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Divergence in Reproductive Ecology of the Three-Spined Stickleback, *Gasterosteus aculeatus*

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Abstract An anadromous population (*trachurus* form) and three freshwater populations (*leiurus* form) of the three-spined stickleback, *Gasterosteus aculeatus*, in central Japan were compared with one another in the reproductive traits: body length at maturity, egg size, clutch size, the swell of abdomen and the number of eggs per nest. The anadromous fish which become larger in body size at maturity spawn eggs smaller in size and greater in number than the freshwater fish. The abdomen swell of gravid females expressed by the proportion of abdomen width to body length was greater in the freshwater fish. The anadromous male fish collected a mean of 2,638 eggs with a range of 1,119 to 4,052 eggs from about 6–7 females. In the three freshwater (the Yamayoke, the Tsuya and the Jizo) populations, males must have mated with about 9–22, 7–18 and 4–7 females respectively. It seems that the *leiurus* form increases its reproductive success by its much more mating opportunities and the parental efforts of nesting males as well as by spawning large eggs. Furthermore, among the freshwater populations, the Jizo one inhabiting the upper stream was clearly larger in body size, in egg size and in clutch size than the Yamayoke and the Tsuya ones which inhabit stable waterbodies with springs. It is possible that the Jizo population adopted the strategy of spawning a few large eggs as an adaptation to its habitat. The causal and functional explanations in reproductive characteristics among the four populations are discussed in regard to differences in the environmental conditions.

The three-spined stickleback, *Gasterosteus aculeatus*, has both a freshwater type (*leiurus* form, low plated morph) occupying freshwater permanently and an anadromous type (*trachurus* form, complete plated morph) migrating into freshwater from the sea to breed in spring. The complete plated morph also occurs in some freshwater habitats permanently northward to 36°N in Japan. The differences between the two types have been attributed not only to their habitat but also to morphological aspects (Heuts, 1947; Münzing, 1963; Hagen, 1967, 1973; Miller and Hubbs, 1967; Hagen and Gilbertson, 1972, 1973a, b; Hagen and Moodie, 1982). Furthermore, Hagen (1967), Wilz (1973), Hay and McPhail (1975) and McPhail and Hay (1983) found that reproductive isolation ethologically occurred between the two types using mate selection tests.

This study, in addition to the aforesaid differences, rates ecological divergences in reproductive traits (body length at maturity, egg size, fecundity and egg numbers per nest) between the anadromous and the freshwater types of *G. aculeatus*, and reproductive differences among interpopulations of the latter type. I also argue here that intraspecies and interpopulation variations in reproductive characteristics reflect their adaptations to different features of environmental conditions in each habitat. Further, I evaluate the opinion that the freshwater type is not a subspecies of *G. aculeatus* but an independent species.

Materials and methods

Fish were collected in the Yamayoke and the Tsuya Rivers of Gifu Prefecture (Mori, 1984, 1985), in Jizo Creek (Mori, 1984, 1987) a tributary of the Amano River flowing into Lake Biwa, Shiga Prefecture, and Kahoku-gata lagoon of Ishikawa Prefecture using seines in March to June, from 1982 to 1984 (Fig. 1). The populations in the first three locations represented the *leiurus* form, and inhabited freshwater permanently. Those in the last locality are of the *trachurus* form, and

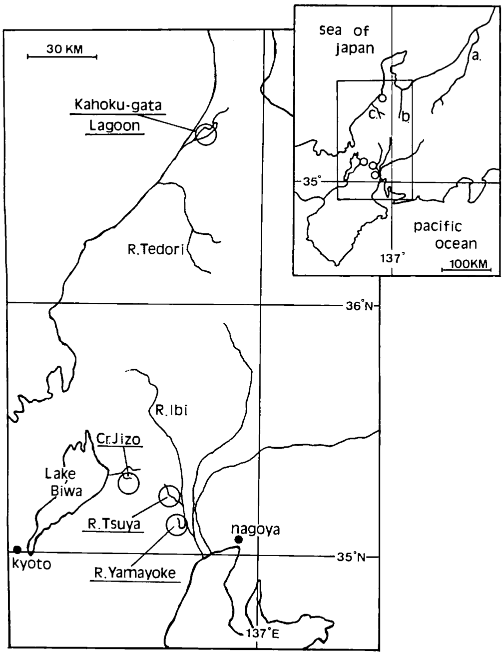

Fig. 1. Locations of sampling stations in central Japan. The anadromous *trachurus* form was collected in the Kahoku-gata lagoon facing the Sea of Japan. The *leiurus* form was collected in the Jizo, the Tsuya and the Yamayoke Rivers. a, b and c show the Shinano, the Shoh and the Tedori Rivers, respectively.

inhabited marine habitats except during the breeding season: the anadromous type.

Samples were preserved in 10% formalin. Body length from snout to hypural fold (standard length) and width of abdomen were measured to the nearest millimeter. Maturity was determined by examination of the reproductive organs under a microscope. Total number of eggs were counted from each ovary at maturity stage IV or V of Nikolsky (1963) in the female. The diameter of about 25 unfertilized eggs chosen at random from each of 30 females was measured using calibrated micrometer eyepiece. Clutch size of nest was determined by counting the number of pre-eyed eggs and eyed eggs (Kynard, 1978).

Results

Breeding season. Many authors have reported that the breeding season of the three-spined stickleback, *G. aculeatus*, is generally in spring and/or summer, and the length of the season appears to vary from two to five months (Bertin, 1925; Craig-Bennett, 1931; Ikeda, 1933; Vart, 1949; Greenbank and Nelson, 1959; Hagen, 1967; Van Mullem, 1967; Coad and Power, 1973; Worgan and FitzGerald, 1981; Borg, 1982; Rowland, 1983).

The *leiurus* form of the Yamayoke and the Tsuya Rivers tend to nest and breed throughout the year with a peak in spring. Nest sites are in water areas with springs and along shores (Mori, 1985). Jizo Creek has a spring only at the uppermost part of the stream (120 m above the sea level) unlike the above two rivers, and has a faster stream current, more gravel on the substratum and larger fluctuation of water temperature (Mori, 1987). The breeding period (February to August) of the Jizo population is not as prolonged as in the Yamayoke and the Tsuya Rivers.

The *trachurus* form migrates to breed along the shore of lagoons, at the lower reaches of the river and drainages close to it, and initiates breeding activities in late March. After spawning, mass mortalities of adult fish begin to appear at breeding sites along the shore in late May. By June, young fish can be seen in lagoons and ditches. The breeding period of the anadromous fish from Japan coincides with that of other populations reported in the literature.

Body length at maturity. Frequency distribution of the body length of adult females is given in Fig. 2. Females of the anadromous *trachurus* form were apparently larger in body size than those of *leiurus*. Differences in the standard length of females were statistically significant between the Yamayoke and the Jizo populations and between the Tsuya and the Jizo populations (t-test, $p<0.01$). Accordingly, Jizo females differed from those of two populations in the Gifu district in maturity size. The length of females from the Yamayoke, the Tsuya and the Jizo populations ranged from 3.15 to 6.06 cm with a mean of 5.14 cm ($N=75$), from 3.85 to 5.82 cm with 4.99 cm ($N=99$) and from 4.72 to 7.01 cm with 5.72 cm ($N=72$), respectively. Fecund females from Kahoku-gata lagoon ranged in body size from 6.40 to 8.03 cm with a mean length of 7.46 cm ($N=48$).

Egg size. The egg diameters of freshwater populations were remarkably larger than those of anadromous populations (Mann-Whitney's U-test, $p<0.01$; Fig. 3). Egg sizes were similar to each other among three freshwater populations. How-

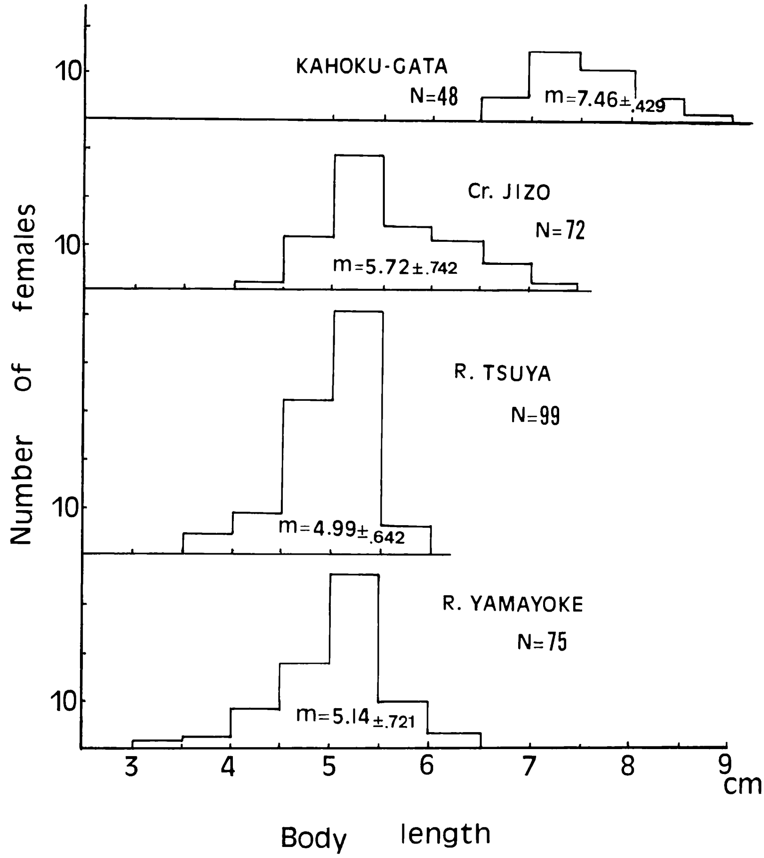

Fig. 2. Frequency distributions of body length at sexual maturity in female of each station.

ever, egg sizes of the Jizo population were significantly larger than those of the other two freshwater populations ($p<0.05$). No significant correlations were recognized between egg size and body length of females within each population.

Fecundity of females. Female of *trachurus* were far more fecund than those of *leiurus* (Fig. 4). The mean number of eggs per female was 401 (range 203–578) for Kahoku-gata lagoon, 168 eggs (range 48–304) for the Yamayoke, 122 eggs (range 41–236) for the Tsuya and 172 eggs (range 109–298) for the Jizo fish. Covariance analyses of the length-fecundity regression lines for anadromous *trachurus* and for each freshwater *leiurus* vastly differed from each other (Okuno et al., 1971). There were no significant differences in regression coefficients (slopes) among the three freshwater populations ($p<0.05$).

Female *leiurus* with remarkably distended abdomens were more fecund than the anadromous *trachurus* (Table 1). Moreover, Fig. 5 shows that the slope of the regression line for the abdomen width-body length relationship was much smaller for the anadromous fish than for the freshwater ones. Consequently, the slopes of regression lines indicate that the increase in abdomen width in ratio to body length was considerably fewer for the former fish than for the latter. The ratio of abdomen width to body length of the Jizo population was apparently lower than those of the other two populations.

Table 1. Means and standard deviations of the ratio of body length to abdomen width indicating the abdomen expansion.

Locality	Abdomen width/Body length
Kahoku-gata	0.134 ±0.0100
Cr. Jizo	0.181 ±0.0178
R. Tsuya	0.202 ±0.0078
R. Yamayoke	0.204 ±0.0130

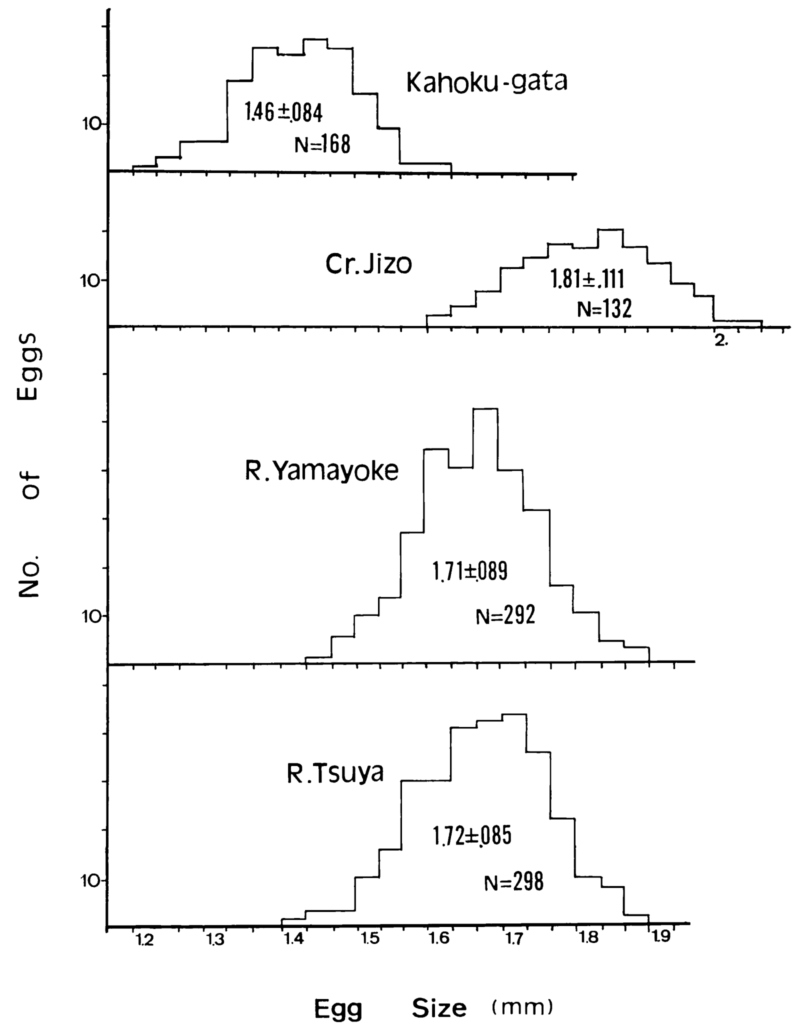

Fig. 3. Frequency distributions of egg sizes in diameter with means and standard deviations.

Egg number per nest. Fig. 6 shows the monthly variation in the mean and range of egg numbers per nest for *leiurus*. The variation in egg numbers ranged from 300 to more than 3,000. The average clutch size per nest in the Yamayoke population was 1,815 eggs (range 464–2,947), and that of the Tsuya one was 1,518 (358–3,164). Males of Jizo Creek guarded 648 eggs on the average, with a range from 264 to 1,645. In Jizo Creek, I have also observed the interior of each of 26 nests in the field, counting eggs by the naked eye, so that egg numbers in all the nests were presumed less than 1,500. In summer (late July to early September), the number of eggs per nest in both the Yamayoke and the Tsuya populations significantly decreased to less than 1,000. The anadromous *trachurus* form ranged in egg number per nest from 1,119 to 4,052 eggs with a mean of 2,638. The clutch size per nest of the anadromous population was 1.45 to 1.74 times, on the average, larger than those of the freshwater populations. The difference between *leiurus* and *trachurus* was statistically significant (Mann-Whitney's U-test, $p<0.01$).

As for the *leiurus* form, males appear to mate with 9 to 22 females in the Yamayoke population, 7 to 18 females in the Tsuya population, because most females examined contained 80 to 200 eggs. In the case of the Jizo population, males probably

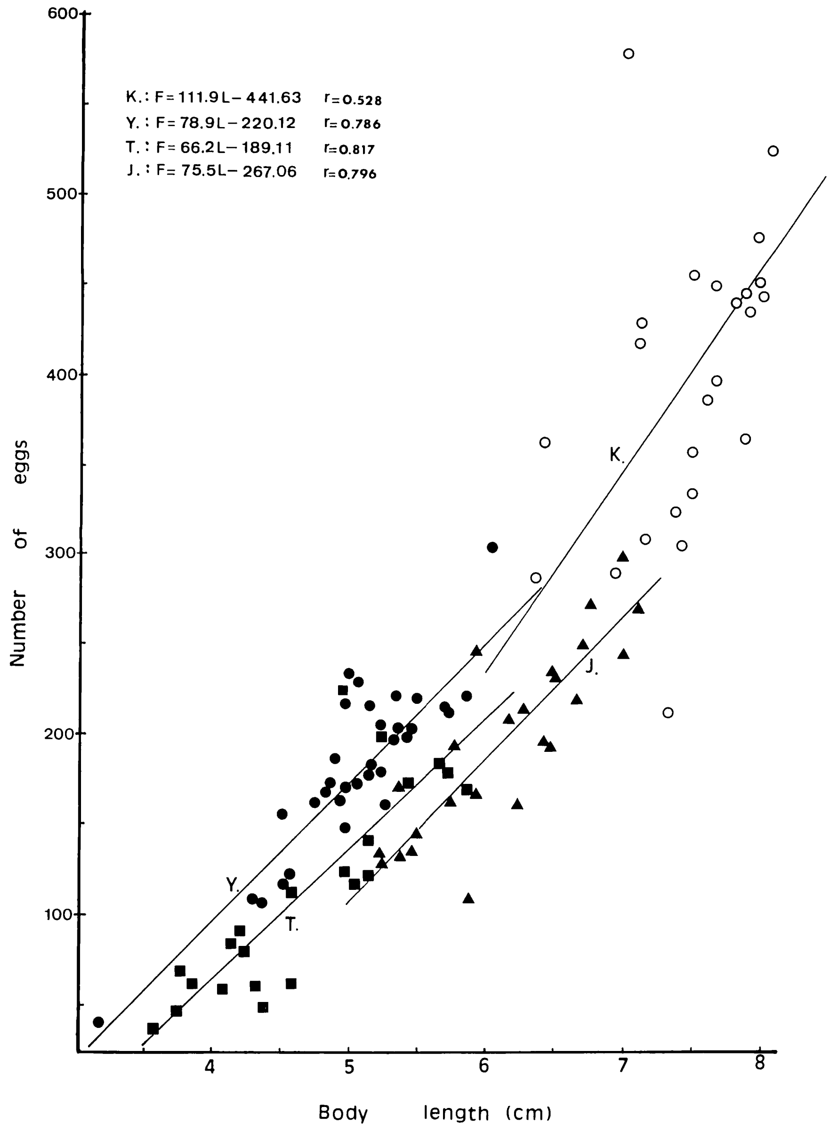

Fig. 4. Regression equations of length-fecundity relationships on four populations ($p<0.01$). Open circles, the anadromous *trachurus* form (K); black triangles, the Jizo population (J); black squares, the Tsuya population (T); black circles, the Yamayoke population (Y).

mate with 4 to 7 females on the average. For the anadromous *trachurus* form, 5 to 7 times of mating per nest was very likely. This is estimated from the relation between mean fecundity and egg number in the nest. There were no significant differences in the egg number per nest within any population between years.

No correlation was found between the number of fungous eggs and the total number of eggs in the nest. This study did not indicate that eggs on the bottom of the nest or in the interior of egg mass were particularly susceptible to fungus. Ratios of dead eggs to total eggs per nest ranged from 1.2% (24/1927) to 21.1% (536/2536) in the Yamayoke, from 0.4% (11/2690) to 11.5% (191/1655) in the Tsuya, from 1.4% (12/864) to 4.6% (32/690) in the Jizo and from 0.9% (32/3741) to 7.2% (168/2339) in the Kahoku-gata lagoon. Maximum loss of eggs due to fungus in a nest was found in mid-November and in late June, outside

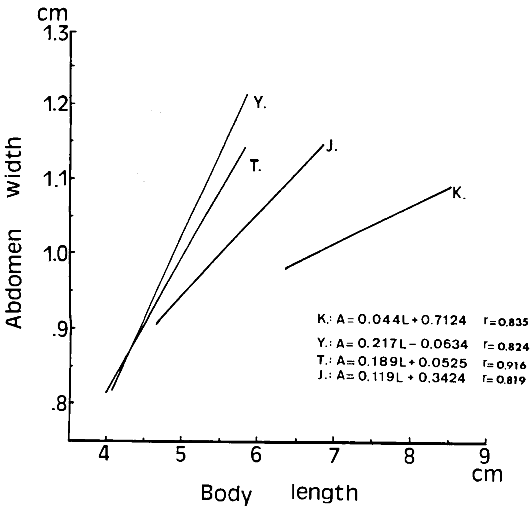

Fig. 5. Regression equations of the relations between abdomen width and body length for each population ($p<0.01$). Abbreviations represent the same as in Fig. 4.

the peak of breeding season (March to May) in the Yamayoke and the Tsuya Rivers, respectively. The highest ratio of egg loss was found in nests of the Yamayoke population. The ratio of egg loss in the anadromous population was clearly the lowest among all populations. The nests examined in this study had a far greater number of eggs than the three-spined sticklebacks studied outside Japan, whereas the hatching ratio was relatively constant for a nest.

Discussion

Divergences between anadromous and freshwater types. It is well known that in freshwater types and marine or anadromous types of various species, the former produces a smaller number of large eggs, in contrast the latter lays many small eggs (Mizuno, 1960; Mizuno and Niwa, 1961; Goto, 1975a, b). A survey of the literature shows that differences in reproductive traits between the two types are convincingly related to differences in environmental conditions.

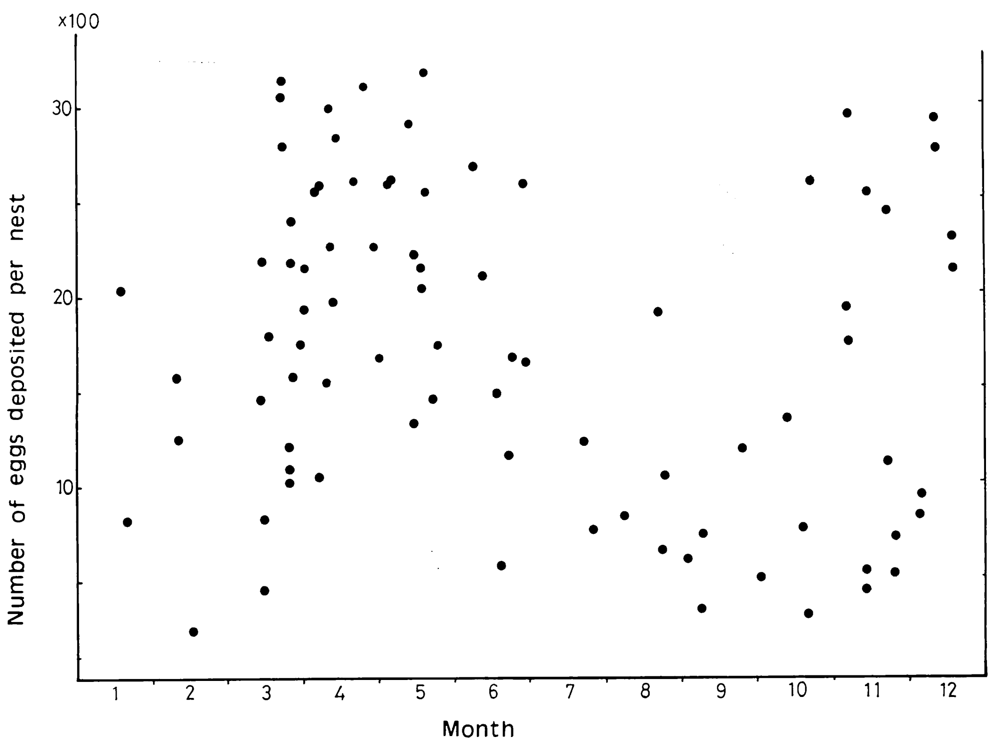

Fig. 6. Seasonal change on the egg number per nest in Gifu populations (from the Yamayoke and the Tsuya Rivers).

Table 2. Comparisons of reproductive characteristics among populations studied in the previous papers. * freshwater type, ** total length, † calculation by Wootton (1973). The numbers in parentheses show the range.

Localities	Species or form	Body length (cm)	Egg size in diameter (mm)	Clutch size	Estimated no. of eggs for 5 cm BL	Reference
Little Campbell	*trachurus*	5.8 (5.2–6.4)	—	241 (157–292)	163†	Hagen (1967)
River (west Canada)	hybrid	5.3 (4–6.3)	—	190 (83–296)	154†	
	leiurus	4.5 (3.4–7.5)	—	105 (49–234)	133†	
Amory Cove	*G. aculeatus*	6.1 (3.9–7.1)	1.25 (1.01–1.60)	265 (120–515)	—	Coad and Power
(east Canada)	*G. wheatlandi*	3.3 (2.8–4.0)	1.05 (0.86–1.21)	126 (75–168)	—	(1973a)
Matamek River	*G. aculeatus**	—	1.56	88	—	Coad and Power
(east Canada)						(1973b)
Mayer Lake	Black *leiurus**	8–9 (max. 11.6)	1.9	257	133	Moodie (1972)
(west Canada)	*leiurus**	5.1	1.87	105	131	
Wales (U. K.)	*leiurus**	4.8 (4.1–7.4)**	—	87 (40–295)	103	Wootton (1973)
Wapato Lake	*G. aculeatus**	May: 4.24	—	95.8±36.8	137	Kynard (1978)
(west Ameri.)		July: 5.39	—	159.6±54.5		
Woods Hole	*G. aculeatus*	4–5	1.31±0.05	112±19	—	Wallace and
(Massachusetts)						Selman (1978)
St. Lawrence	*G. aculeatus*	6.4 (5.1–7.0)	1.39 (1.3–1.52)	366 (116–838)	104	Craig and Fitz-
Estuary	*G. wheatlandi*	3.3 (2.7–4.1)	1.25 (1.10–1.43)	80 (45–142)	140	Gerald (1982)

Similarly, within the species *G. aculeatus*, the *leiurus* form inhabiting freshwater was smaller in body length, larger in egg size and, therefore, less in fecundity than the anadromous *trachurus*. Other anadromous populations (*trachurus* form) from the Tedori (Ishikawa Pref.), the Shoh and the Oyabe (Toyama Pref.) rivers, all flowing into the Sea of Japan, were similar to the population studied in the present paper (Mori, unpubl.).

Reproductive characteristics of populations in North America (Hagen, 1967; Moodie, 1972; Coad and Power, 1973a, b; Scott and Crossman, 1973; Wallace and Selman, 1979; Kynard, 1978; Pressley, 1981; Carig and FitzGerald, 1982) and Europe (Wootton, 1973, 1984) are indicated in Table 2. It is generally known that the freshwater population of *G. aculeatus* has larger egg sizes than the anadromous population, in contrast, egg number per female in the former is less than that in the latter. These differences in reproductive traits may not result from differences in body length at sexual maturity. The *leiurus* form has not compensated small body length at maturity by producing small eggs.

Itô (1978) argued that large-size eggs of a relatively small number is adaptation to poor food supply for the young as in rivers, while small-sized eggs of a large number represent adaptation to rich food supply as in brackish or sea waters. This hypothesis may apply to the situation of the *leiurus* and *trachurus* forms. For a relatively low food supply and severe environmental fluctuations in comparison with the marine conditions, *leiurus* in freshwater may have advanced to a more adaptive stage by means of laying a few large-size eggs.

It has been suggested that the anadromous type is primitive within the genus *Gasterosteus* (Ikeda, 1933; Hagen, 1967; McPhail and Lindsey, 1970; McPhail and Hay, 1983). Assuming that the *leiurus* form is a landlocked fish derived from the anadromous type or its allied fish, the remarkable variations for reproductive traits (body size at maturity, egg size, clutch size and egg number per nest) between the two types may have beeen acquired in the course of landlocking, from an anadromous life-history to a completely freshwater one. Subsequently, the *leiurus* form has probably diversified its reproductive potential. Furthermore, I propose here that the *leiurus* form (freshwater type) be regarded as an independent species of the *trachurus* form (anadromous type), because of the remarkable differences of reproductive ecology examined in the present study.

Differences among freshwater populations. Among populations of the *leiurus* form, the reproductive pattern of the Jizo population (relatively few large eggs) definitely differed from that of the Yamayoke and the Tsuya populations on the strength of the differences of environmental conditions of their habitats. The females of the Jizo population have adopted a spawning pattern of fewer and larger eggs and are significantly larger in body size than those of the Yamayoke and the Tsuya populations. The Jizo fish were also smaller both in estimated egg production for a set body length and in the ratio of abdomen width to body length.

Moreover, the egg number per nest was distinctly fewer in the Jizo population than in the other two freshwater populations. Probably, such traits of the Jizo population are adaptive to severe environmental conditions: unsteady flow of water, few inlets in which to build nests, unstable water level, high fluctuations in water temperature, gravelly bottom substratum, and predation pressure (by *Salmo gairdneri*; Mori, 1987).

In the case of Jizo Creek with impetuously fluctuating habitable environment, it could be hypothesized that when a nest was damaged and lost due to a particular cause, egg loss would be restrained owing to fewer eggs per nest. Although the Jizo population has fewer eggs in a nest, it might have achieved a superior reproductive success against the seasonal change of environmental conditions by laying larger sized eggs. On the otherhand, in the Yamayoke and the Tsuya populations, laying many eggs per nest resultsfrom adaptation to waters with constant temperature, relatively rich food supply even in winter, and many standing water areas in which to nest. Accordingly, the Yamayoke and the Tsuya Rivers, being stable habitats, have reproductive advantages for maintaining nests and mating behaviours.

Abundance of nest eggs in Gifu populations. The increase of reporoductive success in the genus *Gasterosteus* largely depends not only on egg size and egg number but also on the number of femles that a male can mate with and of hatched fry on nests as a result of parental care (Van Iersel, 1953). As Wootton (1984: p. 147) also stated, the fecundity of a male is defined as "the number of eggs he fertilizes per parental cycle", i.e. the clutch size of the nest. Unfortunately, data on eggs in the nest have not provided enough material for comparison. Moodie (1972) found that the mean clutch size in nests of the large black stickleback (lacustrine *leiurus* form of *G. aculeatus*) was 773 (N=133) with a maximum of 2,001 eggs. Kynard (1978) reported that nest egg sizes are about 1,000 per nest in vegetated areas and less than 400 in rocky areas in Wapato Lake, Washington State. In addition, Pressley (1981) reported that males in Trout Lake and Garden Bay Lake, British Columbia, had an average of 350 eggs and 152 eggs, respectively.

The male fish examined in this study demonstrated more numerous egg masses per nest than those of North American populations. More than 2,000 eggs per nest were not hard to find in Japan (35% of total nests studied in the Yamayoke, 28% of the Tsuya and 67% of the Kahoku-gata populations). Estimated from the average clutch per nest, the black stickleback male probably mates with about three females, and the *leiurus* male in Wapato Lake mates with about 10 females in May and 3–4 females in June. In Japanese sticklebacks, the mating number per male during the breeding cycle in the anadromous *trachurus* and in the Gifu freshwater *leiurus* may be 5–7 and 7–20, respectively. Thus, the number of females per male is greater in Gifu populations than in North American ones.

According to Wootton (1974), the length of inter-spawning interval of English *leiurus* is most commonly 3–5 days with the shortest being 60 hours under laboratory conditions. For this reason, females of *leiurus* with relatively low fecundity have much more spawning opportunities during the breeding season than those of *trachurus* with a high fecundity. Moreover, the relative number of maturefemales is likely to be large as a consequence of the yearlong prolongation of the breeding season as well Mori, 1985). Hence, a male will achieve greater mating opportunity (Knowlton, 1979; Krebs and Davies, 1981) though the high variation in egg number per nest may be related to difference in population density among the study areas. In addition, lower clutch sizes in July and August are probably caused by low breeding activities of *leiurus* in those months. Further, causal problems such as why many matings occurred in *leiurus* from the Gifu district might be explained in relation to the diversity of some releaser at courtship. In fact, Rowland (1982) found by ethological dummy experiments that males of *G. aculeatus* prefer models with more distended abdomens during courtship behaviour. Such mate preference suggests that male *leiurus* may have higher frequence of mating per breeding cycle due to more swollen abdomen of gravid females; ethological condition that has adaptive significance as a releaser for the sequent mating behaviour of males. The role of the swollen abdomen as a probable releasing mechanism to males is a problem to be examined in the future ethological study.

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イトヨ類の繁殖特性における分化

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石川県河北潟産溯河型イトヨと滋賀県地蔵川産，岐阜県津屋川及び山除川産ハリヨにおける繁殖的特性，成熟期の体長，卵径，一腹卵数，孕卵時の体幅，そして一巣卵数の比較をした．また，アメリカ，ヨーロッパ産のイトヨ類個体群とも比較し，日本産イトヨ類の生態学的な繁殖特性を示した．

体長は溯河型イトヨ，地蔵川産，山除川・津屋川産の順に大きく，卵径においては明らかに地蔵川産が大きく，溯河型イトヨが最小であった．一腹卵数の平均は体長の大きさにより溯河型イトヨが最多であるが，体長 50 mm における推定卵数は岐阜県産が有意に多く，体長に対する体幅比も大きかった．またさらに，一巣卵数において溯河型イトヨは平均 2,638 (範囲，1,119–4,052)，山除川産ハリヨは 1,815 (464–2,947)，津屋川産は 1,518 (358–3,164)，地蔵川産は 648 (264–1,645) であるが，巣をもつ雄の配偶回数を平均一腹卵数から推定すると，山除川・津屋川産ハリヨは十数回にもなり，外国産イトヨ個体群を比べても最多であるといえる．

これら溯河型イトヨとハリヨ間，及びハリヨ個体群間の繁殖的特性における相異について，生態学的な意義を究極，至近（行動学的意味を含めて）要因の両面から考察した．

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