Bueno et al. / The Philippine Journal of Fisheries 32(1): 197 - 213
DOI: 10.31398/tpjf/32.1.2025-0007

January - June 2025

RESEARCH ARTICLE

Identification and Allometric Scaling of Megamouth Shark (*Megachasma pelagios*) Mother-Offspring Specimens from Dipaculao, Aurora, Luzon Island, Philippines

Kyara Patricia R. Bueno[1], Mudjekeewis D. Santos[2], Jade Tiffany S. Rey[2], Princess Ann P. Tayag[3], Clien Yvan A. Ongkiatco[4], Arnel Andrew S. Yaptinchay[5]*

[1] *The Graduate School, University of Santo Tomas, España Blvd., Sampaloc Manila, Metro Manila, 1008 Philippines*
[2] *Genetic Fingerprinting Laboratory, National Fisheries Research and Development Institute, Fisheries Building Complex, BPI Compound, Visayas Ave., Quezon City, Metro Manila 1128 Philippines*
[3] *Bureau of Fisheries and Aquatic Research Region 3, Diosdado P. Macapagal Government Center, City of San Fernando, Pampanga, 2000 Philippines*
[4] *Zoology Division, National Museum of the Philippines, Padre Burgos Ave, Ermita Manila, Metro Manila 1000 Philippines*
[5] *Marine Wildlife Watch of the Philippines, Barangay San Isidro, Makati City, 1234 Metro Manila, Philippines*

ABSTRACT

Megachasma pelagios, commonly known as the megamouth shark, is the lone extant shark species belonging to the family Megachasmidae and genus *Megachasma.* It was first described in 1978 by Taylor et al. (1983), with fewer than three hundred specimens recorded to date. Given its rarity and elusiveness, no pregnant or neonate megamouth sharks have ever been documented. On 14 November 2023, a freshly dead adult female megamouth shark carrying seven pups washed up on the shores of Barangay Ipil, Dipaculao, Aurora, Luzon Island, Philippines. This event has confirmed that megamouth sharks are ovoviviparous. Here, we establish the identity of the specimens using morphological and molecular methods and identify their morphometric differences through allometric analysis. Morphological identification was performed using available photo documentation and morphometric data, with results compared with published literature. On the other hand, the mitochondrial cytochrome c oxidase subunit 1 (MT-COI) gene was used for molecular identification. A phylogenetic tree was constructed using the Kimura two-parameter (K2P) model with 1000 bootstrap replicates. Allometric analysis was investigated using linear regression of each of the 19 morphometric trait measures against the total body length of the specimens. Based on morphological and molecular evidence, the results confirmed the identity of the stranded sharks as *M. pelagios.* Furthermore, morphological scaling of the mother *vis-à-vis* pups revealed that while some traits scale isometrically, the presence of negative and positive allometry in most traits indicates that the offspring are not completely isometric with the mother. Thus, it implies that the pups are morphologically distinct from the mother. Overall, this study provides a definitive identification of the stranded megamouth sharks, and the allometric measurements show new information on the basic biology of this rare fish species.

*Corresponding Author: *aayaptinchay@mwwphilippines.org*

Received: *February 12, 2025*
Accepted: *May 15, 2025*

Keywords: *Fish, Rare Species, Taxonomy, Comparative Anatomy, Conservation*

1. INTRODUCTION

The megamouth shark (*Megachasma pelagios*), popularly known for its gigantic size and distinctive morphology, has been one of the most novel ichthyological discoveries of the 20th Century (Nakaya 2010). It was on 15 November 1976, off the coast of Oahu, Hawaii, when a group of U.S. Navy research vessel accidentally captured a large, strange-looking shark due to entanglement in a parachute sea anchor at a depth of approximately 165 m in water with a bottom depth of about 4,600 m (Berra and Hutchins 1990). The 4460 mm long adult male shark, weighing 750 kg, has a stout body with whitish coloration on the ventral side while dark grayish on the dorsal surface (Ebert et al. 2021). It has a broad and large head, an extremely long terminal mouth that protrudes past its eyes, and a short, round snout (Rodriguez-Ferrer et al. 2017). Inside its massive mouth are relatively small, numerous, over a hundred hooked teeth on both top and bottom jaws, and an unusual white band, hidden in a groove between the snout and the jaw, which is barely visible when the mouth is closed but observed when protruded (Duchatelet et al. 2020). These notable morphological features have subsequently led to the identification of a new family of lamniform sharks, Megachasmidae, and a new genus and species described as *M. pelagios* by Taylor et al. (1983).

Since its first appearance, there have been fewer than three hundred specimens found to date (Skelton et al. 2023; Beuningen et al. 2023) across the deep waters of the Pacific, Atlantic, and Indian Oceans (Nakaya 2010; Diez et al. 2022). Given its elusive nature, no gravid megamouth shark (Yu et al. 2021) and/or neonates have ever been documented. However, it was not until 14 November 2023 that an adult female megamouth shark washed up along the shores of Barangay Ipil Dipaculao, Aurora, Luzon Island, Philippines. It was found pregnant with six pups, while the seventh pup was found nearby on the shore (Figure 1). This incident has solved the long-standing mystery surrounding its reproductive biology, confirming that the megamouth shark is ovoviviparous. Its eggs are hatched internally and give birth to live young.

Life-history theory, a framework that provides an understanding of how organisms allocate resources between survival and reproduction to optimize their fitness, including the passing of genetic material (Kavanagh and Kahl 2016), suggests that organisms necessarily need to allocate an optimal degree of parental investment or energy expenditure to enhance offspring survival and future reproductive success, whilst balancing this against their survival, maintenance, and chances of reproduction (Clutton-Brock 1991; Stearns 1998). In elasmobranchs (rays, skates, and sharks), unlike males that contribute no parental care (Hussey et al. 2010), females provide significant maternal investment strategies to nurture their young during development, influencing the offspring size at birth, growth rate, physical traits, and litter number (Evans 1990; Hamlett 2011; Cotton et al. 2015). Comparative analysis of life-history traits across

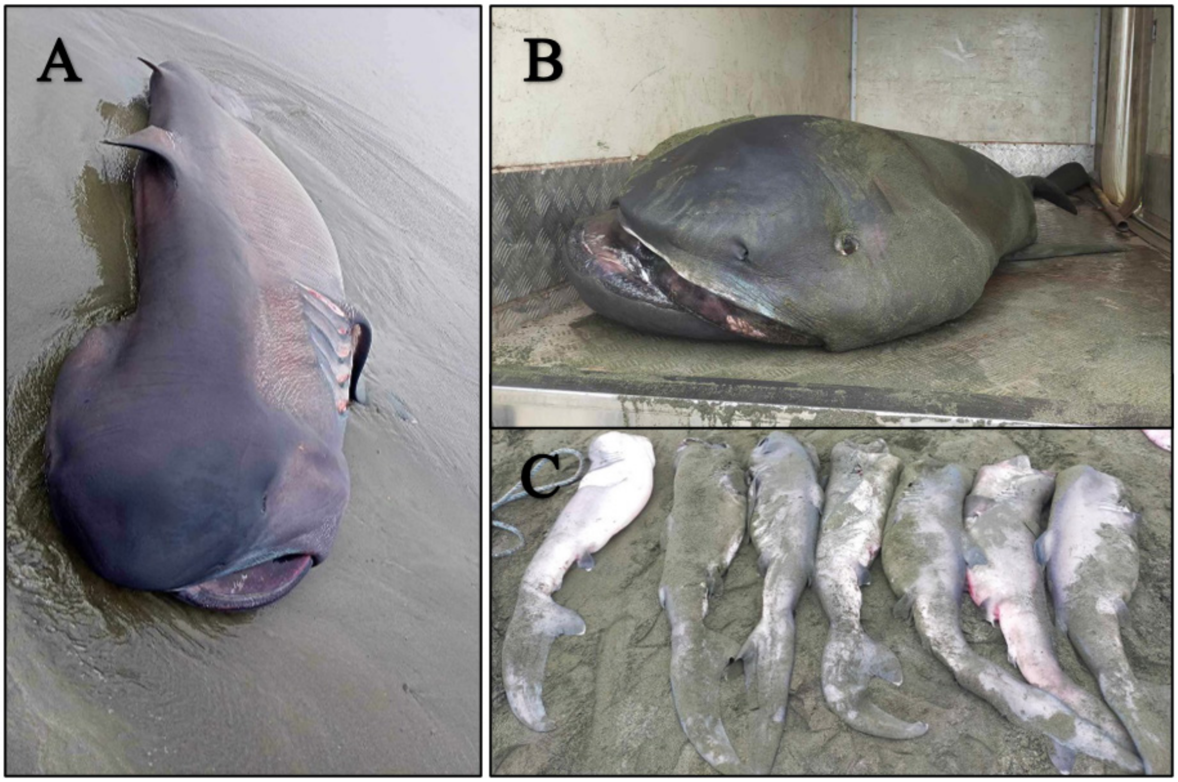


Figure 1. Stranding photos of megamouth sharks, *Megachasma pelagios*. (A) Mother megamouth shark dorsal view; (B) Mother megamouth shark anterior view; and (C) Megamouth shark litter of pups. Photo credits: Marine Wildlife Watch of the Philippines and Bureau of Fisheries and Aquatic Resources (BFAR) Region 3.

animal taxa, including fish, suggests that the offspring phenotype is influenced by the mother's phenotype, regardless of genotype (Bernardo 1996; Mousseau and Fox 1998). Maternal phenotypic effects are typically determined by the age or size and experience of the females, which often leads to a positive correlation between the size of the mother and the size of the offspring (Green and McCormick 2005; Skibiel et al. 2009), as well as the number of offspring produced (Morris 1996; Sogard et al. 2008).

The maternal size in relation to the offspring size can further be elaborated through allometry, which, in this context, refers to the scaling relationship between the size of an organism's particular body part and its total body size that both grow during development (Shingleton 2010). Thus, this provides an understanding of whether offspring size changes proportionally or disproportionately with maternal size, implying that morphology may vary with ontogeny (Muir et al. 2013). Ontogenetic morphometry has been investigated in some shark species and has found that small-bodied sharks, such as the spiny dogfish *Squalus acanthias*, are likely to display isometric growth (Reiss and Bonnan 2010), retaining overall proportions throughout ontogeny (Irschick and Hammerschlag 2014; Irschick et al. 2017), whereas larger species, including Carcharhiniformes and Lamniformes, are more inclined to exhibit varying degrees of allometric growth (Lingham-Soliar 2005; Fu et al. 2016; Ahnelt et al. 2020). For instance, the large pelagic filter-feeder basking shark *Cetorhinus maximus* displays negative allometry in the head and caudal fin, similar to large pelagic carnivorous sharks, such as the white shark *Carcharodon carcharias* and tiger shark *Galeocerdo cuvier* (Ahnelt et al. 2020). Contrarily, the megamouth shark *M. pelagios*, the third-largest extant filter-feeder shark, exhibits positive allometry in the head and isometry in the caudal fin. This growth pattern differs from that of the large-bodied sharks, which have negative allometry in the head, and intriguingly resembles that of small-bodied sharks with isometric growth in the caudal fin (Yun and Watanabe 2023).

This study, provided with the first ever mother-offspring megamouth shark specimens from an opportunistic sampling, aimed to establish the identity of the specimens using morphological and molecular methods and investigate the morphometric differences of mother *vis-à-vis* pups using the principle of ontogenetic allometry. Significantly, this study facilitates a comparison of the mother and offspring morphology of megamouth sharks, which is a rare opportunity due to their elusive nature. Furthermore, this uncovers noteworthy insights into the developmental progression and adaptive significance of morphological features in megamouth sharks.

2. METHODS

2.1 Morphological and molecular identification

On 14 November 2023, at 1:32 in the afternoon, a gravid megamouth shark was found ashore in Barangay Ipil, Municipality of Dipaculao, Aurora Province, Luzon Island, Philippines (15.82561 N, 121.55323 E) (Figure 2). Unfortunately, on her way to giving birth, the mother died along with the one pup on her side and six pups inside her womb. The incident was immediately reported to the Office of the

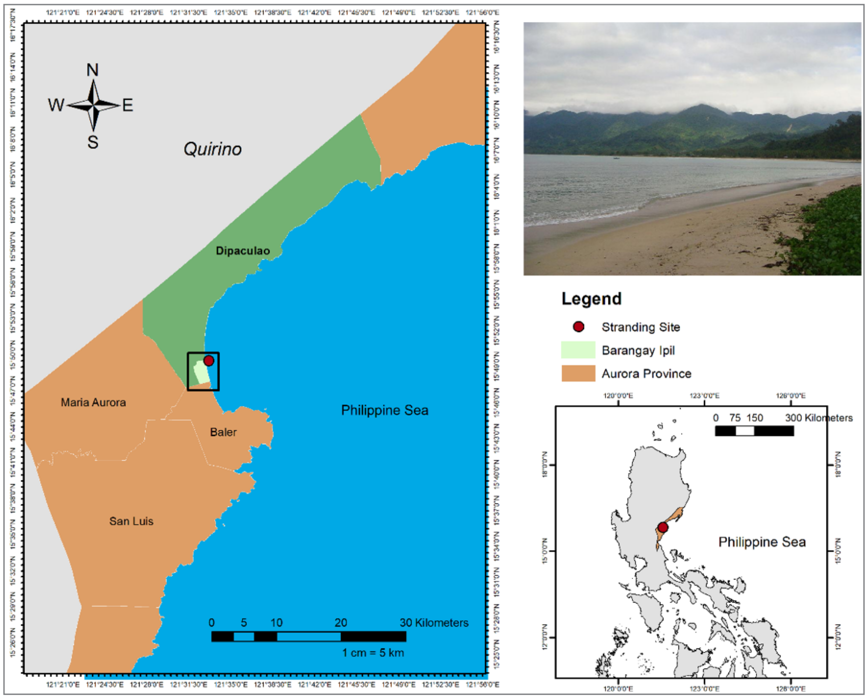


Figure 2. Map showing where the stranding happened, Brgy. Ipil, Dipaculao, Aurora, Luzon Island, Philippines.

Municipal Agriculturist, which, in turn, notified the Bureau of Fisheries and Aquatic Resources (BFAR) Regional Office 3. The mother and one of the pups ("labeled here in this study as "23MMS-PUP2") were necropsied on-site in the evening (Supplementary Figure 1). The cause of the mother's death is unknown; however, necropsy revealed stomach ulcerations and a pale liver, with no signs of injury from fishing gear.

On the other hand, the remaining six pups were transported to the National Museum of the Philippines on 17 November 2023, where they were further processed and examined (Supplementary Figure 2). The specimens were received in an intact and viable condition to acquire morphometric data and tissue samples. The Philippine Aquatic Wildlife Rescue and Response Manual Series: Sharks and Rays (Marine Wildlife Watch of the Philippines 2014) was used as the guide for the data gathering. Obtained morphometric data and photo documentation (except for “23MMS-PUP2” due to data unavailability) were used for morphological identification, while tissue samples from the eight specimens were processed for molecular analysis.

Briefly, genomic DNA was extracted from the ~25 mg of muscle tissue using the cetyltrimethylammonium bromide (CTAB) method following the protocol of Santos et al. (2010). gDNA quality was checked based on the concentration and absorbance values via spectrophotometer. The mitochondrial cytochrome c oxidase 1 gene (CO1) of each megamouth shark sample was polymerase chain reaction (PCR) amplified using primer sets of Ward et al. (2005) and Ivanova et al. (2007) as presented in Table 1. The composition of the PCR cocktail mix was put together following the protocol of Ward et al. (2005) and its corresponding PCR parameters.

The cocktail mix composed of 12.3 µL double-distilled water (ddH20), 2.5 µL10x PCR buffer, 2.5 µL 2 mM diluted deoxyribonucleoside triphosphate (dNTP), 2.5 µL 25 mM MgCl2, 2 µL forward primer (1 µM), 2 µL reverse primer (1 µM), 0.2 Taq DNA polymerase (5U/ µL), and 2 µL DNA template (with ranges from 60 to 1000 ng/µL). PCR parameters are as follows: 94°C at 5 minutes for initial denaturation, 40 cycles of 94 °C at 1 minute for denaturation, 50 °C at 1 minute for annealing, 72 °C at 1 minute for extension, and finally, 72 °C at 5 minutes for final elongation (Ward et al. 2005). The amplified fragment of the MT-COI gene, used as the DNA barcode, is expected to have an average length of about 650 bp. Subsequently, the said PCR amplicons were electrophoresed through a 1% agarose gel stained with Ethidium Bromide (EtBr) and submerged in 1% TAE buffer. Moreover, a hundred-base pair ladder was used in this analysis. Finally, the positive amplicons obtained were sent to 1st BASE, Malaysia, for purification and Bi-directional Sanger sequencing.

For the data analysis, Bi-directional sequence chromatogram results in AB1 file format were visualized, aligned, and edited using Geneious Prime version 6.1.8 software to generate consensus sequences, which were used for homology search in nucleotide Basic Local Alignment Tool (blastn). Reference MT-COI sequences from *M. pelagios,* ingroups - *Centorhinus maximus, Alopias pelagicus,* and *Isurus oxyrinchus,* and outgroup - S*cyliorhinus canicula,* were acquired from GenBank and compiled together in a single Notepad file saved as a FASTA output file. The ingroups consisted of representative species from the sister taxa of Megachasmidae: Cetorhinidae, Alopiidae, and Lamnidae, from the Order Lamniformes (Compagno 1990). On the other hand, *Scyliorhinus* was designated as the outgroup because Carcharhiniformes is sister to Lamniformes, with Scyliorhinidae being one of the closest relatives of lamniforms among carcharhiniforms (Shimada 2005). The FASTA file containing the sequences was uploaded and analyzed in Molecular Evolutionary Genetics Analysis (MEGA) version 11 software (Tamura et al. 2021), then subjected to ClustalW alignment and cut to a uniform length of 554 nucleotides. This was followed by phylogenetic tree construction using the Neighbor-

Table 1. Set of primers used to amplify mitochondrial DNA genes COI.

Gene Marker	Name of Primer	Primer 5’-3’	References
CO1	FishR1	5’-TAGACTTCTGGGTGGCCAAAGAATCA-3’	Ward et al. (2005)
	FishF2	5’-TCGACTAATCATAAAGATATCGGCAC-3’	Ward et al. (2005)
CO1	FishF2_t1	5’-TGTAAAACGACGGCCAGTCGACTAAT CATAAAGATATCGGCAC-3’	Ivanova et al. (2007)
	FishR2 t1	5’-CAGGAACAGCTATGACACCTCAGGGT GTCCGAARAAYCARAA-3’	Ivanova et al. (2007)
		5’-CAGGAAACAGCTATGACACTTCAGGG TGACCGAAGAATCAGAA-3’	

Joining method based on Kimura 7 two-parameter (K2P) with 1000 bootstrap replicates, executed in the same software. Following the procedures of Ward et al. (2008) in species identification of chondrichthyans, the K2P substitution model was employed due to its effectiveness in accounting for a higher rate of transitions relative to transversion in mitochondrial DNA, facilitating a standard and accurate estimate of genetic divergence among species (Hebert et al. 2003). The pairwise distance and sequence data were also acquired and analyzed to strengthen the evidence of identification using DNA forensics. Furthermore, nucleotide sequences and supplementary metadata of the eight specimens analyzed in this study, coded as 23MMS-MOM, 23MMS-PUP1, 23MMS-PUP2, 23MMS-PUP3, 23MMS-PUP4, 23MMS-PUP5, 23MMS-PUP6, and 23MMS-PUP7, were uploaded to the Barcode of Life Database (BOLD) systems. All the sequences were submitted to GenBank and were assigned accession numbers PQ299136, PQ299137, PQ299138, PQ299139, PQ299140, PQ299141, PQ2991342, and PQ299143, respectively.

2.2 Allometric scaling analyses

A total of 20 morphometric, straight-line measurements of the different body parts of the megamouth sharks were analyzed in this study (Figure 3). Following the methodology of Yun and Watanabe (2023), these measurements were log-10 transformed to normalize the distribution, minimize heteroscedasticity, reduce the effect of extreme outliers, and facilitate linear visualization of data for simplified slope comparisons (Campione and Evans 2012). Each body part length (x) was subjected to linear regression against the total body length represented as Log_{10} (y) = m Log_{10} (x) + b. Regression analyses were performed using a customized R script incorporating the formula adopted from Yun and Watanabe (2023) and executed in RStudio for statistical data and scatter plot visualization.

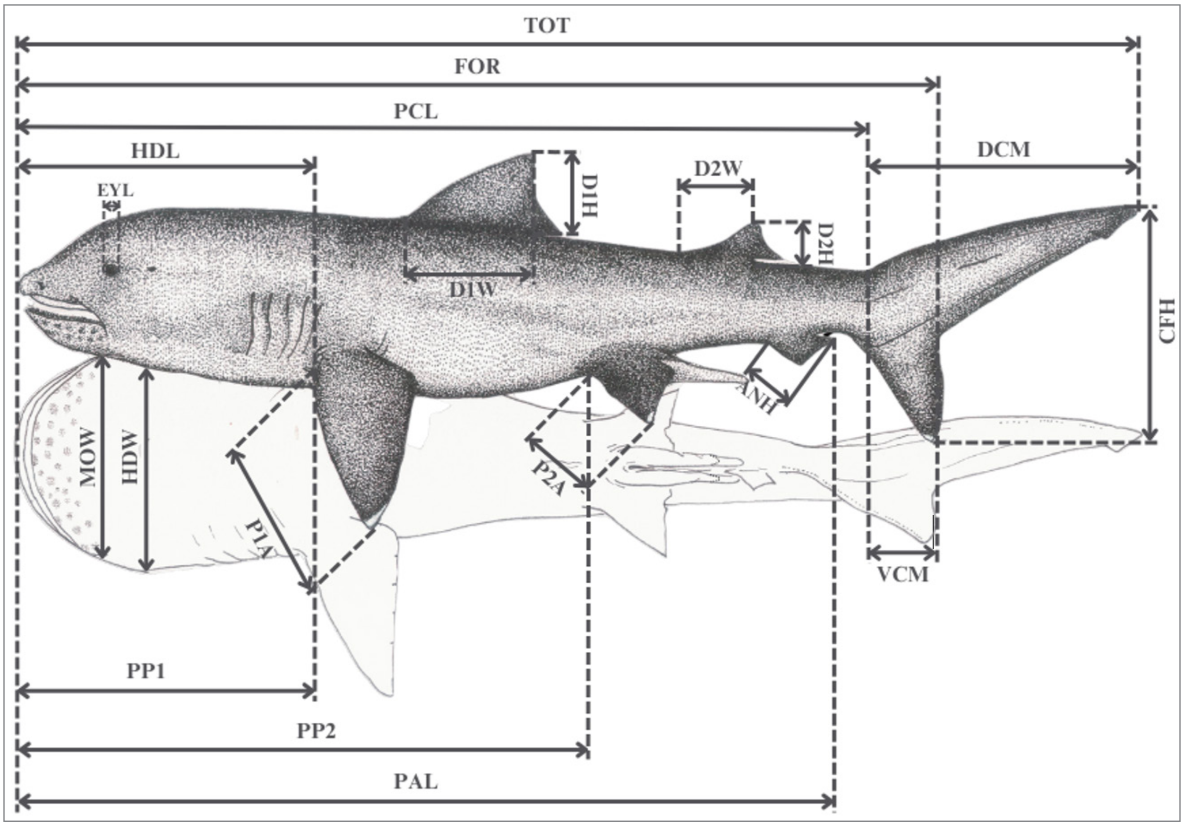


Figure 3. Morphometric, straight-line measurements used in the study. (A) Body Measurements: TOT (Total Length); FOR (Fork Length); PCL (Pre-Caudal Length); PP1 (Pre-Pectoral Length); PP2 (Pre- Pelvic Length); PAL (Pre-Anal Length); (B) Head Measurements: HDL (Head Length); HDW (Head Width); EYL (Eye Length); MOW (Mouth Width); (C) Pectoral, Pelvic, and Fin Measurements: P1A (Pectoral Fin Anterior Margin); P2A (Pelvic Fin Anterior Margin); ANH (Anal Fin Height); (D) Dorsal Fin Measurements: D1H (First Dorsal Fin Height); DIW (First Dorsal Fin Base Width); D2H (Second Dorsal Fin Height); D2W (Second Dorsal Fin Base Width); (E) Caudal Fin Measurements: CFH (Caudal Fin Height); DCM (Dosal Caudal Fin Margin); VCM (Ventral Caudal Fin Margin).

3. RESULTS AND DISCUSSION

Morphological and molecular methods are primarily utilized to describe species identity, offering complementary advantages for improved identification accuracy (Hebert et al. 2003). The morphological approach heavily relies on character-based delineation through visual assessments of physical traits and analysis of morphometric measurements. On the other hand, molecular techniques, particularly DNA barcoding, focus on DNA-based approaches that use genetic markers, such as the MT-COI gene, to discriminate species with high precision (Ward et al. 2005). Table 2 presents the 20 morphometric measurements (in % total length) of the gravid megamouth shark and neonates. The adult female shark measured 5600 mm, while the pups' total length ranged from 1650 mm to 1835 mm. Four of the seven pups were identified as females (including "23MMS-PUP2"), while the rest were males.

Based on morphological observations, specimens display a tadpole-like body with a cylindrical trunk tapering posteriorly from the head. They were coated with a greyish-black color on the dorsal region and a whitish shade on the ventral side. Their heads were broad, large, and longer than the abdomen, situated between the pectoral and pelvic bases. Eyes are placed laterally on the head. Snouts were broadly rounded, short, and depressed, while their mouths were greatly enlarged and terminal on the head, containing about a hundred, blade-like teeth on both the upper and lower jaws and, at the same time, a bright white band that ran horizontally along the dorsal border of the upper jaw. More so, there were conspicuously visible dark spots under the lower jaw.

Dark wavy grooves running parallel were observed on the outer edges of the upper surfaces of the pectoral and pelvic fins, which are channels of bare skin interspersed with areas of denticulated skin. Pectoral fins demonstrate a plesodic structure

Table 2. Morphometric measurements of the mother and pups. Data credit: Marine Wildlife Watch of the Philippines and Bureau of Fisheries and Aquatic Resources (BFAR) Region 3.

Specimen code	**23MMS-MOM**	**23MMS-PUP1 23MMS-PUP5 23MMS-PUP7**	**23MMS-PUP3 23MMS-PUP4 23MMS-PUP6**
Gender	♀	♂	♀
Weight (kg)	>500	11.96-13.53	9.16-10.91
Total length (TOT)	5600 mm	1755 mm - 1835 mm	1650 mm - 1791 mm
Scale	% TOT	% TOT	% TOT
Fork length (FOR)	71.4	77.2 - 80.7	78.5 - 79.3
Pre-caudal fin length (PCL)	62.3	64.4 - 69.2	66.7 - 71.3
Pre-pectoral length (PP1)	21.4	19.9 - 23.9	22.2 - 23.6
Pre-pelvic length (PP2)	45.4	42.5 - 50.7	42.0 - 49.1
Pre-anal length (PAL)	52.3	53.9 - 60.4	50.7 - 60.4
Head length (HDL)	17.1	16.5 - 20.7	16.4 - 20.7
Head width (HDW)	19.6	16.8 - 19.6	14.5 - 19.2
Eye length (EYL)	1.1	1.0 - 1.6	1.3 - 1.5
Mouth width (MOW)	19.6	12.4 - 13.7	11.8 - 13.3
Pectoral fin anterior margin (P1A)	16.1	16.4 - 18.8	17.5 - 18.4
Pelvic fin anterior margin (P2A)	4.6	5.5 - 6.9	5.6 - 6.7
Anal fin height (ANH)	6.1	2.1 - 2.8	2.2 - 2.6
First dorsal fin height (D1H)	5.0	4.7 - 6.0	4.6 - 6.1
First dorsal fin base width (DIW)	7.1	7.6 - 8.6	6.7 - 9.1
Second dorsal fin height (D2H)	2.7	2.3 - 2.7	1.8 - 2.9
Second dorsal fin base width (D2W)	3.6	2.7 - 3.5	3.9 - 5.0
Caudal fin height (CFH)	11.3	22.2 - 28.6	23.9 - 31.2
Dorsal caudal fin margin (DCM)	28.6	23.7 - 29.6	27.4 - 29.5
Ventral caudal fin margin length (VCM)	12.5	11.1 - 13.0	11.4 - 14.0

characterized as relatively narrow, long, and blunted white-tipped. Dorsal fins were moderately large, angular, and low, featuring a narrowly rounded tip and aplesodic fin structure. The anal fins were relatively small and low. Their caudal fins were relatively long but displayed unequal upper and lower lobes, in which the dorsal lobe is longer than the ventral lobe and features a subterminal notch. Actual photos of the mother and pups are shown in the supplementary file (Supplementary Figures 3-9).

Overall, these morphological characters were consistent with the description of the megamouth shark, *M. pelagios*, as Taylor et al. (1983) described. Furthermore, some of the notable morphometric trait measurements of megamouth shark specimens documented in literature on adults from Hawaii, Western Australia, Mie Japan, Taiwan (Hualien & Taitung Country), and Kuroshio Extension (Taylor et al. 1983; Berra and Hutchins 1990; Yano et al.1997; Lee and Shao 2009; Sawamoto and Matsumoto 2012), and juveniles from Brazil, Indonesia, and Mexico (Amorim et al. 2000; White et al., 2004; Castillo et al., 2012) were relatively close to that of the mother and pups characterized in this study based on their morphometric measurements as shown in Table 3.

Using a molecular approach, the phylogenetic tree (Figure 4) inferred from the Neighbor-Joining method using the K2P parameter model revealed that the mitochondrial COI sequences of the adult female shark and the seven pups have 100% similarity with published reference sequences of *M. pelagios*; thus, they clustered in the same clade. On the other hand, reference published sequences of *A. pelagicus* from the family Alopiidae obtained 84% similarity, being the closest relative of megamouth sharks among the group of species. Computed average pairwise distances validated the identity of the beached mother shark and pups as *M. pelagios*, with a mean genetic distance of 0.000 (Table 4). Multiple alignment of MT-COI sequences of specimens examined with the reference species is shown in the supplementary file (Supplementary Figure 10), which provided a brief comparison of the different sequences of specimens examined and enabled the identification of conserved and variable sites among species.

Megamouth shark, *M. pelagios*, the lone extant species of the genus Megachasma, is among the rarest shark species, with inadequate biological and fishery data to date. With less than 300 specimens documented, no gravid female and neonate megamouth sharks have ever been recorded prior to this study. Using morphological and molecular approaches, the results of the present study identified that the freshly deceased gravid shark and her

Table 3. Morphometric measurements of megamouth shark specimens from published literature and the specimens analyzed in the present study.

Ontogenic stage and origin of specimen	Juvenile (Indonesia, Brazil, Mexico)	Pups (Philippines)	Subadult - Adult (Hawaii, Western Australia, Japan, Taiwan, Kuroshio Extension)	Mother (Philippines)
Gender	♀♂	♀♂	♀♂	♀
Total length (TOT)	1767 mm - 2265 mm	1700 mm - 1835 mm	3667 mm - 5440 mm	5600 mm
Scale	%TOT	%TOT	%TOT	%TOT
Pre-caudal fin length (PCL)	64.0 - 64.7	64.4 - 71.3	67.0 - 70.4	62.3
Head length (HDL)	24.3 - 25.4	16.4 - 20.7	25.4 - 28.7	17.1
Eye length (EYL)	1.4 - 1.8	1.0 - 1.6	1.1 - 1.4	1.1
Mouth width (MOW)	11.6 - 13.1	11.8 - 13.7	11.3 - 19.1	19.6
Pre-pectoral length (PP1)	23.8 - 24.3	19.9 - 23.9	24.5 - 28.9	21.4
Pectoral fin anterior margin (P1A)	17.2 - 19.9	16.4 - 18.8	18.7 - 20.1	16.1
Pre-pelvic length (PP2)	-	42.0 - 50.7	48.7 - 55.9	45.4
First dorsal fin height (D1H)	4.9 - 6.7	4.5 - 6.1	4.9 - 6.1	5.0
First dorsal fin base width (DIW)	6.4 - 8.9	7.6 - 9.1	7.5 - 10.8	7.1
Second dorsal fin height (D2H)	2.2 - 4.9	2.2 - 2.9	1.9 - 2.8	2.7
Second dorsal fin base width (D2W)	3.8 - 4.0	2.7 - 4.1	4.1 - 5.5	3.6
Dorsal caudal fin margin (DCM)	32.8 - 35.3	23.7 - 29.6	30.5 - 36.5	28.6
Ventral caudal fin margin length (VCM)	14.3 - 16.4	11.1 - 14.4	13.5 - 14.7	12.5

seven pups washed ashore in Aurora, Philippines, were indeed megamouth sharks. Morphometric measurements of the mother and pups closely resemble those of adult and juvenile megamouth sharks documented in published literature. Slight differences in observed measurements can be attributed to external factors, including post-mortem changes, preservation, and storage. DNA barcoding, on the other hand, was also an efficient method for species identification, as it offers an independent line of evidence that substantiates the morphological identification. Integrating morphological and molecular data improves the overall robustness and credibility of identification, which is crucial for rare species. Furthermore, only a few megamouth shark reference sequences are available in GenBank and BOLD systems. The present study contributed eight MT-COI sequences to the databases, which can be used for future studies.

Out of the less than 300 specimens documented, Yu et al. (2021) investigated approximately 90% of reported cases and found that females were significantly larger than males. The total length of females ranges from 4000 mm to 6000 mm, whereas males vary between 4000 mm and 5000 mm. Small individuals or juveniles have a total length of approximately less than 2000 mm. The smallest free-swimming megamouth shark documented was 1767 mm in total length, reported in Northern Sumatra, Indonesia. (White et al. 2004). Potential reasons why females are larger compared to males are because of their necessity for additional space in the coelom to accommodate large and well-developed pups and as a form reproductive strategy, allowing females to achieve greater reproductive fitness through their growth, as larger females may deliver more pups (Goodwin et al. 2002; Baremore and Hale 2012). With no gravid female and neonate megamouth sharks ever being reported, Castro et al. (1997) initially thought that megamouth sharks may exhibit viviparity with oophagy owing to their resemblance to other lamniform sharks (Ebert et al. 2021). Meanwhile, Yu et al. (2021) inferred that it is convincing to believe that megamouth sharks may instead specifically display aplacental also known as ovoviviparity, giving birth to a limited number of well-developed pups akin to *C. maximus* (Tanaka & Yano 1997). The present study, through the first-ever gravid female and neonate megamouth shark specimens reported in the Philippine waters, confirmed that the rare shark species demonstrates ovoviviparity as their reproductive strategy.

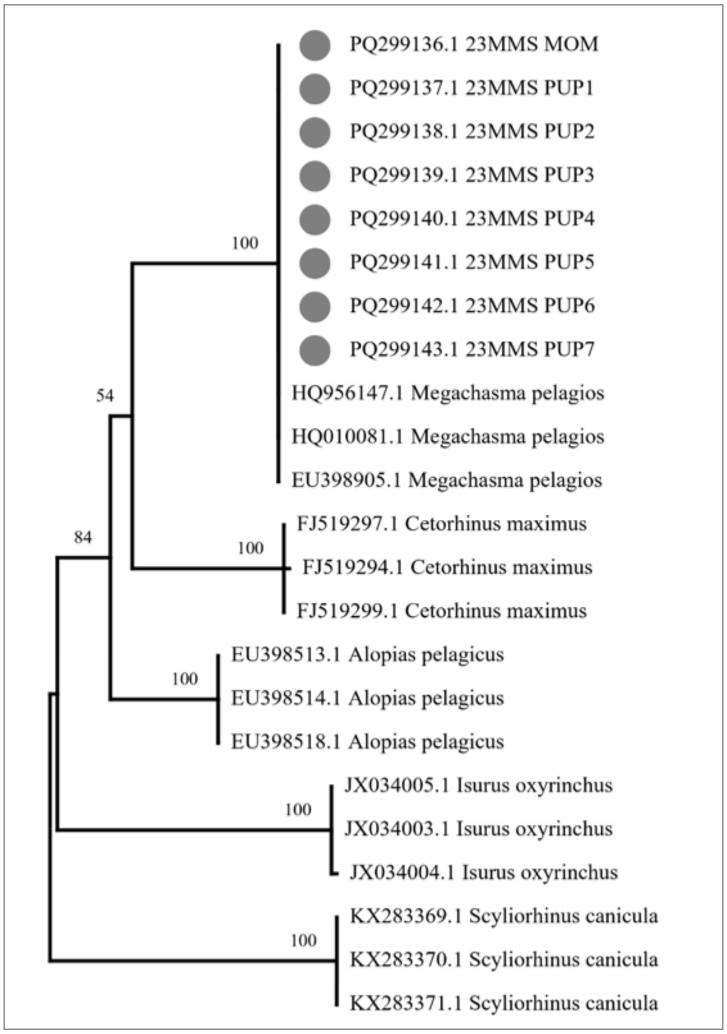


Figure 4. Neighbor-Joining tree of the mother megamouth shark and seven pups based on 554 nucleotides of the MT-COI gene using the K2P model of DNA substitution. Number on nodes represent percentage bootstrap support out of 1000 bootstrap samples; values less than 50% are not shown. Scale bar represents two nucleotide substitutions for every 100 nucleotides.

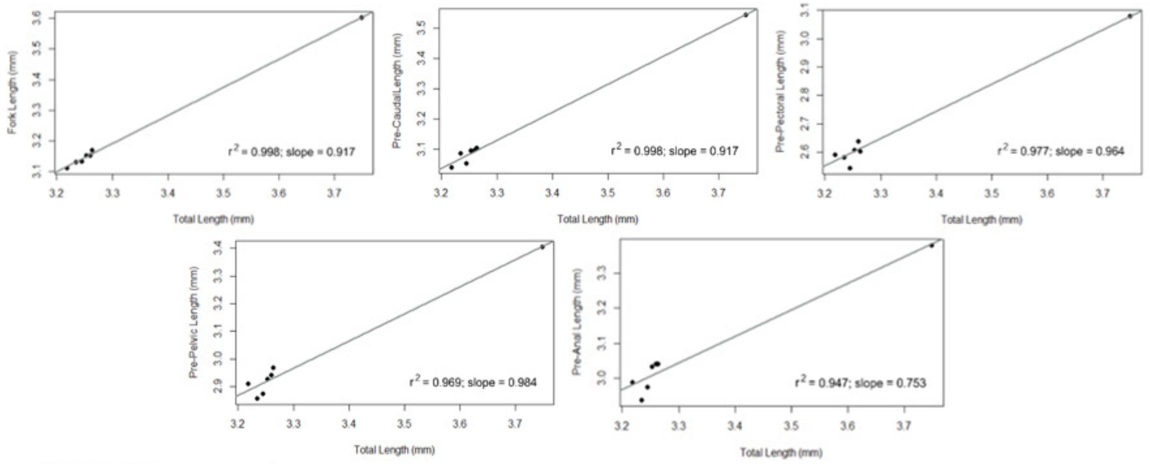
Allometry provides insights into the scaling relationship of proportionality between the size of different body parts relative to the total body size of organisms that grow during development, which

Table 4. Pairwise genetic distances of MT-COI sequences of specimens examined and reference species.

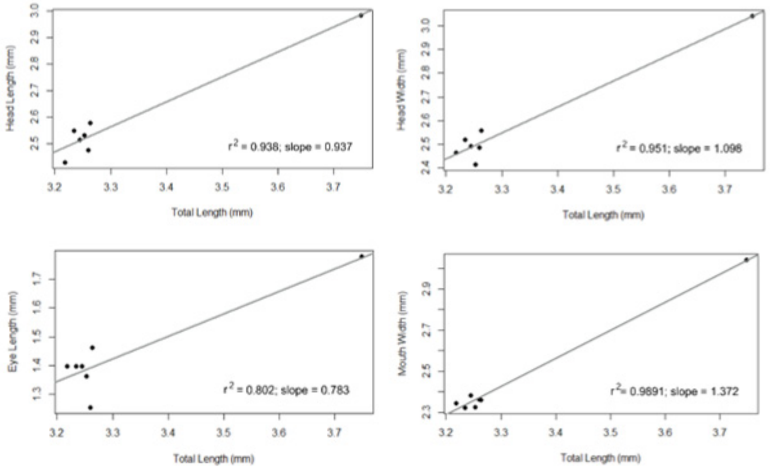
PQ299136.1_23MMS_MOM		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
PQ299137.1_23MMS_PUP1	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
PQ299138.1_23MMS_PUP2	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
PQ299139.1_23MMS_PUP3	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
PQ299140.1_23MMS_PUP4	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
PQ299141.1_23MMS_PUP5	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
PQ299142.1_23MMS_PUP6	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
PQ299143.1_23MMS_PUP7	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
HQ956147.1_Megachasma_pelagios	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
HQ010081.1_Megachasma_pelagios	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
EU398905.1_Megachasma_pelagios	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.015	0.015	0.015	0.017	0.017	0.017	0.024	0.024	0.024	0.023	0.023	0.023
EU398513.1_Alopias_pelagicus	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115		0.000	0.000	0.017	0.017	0.017	0.022	0.022	0.022	0.021	0.021	0.021
EU398514.1_Alopias_pelagicus	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.000		0.000	0.017	0.017	0.017	0.022	0.022	0.022	0.021	0.021	0.021
EU398518.1_Alopias_pelagicus	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.115	0.000	0.000		0.017	0.017	0.017	0.022	0.022	0.022	0.021	0.021	0.021
FJ519294.1_Cetorhinus_maximus	0.128	0.128	0.128	0.128	0.128	0.128	0.128	0.128	0.128	0.128	0.128	0.135	0.135	0.135		0.002	0.002	0.022	0.022	0.022	0.022	0.022	0.022
FJ519297.1_Cetorhinus_maximus	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.132	0.132	0.132	0.002		0.000	0.022	0.022	0.022	0.022	0.022	0.022
FJ519299.1_Cetorhinus_maximus	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.132	0.132	0.132	0.002	0.000		0.022	0.022	0.022	0.022	0.022	0.022
JX034003.1_Isurus_oxyrinchus	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.193	0.193	0.193	0.198	0.195	0.195		0.002	0.000	0.024	0.024	0.024
JX034004.1_Isurus_oxyrinchus	0.211	0.211	0.211	0.211	0.211	0.211	0.211	0.211	0.211	0.211	0.211	0.195	0.195	0.195	0.200	0.198	0.198	0.002		0.002	0.024	0.024	0.024
JX034005.1_Isurus_oxyrinchus	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.208	0.193	0.193	0.193	0.198	0.195	0.195	0.000	0.002		0.024	0.024	0.024
KX283369.1_Scyliorhinus_canicula	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.181	0.181	0.181	0.207	0.205	0.205	0.241	0.238	0.241		0.000	0.000
KX283370.1_Scyliorhinus_canicula	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.181	0.181	0.181	0.207	0.205	0.205	0.241	0.238	0.241	0.000		0.000
KX283371.1_Scyliorhinus_canicula	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.219	0.181	0.181	0.181	0.207	0.205	0.205	0.241	0.238	0.241	0.000	0.000	

may influence structural and functional differences (Shingleton 2010). In here, results of regression analyses revealed that all 19 morphological traits showed strong and positive relationships with the total length (Figure 5). The r-squared values between the total length and the morphological traits examined ranged from 0.50 to 0.99, with most relationships having values greater than 0.75. On the other hand, the slope values were used to describe isometry or allometry, with a slope of one indicating isometry, less than one representing negative allometry, and greater than one signifying positive allometry.

(A) Body Measurements



(B) Head Measurements



(C) Pectoral, Pelvic, and Anal Fin Measurements

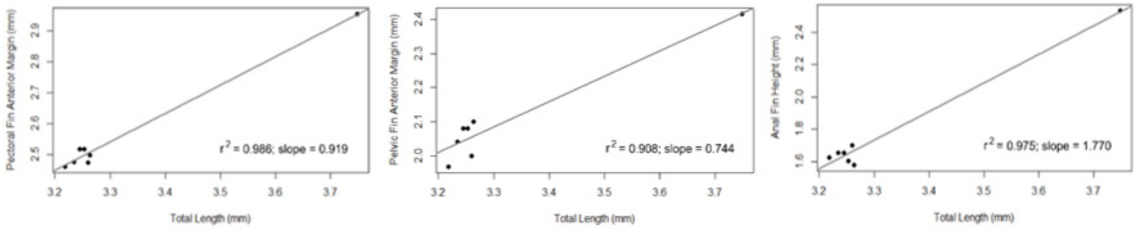
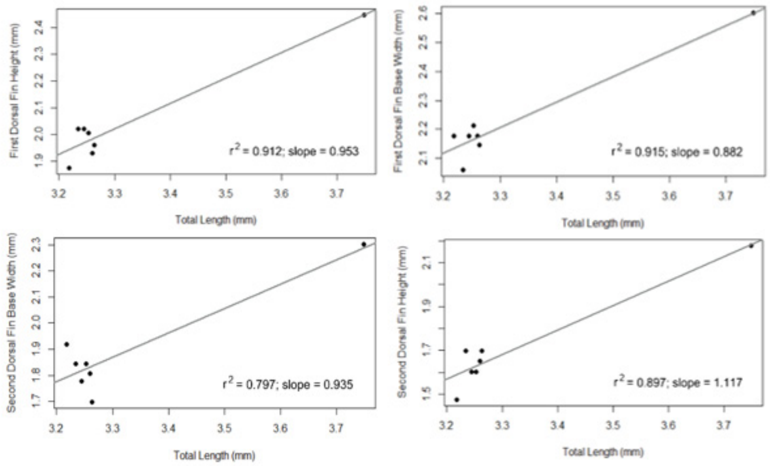
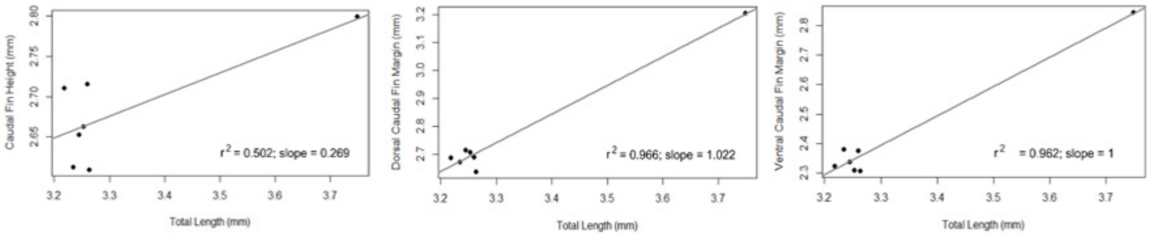


Figure 5. Scatter plots with r^2 and slope values of (A) Body Measurements; (B) Head Measurements; (C) Pectoral, Pelvic, and Anal Fin Measurements; (D) Dorsal Fin Measurements; and (E) Caudal Fin Measurements.

(D) Dorsal Fin Measurements



(E) Caudal Fin Measurements



Continuation of Figure 5. Scatter plots with r^2 and slope values of (A) Body Measurements; (B) Head Measurements; (C) Pectoral, Pelvic, and Anal Fin Measurements; (D) Dorsal Fin Measurements; and (E) Caudal Fin Measurements.

For body measurements, the fork length, pre-caudal length, pre-pectoral length, pre-pelvic length, and pre-anal length showed a slope that ranged from 0.753 to 0.964, indicating negative allometry. In head measurements, the head length and eye length have a slope lower than 1, suggesting negative allometry, whereas the head width and mouth width demonstrated positive allometry. The pectoral and pelvic anterior margins have a slope of 0.919 and 0.744, respectively, indicating negative allometry, while the anal fin has a slope of 1.770, representing positive allometry. For dorsal fin measurements, the first dorsal fin height and first dorsal fin base width both displayed negative allometry. On the other hand, the second dorsal fin height exhibited positive allometric growth, in contrast to the second dorsal fin base width, which has negative allometric growth. Furthermore, for caudal fin measurements, the caudal fin height has a relatively low slope, 0.502, indicating negative allometry, whereas both dorsal and ventral caudal margins demonstrated isometry, where the slope is equal to 1.

Yun and Watanabe (2023) pointed out in their study that despite minor variations observed by Amorim et al. (2000), the body proportion of a juvenile megamouth shark agrees well with that of adults, suggesting an isometric growth. However, based on the results of the present study, while some measurements, such as the dorsal and ventral caudal margin, showed isometry, most of the traits demonstrated clear allometry. Therefore, while some traits scale isometrically, the presence of both positive and negative allometry in other traits imply that the pups do not completely scale proportionally with the mother megamouth shark. For instance, crucial morphometric characteristics that play a significant role in feeding, stability, and propulsion, such as the head length and mouth width, anal fin, and caudal fin, respectively, showed allometric growth.

Negative allometry was observed in head length and caudal fin, indicating that adults have relatively smaller heads and caudal fins than juveniles, similar to the tiger shark, white shark (Irschick and Hammerschlag 2014), and basking shark (Ahnelt et al. 2020). Megamouth sharks possess a heterocercal caudal fin, which means it is also applicable to assume that the more the caudal fin shaped heterocercal in juveniles, the greater their swimming speed is compared to adults (Lingham-Soliar 2005; Irschick and Hammerschlag 2014; Fu et al. 2016). There are two advantages it may provide for the young, as hypothesized by Ahnelt et al. (2020): the first is for escape behavior against large predators, and the second is for reduced energy expenditure, provided that juveniles need their energy to grow, thus an energy-saving swimming mode may be served as an advantage. Both of these have the common goal of ensuring the survival of the early ontogenetic stage under certain environmental pressures. The result of negative allometry in head length and caudal fin may vary from Yun and Watanabe (2023), which showed positive allometry and isometry on the two traits, respectively, in megamouth sharks as they have included the sub-adult stage that may have influenced the differences in the result.

On the other hand, the mouth width demonstrated positive allometry. The mouth width of megamouth sharks increases disproportionately relative to the overall size, indicating that as they mature, the mouth becomes larger, enhancing their ability to filter large volumes of water and feed on their schools of prey. Most of their prey are planktonic prey, which includes krill, sea jellies, copepods, squat lobsters, and shrimp and crab larvae (Taylor et al., 1983; Berra and Hutchins 1990; Sawamoto and Matsumoto 2012; Yu et al. 2024). Megamouth sharks were initially considered ram-filter feeders by Taylor et al. (1983), similar to basking sharks. Basking sharks, inhabiting the cold-temperate oceans and aggregate in coastal waters of the continental shelves, prey on zooplankton by swimming forward with an open mouth, allowing passive water flow to pass over their gills through the bristle-like rakers found on the gill arches; hence, regarded as ram filter-feeder (Sims 2008). However, Compagno (1990) argued that megamouth sharks are suction-filter feeders, akin to whale sharks, supported by their relatively weak body musculature, anteroposteriorly elongated jaw, restrictive internal gill openings, and comparatively soft fins. Whale sharks, the largest filter-feeder fish often found in tropical and warm temperate oceans, forage on zooplankton in shallow waters through active suction-filtering behavior, rapidly expanding their mouth to provide suction forces for prey capture (Cade et al. 2020).

Intriguingly, Tomita et al. (2011) found that the ceratohyal cartilage of megamouth sharks, which facilitates jaw opening, lacks sufficient rigidity to generate suction force, refuting suction filter-feeding behavior. Megamouth sharks possessing extraordinary mouth morphology, characterized by a large buco-pharyngeal elongated jaw cartilages, long ethmopalatine ligament, long palatoquadrate levator and preorbital muscles, and elastic skin around the pharynx, collectively may indicate a potential for engulfment feeding (Nakaya et al. 2008). Further supported by Yu et al. (2024), megamouth sharks forage in deep waters through engulfment feeding, a different feeding mode from basking and whale sharks. Therefore, these inferences suggest that filter-feeder sharks explore different foraging modes and habitats. Additionally, while some sharks have an absent anal fin, including the Order Squatiniformes (Stevens 2005), *M. pelagios* possesses one and was found in this study to demonstrate pronounced positive allometric growth. Similarly, White et al. (2004) documented a 1767 mm juvenile megamouth shark and found significant differences in the shape and size of the anal fin relative to other reported specimens. The anal fin primarily serves as a stabilizing structure that enhances maneuverability and control during swimming, as well as significantly contributes to the overall hydrodynamic efficiency of sharks (Compagno 2001).

Allometric change affects the relative morphology of structures that aid organisms thrive with varying environmental conditions during growth (Ahnelt et al. 2020). Likewise, it also influences various facets of animal behavior, including foraging, predation, defense and adaptive response, and even social interactions (Dial et al. 2008). The study of allometry provides an opportunity to infer undescribed changes in life history that, in turn, may suggest vital insights into the strategies of species to adapt to differing ecological niches and behavioral mechanisms as they grow during ontogeny (Gratwicke et al. 2006; Carlisle et al. 2015). Due to the scarcity of information concerning the megamouth shark, the International Union for Conservation of Nature has listed the megamouth shark as Least Concern (Kyne et al. 2019). However, increased specimen reports were attributed mainly to accidental strandings and bycatch in fisheries. According to Dulvy et al. (2014), given the body size and depth distribution of megamouth sharks, they are likely to be threatened with an elevated risk of extinction if continuously subjected to significant fisheries. Therefore, studying their allometric growth patterns is crucial for understanding their vulnerability to environmental pressures throughout life stages. With this, conservation and management strategies can be made, thereby mitigating the species extinction risk.

4. CONCLUSION

Morphological and molecular analyses confirmed that the adult female shark and pups washed ashore in Aurora, Philippines, were indeed megamouth sharks. This set of specimens was considered the world's first-ever recorded specimens of gravid megamouth shark and a litter of pups. The recent event has also confirmed that megamouth sharks are ovoviviparous. Furthermore, morphological scaling of the mother *vis-à-vis* pups revealed that while some traits scale isometrically, the presence of allometry in most traits, including those that have significant functional roles in feeding, stability, and propulsions, such as the head length and mouth width, anal fin, and caudal fin respectively, imply that the offspring do not completely scale proportionally with the mother megamouth shark. This also suggests that the pups are morphologically distinct from the mother. However, the results of this study only represent the specimens examined and not the overall population; thus, further studies are warranted.

ACKNOWLEDGEMENT

The authors would like to acknowledge the National Museum of the Philippines (NMP) Zoology Division and the Bureau of Fisheries and Aquatic Resources (BFAR) Region 3 for providing the morphometric data, photos, and tissue samples. The authors would also like to thank the Marine Wildlife Watch of the Philippines (MWWP) for assisting with data and tissue sample acquisition and providing the necessary funding for the study, as well as the National Fisheries Research and Development Institute - Genetic Fingerprinting Laboratory (NFRDI-GFL) for the provision of materials and apparatuses used in the study. Furthermore, the authors would like to recognize the University of Santo Tomas - Graduate School for their invaluable support and the Department of Science and Technology Science Education Institute (DOST-SEI) Accelerated Science and Technology Human Resource Development Program - National Science Consortium (ASTHRDP-NSC) for the scholarship and research support grant.

SUPPLEMENTARY MATERIAL

Link to the electronic supplementary material. Supplementary file.

CONFLICTS OF INTEREST

The authors report no conflicts of interest.

ETHICS STATEMENT

The samples used in the study were received by the National Fisheries Research and Development Institute from the Bureau of Fisheries and Aquatic Resources Region 3, which requested the former to conduct species identification and genetic analysis dated 8 January 2025.

AUTHOR CONTRIBUTIONS

Bueno KPR: Conceptualization, Investigation, Formal Analysis, Data curation, Writing – Original Draft. **Santos MD**: Conceptualization, Validation, Supervision, Project administration, Writing – Review & Editing. **Rey JTS**: Investigation, Formal Analysis. **Tayag PAP:** Investigation, Resources. **Ongkiatco, CYA:** Investigation, Resources. **Yaptinchay AAS**: Supervision, Resources, Funding acquisition.

REFERENCES

Ahnelt H, Sauberer M, Ramler D, Koch L, Pogoreutz C. 2019. Negative allometric growth during ontogeny in the large pelagic filter-feeding basking shark. Zoomorphology. 139(1):71–83. https://doi.org/10.1007/s00435-019-00464-2

Amorim AF, Arfelli CA, Castro JI. 2000. Description of a Juvenile Megamouth Shark, *Megachasma pelagios,* Caught off Brazil. Environmental Biology of Fishes. 59(2):117–123. https://doi.org/10.1023/a:1007609617773

Baremore IE, Hale LF. 2012. Reproduction of the Sandbar Shark in the Western North Atlantic Ocean and Gulf of Mexico. Marine and Coastal Fisheries. 4(1):560–572. https://doi.org/10.1080/19425120.2012.700904

Bernardo J. 1996. Maternal Effects in Animal Ecology. American Zoologist. 36(2):83–105. https://doi.org/10.1093/icb/36.2.83

Berra TM, Hutchins JB. 1990. A specimen of megamouth shark, *Megachasma pelagios* (Megachasmidae) from Western Australia. Rec. West. Aust. Mus. 14(4):651–656.

Beuningen DV, Bennette RH, Abdulla AS. 2023. First record of the megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae), from the United Republic of Tanzania. Zootaxa. 5380(6):595–598. https://doi.org/10.11646/zootaxa.5380.6.7

Cade DE, Levenson JJ, Cooper R, de la Parra R, Webb DH, Dove ADM. 2020. Whale sharks increase swimming effort while filter feeding but appear to maintain high foraging efficiencies. Journal of Experimental Biology. 223(11):jeb224402. https://doi.org/10.1242/jeb.224402

Campione NE, Evans DC. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. BMC Biology. 10(1):60. https://doi.org/10.1186/1741-7007-10-60

Carlisle AB, Goldman KJ, Litvin SY, Madigan DJ, Bigman JS, Swithenbank AM, Kline TC, Block BA. 2015. Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. Proceedings of the Royal Society B: Biological Sciences. 282(1799):20141446. https://doi.org/10.1098/rspb.2014.1446

Castillo-Géniz J, Ocampo-Torres A, Shimada K, Rigsby C, Nicholas A. 2012. Juvenile megamouth shark, *Megachasma pelagios,* caught off the Pacific coast of Mexico, and its significance to chondrichthyan diversity in Mexico. Ciencias Marinas. 38(2):467–474. https://doi.org/10.7773/cm.v38i2.2071

Castro JI, Clark E, Yano K, Nakaya K. 1997. The gross anatomy of the female reproductive tract and associated organs of the Fukuoka megamouth shark *(Megachasma pelagios).* In: Yano K, Morrissey JF, Yabumoto Y, Nakaya K, editors. Biology of the megamouth shark. Tokai: Tokai University Press. pp. 115–119.

Clutton-Brock TH. 1991. The Evolution of Parental Care. Princeton, N.J: Princeton University Press. https://doi.org/10.2307/j.ctvs32ssj

Compagno LJ. 1990. Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits. NOAA Tech. Rep. NMFS. 90:357-379.

Compagno LJ. 2001. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Vol. 2, Bullhead, mackeral and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). Rome; Great Britain: Food And Agriculture Organization Of The United Nations.

Cotton CF, Dean Grubbs R, Dyb JE, Fossen I, Musick JA. 2015. Reproduction and embryonic development in two species of squaliform sharks, *Centrophorus granulosus* and *Etmopterus princeps*: Evidence of matrotrophy? Deep Sea Research Part II: Topical Studies in Oceanography. 115:41–54. https://doi.org/10.1016/j.dsr2.2014.10.009

Dial KP, Greene E, Irschick DJ. 2008. Allometry of behavior. Trends in Ecology & Evolution. 23(7):394–401. https://doi.org/10.1016/j.tree.2008.03.005

Diez G, Ruiz J, Salgado A. 2022. Record of three specimens of megamouth sharks – *Megachasma pelagios* – in tropical tuna purse seine fisheries in the Atlantic and Indian Oceans. Journal of the Marine Biological Association of the United Kingdom. 102(1–2):153–156. https://doi.org/10.1017/s0025315422000224

Duchatelet L, Moris VC, Tomita T, Mahillon J, Sato K, Behets C, Mallefet J. 2020. The megamouth shark, *Megachasma pelagios*, is not a luminous species. Schubert M, editor. PLOS ONE. 15(11):e0242196. https://doi.org/10.1371/journal.pone.0242196

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LN, Fordham SV, Francis MP, et al. 2014. Extinction risk and conservation of the world's sharks and rays. eLife. 3:e00590. https://doi.org/10.7554/eLife.00590

Ebert DA, Dando M, Fowler S. 2021. Sharks of the World. Princeton University Press. https://doi.org/10.2307/j.ctv1574pqp

Evans RM. 1990. The relationship between parental input and investment. Animal Behaviour. 39(4):797–798. https://doi.org/10.1016/s0003-3472(05)80391-4

Fu AL, Hammerschlag N, Lauder GV, Wilga CD, Kuo C-Y, Irschick DJ. 2016. Ontogeny of head and caudal fin shape of an apex marine predator: The tiger shark *(Galeocerdo cuvier)*. Journal of Morphology. 277(5):556–564. https://doi.org/10.1002/jmor.20515

Goodwin NB, Dulvy NK, Reynolds JD. 2002. Life-history correlates of the evolution of live bearing in fishes. Balshine S, Kempenaers B, Székely T, editors. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences. 357(1419):259–267. https://doi.org/10.1098/rstb.2001.0958

Gratwicke B, Petrovic C, Speight MR. 2006. Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. Environmental Biology of Fishes. 76(2-4):191–210. https://doi.org/10.1007/s10641-006-9021-8

Green BS, McCormick MI. 2005. Maternal and paternal effects determine size, growth and performance in larvae of a tropical reef fish. Marine Ecology Progress Series. 289:263–272. https://doi.org/10.3354/meps289263

Hamlett WC. 2011. Reproductive Biology and Phylogeny of chondrichthyes: Sharks, Batoids, and Chimaeras. CRC Press. 3. https://doi.org/10.1201/9781439856000

Hebert PDN, Cywinska A, Ball SL, deWaard JR. 2003. Biological Identifications through DNA Barcodes. Proceedings Biological Sciences. 270(1512):313–21. https://doi.org/10.1098/rspb.2002.2218

Hussey NE, Wintner SP, Dudley SFJ, Cliff G, Cocks DT, Aaron MacNeil M. 2010. Maternal investment and size-specific reproductive output in carcharhinid sharks. Journal of Animal Ecology. 79(1):184–193. https://doi.org/10.1111/j.1365-2656.2009.01623.x

Irschick DJ, Fu A, Lauder G, Wilga C, Kuo C-Y, Hammerschlag N. 2017. A comparative morphological analysis of body and fin shape for eight shark species. Biological Journal of the Linnean Society. 122(3):589–604. https://doi.org/10.1093/biolinnean/blx088

Irschick DJ, Hammerschlag N. 2014. Morphological scaling of body form in four shark species differing in ecology and life history. Biological Journal of the Linnean Society. 114(1):126–135. https://doi.org/10.1111/bij.12404

Ivanova NV, Zemlak TS, Hanner RH, Hebert PDN. 2007. Universal primer cocktails for fish DNA barcoding. Molecular Ecology Notes. 7(4):544–548. https://doi.org/10.1111/j.1471-8286.2007.01748.x

Kavanagh PS, Kahl BL. 2021. Life History Theory. In: Shackelford TK, Weekes-Shackelford VA, editors. Encyclopedia of Evolutionary Psychological Science. pp. 4569–4580. Springer, Cham. https://doi.org/10.1007/978-3-319-19650-3_1914

Kyne PM, Liu KM, Simpfendorfer C. 2019. *Megachasma pelagios*. The IUCN Red List of threatened species 2019:e.T393 38A124402302. https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39338A124402302.en

Lee P, Shao K. 2009. Two New Records of Lamniform Shark from the Waters Adjacent to Taiwan. J.Fish. Soc. Taiwan. 36(4):303–311. https://doi.org/10.29822/jfst.200912.0006

Lingham-Soliar T. 2005. Caudal fin allometry in the white shark *Carcharodon carcharias*: implications for locomotory performance and ecology. Naturwissenschaften. 92(5):231–236. https://doi.org/10.1007/s00114-005-0614-4

Marine Wildlife Watch of the Philippines. 2014. Philippine Aquatic Wildlife Rescue and Response Manual Series: Sharks and Rays. Marine Wild Fauna Watch of the Philippines, Inc. 70 p.

Morris DW. 1996. State-Dependent Life Histories, Mountford's Hypothesis, and the Evolution of Brood Size. The Journal of Animal Ecology. 65(1):43. https://doi.org/10.2307/5698

Mousseau TA, Fox CW. 1998. Maternal effects as adaptations. Oxford University Press.

Muir AM, Vecsei P, Pratt TC, Krueger CC, Power M, Reist JD. 2013. Ontogenetic shifts in morphology and resource use of cisco *Coregonus artedi*. Journal of Fish Biology. 82(2):600–617. https://doi.org/10.1111/jfb.12016

Nakaya K, Matsumoto R, Suda K. 2008. Feeding strategy of the megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae). Journal of Fish Biology. 73(1):17–34. https://doi.org/10.1111/j.1095-8649.2008.01880.x

Nakaya K. 2010. Biology of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae). In Proceedings of an international symposium—into the unknown, researching mysterious deep-sea animals. Okinawa: Okinawa Churaumi Aquarium. pp. 69–83.

Reiss KL, Bonnan MF. 2010. Ontogenetic Scaling of Caudal Fin Shape in Squalus acanthias (Chondrichthyes, Elasmobranchii): A Geometric Morphometric Analysis With Implications for Caudal Fin Functional Morphology. The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology. 293(7):1184–1191. https://doi.org/10.1002/ar.21155

Rodriguez-Ferrer G, Wetherbee BM, Schärer M, Lilyestrom C, Zegarra JP, Shivji M. 2017. First record of the megamouth shark, *Megachasma pelagios*, (family Megachasmidae) in the tropical western North Atlantic Ocean. Marine Biodiversity Records. 10:20. https://doi.org/10.1186/s41200-017-0117-y

Santos MD, Lopez GV, Barut NC. 2010. A pilot study on the genetic variation of eastern little tuna *(Euthynnus affinis)* in Southeast Asia. Philippine Journal of Science. 139(1):43-50.

Sawamoto S, Matsumoto R. 2012. Stomach contents of a megamouth shark *Megachasma pelagios* from the Kuroshio Extension: evidence for feeding on a euphausiid swarm. Plankton and Benthos Research. 7(4):203–206. https://doi.org/10.3800/pbr.7.203

Shimada K. 2005. Phylogeny of lamniform sharks (Chondrichthyes: Elasmobranchii) and the contribution of dental characters to lamniform systematics. Paleontological Research. 9(1):55–72. https://doi.org/10.2517/prpsj.9.55

Shingleton AW. 2010. Allometry: the study of biological Scaling. Nature Education Knowledge. 3(10):2. https://www.nature.com/scitable/knowledge/library/allometry-the-study-of-biological-scaling-13228439/

Sims D. 2008. Chapter 3: Sieving a Living: A Review of the Biology, Ecology and Conservation Status of the Plankton-Feeding Basking Shark *Cetorhinus Maximus*. Advances in Marine Biology. 54:171–220. https://doi.org/10.1016/S0065-2881(08)00003-5

Skelton ZR, Kacev D, Frable BW, Chang A, Costescu V, Stabile D, Ebert DA. 2023. Two's company: first record of two free-swimming megamouth sharks, *Megachasma pelagios* (Lamniformes: Megachasmidae), off the California coast. Environmental Biology of Fishes. 106(4):717–724. https://doi.org/10.1007/s10641-023-01406-0

Skibiel AL, Dobson FS, Murie JO. 2009. Maternal influences on reproduction in two populations of Columbian ground squirrels. Ecological Monographs. 79(2):325–341. https://doi.org/10.1890/08-0718.1

Sogard S, Berkeley S, Fisher R. 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. Marine Ecology Progress Series. 360:227–236. https://doi.org/10.3354/meps07468

Stearns SC. 1998. The Evolution Of Life Histories. Oxford University PressOxford. https://doi.org/10.1093/oso/9780198577416.001.0001

Stevens JD. 2005. Taxonomy and field techniques for identification and available regional guides. FAO Fisheries Technical Paper. 474:15.

Tamura K, Stecher G, Kumar S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Molecular Biology And Evolution.

38(7):3022–3027. https://doi.org/10.1093/molbev/msab120

Tanaka S, Yano, K. 1997. Histological observations on the reproductive organs of a female megamouth shark, *Megachasma pelagios*, from Hakata Bay, Japan. In: Yano K, Morrissey JF, Yabumoto Y, Nakaya K, editors. Biology of the megamouth shark. Tokyo, Japan: Tokai University Press. pp. 121–129.

Taylor LR, Compagno LJV, Struhsaker PJ. 1983. Megamouth- a new species, genus, and family of lamnoid shark (*Megachasma pelagios,* family Megachasmidae) from the Hawaiian Islands. 43(8):87-110. http://biostor.org/reference/3316

Tomita T, Sato K, Suda K, Kawauchi J, Nakaya K. 2011. Feeding of the megamouth shark (Pisces: Lamniformes: Megachasmidae) predicted by its hyoid arch: A biomechanical approach. Journal of Morphology. 272(5):513–524. https://doi.org/10.1002/jmor.10905

Ward RD, Holmes BH, White WT, Last PR. 2008. DNA barcoding Australasian chondrichthyans: results and potential uses in conservation. Marine and Freshwater Research. 59(1):57–71. https://doi.org/10.1071/MF07148

Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PDN. 2005. DNA barcoding Australia's fish species. Philosophical Transactions of the Royal Society B: Biological Sciences. 360(1462):1847–1857. https://doi.org/10.1098/rstb.2005.1716

White WT, Fahmi MA, Sumadhiharga K. 2004. A juvenile megamouth shark *Megachasma pelagios* (Lamniformes: Megachasmidae) from northern Sumatra, Indonesia. Raffles Bulletin of Zoology. 52(2):603–607. https://www.researchgate.net/publication/235659736_A_juvenile_megamouth_shark_Megachasma_pelagios_Lamniformes_Megachasmidae_from_Northern_Sumatra_Indonesia

Yano K, Yabumoto Y, Tanaka S, Tsukada O, Furuta M. 1997. Capture of a mature female megamouth shark, *Megachasma pelagios,* from Mie, Japan. In: Proceedings of the 5th Indo-Pacific Fish Conference. pp. 335-349. https://www.researchgate.net/publication/256835495_Capture_of_a_mature_female_megamouth_shark_Megachasma_pelagios_from_Mie_Japan

Yu C, Joung S, Hsu H, Liu K, Yamaguchi A. 2024. Feeding ecology of two filter feeding sharks in the northwestern Pacific Ocean. Preprint (Version 1). Research Square (Research Square). https://doi.org/10.21203/rs.3.rs-4166667/v1

Yu C-J, Joung S-J, Hsu H-H, Lin C-Y, Hsieh T-C, Liu K-M, Yamaguchi A. 2021. Spatial–Temporal Distribution of Megamouth Shark, *Megachasma pelagios*, Inferred from over 250 Individuals Recorded in the Three Oceans. Animals. 11(10):2947. https://doi.org/10.3390/ani11102947

Yun C, Watanabe YY. 2023. Allometric Growth of the Enigmatic Deep-Sea Megamouth Shark *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983 (Lamniformes, Megachasmidae). Fishes. 8(6):300. https://doi.org/10.3390/fishes8060300