Biology of the Megamouth Shark, *Megachasma pelagios* (Lamniformes: Megachasmidae)

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Abstract

All records to date (end of June, 2008) of the megamouth shark, *Megachasma pelagios* were analyzed and the biology of the megamouth shark was inferred from them. The megamouth shark is a wide-ranging species, distributed from the tropical to temperate seas, with the most numerous occurrences in the western North Pacific Ocean. Young individuals tend to be distributed in warmer waters, while mature individuals broaden their habitat to higher latitudes. Males become mature at about 4 m in total length and females at about 5 m. The megamouth shark may copulate all year round, giving birth to young in warmer waters, and may be spatially segregated by sex.

The discovery of the megamouth shark was one of the ichthyological highlights of the last century. The first specimen of the megamouth shark was accidentally collected in Hawaii in 1976, and the species was eventually named *Megachasma pelagios* by Taylor, Compagno and Struhsaker (1983). The second specimen was captured in 1984 in California, U.S.A., eight years after the capture of the first Hawaiian specimen (Lavenberg and Seigel, 1985). The third specimen was found stranded in 1988 off western Australia in the Indian Ocean (Berra and Hutchins, 1990). Then, the fourth and fifth specimens were reported from Japan in 1989 (Nakaya, 1989; Miya et al., 1992). The sixth specimen was captured and released in California with a sonic transmitter (Lavenberg, 1991), and its horizontal and vertical movements were recorded for a few days (Nelson et al., 1997). These specimens were

Fig. 1. Megamouth shark (#7), stranded in Fukuoka Prefecture, Japan. (Photograph by Marine World Umino-Nakamichi, Fukuoka, Japan)

all giant males of about five meters in total length, except for the fifth one of unknown sex, and finally the first female megamouth (Fig. 1) was caught in Japan in 1994 (Takada et al., 1997).

At present, the worldwide total of megamouth shark captured, found stranded or sighted is forty specimens. Some of the specimens were studied for their morphology and phylogenetic relationships, but most of them were discarded, consumed or not studied. Among the few studies available, Nelson et al. (1997) reported part of their way of life, showing that the megamouth shark makes clear daily vertical movements within depths shallower than 200 meters. However, most of the biology of the megamouth shark still remains to be disclosed.

The purposes of the present study are to synthesize the scattered information of the 40 specimens recorded as of June, 2008, to study the morphological and biological evidence of each specimen, to analyze their capture data, and to discuss the biology of the megamouth shark.

Materials and methods

This paper is based on information from the 40 specimens captured, stranded or sighted in the world by the end of June, 2008 (Table 1). Information on each specimen was obtained from published papers, internet reports, the homepage of the American Elasmobranch Society, and/or directly from the collectors of the specimens. Maturity stages follow Nakaya and Stehmann (1998). Precaudal length (PCL) was converted into total length (TL) by referring to proportional measurements in Taylor et al. (1983), Berra and Hutchins (1990) and Nakaya et al. (1997).

Results and discussion

Size and sex ratio

Forty records of the megamouth shark are summarized in Table 1. The smallest megamouth ever found was 176.7 cm TL collected in Indonesia, and the most reliable largest specimen was 627 cm TL (4.2 m PCL) from Ecuador. Thirteen individuals were males, 21 were females and six individuals were of unknown sex.

History of megamouth records

Figure 2 shows the records of the megamouth shark by year. The first Hawaiian specimen was caught in 1976, and the second one was captured in 1984, eight years after the first discovery. Four specimens were captured or photographed during 1988 and 1990. Eight more specimens were captured, observed, or landed before 2000, totaling to 14 specimens in the 20th century. However, 26 specimens have already been captured, landed, or sighted to date in the 21st century (2001-2007).

During the twenty years since the capture of the first megamouth in Hawaii, records of the megamouth shark were quite few, i.e., one more record in the first decade (1976-1985) and seven records in the second decade (1986-1995). However, the records suddenly increased to 24 in the third decade (1996-2005). Seven megamouth sharks were recorded in 2006 and 2007.

Table 1. Megamouth sharks recorded to date (by June 30, 2008).
1, Taylor et al. (1983); 2, Lavenberg and Seigel (1985); 3, Berra and Hutchins (1990); 4, Nakaya (1989); 5, Miya et al. (1992); 6, Lavenberg (1991); 7, Nakaya et al. (1997); 8, Seret (1995); 9, Amorim et al. (2000); 10, Yano et al. (1999); 12, Yano et al. (1998); 17, Smale et al. (2002); 23, White et al. (2004); 25, Iida (2004)

#	Country	Capture date	TL(cm)	Sex	Method	Status	Depth(m)
1	Hawaii, USA	1976.11.15	446	♂	Entangled	Specimen	165
2	California, USA	1984.11.29	449	♂	Gill net	Specimen	< 38
3	Mandurah, W. Australia	1988.8.18	515	♂	Stranded	Specimen	
4	Shizuoka, Japan	1989.1.23	400<	♂	Stranded	Lost	
5	Shizuoka, Japan	1989.6.12	490	?	Set net	Released	< 40
6	California, USA	1990.10.21	495	♂	Gill net	Released	23
7	Fukuoka, Japan	1994.11.29	471	♀	Stranded	Specimen	
8	Dakar, Senegal	1995.5.4	180	♂	Purse seine	Discarded	
9	Southern Brazil	1995.9.18	190	♂	longline	Specimen	15-40
10	Mie, Japan	1997.4.30	544	♀	Purse seine	Specimen	< 150
11	Cagayan de Oro,	1998.2.21	ca 549	♂	Stranded	Consumed	
12	Mie, Japan	1998.4.23	550(*520)	♀	Set net	Discarded	35-40
13	Manado, Indonesia	1998.8.30	ca 500	?	Watching	Disappeared	0
14	California, USA	1999.10.1	ca 17 ft	♀	Gill net	Released	
15	California, USA	2001.10.19	ca 18ft FL	♂	Gill net	Released	
16	East Indian Ocean	2002.1.18	235	♂	Purse seine	Discarded	150
17	Western Cape, South Africa	2002.4.20	ca460	♀	Stranded	Specimen	ca180
18	Cagayan de Oro,	2003.1.6	497	♀	Gill net	Consumed	
19	California, USA	2003.5.26	20-25 ft	?	spotted	Disappeared	
20	Hualien, Taiwan	2003.7.3	ca 250	♀	Gill net?	Consumed	
21	Shizuoka, Japan	2003.8.7	425.5	♂	Purse seine	Specimen	
22	Guayas, Ecuador	2004.3.8	420 PCL	♂	Gill net	Consumed	
23	Sumatra, Indonesia	2004.3.13	176.7	♂	Stranded	Specimen	
24	Chiba, Japan	2004.4.19	563	♀	Stranded	Jaw preserved	
25	Shizuoka, Japan	2004.4.23	490	♀	Set net	Discarded	200
26	Iloilo, Philippines	2004.11.4	504	♀	Stranded	Specimen	
27	Mie, Japan	2005.1.23	528	♀	Purse seine	Mounted	
28	Macajalar Bay, Philippines	2005.1.30	417	♀	Gill net	Buried	35
29	Hualien, Taiwan	2005.4.25	?	?	Gill net	Consumed	
30	Hualien, Taiwan	2005.5.2	?	?	Gill net	Consumed	
31	Hualien, Taiwan	2005.5.4	480	♀	Gill net	Specimen	
32	Hualien, Taiwan	2005.5.5	570	♀	Gill net	Specimen	
33	Hualien, Taiwan	2005.5.5	?	?	?	?	
34	Bayawan, Philippines	2006.1.26	500	♀	Gill net	Buried	
35	Cagayan de Oro,	2006.3.12	7 ft 5 inch	♀	Gill net	?	
36	Zhejiang, China	2006.3.23	570	♀	?	Mounted	
37	Kanagawa, Japan	2006.5.2	568.8	♀	Set net	Mounted	
38	Tortugas Bay, Mexico	2006.11.16	214.9	♀	Gill net	Specimen	35
39	Shizuoka, Japan	2007.6.7	540	♀	Set net	Releasd	70
40	far off Ibaragi, Japan	2007.7.9	320 PCL	♀	Purse seine	Specimen	

The sudden recent increase in records may simply reflect an increase in reports of catches or sightings, as the megamouth shark has been steadily gaining public attention and the interest of people worldwide because of its very impressive morphology.

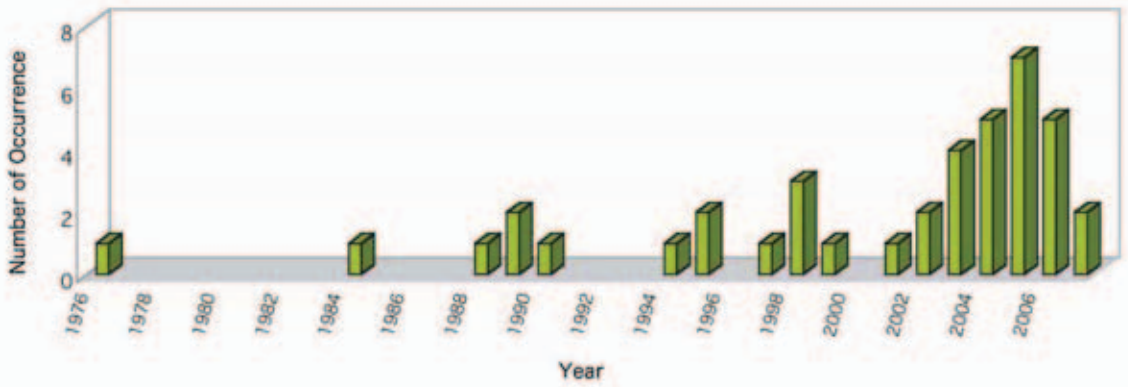

Fig. 2. World occurrences by year.

Geographical distribution

Figure 3 shows the latitudinal occurrence of the megamouth shark. Megamouth sharks are reported from the tropical to temperate waters of the world oceans between 36°5'N and 33°9'S. Thirty five records come from the northern Hemisphere, and only five are from the southern Hemisphere. Sixteen records came from the waters of 33°N and north. The second most frequent records are between 24-27°N.

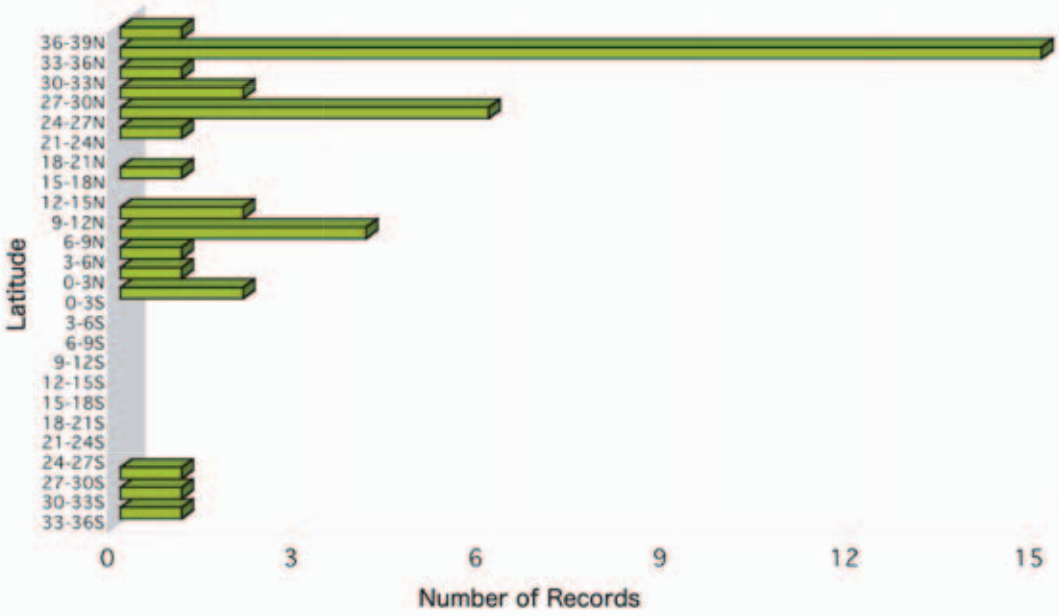

Fig. 3. World occurrences by latitude.

Thirty four specimens (or 85 % of the total records) have been reported from the Pacific Ocean, and only two (5%) and four (10%) specimens were captured or confirmed in the Atlantic Ocean and in the Indian Ocean, respectively (Fig. 4). Twenty six specimens (76% of 34 Pacific records) were recorded in the western North Pacific, with 12 records from Japan, six each from Taiwan and the Philippines, and one each from Indonesia and China. Seven records came from the eastern Pacific, with five from the United States (California) and one each from Mexico and Ecuador. The Ecuador specimen is the only one from southern latitudes in the Pacific. No specimens are known from the western South and central South Pacific Ocean.

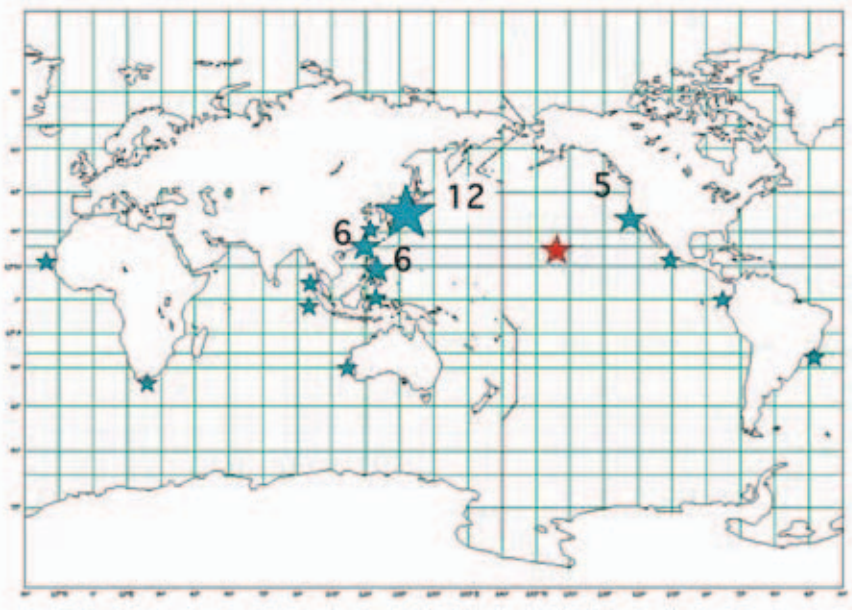

Fig. 4. World geographical occurrences. Red star indicates the holotype. One small star indicates one occurrence. Larger stars indicate plural occurrences shown by the number.

The Atlantic records are scattered, one each from Senegal and Brazil. No reports have been made from the western North Atlantic nor from the eastern North Atlantic north of Senegal. Three of the four Indian Ocean records were reported in the eastern region, and one specimen was stranded in South Africa. No reports have been made from the middle and western north Indian Ocean.

The first megamouth from Hawaii, 16th from the Indian Ocean and 40th from Japan are the pelagic records. All the other specimens were caught or sighted in waters near the continents, with eight stranding records.

As seen above, reports of the occurrences of the megamouth sharks appear to be strongly biased, perhaps as a result of sampling artifacts, such as differences in fishing effort, fishing gear, or interest of the local people, or they may indeed indicate actual differences in local population sizes of the shark.

Seasonal distribution

Figure 5 shows the monthly occurrence of the species. Seven specimens were recorded in May, and six specimens each were in January and April, followed by five records in November. No specimen has been captured in December.

Table 2 is a combination of the monthly and latitudinal occurrences for the world, indicated by the catch number shown in Table 1. Megamouth sharks occurred throughout year except in September and December in the northern Hemisphere, but occurrences for the southern Hemisphere are scattered, one each in January, March, April, August and September.

Eight records were reported from the waters of lower latitudes during January through March. More than half (23 records) of the total records were reported from the waters north of □ □□□ of the Pacific Ocean from January to November, with six records in May and five records in April. Only four

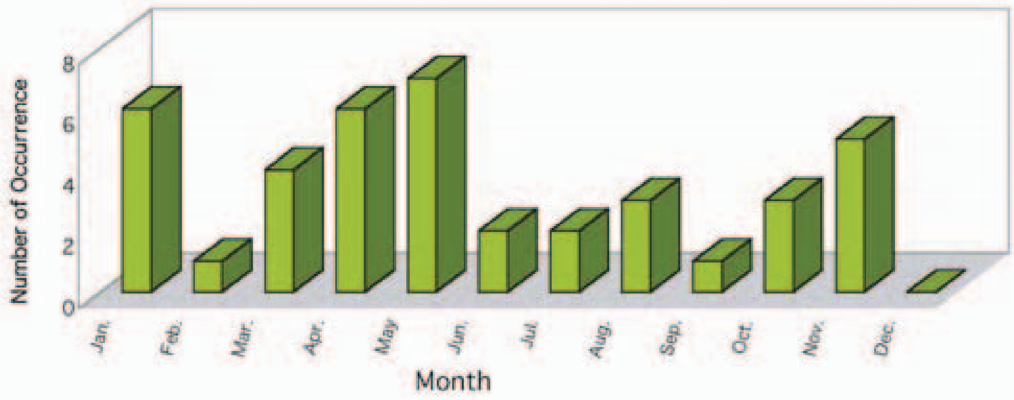

Fig. 5. World occurrences by month.

Table 2. Latitude and month of each capture (by June 30, 2008). Number indicates the serial individual number of the catch given in Table 1.

Latitude	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
36-39N							40	21					1
33-36N	4,27			10, 12, 24, 25	19, 37	5,39				6,15	2,7		15
30-33N										14			1
27-30N											38		2
24-27N			36	29	30, 31, 32, 33		20						6
21-24N											1		1
18-21N													
15-18N					8								1
12-15N													
9-12N	34										26		2
6-9N	18,28	11	35										4
3-6N			23										1
0-3N													1
0-3S	16		22					13					2
3-6S													
6-9S													
9-12S													
12-15S													
15-18S													
18-21S													
21-24S													
24-27S													
27-30S									9				1
30-33S								3					1
33-36S				17									1
Total	6	1	4	6	7	2	2	3	1	3	5	0	40

megamouth sharks appeared in the waters between [illegible] and [illegible] from April to December. One each was [illegible] April, August and September.

Figure 6 shows the monthly and latitudinal occurrences for Pacific megamouth sharks. Thirty three out of 34 records were from the North Pacific (north of the Equator), and only one was collected in the South Pacific off Ecuador. The megamouth shark occurred throughout the year in the higher latitudes (north of 20°N). For the records of the lower latitudes (20°N and south), six specimens were recorded during January and March, and one specimen each appeared in August, and in November. All of the

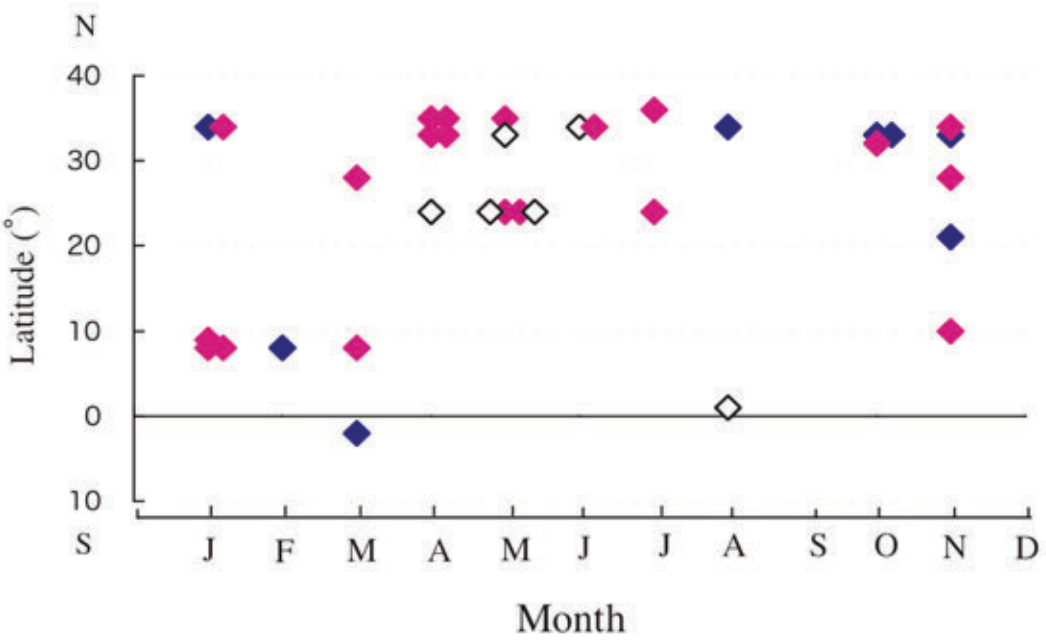

Fig. 6. Latitudinal occurrences in the Pacific Ocean by month. Solid blue diamond, male; solid red diamond, female; open diamond, unknown sex.

records from the lower latitudes are actually confined in the waters of 10°N and south. There are no reports from the waters between 10°N and 20°N.

These facts suggest that the megamouth shark is distributed in the waters of higher latitudes all the year round, and the absence of records from the lower latitudes during April and October might mean that the sharks leave the lower latitudes for several months.

The records from the Atlantic and Indian Oceans are too few for speculation about their seasonal movements.

Geographical distribution by size

The latitudinal occurrences by size are given in Figure 7. Smaller specimens less than 2.5 meters are confined in the lower latitudes between 27°39'N and 27°08'S, and do not appear in the higher latitudes north of 30°N and south of 30°N. Specimens between three and four meters have not been recorded. On the other hand, specimens larger than 4 meters appeared not only in the lower latitudes south of 30°N, but also in the higher latitudes north of 30°N in the North Pacific Ocean. In addition, 4.6 m TL and 5.15 m TL specimens were recorded in the higher latitudes at 34°S and 32°S, respectively, in the Indian Ocean. More than half of the larger specimens have been captured or sighted in waters of the higher latitudes.

As mentioned above, individuals smaller than 2.5 m TL and specimens larger than 4 m TL have numerously been reported, while those between 2.5 m TL and 4 m TL have not yet been reported.

These facts may indicate that while they are young, the megamouth sharks are rather confined in the lower latitudes, and as they grow, they broaden their distribution to the higher latitudes. The complete absence of 2.5-4 m TL specimens might reflect some kind of sampling artifact, but this is rather strange, because so many individuals of the smaller or the larger sizes were frequently recorded. These facts might

also suggest some biological characteristics of the megamouth shark.

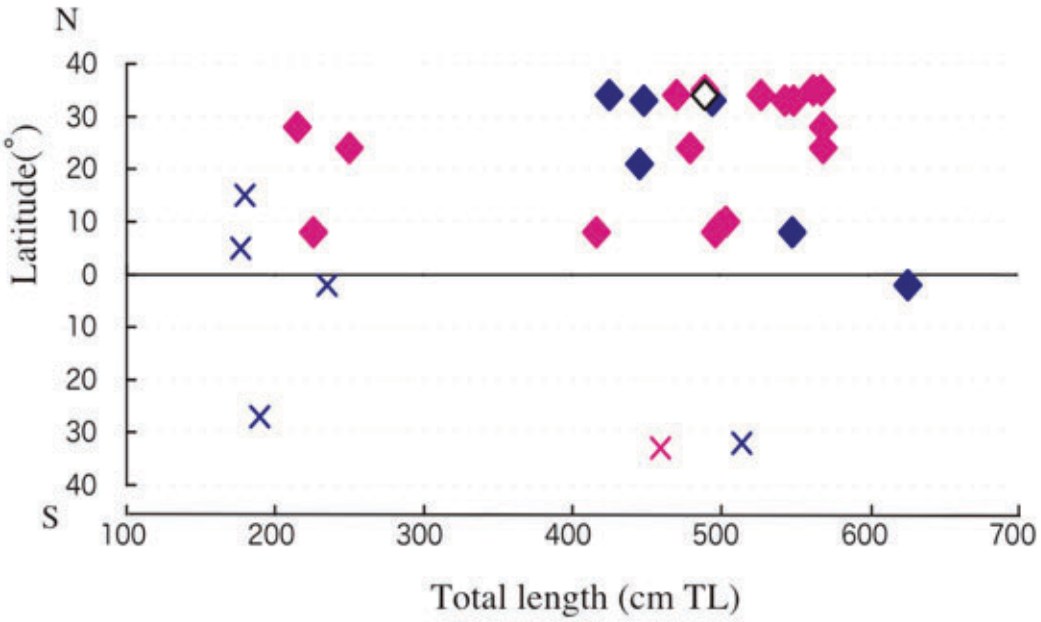

Fig. 7. World latitudinal occurrences by total length. Solid blue diamond, Pacific male; solid red diamond, Pacific female; open diamond, unknown sex (Pacific); blue cross, Indian/Atlantic male; red cross, Indian female.

Maturity

The maturity stages of the available specimens are summarized in Fig. 8. The data on the maturity were taken either directly from the specimens or photographs, or from the descriptions in reports of occurrence.

Specimens between 190 cm TL and 235 cm TL (three males and one female) were all immature, which is shown as maturity stage 1 in Fig. 8. A male of 426 cm TL (#21) has well developed claspers, and this is the smallest mature male (maturity stage 3) among available specimens. A 449 cm male (#2) was oozing spermatophores from its claspers (Lavenberg and Seigel, 1985). The larger males were fully mature. Two females of 460 cm TL (#17; Smale et al, 2002) and 471 cm TL (#7; Castro et al., 1997) were adolescent, with developing reproductive organs (maturity stage 2). Females of 497cm TL (#18; Compagno et al., 2005), and 544 cm TL and 550 cm TL (#10 and #12, respectively; Yano et al., 1999) had mating scars on their bodies. A 563 cm TL female (#24) was fully mature without embryos (personal communication with M. Miya). These are shown as maturity stage 3.

These facts indicate that the megamouth shark reaches maturity at about 4 meters (less than 4.3 meters) in males, and about 5 meters in females.

Geographical distribution by sex and maturity

Based on the above discussion, the maturity stages of the unknown individuals were determined

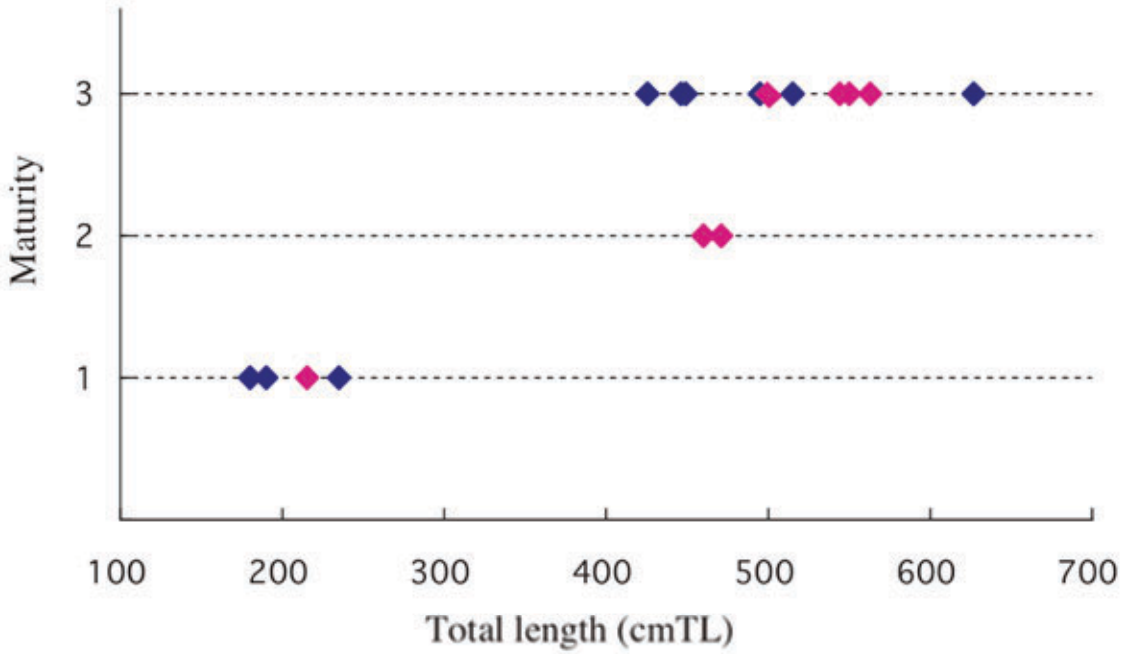

Fig. 8. Maturity stages. 1, immature; 2, adolescent; 3. mature. Blue, male; red, female.

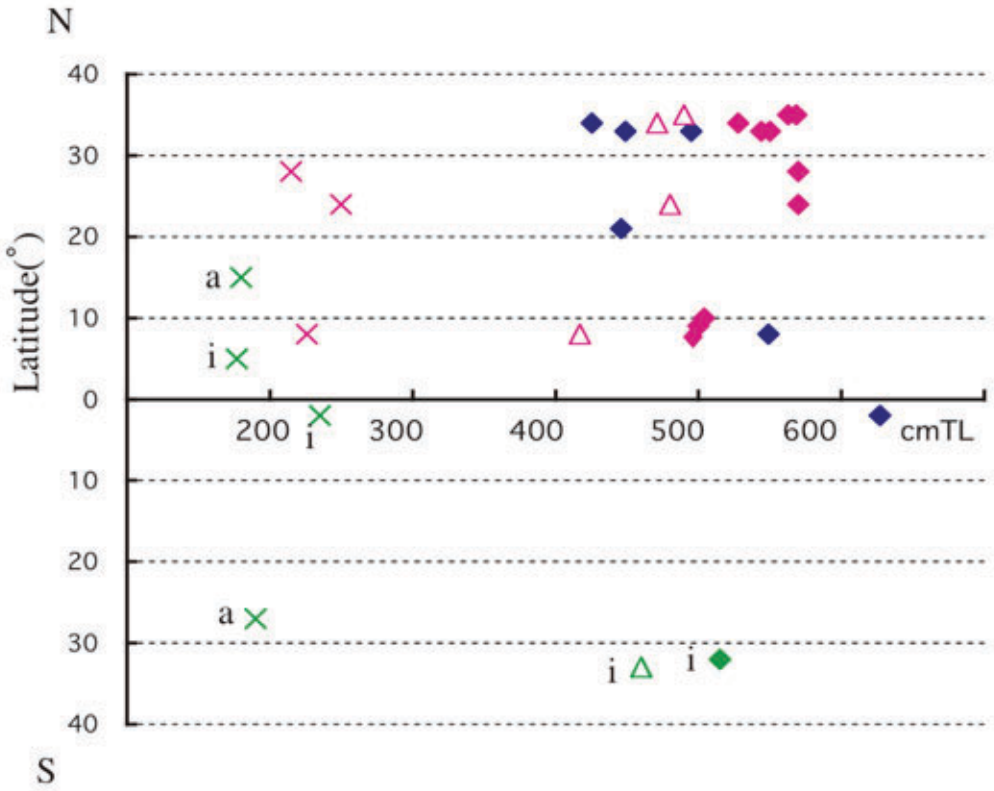

Fig. 9. Latitudinal occurrences by maturity stage and total length. Solid blue diamond, mature male (Pacific Ocean); solid red diamond, mature female (Pacific); red triangle, adolescent female (Pacific); red cross, immature female (Pacific); green solid diamond, mature male (Indian); green open triangle, adolescent female (Indian); green cross, immature male (Indian/Atlantic). a, Atlantic Ocean; i, Indian Ocean.

according to the following rule. The males smaller than 2.5 m TL were treated as immature, and those larger than 4 m TL as mature. The females smaller than 2.5 m TL were treated as immature, those between 4 and about 5 m TL (excluding the 497 cm TL specimen, which had bite marks) were treated as adolescents, and those larger than 5 m TL (including the 497 cm TL specimen above) were mature.

Figure 9 shows latitudinal and length distribution by maturity stages for world records. Among Pacific megamouth sharks, the immature individuals (only females) appeared in the lower latitudes south of 28°N. Atlantic/Indian immature individuals (only males) appeared in the lower latitudes between 15°N and 28°S.

Pacific adolescent females appeared between 8°N and 37°N, expanding their distribution to more northern waters higher than 30°N, and a single adolescent Indian female was recorded at 34°S. Adolescent males have not yet been found.

Mature Pacific females appeared between 8°N and 36°N. Mature Pacific males appeared between 35°N and 3°S, and a single mature Indian male appeared at 32°S.

These facts suggest that the megamouth sharks stay in the waters of lower latitudes while immature, and invade waters of higher latitudes as they mature, although some mature individuals still stay in the lower latitudes.

Figure 10 shows occurrences in the four local regions of the Pacific Ocean by sexual maturity stages, i.e. Japan (A), Taiwan/China (B), the Philippines/Indonesia (C) and the Central/Eastern Pacific (D). In Japanese waters, three adolescent and six mature females of larger sizes, and two mature males (including one of unknown length, but with developed claspers) were captured, but no immature individual is known. In Taiwan/China, only four females (one immature, one adolescent and two mature individuals) are known, with three individuals of unknown sex. In the Philippines/Indonesia, five females (one immature, one adolescent and three mature individuals) and one mature male were captured, and one individual of unknown sex was sighted and photographed.

In the Central/Eastern Pacific, five mature males (including one individual of unknown length), one mature female of unknown length, one immature female and one individual of unknown sex/length were recorded.

Many adolescent and mature females, and only a few males appeared in the western Pacific Ocean (Fig. 10, A-C), while five mature males and two females were seen in the eastern Pacific Ocean (Fig. 10, D). The sexual bias seen between the western and the eastern Pacific Oceans may suggest spatial segregation by sex in the megamouth shark.

In the western Pacific, immature, adolescent and mature females occurred in Taiwan/China and the Philippines/Indonesia, while many adolescent and mature females occurred, and no immature female was found in Japan. These facts also might suggest that females tend to move into the waters of higher latitudes as they mature.

For the Indian Ocean, one adolescent female was found in the western part, and three males (two immature and one mature) were reported in the eastern part.

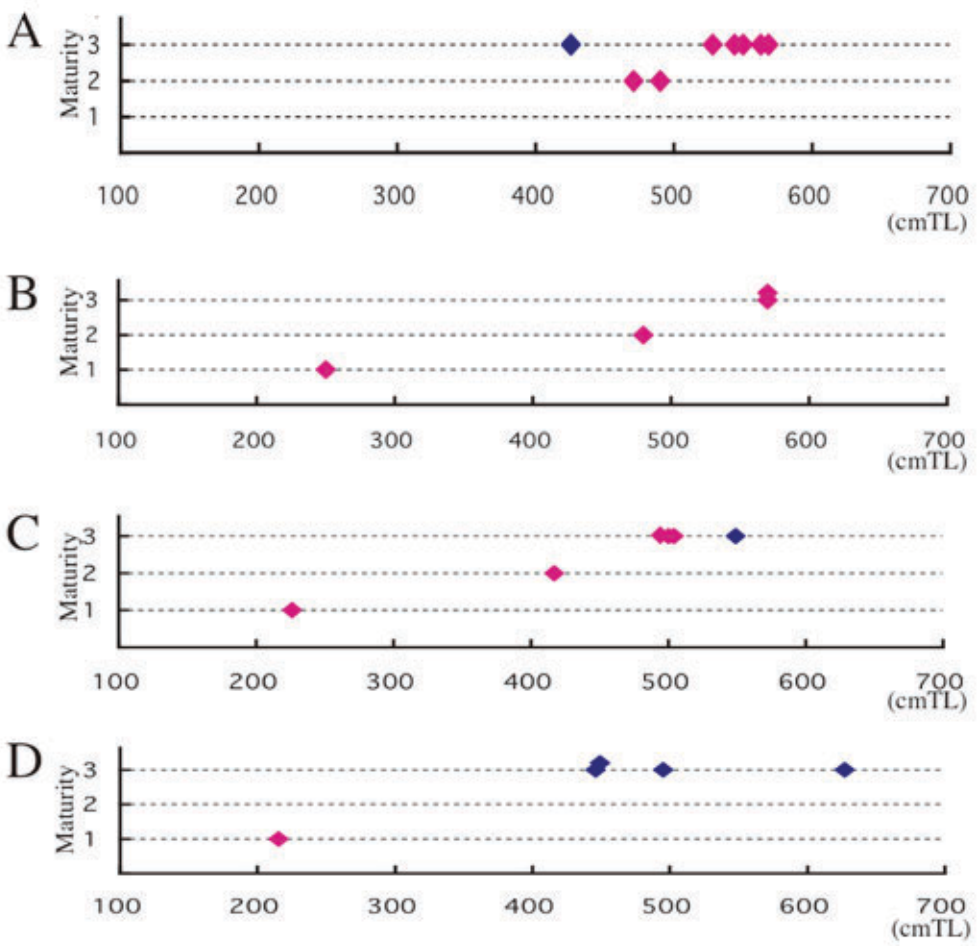

Fig. 10. Regional occurrences by maturity stages. A, Japan; B, Taiwan/China; C, The Philippines/Indonesia; D, the Eastern Pacific/Hawaii. Blue, male; red, female.

Seasonal distribution by sex and maturity

Figure 11 shows monthly latitudinal distribution by maturity level for the world. Among Pacific megamouth sharks, the females of all maturity stages appeared from November through May. Females appeared between 8°N and 34°N in January, 8°N and 28°N in March, 33°N and 35°N in April, 24°N and 35°N in May, 35°N in June, 24°N and 36°N in July, and 10°N and 34°N in November. Pacific mature males were found in January (34°N), February (8°N), March (2°N), August (34°N), October (33°N) and November (21°N and 33°N).

Atlantic immature males appeared in May (15°N) and September (27°S), and Indian immature males appeared in January (2°S) and March (5°N). One adolescent female was found in April (33°S) and one mature male in August (32°S) in the Indian Ocean.

For Pacific megamouth sharks, it seems that the adolescent and mature individuals of both sexes stay in the waters of the lower to higher latitudes from November through March. Because of their almost complete absence in the lower latitudes from April through October, it may be presumed they leave the lower latitudes during this period. The immature individuals, however, may be found year-round in the lower latitudes within the distributional range of the species.

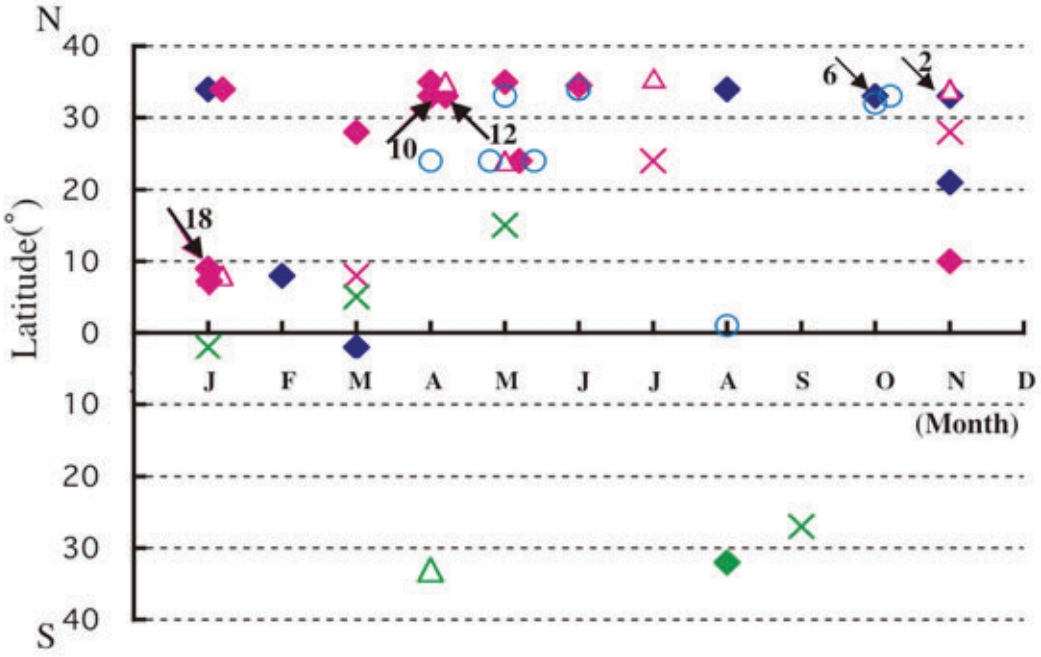

Fig. 11. World latitudinal occurrences by month. Arrow with record number indicates individual with mating scars or active claspers (see text). Solid blue diamond, mature male (Pacific); solid red diamond, mature female (Pacific); open red triangle, adolescent female (Pacific); red cross, immature female (Pacific); solid green diamond, mature male (Indian); open green triangle, adolescent female (Indian); green cross, immature male (Indian/Atlantic); open blue circle, unknown length and/or unknown sex (Pacific).

Reproduction

Spermatophores were oozing from the claspers of a 449 cm TL male (#2, arrow 2 in Fig. 11) captured in November, 1984 in California (Lavenberg and Seigel, 1985, and a 495 cm TL male (#6, arrow 6 in Fig. 11) captured and released in October, 1990 in California had evidence of recent use of the claspers (Lavenberg, 1991). Fresh mating scars were found in a 544 cm TL female (#10, arrow 10 in Fig. 11) and healing mating scars were reported in a 550 cm TL female (#12, arrow 12 in Fig. 11), both captured in April in Japan (Yano et al., 1998, 1999). In addition, a 497 cm TL female (#18, arrow 18 in Fig. 11), from the Philippines in January was reported to have mating scars (Compagno et al., 2005). These facts may indicate that the megamouth shark mates all year round.

It may be also inferred that they give birth to young in the waters of lower latitudes, because the immature individuals are reported only in the lower latitudes between 28°N and 28°S, and the immature individuals may stay in the waters of the lower latitudes for a while.

Depth distribution

The few depth data available at present show sharks being caught in depths between 23 and 200 meters. Daily movements of a megamouth shark (#6) were recorded by Nelson et al. (1997), and the shark showed a very clear vertical movement. The shark swam at depths a little shallower than 200 meters in depths during the daytime, moved to the surface at dusk, stayed around 20 meters during nighttime, and sank again to the original deeper layers at dawn. The present available depths of capture are almost within

the ranges shown by Nelson et al. (1997), but because no accurate time of capture was reported in most records, the vertical movements cannot be conclusively speculated upon here. The only exception is the Indonesian individual (#13), which was sighted and photographed during an attack by a sperm whale. The photograph was taken at the surface at 10:00 am, the time megamouth sharks normally stay deep, near 200 meters below the surface. This case appears to be abnormal.

Length weight relationship

The length-weight relations of the megamouth shark are given in Fig. 12. As the body lengths and the body weights, especially of larger individuals, are often inaccurate and were reported as estimates, only lengths and weights that seem to be reliable are included in the figure. The specimens around 2m in total length range from 176.7cm TL (13.8 kg, #23) to 235 cm TL (120 kg, #16) for males, and 214.9 cm TL (27kg, #38) and 226 cm TL (70kg, #35) for females. Body weights of those around the 5m TL range from 700 to 1,000 kg. A Taiwanese specimen (ca 250 cm TL, 490 kg, # 20 in Fig. 11), and a South African specimen (ca 460 cm TL, 260 kg, #17 in Fig. 11) are somewhat different from the others.

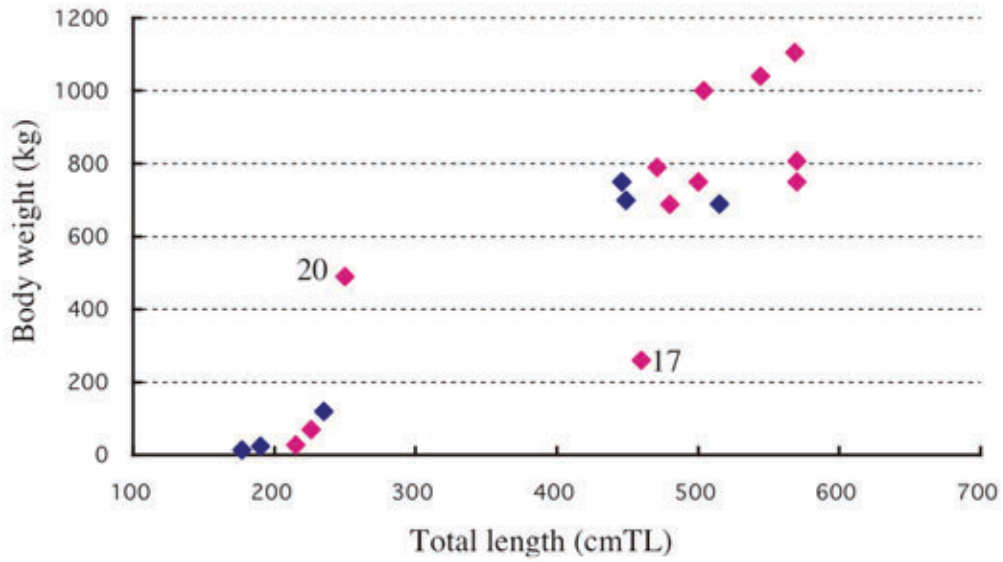

Fig. 12. Length/weight relationship. Number indicates record number. Blue, male; red, female.

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