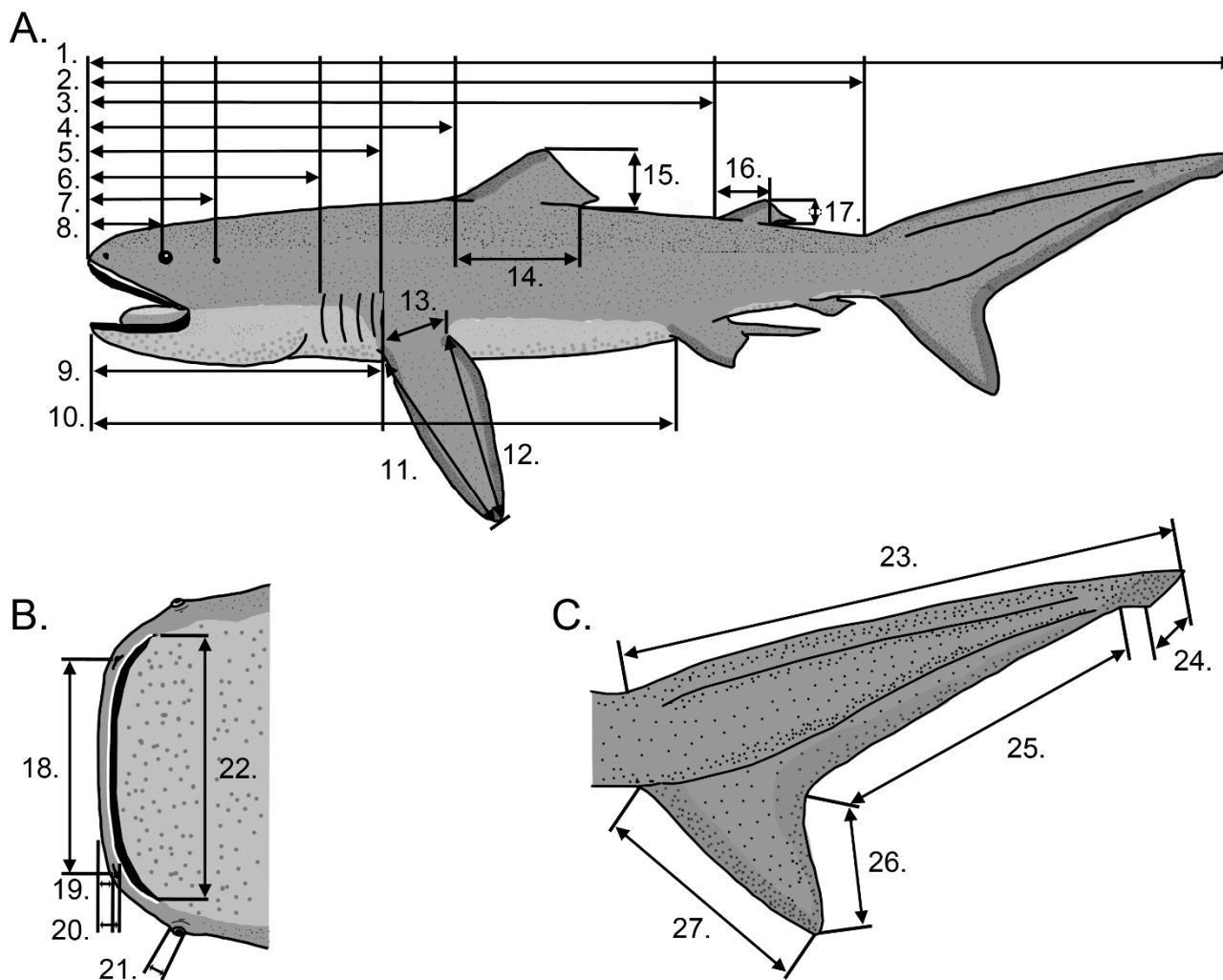
Figure 1. Morphometric measurements used in this study. (**A**). Body measurements. (**B**). Head measurements. (**C**). Caudal fin measuresments. 1. Body length; 2. Precaudal length; 3. Presecond dorsal length; 4. Prefirst dorsal length; 5. Head length; 6. Prebranchial length; 7. Prespiracular length; 8. Preorbital length; 9. Prepectoral length; 10. Prepelvic length; 11. Pectoral anterior margin length; 12. Pectoral height; 13. Pectoral base length; 14. First dorsal base length; 15. First dorsal height; 16. Second dorsal base length; 17. Second dorsal height; 18. Internarial distance; 19. Prenarial length; 20. Preoral length; 21. Eye length (horizontal); 22. Mouth width; 23. Dorsal caudal margin length; 24. Terminal caudal lobe length; 25. Upper postventral caudal margin length; 26. Lower postventral caudal margin length; 27. Preventral caudal margin length. Illustrations are after Compagno [5] and Ebert and Dando [9].

Table 1. A list of individuals of megamouth sharks used in this study.

Specimen ID	BPBM 22730	N/A	WAM P.29940-001	N/A	MZB12906	ASIZP0071582	NMMBP8950	SIO 07-53	N/A
Ontogenetic stage	Adult	Juvenile	Adult	Adult	Juvenile	Adult	Adult	Juvenile	Subadult
Sex	Male	Male	Male	Female	Male	Female	Female	Female	Female
Body Length (mm)	4460	1900	5150	5440	1767	4830	4870	2265	3667
Location	Hawaii, USA	Brazil	Australia	Mikizaki, Japan	Sumatra, Indonesia	Hualien, Taiwan	Hualien, Taiwan	Mexico	Ibaraki, Japan
Source	[1]	[23]	[25]	[26]	[27]	[28]	[28]	[29]	[30]

The measurements were log 10-transformed, and rounded to three decimal places. Log 10-transformation of the measurement data (with positively skewed distributions) allowed us to normalize the distributions [31], reduce the effects of outliers, and reduce the level of heteroscedasticity in the analyses of allometric relationships [32]. Each length(x) was linearly regressed against total body length (y) as $\text{Log}_{10}(y) = m\,\text{Log}_{10}(x) + b$. The regression analyses were performed with Microsoft Excel and GraphPad (https://www.graphpad.com (accessed on 9 November 2022)), and 95% confidence intervals of slopes were calculated. Additionally, to examine whether growth patterns of megamouth sharks are unique, the changes in head length and mouth width associated with change in body length were compared with those of six other lamniform species [33].

Institutional abbreviations are as follows: ASIZP, Academia Sinica, Taipei, Taiwan; BPBM, Bishop Museum, Honolulu, HI, USA; MZB, Museum Zoologicum Bogoriense, Cibinong, Bogor, Indonesia; NMMB, National Museum of Marine Biology and Aquarium, Taipei, Taiwan; SIO, Marine Vertebrate Collection of the Scripps Institution of Oceanography, CA, USA; WAM, Western Australian Museum, Perth, Australia.

3. Results

Results of all linear regressions are summarized in Table S2 and Figures S1–S4.

3.1. Head Measurements

Head length showed slightly positive allometry with a slope (with 95% confidence interval) of 1.103 (1.057–1.149) (Figure 2A). Similarly, prebranchial length showed slightly positive allometry with a slope of 1.155 (1.013–1.298) (Figure S1, Table S2). Internarial distance (i.e., the width between the nares) also showed positive allometry with a slope of 1.245 (1.159–1.332) (Figure S1, Table S2).
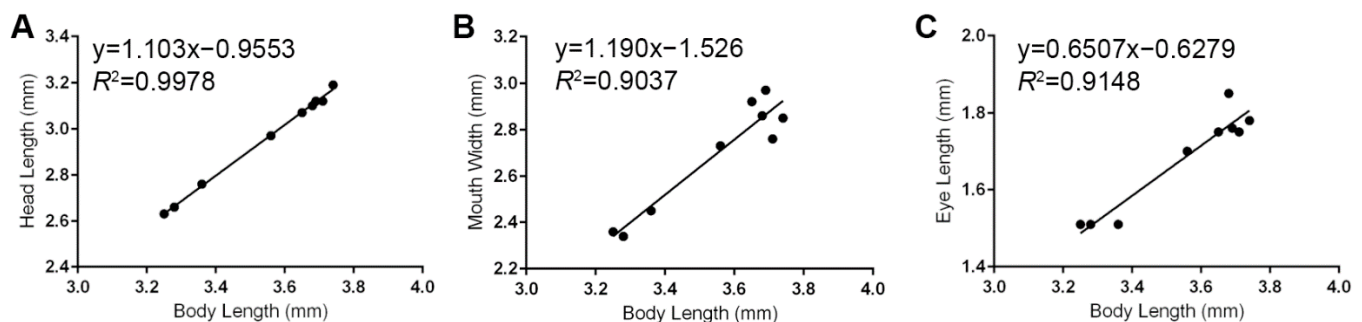

Figure 2. Linear regressions of selected $\log_{10}$-transformed *Megachasma pelagios* head measurements against $\log_{10}$-transformed total body length. (**A**). Head length. (**B**). Mouth width; (**C**). Eye length.

While prespiracular length (Figure S1) and preorbital length (Figure S1) had slopes of >1 (1.205 and 1.243, respectively), 95% confidence intervals included 1 (0.8384–1.572 and 0.9365–1.549, respectively). Prenarial length (Figure S1) had a slope of 1.424 with 95% confidence intervals including 1 (0.8036 to 2.044). Likewise, mouth width (Figure 2B) and anteroposterior length of the region between the snout tip and the mouth (Figure S1) had slopes of >1 (1.190 and 1.381, respectively), but 95% confidence intervals included 1 (0.8426–1.537 and 0.2888–2.474 respectively). Collectively, a majority of head measurements showed positive allometry against total lengths, although the results are provisional for some parts in which 95% confidence intervals overlapped 1.

As an exception, eye length exhibited negative allometry (Figure 2C), with a slope of 0.6507 (0.4732–0.8283).

3.2. Body Measurements

Length between the snout tip and the point just anterior to the caudal fin (Figure S2) showed slightly positive allometry with a slope of 1.070 (1.033–1.106). Similarly, length between the snout tip and the first dorsal fin showed weak positive allometry (Figure S2)

with a slope of 1.114 (1.050–1.179). Likewise, length between the snout tip and the second dorsal fin (Figure S2) showed positive allometry with a slope of 1.076 (1.001–1.152) (Figure S2, Table S2). Additionally, the length of the region anterior to the pectoral fin (Figure S2) showed positive allometry with a slope of 1.120 (1.048–1.192).

Prepelvic length (Figure S2) showed isometric scaling with a slope of 1.004 (0.6213–1.387).

3.3. Dorsal Fin Measurements

Length of the first dorsal fin base (Figure S3) showed a slope of 1.161 (0.8637–1.458), indicating an isometric growth. Height of the first dorsal fin also scaled isometrically (Figure S3) with a slope of 0.8800 (0.6585–1.102). The second dorsal fin height (Figure S3) had a slope of <1 (0.6622) but its 95% confidence intervals encompassed 1 (0.2332–1.091). While the correlation coefficient was statistically significant ($p = 0.0082$), R^2 value was low (0.6556) for this variable.

Anteroposterior length of the base of the second dorsal fin (Figure S3) showed positive allometry with a slope of 1.229 (1.079–1.379).

3.4. Pectoral Fin Measurements

Length of the pectoral fin base showed positive allometry (Figure 3A) with a slope of 1.224 (1.008–1.440). Other pectoral fin regions exhibited isometric scaling. The anterior margin of pectoral fin (Figure 3B) showed a slope of 1.031 (0.9203–1.142). Pectoral fin height (Figure 3C) had a slope of 0.9923 (0.8254–1.159).
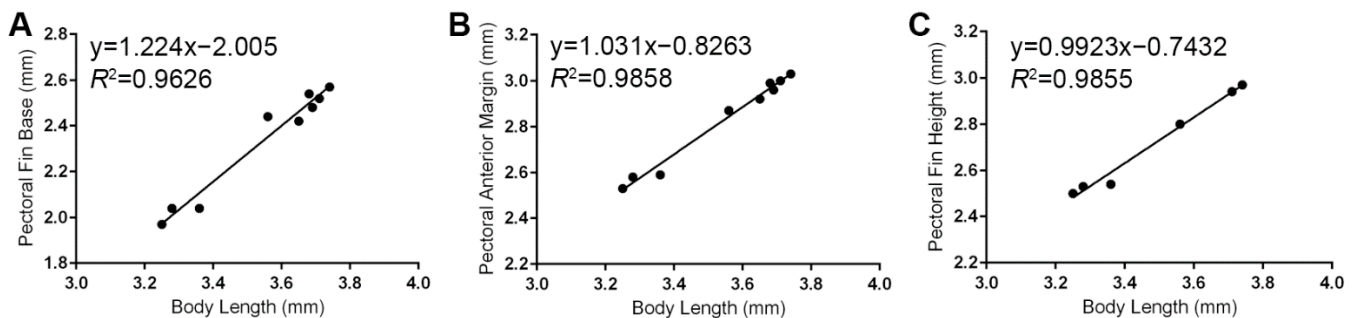

Figure 3. Linear regressions of $\log_{10}$-transformed *Megachasma pelagios* pectoral fin measurements against $\log_{10}$-transformed total body length. (**A**). Pectoral base length. (**B**). Pectoral anterior margin length. (**C**). Pectoral height.

3.5. Caudal Fin Measurements

Dorsal caudal margin of the dorsal lobe of the caudal fin (Figure 4A) showed isometric growth with a slope of 0.9533 (0.8414–1.065). Similarly, length between the fork of the caudal fin and the terminal caudal lobe also scaled isometrically (Figure S4), with a slope of 1.088 (0.8133–1.363). Lastly, the length of terminal caudal lobe (Figure S4) showed isometric growth with a slope of 1.038 (0.7062–1.370). Collectively, all measurements on the upper lobe of the caudal fin showed isometric growth.

Preventral margin of the lower lobe (Figure 4B) showed negative allometry with a slope of 0.9065 (0.8343–0.9786). In contrast, length of the postventral caudal margin of the lower lobe showed isometric scaling (Figure 4C) with a slope of 0.9419 (0.6271–1.212).

3.6. Comparisons with Other Lamniform Shark Species

The allometric slopes of head length and mouth width against body length in megamouth sharks tended to be steeper than those seen in other lamniform shark species (Figure 5). The slopes tended to be close to, or lower than, 1.0 in lamniforms (except for megamouth sharks), indicating isometric or negatively allometric scaling. Additionally, megamouth sharks had wider mouths than other lamniform species for a given body length (Figure 5B). Collectively, head dimensions increased at faster rates relative to body length in megamouth sharks compared to other lamniform species.
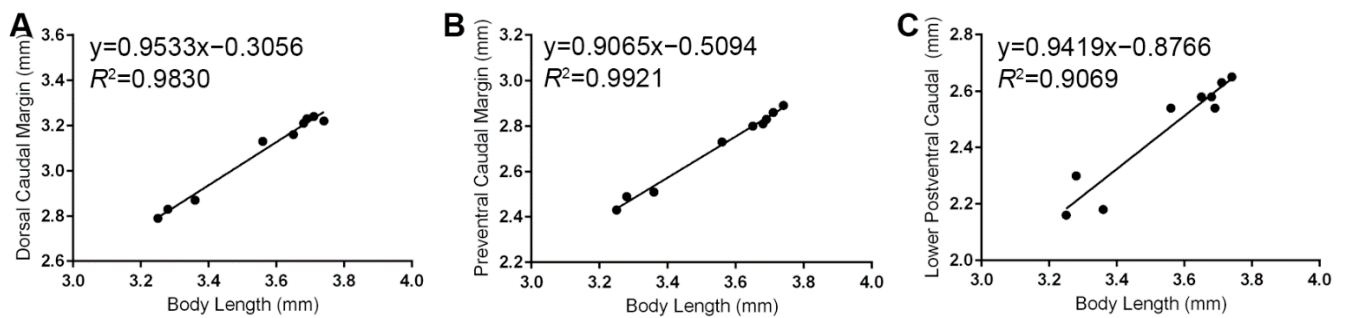
Figure 4. Linear regressions of selected $\log_{10}$-transformed *Megachasma pelagios* caudal fin measurements against $\log_{10}$-transformed total body length. (**A**). Dorsal caudal margin length. (**B**). Preventral caudal margin length. (**C**). Lower postventral caudal margin length.
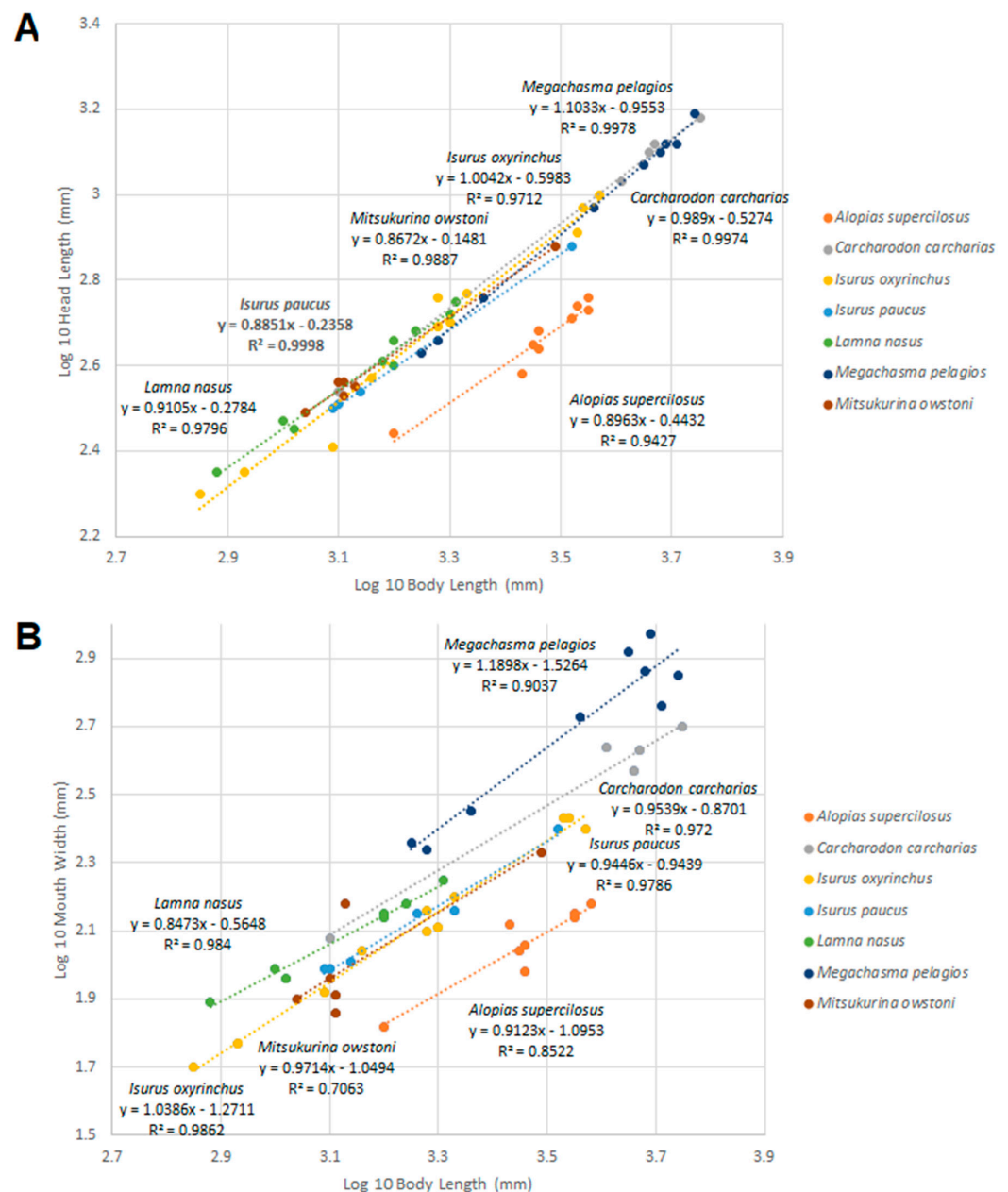

Figure 5. Linear regressions of selected $\log_{10}$-transformed head measurements of lamniform sharks against $\log_{10}$-transformed total body length. (**A**). Head length. (**B**). Mouth width.

4. Discussion

We showed that 14 of the 26 measurements taken from megamouth sharks scale positively and 9 of them scale isometrically against total length (Table S2). Although 95% confidence intervals of slopes included 1 for the five variables from the head (Table S2), these results might represent "soft" isometry [34], associated with small sample sizes and wide confidence intervals. Indeed, the estimates of slopes (1.190–1.424) are well above 1. Moreover, we found at least one of these variables (the mouth width) is larger and increases at a faster rate in megamouth sharks than other lamniform species. This result shows that megamouth sharks deviate from the main trend of negative allometry to isometry seen in other lamniform species (Figure 5B). Collectively, our results indicate that head measurements generally scale positively in megamouth sharks, unlike other lamniform species.

Intriguingly, only three variables we examined show negative allometry. One of them (second dorsal fin height) had a low R^2 value, suggesting that this result represents individual variations rather than general patterns during growth (Table S2). Collectively, our results showed largely positive allometric growth during the ontogeny of megamouth sharks, especially around the head, as well as isometric scaling in the caudal fin. Such a growth trend differs from that of basking sharks, which show negative allometric growth in the caudal fin and head [15]. It also differs from the growth patterns of white sharks and tiger sharks, in which the caudal fin scales negatively [14,15,19,20,22]. Isometric growth trends in caudal fins, as we observed for megamouth sharks, were reported for a variety of small-bodied sharks, such as nurse sharks *Ginglymostoma cirratum* Bonnaterre, 1788, and spiny dogfish [14,18]. Given that megamouth sharks are the third largest extant shark species in the world, being only smaller than whale sharks *Rhincodon typus* Smith, 1828, and basking sharks [11], it is intriguing that the changes in relative length of multiple body regions during the growth of this species are similar to those of smaller shark species, rather than its distant large relatives. It should be emphasized, however, that the results presented in this work should be considered preliminary due to the relatively small sample size (*n* = 9). In some cases, we may have failed to detect allometric relationships ("soft" isometry) [34], as discussed earlier. While individuals of both sexes were pooled in our analyses, we feel this is reasonable due to the absence of sex differences in body shapes in this species. Moreover, although our dataset covers an extensive size range (177–544 cm in total length), medium-sized individuals (250–350 cm) are lacking [8], partially limiting our analyses. Note, however, that some studies of fossil organisms used even fewer specimens than this study to successfully detect allometric growth trends [35–37]. To advance our understanding of the relative growth of megamouth sharks, detailed length measurements from various parts of the body, rather than just total length and weight, should be reported when new individuals are found in future studies.

The heterocercal caudal fin of megamouth sharks bears a horizontally directed vertebral column with a small curvature (low "Cobb's angle") and posteriorly directed hypochordal rays [38]. Such fin morphology is a basal condition for lamniforms, and the caudal fin with a dorsally oriented vertebral column seen in basking sharks and Lamnidae is a derived character [38]. Although our results should be considered somewhat provisional, we suggest several explanations for why megamouth sharks retain isometric growth patterns in the caudal fin instead of the negative allometry seen in white and basking sharks. Megamouth sharks feed primarily on slow-moving zooplankton such as euphausiids, copepods, and jellyfishes [11,26,30]. Although little information is available for the diet of juveniles, tooth morphology does not appear to change during growth [27], suggesting that diets do not change, either. It is possible, therefore, that no change in feeding ecology is reflected by little changes in the shape or proportion of caudal fins. Indeed, isometric growth in the caudal fin was reported for nurse sharks [14], which also prey on slow-moving organisms, including benthic fishes and invertebrates, without showing dramatic changes in diets during growth [20,39]. Of note, basking sharks also prey on small zooplankton and do not exhibit ontogenetic changes in diets, yet this species

shows negative allometry in the caudal fin [15]. Basking sharks have a unique caudal fin morphology among lamniforms with a dorsally oriented vertebral column, yet they have posteriorly directed hypochordal rays, unlike ventrally directed hypochordal rays in Lamnidae. Thus, their caudal fin is morphologically intermediate between heterocercal and homocercal morphotypes [15,38]. Such distinct morphology is thought to reflect a unique lifestyle of this species, cruising at a slow speed with the mouth opened to collect foods [15,38,40]. Perhaps the difference in the shape of the caudal fin, or the growth trend, raises the possibility that the foraging mode of megamouth sharks is different from that of basking sharks. Another explanation, perhaps simpler, is that because megamouth sharks are phylogenetically less derived than basking sharks and other lamnid species within Lamniformes (e.g., [11,41–43]), they retain their morphologically basal condition throughout their lifespan.

We found that the heads of megamouth sharks show positive allometry during growth, unlike basking sharks which exhibit negative allometry [15]. While eye size shows negative allometry, this trend is common among vertebrates, including large sharks [15,44,45]. Given that head shape in vertebrates, including sharks, is closely linked to their diet and feeding modes [19], our findings raise the possibility that megamouth and basking sharks, both of which are filter feeders, use different feeding modes. Interestingly, the feeding mode of megamouth sharks is controversial. It was initially suggested that megamouth sharks are a ram feeder (i.e., swimming towards prey and catching it without using suction forces generated by the mouth) like basking sharks [1]. However, Compagno [46] raised the possibility of suction feeding (i.e., quickly opening the mouth to generate suction forces to collect prey), as in whale sharks, based on the morphological characteristics of megamouth sharks, including the heavy and anteroposteriorly elongated jaw, restricted internal gill openings, relatively weak body musculature, and relatively soft fins. Further, Nakaya et al. [47] suggested that megamouth sharks are an engulfment feeder (similar to rorqual and humpback whales) in that they approach zooplankton swarms and engulf prey-laden water by expanding the gape laterally and ventrally. Tomita et al. [48] provided support for the ram feeding mode, based on their analyses which showed that the ceratohyal of megamouth sharks is not stiff enough to produce suction forces.

Comparing the scaling pattern of the megamouth shark's head and mouth to that of other aquatic animals with known feeding modes may shed some light on this issue. Mobulid rays are large planktivorous elasmobranchs that employ ram feeding [49]. Setyawan et al. [50] showed that the head width of the reef manta ray *Mobula alfredi* Krefft, 1868, scales negatively against body length, similar to basking sharks. Additionally, we found that in lamniform sharks with a conical head similar to basking sharks, mouth width and head length scale isometrically or negatively (Figure 5). In general, Lamniform sharks with a conical head are fast swimmers, and they ram-feed on their prey by approaching close enough to consume it [48,51]. While one species included in our analyses (goblin sharks *Mitsukurina owstoni* Jordan, 1898) has a slightly different head morphology compared to typical conical shape in lamniforms (i.e., elongated and flattened), it nevertheless shares a pointed head tip and also performs ram-feeding [48,52]. Given that mouth width is strongly correlated with the perimeter of the upper jaw in sharks [33], isometric to negatively allometric scaling of the mouth width in lamniforms (excluding megamouth sharks) suggest that the shape of the head remains conical or becomes more pointed as the shark grows. Given that conical head shape in sharks reduces drag while swimming [14,19], narrowing or conserving the conical morphology of the head in "typical" lamniform might be advantageous to their ram-feeding behavior, as they have to swim fast enough to approach the prey [51]. While basking sharks cruise at a slower speed during feeding than expected for their size, they nevertheless capture zooplankton by strong forward swimming [53–56].

In contrast, the lack of conical head morphology [1,11] combined with the apparent positive scaling of the head size suggests that head shape and its growth pattern in megamouth sharks are not optimal for the obligate ram-feeding mode seen in basking sharks and other lamnid species. Our result of positive allometry for the heads of meg-

amouth sharks is similar to that of whale sharks [44,57]. Additionally, the largemouth bass *Micropterus salmoides* Lacépède, 1802, considered as a behavioral analogue of megamouth sharks by Nakaya et al. [47] in its being a slow-swimming, high-volume suction feeder [51,58], show isometric [59,60] to positive allometry in the heads [61]. In rorqual and humpback whales, considered as another behavioral analogue of megamouth sharks by Nakaya et al. [47] by their engulfment feeding mode, the dimensions of the jaw and skull scale positively [62,63]. These comparisons suggest that the head of megamouth sharks' scales like that of a suction or engulfment feeder. Although Tomita et al. [48] argued against the obligate suction feeding mode in megamouth sharks, these authors noted that the engulfment feeding mode is not inconsistent with their results given that the engulfment feeding is a derived mode of ram feeding. Their suggestion that the ceratohyal of megamouth sharks is not stiff enough to perform obligate suction feeding [48], coupled with the results of this study, might imply that the feeding mode of this species is engulfment, or at least differs from the obligate ram feeding mode of basking sharks. By having a larger head relative to body, larger megamouth sharks may be able to engulf larger amounts of food and water, increasing the efficiency of their feeding activities. Another potential piece of evidence that megamouth sharks are engulfment feeders comes from their diet; stomach contents analyses showed that megamouth sharks feed primarily on krill (euphausiid) that form dense swarms [30], rather than the dispersed prey of basking sharks [55]. To capture such dense swarms, suction or engulfment feeding modes are more efficient than the ram-feeding mode employed by basking sharks [56]. Nevertheless, as Watanabe and Papastamatiou [11] noted, the feeding behavior of megamouth sharks should be directly observed by biologging technology with animal-borne video cameras [64] in future studies to resolve this debate.

The anterior margin and the height of pectoral fins show isometric scaling. This result is consistent with the studies on other shark species, including other lamniforms [20,21]. In contrast, pectoral fin bases showed positive allometry. This result is different from other lamniform species [21], in which pectoral fin width scales isometrically. Tomita et al. [24] found that the pectoral fins of megamouth sharks are highly flexible and mobile, unlike those of fast-swimming sharks (such as shortfin mako and salmon sharks) which have stiff, relatively immobile fins. Based on this, Tomita et al. [24] suggested that the pectoral fins of megamouth sharks are specialized for maintaining body posture during slow-speed swimming. Given that pectoral fin bases are attachment sites for various pectoral muscles [24], the positive allometric scaling of megamouth sharks in this part may indicate that muscle volumes supporting pectoral fins increase disproportionally as they grow in order to maintain maneuverability in the water.

5. Conclusions

Despite the small sample size, we show that megamouth sharks exhibit positive allometric scaling in the head and isometric growth in the caudal fin. Such trends differ from another planktivorous lamniform species, basking sharks, in which both the head and the caudal fin scale negatively. We also found that the head length and mouth width of megamouth sharks grow faster (relative to body length) compared to other lamniform sharks. Such allometric trends are different from the isometric to negatively allometric growth trends seen in many ram-feeding sharks, but rather similar to those of suction-feeding whale sharks and engulfment-feeding rorqual whales. We suggest that megamouth sharks have different feeding mode from obligate, ram-feeding basking sharks, the species often thought to have a comparable ecology to megamouth sharks. However, the sample size should be expanded and electronic tagging experiments are needed in future studies to draw firm conclusions.

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