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Geographic variations in reproductive parameters of the starspotted dogfish, *Mustelus manazo*, from five localities in Japan and in Taiwan

Atsuko Yamaguchi[a], Toru Taniuchi[b] & Makoto Shimizu[b]
[a]*Department of Food and Nutrition, Faculty of Home Economics, Kyoto Women's University, 35, Kitahiyoshi-cho, Imakumano, Higashiyama-ku, Kyoto 605-8501, Japan (e-mail: IZP 01552@niftyserve.or.jp)*
[b]*Department of Fisheries, Faculty of Agriculture, University of Tokyo, Yayoi, Bukyo, Tokyo113-8657, Japan (e-mail: atoru@hongo.u-tokyo.ac.jp)*

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Synopsis

Geographic variations in reproductive parameters of *Mustelus manazo* from five localities, four in Japan (Aomori, Tokyo Bay, Maizuru, and Shimonoseki) and one in Taiwan, were investigated from November 1994 to June 1996. Differences in age and length at sexual maturity from Aomori to Taiwan were approximately 3 years and 300 mm in TL, respectively, for both sexes. The sharks appeared to mature at a later age and to a larger size in the most northern population, Aomori, and to be faster and smaller in the southern population, Taiwan. Mating, ovulation and fertilization periods were generally during May and August in the four localities of Tokyo Bay, Maizuru, Shimonoseki, and Taiwan. In Aomori, males showed no clear monthly variation in gonad index, and females in Aomori had a protracted reproductive period. Females became pregnant every year in all localities, except Aomori. The Aomori population apparently has a different reproductive cycle. The Tokyo Bay population is distinctive regarding growth and sex ratios of embryos. In all localities, the number of embryos per litter increased relative to total length of mother. There was no geographic variation in reproductive parameters between Maizuru and Shimonoseki. The coast between these last two sampling areas is a continuous steep slope with similar environmental conditions, and mixing of the two populations may occur.

Introduction

There are two species of *Mustelus*, *M. manazo* and *M. griseus*, around Japan. The starspotted dogfish, *M. manazo*, occurs widely from Hokkaido in northern Japan to Taiwan, where it is one of the most abundant shark species. *M. manazo* is caught commercially as a bycatch around most of Japan, mainly by bottom trawl, long lines, and set net. Recently, according to fishermen, the catch size of *M. manazo* has decreased in many localities. In Taiwan, this species is fished in a limited northern area. However, there are no exact catch data on this species in Japan or Taiwan.

Species of the genus *Mustelus* are viviparous and the embryos are of two types, non-placental or placental. *M. manazo* from Shimonoseki, described by Teshima (1981), is a non-placental type. Females develop uterine compartments during gestation and throughout life, and only the right ovary is functional (Teshima 1981). Some information is available on the reproductive biology of *M. manazo* from the East China Sea (Tanaka & Mizue 1979), the Bungo Channel (Kudo 1958), off Choshi (Taniuchi et al. 1983), and in Tokyo Bay (Yamaguchi et al. 1997). In recent years, geographical variations in maximum length and age, and growth rate of *M. manazo* from five localities among Japan and Taiwan were found by Yamaguchi et al. (1998). The species tended to grow larger and have a longer life span in the eastern and northern areas, though the water temperature may not be a major factor for differences in growth. Rather, such variations among localities indicate the existence of many separate stocks of *M. manazo* around Japan and Taiwan. However, there is little published information on reproductive variations in *M. manazo*. Our objectives in this study were to examine the reproductive biology of *M. manazo* in each locality and to elucidate geographic variations in reproductive parameters of *M. manazo* among four localities, Aomori, Tokyo Bay, Maizuru, and Shimonoseki in Japan, and one in Taiwan.

Materials and methods

Specimens were collected from five localities (Figure 1): Aomori (n = 317), Maizuru (n = 144), Shimonoseki (n = 147), Tokyo Bay (n = 565, Yamaguchi et al. 1996), and Taiwan (n = 201, Yamaguchi et al. 1998), during May 1994 and June 1996 (Table 1, Figure 2). Most of the specimens were caught by bottom trawlers. Information on fishing grounds, catch depth, and fishing gear were given in Yamaguchi et al. (1998). In Aomori, specimens were collected at the Hachinohe fish market, though only a few pregnant females were found there. Therefore, we also collected *M. manazo* at the Tairadate fish market in Aomori to procure more pregnant females. Specimens marketed at Hachinohe were caught in depths greater than 200 m in the Tsugaru Strait, and those at Tairadate were caught in depths less than 50 m in Mutsu Bay (Figure 1). Pregnant females were frequently caught at other localities.

Maturity stages were defined following those set out by Yamaguchi et al. (1997). Males – immature, claspers not calcified, testis not developed; premature, claspers more or less calcified, testis developed but no sperm in the seminal vesicle; mature, claspers calcified, and sperm in the seminal vesicle. Females – immature, uteri threadlike and no obviously developed ova in the ovary; premature, uteri thickening but not obviously vascularized, developed ova more or less distinct; mature, embryos present or uteri enlarged and flaccid; uncertain (mature or premature), no embryo, uteri flaccid and developed ova more or less distinct.

Age at sexual maturity for both sexes was estimated based upon a previous aging study (Yamaguchi et al. 1998). The gonad index (GI) for males was calculated with the following formula; GI = testis weight (g)/ (TL (mm))^3 $\times$ 10^9 (Yamaguchi et al. 1997). The mating season was estimated from the GI following Teshima

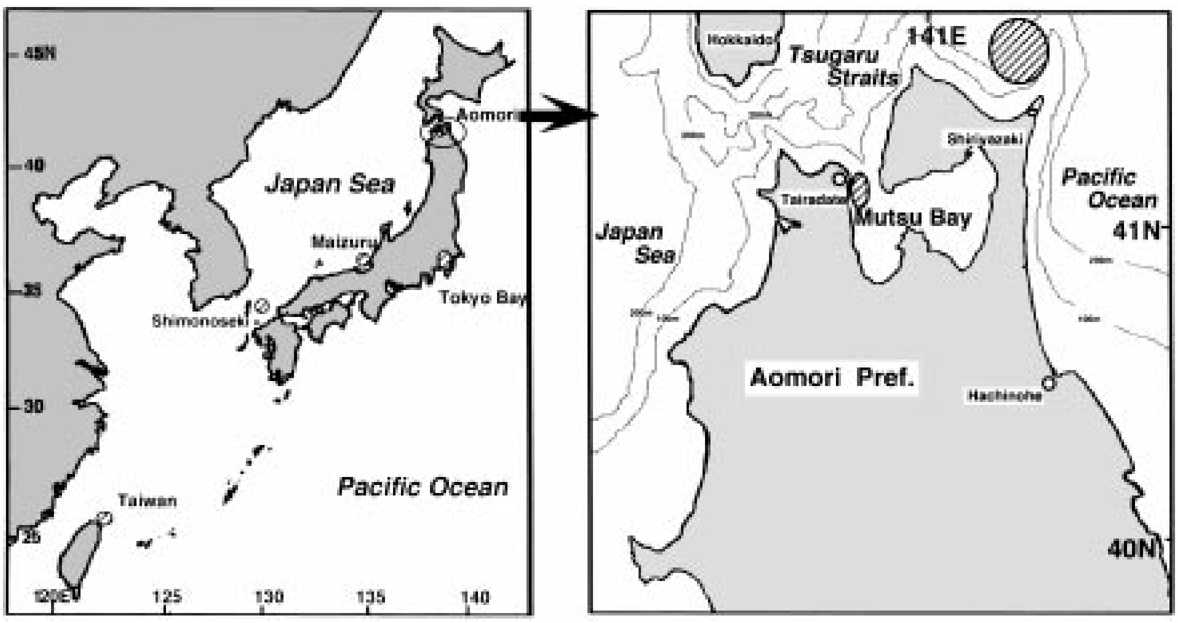

Figure 1. Sampling locations in Japan and Taiwan. Circles with oblique bars denotes collecting areas for *Mustelus manazo.*

Table 1. The number of specimens of *Mustelus manazo* by month in five localities.

Locality		Month													Total
		J	F	M	A	M	J	J	A	S	O	N	D	Total	
Aomori	Male	22		1	2	28	13		7			13	20	106	
	Female	30	1	3	6	48	41	10	2	12	5	18	35	211	317
Tokyo Bay	Male	14	9	2	13	30	35	5	27	50	32	23	6	246	
	Female	23	15	13	30	39	25	24	42	43	26	19	20	319	565
Maizuru	Male	1	28	36		20	3				8		1	97	
	Female	1	12	13	5	5	6		4				1	47	144
Shimonoseki	Male	5	6	8	2	19				18		14	3	75	
	Female	7	11	12	14	5				11		3	9	72	147
Taiwan	Male	7			3		16	9	15		5	17	6	78	
	Female	12			18		15	4	13	7	7	18	29	123	201

(1981). The maximum ova diameters were measured using the largest ova in the ovary from each specimen. Sex ratios of embryos ($0 \leqq x \leqq 1$) were calculated as male/(male + female). Clasper length was measured from the cloaca to the tip of the clasper.

Results

Age at sexual maturity

Males attained sexual maturity earlier than females at all localities (Figure 3). In Taiwan, 23.1% of males were mature at age 1 and 44.1% at age 2. In Taiwan, Shimonoseki, and Maizuru 90–95% were mature at age 3, but in Tokyo Bay only 26.1% were mature at this age, and none were in Aomori. In Tokyo Bay, all specimens were mature at age 5, while in Aomori only 63.2% of the specimens were mature at this age. In Aomori, all specimens were fully mature at age 7. Thus, first sexual maturity in Taiwan was age 1, in Shimonoseki and Maizuru age 2, in Tokyo Bay age 3, and in Aomori age 4. Age at 100% sexual maturity was for Taiwan and Shimonoseki 4, for Maizuru and Tokyo Bay 5, and for Aomori 7.

As was the case with males, females in Taiwan matured the earliest, with 7.1% already mature at age 2. In Taiwan, Shimonoseki, and Maizuru, all specimens at age 5 were mature. However, in Tokyo Bay, 67% were mature at age 5, and 100% at age 6. It was assumed sexual maturity occurred latest in Aomori, because in Tokyo Bay immature specimens at age 5 amounted to 8%, while in Aomori 10% at age 6 were immature. Thus, first sexual maturity for females was age 2 for Taiwan, age 3 for Shimonoseki, Maizuru and Tokyo Bay, and age 5 for Aomori, and age at 100% sexual maturity was 5 for Taiwan, Shimonoseki and Maizuru, 6 for Tokyo Bay, and later than 6 in Aomori. The largest geographical difference with respect to age at sexual maturity was approximately 3 years for both sexes.

Length at sexual maturity

Length at sexual maturity was smallest in Taiwan for both sexes (Figure 4). Some specimens of <500 mm had already reached the premature stage. Most males in Taiwan, in a range of 601–700 mm were mature. However, in Tokyo Bay, only 3% of the males in this length group were mature, while in Aomori in this group only premature specimens (6%) were found. In Taiwan, Shimonoseki, and Maizuru, all male specimens 701–800 mm long were mature, in Tokyo Bay 87% were mature, but in Aomori only 4% were mature.

Females in Taiwan in the 601–700 mm length group were mature in half of the specimens 7–8% in Shimonoseki and Maizuru, while in Tokyo Bay, only first premature specimens occurred (11%) and in Aomori, all specimens in this length group were immature. In Taiwan and Shimonoseki, all specimens in the 701–800 mm length groups were mature, in Maizuru and Tokyo Bay 80% and 41%, respectively in this length group were mature, and no specimens from Aomori were mature, though some uncertain specimens (non-pregnant) occurred (18%). In Aomori, some specimens in the 801–900 mm and 901–1000 mm length groups were immature (24% and 5%, respectively). No immature specimens were found in the >801 mm length groups in the other four localities. Length at 100% sexual maturity was not determined

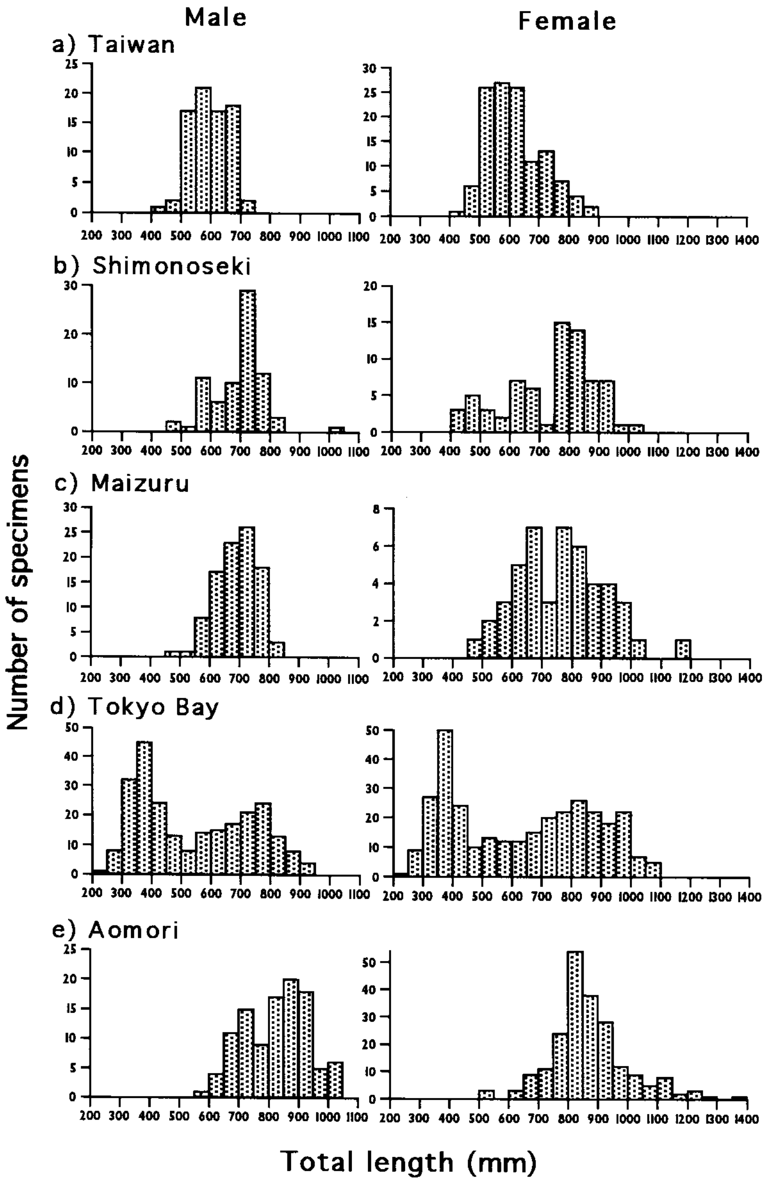

Figure 2. Length frequency histograms of *Mustelus manazo* collected from five localities.

for specimens from Aomori. Sexual maturity in order of length was attained first in Taiwan, Shimonoseki and Maizuru, Tokyo Bay and last in Aomori. The largest difference between localities was approximately 300 mm of total length for both sexes.

Clasper length

Clasper length increased with total length at all localities. In the immature phase, claspers lengthened slowly with respect to total length. In the premature phase, the elongation was rapid, and in the mature phase, calcification of the claspers was completed. Thereafter, claspers showed little elongation.

The ratios of clasper length to total length for the five localities are given in Figure 5. Differences were found among values of total length from these localities when the elongation of the claspers first occurred, however, no differences were found in the ratio of clasper length to total length at any locality. That is, in all

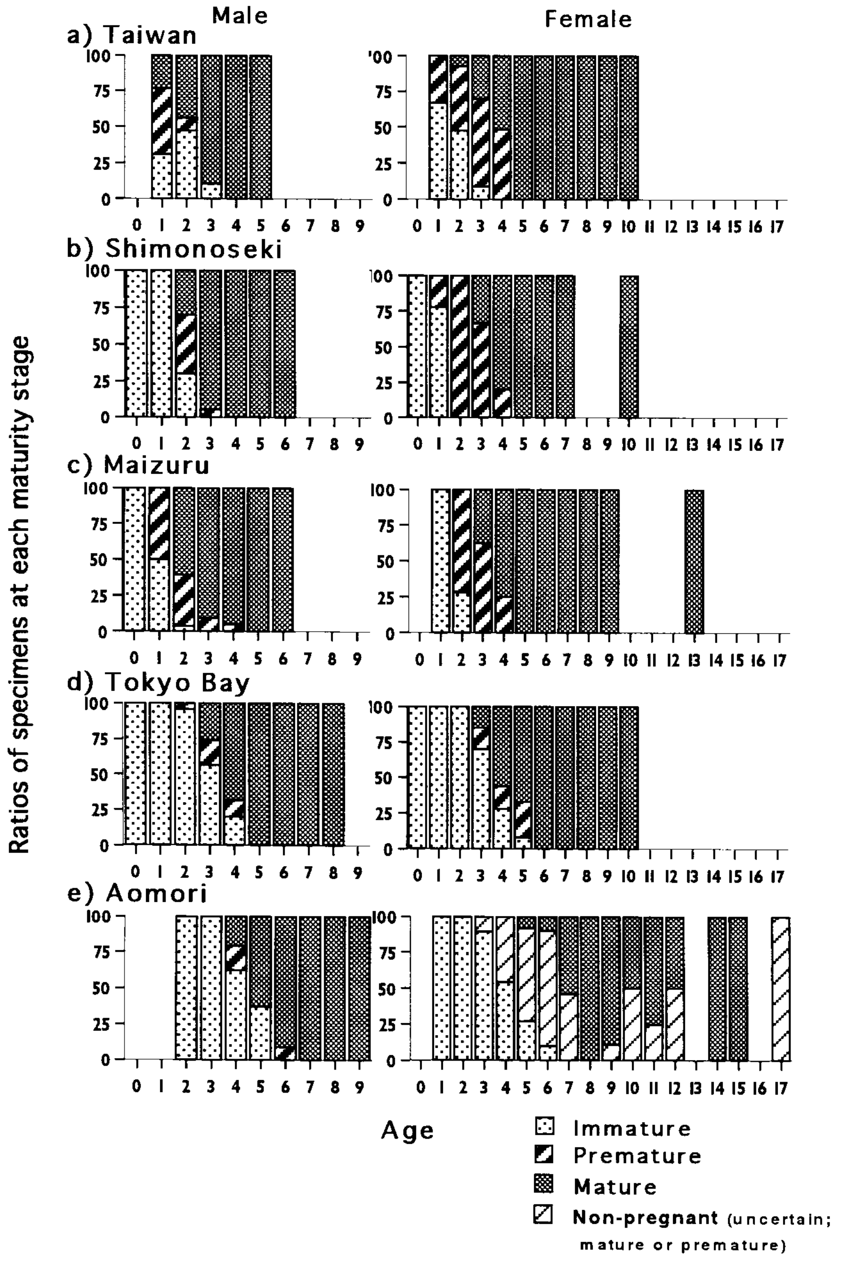

Figure 3. Age at sexual maturity of *Mustelus manazo* in five localities.

localities, the ratio of clasper length to total length in the immature phase was 6–8%; claspers started rapid elongation when the ratio attained approximately 8%; and clasper length ratio when specimens had attained the mature phase were 15–16%. At that point, clasper length to total length ratio declined because claspers showed little further elongation.

Reproductive cycles for males

Seminal vesicles of *M. manazo* are full of spermatozoa as the GI value reaches its minimum, and mating occurs soon afterward (Teshima 1981). Mating periods estimated from monthly variations in GI were generally during May and August for Taiwan, Shimonoseki,

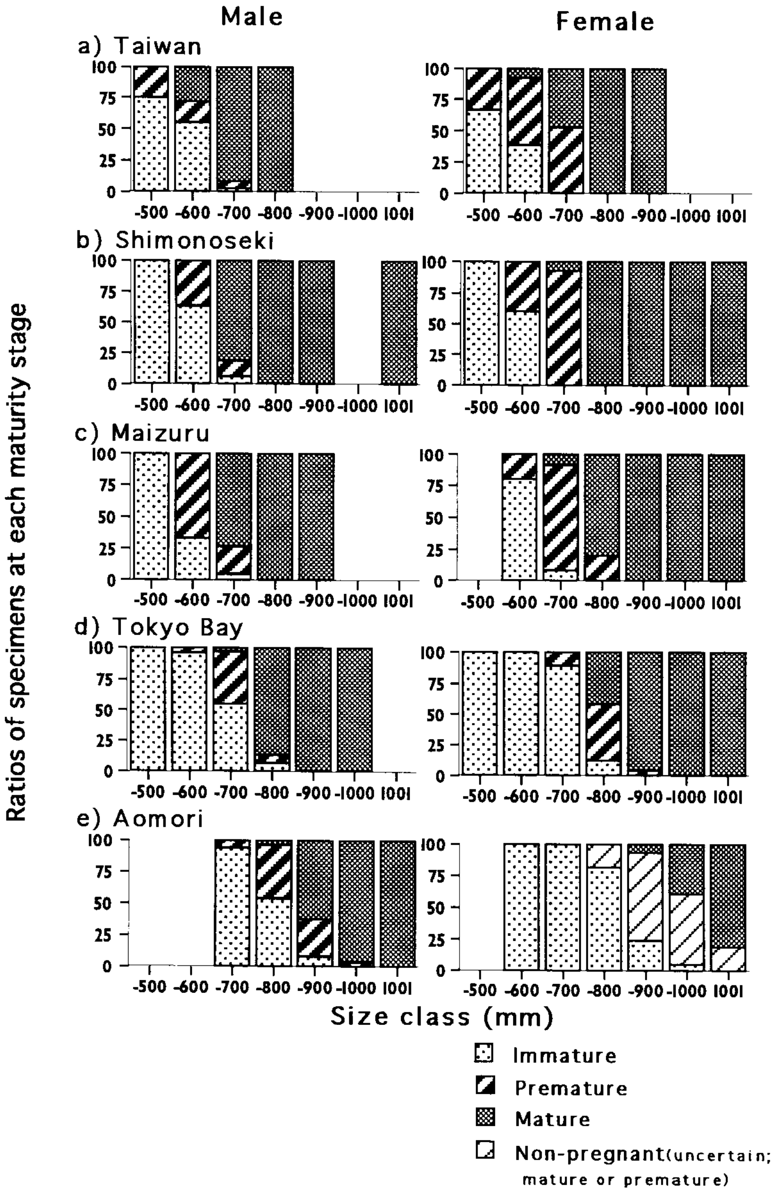

Figure 4. Length at sexual maturity of *Mustelus manazo* in five localities.

Maizuru, and Tokyo Bay (Figure 6). However, in Aomori, no clear cycle in GI was shown.

Reproductive cycles for females

The maximum ova diameter for mature females increased gradually from September to March, and showed rapid development in April (Figure 7). Ovulation occurred when ova diameter was the largest. Estimated periods of ovulation and fertilization occurred in August in Taiwan, and during May and June in Shimonoseki, Maizuru, and Tokyo Bay. In Aomori, where pregnant females were collected only during April and September, the maximum ova diameter for mature and uncertain (mature or premature, non-pregnant) females was largest in June, and fertilized

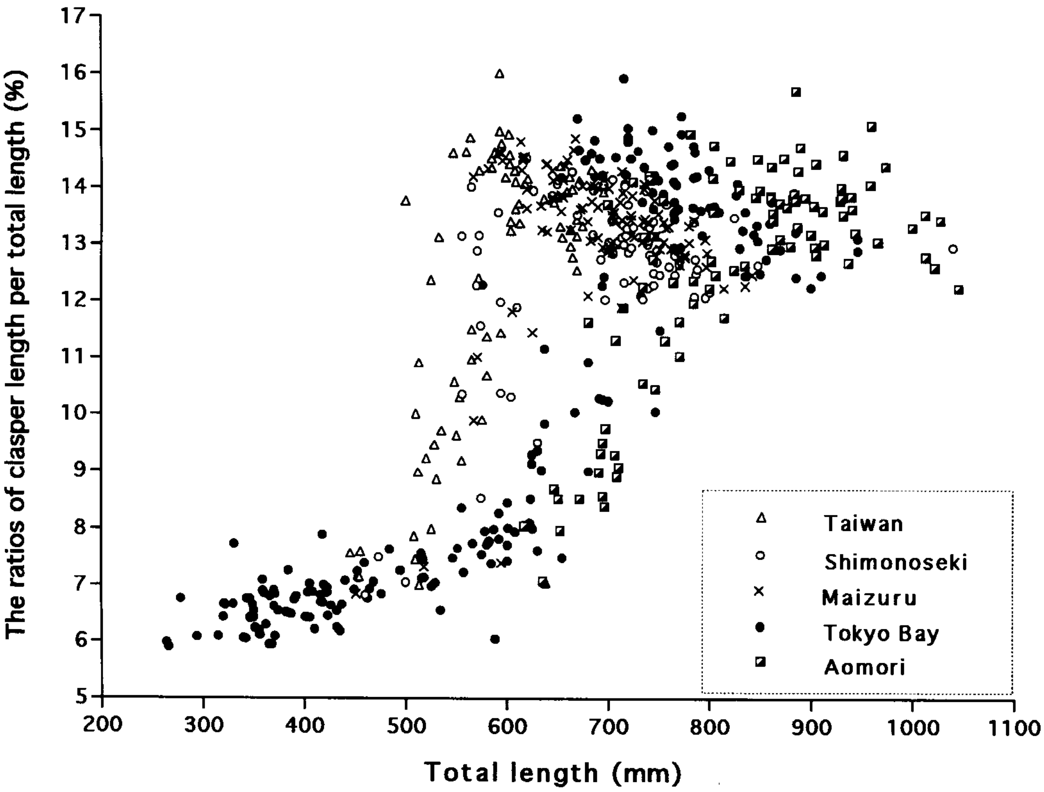

Figure 5. Relationships between total length and the ratio of clasper length to total length of *Mustelus manazo* in five localities.

eggs were found in April and August. Thus, ovulation and fertilization periods were lengthened, and ovulation during April and August.

The ova in the ovary of late term pregnant females showed differences between specimens from Aomori and those from all other localities (Figure 8). All pregnant specimens in Taiwan, Shimonoseki, Maizuru, and Tokyo Bay had the largest ova (diameter 15–20 mm) in the ovary at a late stage of pregnancy. This suggests that the female becomes pregnant soon after parturition, and that parturition occurs annually after sexual maturity. In Aomori, however, late-term pregnant females had only immature ova (less than 5 mm in diameter) in the ovary. This indicates that females in Aomori do not breed every year, and that the reproductive cycle for females is different from that of females at other localities, which parallels the case for males.

The parturition occurred during May and June, and the gestation period was estimated at 12 months in Tokyo Bay (Yamaguchi et al. 1997). Mature females in Maizuru had the largest embryos or fertilized eggs in May; it was estimated, therefore, that the parturition period was in May and the gestation period was approximately 12 months. In Shimonoseki, fertilized eggs were not found because no specimens were taken during June and August, but the largest embryos occurred in May and the smallest embryos occurred in September (Figure 9). Thus, the gestation period was estimated at 10–12 months in Shimonoseki. Mature females in Taiwan had the largest embryos in April and no embryos in May, and fertilized eggs were found in August; the parturition period was, therefore, April or May and the gestation period was estimated at approximately 10 months.

Growth and sex ratios of embryos

Recently ovulated eggs in the uteri weighed 5–10 g, and were enclosed in a brownish transparent egg case. Embryos were separated from each other in compartments created by the ridges on the uterine wall. Five or 6 months after fertilization, the external yolksac is consumed. Just before parturition, embryos weighed 70–100 g, more than 20 times the weight of fertilized eggs.

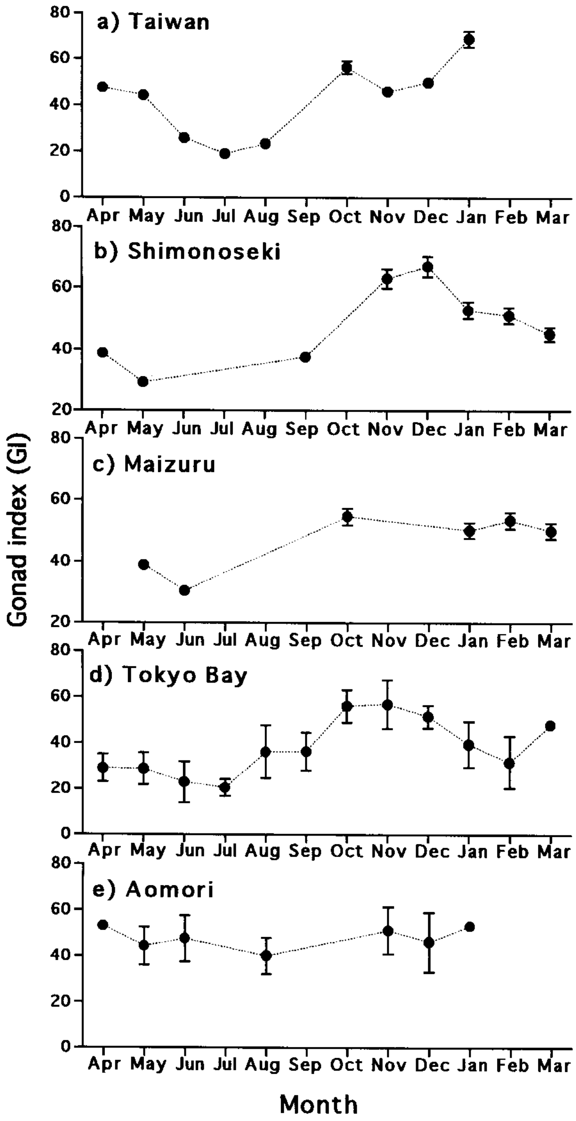

Figure 6. Monthly average gonad index for mature males in five localities.

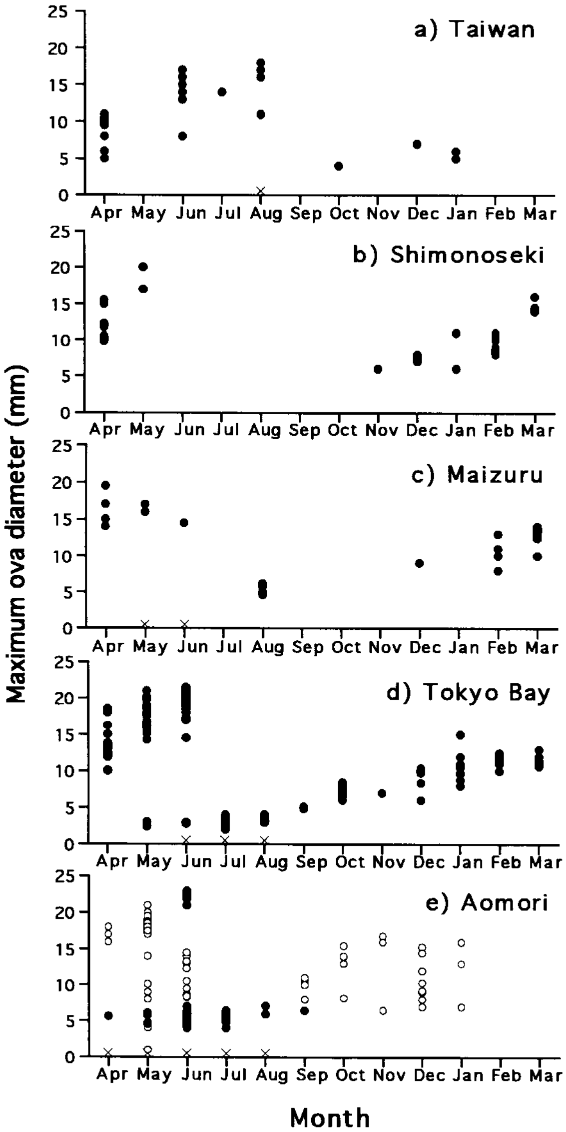

Figure 7. Monthly maximum ova diameter for mature (pregnant) females in five localities. The opened circles denote uncertain (mature or premature) specimens from Aomori. The crosses show the months with fertilized eggs in uteri.

The monthly mean length of embryos per litter for each locality is shown in Figure 9. The smallest embryos occurred during August and September in all localities except Aomori, and the mean length in Tokyo Bay was the largest by February. Embryos in Tokyo Bay grew quickly until February but showed no clear growth from February to May, while in Maizuru and Shimonoseki the growth of embryos was constant until full-term. Thus, by May, the mean lengths of embryos in Maizuru and Shimonoseki were larger than that of those in Tokyo Bay, even though the latter had been larger in September. Embryonic growth in Maizuru and Shimonoseki were similar throughout gestation. Taiwan had the smallest embryos in December and January. However, by April, the embryos were smaller in size than those of other localities. In Aomori, the mean length of embryos per litter in December was slightly smaller than that in Tokyo Bay. However in June the mean length of embryos per litter in Aomori

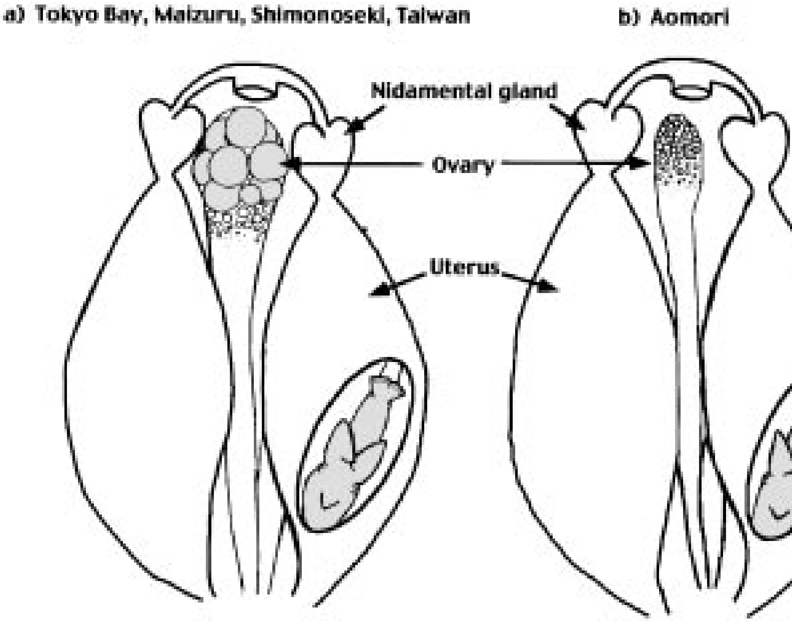

Figure 8. Conditions of ovarian eggs when specimens have full-term embryos in their uteri: a – Taiwan, Shimonoseki, Maizuru and Tokyo Bay; maximum ova diameter was approximately 15–20 mm, the ovulation soon to occur, b – Aomori; ovarian eggs were less than 5 mm.

was more than 300 mm. It appears that the growth of embryos assumes one of two patterns in *M. manazo.* In Tokyo Bay, growth is faster in the early interval of development. In Aomori, Maizuru, Shimonoseki, and Taiwan, growth is constant until full-term. Lengths at birth were estimated at 200–300 mm TL in Tokyo Bay (Yamaguchi et al. 1997), 250 mm TL in Taiwan, 300 mm TL in Maizuru and Shimonoseki, and 300–350 mm TL in Aomori.

The sex ratio of embryos in Tokyo Bay showed a significant predominance of males (0.55, $n = 374$, Yamaguchi et al. 1997); however, in the other localities, the χ^2 test showed no significant departure from the expected 1 : 1 ratio (Aomori 0.51, $n = 233$, $\chi^2 = 0.039$, $p > 0.1$; Maizuru 0.52, $n = 149$, $\chi^2 = 0.17$, $p > 0.1$; Shimonoseki 0.48, $n = 272$, $\chi^2 = 0.53$, $p > 0.1$; Taiwan 0.61, $n = 64$, $\chi^2 = 3.06$; $p > 0.1$). Embryos in Tokyo Bay may have distinctive growth and sex ratios.

Litter size

The number of embryos per litter ranged from 2 to 19 ($n = 18$) in Aomori, 1 to 16 ($n = 27$) in Maizuru, 1 to 14 ($n = 42$) in Shimonoseki, 2 to 10 ($n = 30$) in Taiwan, and 2 to 13 ($n = 69$) in Tokyo Bay (Yamaguchi et al. 1997). The number of embryos increased relative to the total length of females in all localities (Figure 10). Almost all of the females had an equal number of embryos in both uteri.

Because positive significant correlations between litter size (LS) and total length of the female (TL) were shown in all localities, relationships between localities were compared by analysis of covariance. Taiwanese *M. manazo* had the most embryos per litter relative to size of female (ANCOVA, all $p < 0.01$). Tokyo Bay had the smallest litter size relative to size of female, and the differences between Shimonoseki or Maizuru were significant (ANCOVA, both $p < 0.01$), though no significant difference was found between Tokyo Bay and Aomori (ANCOVA, $p > 0.1$). There was no significant difference between Maizuru and Shimonoseki (ANCOVA, $p > 0.1$), both being lower than Taiwan when TL was at nearly equal size. Again, the differences between Shimonoseki and Aomori were not significant (ANCOVA, $p > 0.1$).

Discussion

Our data show that maturity of *M. manazo* tended to be slow in populations living in lower water temperature. Maturity was the slowest in the most northern population, Aomori, and the fastest in the most southern

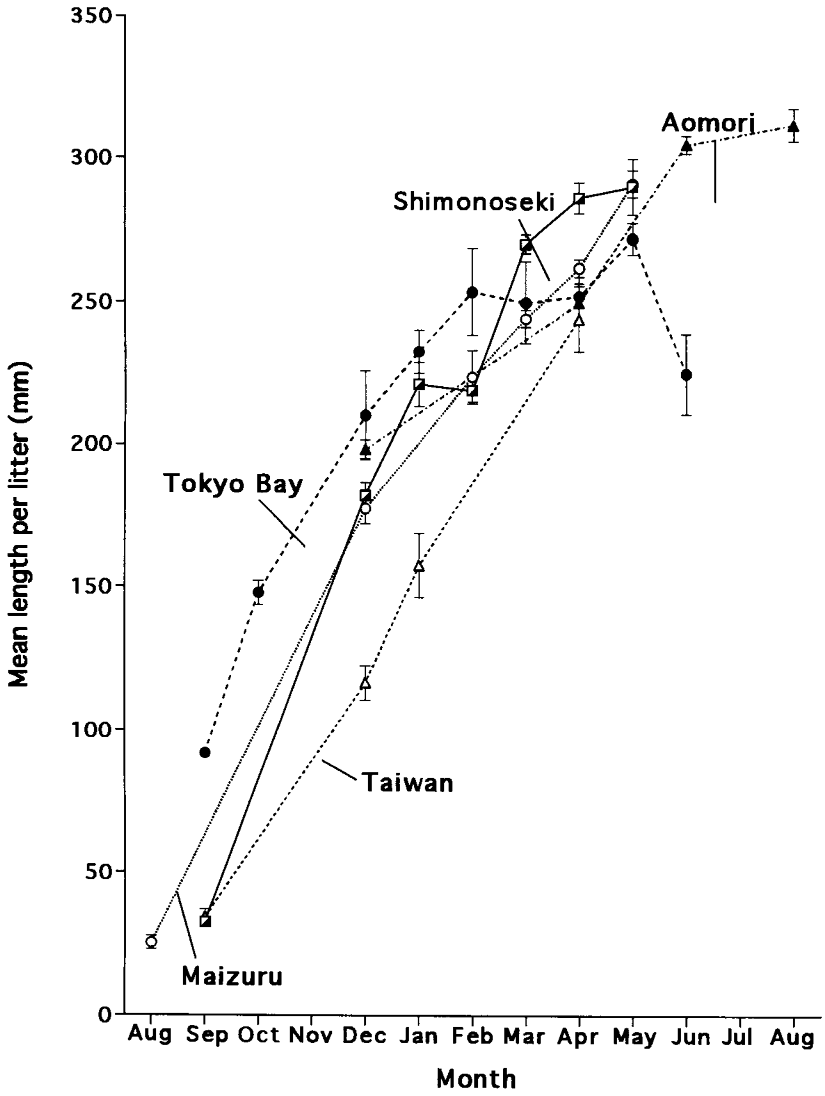

Figure 9. Monthly mean length per litter of *Mustelus manazo* in five localities. The symbols and bars denote mean and 95% confidence intervals, respectively.

population, Taiwan. The water temperature in Tokyo Bay is higher than that at Shimonoseki and Maizuru in all seasons, however, maturity for both sexes in Tokyo Bay was slower than that in Shimonoseki and Maizuru. Comparisons of water temperature for the five study areas were reported by Yamaguchi et al. (1998). Aomori is the lowest at every season (3–10°C at 200 m depth); Shimonoseki and Maizuru is similar (11–17°C at 100 m depth); the locality showing the greatest variation is Tokyo Bay (12–22°C at 40 m depth); and Taiwan is constant throughout the year (17–18°C at 100 m depth). Parsons (1993) reported a converse difference between the rate of maturity for *Sphyrna tiburo* in the warm temperate Tampa Bay and the tropical Florida Bay populations. Maturity in Florida Bay was slightly slower than in Tampa Bay because of warmer temperature and a smaller quantity of available food.

In our study, the differences in number of embryos per litter showed a trend from north to south in which

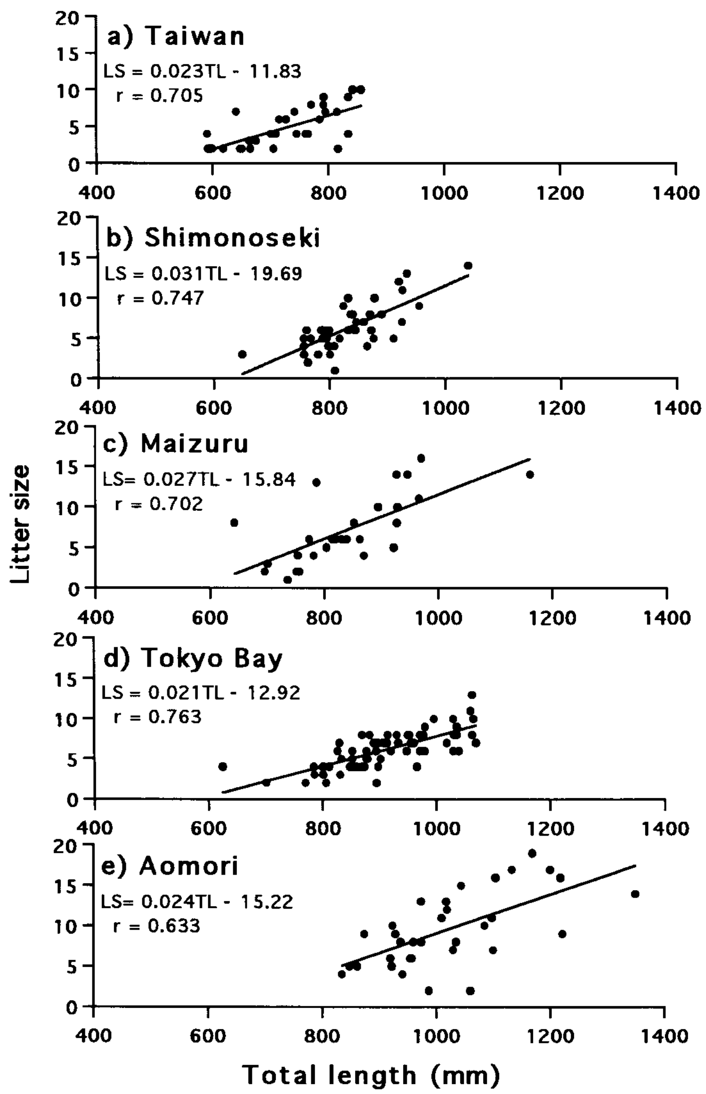

Figure 10. Relationships between total length and litter size of *Mustelus manazo* in five localities.

the northern population had the smallest litter size when the length of the mother was the same. However, in the northern population, a higher number of total offspring may have resulted from slower growth, larger size at maturity, and longer life span. In fact, we obtained data that the maximum litter size in Aomori was 19 embryos compared with only 10 in Taiwan. No explanation can be proposed for the geographic variations in litter size, though it may be related with aspects of latitude or water temperature. Different results were reported for *Squalus mitsukurii* by Taniuchi et al. (1993), who observed that litter size increased with latitude. The relationship between litter size and length of female was the same among localities, in other words, *S. mitsukurii* exhibited a uniform reproductive style (Taniuchi et al. 1993). Chen et al. (1981) also noted that the features of *S. japonicus* between Nagasaki and Choshi corresponded to those of *S. mitsukurii.*

The mating season may not be fixed for *M. manazo* in Aomori. This phenomenon is well known for deep-sea or tropical fish that live in stable environmental conditions. For example, recently Chen et al. (1996) reported on the fluctuating mating season of *Galeus sauteri* in Taiwan. However, it cannot be explained solely by seasonal changes in water temperature, because Taiwan, not Aomori, demonstrated little seasonal shift in water temperature. Mating behavior may be related to specific life history parameters in Aomori.

Only a few pregnant females were found at Hachinohe fish market in Aomori, which had been caught at Tsugaru Strait, though many pregnant females and newborn specimens were collected at Mutsu Bay (Tairadate fish market) in Aomori. No males were caught in Mutsu Bay. *M. manazo* is rarely caught on the coast from Shiriyazaki to Hachinohe by small bottom trawlers. At other localities, specimens at all reproductive stages for both sexes were frequently caught. Our findings suggest that migration of pregnant females from the deep water of Tsugaru Strait to the shallow coastal water of Mutsu Bay was due to parturition and feeding. Many fish-feeding sharks such as *Squalus acanthius* (Mikawa 1971) or large bony fishes are abundant in Tsugaru Strait, while there are few natural predators for *M. manazo* in Mutsu Bay. Similar sexual segregation and migration have been reported for *M. lenticulatus* from New Zealand (Francis 1980, King 1984, Francis 1988, Massey & Francis 1989). The results of a tagging study for *M. lenticulatus* suggest that mature females move over greater distances than do males (Francis 1988). More investigation on the reproductive migration of *M. manazo* in Aomori is necessary.

Embryos of *M. manazo* in Tokyo Bay showed different growth patterns from those at other localities. In Tokyo Bay, the water is not as deep as that of the other localities investigated, and the water temperature during August and November the highest. These conditions may account for the initial fast growth of embryos in Tokyo Bay. The predominance of male embryos in Tokyo Bay established a sex ratio different from that at other localities. However, we have found yearly variations in Tokyo Bay. The sex ratio in the 1994 and 1996 year classes did not show significant departures from 1 : 1, though the ratio in 1995 year class showed a significant predominance of male embryos (Yamaguchi et al. 1997). The cause of a predominance of males in Tokyo Bay is as yet unknown.

The reproductive mode of *M. manazo* is that of an obligate lecithotrophic live bearer (Balon 1990). Each embryo is wrapped in a shell, and completes its development in a uterine compartment, that develops during gestation. Uterine compartments in mature females in Shimonoseki were found from early gestation to full-term. However, Aomori females were exceptional in that they did not have uterine compartments throughout the term of gestation. Teshima (1981) noted that uterine compartments of *M. manazo* in Shimonoseki were completed when the length of embryos attained 100 mm TL, then disappeared just before parturition in preparation for the next pregnancy. In Tokyo Bay, we found uterine compartments at mid-term gestation, though not once the embryos were full-term. We could not tell the precise time the compartments disappeared. MacDonald (1988) pointed out, on the basis of Heemstra (1973), that intraspecific variability of many characteristics is used to identify *Mustelus* species; he described the taxonomic confusion that had arisen from the publication of apparently conflicting descriptions, particularly of uterine and embryo morphology. Whitley (1945), for example, used the presence or absence of uterine compartments as a criterion in the classification of the genus *Mustelus*. Our study shows variation of this character within *M. manazo.*

In the present study, we found large geographic variations in the reproductive parameters of *M. manazo*, particular between Aomori and Taiwan populations. Similar differences in growth of *M. manazo* were previously obtained by Yamaguchi et al. (1998). Observed maximum ages and length were the youngest and smallest in Taiwan (male, age 5, 707 mm; female, age 9, 865 mm), and the oldest and largest in Aomori (male, age 9, 1045 mm; female, age 17, 1350 mm). The Taiwan population, compared to the other populations of this species, may be characterized as having an earlier and smaller size at maturity, fewer embryos per female, faster growth, smaller size, and shorter life spans. Taiwan may have a fluctuating environment, including aspects of food availability, that is not advantageous for *M. manazo*. The Aomori population has a larger size and later maturity, more embryos per female, slower growth, larger size, and a longer life span. Thus Aomori is probably a better locality for *M. manazo*, due to an abundant food supply and more suitable lower water temperatures. No geographic variations in reproductive parameters occur between Maizuru and Shimonoseki, except a difference in growth (Yamaguchi et al. 1998). The distance between these two sampling areas is about 600 km, however, the coast between these two areas is a continuous steep slope and they have similar environmental conditions. Uneven mixing of these two populations may occur.

Acknowledgements

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