

**REVIEW PAPER**

**Distribution, body size and biology of the megamouth shark *Megachasma pelagios***

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**ABSTRACT**

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We compiled historical reports of megamouth sharks *Megachasma pelagios* (mostly fishery by-catch and strandings) from 1976 to 2018 ( $n = 117$ ) and found that they are distributed globally (highest latitude,  $36^\circ$ ) with three hotspots: Japan, Taiwan and the Philippines. Despite possible biases due to variability in fishing effort, more individuals were reported at higher latitudes in the summer, suggesting seasonal, latitudinal migrations. Sex ratios were female-biased in Japan, but even more so in Taiwan and the Philippines, suggesting some sexual segregation. Females (total length,  $L_T = 3.41\text{--}7.10$  m) were larger than males ( $L_T = 1.77\text{--}5.39$  m) and matured at a larger  $L_T$  (5.17 m) than males (4.26 m). Also, we reviewed the systematics, feeding ecology and swimming behaviour of *Megachasma pelagios* based on the literature. Our review shows that, compared with their morphology, anatomy and genetics, behavioural ecology of this species remains largely unknown and electronic tagging studies are warranted.

## KEYWORDS

filter feeding, fishery by-catch, maturity, seasonal movement, sexual segregation, stranding

## 1 | INTRODUCTION

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In 1976, while hauling up a parachute-type sea anchor from 165 m depth off Oahu, Hawaii, a US research vessel found a large, strange-looking creature entangled in the anchor. It was a shark, with a peculiar morphology; an enormous mouth with a tadpole-like body shape (Figure 1a). It was assigned to a new family (Megachasmidae) and genus (*Megachasma* Taylor, Compagno & Struhsaker 1983) and named the megamouth shark *Megachasma pelagios* (Taylor *et al.*, 1983). Subsequently, new specimens were occasionally captured in fishing nets (Lavenberg & Seigel, 1985) or found stranded (Berra & Hutchins, 1990) in various parts of the world, with the number of reports increasing slowly. Since the early 2000s, however, an increasing number of *M. pelagios* have been reported, presumably due to increasing publicity, with *c.* 100 individuals being recorded to date (Liu *et al.*, 2018).

Despite increased reports, information on the general biology and ecology of *M. pelagios* is still fragmented. Based on 40 sharks reported pre 2008, information on their distribution, body size, maturity *etc.* was provided by Nakaya (2010). However, given that the number of reports has greatly increased since 2008, an updated analysis is warranted. Moreover, while some aspects of their biology and ecology have been investigated, including

morphology (Taylor *et al.*, 1983), anatomy and systematics (Compagno, 1990), feeding ecology (Nakaya *et al.*, 2008; Tomita *et al.*, 2011), genetics (Martin & Naylor, 1997; Liu *et al.*, 2018) and movement patterns (Nelson *et al.*, 1997), no study has synthesised all available information to capture the general features of this species.

Here we compiled the historical reports of *M. pelagios* to investigate their distribution, seasonal occurrences, body size distribution and body size at maturity. We also review the literature on this species to summarise what is known (or unknown) of its general biology and ecology. By doing so, we update and synthesise our knowledge on this evolutionarily interesting yet enigmatic species.

## **2 | DATA COLLECTION**

Case reports were collected from the literature and two online databases: Florida Museum of Natural History ([www.floridamuseum.ufl.edu/discover-fish/sharks/megamouths/](http://www.floridamuseum.ufl.edu/discover-fish/sharks/megamouths/)) and *Sharkman's World* ([www.sharkmans-world.eu](http://www.sharkmans-world.eu)). As of December 2018 (when our data collection was completed), the former website lists historical reports up until April 2016,

whereas the latter website, created by a shark enthusiast, was still being updated. The information on the two websites is consistent with the literature (Supporting Information Table S1) and recent information we found from different internet sources (*e.g.*, current news sources). Therefore, the websites were considered reliable, at least for date, location, situation (*e.g.*, captured or stranded) and sex of the individuals (which is readily determined by the presence or absence of claspers). However, body length and mass were not extracted from the internet sources, because it was often unclear if the values were measured or approximated. Information on body size was extracted only from the literature that measured (rather than estimated) these variables.

Information on sexual maturity (*i.e.*, mature or immature) was also extracted from the literature. Maturity for females was assessed by the development of ovaries and uterus or by the presence of mating scars on the body, whereas maturity for males was based on the state of claspers or the development of testes (Lavenberg & Seigel, 1985; Yano *et al.*, 1997; Smale *et al.*, 2002; Liu *et al.*, 2018), although some reports did not specify the criteria used. Because we were interested in the body length at which sharks reach sexual maturity, sub-adults (Liu *et al.*, 2018) were referred to as immature in this study.

### 3 | DATA ANALYSIS

#### 3.1 | Distribution and seasonality

A total of 117 individuals (55 females, 36 males, 26 unknown sex) were reported from 1976 to 2018 (Supporting Information Table S1). The locations (Figure 1b) show that *M. pelagios* are a cosmopolitan species distributed widely in temperate and tropical waters of the Pacific, Atlantic and Indian Oceans. The highest latitudes for a megamouth report were 36° N and 34° S. The three most important hotspots were Japan ( $n = 21$ ), Taiwan ( $n = 46$ ) and the Philippines ( $n = 24$ ). These areas are located adjacent to the Kuroshio Current and *M. pelagios* might be associated with this strong, warm current (Liu *et al.*, 2018). Other important areas included California ( $n = 5$ ). Because the majority (84 of 117) of *M. pelagios* were reported as fishery by-catch, our results may be biased by regional and seasonal variability in fishing effort. However, when we restricted our analyses to stranded individuals ( $n = 23$ ), the highest number ( $n = 12$ ) was recorded in the Philippines followed by Japan ( $n = 3$ ); therefore, our finding that the east Asian continental

waters along the Kuroshio Current is the most important region, is robust.

In the northern hemisphere, *M. pelagios* were reported throughout the year, but some seasonality was detected (Figure 2a). In winter (January–March), *M. pelagios* occurred mostly in lower latitudes ( $< 13^\circ$ ), except for four individuals reported in Japan ( $34\text{--}35^\circ$ ) in January. In April–July, when sea surface temperatures increase, *M. pelagios* were reported at a higher latitudinal range ( $7\text{--}36^\circ$ ). In August–October, when sea surface temperatures are highest, the majority of *M. pelagios* were reported at relatively high latitudes ( $24\text{--}35^\circ$ ). The seasonality of occurrence was highlighted in Taiwan (the most important hotspot), where all 27 individuals caught by drift-gillnet fishery from 2013 to 2015 were reported from late April to early August, although the fishery operated year round (Liu *et al.*, 2018). In contrast, in the Philippines (located in lower latitudes than Taiwan), nine of the 11 fishery-caught individuals were reported from January to March. Overall, these results suggest that *M. pelagios* may perform latitudinal migration to buffer seasonal changes in water temperature and prey availability, as reported for other shark species (Weng *et al.*, 2008). Our result, however, should be interpreted with caution, due to complex regional and seasonal variability in fishing effort. When we restricted our analyses to stranded individuals, no clear seasonal patterns were observed (Figure 2b). In the

southern hemisphere, information was too scarce to detect any seasonal patterns.

Interestingly, in the northern hemisphere, more females were reported at higher latitudes (Figure 2a). In Japan, 18 of 20 sexed individuals (90%) were females, whereas sex ratios were less biased in Taiwan (60% females) and the Philippines (62% females; Figure 1b), suggesting some sexual segregation in *M. pelagios*. Sexual segregation is common in both coastal and pelagic elasmobranchs, presumably due to sex-specific environmental preferences or females avoiding male harassment outside of the mating season (Wearmouth and Sims, 2008).

### 3.2 | Body size and maturity

The total length and body mass ( $M$ ) of *M. pelagios* were  $L_T = 1.77\text{--}7.10$  m and  $M = 13.8\text{--}1137$  kg (Figure 3). Females ( $L_T = 3.41\text{--}7.10$  m) were significantly larger than males ( $L_T = 1.77\text{--}5.39$  m;  $t = 2.46$ ,  $df = 43$ ,  $P < 0.05$ ). Only whale sharks *Rhincodon typus* Smith 1828 and basking sharks *Cetorhinus maximus* (Gunnerus 1765) reach larger sizes (Compagno *et al.*, 2005) and *M. pelagios* are confirmed as the third biggest shark species in the world.

The length–mass relationship showed large variability around the regression curve,

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especially in females (Figure 4a–c), but overall could be described by  $M = 9.86 L_T^{2.70}$  ( $L_T$  range, 1.77–5.67 m; Figure 4d). This variability probably comes from natural variation in individual body condition and measurement errors associated with difficulties in weighing very heavy animals. Notably, data in Liu *et al.* (2018) ( $n = 27$ ) show a large variability; *e.g.*, a 3.52 m female weighed 210 kg and a 3.41 m female weighed 916 kg. Excluding data from Liu *et al.* (2018) provided a less variable relationship with an exponent of 2.7 (Figure 4d), within a range of exponents (2.5–3.5) reported for many other shark species (Kohler *et al.*, 1995). Although stranded individuals can be thin, presumably due to poor health (Smale *et al.*, 2002), the residuals of the length–mass relationship did not statistically differ between fishery-caught individuals (including an individual caught by a sea anchor) and stranded individuals for all data (Figure 4a,  $t = 0.58$ ,  $df = 37$ ,  $P > 0.05$ ) and the data excluding Liu *et al.* (2018) (Figure 4d,  $t = 1.70$ ,  $df = 10$ ,  $P > 0.05$ ). Total length was highly correlated with precaudal length ( $L_{PC}$ ), with 69% of total length representing the precaudal length (Figure 4e).

Maturity was assessed for 23 females and 20 males, of which 7 females and 7 males, respectively, were fully mature. The smallest mature individuals were 4.76 m and 4.00 m  $L_T$  for females and males, respectively (Figure 5). Logistic regression models indicated that the

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lengths at which 50% of the individuals reach sexual maturity are  $L_{T50}$  5.17 m and 4.26 m for females and males, respectively (Figure 5). A large individual variability in  $L_{T50}$ , especially in females, may be partly because maturity was assessed by different researchers using different criteria; therefore, the length at  $L_{T50}$  determined statistically might be more useful than the length of the smallest mature individuals. As in many other elasmobranch species (Compagno *et al.*, 2005), female *M. pelagios* reach sexual maturity at larger body size than males. The age at maturity cannot be estimated, due the lack of age determination studies for this species. Pregnant females or neonates have never been found, precluding us from understanding their reproductive biology. It is known, however, that the ovary of this species is similar to that of Lamnidae [*e.g.*, white sharks *Carcharodon carcharias* (L. 1758)] and Alopiidae [*e.g.*, thresher sharks *Alopias vulpinus* (Bonnaterre 1788); Castro *et al.*, 1997]. It suggests that *M. pelagios* embryos are oophagous (*i.e.*, eating eggs; Castro *et al.*, 1997; Tanaka ± Yano, 1997), although the modes of embryonic nourishment may change during gestation periods as reported for white sharks (Sato *et al.*, 2016).

### 3.3 | Systematics

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The systematics of *M. pelagios*, a filter-feeding species, are of particular interest, because they could indicate when and how many times filter feeding has evolved in sharks. Based on morphology, *M. pelagios* were thought to be a close relative of *C. maximus* in the order Lamniformes (Maisey, 1985). *Rhincodon typus*, the other filter-feeding shark, is a distant relative of the two species, being classified in the Orectolobiformes. Under this scenario, filter feeding evolved at least twice in sharks. Subsequent morphological studies, however, argued that Megachasmidae (the family only including *M. pelagios*) are a sister group to the Alopiidae, Cetorhinidae (including *C. maximus*) and Lamnidae and that *M. pelagios* and *C. maximus* do not form a single clade (Compagno, 1990). Under this scenario, filter feeding evolved at least three times in sharks. Molecular studies supported the latter scenario (Martin & Naylor, 1997; Morrissey, 1997; Martin *et al.*, 2002), although the phylogenetic trees constructed varied depending on the models used.

The origination time for *M. pelagios* remains unclear. The morphologically distinct, crown-like teeth of *M. pelagios* (Figure 6) allowed palaeontologists to identify fossilised teeth of *Megachasma* spp. (Shimada, 2007; Spadini & Manganelli, 2015; Tomita & Yokoyama, 2015;

Shimada & Ward, 2016). Such fossils have been found in North and South America, Europe and East Asia (Shimada & Ward 2016, figure 3). The oldest fossil record is from the late Eocene in Denmark, suggesting that *Megachasma* spp. inhabited offshore waters about 36 M years ago (Shimada & Ward, 2016). However, there is a large gap between this estimate and the estimated origination time based on molecular studies (the late Cretaceous about 100 M years ago; Martin *et al.*, 2002).

### 3.4 | Feeding ecology

Stomach contents analyses show that *M. pelagios* feed primarily on krill (euphausiids; Taylor *et al.*, 1983; Yano *et al.*, 1997; Sawamoto & Matsumoto, 2012), but also copepods and gelatinous zooplankton (Berra & Hutchins, 1990). These observations are supported by a stable-isotope analysis, showing that *M. pelagios* prey on low trophic-level foods in offshore environments (de Moura *et al.*, 2015). Coupled with their specialised morphology (large protrudable mouth, small teeth, densely packed gill-raker papillae), there is no doubt that *M. pelagios* are planktivorous filter feeders, along with two other extant shark species (*C. maximus* and *R. typus*).

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However, it is still unclear how they feed on plankton. *Cetorhinus maximus* and *R. typus* employ different feeding modes. *Cetorhinus maximus* swim continuously through schools of plankton with their mouth open, a mode called ram-filter feeding. *Rhincodon typus*, on the other hand, generate suction pressure by opening their mouth rapidly to draw in water, a mode called suction-filter feeding, although they also employ ram-filter feeding. Originally, *M. pelagios* were thought to be ram-filter feeders (Taylor *et al.*, 1983), but a later study by Compagno (1990) suggested that *M. pelagios* are suction-filter feeders based on their weak body musculature, soft fins, restricted internal gill openings and jaw morphology. Another study (Nakaya *et al.*, 2008) pointed out that *M. pelagios* have an unusually big gulp for a shark with relatively small gill openings and suggested that they are neither ram-filter nor suction-filter feeders, but engulfment feeders as in rorqual whales. Using a different approach, Tomita *et al.* (2011) analysed the morphological data for 21 species of sharks to show that ram or suction-filter feeders can be identified by the morphology of ceratohyal (cartilage used for opening jaws). They concluded that the ceratohyal of *M. pelagios* is not stiff enough to produce suction force and that *M. pelagios* might be ram-filter feeders (Tomita *et al.*, 2011). This debate can only be resolved by directly observing their feeding behaviour. Recently developed animal-borne video

cameras, coupled with multi-sensor data loggers (*e.g.*, accelerometer), are promising tools for that purpose (Papastamatiou *et al.*, 2018).

As in other shark species, *M. pelagios* have electroreceptor ampullae of Lorenzini on the surface of the head anterior to the first gill slit. Interestingly, *M. pelagios* (Kempster & Collin, 2011b) and *C. maximus* (Kempster & Collin, 2011a) have the lowest density of ampullary pores among shark species that have been studied; therefore, filter-feeding sharks may rely less on passive electroreception for detecting prey compared with other sharks. The pectoral fins of *M. pelagios* have multiple features (*i.e.*, large number of radial segments, high skin elasticity and hinge joint structure) that suggests greater flexibility compared with other sharks such as shortfin mako *Isurus oxyrinchus* Rafinesque 1810 and salmon sharks *Lamna ditropis* Hubbs & Follett 1947 (Tomita *et al.*, 2014). Therefore, they may be able to control their bodies by using the pectoral fins (in addition to the caudal fin) to pursue krill swarms in the water. In addition, *M. pelagios* have a conspicuous white band on the upper jaw (Figure 6a), which is barely visible when the mouth is closed, but is exposed when the mouth is protruded. It has been speculated that this band may have a luring or attracting function on planktonic prey under dark conditions (Nakaya, 2001).

### 3.5 | Swimming and migratory behaviour

The swimming behaviour of *M. pelagios* remain largely unknown. To date, only a single individual has been electronically tagged and tracked (Nelson *et al.*, 1997). It was acoustically tracked for 50 h off California where it exhibited distinct vertical migration by staying shallow (12–25 m depth) at night and diving deep (120–166 m) during the day. A similar vertical migration has been reported for *C. maximus*, although they also exhibit reverse vertical migration (*i.e.*, diving deep at night and stay shallow during the day) depending on the location (Sims *et al.*, 2005). Vertical migrations reported for other shark species (Weng *et al.*, 2007) are not that distinct, suggesting that filter-feeding sharks follow vertically migrating zooplankton (*i.e.*, deep scattering layer) to maximise foraging efficiencies. Swimming speed (relative to water) of the 4.9 m shark was estimated to be 0.4–0.6 m s<sup>-1</sup> (Nelson *et al.*, 1997), which is slower than 1.0 m s<sup>-1</sup> that is predicted for its estimated body mass (720 kg; Figure 4e) and ectothermic physiology based on a published allometric relationship (Watanabe *et al.*, 2015). It supports the previous suggestion that *M. pelagios* are slow swimmers based on their morphology (*e.g.*, weak body

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musculature, soft fins, lack of a keel on the caudal peduncle; Taylor *et al.*, 1983; Compagno, 1990).

No conventional or electronic tagging studies have been published on *M. pelagios* to record their seasonal migratory patterns. Seasonality detected in this study (despite possible biases due to fishing effort; Figure 2a) suggests that *M. pelagios* may perform latitudinal, seasonal migrations to buffer changes in water temperature and prey availability. Moreover, a recent genetic analysis indicated that specimens from Taiwan, Indonesia, Mexico and Puerto Rico shared a haplotype (Liu *et al.*, 2018), suggesting connectivity of different populations across the Pacific Ocean. Trans-oceanic migrations have been recorded for several large-bodied sharks, including filter-feeding *C. maximus* (Gore *et al.*, 2008) and *R. typus* (Eckert & Stewart, 2001); therefore, it is possible that *M. pelagios* are long-distance migrators and satellite-tracking studies are warranted.

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### **Contributions**

Y.Y.W. conceived the idea, collected and analysed the data. Y.Y.W. wrote the paper with input from Y.P.P.

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### **Significance Statement**

The general biology and ecology of megamouth sharks is poorly understood. We compiled historical reports (1976–2018) to show their distribution, seasonal occurrence patterns, body size distribution, and body size at maturity. We also reviewed the literature on this species to point out that electronic tagging studies are warranted.

## Figure captions

**FIGURE 1** (a) A 4.46 m total length *Megachasma pelagios* captured in Japan in 2014. (b) World map showing where megamouth sharks were reported from 1976 to 2018. Sex compositions are shown by pie charts for Japan, Taiwan, and the Philippines, the three hotspots of this species.

Typesetter: capital first letter for Female, Male and Unknown.

**FIGURE 2.** Latitudes of the locations where *Megachasma pelagios* were reported, plotted against time of the year, based on (a) all data and (b) stranded individuals. As a reference, monthly mean sea surface temperature at 180° longitude, provided by the US National Oceanic and Atmospheric Administration (NOAA), is shown by colour in the background.

Typesetter: capital first letter for Female, Male and Unknown.

**FIGURE 3.** Frequency distributions of (a) total length ( $L_T$ ) and (b) body mass ( $M$ ) based on physically measured data for *Megachasma pelagios*.

**FIGURE 4.** Least-square regression relationships between total length ( $L_T$ ) and body mass ( $M$ ) (based on physically measured data) for *Megachasma pelagios*: (a) all data ( $y = 47.23x^{1.63}$ ,  $r^2 = 0.57$ ,  $n = 63$ ), (b) female only data ( $y = 69.88x^{1.41}$ ,  $r^2 = 0.41$ ,  $n = 23$ ), (c) male only data ( $y = 15.45x^{2.36}$ ,  $r^2 = 0.85$ ,  $n = 16$ ) and (d) data excluding Liu *et al.* (2018) ( $y = 9.86x^{2.70}$ ,  $r^2 = 0.83$ ,  $n = 12$ ). Stranded individuals are represented by different symbols in (a)–(d). (e) Relationship between  $L_T$  and precaudal length ( $L_{PC}$ ;  $y = 0.688x^{-0.05}$ ,  $r^2 = 0.99$ ,  $n = 13$ )).

**FIGURE 5.** Maturity (mature or immature) plotted against total length ( $L_T$ ) for (a) female and (b) male *Megachasma pelagios*. Logistic regression models between  $L_T$  and the probability of mature are also shown: female,  $\text{logit}(y) = -18.2 + 3.52x$ ; male,  $\text{logit}(y) = -18.4 + 4.32x$ .

**FIGURE 6.** (a) Mouth of *Megachasma pelagios*, showing a number of small teeth (↓) and a white band on the upper jaw (↓). Photo courtesy: Sho Tanaka. (b) Teeth taken from a different individual, showing distinct, crown-like shape. Photo courtesy: Asako Numaguchi.

(a)

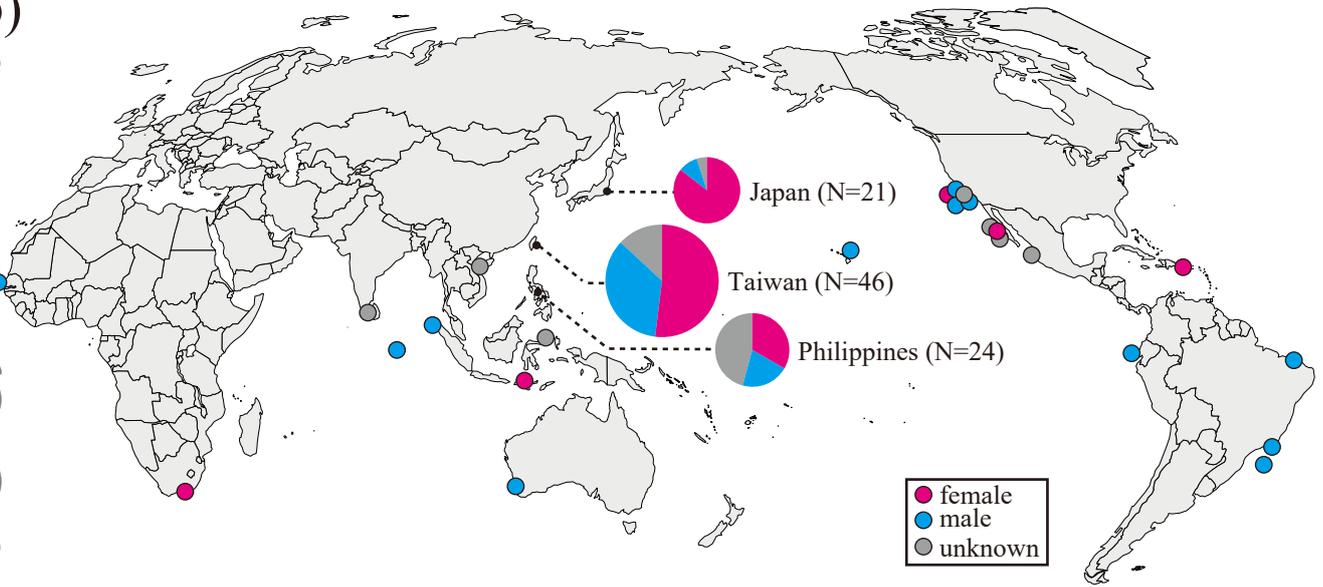
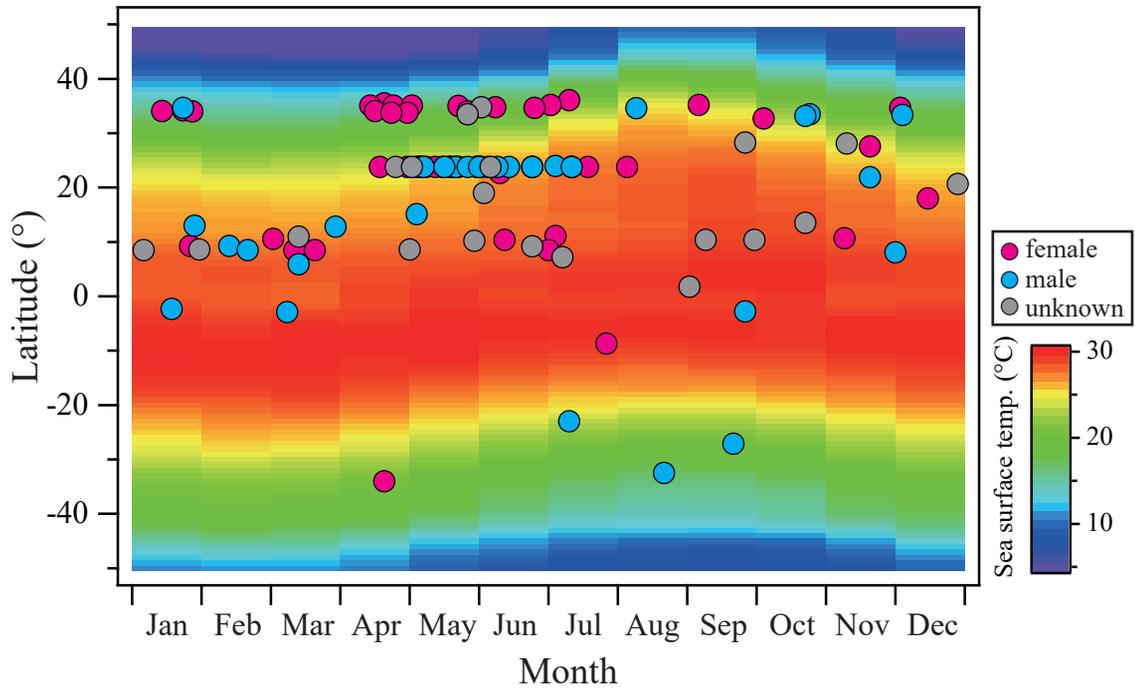


Fig. 1

(a) All data



(b) Stranding only

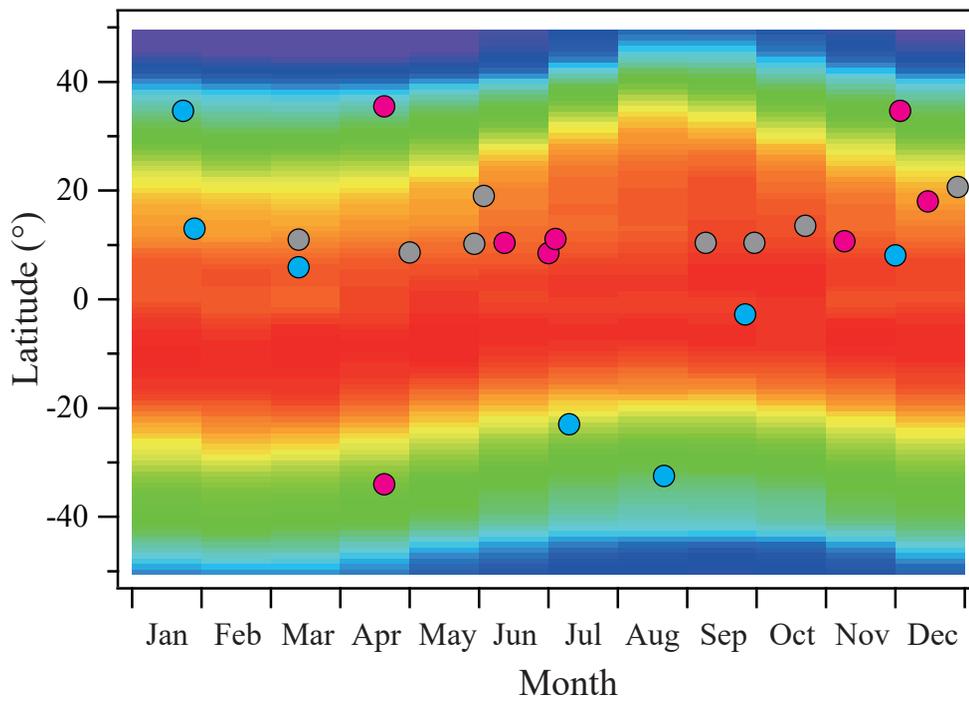


Fig. 2

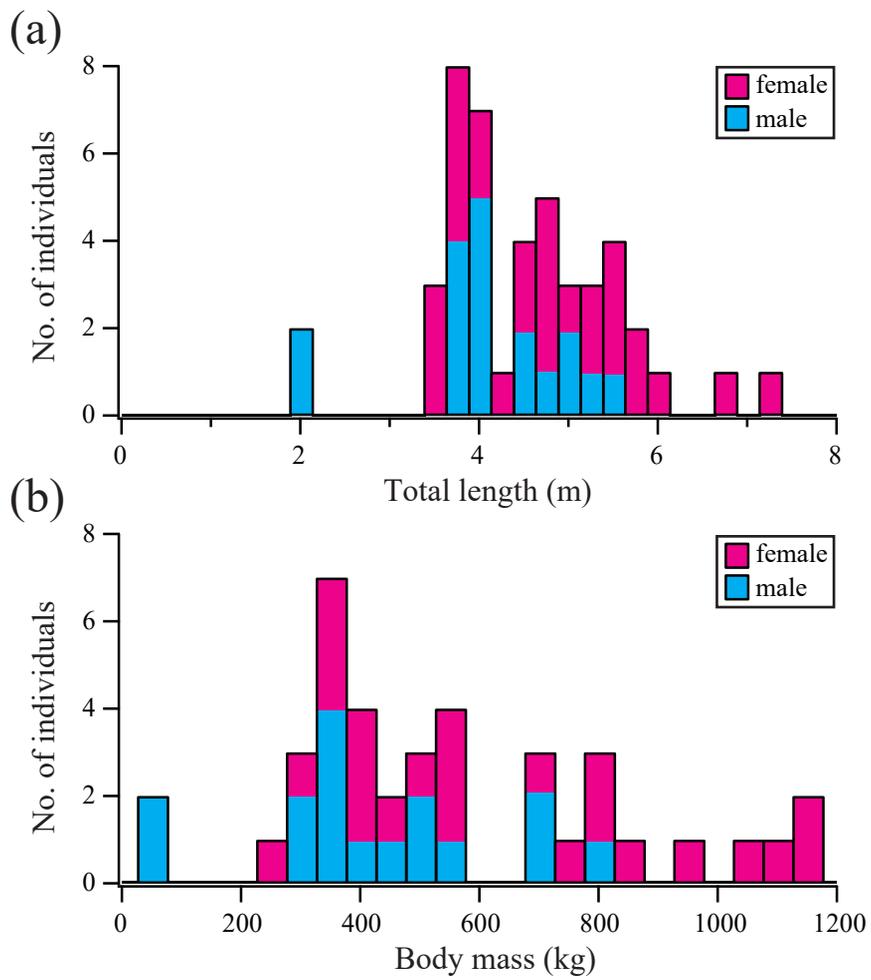


Fig. 3

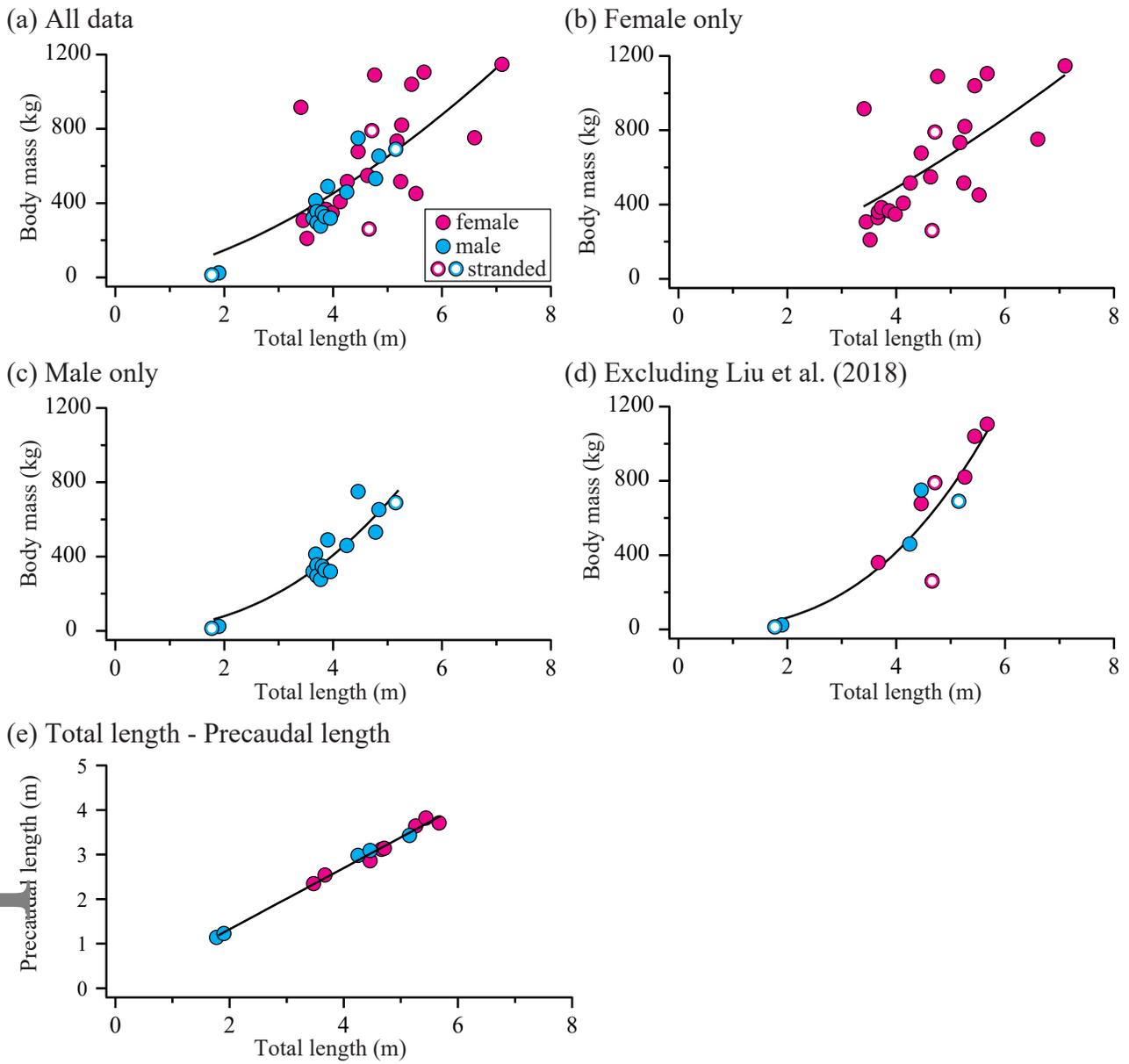


Fig. 4

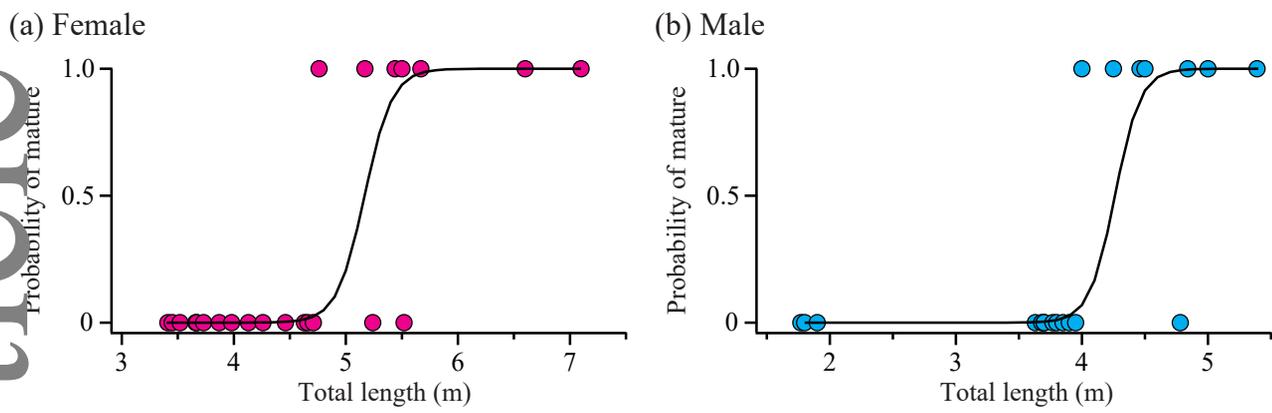
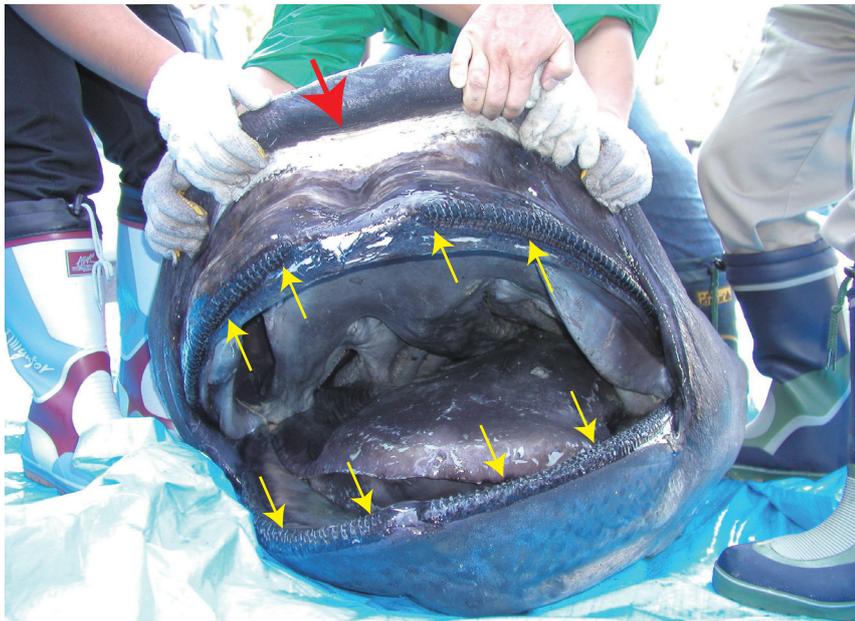


Fig. 5

(a)



(b)



Fig. 6