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Geographical Variations in Freshwater Populations of the Three-Spined Stickleback, *Gasterosteus aculeatus*, in Japan

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Abstract This paper describes an investigation of morphological variation among six freshwater populations (dominantly low-plated morph) of the three-spined stickleback, *Gasterosteus aculeatus*, in Japan. Such populations are mainly distributed in restricted water areas within a band from Ise to Wakasa Bays, the most constricted part of Honshu Island. According to some differences in morphological variation, i.e. plate morph, number of lateral plates, body size, body shape and body colour, they were classified into two types corresponding to occurrence in the Ibi River and Lake Biwa water systems. The former type was monomorphic dominated by low-plated morphs in spring-fed water, whereas the latter was a dimorphic population consisting of low- and partially-plated morphs. My results suggest that the plate morph type is not correlated with climate nor predation but is related to geological isolation patterns during the course of the landlocking process. Conversely, variations in meristic (number of dorsal and anal fin rays and gill rakers) and morphometric (body shape and body colour) characteristics may have been related to different environmental conditions. This study also provides supporting evidence that the freshwater three-spined stickleback is a distinct species from the anadromous stickleback, *G. aculeatus*.

Within Japan, the freshwater three-spined stickleback, *Gasterosteus aculeatus*, is locally distributed in northern inland waters of more than 35°N. In Honshu Island, with the exception of two places (Mori, 1985, 1986), the species is restricted to spring-fed waterbodies. According to lateral plate phenotype, this species has differentiated into three distinct plate morphs: completely plated, partially plated and low plated (Hagen and Gilbertson, 1972, 1973a), all of which occur in the freshwater population in Japan (Ikeda, 1933). For Japanese populations, there are only three preliminary works concerning plate morph type (Ikeda, 1933, 1934; Igarashi, 1970) and when compared to the situation in Europe (Heuts, 1947; Münzing, 1963) and North America (Greenbank and Nelson, 1959; Hagen, 1967; Miller and Hubbs, 1969; Hagen and Gilbertson, 1972, 1973a, b; Coad and Power, 1973, 1974; Bell, 1982a; McPhail, 1984), there have been very few meristic studies on this fish performed in Japan or East Asia (Ikeda, 1933, 1934; Mori, 1984, 1986).

I present here the morphological features of freshwater populations in which the low-plated morph is dominant from probably the southernmost habitat on the west side of the Pacific Ocean (Mori, 1985). The purpose of this study was to document any geographic variation in meristic characteristics of the freshwater three-spined stickleback within a monomorphic population of the low-plated morph and dimorphic (or mixed) population of the low- and partially-plated morphs, and to detect any relationship between the phenotypic variant of morph and the variation of environmental conditions. Although the low-plated morph from Japan has previously been regarded as a subspecies, *G. a. microcephalus* (Ikeda, 1933, 1934; Igarashi, 1965; Mori, 1984, 1985), I propose that this stickleback is a distinct species at least from the anadromous type of *G. aculeatus*. However, no suggestion regarding the taxonomic nomenclature of this new species is given.

Materials and methods

Freshwater three-spined sticklebacks, *Gasterosteus aculeatus*, were collected from the Yamayoke and Tsuya Rivers (May 1981 to July 1982) and Nakagawa Creek (September 1983, January and

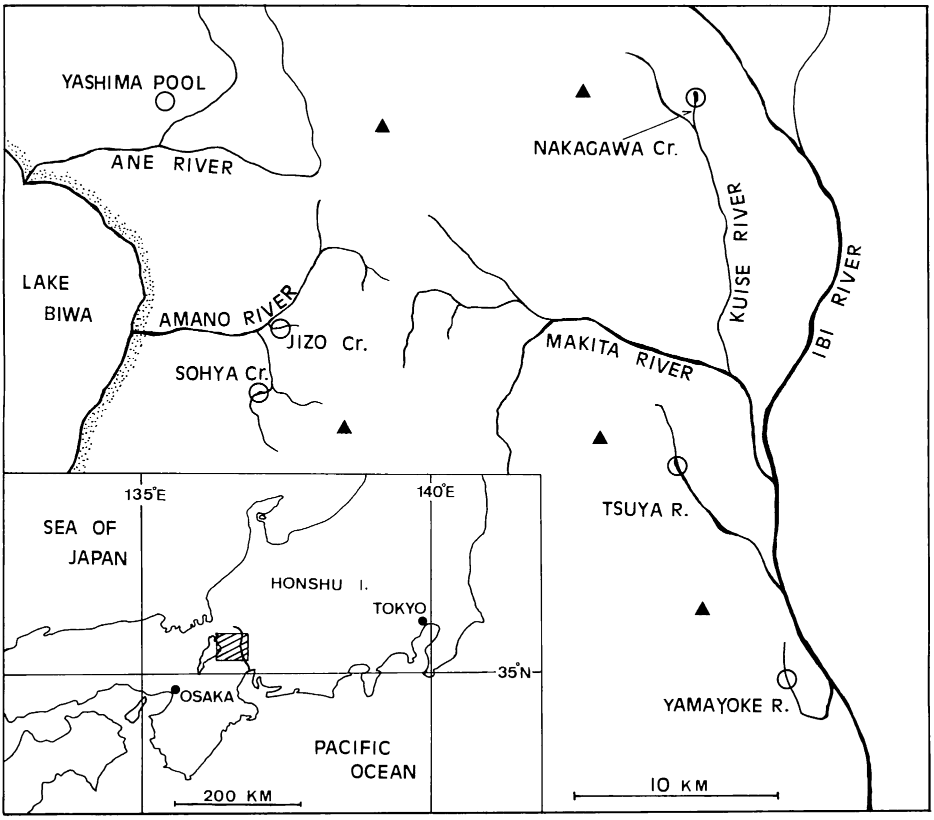

Fig. 1. Sampling stations (open circles) of the freshwater three-spined stickleback, *Gasterosteus*. ▲, top of a mountain.

May 1985) in Gifu Prefecture and from Jizo Creek (October 1981, May to July 1982, March, April and September 1984), Sohya Creek (April, May and July 1985) and Yashima Pool (December 1982 to March 1983, December, 1984) in Shiga Prefecture (Fig. 1). A total of 1,651 specimens were collected; 618 from Yamayoke River and 547 from Tsuya River, including fish under 25 mm in standard length (SL) to examine the progressive formation of plates; 66 from Nakagawa Creek, 213 from Jizo Creek, 75 from Sohya Creek, and 132 from Yashima Pool. The low number of fish collected from the Nakagawa and Sohya Creeks was due to the short sampling period and to the small number of fish inhabiting three very restricted habitats.

All specimens were fixed and preserved in 10% formalin. Lateral plates, excluding the plate forming the caudal keel, were counted by pricking or removing them with tweezers under a binocular microscope. The absence or presence of the caudal keel was noted. Plates of fish over 30 mm SL were counted without staining with an alkaline solution of Alizarin red S (Hagen and McPhail, 1970). A comparison between stained and unstained fish counts revealed no difference in accuracy. The discussion refers to fish over 25 mm SL and to the lateral plates on the left side, unless noted.

On most specimens, I recorded the anterior lateral plates of each side, standard length, head length, head depth (the vertical distance from the top of head to the lower margin of the preopercle; McPhail, 1984), body depth (measured beneath the first and second dorsal spines; Moodie, 1972b; Mori, 1984), body colour and sex. In addition, the relationships of head length, head depth and body depth to standard length were noted in order to compare the body shape among populations.

I also counted the number of gill rakers on the first right branchial arch, including rudimentary rakers, and the dorsal, anal, pectoral and caudal fin rays for specimens chosen at random from each collection. The numbers of dorsal and anal fin rays were differentiated between spine and soft rays, and the last two soft fin rays of dorsal and anal were counted separately (Coad and Power, 1973).

Results

Habitat situation. In Japan, the range of geographic distribution of the freshwater three-spined stickleback (the low-plated morph, termed the leiurus form) is mainly restricted to the immediate vicinity of the Ibi River (103 km long) in Gifu Prefecture and to an area adjacent to the east of Lake Biwa in Shiga Prefecture. Both these areas are located in the most constricted region in Honshu Island, Central Japan (Fig. 1).

Table 1 shows a synopsis of habitat conditions in each water area. The Yamayoke and Tsuya Rivers, and the Nakagawa Creek have relatively many springs (Mori, 1984, 1985) which result in a constant water temperature throughout the year. For convenience, these streams are named the Ibi River system and the described habitats are completely isolated from each other. Streams of this system have abundant aquatic vegetation and muddy bottoms, and riffles are almost absent. The streams can be classified as Bc type according to the classification of Kani (1981). Nakagawa Creek is a very short stream (about 1 km long, 8–30 m in width) overgrown with aquatic vegetation, and flows into the Kuise River, a tributary of the Ibi River. The water source (20 m a.s.l.) is a relatively wide, flat area (23 m × 28 m, 0.5–1.5 m deep) with springs. In Nakagawa Creek, the stickleback usually inhabits only the upper stream within a distance of about 300 m from the source and is absent from the Kuise River.

Jizo and Sohya Creeks are tributaries of the Amano River which flows into Lake Biwa. Jizo Creek is less than 2 km long and has a spring only in the water source area (110 m a.s.l.) and is dominated by riffles. This creek is usually only a few meters wide and less than 80 cm deep. The fish habitat is mainly restricted to the lower and middle regions of the stream flowing throughout a row of houses in Santo-cho town, Shiga Prefecture. During the breeding season, the fish often occurs in the Amano River at the mouth of Jizo Creek. Sohya Creek is mostly a rushing stream (Aa type, sensu Kani, 1981) and about 6 km long. Sticklebacks occur in only a small section of the middle stream (about 160 m a.s.l.) located immediately above a notched weir (4 m in height) consisting of a partially mud-bottomed pool (100 m long × 30 m wide, 2 m maximum depth) with abundant aquatic vegetation. The water current flows sluggishly through a channel on the left side of the pool. In Sohya Creek, rainbow trout (*Salmo gairdneri*) are extremely abundant because of the Prefectural Trout Fish-farm on both shores of the upper stream. Although Sohya and Jizo Creeks are connected by the Amano River, little dispersal of fish between the two creeks seems to occur. These creeks of the Lake Biwa water system are often flooded after severe rainfall. They generally possess more fluctuating environmental conditions than the habitats of the Ibi River system. Yashima Pool is a spring area of 4 m × 4 m square with a maximum depth of 2.5 m. With the exception of a small part of the adjacent brook, sticklebacks were restricted to the pool area (Fig. 1, Table 1). No collection of sticklebacks were made in Lake Biwa itself.

From this description of habitat conditions, it will be seen that in Japan, the low-plated morph inhabits two contrasting habitat types. One is that seen in the creeks of the Ibi River system and Yashima Pool characterized by standing water, very low gradients and a mud bottom with a spring. The other habitat type is seen in the Sohya and Jizo Creeks, which are streams with high gradients and a large proportion of gravel substrate.

Plate variation among populations. In the Yamayoke and Tsuya Rivers and Jizo Creek, the plate number of all stickleback specimens over 15 mm SL was plotted for each 5 mm length size class (Fig. 2). This result shows that the number of lateral plates was fixed and completed at a length of more than 25 mm. Also, since the specimens having 8 and 9 plates (relatively many anterior plates within low-plated morph) on the left side were 53.2 mm and 34.2 mm in SL, respectively, it was inferred that the plates did not increase with growth but were probably completed genetically during the juvenile phase (Igarashi, 1964, 1965; Hagen and McPhail, 1970; Garside and

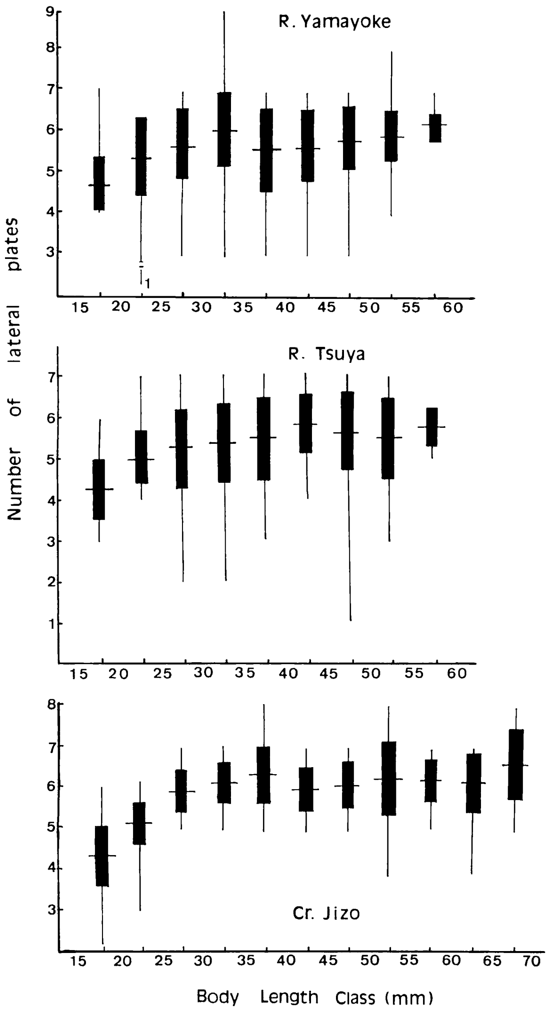

Fig. 2. Plate formation per 5 mm in SL from the Yamayoke and Tsuya Rivers.

Hamor, 1973; Bell, 1981; Coad and Power, 1973; Hagen and Moodie, 1982). Therefore, the results and discussion in this paper will only be concerned with specimens over 25 mm SL. Since differences from between-year comparisons of the Yamayoke and Tsuya Rivers and Jizo Creek were non-significant ($p<0.05$), the samples taken over the years can be used with confidence to detect geographic patterns of differentiation in plate number (McPhail, 1984).

The lateral plate counts of both body sides are summarized in Table 2. Fish from the Ibi River System tended to have a low number of anterior plates (minimum of one plate on left side from the Tsuya River and no plate on right side from the Yamayoke River), while the Lake Biwa population had a higher number (maximum of 9 plates on left side and 11 plates on right side from Sohya Creek). It was also found that fish with a plate (keel) on the caudal peduncle (the partial plated morph) frequently occurred in the Lake Biwa water system, especially in Sohya Creek (Table 2, Fig. 3). Specimens with 6 plates were the most abundant in all populations, followed by 5 and 7 plated morphs found in the Ibi River system and Lake Biwa water system respectively.

Partially-plated morphs were absent from the Ibi River system except for one fish (on right side) from the Tsuya River. In contrast, the partially-plated morph was often found in the Lake Biwa water system, notably within the Sohya Creek population, where the frequency exceeded 70% of the total. The caudal keels, however, were essentially rudimentary. In Lake Biwa populations, the keels were absent in specimens smaller than 33.0 mm in Jizo Creek, 34.1 mm in Sohya Creek, and 37.1 mm in Yashima Pool.

All specimens studied possessed some plates and were not the hologymnura form (no plated morph; Heuts, 1947). No sexual difference in plate number was evident in any population. There were no significant differences in the number of anterior plates between the samples from the Yamayoke and Nakagawa River, nor among the samples from the Nakagawa River, Jizo River and Yashima Pool (Student's t-test, $p>0.05$).

Asymmetry in plate number between body sides. No significant difference was seen between plate number on each side of the body within each population ($p>0.05$). Table 3 gives the frequency of asymmetry for plate number between left and right sides of body. It was found that over 30% of all specimens had azygous plate counts. The plate number of most fish was 6 on both sides. Differences in plate number between both sides was mostly one count, with a maximum of 5 counts seen on a fish from the Yamayoke River.

Morphometrics. Mature males and females from each area were used to obtain the frequency distributions of body length, mean length and standard deviation as given in Fig. 4. The mature female was larger than the male in all morphometric measurements except for the minimum length at maturity of fish from Jizo Creek. A difference in mean body length between both sexes

Table 1. Synopsis of habitat conditions at the time of collection. Temperature was stable for 15°C in spring bodies.

	Yamayoke R.	Tsuya R.	Nakagawa Cr.	Jizo Cr.	Sohya Cr.	Yashima Pl.
Situation	Spring pool, brook and main stream	Spring pool, brook and main stream	Spring pool and main stream	Small stream	Pool, just upstream of dam	Spring pool
Water velocity	Near stillness —35 cm/sec.	Near stillness —28 cm/sec.	7–39 cm/sec.	7–65 cm/sec.	5–60 cm/sec.	Stillness
Temperature flux of main stream through the year	12–20°C	11–19°C	12–17°C	13–19°C	4–17°C	12–16°C
Water colour	Clear (partly greenish)	Mostly clear	Clear to grayish	Clear to tea colour	Clear to tea colour	Clear
Substrate type	Mud	Mostly mud & sand	Mud	Sand, gravel & rubble	Sand, gravel & rubble	Sand & gravel
Common fish	*Zacco platypus* *Carassius auratus* *Cyprinus carpio* *Odontobutis obscurus* *Rhinogobius flumineus* *Channa argus*	*Z. platypus* *C. auratus* *C. carpio* *O. obscurus* *R. flumineus* *C. argus* *Hemibarbus barbus* *Moroco steindachneri*	*Z. platypus* *C. auratus* *M. steindachneri* *Salmo gairdneri* *Plecoglossus altivelis*	*M. steindachneri* *S. gairdneri*	*S. gairdneri* *M. steindachneri*	*M. steindachneri*

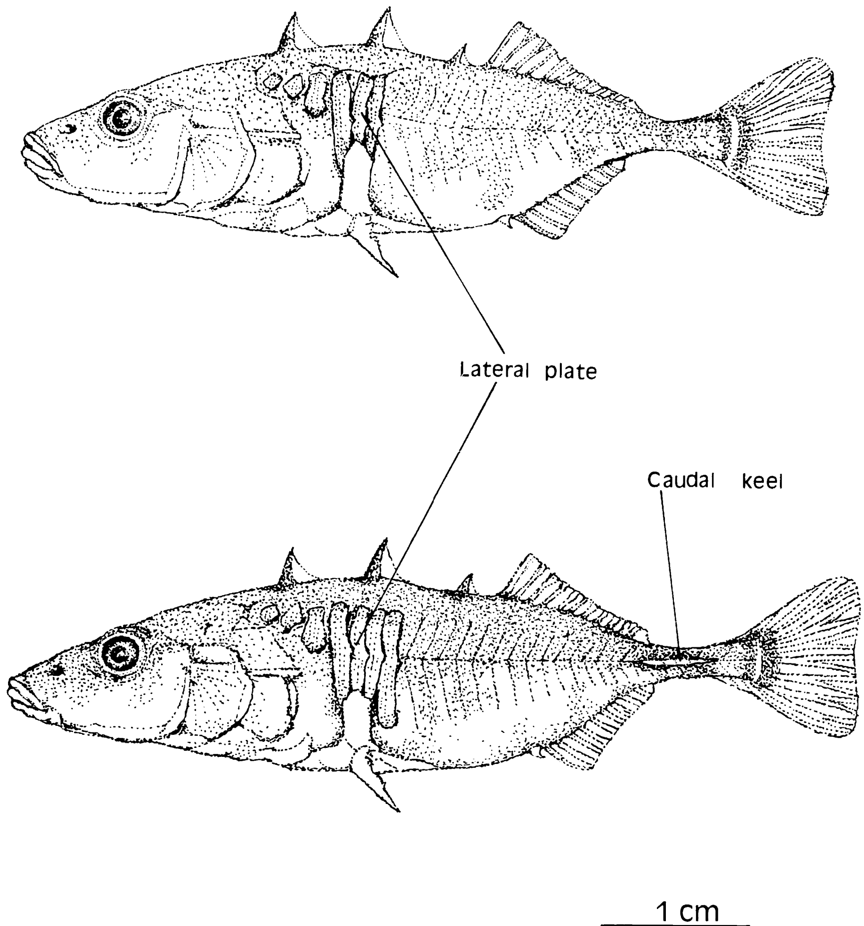

Fig. 3. Adults of low-plated (above, from the Ibi River system) and partially-plated (below, from the Lake Biwa water system) morphs. The pectoral fin has been removed.

was evident in both Jizo and Sohya Creeks. Fish larger than 60 mm SL composed over 20% of the population from Jizo Creek and 18% from the Sohya Creek population. Specimens from the Lake Biwa water system were usually larger with a more streamlined body than those from the Ibi River populations. The proportions of body and head depths to body length differed significantly between fishes from the two water systems. In addition, the relationship between head length and body length suggests sexual dimorphism (Mori, 1984), males being clearly larger than females within all populations (Table 4).

The low-plated morph has lateral plates only on the anterior part of the vertical bone and has irregular dark figures on the posterior ventral region. Ikeda (1933) reported a variation in body colour between low-plated and completely-plated morphs. In the current study, a difference in body colour within the low-plated morph populations of the two water systems was detected. The body colour was more uniformly dark green and drab on sticklebacks from the Lake Biwa water system than on those from the Ibi River system. Fish from areas adjacent to Lake Biwa did not generally possess distinct melanic figures on the lateral body, but showed a blackish abdomen as a whole.

Spine number and ascending process. The number of dorsal spines was usually 3, and rarely 4 (0.3% of all specimens collected) or 2 (one specimen). In all specimens with 4 spines, the fourth spine was small and inserted just poserior to the third one as shown in Greenbank and

Table 2. Variation in plate number per body side and proportion of partially-plated fish in each population. M=mean, S. D.=standard deviation.

	Number of plates											Total	M±S.D.	% of partially-plated morph
	0	1	2	3	4	5	6	7	8	9	11			
Yamayoke R.														
Left side				12	18	85	337	52	1	1		506	5.80±0.783	0
%				2.4	3.6	16.8	66.6	10.3	0.2	0.2				
Right side	1	2	5	7	9	91	329	61	1			506	5.80±0.889	0
%	0.2	0.4	1.0	1.4	1.8	18.0	65.0	12.1	0.2					
Tsuya R.														
Left side		1	3	17	44	145	255	26				491	5.44±0.924	0.2
%		0.2	0.6	3.5	9.0	29.5	51.9	5.3						
Right side		1	5	19	39	153	244	28	2			491	5.43±0.968	0
%		0.2	1.0	3.9	7.9	31.1	49.7	5.7	0.4					
Nakagawa Cr.														
Left side				1		9	46	9	1			66	5.94±0.631	0
%				1.5		13.6	69.7	13.6	1.5					
Right side				1		10	47	8				66	5.92±0.688	0
%				1.5		15.2	71.2	12.1						
Jizo Cr.														
Left side				1	4	22	142	43	1			213	6.06±0.662	42.1
%				0.5	1.9	10.3	66.7	20.2	0.5					
Right side				1	3	20	140	49				213	6.09±0.643	48.6
%				0.5	1.4	9.4	65.7	23.0						
Sohya Cr.														
Left side						1	36	34	3	1		75	6.56±0.658	72
%						1.3	48	45.3	4	1.3				
Right side						1	30	40	2	1	1	75	6.68±0.803	78.7
%						1.3	40	53.3	2.7	1.3	1.3			
Yashima Pl.														
Left side					1	12	95	22	2			132	6.09±0.583	48.7
%					0.8	9.0	72.0	16.7	1.5					
Right side					2	14	87	27	2			132	6.10±0.650	40.7
%					1.5	10.6	65.9	20.5	1.5					

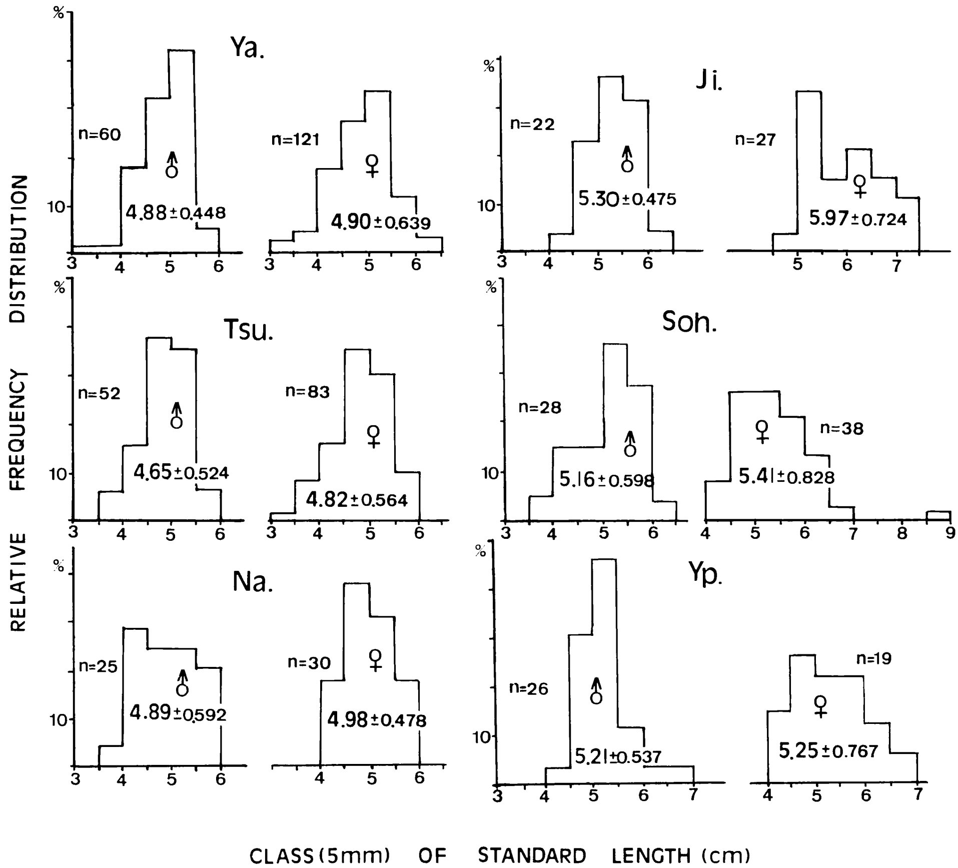

Fig. 4. Frequency distribution of body length of adult fish for each sex. Ya, Yamayoke R.; Tsu, Tsuya R.; Na, Nakagawa Cr.; Ji, Jizo Cr.; Soh, Sohya Cr.; Yp, Yashima Pool.

Table 3. Frequency of individuals with azygous plate number between body sides in each population.

Locality	Difference in plate number				Total of fish with azygous plate number	% of fish with azygous plate number
	1	2	3	5		
Yamayoke River	139	23	4	1	167	33.0
Tsuya	176	24	5		205	41.8
Nakagawa Creek	17	2			19	28.8
Jizo Creek	74	2			76	57.6
Sohya Creek	24	1	1		26	34.7
Yashima Pool	40	1	1		42	31.8

Nelson (1959). The ascending process, "the vertical arm of the pelvic girdle" (Lindsey, 1962), of the Jizo specimens was underdeveloped compare to other populations. In 13 fish (8.3% of total) from Jizo Creek, the ascending process was so small that it did not even about on the well-developed plate.

Numbers of fin rays and gill rakers. Significant differences ($p<0.01$, Student's t-test) in the numbers of dorsal and anal fin rays were found between the samples from the Ibi River population and from the two creeks populations in the

Lake Biwa water system (Fig. 5). The highest average number of gill rakers was found in the Nakagawa Creek population. However, the number of gill rakers was not significantly different between the two systems and no correlation or trend among population was detected.

Comparison with habitats in 1930's. From this study, the low-plated morph from the Lake Biwa water system can be morphologically distinguished from those originating from the Ibi River system. The results of Ikeda's (1933) preliminary works on the Japanese stickleback (Fig. 6) also show the general morphological differences between fishes from the two water systems, and the partially-plated morph occurred only in the Lake Biwa water system. The phenotypes may therefore be regarded to have been stable for a period of at least 50 years. Ikeda (1933) showed that vertebrae number is also different between the two area populations.

Ikeda's samples are invaluable to enable a comparison with now extinct habitats. The habitats in the two water systems shown in Fig. 6 are all spring bodies and not the main stream. Unfortunately, at present, the stickleback does not inhabit all the above loci, but only a few areas of the Ibi River system. The present patchy distribution is limited to restricted spring-fed water-bodies or to the upper stream where the water temperature remains below 20°C, even in summer. The habitats of stickleback have undergone a progressive reduction within the last 30 years, mainly due to artificial environmental modification or pollution.

Discussion

Plate variation and climate condition. Hagen and Moodie (1982) suggested that much of the polymorphism for plate morphs in freshwater stickleback were strongly associated with climatic conditions. According to this hypothesis, monomorphic populations for low-plated, or polymorphic populations with high frequencies of low-plated morphs are distributed in warm or mild climates with a small annual temperature flux. On the other hand, completely-plated morph populations favour cold areas with a greater temperature fluctuation. The occurrence of low-plated morphs in spring-bodies of the Ibi River system which have a small annual temperature flux and a water temperature that is generally below 20°C all year round (Table 1; Mori, 1985), seems to be explicable by this theory. However, the monomorphic low-plated morph population inhabits the main stream which has a relatively large water temperature fluctuation (8–25°C), and the spring bodies which have a nearly constant temperature (Mori, 1982, 1985). Therefore, the correlation between plate morph and climate situation does not always hold true.

Moreover, the freshwater completely-plated morph is found mainly in restricted spring-fed loci: in Ono City of Fukui Prefecture, 36°N; in Aizu district of Fukushima Pref., 37°40′N; Nasu district of Tochigi Pref., 37°N; all in more northern places than this study area. In the Ono and Aizu areas, the monomorphic populations of completely-plated morph commonly inhabit the spring bodies that are 12–18°C throughout the year (Hirai et al., 1973;

Table 4. Mean and standard deviation of the relationships of body length to head length and body depth, respectively, in each sex of population.

Localities	Sex	Head length/body length	Body depth/body length	No. examined
Yamayoke River	♂	0.332±0.0137	0.252±0.0177	66
	♀	0.287±0.0107	0.253±0.0184	81
Tsuya River	♂	0.325±0.0122	0.255±0.0164	66
	♀	0.292±0.0115	0.257±0.0189	75
Nakagawa Creek	♂	0.339±0.0117	0.258±0.0144	24
	♀	0.310±0.0066	0.260±0.0128	14
Jizo Creek	♂	0.323±0.0105	0.255±0.0109	40
	♀	0.299±0.0103	0.254±0.0106	67
Sohya Creek	♂	0.323±0.0083	0.226±0.0125	24
	♀	0.301±0.0085	0.227±0.0211	51
Yashima Pool	♂	0.336±0.0065	0.246±0.0110	20
	♀	0.318±0.0052	0.248±0.0056	15

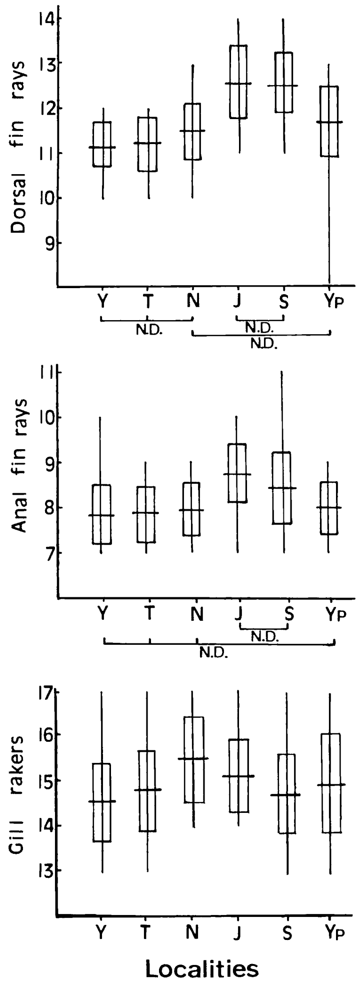

Fig. 5. Geographic variation in numbers of dorsal and anal fin rays and gill rakers. Horizontal line, rectangle and bar indicate mean, standard deviation and range, respectively. Abbreviations represent the same localities as in Fig. 4. Localities on the same under line do not show significant difference (5% level) in mean.

Yamanaka, 1981). Besides, only a single population in the Nasu area is polymorphic with three forms: complete, partial and low plated morphs, and with a mean of 26.09 (Igarashi, 1970) or 25.8 plates (Mori, unpubl.) including keels on the caudal peduncle. Thus, since the freshwater completely-plated morph occurs in spring bodies with a small temperature flux, the suggestion of Hagen and Moodie (1982) appears to be inapplicable to the Japanese stickleback populations. Climate seldom influences the condition of spring-fed water and I suggest that it is not atmosphere as Hagen and Moodie stated, but water temperature that influences morph pattern frequencies.

Furthermore, a monomorphic population for the completely-plated morph is ordinarily distributed throughout Lake Ohnuma (513 ha, 41°59′N), the southern part of Hokkaido Island. In this lake, climate influences water temperature due to the absence of springs in the vicinity, and thus, large temperature fluctuations occur annually (0–23°C) (Mori, unpubl.). It is evident that the frequencies of completely-plated morphs tend to dominate in the northern regions where climate is much colder in winter. Presumably, a global or general trend between plate morph and climate or latitudinal locale exists in the world-wide distributional range of the three-spined stickleback, although it is necessary to detect detailed local variations in environmental factors for morph frequencies (Münzing, 1963; Hagen and Moodie, 1982).

Slight selective adaptation under predation pressure. Predatory fishes, especially trout, have been known to function as a selective factor for plate number (Moodie, 1972a; Hagen and Gilbertson, 1972, 1973a, b; Bell, 1981, 1982a). For example, Hagen and Gilbertson (1973a) found that the selective advantage of seven plates in low plate morph was highly significant under predation pressure. The correlation was also shown by occurrence of a dimorphic population with a relatively high proportion of 7 plates in the Sohya Creek in which many trout were present. However, although predatory fishes were absent from Yashima Pool and were very few in the lower stream of Jizo Creek, the two habitats were occupied by dimorphic stickleback populations. Furthermore, though Ikeda (1933) did not state plainly, we can conclude that trout and high predation may have been absent in the past spring-fed habitat areas of Toyosato, Imajuku and Moriyama districts (Fig. 6). Even today, there are still very few known predators of the stickleback distributed in these districts. Thus, it will be seen that the relatively high number of plated morphs and the dimorphic population with a high frequency of partially plated fishes found in the Lake Biwa water system are not related to the presence or absence of severe predation. The fact that there was little predation evident

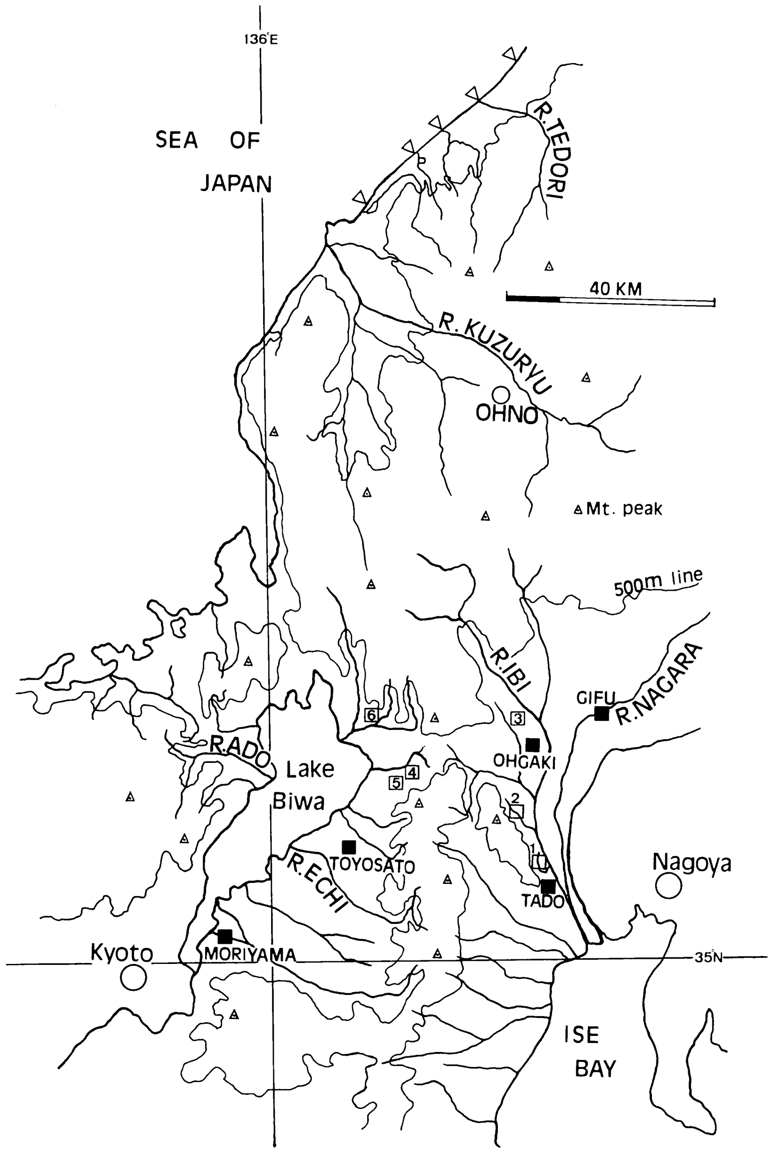

Fig. 6. Collecting sites by Ikeda (1933) shown as black squares. Open squares (1–6) show localities sampled in this study. Triangles in the Sea of Japan indicate the distribution of the anadromous three-spined stickleback during breeding season (March to early June).

in Ono, Aizu and Ohnuma areas also tends to refute the suggestion that predation pressure acts upon the number of plates since these places possess monomorphic populations for complete plated morphs.

Plate variation with regard to historical processes. Some data have indicated that within any river system, the number of lateral plates tends to be larger in the downstream areas (Hagen, 1967; Narver, 1969; Bell and Richkind, 1981; Bell, 1982b). Nevertheless, as Hagen and Gilbertson (1972), Hagen and Moodie (1982), Bell (1982a) and the present paper demonstrated, there is no correlation between morph frequencies and distance from the sea. Moreover, it is not possible to compare these factor among populations in the present study since habitats adjacent to Lake Biwa are at almost equal distances from three sea areas, Wakasa, Ise and Osaka Bays (Figs. 1, 6). Additionally, in the Pliocene Epoch, the water areas of Lake Biwa (the Ancient Lake Biwa) and the Ibi River (the Ancient Ise Bay or Lake Tohkai-ko) system were joined at a pass (existing elevation of 150–200 m) between the Amano and Makita Rivers (Figs. 1, 6; Ichihara, 1964). Hence, such sparsely distributed freshwater populations must be examined in association with both the past and the present water systems.

The freshwater populations of the stickleback are derived from the anadromous and monomorphic completely scaled morph (Ikeda, 1933, 1934; Münzing, 1963; Igarashi, 1965, 1970; McPhail and Lindsey, 1970; Moodie and Reimchen, 1973; Bell, 1981; McPhail, 1984; Mori, 1985, 1986). Igarashi (1970) and Bell (1981) argued that neoteny plays the most important role in the retention of plate formation in low- and partially-plated morphs. Various reductions of plate number may depend on the landlocking period which is related to the occurrence of a neoteny involved in physiological matters of osmoregulation, buoyancy control (Is the lateral plate heavy for the fish in the freshwater?), etc.

In this paper, the relatively high frequency of asymmetry in plate number contradicts the results of Ikeda (1933). Fish were most frequently asymmetric by one and rarely two plates between sides, although up to five plate difference was recorded. Hagen (1973) proposed that asymmetry of plates has been caused by intense directional selection based on a genetic component. The frequent symmetry in plate number may imply an unstable phenotype, indicating the course of alteration under directional selection. In order that plate number and morph type in relation to the landlocking process be investigated fully in Japan, there is a need for further morphological surveys on freshwater and anadromous monomorphic populations, and for a detailed paleontological and geological investigation.

Body size. Nikolsky (1963) pointed out that a fish has an adaptive pattern of becoming small-sized under severe or poor environmental conditions. However, stickleback from around Lake Biwa, where it was thought inferior conditions occurred, grew to a large size (the largest individual was 85.2 mm from the Sohya Creek). Conversely, the adult body size of fish from creeks in the Ibi River system (relatively stable water area) was generally small with a mean of less than 50 mm. Moodie (1972b) proposed that the large body size is a defence against predators. From this viewpoint, the large body size of fish from around Lake Biwa may reflect the existence of abundant predatory fishes. However, as already mentioned, with the exception of Sohya Creek, there was no intense predation evident on the stickleback in any of these habitats. Therefore, in Japan, large body size is not correlated with the presence of predation. Rather, the large-sized stickleback from the Lake Biwa system probably evolved for the consumption of large-sized prey and the limited supply or distribution of prey (Larson, 1976). A further possibility is that in areas of cold and severely fluctuating water temperatures, longevity incurs the large body size.

Fish from Jizo and Sohya Creeks apparently have a more streamlined body than those from the Ibi River system, resulting in the former being smaller in the ratios of body length to body and head depths than the latter. The streamlined fish also has a more sharply curved branchial arch. Such a streamlined body shape appear to be an adaptation to stream life.

Meristic counts. Since gill rakers are a trophic apparatus, any differences may be inferred as being adaptations to various feeding conditions. Larson (1976) and McPhail (1984) showed that sticklebacks with a high number of gill rakers fed on smaller food particles than those with lower numbers of gill rakers. Ecological evidence supports this view. Stickleback in the eutrophic Nakagawa Creek (Mori, 1986) may mainly eat smaller planktonic food, whereas those in other streams mainly eat benthic organisms.

Numbers of dorsal and anal fin rays were larger in the specimens from around Lake Biwa. A large number of fin rays may be related to the large body size, although a further consideration of the development of fin rays accompanied with the growth is necessary. As shown by Lindsey (1962), the numbers of dorsal and anal fin rays may increase owing to the lower water temperatures (7–18°C in the annual flux) as seen in Jizo and Sohya Creeks. Thus, these meristic phenotypic variations possibly arose from differences in habitat conditions.

In summary, phenotypic variations, except for plate morph, among populations of the freshwater three-spined stickleback may have been related to a variety of physical and biotic environmental factors. The specific phenotype of low plate numbers in *G. aculeatus* might have been evolved basically by the neoteny associated with a dwarfish body size resulted from the landlocking though fish predation has probably played a partial role.

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ハリヨの形態における地理的変異

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ハリヨの鱗板数を中心とした形態に関して6つの水域の地理的変異を調査した．鱗板数，最大体長，体長—体高関係及び体長—頭長関係，背鰭及び臀鰭軟条数などにおいて，揖斐川水系型と琵琶湖水系型とに区分することができた．特に，尾柄部にも鱗板（竜尾骨）があるのは殆んど琵琶湖水系産であり，これは体形がより流線型をなしていた．鰓耙数の変異については何らの傾向もみられず，これは生息水域の環境条件の相異を反映し，食性の差によると思われる．

また，揖斐川水系と琵琶湖水系との形態的相異は，各水域ごとの捕食者や水温などとの関係によるよりも，陸封化過程に伴うネオテニーの進行度とより関連があるかもしれない．

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