

Clinal Life-history Variation in the River-sculpin, *Cottus hangiongensis*: an Example of Phenotypic Plasticity

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Abstract An amphidromous sculpin, *Cottus hangiongensis*, distributed freely in a natural river system, exhibited clinal differences in population density, sex ratio, age composition and life-history. In a second river, in which the distribution was restricted to a narrow area in the lower reaches by a notched weir, the species was characterized by high population density and a similar population structure in two different habitats. Little life-history variation was evident. Field observations suggested that clinal life-history variations in *C. hangiongensis* were not genotypic, but environmentally-induced, phenotypic responses. Rearing experiments demonstrated that the maturity of one-year old males was delayed under low density conditions, and that no relationship existed between the timing of maturity and the sex ratio. This suggests that phenotypic life-history variation in *C. hangiongensis* is induced primarily in response to population density. Such phenotypic plasticity in life-histories of individual *C. hangiongensis* populations may be an adaptation for exploitation of broad and heterogeneous river habitats.

According to life-history theory (Stearns, 1976, 1980; Stearns and Crandall, 1984), a species occupying a variety of habitats should exhibit different life-history patterns as a result of different selection pressures. In freshwater fishes there are many examples of geographical variation in life-history strategies of a single species (Schaffer and Elson, 1975; Fox, 1978; Leggett and Carscadden, 1978; Reznick and Endler, 1982; Mann et al., 1984; Jonsson et al., 1991). In American shad, *Alosa sapidissima*, the age of sexual maturity and the frequency of repeat spawners, which increase with latitude along the east coast of North America (Leggett and Carscadden, 1978), are thought to be adaptations to differences in water temperature (Glebe and Leggett, 1981).

From an evolutionary point of view, however, it is important to determine whether such variations are the consequence of local genetic variation due to natural selection (Endler, 1986), or are environmentally induced, i.e., phenotypic plasticity (Via and Lande, 1985). Although intraspecific life-history variation may be evident on a broad geographic scale, such as in the American shad, there are few studies that have compared the life-history patterns among habitat groups of a single population.

The river-sculpin, *Cottus hangiongensis* Mori, is a bottom-dwelling fish abundantly distributed in southern Hokkaido rivers, which empty into the Sea of Japan (Sato and Kobayashi, 1951; Goto, 1981).

This species, which has an amphidromous life cycle, lives a sedentary benthic life primarily in the lower river courses after a month-long pelagic period and reproduces as a nest-spawner like its congeners (Goto, 1988, 1990). Its mating system is polygynous, with females preferring to mate with larger nesting males, which is believed to increase their reproductive success (Goto, 1987a). Recently, Goto (1987b, 1989a, b) demonstrated that the life-history traits of *Cottus hangiongensis* varied along the course of a natural river, with sexual maturity occurring earlier in life and at a smaller body size downstream, but later in life and at a larger body size upstream. Such life-history differences were more striking for males than females.

This study presents field data which suggest that variations in life-history patterns of *C. hangiongensis* are environmentally-induced (phenotypic). Rearing of young males enabled identification of the primary factors determining phenotypic variation. Finally, the reflection of developmental plasticity and adaptation to successively different environments along a river course by variations in life-history are discussed.

Materials and Methods

Field study. Field studies on the life-history patterns of *C. hangiongensis* were conducted from Octo-

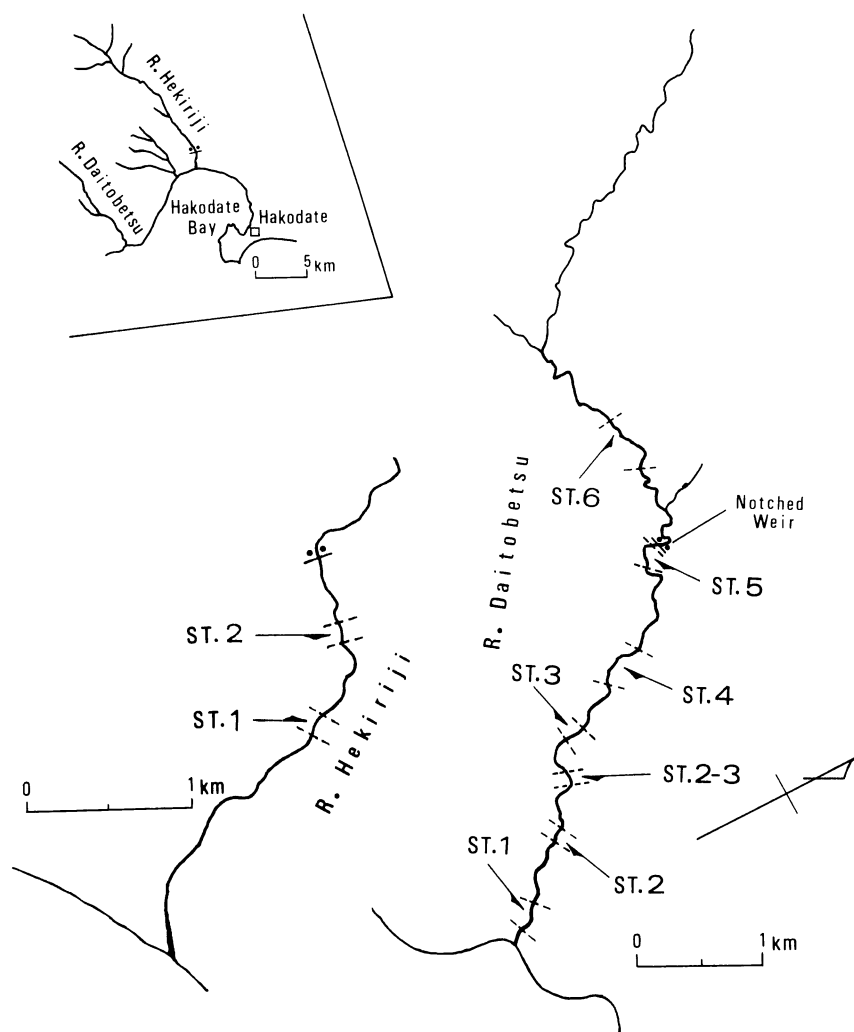


Fig. 1. Location and map of the Daitobetsu and Hekiriji rivers, showing the study sections.

ber 1983 to December 1990 in the Daitobetsu and Hekiriji rivers, southern Hokkaido, Japan (Fig. 1). These rivers are characterized by their relatively steep gradients and short lengths, about 17 km and 24 km, respectively. In the Hekiriji River, a large notched weir located approximately 3 km upstream from the river mouth blocks further upstream migration of sculpins (Goto, 1984). Two study sections were selected at 0.7 km and 1.4 km downstream of the notched weir (Fig. 1). In the Daitobetsu River, a small notched weir about 4 km upstream from the river mouth allows sculpins over 4 cm in body length to migrate upstream, resulting in a small number of individuals above the weir (Goto, 1986). Six study

sections were established along the lower 6 km of the river (Fig. 1). The biotic and abiotic characteristics of each study section has been described by Goto (1986, 1987b).

Throughout the study period, *C. hangiongensis* were sampled monthly with 3 mm stretched mesh dip nets in each section of the two rivers (except from January to March when the rivers were ice-covered). Individuals larger than 50 mm in standard length (SL) were marked by removing dorsal fin spines and rays (Goto, 1985). Mark-and-recapture methods allowed assessment of the population density, sex ratio, and individual growth rates of male sculpins in each study section. The population size and density were

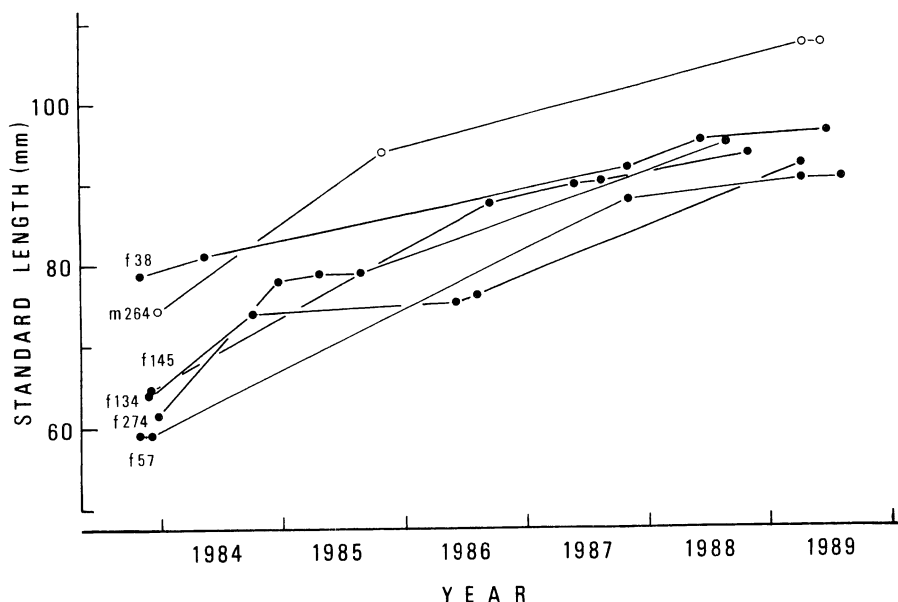


Fig. 2. Successive recapture and growth of individually-marked *Cottus hangiongensis* showing their long-term residence in the original habitat, St. 1 of the Daitobetsu River. ●, female; ○, male.

estimated for each section using the Jolly-Seber method (Seber, 1973). For each fish, sex was determined by its external sexual characters (Goto, 1984), and standard length (SL) measured to the nearest 0.1 mm using a caliper. The maturity of males was determined according to whether or not they oozed milt during the pre-spawning and spawning periods (March to May). Age at maturity was estimated by examining the successive growth patterns of each fish, but could only be used for individuals smaller than 70 mm SL at the time of marking.

Rearing experiments. One-year-old *C. hangiongensis* were collected by cast-nets from the lower course of the Hekiriji River in early July 1986 and transported to the Nanae Fish Culture Experimental Station, Hokkaido University. Once acclimatized to the rearing conditions at the Station (about one month), 70 male sculpins of 50 to 65 mm SL were selected and individually marked for use in the following experiments: 1) 2 replicates of 20 individuals were reared in 200 liter containers (78 × 73 cm), representing high-density conditions, 2) 2 replicates of 5 individuals were reared in 200 liter containers, representing low-density conditions, and 3) 20 individuals were separately reared in 3.5 liter containers (21 × 13 cm), representing solitary conditions.

The experiments were initiated in the first week of August 1986 and continued until the third week of

December of the same year. During this period, fish were maintained in flowing water and fed 10% of their total body weight in opossum shrimp, *Neomysis intermedia*, once a day. No attempts were made to control the natural photoperiod or water temperature. The latter gradually decreased from 22° to 6°C between August and December. The body length (SL) and weight (BW) of each fish were measured three times, at intervals of two months.

After the experiments, the surviving fish were sacrificed for determination of sexual maturity. Testes were dissected, weighed and fixed in Bouin's solution for histological observations. Representative, paraffin-embedded 8-μm sections were prepared and stained with Delafield's aematoxylin and eosin. The gonadosomatic index (GSI) was calculated as the percentage of testis weight to body weight.

Results

Field study. In the Daitobetsu River, young and adult individuals of *C. hangiongensis* were strongly sedentary in their own habitats along the river course. At St. 1, for example, the lowest study section, one male and five females, which had been individually marked in the early winter season of 1983, were recaptured several times in succession until 1988 or 1989 (Fig. 2), demonstrating their

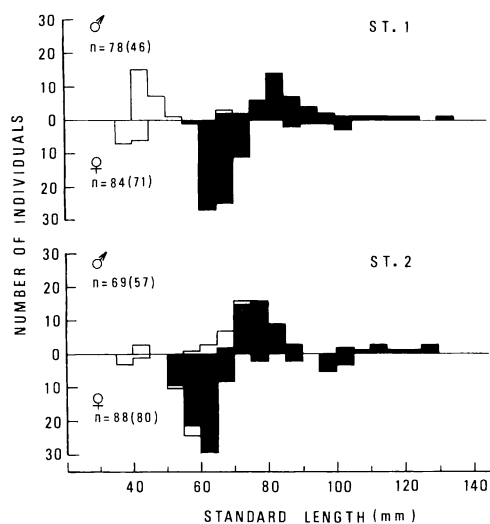


Fig. 3. Length-frequency distribution of male and female *Cottus hangiongensis* captured in two sections of the Hekiriji River in April 1989. Figures in parentheses indicate the number of mature fish. □, immature fish; ■, mature fish.

long-term sedentary nature in their original habitat. More particularly, it suggests that fish inhabiting each of the study sections can be referred to as a habitat group.

The population structures of six habitat groups of *C. hangiongensis* along the river course were characterized as follows (Table 1): 1) The density decreased toward the upstream habitats from 3.5 fish/m² at St. 1 to 0.03 fish/m² of St. 6. 2) The sex ratio changed strikingly, being skewed toward females in the downstream habitats, from 0.17 male/female at St. 1 to 0.89 at St. 4, nearly 1:1 at St. 5, and skewed heavily toward males (8.4) at St. 6. 3) Although the minimum age class became progressively older in the upstream habitats (reflecting early recruitment in the lower habitats and delayed recruitment in upstream habitats), the age composition did not differ greatly among the six habitat groups.

In the Hekiriji River, where sculpin distribution was restricted to the lower reaches by a notched weir, the population density was very high and showed little variation (Table 2). The sex ratio skewed slightly toward females in both sections. The age composition was the same in the two habitat groups, and no older age classes were found, as had been in the Daitobetsu River population.

The males attained sexual maturity at lengths greater than 65 mm (2 years and older) in both sections (Fig. 3), although the proportion of mature fish at age 2 was slightly higher in St. 1 (90%) than in St. 2 (76%) (Table 3).

Table 1. Population structure of each habitat group in the Daitobetsu River during the non-breeding season (see text)

Station	Population size (fish)	Population density (fish/m ²)	Sex ratio		Age composition (year)	
			female	male	female	male
1	3970	3.5	1	0.17	0-VII	0-VII
2	500	0.5	1	0.27	0-VII	0-VII
3	180	0.2	1	0.40	0-VII	0-VII
4	850	0.3	1	0.89	I-VIII	I-VII
5	130	0.1	1	1.07	I-IX	I-VII
6	40	0.03	1	8.4	II-VIII	II-VI

Table 2. Maturity of male and female *Cottus hangiongensis* collected from two stations in the Hekiriji River in April 1989

Sex	Station	Maturity at each age (year)									
		II		III		IV		V		VI	
		n	% mature	n	% mature	n	% mature	n	% mature	n	% mature
Male	1	20	90	19	100	4	100	4	100	1	100
	2	42	76	17	100	6	100	4	100	0	0
Female	1	64	92	4	100	3	100	0	0	0	0
	2	70	94	4	100	3	100	6	100	0	0

Rearing experiments. Of the 20 young males, which were reared under solitary conditions, 12 survived the full term of the experiment, 4 attaining sexual maturity (Table 4). The latter had larger body sizes (over 60 mm SL; body weight 3.6 g) than the remaining 8 fishes.

Under high density conditions, 11 out of 19 survivors had reached maturity by the end of the experiments, all being over 60 mm SL and 4.0 g BW (Fig. 4). In contrast, no males had attained maturity when reared under low density conditions. Although two males in the low density group had attained large body sizes (over 62 mm SL and 4.1 g BW), they had not matured sexually (Fig. 4). The remaining 8 males showed less growth than the minimum size at maturity found in the solitary rearing experiment.

Discussion

Remarkable geographic variation in the life-history strategies of the European freshwater sculpin, *Cottus gobio*, have been observed. Fast growth, early maturation, short life-span and multiple annual egg batches have been found in unproductive, northern streams, whereas slow growth, late maturation, long life-span and a single annual egg batch have

been found in more productive, southern streams (Fox, 1978; Mann et al., 1984). Reciprocal transfer experiments indicated that the variation in the number of egg batches and differences in growth rate at least are not genotypic in origin, but are environmentally-induced, phenotypic characteristics (Mann et al., 1984).

In the case of the amphidromous sculpin, *C. hangiongensis*, significant life-history variations have been found in males (Goto, 1987b, 1989a) and females (Goto, 1989b) within a population along the course of a natural river. In the Daitobetsu River, where *C. hangiongensis* is distributed almost freely throughout, the population showed clinal differences in population density, sex ratio, age composition, and life-history patterns along the stream course. In the Hekiriji River population, the distribution of *C. hangiongensis* is restricted to a narrow area in the lower reaches by a notched weir and was characterized by high density, similar population structure and little life-history variation.

The field data suggest that the significant life-history variations of *C. hangiongensis* in the Daitobetsu River are not genotypic but environmentally-induced, phenotypic characteristics. The allelic frequencies of the Daitobetsu and Hekiriji River popu-

Table 3. Population structure of two habitat groups in the Hekiriji River

Station	Population density (fish/m ²)	Sex ratio		Age composition (year)	
		female	male	female	male
1	4.1	1	0.65	0-IV	0-VI
2	4.3	1	0.71	0-V	0-V

Table 4. Body size and sexual maturity of surviving males reared under solitary conditions (see text). +, mature; -, immature

No. of individual	August		December			
	SL (mm)	BW (g)	SL (mm)	BW (g)	GSI	Maturity
1	61.5	3.43	68.3	5.39	1.76	+
2	59.9	2.84	68.0	5.51	1.64	+
3	58.7	3.20	60.9	3.62	1.51	+
4	58.0	2.91	61.3	3.28	0.11	-
5	56.5	2.60	62.3	3.99	0.45	+
6	53.4	2.84	54.2	2.70	0.18	-
7	53.3	2.45	56.7	3.20	0.13	-
8	53.1	2.19	54.8	2.35	0.09	-
9	52.4	2.34	53.7	2.12	0.09	-
10	52.2	2.16	52.7	1.95	0.10	-
11	51.7	2.06	52.9	2.13	0.09	-
12	49.6	1.80	52.6	2.14	0.09	-

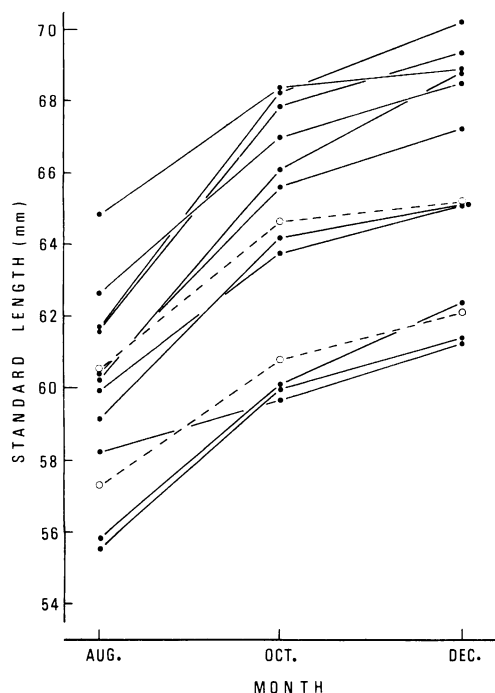


Fig. 4. Individual growth patterns of 11 males (solid circles) which attained sexual maturity under high density rearing conditions; and 2 males (open circles), reared under low density conditions, which attained over 60mm SL but remained sexually immature.

lations were homogeneous, probably due to gene flow along the coast during the larval period (Goto, unpubl. data).

In the Daitobetsu River population, increased growth in males in the upper reaches is most likely the result of differences in sculpin population density (Goto, 1986) and/or food abundance (Yamamoto et al., 1988) along the river course, and is apparently reflected by variations in their life-history (Goto, 1987b, 1989a). The size and age at maturity of males differ among the habitat groups, males upstream attaining maturity at larger body size and older age. Such differences in later ontogenetic trajectory among the habitat groups are schematically represented in Fig. 5, which shows similar length embryonic and larval periods.

The differences in the timing of maturity among the habitat groups may be related to differences in population density and/or sex ratio. The rearing experiments demonstrated that the maturity of one-year-old males was delayed under low density condi-

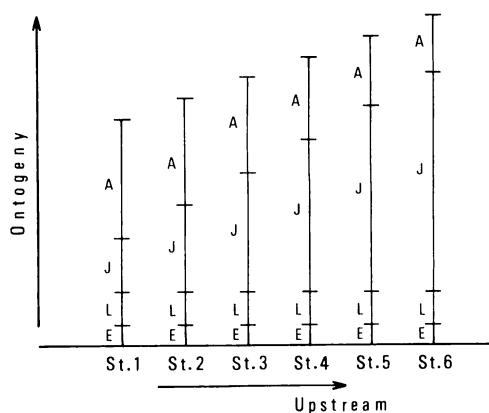


Fig. 5. Schematic diagram representing the ontogenetic trajectories of the six habitat groups of male *Cottus hangiongensis* in the Daitobetsu River. E, embryonic period; L, larval period; J, juvenile period; A, adult period.

tions compared with those under high density conditions. Furthermore, there was no relationship between the timing of maturity and the sex ratio because the differences in the timing of maturity occurred in males-only experiments. Therefore, the experimental data suggest also that the phenotypic life-history variation of *C. hangiongensis* is primarily related to population density, which may itself reflect the habitat space available. Although no retardation in the timing of maturity was observed under solitary rearing conditions, such life-history variations would not likely be induced by a lack of interaction among individual sculpins.

Phenotypic plasticity in life-history patterns, as found in *C. hangiongensis*, is important when considering the adaptation of a species to environmental differences along the course of a river. If the population had a single, specific life-history pattern, the sculpins, in this case, could not exploit the broad range of habitats along a stream course. In many freshwater fishes, the ability to develop along different trajectories in different environments (plasticity), as demonstrated in several poeciliids (Trexler, 1989; Meffe, 1992) and in a freshwater sculpin (Goto, 1978b, 1989a; this study), may be more important than selection for one specific life-history tactic.

Similar plasticity in life-histories has been observed in several freshwater snails (Russell-Hunter, 1978; Brown, 1985; Brown et al., 1985). In his study on intraspecific life-history variation in the pond snail *Lymnaea elodes*, Brown (1985) argued that

plasticity in life-histories may itself be adaptive for the inhabitants of unpredictable, vernal ponds. Clearly, high degrees of phenotypic plasticity in life-histories can be expected both within and between populations of many freshwater animals.

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表現型的可塑性としてのカンキョウカジカにおける流程に沿った生活史変異

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両側回遊性の生活環を送るカンキョウカジカ個体群には、その遡上を妨げる障害物のない河川では、流程に沿って個体群密度、性比、齢構成に傾斜的变化が存在し、各ハビタート集団間に顕著な生活史変異が認められた。一方、下流域に遡上を妨げる堰堤のある河川では、その流程に沿った各ハビタート集団は高い個体群密度、類似した個体群構造をもち、集団間にはほとんど生活史変異が観察されなかった。本種の未成熟雄1年魚を8月から12月までの期間、単独、低密度および高密度条件下で水槽飼育した結果、低密度条件下で飼育された個体は高密度飼育個体と比較して、性成熟が遅滞することを示した。また、単独飼育条件では、その中の大型に成長した個体は性成熟に達することが認められた。以上の野外観察と飼育実験結果から、カンキョウカジカの個体群内に出現する生活史変異は、遺伝子型の違いによってではなく、生息環境条件に対する各個体の反応としての表現型の可塑性によって起因すること、およびその環境要因としては各生息場所での個体群密度の違いが重要であることが示唆された。そして、このような個体発生軌道における可塑性が、河川の流程に沿った異質な環境下に生息する本種個体群にとって、どのような適応的意味を持つのかについて考察した。

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