

Distribution and feeding ecology of
megamouth shark, *Megachasma pelagios*

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長崎大学大学院水産・環境科学総合研究科

游 紀汝

(Yu Chi-Ju)



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Abstract

Research on large filtering shark species, especially the biological information and movement pattern is extremely difficult due to the rarity and unpredictable behavior. Fortunately, the advancement in science and technology is a powerful tool for scientists to better understand these animals. The megamouth shark (*Megachasma pelagios*) is one of the rarest shark species in the three oceans, and its biological and fishery information is still very limited. Due to the scarcity of biological and catch data, it has been categorized as of least concern on the red list by the IUCN. Previous evidence showed that *M. pelagios* was panmictic population with no genetic structure, indicating the vulnerable situation under high strength fishery development. Some resource management strategy had established in order to protect *M. pelagios*, indicating it is high-profile species and needed to be studied. Therefore, the aims of this study were to integrate scattered records of *M. pelagios* from the three oceans, refine previous results, and provide additional information on the biology of *M. pelagios*.

Firstly, the data from published scientific articles, gray literature, online information, news, social network service (SNS) resources, private contact with research institutes, interviews with fishermen, and public websites were collected, cross-validated and checked each record from the above sources for further estimation of the spatial–temporal distribution of *M. pelagios*. A total of 261 landing/stranding records were examined, including 132 females, 87 males, and 42 sex unknown individuals, to provide the most detailed information on global *M. pelagios* records, and the spatial–temporal distribution of *M. pelagios* was inferred from these records. The vertical distribution of *M. pelagios* ranged 0 – 1203 m in depth, and immature individuals were mostly found in the waters shallower than 200 m. Mature individuals are not only able to dive deeper, but also move to higher latitude waters. The majority of *M. pelagios* are found in the western North Pacific Ocean ($> 5^{\circ}$ N). The Indian and Atlantic Oceans are the potential nursery areas for this species, immature individuals are mainly found in Indonesia and Philippine waters. Large individuals tend to move towards higher latitude waters ($> 15^{\circ}$ N) for foraging and growth from April to August. Sexual segregation of *M. pelagios* is found, females tend to move to higher latitude waters ($> 30^{\circ}$ N) in the western North Pacific Ocean, but males may move across the North Pacific Ocean.

In the second part, feeding information were compared between two filtering shark species in this study, megamouth shark (*Megachasma pelagios*) and whale shark (*Rhincodon typus*). Through the mandatory catch and report system in Taiwan, some

stomach composition specimens of *M. pelagios* and tissue sample of two species were collected and analyzed. A total of 19 stomachs were investigated by this study. Five stomachs content were unrecognized due to the high digested level or empty situation, and the result of stomach composition analysis (SCA) of 14 stomach specimens showed that *M. pelagios* mainly feed on zooplanktonic prey, including krill (Euphausiacea), jellyfish (Medusozoa), shrimp larvae (Dendrobranchiata), squat lobsters (Anomura), and crab larvae (Brachyura), indicating the low trophic diet. The stable isotope analysis (SIA) between *M. pelagios* ($n = 91$) and *R. typus* ($n = 90$) inferred different feeding strategies and diet composition. *M. pelagios* is an inactive feeder, which displays engulfment feeding. While *R. typus* was an active suction filtering feeder, which is not only able to prey on swimming small fish and squids, but also exhibit ontogenetic change in diet. Both *M. pelagios* and *R. typus* were believed born in less productive waters and move gradually to more nutritious habitat through they grow. The ontogenetic change was found in *R. typus* due to well-developed swimming behavior and gill-rakers for more active suction feeding. On the other hand, *M. pelagios* show no diet shift during growth, but there is a different isotope structure between males and females, indicating the sexual segregation and leading to different isotope signatures. However, more evidence from different size class individuals for both *M. pelagios* and *R. typus* are needed.

In general, this study not only gives the spatial–temporal movement frame of *M. pelagios*, but also provides feeding information of two filtering feeders. It is hoped that the complete global landing data, distribution, and feeding ecology of *M. pelagios* derived from these records can provide useful information on better understand the ecology of this mysterious species.

Keywords: *Megachasma pelagios*, megamouth shark, spatial–temporal movement, feeding ecology, elasmobranchs, western North Pacific.

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1. Introduction

1.1 *Megachasma pelagios*

The megamouth shark, *Megachasma pelagios* (Taylor, Compagno, and Struhsaker, 1983), is one of the mysterious and rare large shark species all over the world (Figure 1). The first *M. pelagios* was accidentally caught by entangling in the parachutes from the research vessel of the Naval Undersea Center, Kaneohe, Hawaii on 15 November 1976, and it was identified as a new species in 1983 (Taylor et al., 1983). This large adult male shark was 446 cm (14.6 ft) in total length (TL) and 750 kg (1653 lbs) in total weight. This species is tadpole-like with large head, stout and tapering posteriorly body, its mouth is very board and extending behind the eyes (Compagno, 2001). This shark is a large pelagic filtering species, which could be found in the three ocean. Its teeth are very small and hooked shape, and be believed taking engulfment feeding strategy (Nakaya et al., 2008). This is primarily an oceanic species usually found offshore in very deep water from 0 to 1500 m deep but may also occasionally occur over continental shelf waters at 5–40 m depth (Ebert et al., 2021). Due to the scarcity of biological and catch data, it has been categorized as least concern on the red list by the IUCN (Kyne et al., 2019).

1.2 Research background

Megachasma pelagios is one of the rarest shark species all over the world, due to no more than 200 individuals be recorded in the past 40 years since the first one was found, and the catch information of this species is still unclear (Nakaya, 2010; Liu et al., 2018; Watanabe and Papastamatiou, 2019). There were some literatures for *M. pelagios* in the past, most of these were single or few individual record, including morphology, movement, molecular biology, physiology, new specimen record, etc (Ishida et al., 1996; Martin and Naylor, 1997; Nelson et al., 1997; Yano et al., 1997; Chang et al., 2014; Tomita et al., 2014; Ju et al., 2021). *M. pelagio* has the preference for the zooplanktonic prey, mainly *Euphausia pacifica*, but *Nematoscelis difficilis* also used to be found in the stomach (Yano et al., 1997; Sawamoto and Matsumoto, 2012; de Moura et al., 2015). The female *M. pelagio* develops only one ovary and may be the oophagous shark species according to the observation (Castro et al., 1997). Vertical movement behavior was discovered for *M. pelagio* according to acoustic tagging research, indicating that this species will move to shallower water in the dusk and move to deeper water in the dawn (Nelson et al, 1997). However, these results were based on single individual, more information from multiple individuals were needed. Large

sharks such as *Rhincodon typus* and *M. pelagios* are hard to collect sample due to their huge body size and usually highly mobile and spend only a short time at any specific location. Therefore, most published researches are based on few individual observation, providing only part of the biological message.

On the other hand, there are three published articles for multiple *M. pelagios* individuals record, these studies suggest that *M. pelagios* can be found in the three ocean, but numerous *M. pelagios* were found in the western Pacific Ocean (Nakaya, 2010; Liu et al., 2018; Watanabe and Papastamatiou, 2019). *M. pelagios* reaches mature at about 4 m TL for males and 5 m TL for females (Nakaya, 2010). Mature individuals have the ability to move to higher latitudes and they are potentially segregated by sex, the gravid females may delivery pups in the warm waters (Nakaya, 2010; Watanabe and Papastamatiou, 2019).

1.3 Motivation

Although there are many studies for *M. pelagios*, some limitations and questions were found in the previous multiple individual studies: (i) The length-weight relationship was developed based on few sample size, (ii) Few individuals between 250 and 400 cm TL were included, (iii) The individuals were few in lower latitudes from April to October, and (iv) There was insufficient information on latitudinal distribution to reach any conclusion. Moreover, the biological information of multiple individuals was also inadequate, large shark species are usually K-selection animals, with the characteristic of late maturity, small numbers of offspring, and slow growth rate, and were vulnerable to overfishing (Holden, 1977; King and McFarlane, 2003). A resource management strategy has been followed and *M. pelagios* retention has been prohibited in United States Pacific fisheries since 2004, but the rule was refined for scientific or educational use in 2015, indicating the lack of information regarding this species. There was a mandatory catch and report system for *M. pelagios* from Taiwan Fishery Agency since 2013. Fishermen have to cooperate with scientific institutions and Fishery Agency when they catch the *M. pelagios*, including sample collection and information reports. Afterward, the Taiwan Fisheries Agency announced a ban fishing management measure on *M. pelagios* on 10 November 2020 for conservation purposes; however, further effectiveness and study remain to be elucidated. Therefore, scientists should put more effort on collecting detailed biological information of large shark species for sustainable management of these animals.

As stated above, previous *M. pelagios* landing records are very scattered and incomplete and need to be integrated. There were many unpublished data or unreleased

information that needed to be included; for example, numerous individuals were recorded by the mandatory catch and report system of the Taiwan Fisheries Agency, and some individuals were recorded by the Japanese Society for Elasmobranch Studies in Japanese. In addition, some insides, stomach, and tissue sample were collected through the catch and report system for further studies. Thus, the feeding analysis include stomach composition analysis (SCA) and stable isotope analysis (SIA) would be doable in this study. Stable isotope analysis is an appropriate tool for better understanding the feeding information of animals. Different from traditional stomach composition analysis, which are limited by sample size, high empty rate or digestive rate, SIA could not only get information form few specimens such as dermal tissue, but also make sure nonlethal to animal. Various isotope value provides different information, e.g. the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from individuals reflects the inhabited environment and assimilated food habits over time, respectively (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981; Peterson and Fry, 1987). The $\delta^{13}\text{C}$ indicated how productive the environment is, while the $\delta^{15}\text{N}$ shown the relative trophic position.

1.4 Purpose of this study

The present study aims to (1) integrate records of *M. pelagios* from the three oceans, (2) refine previous results and solve problems such as small sample sizes or uncertain body size estimations, (3) provide additional information on the horizontal and vertical distributions, (4) give some knowledge of feeding ecology of *M. pelagios*. It is hoped that the complete global landing data and spatial–temporal distribution of *M. pelagios* derived from these records, and feeding information can provide useful knowledge for better understanding the ecology of this mysterious species.

2. Material and methods

2.1 World recorded data integration

The world recorded data used in this study were collected from published scientific articles, gray literature, online information, news, social network service (SNS) resources, private contact with research institutes, and interviews with fishermen and researchers. In addition, the following public websites were reviewed for *M. pelagios* records: Florida Museum (<https://www.floridamuseum.ufl.edu/discover-fish/sharks/megamouths/>), Sharkmans-world (<https://sharkmans-world.blogspot.com/>), Summary of Megamouth Sharks (<http://elasmollet.org/Mp/Mplist.html>), Japanese Society for Elasmobranch Studies (<http://www.jses.info/index.html>), and catch and report data from the Taiwan Fisheries Agency, Council of Agriculture (<https://www.fa.gov.tw/cht/index.aspx>). To confirm the accuracy of these data, we cross-validated and checked each record from the above sources, including date, time, method (fishing gear, sighting, or stranded), location, operation depth, record country, length, sex, and mature stage if available. The data published in journals would be the most convincing, others were cross-checked from different sources. This information was used for further estimation of the spatial-temporal distribution of *M. pelagios*.

2.2 Sample collection and preparation

SCA and SIA sample of *M. pelagios* were collected from 2013 to 2019. There has been a mandatory catch and report system for *M. pelagios* in Taiwan since 2013, and fishermen have to report their catch information to scientific institutions and the Fishery Agency when they catch sharks. Almost all *M. pelagios* records from Taiwan were from the bycatch of large-mesh (mesh size= 90 cm) drift net vessels, which operated in the eastern waters of Taiwan, targeting ocean sunfish (*Mola mola*), sharptail mola (*Masturus lanceolatus*), and Indo-Pacific sailfish (*Istiophorus platypterus*), especially during April-August (Figure 2). According to interviews with fishermen, the large-mesh drift net fishery operates primarily in the evening (18:00- 24:00) with net deployment ranging from 10 to 140 m in depth and ~2000 m wide, soaking for 2-3 hours. Only a few landed specimens were accidentally caught by trawl nets and longline vessels.

After the shark landing in the port or fish market, the total length (TL, cm), weight (kg), and sex were recorded. The stomach composition and tissue specimens were collected right after the sharks were dissected if the condition for sampling is possible, all the specimens were preserved in the ice chest at low temperature and brought back to the laboratory. The stomach contents were stored at -20°C and the tissue specimens

were preserved in 95% ethanol for further analysis.

Additionally, to reveal the connection and genetic diversity of *M. pelagios* from different waters, the author cooperated with research team of Marine Biotechnology and Resources, National Sun Yat-Sen University, by analyzing the genomic DNA of 27 specimens from Taiwan (2013-2015) and two specimens from the Baja California, Mexico (Liu et al., 2018). This study also used published sequences from GenBank, including Japan, Indonesia, and Puerto Rico. The 27 tissue specimens were smashed into pieces, adding commercial DNA extraction kits for extracting the genomic DNA (Table 1). The extracts were diluted in TE buffer, preserved at -20 °C until amplified by PCR (polymerase chain reaction). Two genetic markers (*cox1* and *Loc6*) were used reveal the genetic diversity and connectivity pattern of *M. pelagios*, the approach gives a way to indirectly measure gene flow among populations (Martin et al., 2002; Ward et al., 2005; Liu et al., 2018).

This study also collected tissue sample from another filtering shark, *R. typus* for comparing feeding habits with *M. pelagios*. Although Taiwan's fisheries prohibited the capture of *R. typus* in 2008, sample collecting without hurt the animal was allowed. The skin tissue was collected from the caudal fin of *R. typus* from 2008 to 2018, which barged into the set net (Figure 2). Taking a small piece skin tissue sample from the shark is not only harmless, but also available for further population or genetic study, and in this study, we use these specimens for stable isotope analysis. The specimens were preserved in the ethanol with label noted time, location, body length, and sex information of the sharks.

2.3 Meristic measurement and maturity stage division

Measurements of *M. pelagios* were taken on total length (TL in cm), precaudal length (PCL), fork length (FL), body weight (BW in kg), mouth width (MW), 1st dorsal fin anterior margin, (D1A), 1st dorsal fin height (D1H), 1st dorsal fin base (D1B), pectoral fin anterior margin (P1A), and caudal fin dorsal margin (CDM) of those sharks landed at Taiwanese fish markets following the protocol described by Ebert et al. (2021). These data were used to develop conversion equations between different measurements and length-weight relationships of *M. pelagios*.

To understand the monthly horizontal distribution of *M. pelagios* in different life stages, the maturity stage was identified by macroscopic examination of reproductive organs if possible. Three maturity stages of *M. pelagios* were categorized as: immature, maturing, and mature. The maturity individuals not in Taiwanese waters was based on

the descriptions of other resources. On the other hand, the maturity stage of *M. pelagios* in Taiwanese waters was determined by the following criteria (Figure 3). Stage I (immature): immature males and females have undeveloped gonads, testis and ovaries were small or nondistinguishable, vas deferens and oviducts were small in diameter, clasper were uncalcified, and uteri were threadlike (Figure 3a, c). Stage II (maturing): developing (transitional) reproductive organs were observed in males by clasper development (could be slightly rotated) and the presence or absence of semen, and inflating ovaries or uteri were observed in females (Figure 3d). Stage III (mature): developed claspers (could be rotated), inflated testis, and semen were found in males; mating scars, inflated ovaries, and large uteri were found in females (Figure 3b, e). The vertical distribution of *M. pelagios* at different sizes and time was plotted, and depth data included reliable catch depths or operation depths from fishermen and observers of NOAA Fisheries.

2.4 Pretreatment of SCA and SIA

Megachasma pelagios is filtering shark species, which feeds on very fragile planktonic prey. Therefore, the stomach composition sample were preserved in the freezer for further analysis. The SCA study would be conduct as soon as possible for making sure the fresh condition of the prey item. 10 g of stomach composition of each specimen were weighted for SCA. We used deionized water to wash out the gastric juice and rinse the prey out. The rinsed prey items were pick out to be classified and weighted (± 0.001 g).

The SIA sample of *M. pelagios* and *R. typus* were dried 2-4 days at 60°C and grinded into homogeneous powder. The tissue powder sample were weighted ~ 3 mg, transferred into tin cup, and sent to Société Générale de Surveillance (SGS) Taiwan Ltd. for further carbon and nitrogen stable isotope analysis. The steps for analysis were as follow: Powder sample were wrapped in the tin cup, sent into the elemental analyzer (EA), and burned at 1000-1050°C. After the carbon and nitrogen from the sample were converted to CO₂ and N₂ under the high temperature and were separated by the chromatography column. The gas was sent into the Finnigan DELTAplus XP stable isotope ratio mass spectrometer through the ConFlo IV or ConFlo III for analysis.

2.4.1 Stomach composition analysis

(1) Measure of Prey Importance

According to observation the stomach composition by the dissecting microscope, the prey of *M. pelagios* were fragmented and unable to be count in number. Therefore,

ranking index (RI) was used to estimate the food importance of *M. pelagios* (Hobson, 1974). The calculation was as below:

$$RI = \%W \times \%FO$$

where the %W is the percentage of each prey by wet weight and %FO is the frequency of occurrence (the number of *M. pelagios* stomachs in which a prey item occurred).

(2) Prey Diversity

We use Shannon-Wiener Index (H') to estimate the feeding diversity of *M. pelagios* (Krebs, 1999). The calculation was as below:

$$H' = -\sum p_i \log p_i$$

where the P_i is the percentage of different prey in the stomach, here we use %W for calculation.

2.4.2 Stable isotope and trophic position analysis

(1) Stable isotope

The results were expressed in delta (δ) notation, and the specimens were analyzed through continuous flow isotope-ratio mass spectrometer (Peterson and Fry, 1987). These values were calculated as:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3$$

where X is ^{13}C or ^{15}N , and R is the isotope ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. The value was relative to Pee Dee Belemnite (PDB) and atmospheric N_2 for ^{13}C and $\delta^{15}\text{N}$. This study also calculate the sample C:N ratio, indicated satisfactory lipid removal efficiency.

(2) Trophic position

The relative trophic position (TP) values of *M. pelagios* and *R. typus* were estimated, the equation is as below:

$$TP = \lambda + \frac{\delta^{15}\text{N}_{\text{secondary consumer}} - \delta^{15}\text{N}_{\text{base}}}{\Delta_n}$$

where λ is the trophic position of reference organism, $\delta^{15}\text{N}_{\text{secondary consumer}}$ is stable isotope of consumer, $\delta^{15}\text{N}_{\text{base}}$ is stable isotope of reference organism, and Δ_n is the trophic

enrichment factor represents a best estimate of isotopic enrichment between consumer and its prey (Post, 2002). According to Post (2002), the species used for estimating $\delta^{15}\text{N}_{\text{base}}$ should come from the same habitat as consumer. Therefore, $\delta^{15}\text{N}$ of euphotic POM (1.1 ‰) from the north-eastern Taiwan water was chosen to be baseline for *R. typus*, in this case λ is 1 (Ho et al., 2021). On the other hand, $\delta^{15}\text{N}$ of identifiable stomach composition ($\delta^{15}\text{N}_{\text{Euphausiacea}} = 6.95 \text{ ‰}$) of *M. pelagios* was used for calculating trophic position in this study, as Euphausiacea is the primary consumer, it was assigned a trophic position of 2. The trophic enrichment was assumed as 3.4 according to Post (2002) because there is no reference for elasmobranchs.

2.5 Data analysis

2.5.1 Length–weight relation and conversion equations

A linear regression analysis was used to describe relationships for TL- FL, TL- PCL, TL- MW, TL- D1A, TL- D1H, TL- D1B, TL- P1A, and TL- CDM. An allometric equation ($\text{BW} = a\text{TL}^b$) was used to describe the relationship between BW and TL, where a and b are parameters. The maximum likelihood ratio test was used to examine the difference in the BW-TL relationships among sexes.

2.5.2 Trophic niche overlap and ontogenetic changes in foraging

The Shapiro-Wilk normality test was used to test normality of isotope value for *M. pelagios* and *R. typus*, respectively. When normal distribution was found, student's t -test will be used to test the differences between sex, otherwise Kruskal-Wallis test will be used in non-normal condition. ANOVA was used to test the difference between sex and size groups. *M. pelagios* and *R. typus* were both grouped into small (I), medium (II), and large (III) for discussing the shift of trophic position. For *M. pelagios* was according to the mature stage I, II, and III, but for *R. typus* was based on sampling size range due to almost no mature *R. typus* in this study, therefore, the individuals ≤ 400 cm TL were in group I, from 401 to 600 cm TL were in group II, and > 600 cm TL were in group III. Statistical significant level (α) was 0.05. Stable Isotope Bayesian Ellipses in R (SIBER) analysis was used to calculate the small sample size corrected SIBER ellipse area (SEAc) for the niche breadth and niche overlap (Jackson et al., 2011). Moreover, the overlap percentage (Overlap%) of both shark between sex and different size groups were calculated, the Overlap% value is low ($\leq 35 \%$), medium (36 – 70%), and high ($> 70\%$), respectively (Jackson et al., 2011). Simple linear regression analyses were carried out between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and length for two species and different sex.

3. Results

3.1 Overall

A total of 261 *M. pelagios* individuals (132 females, 87 males, and 42 sexual unknown) recorded from 15 November 1976 to 7 August 2020 were analyzed in this study (Figure 4, Table S1). There were 154 records from Taiwan fisheries catch and report system, and some of them were used for conversion equations establish.

There were 29 *M. pelagios* (from Taiwan and Mexico) individuals' *cox1* gene and Loc6 microsatellite sequence be amplified and analyzed (others were from GenBank). However, there were three specimens under the low DNA quality situation and failed to amplify on both loci. The *cox1* sequence of 27 *M. pelagios* were made up of three unique haplotypes, meanwhile, the sequences from Taiwan, Mexico, Indonesia, and Puerto Rico shared the dominant haplotype. On the other hand, there were 25 sequences were obtained for Loc6 genetic analyses (some were failed to amplify because the sequence downloaded from GenBank problem), the result showed that the sequences from Taiwan and Mexico were identical. In short, no genetic structure be found between individuals from different region, suggesting *M. pelagios* is a possible panmictic population.

3.1.1 BW–TL relation of *M. pelagios*

The maximum likelihood test indicated that there was a significant difference in the BW–TL between sexes (Chi-square = 7.92, critical value = 5.99, $p < 0.05$), and the sex-specific BW–TL relationships were estimated as follows (Figure 5):

$$BW = 0.014TL^{1.74} \text{ (females, } r^2 = 0.94, n = 93, p < 0.001)$$

$$BW = 0.057TL^{1.49} \text{ (males, } r^2 = 0.95, n = 58, p < 0.001)$$

where BW is the body weight, TL is the total length.

3.1.2 Conversion equations of *M. pelagios*

The linear relationships among measurements were expressed as follows:

$$TL = 1.131PCL + 86.731 \text{ (} r^2 = 0.865, n = 126, p < 0.05)$$

$$TL = 1.257FL + 1.407 \text{ (} r^2 = 0.975, n = 10, p < 0.05)$$

$$TL = 4.236MW - 22.461 \text{ (} r^2 = 0.946, n = 3, p = 0.149)$$

$$TL = 3.520D1A + 330.06 \text{ (} r^2 = 0.068, n = 61, p < 0.05)$$

$$TL = 3.130D1AH + 373.48 \text{ (} r^2 = 0.045, n = 61, p = 0.101)$$

$$TL = 4.948D1B + 280.04 (r^2 = 0.206, n = 54, p < 0.05)$$

$$TL = 5.959P1A - 35.27 (r^2 = 0.876, n = 9, p < 0.05)$$

$$TL = 2.988CDM + 123.62 (r^2 = 0.861, n = 6, p < 0.05)$$

where PCL is the precaudal length, FL is the fork length, MW is the mouth width, D1A is the 1st dorsal fin anterior margin, D1H is the 1st dorsal fin height, D1B is the 1st dorsal fin base, P1A is the pectoral fin anterior margin, and CDM is the caudal fin dorsal margin. For consistency, the lengths from other studies that were not reported in TL were converted to TL using above equations (Table S1).

3.2 Spatial-temporal distribution of *M. pelagios*

3.2.1 Global Distribution

There were 261 *M. pelagios* individuals recorded in this study, the majority of sharks were recorded from the western Pacific ($n = 214$), followed by the eastern Pacific ($n = 35$), with only six specimens being recorded each from the Atlantic and Indian oceans (Figure 6). Females represented slightly more than half (51%) of all sharks recorded with a breakdown by sex, if known, revealing a total of 132 females (226–710 cm TL) and 87 males (176.7 – 690.2 cm TL), with the sex unknown for 42 individuals (180 – 530 cm TL) (Figure 6a). The TL for all females was mostly between 400 and 500 cm, followed by 501 and 600 cm and 301 and 400 cm (Figure 6a). The TL for all males was mostly between 401 and 500 cm, followed closely by 301 and 400 cm (Figure 6a). Females represented the majority of records for the western Pacific (female: male = 125: 65) compared with males, but more males (female: male = 4: 14) were reported in the eastern Pacific (Figure 6).

3.2.2 Size and Sex Distribution in the Three Oceans

The length frequency of *M. pelagios* was estimated by different oceans; individuals ≥ 200 cm TL were found more often in the Indian and Atlantic Oceans, while more males > 400 cm TL were found in the eastern Pacific Ocean (Figure 6b, c, and e). On the other hand, there were 214 individuals, including 125 females (226 – 710 cm TL), 65 males (250 – 570 cm TL), and 24 unknown sexes (213 – ~700 cm TL), in the western Pacific Ocean (Figure 6d).

Furthermore, because no record was from the southwestern Pacific, the records from the western North Pacific Ocean were divided by latitude, (i) $\leq 15^\circ\text{N}$, (ii) $15 - 30^\circ\text{N}$, and (iii) $> 30^\circ\text{N}$, and the ratios of females from zones (i) to (iii) were 43% ($n =$

28), 58% ($n = 158$), and 75% ($n = 28$), respectively (Figure 7). In zone (i), the length of *M. pelagios* ranged from ~300 to 549 cm TL for males ($n = 5$), 226 to 550 cm TL for females ($n = 12$), and 213 to 480 cm TL for sex unknown ($n = 11$); the mean TL was 418 ± 114 cm TL (Figure 7). In zone (ii), the length ranged from 250 to 570 cm TL for males ($n = 57$), 247 to 710 cm TL for females ($n = 92$), and 470 to 700 cm TL for unknown sex ($n = 9$); the mean TL was 446 ± 80 cm TL (Figure 7). In zone (iii), the length ranged from 400 to 425 cm TL for males ($n = 3$), 346.6 to 577 cm TL for females ($n = 21$), and 247 to 710 cm TL for sex unknown ($n = 4$); the mean TL was 496 ± 74 cm TL (Figure 7).

3.2.3 Horizontal Distribution

According to the landing records of *M. pelagios* around the world, no immature individual was landed at latitudes higher than 30° , while mature individuals were widely distributed. To further investigate the spatial-temporal distribution of *M. pelagios*, we eliminated data from the Indian and Atlantic Oceans and uncertain data from the Pacific Ocean. Figure 6 shows the monthly latitudinal occurrence of sex-specific *M. pelagios* at different maturity stages in the Pacific Ocean. Females appeared sporadically in the western Pacific Ocean from January to March and appeared in the higher latitude area (mainly in zone ii) from April to August (Figure 8a). In September, only one female was found in the high latitude area, and the distribution separated in the eastern and western Pacific Ocean after October (Figure 8a). On the other hand, male *M. pelagios* were found mainly in lower latitude waters in both the eastern and western Pacific Oceans from January to March. Males were mostly found in the middle latitude area from April to August (Figure 8b). There was no record for males in September, but mature males occurred in the eastern Pacific Ocean, and immature males occurred in the western Pacific Ocean in October and November (Figure 8b).

3.2.4 Vertical Distribution

Figure 9a shows the 64 *M. pelagios* caught ($n = 60$) or sighted ($n = 4$) from different depths in size. Individuals < 300 cm TL were only found in the shallower water column (no deeper than 200 m), and large individuals were found at all water depths. In addition, the temporal-vertical movements of 23 *M. pelagios* indicated that sharks tended to occur in deep water at dawn (00:00 – 06:00 am) and then appeared in shallow water at dusk (18:00 – 00:00) (Figure 9b). However, one female was recorded around noon, which was a sighting event in which the individual was attacked by a whale.

3.3 Feeding ecology of *M. pelagios*

3.3.1 Stomach composition analysis

There were 19 *M. pelagios* stomachs analyzed, however, 5 of them containing high digestive level preys, it is difficult to further quantify the diet composition. Therefore, only 14 stomach specimens were allowed analysis. Most of the preys were planktonic prey, including krill (Euphausiacea), jellyfish (Medusozoa), shrimp larvae (Dendrobranchiata), crab larvae (Brachyura), and squat lobsters (Anomura) (Figure 10). What's more, nematodes (Nematoda) were also found in the stomach of *M. pelagios*. Smith (1983) indicated that some larvae stage of nematode is parasitic on krill, thus, we exclude the nematode from prey items. Overall, only 6 prey items were found in the stomach of *M. pelagios*, showing a low prey diversity ($H' = 0.22$). Table 2 shows that Medusozoa (%RI = 66.59) and Euphausiacea (%RI = 33.40) were the main preys of *M. pelagios*. Although Medusozoa occupied the highest %RI and %W, Euphausiacea was the most common prey item for *M. pelagios* due to 100% occurrence rate.

3.3.2 Stable isotope analysis

In total, 91 *M. pelagios* (37 males and 54 females) and 90 *R. typus* (58 males and 32 females) tissue samples were used in stable isotope analysis (Table 3, Table 4). The body size of *M. pelagios* ranging from 290-720 cm TL, and of *R. typus* ranging from 284 to 1190 cm TL. The value of $\delta^{13}\text{C}$ in *M. pelagios* was from -18.46 to -14.99 ‰ (-17.2 ± 0.69 ‰, mean \pm SD), and the $\delta^{15}\text{N}$ was from 6.83 to 11.67 ‰ (9.04 ± 0.9 ‰, mean \pm SD) (Table 3). The value of $\delta^{13}\text{C}$ in *R. typus* was from -18.89 to -13.67 ‰ (-15.63 ± 0.78 ‰, mean \pm SD), and the value of $\delta^{15}\text{N}$ was from 5.17 to 13.01 ‰ (9.02 ± 1.79 ‰, mean \pm SD) (Table 4). C: N ratio of both sharks were smaller than 3.5, indicating that freeing from effects of lipid extraction on the stable isotope composition (Post, 2002).

Results of S – W normality test for stable isotope value of *M. pelagios* and *R. typus* indicated that $\delta^{13}\text{C}$ for both species were asymmetrical ($p < 0.05$), but $\delta^{15}\text{N}$ were symmetrical ($p = 0.98$ for *M. pelagios* and $p = 0.75$ for *R. typus*). There was no significant difference between male and female in $\delta^{13}\text{C}$ both for *M. pelagios* (K – W test, $p = 0.46$) and *R. typus* (K – W test, $p = 0.63$) and in $\delta^{15}\text{N}$ for *R. typus* (t-value is 1.23, $p = 0.11$), but significant difference $\delta^{15}\text{N}$ between female and male *M. pelagios* (t-value is 1.23, $p < 0.05$). ANOVA for $\delta^{13}\text{C}$ of *M. pelagios* was $F=1.45$, $p = 0.24$, for $\delta^{15}\text{N}$ of *M. pelagios* was $F=2.53$, $p = 0.09$, for $\delta^{13}\text{C}$ of *R. typus* was $F=0.65$, $p = 0.52$, and $\delta^{15}\text{N}$ of *R. typus* was $F=0.96$, $p = 0.39$, respectively.

The SIBER analysis for different species and sex, the isotopic niche of *M. pelagios*

and *R. typus* were found separated into two groups (overlap% = 0), but the medium to high overlaps were found between male and female for both *M. pelagios* and *R. typus* (Figure 11, Table 5). The $\delta^{13}\text{C}$ of *M. pelagios* (-17.20 ± 0.69 , Mean \pm SD) was lower than $\delta^{13}\text{C}$ of *R. typus* (-15.67 ± 0.78 , Mean \pm SD), indicating different habitat. Although the $\delta^{15}\text{N}$ didn't show different between two species, the TP of *R. typus* (3.33 ± 0.53 , Mean \pm SD) was higher than *M. pelagios* (2.62 ± 0.27 , Mean \pm SD), inferring the higher consumer *R. typus* play around Taiwan waters. To further elaborate, the isotope niche breadth of male is larger than female for both *M. pelagios* and *R. typus*.

There was a positive relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *R. typus*, but negative relationship for *M. pelagios*, indicating different feeding strategies (Figure 11). What's more, $\delta^{13}\text{C}$ increase with body size both in *M. pelagios* and *R. typus*, however, $\delta^{15}\text{N}$ increase with the body size only in *R. typus* (Figure 14, Figure 15). Table 8 showed the trophic position for *M. pelagios* and *R. typus* in different size groups, the scope of trophic position of *R. typus* was wider (1.73 – 4.03) than *M. pelagios*. The mean of trophic position increased slightly in *R. typus*, indicating the ontogenetic change. Overall, the mean trophic position were calculated as 2.87 ± 0.27 (mean \pm SD) for *M. pelagios* and 2.85 ± 0.53 (mean \pm SD) for *R. typus*, revealing both of them are low trophic level consumers.

4. Discussion

This study provided the first complete and detailed landing records, the spatial–temporal distribution, and feeding biological information of *M. pelagios*. The results derived from this study can be used as a reference for future studies on the ecology, conservation, and management of this species.

In this study, we found that the body size of female *M. pelagios* was larger than that of males. One possible reason for this is that females need more space in the coelom to carry large and well-developed pups. Another reproductive strategy was also considered: females will be more reproductively fit through their growth, larger females may delivery more pups (Goodwin et al., 2002; Baremore and Hale, 2012). Although no pregnant *M. pelagios* has ever been found, the observation of its gonad structure showed that it was very similar to *C. maximus* (Matthews, 1950). Additionally, the smallest free-swimming *M. pelagios* was 176.7 cm TL. One convincing inference was that *M. pelagios* is an aplacental viviparous species, delivering a few well-developed pups, which is similar to *C. maximus* (Tanaka and Yano, 1997; White et al., 2004). The ovary and uterus of female *M. pelagios* may become heavy when they reach the mature stage, leading to a length–weight relationship difference between sexes (Figure 5).

Parameter *b* of the length–weight equation of *M. pelagios* is far smaller than the value (2.5–3.0) commonly known from sharks (Wigley et al., 2003). According to the data for allometric equations having been weighed by scientists and fishermen associations, one possible reason for this is that *M. pelagios* is an engulfment filter feeder, the mechanism of energy use such as the metabolic rate and growth may differ from other shark species, leading to different allometric equation results compared with other species (Nakaya et al., 2008; Hsu et al., 2012). The linear regression analysis showed that TL had a good correlation with PCL, FL, P1A, and CDM, but the small sample size for FL, P1A, and CDM remains to be further enforced. On the other hand, the formulas of TL- MW, TL- D1A, and TL- D1B were for reference only due to either a limited sample size or low correlation. However, considering the rarity of *M. pelagios*, this information would still be useful. Furthermore, we attempted to estimate the “~9 m TL male” from Martínez-Ortiz et al. (2017) by using the TL- CDM formula; pursuant to “1700 mm measured at the dorsal margin of the caudal fin”, this male had a 631.58 cm TL rather than ~9 m TL. This result indicated that the regression formulas from the present study provided an opportunity to validate uncertain data regarding *M. pelagios*. Further regression data should be collected from more individuals to be more convincing.

In this study, no evidence indicated that the population of *M. pelagios* is female

biased due to 16% ($n = 42$) sexually unknown records. Some studies have indicated that the sexual segregation of elasmobranchs usually leads to sexual bias when under local investigation (Robbins, 2007; Borrell et al., 2011). In this study, we integrated diverse record resources, including academic journals, conference reports, and public online resources, and the female ratio was 51%, close to half of the records. Additionally, *M. pelagios* is considered a panmictic population with no genetic structure, showing the ability to move across oceans (Liu et al., 2018). However, the specimens for the genetic study were few (less than 30) and most of them were only from Taiwan, further international cooperation for clarifying the whole population structure is essential. The length frequency showed that small (≤ 200 cm TL) free-swimming *M. pelagios* ($n = 4$) were found only in the Indian and Atlantic Oceans, indicating a potential nursery area in these waters (Figure 6b, c). On the other hand, the males ($n = 14$) were more than three times as abundant as females ($n = 4$) in the eastern Pacific Ocean, but females were notably more abundant in the western North Pacific. Both the mean body size and the ratio of large females increased when the latitude was higher. Recent studies have shown that large shark species usually have sexual segregation behavior because (1) females escape forced mating by mature males, (2) to avoid consuming the same prey resources, and (3) gravid females move to habitats that offer stable resources, through which they can gain more energy for offspring from predation (Klimley, 1987; Mucientes et al., 2009). A significant sexual bias of reef manta rays (*Mobula alfredi*) was found in southern Mozambique, and female *M. alfredi* uses this habitat as the breeding and birthing grounds (Marshall and Bennett, 2010). During the mating season, male shortfin mako sharks (*Isurus oxyrinchus*) harass females that lead to fitness consequences, which reflect avoidance behavior (Mucientes et al., 2009). White sharks (*Carcharodon carcharias*) near the Neptune Islands experience segregation due to different physiological strategies, females are absent in the breeding season and only return in the feeding period to increase the growth rate of pups (Robbins, 2007). Large shark species usually have large spatial-scale segregation behavior, and our results showed that female *M. pelagios* mainly inhabit the western Pacific Ocean, while males prefer to inhabit the eastern Pacific Ocean. However, the mechanisms resulting in sex segregation need further investigation in the future.

Immature individuals were found only between 30° N and 30° S, but mature *M. pelagios* could not only move toward higher latitude waters, but also have the ability to dive deeper, where the water temperature is lower (Figures 7, Figures 8). Previous studies have suggested that many Lamnidae sharks, such as *I. oxyrinchus*, big-eye thresher (*Alopias superciliosus*), and pelagic thresher (*A. pelagicus*), have some capability of endothermic regulation; they could conserve heat and arrange their body temperature well to protect against low temperatures (high latitude or winter)

environments (Carey and Teal, 1969; Carey et al., 1985). The most famous endothermic species are the porbeagle (*Lamna nasus*) and salmon shark (*L. ditropis*), which are usually distributed at latitudes higher than 40°; however, limited by thermal inertia, young individuals can only remain in moderate temperature areas until they mature (Goldman et al., 2004; Carlisle et al., 2015). The distribution pattern of *M. pelagios* based on latitude or water depth in this study showed that mature individuals have the ability to protect themselves against low-temperature water compared with immature individuals, although there is a lack of evidence to verify whether *M. pelagios* is an endothermic species.

Records from the western North Pacific Ocean were mostly bycatch from fisheries (85%). According to fishermen, the occurrence of *M. pelagios* seems to be seasonal, some large-mesh drift net fishing vessels in Taiwan operate year-round but do not catch any *M. pelagios* from September to March. On the other hand, *M. pelagios* was mainly recorded between October and March in the eastern Pacific Ocean (74%). These results may indicate that *M. pelagios* move between eastern and western Pacific waters. Large sharks are able to move across the Ocean, a tracking study provided evidence of the trans-Pacific migration of the *R. typus*. One female *R. typus* individual was tracked from the eastern (Panama) to the western (Mariana Trench) Pacific Ocean (Guzman et al., 2018). In addition, the monthly latitudinal occurrence of *M. pelagios* was slightly different between females and males. In the spring, both sexes from lower latitudes (zone i) moved toward middle latitude water (zone ii), but females also went further to the high latitude area (zone iii) in the western North Pacific Ocean. In the summer, *M. pelagios* was dispersed but mainly found in zone ii around Taiwanese waters in the western North Pacific Ocean. Afterward, *M. pelagios* was absent in early autumn (September); by October, females appeared in zone iii and the eastern Pacific, and males mainly appeared in the eastern Pacific. The records from winter were few, but included *M. pelagios* from both the eastern and western North Pacific Oceans and different latitudes.

Geographically, the movement of *M. pelagios* seems to be related to the current flow in the North Pacific Ocean. Many studies have suggested that the migration or movement of large marine animals relates to the current, and they benefit from the current, such as for moving, spawning, or foraging (Bayliff et al., 1999; Dewar et al., 2010). There are different names of current in the North Pacific Gyre (NPG) according to their position and characteristics, including the Kuroshio Current (KC), which is warm, less productive flows pass through the western Pacific Ocean, and extends from the Philippines to Taiwan and Japan year-round. The intensity of the KC increases from May to August; during this period, many migrating fish species are transported by KC,

passing through eastern Taiwanese waters toward northern Japan. The KC merges with the Oyashio Current (OC) at approximately 35° N, forming a good feeding and fishing ground and, finally, turning toward the east across the North Pacific Ocean (Teague et al., 1994). There was evidence shown that large sharks such as *R. typus* prefer to give birth or aggregate in warm waters (Chen et al., 1997; Wilson et al., 2001). *Megachasma pelagios* migrate northward with the KC in the late spring to summer offshore of Taiwan. Tang et al. (2000) suggested that the subsurface Kuroshio water on the shelf along the east coast of Taiwan indicated upwelling and nutrient transport, which could explain why the *M. pelagios* we observed from Taiwan were mostly full with prey in their stomach. Therefore, the middle western Pacific Ocean may be the feeding grounds of *M. pelagios* in the spring and summer; moving northward to 35° N, some females remain and other individuals change direction toward the eastern Pacific Ocean in early autumn and arrive after October. When arriving in the eastern Pacific Ocean, *M. pelagios* move southward with the California Current (CC) until they meet the Peru Current (PC) and then turn to cross the Pacific again toward the western side, which returns to Indonesian or Philippine waters. This inference was based on the lack of genetic structure and panmictic populations in *M. pelagios*, but further study in addition to the genetic study of Liu et al. (2018), such as tagging or analyzing more specimens from different oceans, should be conducted to verify this hypothesis.

Vertical migration behavior has been verified for *M. pelagios* since 1997. One 490 cm TL male was attached with acoustic transmitters and tracked for 50.5 h in the eastern Pacific (southern California), and the results indicated that *M. pelagios* has a very specific vertical movement during dawn and dusk (Nelson et al., 1997). Sharks make vertical movements for different purposes, e.g., *R. typus* spends time daily at the surface to gain energy for thermoregulation (Thums et al., 2013); the basking shark (*Cetorhinus maximus*) spends half a day in deep water (800–1000 m) and reduces depths gradually, indicating foraging behavior (Gore et al., 2008). However, many studies have shown that even the same species may have different horizontal or vertical movement patterns (Dewar et al., 2010; Thums et al., 2013; Araujo et al., 2020). As only one *M. pelagios* individual was successfully tracked in the past, we integrated historical time–depth records of *M. pelagios*. In the present study, the daily vertical movement of *M. pelagios* was found in multiple individuals. The shallow–deep water movement was extremely significant from dusk to dawn, but one record was found at approximately 10 am (Figure 9b). Amorim et al. (2000) noted that one *M. pelagios* was sighted with three sperm whales (*Physeter macrocephalus*), and there was some scarring on the fin and gills of the shark, indicating that it may have been attacked or traced by the sperm whales; therefore, it came to the surface. In addition to the sighting of this individual, other studies have shown a similar temporal vertical movement pattern of *M. pelagios*

with acoustic techniques (Nelson et al., 1997). However, most data were operating depth recorded by the Taiwan large-mesh drift net fishery and NOAA Fisheries; the actual catching depth remains to be further elucidated. According to previous studies, as a filter-feeding shark species, *M. pelagios* seems to prefer euphausiid shrimp. Sawamoto and Matsumoto (2012) observed the stomach composition of one female *M. pelagios*, which was caught by a seine net near Japan, and euphausiids (*Euphausia pacifica*) were the main prey of *M. pelagios* (Yano et al., 1997). Nakagawa et al. (2003) found that *E. pacifica* migrate to the surface at night (20:30), move down to approximately 100 m at midnight (00:30), and move toward deeper water (150 – 300 m) after dawn (06:00). The vertical movement patterns of *M. pelagios* and *E. pacifica* seem very similar, indicating that the vertical movement of *M. pelagios* may be related to its foraging behavior.

The notable number of *M. pelagios* landing records from Taiwanese waters compared with those elsewhere may be attributed to the cooperation between fishermen, research institutes, and the Fishery Agency. Due to the catch and report system, we were able to measure *M. pelagios* at the market. The large-mesh drift net fishery usually operates on the east coast of Taiwan from April to August and targets *M. mola* and *M. lanceolatus* at night. The fishermen change different fishing gear in other months in order to catch other species, e.g., striped bonito (*Sarda orientalis*). Previous studies have suggested that oceanic sunfish movement vertically depends on the temperature and depth of the mixed layer. Moreover, oceanic sunfish also move to shallower water during the night and back to deeper water at dawn, which is similar to *M. pelagios* (Potter and Howell, 2010; Chang et al., 2020). Therefore, *M. pelagios* may be accidentally caught by the drift net due to sharing the same vertical movement as molas. Additionally, the catch and report system plays an important role; nearly 40% of the records from the Philippines and Indonesia are either stranded or sexually unknown because of the scattered islands, which prevents the information from being transmitted effectively. To better understand the information of *M. pelagios*, the reporting system or open platform should be designed and propagated, especially for waters with potential nursery grounds.

The data collected on the spatial–temporal movement of *M. pelagios* provide important insights into their vertical and geographic migration behaviors. This study was the first to include different body part measurements of multiple *M. pelagios* individuals using the same standards. Additionally, we integrated the results from previous studies, refined the data records presented in supplementary materials (Table S1), and established conversion equations for future research. Furthermore, we updated the catch records from Taiwanese waters, including the 250–400 cm TL individuals,

integrated the missing records from April to October, and included the vertical movement data in this study.

Many studies suggested that different tissue type, sample storage method, and experiment treatment will show different metabolic rate or affect the analysis of stable isotopes, however, under economic consideration, this study was only made one methodology for analysis, further study on different treatment effects is needed (Marcus et al., 2017; Wyatt et al., 2019). Sample collecting of large shark species, especially filtering shark is difficult due to the small population and tremendous body. Luckily, this study obtained specimens from the catch and report system of the Taiwan Fisheries Agency. However, the stomach composition of *M. pelagios* were easy to leak out when dissection, only 19 *M. pelagios* stomachs be collected in this study. Besides, the fishing ban for *R. typus* since 2008 leading to no stomach specimen of *R. typus* for analysis.

The planktonic preys were fragile, in most of case the stomach contents of *M. pelagios* were digested into small piece and unable to count number, this situation was similar to previous study (Sawamoto and Matsumoto, 2012). There were only 6 zooplanktonic prey items found for *M. pelagios*, this shark mainly feed on Euphausiacea and Medusozoa, the prey diversity was very low ($H' = 0.22$). According to %RI and %W, jellyfish (Medusozoa) was the most important prey, however, the high moisture content of Medusozoa may affect the result. Through the %F, Euphausiacea was the most common prey item for *M. pelagios*, previous studies which recorded stomach contents were all included Euphausiacea but only few with jelly fish (Taylor et al., 1983; Berra and Hutchins, 1990; Yano et al., 1997; Sawamoto and Matsumoto, 2012). Sawamoto and Matsumoto (2012) analyzed the stomach contents of a 367 cm TL female *M. pelagios*, which was caught by bonito purse seine fishery in Japan in 2007, and found that the euphausiids were main diet of *M. pelagios*, sharing the same result with present study. Also, the worm-like organisms were discovered both in previous study and this study (Sawamoto and Matsumoto, 2012). According to Smith (1983), the nematode was excluded from prey importance calculation. Although this study is the first to provide multiple *M. pelagios* SCA information, the knowledge of its prey is still remained to be improved due to the little stomach sample.

The SIA showed different results between *M. pelagios* and *R. typus*, indicating two feeding strategies of these filtering sharks (Figure 11). Abrantes and Sheaves (2010) inferred that linear negative relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ suggesting the primary producers, primary consumers, or secondary consumers, which is not only fit the SIA result for *M. pelagios*, but also fit that we found *M. pelagios* feed mainly on zooplanktonic preys. However, the significant difference between male and female in $\delta^{15}\text{N}$ for *M. pelagios* may lead by potential sexual segregation or metabolic rate, further

evidence from SCA is needed. On the other hand, the SIA of *R. typus* showed a positive relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, revealing the more complex diet than a filtering feeder. Previous study implied that *R. typus* have the ability to feed on wide spectrum of prey, the wide trophic niche of *R. typus* in this study may fit previous studies (Taylor, 1996; Colman, 1997; Norman, 1999; Duffy, 2002). Nakaya et al. (2008) stated that *M. pelagios* is an engulfment feeder, with special morphological characteristic such as large mouth, long jaw cartilages, and flexible skin around the pharynx, these characters are similar to engulfment feeding whale species such as humpback whale (*Megaptera novaeangliae*). This foraging strategy seems much beneficial for slow swim species such as *M. pelagios*, according to previous tracking study the swim speed of *M. pelagios* was 1.5 km h^{-1} (Nelson et al., 1997). Different from engulfment feeder, *R. typus* shows more active suction-filtering behavior, which means this feeder have more chance to prey on small fishes and squids, who have better ability on swimming (Borrell et al., 2011). Therefore, this study gives the evidence that *M. pelagios* and *R. typus* are both filtering feeder inhabit in western North Pacific Ocean but have different feeding strategies.

Furthermore, the trophic niche overlap between *M. pelagios* and *R. typus* was 0, suggesting the different habitat use of them. Thums et al. (2013) marked that *R. typus* usually spend time gaining energy from sun at the sea surface in order to regulate the body temperature. Also, many studies had observed that *R. typus* aggregate and forage on or near the sea surface, inferred that *R. typus* inhabit mainly at shallow waters (Heyman et al., 2001; Motta et al., 2010; Sequeira et al., 2014; Cade et al., 2020). On the other hand, it is believed that *M. pelagios* inhabit in the deeper water, usually around hundred meters and scarcely near the surface, thus, it is hard to be discovered (Nelson et al., 1997; Ebert et al., 2021). Besides, the two filtering feeders were found from different part of Taiwan, *R. typus* were collected from coastal set net fishery around Taiwan waters, but *M. pelagios* were mainly caught by large-mesh driftnet from eastern waters of Taiwan, also indicating the different distribution of two species around Taiwan waters (Figure 2).

The trophic niche of males were larger in both *M. pelagios* ($\text{SEAc} = 2.11$) and *R. typus* ($\text{SEAc} = 4.49$), inferring the wide distribution in males. It seems that many sharks display more active movement in males than females. Kock et al. (2013) expressed that the female great white sharks (*Carcharodon carcharias*) were frequently found offshore area, while male were rarely discovered in False Bay. The female bull sharks (*Carcharhinus leucas*) were caught and monitored more frequently in coastal waters, however, males were only found at isolated waters far from coast in New Caledonia (Werry and Clua, 2013). Male *M. pelagios* were found wide spread in different waters,

including western and eastern Pacific Ocean, but females were mainly appeared in the western North Pacific Ocean. Previous studies inferred that male sharks undertake more wide scope movement in order to have more chance on meeting females and mating, while females usually choose various coastal areas, which enrich foods to stay at particular place for giving birth (Keeney et al., 2005; Knip et al., 2012).

Although the mean calculated TP exhibiting that both *M. pelagios* and *R. typus* are lower trophic level consumers, the stable isotope showed different information of their life history and feeding habits. Sexual segregation and ontogenetic change were also be found through *M. pelagios* and *R. typus* growth, the niche overlap between male and female in group III were medium in *M. pelagios* but low in *R. typus* (Figure 12, Figure 13). Recent studies inferred that the sexual segregation lead by different reasons such as force mating behavior from male, reducing the resources competition, and finding appropriate area for offspring (Mucientes et al., 2009). Besides, ontogenetic shift was common in elasmobranchs through their different life stages. The greenland shark (*Somniosus microcephalus*) shifted their diet from low trophic level squids to seals and benthic fishes, supports that this species is able to prey on fast swimming prey species (Nielsen et al., 2019). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showed the ontogenetic changes in prey consumption and habitat use of blue shark (*Prionace glauca*) between life stages, small and large individuals preferred inhabit in coastal waters, while large juvenile shown ocean preference (Estupiñán-Montaña et al., 2019).

There was a slightly positive correlation between $\delta^{13}\text{C}$ and body length for both filtering feeders, indicating that they will move to more productive environment through they growth, and where *R. typus* inhabits is more productive (sea surface) than *M. pelagios* (Figure 14). The *R. typus* caught from set net around Taiwan were all from coastal waters no deeper than 50 m, which were enrich producers. While *M. pelagios* inhabit mainly in deeper water column, usually around 100 m according to operation depth of gillnet and tracking study (Nelson et al., 1997). Basic on previous studies, *M. pelagios* may born in tropical warm water, which is lower productive environment, and move tower zooplankton rich current as they growth (Nakaya, 2010; Sawamoto and Matsumoto, 2012; de Moura et al., 2015). Borrell et al. (2011) shared the similar result on $\delta^{13}\text{C}$ and body length for *R. typus* as present study, it is believing that *R. typus* born in open or deeper water and growth for a period, then move tower productive coastal water to feed on planktonic prey (Wolfson, 1983; Kukuyev, 1995; Rowat et al. 2008). Marcus et al. (2019) also suggest the much dietary component from benthic and coastal habitats of juvenile and sub-mature *R. typus*. To give birth at lower productive waters may be a protective strategy of these filtering shark species, in order to avoid their young be prey by other predators (Rowat et al. 2008).

There were different tendencies of $\delta^{15}\text{N}$ – body length correlation between *M. pelagios* and *R. typus*, the $\delta^{15}\text{N}$ of *M. pelagios* decreased slightly through its growth, the $\delta^{15}\text{N}$ of *R. typus* showed increasing through its growth (Figure 15). The present study indicated that *M. pelagios* is a secondary consumer, who mainly feeds on small zooplanktonic prey such as Euphausiacea and Medusozoa even during different life stages because of their engulfment behavior (Table 2). However, if the metabolic rate changes as it grows would affect the $\delta^{15}\text{N}$ is still remaining to be understood. On the other hand, $\delta^{15}\text{N}$ tendency showed that *R. typus* may feed on higher trophic level prey. Previous study implied that *R. typus* may change their habitat and prey as they grow, juveniles may cruise various waters for feeding and growth, leading to the wide scope of $\delta^{15}\text{N}$ at their young stage (Taylor, 1996; Duffy, 2002; Borrell et al., 2011; Whitehead et al., 2020). As *R. typus* grows, large individuals may have the ability to feed on the higher trophic spectrum of prey according to their swim ability and well-developed filtering structures on the gills (Garrick, 1964; Borrell et al., 2011).

In general *M. pelagios* and *R. typus* were both filtering shark species occurred in the western North Pacific Ocean, but play different roles and have different feeding strategies. *M. pelagios* is an engulfment feeder, which only preys on small zooplanktonic preys through their life without changing their diet, but sexual segregation was found in large individuals. On the other hand, *R. typus* has ontogenetic change in both diet and habitat use, the well-developed swimming behavior and gill-rakers in large individuals allow *R. typus* a better ability to do suction feeding. Nevertheless, little and no stomach composition specimens of *M. pelagios* and *R. typus* implied that more SCA evidence and SIA information are needed among waters, gender, and sizes. The results of this study not only provide information of feeding ecology of two rare filtering feeders, but also are important reference for management strategy making in the future.

5. Conclusion

This is the first study that provides complete records, spatial–temporal distribution, and feeding information of *M. pelagios*. Also this is the only research try to compare the feeding ecology of two filtering shark species in the western North Pacific Ocean. One hypothesis was proposed in this study: *M. pelagios* give birth in the eastern Indian Ocean near the Philippines and Indonesia; during growth, they move northward to the western Pacific Ocean, joining the NPG in the spring and arriving in Taiwanese waters, foraging on planktonic prey from late spring to summer (Figure 16). Some mature females, which can withstand cool temperatures, keep following the KC and arrive in Japanese waters in the spring. In late summer, females remain in the water around Japan, and males remain across the Pacific Ocean toward the eastern side by following the North Pacific Current (NPC), indicating sexual segregation. *M. pelagios* arrive in Californian waters in late summer or autumn by following the CC and PC south to Mexico, Ecuador, and Peru. Afterward, some *M. pelagios* may follow the North Equatorial Current (NEC) across the Pacific again toward the western side, thereby returning to Indonesian or Philippine waters. However, (1) how does the Atlantic Ocean serve as a potential nursery area for *M. pelagios*? (2) Where do males and females mate? (3) Where do the gravid females go? These questions remain poorly known and need further study. The catch and retention of *M. pelagios* have been banned in Taiwan, fishermen have to release the shark no matter if it is alive or dead (Taiwan Fisheries Agency, 2021). Therefore, data collection and biological study, such as reproduction and age growth, will be difficult in the future. Future studies, such as satellite tracking or international data exchange, would help confirm our hypothesis.

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Figure 1 The female megamouth shark, *Megachasma pelagios* (503 cm in total length, TL), caught by large-mesh drift net in Hualien, eastern Taiwan.

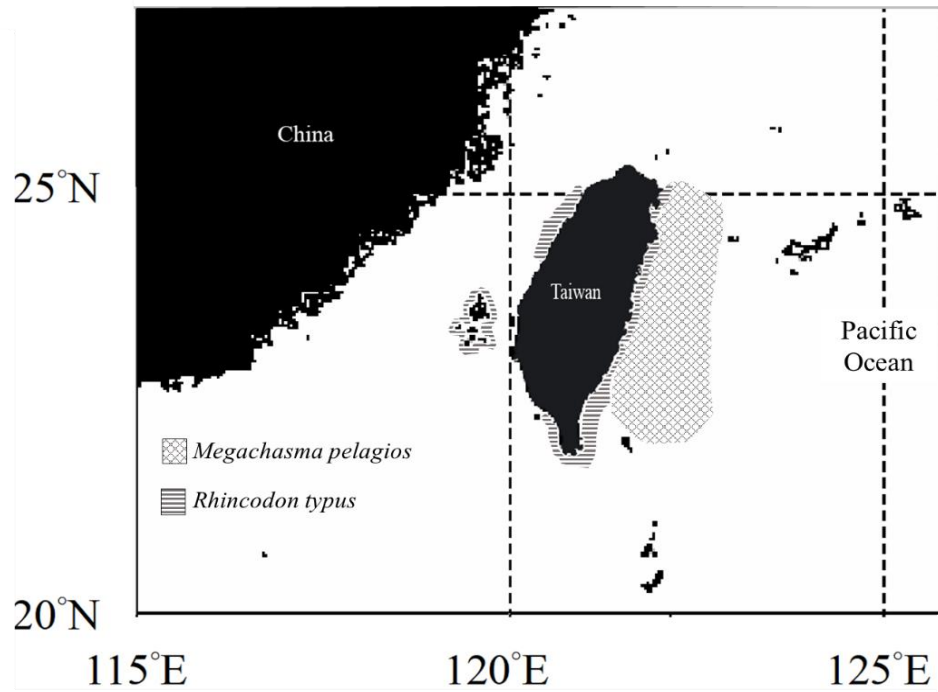


Figure 2 Fishing ground of *M. pelagios*, in the eastern Taiwan waters (the operation area of large-mesh drift net fishery) and of *R. typus*, around Taiwan waters (the operation area of set net fishery).

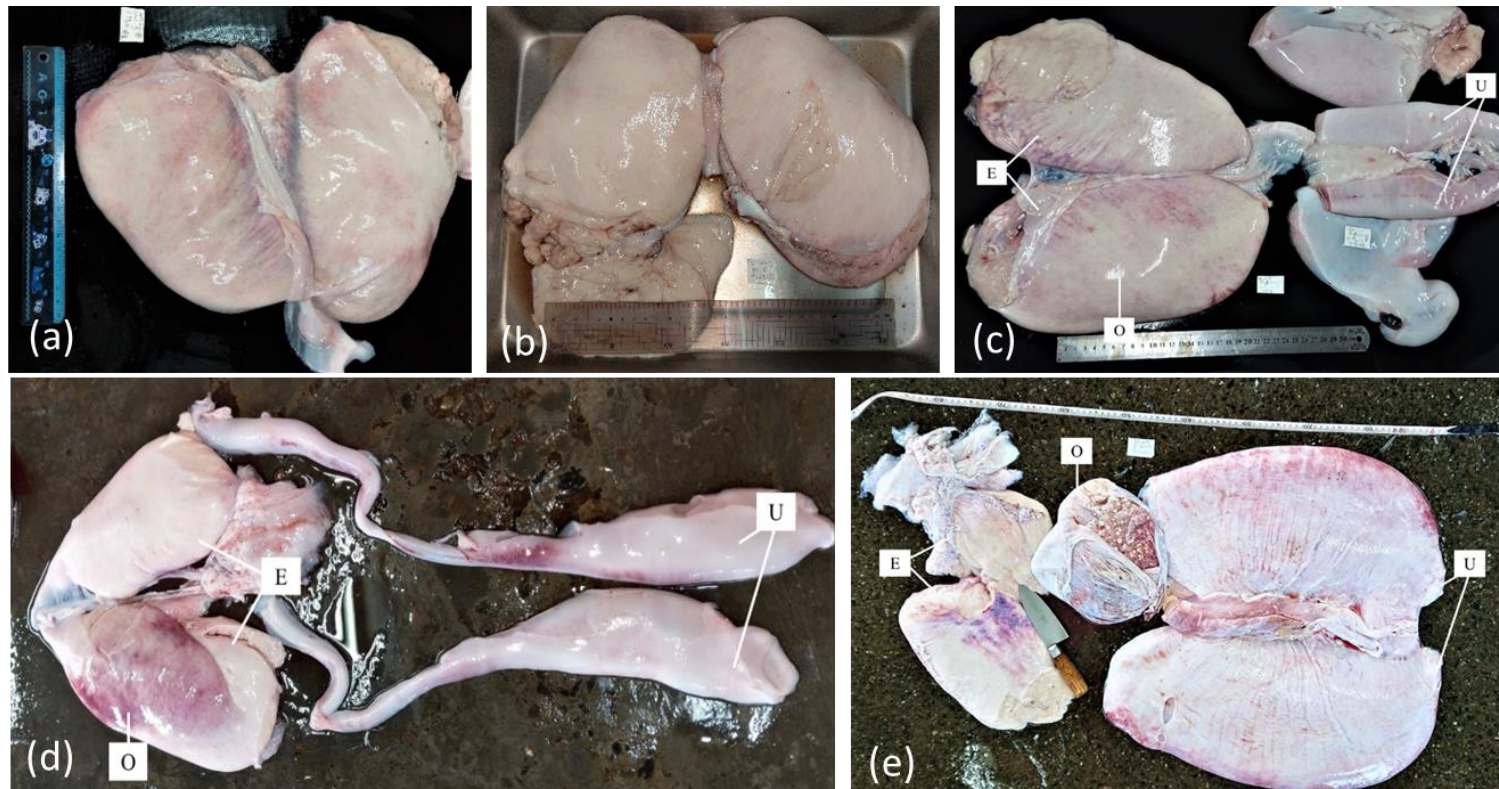


Figure 3 Gonad developing stages of *M. pelagios*. (a) The testis of immature male (374 cm TL), (b) the testis of mature male (445 cm TL), (c) immature female (409 cm TL); (d) maturing female (496 cm TL); (e) mature female (576 cm TL). E: Epigonal organ; O: Ovary; U: Uterine.

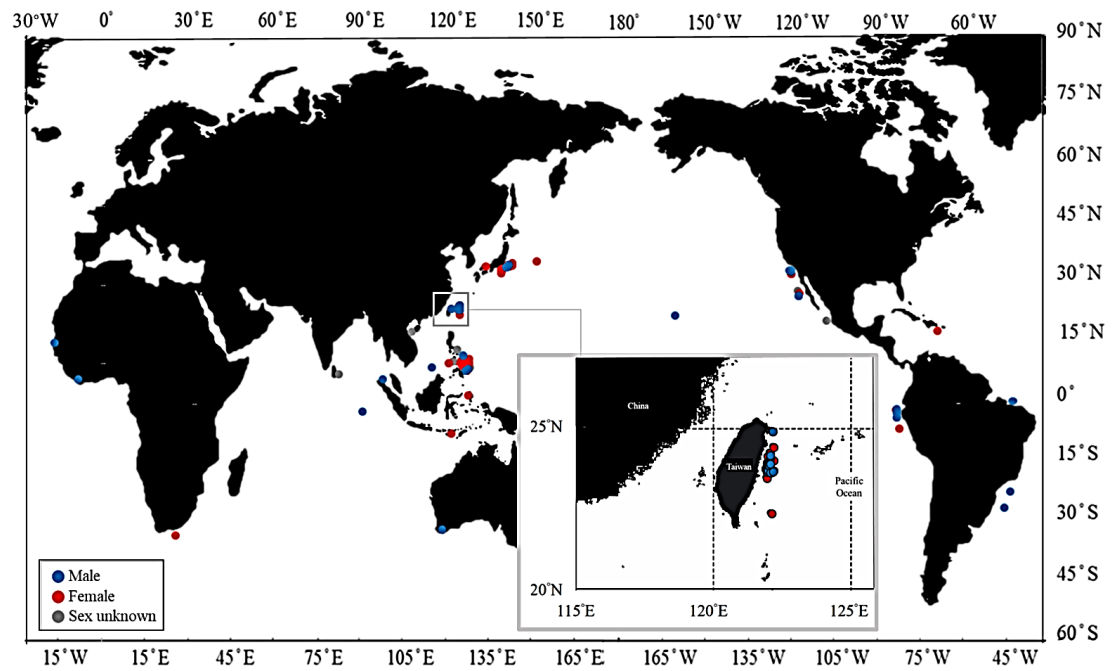


Figure 4 Records of *M. pelagios* in the world and in the eastern Taiwan waters.

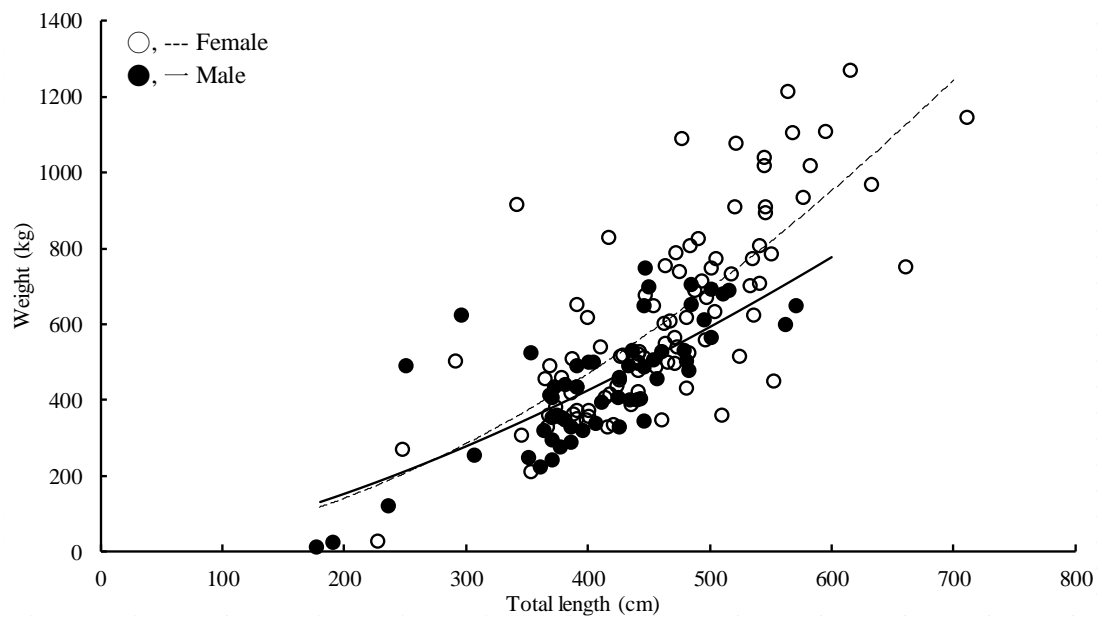


Figure 5 Total length- weight relationship of *M. pelagios*.

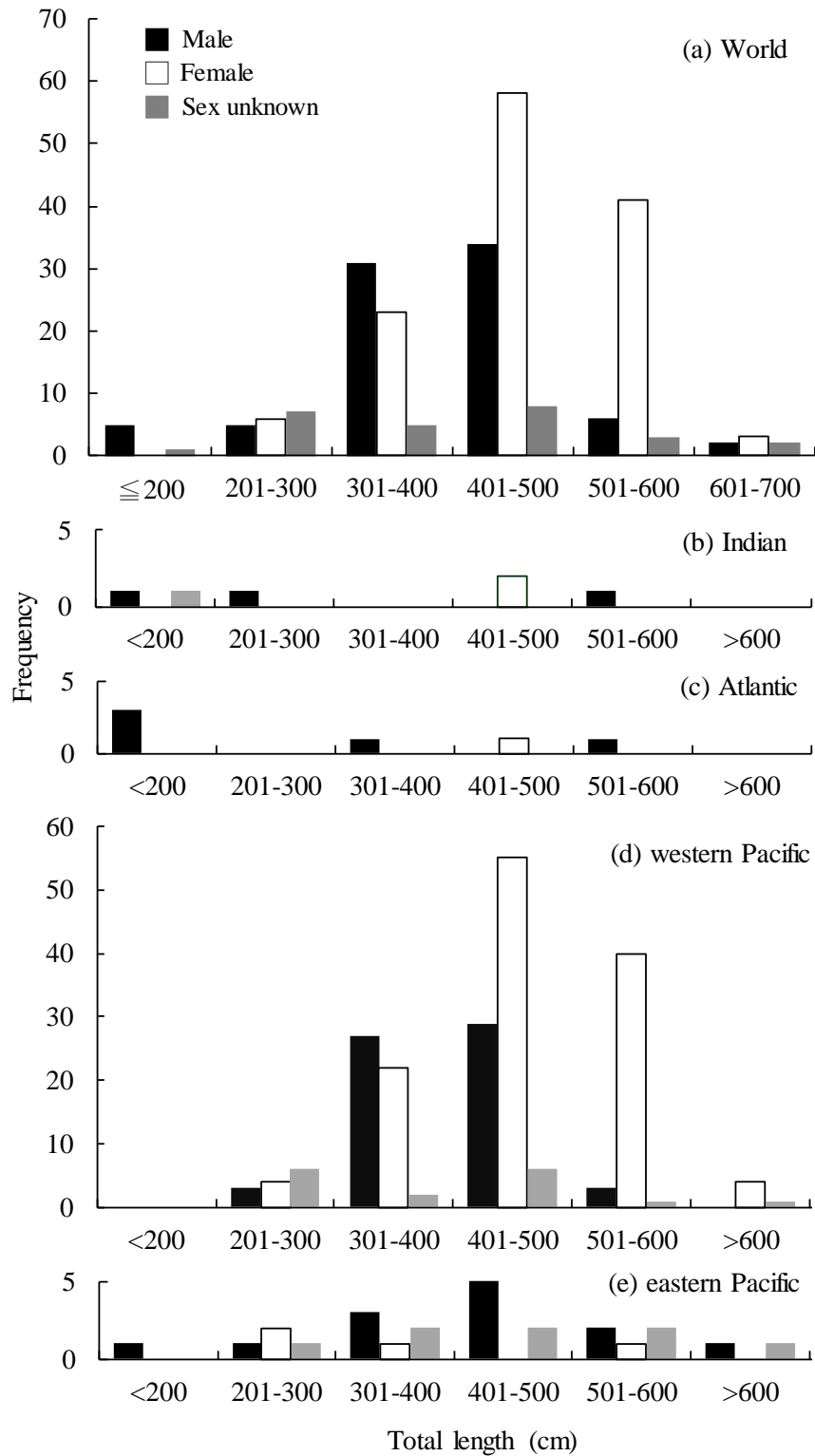


Figure 6 Total length frequency of *M. pelagios* in the (a) three oceans, (b) Indian Ocean, (c) Atlantic Ocean, (d) Western Pacific Ocean, and (e) Eastern Pacific Ocean.

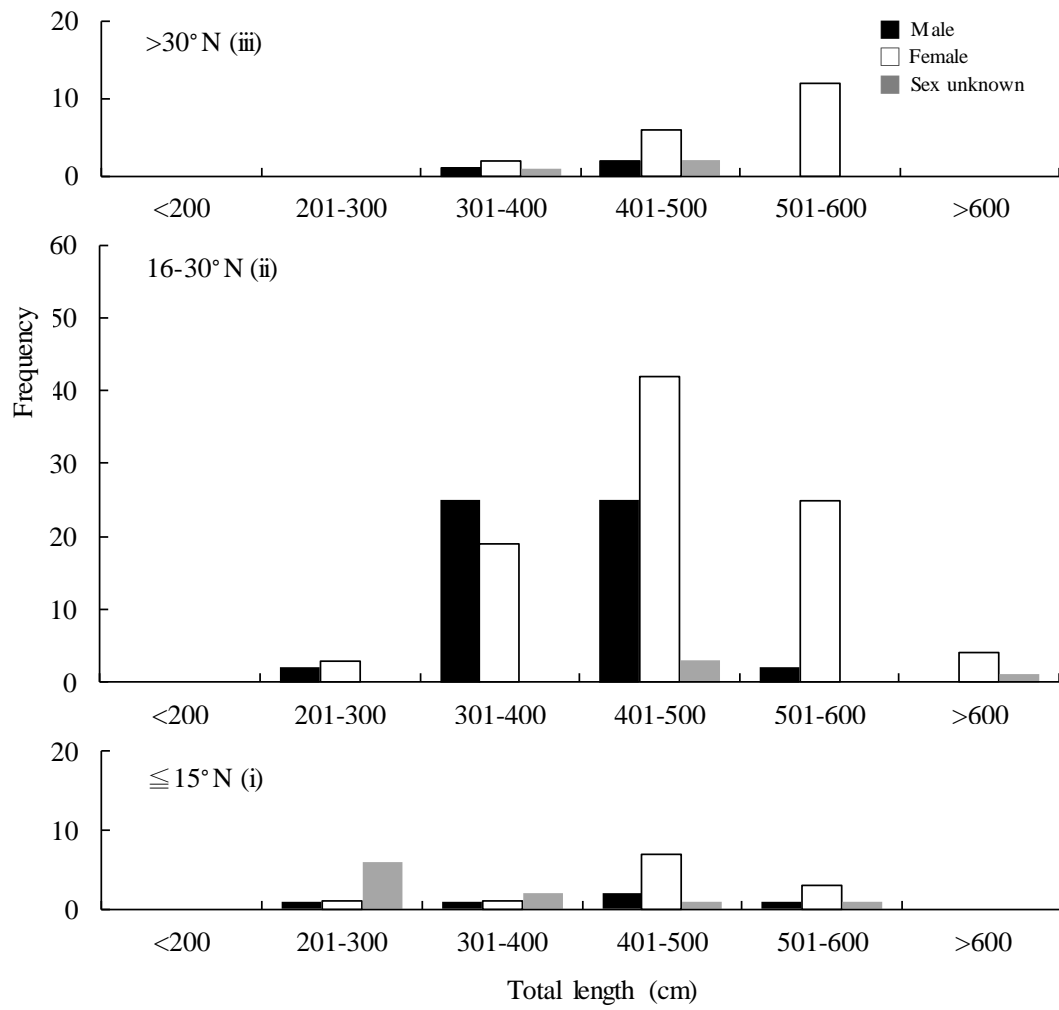


Figure 7 The length frequency of *M. pelagios* in the western Pacific Ocean.

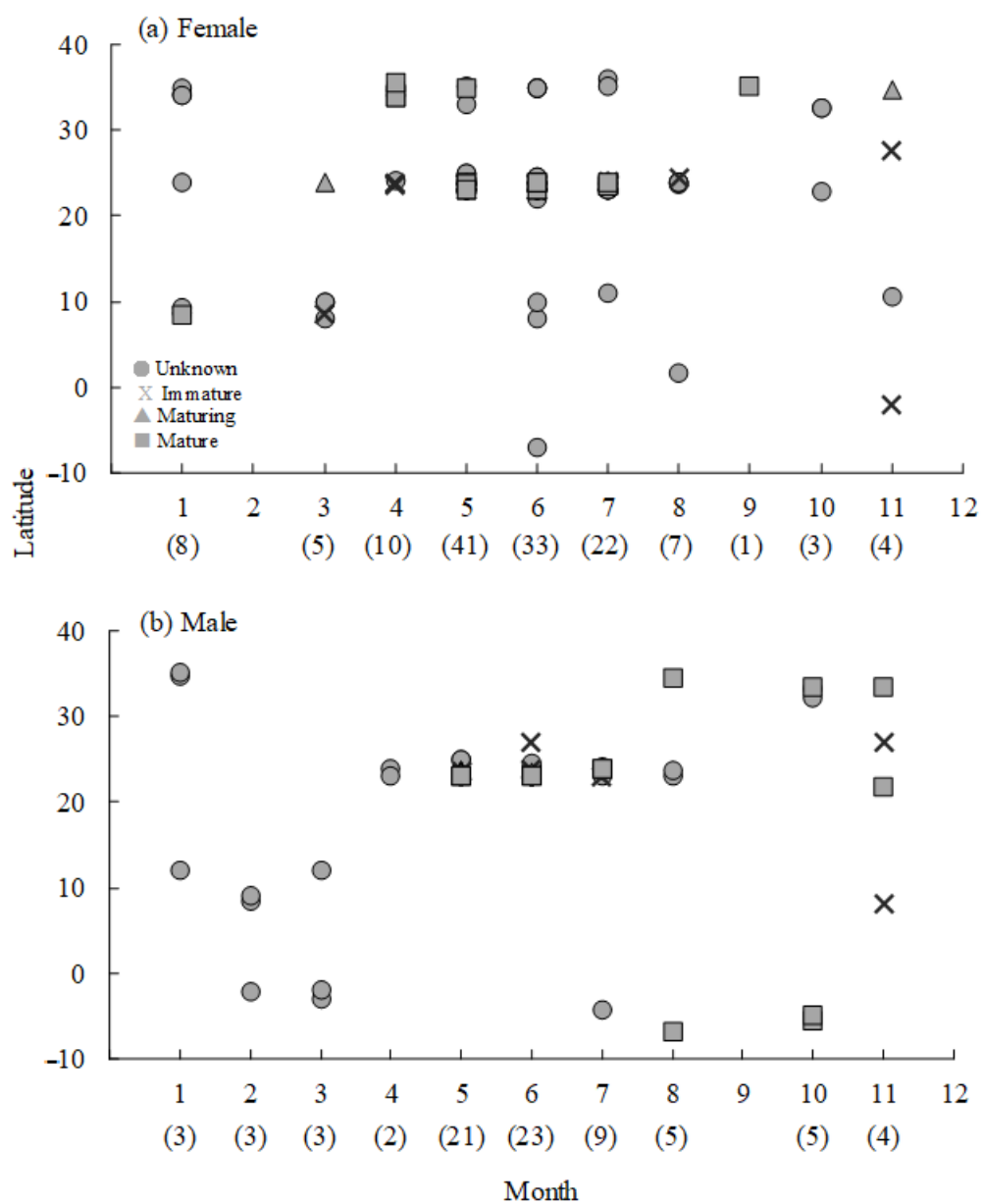


Figure 8 The monthly-latitudinal occurrence in the Pacific Ocean of *M. pelagios* for (a) females and (b) males, number in the parentheses brackets was individual number.

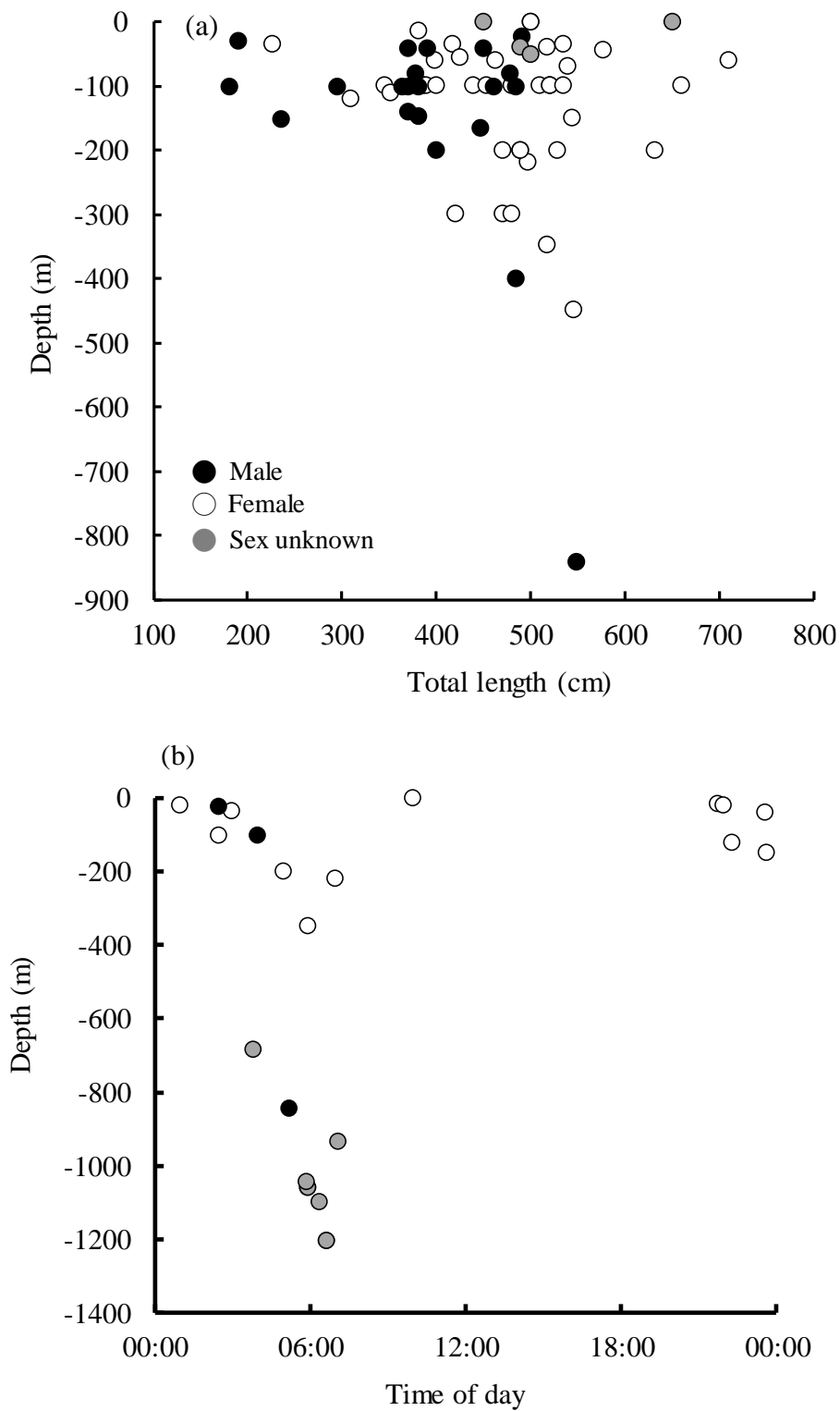


Figure 9 Vertical movement of *M. pelagios*. (a) The *M. pelagios* caught or sighted from different depths in size ($n = 64$). (b) Temporal vertical movement of *M. pelagios* ($n = 23$).

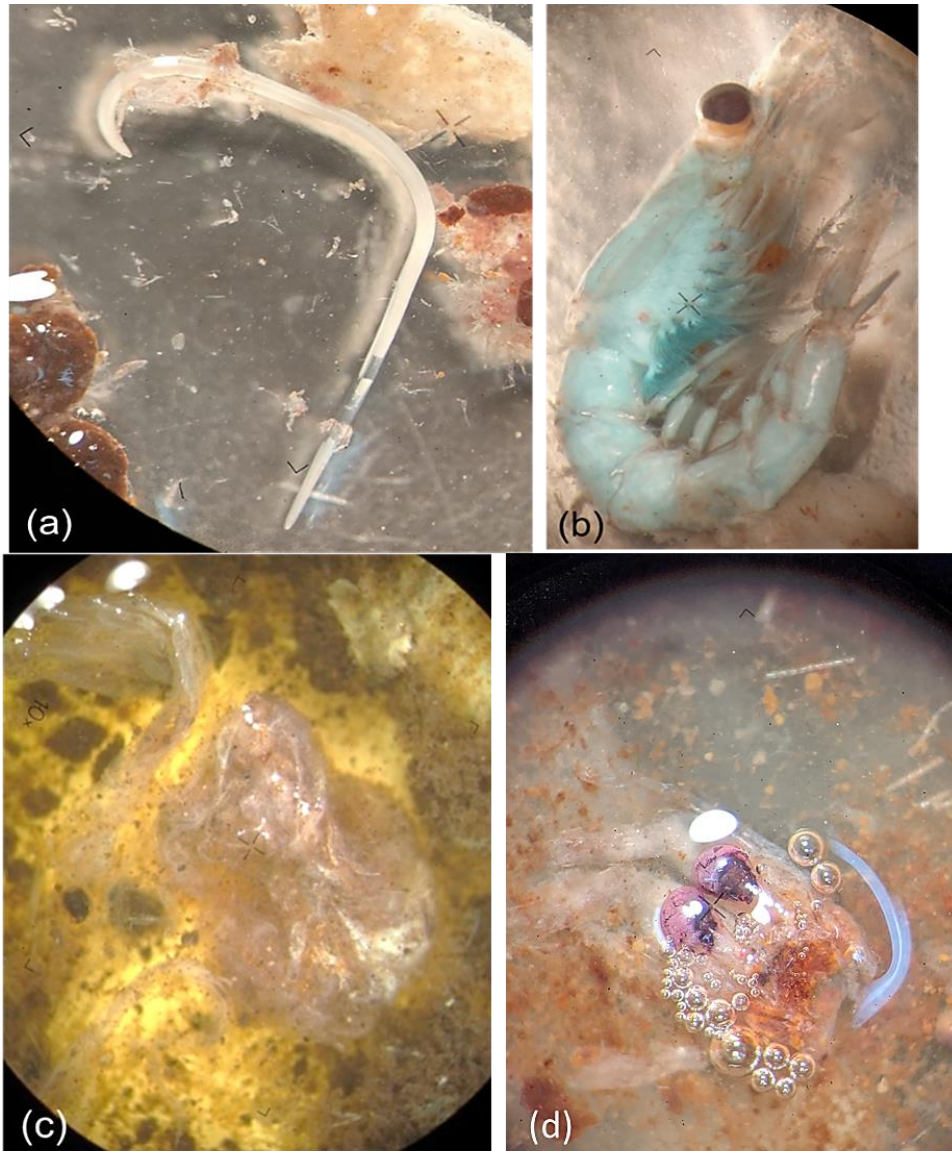


Figure 10 Stomach composition of *M. pelagios*. (a) Nematoda, (b) Euphausiacea, (c) Medusozoa, and (d) Anomura.

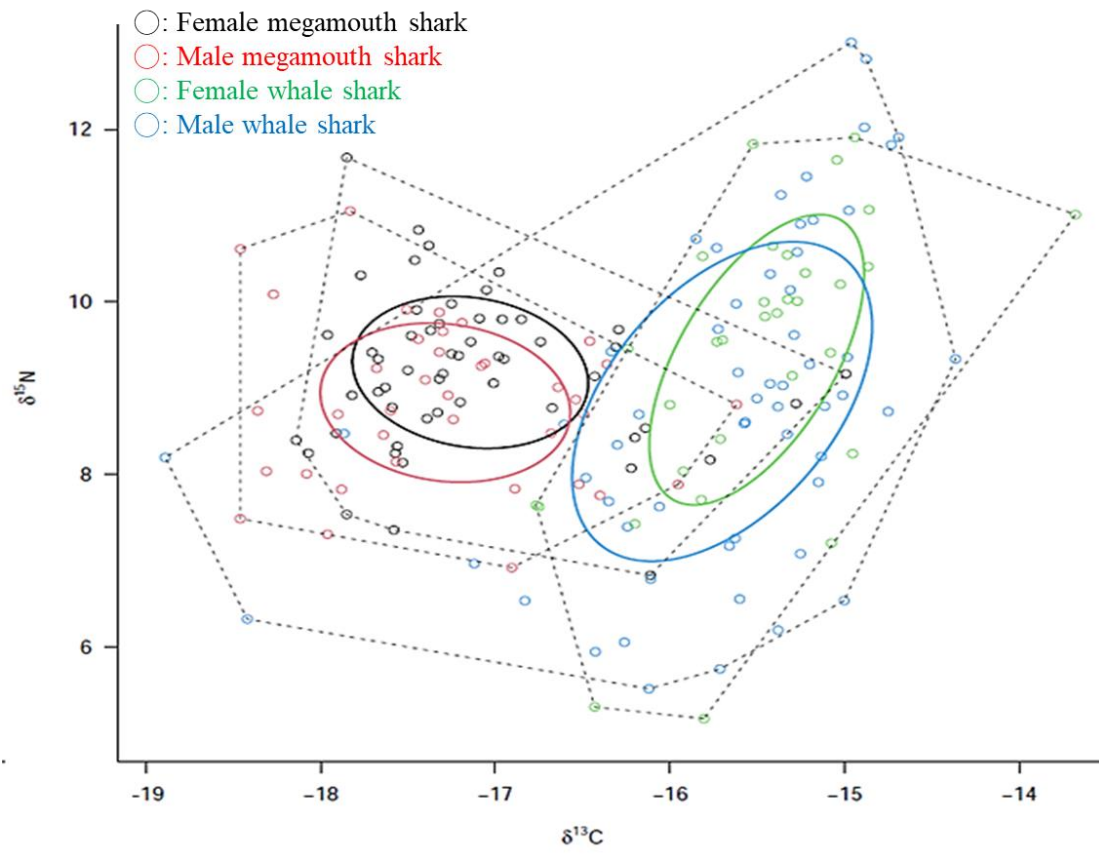


Figure 11 Relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the tissue of *M. pelagios* and whale shark (*Rhincodon typus*).

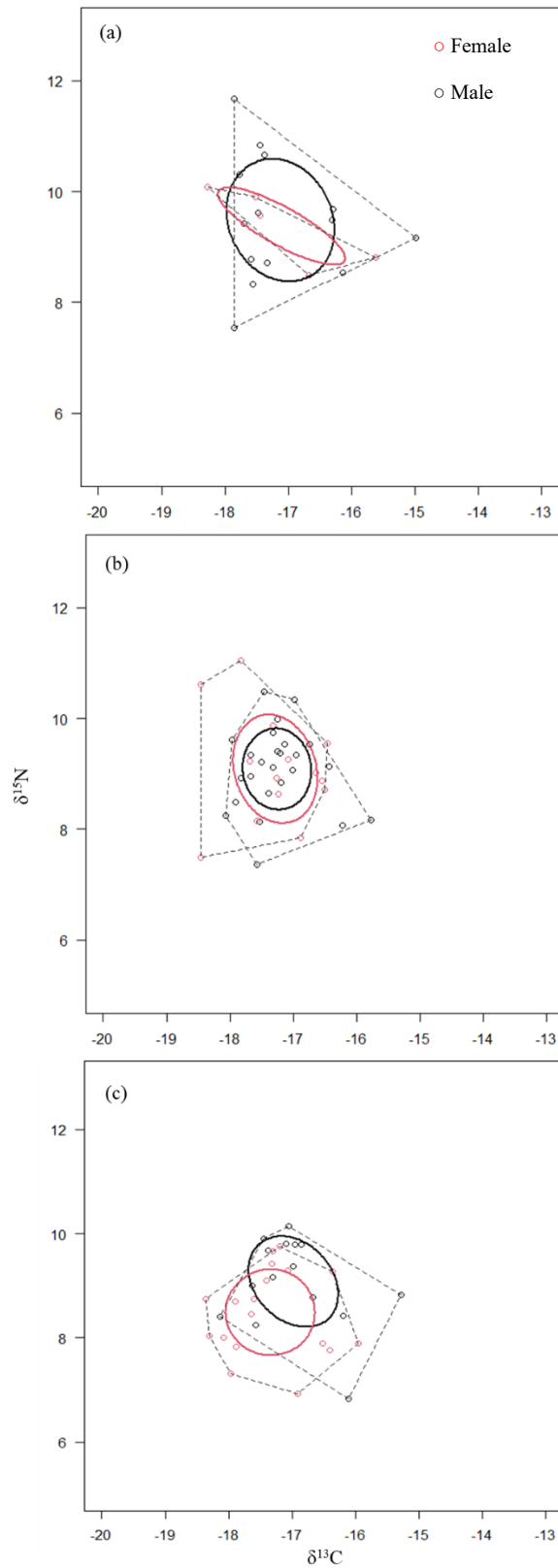


Figure 12 The SEAc (small sample size corrected SIBER ellipse area) and TA (total area of the convex hull encompassing the data points) difference between size groups of female and male *M. pelagios*. (a) group I, (b) group II, and (c) group III.

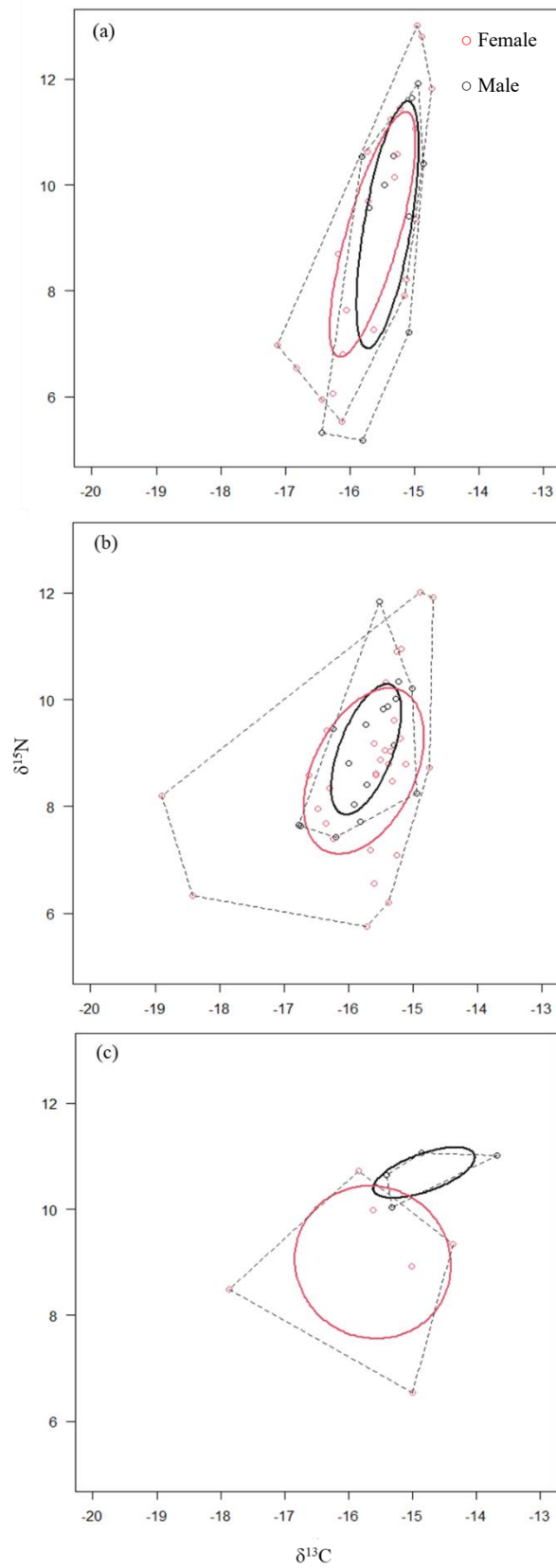


Figure 13 The SEAc (small sample size corrected SIBER ellipse area) and TA (total area of the convex hull encompassing the data points) difference between size groups of female and male *R. typus*. (a) group I, (b) group II, and (c) group III.

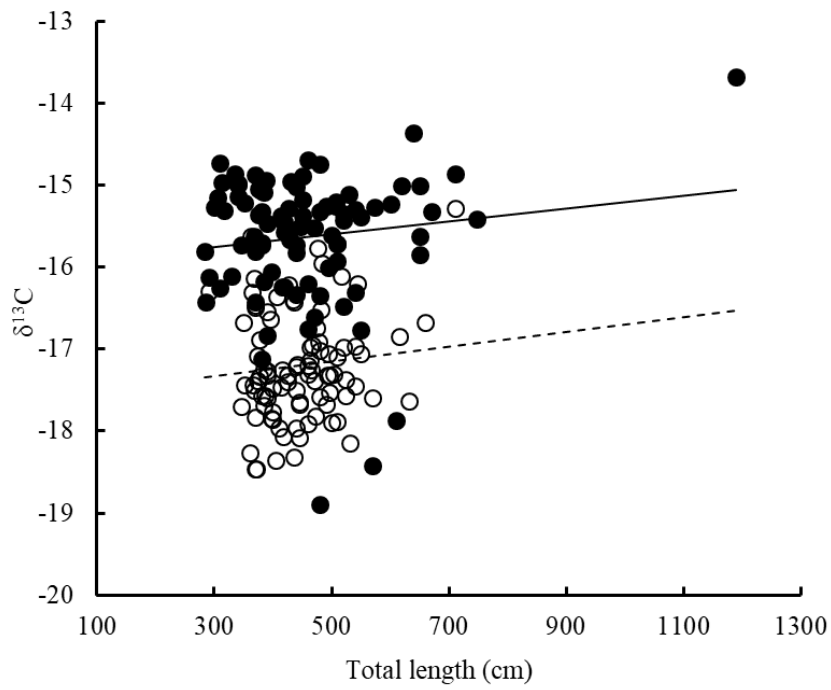


Figure 14 Relationship between $\delta^{13}\text{C}$ value and total length of *M. pelagios* (\circ , ---) and *R. typus* (\bullet , —).

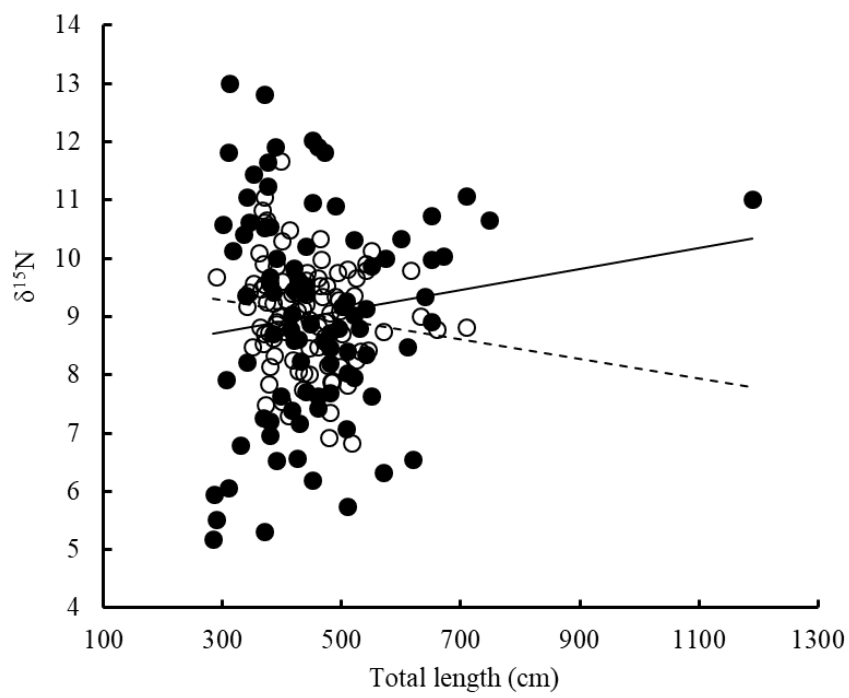


Figure 15 Relationship between $\delta^{15}\text{N}$ value and total length of *M. pelagios* (\circ , ---) and *R. typus* (\bullet , —).

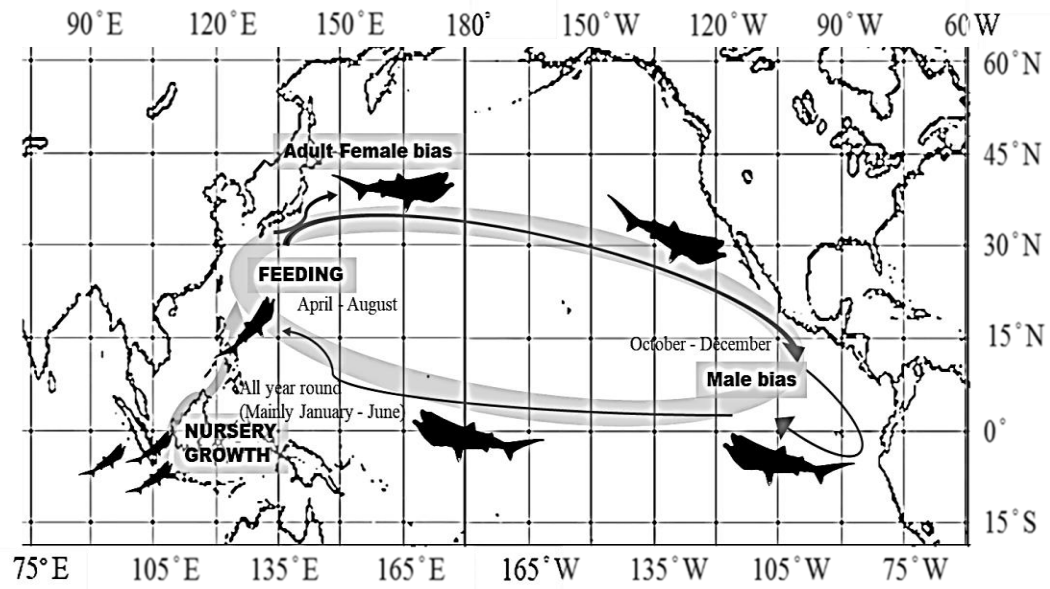


Figure 16 Schematic *M. pelagios* spatial-temporal distribution model proposed by this study.

Table 1 Biological information of 27 *M. pelagios* for genetic research.

No	Date	Sex	TL (cm)	Weight (kg)
1	2013/4/18	F	387	366
2	2013/4/30	F	373	383
3	2013/5/6	F	476	1090
4	2013/5/6	M	368	413
5	2013/5/7	M	385	328
6	2013/5/8	F	413	408
7	2013/5/18	F	524	516
8	2013/5/18	F	552	452
9	2013/5/19	M	395	320
10	2013/5/21	M	363	320
11	2013/5/30	F	426	516
12	2013/6/13	M	380	348
13	2013/7/10	F	463	549
14	2013/7/10	F	398	348
15	2013/7/10	M	484	653
16	2013/7/17	F	710	1147
17	2014/5/5	F	341	916
18	2014/5/22	F	352	210
19	2014/5/30	F	660	752
20	2014/5/31	M	478	532
21	2014/5/31	M	377	277
22	2014/5/31	F	517	734
23	2014/6/1	M	370	355
24	2014/6/4	M	390	490
25	2014/6/8	M	370	296
26	2014/8/3	F	366	330
27	2015/5/15	F	345	307

Table 2 Stomach composition of *M. pelagios* by weight (W), weight importance (%W), frequency occurrence (F), percent frequency of occurrence (%F), relative importance (RI), and percent relative importance (%RI)

Prey item	W	%W	F	%F	RI	%RI
Euphausiacea sp.1	10.820	23.863	14	100.000	2386.256	31.709
Other Euphausiacea	2.698	5.950	3	21.429	127.504	1.694
Unid. Dendrobranchiat	0.001	0.002	2	14.286	0.032	0.000
Unid. Brachyura	0.001	0.002	1	7.143	0.016	0.000
Unid. Anomura	0.010	0.022	1	7.143	0.158	0.002
Unid. Medusozoa	31.813	70.161	10	71.429	5011.484	66.594

Table 3 Number of sampled *M. pelagios*, results of the stable isotope analyses conducted in this study

2013-2019	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		Range	Mean \pm SD	Range	Mean \pm SD
Male	37	-18.14 – -14.99	-17.14 \pm 0.67	6.83 – 11.67	9.19 \pm 0.87
Female	54	-18.46 – -15.62	-17.27 \pm 0.71	6.92 – 11.05	8.84 \pm 0.91
Overall	91	-18.14 – -14.99	-17.20 \pm 0.69	6.84 – 11.67	9.04 \pm 0.90

Table 4 Number of sampled *R. typus*, results of the stable isotope analyses conducted in this study

2008-2018	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		Range	Mean \pm SD	Range	Mean \pm SD
Male	58	-16.77 – -13.67	-15.50 \pm 0.61	5.17 – 11.91	9.33 \pm 1.66
Female	32	-18.89 – -14.36	-15.70 \pm 0.85	5.52 – 13.01	8.85 \pm 1.83
Overall	90	-18.89 – -13.68	-15.63 \pm 0.78	5.17 – 13.01	9.02 \pm 1.79

Table 5 The SEAc (small sample size corrected SIBER ellipse area) and trophic overlap between *M. pelagios* and *R. typus* in different sex

	<i>M. pelagios</i>		<i>R. typus</i>	
	Female	Male	Female	Male
SEAc	1.88	2.11	2.72	4.49
Overlap _{intraspecies}	1.41		2.53	
Overlap% (intraspecies)	75.00	66.82	93.01	56.35
Overlap _{interspecies}	0			

Table 6 The SEAc (small sample size corrected SIBER ellipse area) and trophic overlap between stages for female and male *M. pelagios*

<i>M. pelagios</i>	Size group I		Size group II		Size group III	
	Female	Male	Female	Male	Female	Male
SEAc	3.17	1.63	1.30	2.19	1.99	1.94
Overlap	1.35		1.30		0.87	
Overlap%	42.59	82.82	100.00	59.36	43.72	44.85

Table 7 The SEAc (small sample size corrected SIBER ellipse area) and trophic overlap between stages for female and male *R. typus*

<i>R. typus</i>	Size group I		Size group II		Size group III	
	Female	Male	Female	Male	Female	Male
SEAc	3.01	3.25	1.8	4.27	1.41	6.91
Overlap	2.15		1.77		0.34	
Overlap%	71.43	66.15	98.33	41.45	24.11	4.92

Table 8 Trophic position of *M. pelagios* and *R. typus* in different body size groups

Size group	n	Trophic position of <i>M. pelagios</i>			n	Trophic position of <i>R. typus</i>		
		Min	Max	Mean \pm SD		Min	Max	Mean \pm SD
I	19	2.42	3.64	2.99 \pm 0.29	33	1.73	4.03	2.89 \pm 0.64
II	39	2.37	3.46	2.88 \pm 0.24	47	1.90	3.74	2.8 \pm 0.42
III	33	2.22	3.19	2.78 \pm 0.26	10	2.13	3.46	3.05 \pm 0.39

Table S1 A complete *M. pelagios* records from November 1976 to August 2020

No	year	month	Country	Sex	TL (cm)	Weight (kg)	Method	Reference/ Sources
1	1976	11	USA	M	446	750	Entangling	[1]
2	1984	11	USA	M	449	700	Gill net	[2]
3	1988	8	Australia	M	515	690	Stranded	[3]
4	1989	1	Japan	M	>400	-	Stranded	[4]
5	1989	6	Japan	-	~490	-	Set net	[5]
6	1990	10	USA	M	490	-	Gill net	[6]
7	1994	11	Japan	F	471	790	Stranded	[7]
8	1995	5	Senegal	M	180	-	Purse seine	[8]
9	1995	9	Brazil	M	190	24	Longline	[9]
10	1997	4	Japan	F	544	1040	Purse seine	[10]
11	1998	2	Philippines	M	~549	-	Gill net	[9]
12	1998	4	Japan	F	520-549	-	Set net	[9]
13	1998	8	Indonesia	F	~500	-	Sighting	[9]
14	1999	10	USA	F	518	-	Gill net	[3]
15	2001	10	USA	M	690.24*	-	Gill net	[3]
16	2002	1	East Indian Ocean	M	235	120	Purse seine	[3]
17	2002	4	South Africa	F	~460	260	Stranded	[12]
18	2003	1	Philippines	F	497	-	Gill net	[3]
19	2003	5	USA	-	610-760	-	Sighting	[3]
20	2003	7	Taiwan	M	250	490	-	[13]
21	2003	8	Japan	M	425	460	Purse seine	[14]
22	2004	3	Ecuador	M	529.35*	600	Gill net	[3]
23	2004	3	Indonesia	M	176.7	14	Stranded	[15]

24	2004	4	Japan	F	563	1215	Stranded	[16]
25	2004	4	Japan	F	~490	-	Set net	[16]
26	2004	11	Philippines	F	504	~1000	Stranded	[3]
27	2005	1	Japan	F	528	-	Purse seine	[3]
28	2005	1	Philippines	F	417	~1000	Net	[3]
29	2005	4	Taiwan	-	-	580-630	Trawl net	[13]
30	2005	5	Taiwan	-	-	580-680	Trawl net	[13]
31	2005	5	Taiwan	F	487	689	Trawl net	[13]
32	2005	5	Taiwan	F	483	807	Trawl net	[13]
33	2005	5	Taiwan	-	350-400	400-500	Drift net	[28]
34	2006	1	Philippines	F	500	750	Gill net	[3]
35	2006	3	Philippines	F	226	60-80	Gill net	[3]
36	2006	3	off China Sea	-	470	650	-	[28]
37	2006	5	Japan	F	567	1105	Set net	[3]
38	2006	11	Mexico	F	227	27	Gill net	[18]
39	2007	5	Philippines	-	249-250	40-50	-	[19]
40	2007	6	Japan	F	540	-	Set net	[3]
41	2007	7	Japan	F	367	361	Purse seine	[20]
42	2007	9	Mexico	-	-	-	Gill net	[18]
43	2007	9	Philippines	-	274	-	Stranded	[19]
44	2008	6	Taiwan	M	-	>200	-	[13]
45	2008	7	Taiwan	M	500-550	870	-	[13]
46	2008	9	Philippines	-	213	-	Stranded	[19]
47	2009	3	Philippines	M	400	500	Gill net	[19]
48	2009	6	Taiwan	F	390	350	-	[13]
49	2009	7	Brazil	M	539	-	Stranded	[21]

50	2009	11	Mexico	M	180-200	-	Net	[18]
51	2010	4	off China Sea	M	~400	>1000	-	[28]
52	2010	6	Taiwan	-	700	~770	-	[28]
53	2010	6	Japan	F	570	-	-	[22]
54	2010	-	Philippines	-	-	-	-	[19]
55	2011	1	Japan	F	~500	-	Set net	[23]
56	2011	5	Japan	-	>300	-	set net	[24]
57	2011	6	Mexico	M	300	-	Gill net	[25]
58	2011	6	Japan	F	540	-	Set net	[26]
59	2011	7	Japan	F	346.6	-	Set net	[22]
60	2011	11	Ecuador	F	243	-	Gill net	[27]
61	2012	1	off China Sea	F	565-570	1150-1250	-	[28]
62	2012	3	Ecuador	M	-	-	Gill net	[27]
63	2012	7	Sri Lanka	-	180	-	Gill net	[28]
64	2012	10	Taiwan	F	571.93*	800-900	-	[29]
65	2012	11	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)
66	2012	11	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)
67	2013	1	Japan	-	-	-	Set net	[30]
68	2013	1	Japan	F	450	-	Set net	[30]
69	2013	1	Japan	F	-	-	-	[19]
70	2013	4	Taiwan	F	387	365	Drift net	This study
71	2013	4	Taiwan	F	250	200-300	Drift net	This study
72	2013	4	Taiwan	F	373	383	Drift net	This study
73	2013	5	Taiwan	M	500	565	Drift net	This study
74	2013	5	Taiwan	F	476	1090	Drift net	This study
75	2013	5	Taiwan	M	368	413	Drift net	This study

76	2013	5	Taiwan	M	385	328	Drift net	This study
77	2013	5	Taiwan	F	413	408	Drift net	This study
78	2013	5	Taiwan	F	400	356	Drift net	This study
79	2013	5	Taiwan	F	545	910	Drift net	This study
80	2013	5	Taiwan	F	524	516	Drift net	This study
81	2013	5	Taiwan	F	552	452	Drift net	This study
82	2013	5	Taiwan	F	509	360	Drift net	This study
83	2013	5	Taiwan	M	395	320	Drift net	This study
84	2013	5	Taiwan	M	363	320	Drift net	This study
85	2013	5	Taiwan	F	453	650	Drift net	This study
86	2013	5	Taiwan	F	426	516	Drift net	This study
87	2013	6	Taiwan	M	380	348	Drift net	This study
88	2013	7	Taiwan	F	463	549	Drift net	This study
89	2013	7	Taiwan	F	398	348	Drift net	This study
90	2013	7	Taiwan	M	484	653	Drift net	This study
91	2013	7	Taiwan	F	710	1147	Drift net	This study
92	2013	9	Japan	F	577	-	-	[31]
93	2013	11	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)
94	2013	11	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)
95	2014	2	Ecuador	M	582-650	-	Gill net	[27]
96	2014	3	Philippines	F	>400	-	Stranded	[19]
97	2014	4	Japan	F	446	677	Set net	[30]
98	2014	5	Taiwan	F	341	916	Drift net	This study
99	2014	5	Taiwan	F	352	210	Drift net	This study
100	2014	5	Taiwan	F	660	752	Drift net	This study
101	2014	5	Taiwan	M	478	532	Drift net	This study

102	2014	5	Taiwan	M	377	277	Drift net	This study
103	2014	6	Taiwan	F	517	734	Drift net	This study
104	2014	6	Taiwan	M	370	355	Drift net	This study
105	2014	6	Taiwan	M	390	490	Drift net	This study
106	2014	6	Taiwan	M	370	296	Drift net	This study
107	2014	6	Philippines	-	>300	~1000	Net	[19]
108	2014	6	Philippines	F	548	400-500	-	[19]
109	2014	8	Taiwan	F	366	330	Drift net	This study
110	2014	12	Japan	-	~500	-	Set net	[32]
111	2015	1	Philippines	M	457	-	Net	[19]
112	2015	3	Philippines	F	~365	-	Net	[19]
113	2015	5	Taiwan	F	-	-	Drift net	This study
114	2015	5	Taiwan	F	345	307	Drift net	This study
115	2015	5	Taiwan	M	-	540	Drift net	This study
116	2015	6	Vietnam	-	~500	540	Stranded	[19]
117	2015	6	Taiwan	F	386	510	Drift net	This study
118	2015	6	Taiwan	M	456	456	Drift net	This study
119	2015	6	Taiwan	F	535	625	Drift net	This study
120	2015	6	Taiwan	F	521	1077	Drift net	This study
121	2015	6	Taiwan	F	440	523	Drift net	This study
122	2015	7	Taiwan	F	247	271	Drift net	This study
113**	2015	7	Taiwan	F	290	502	Drift net	This study
123	2015	11	Philippines	-	>300	-	Net	[19]
124	2015	12	Mexico	-	530	-	Stranded	[19]
125	2016	4	Japan	F	~500	-	Set net	[33]
126	2016	5	Taiwan	-	-	-	Drift net	This study

127	2016	5	Taiwan	-	-	-	Drift net	This study
128	2016	11	Peru	-	~350	-	Gill net	[34]
129	2016	12	Puerto Rico	F	457	-	Stranded	[35]
130	2017	5	Philippines	-	~300	~600	Stranded	[19]
131	2017	5	Taiwan	F	440	498	Drift net	This study
132	2017	5	Taiwan	M	484	705	Drift net	This study
133	2017	5	Taiwan	F	480	617	Drift net	This study
134	2017	5	Japan	F	540	-	Set net	[36]
135	2017	5	Japan	F	510	-	Set net	[19]
136	2017	5	Taiwan	M	295	625	Drift net	This study
137	2017	5	Taiwan	M	460	528	Drift net	This study
138	2017	6	Philippines	F	400-500	-	Stranded	[19]
139	2017	6	Taiwan	F	520	910	Drift net	This study
140	2017	6	Taiwan	F	390	653	Drift net	This study
141	2017	6	Taiwan	M	370	407	Drift net	This study
142	2017	7	Taiwan	F	490	827	Drift net	This study
143	2017	7	Indonesia	F	~500	-	Sighting	[19]
144	2017	7	Taiwan	F	632	969	Drift net	This study
145	2017	8	Taiwan	F	470	567	Drift net	This study
146	2017	8	Taiwan	F	480	432	Drift net	This study
147	2017	8	Taiwan	F	420	335	Drift net	This study
148	2017	8	Taiwan	F	470	498	Drift net	This study
149	2018	2	Philippines	M	434	-	Gill net	[19]
150	2018	3	Philippines	F	>400	-	Net	[19]
151	2018	4	Taiwan	F	534	773	Drift net	This study
152	2018	5	Taiwan	-	495	613	Drift net	This study

153	2018	5	Taiwan	M	306	254	Drift net	This study
154	2018	5	Taiwan	F	437	~1200	Drift net	Paul J Clerkin (personal communication)
155	2018	5	Taiwan	F	440	500	Drift net	This study
156	2018	5	Taiwan	F	385	420	Drift net	This study
157	2018	5	Taiwan	F	415	329	Drift net	This study
158	2018	5	Taiwan	M	433	490	Drift net	This study
159	2018	5	Taiwan	M	410	~650	Drift net	Paul J Clerkin (personal communication)
160	2018	5	Taiwan	F	565	~1200	Drift net	Paul J Clerkin (personal communication)
161	2018	5	Taiwan	F	428	520	Drift net	This study
162	2018	5	Taiwan	F	455	487	Drift net	This study
163	2018	5	Taiwan	F	364	456	Drift net	This study
164	2018	5	Taiwan	F	368	492	Drift net	This study
165	2018	5	Taiwan	M	500	692	Drift net	This study
166	2018	5	Taiwan	M	372	436	Drift net	This study
167	2018	5	Taiwan	F	400	373	Drift net	This study
168	2018	5	Taiwan	F	445	513	Drift net	This study
169	2018	5	Taiwan	F	390	372	Drift net	This study
170	2018	5	Taiwan	F	416	830	Drift net	This study
171	2018	5	Taiwan	M	570	649	Drift net	This study
172	2018	5	Taiwan	F	465	500	Drift net	This study
173	2018	5	Taiwan	F	472	540	Drift net	This study
174	2018	5	Taiwan	M	404	500	Drift net	This study
175	2018	5	Taiwan	M	436	530	Drift net	This study
176	2018	5	Taiwan	F	440	424	Drift net	This study
177	2018	5	Taiwan	M	360	223	Drift net	This study
178	2018	6	Taiwan	F	440	480	Drift net	This study

179	2018	6	Taiwan	F	463	755	Drift net	This study
180	2018	6	Taiwan	M	445	346	Drift net	This study
181	2018	6	Taiwan	F	417	417	Drift net	This study
182	2018	6	Taiwan	F	399	618	Drift net	This study
183	2018	6	Taiwan	F	493	716	Drift net	This study
184	2018	6	Taiwan	M	445	650	Drift net	This study
185	2018	6	Taiwan	M	380	440	Drift net	This study
186	2018	6	Taiwan	M	370	243	Drift net	This study
187	2018	6	Taiwan	M	453	508	Drift net	This study
188	2018	6	Taiwan	M	420	~300	Drift net	This study
189	2018	6	Taiwan	M	-	~220	Drift net	This study
190	2018	6	Taiwan	M	410	396	Drift net	This study
191	2018	6	Taiwan	M	406	338	Drift net	This study
192	2018	6	Taiwan	F	435	390	Drift net	This study
193	2018	7	Philippines	F	550	-	Stranded	[19]
194	2018	7	Taiwan	F	378	460	Drift net	This study
195	2018	7	Taiwan	F	544	1020	Drift net	This study
196	2018	7	Peru	M	364-411	-	Gill net	[34]
197	2018	7	Taiwan	F	460	348	Drift net	This study
198	2018	7	Taiwan	F	441	527	Drift net	This study
199	2018	7	Taiwan	M	425	330	Drift net	This study
200	2018	7	Taiwan	F	425	454	Drift net	This study
201	2018	7	Peru	-	370	-	Stranded	[34]
202	2018	8	Taiwan	M	434	400	Drift net	This study
203	2018	9	Brazil	M	>100	-	Stranded	[19]
204	2018	10	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)

205	2018	10	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)
206	2018	10	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)
207	2018	10	Philippines	-	>200	-	Stranded	[19]
208	2018	10	Peru	-	>500	-	Gill net	[37]
209	2018	11	Philippines	M	~300	-	Stranded	[19]
210	2018	12	USA	-	-	-	Gill net	NOAA Fisheries (personal communication)
211	2019	1	Japan	M	~400	-	Stranded	[19]
212	2019	3	Peru	-	470	-	Gill net	[37]
213	2019	4	Philippines	-	~480	-	Stranded	[19]
214	2019	4	Taiwan	M	300-350	420	Drift net	This study
215	2019	5	Taiwan	M	495	612	Drift net	This study
216	2019	5	Taiwan	M	390	435	Drift net	This study
217	2019	5	Taiwan	F	503	633	Drift net	This study
218	2019	5	Taiwan	F	550	787	Drift net	This study
219	2019	5	Taiwan	F	496	558	Drift net	This study
220	2019	6	Taiwan	F	540	808	Drift net	This study
221	2019	6	Taiwan	M	385	289	Drift net	This study
222	2019	6	Taiwan	M	480	503	Drift net	This study
223	2019	6	Taiwan	M	442	403	Drift net	This study
224	2019	6	Taiwan	F	>500	998	Drift net	This study
225	2019	6	Peru	F	>300	-	Seine net	[34]
226	2019	6	Taiwan	M	445	487	Drift net	This study
227	2019	6	Taiwan	F	467	610	Drift net	This study
228	2019	6	Taiwan	F	474	740	Drift net	This study
229	2019	6	Taiwan	M	374	359	Drift net	This study
230	2019	6	Taiwan	F	497	671	Drift net	This study

231	2019	6	Peru	-	215	-	Gill net	[37]
232	2019	7	Philippines	-	~300	-	Net	[19]
233	2019	7	Taiwan	F	540	708	Drift net	This study
234	2019	7	Taiwan	M	424	408	Drift net	This study
235	2019	7	Taiwan	F	615	1270	Drift net	This study
236	2019	7	Taiwan	M	390	436	Drift net	This study
237	2019	7	Taiwan	M	352	525	Drift net	This study
238	2019	7	Taiwan	F	532	703	Drift net	This study
239	2019	7	Taiwan	F	439	401	Drift net	This study
240	2019	7	Taiwan	M	510	682	Drift net	This study
241	2019	7	Taiwan	M	350	248	Drift net	This study
242	2019	8	Taiwan	M	482	480	Drift net	This study
243	2019	8	Peru	M	375	-	Gill net	[37]
244	2019	8	Peru	M	400	-	Gill net	[37]
245	2019	10	USA	-	~450	-	Sighting	[19]
246	2019	10	Peru	M	>400	-	Gill net	[37]
247	2019	10	Peru	M	>400	-	Gill net	[37]
248	2020	3	Liberia	M	380	-	Gill net	[19]
249	2020	3	Taiwan	F	545	895	Drift net	This study
250	2020	5	Taiwan	F	423	439	Drift net	This study
251	2020	6	Philippines	-	~600	-	Stranded	[19]
252	2020	6	Japan	F	~600	-	Set net	[19]
253	2020	6	Taiwan	F	462	602	Drift net	This study
254	2020	6	Taiwan	F	582	1018	Drift net	This study
255	2020	6	Taiwan	M	378	354	Drift net	This study
256	2020	6	Taiwan	F	576	935	Drift net	This study

257	2020	6	Taiwan	F	594	1110	Drift net	This study
258	2020	6	Taiwan	F	482	526	Drift net	This study
259	2020	7	Taiwan	F	504	774	Drift net	This study
260	2020	7	Taiwan	F	409	542	Drift net	This study
261	2020	8	Taiwan	F	381	-	Longline	This study

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