

Growth Patterns, and Age and Size at Maturity in Female *Cottus hangiongensis*, with Special Reference to Their Life-History Variation

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Abstract Growth patterns of the 1982 year-class, individual growth patterns, age and size at sexual maturity and longevity in females of the river-sculpin, *Cottus hangiongensis* (Cottidae), were examined along the course of the Daitobetsu River of southern Hokkaido, Japan. Growth of females slightly varied both along the river course and among individual fishes: slow growth occurs in females from the lower reaches, while more rapid growth occurs in females from upstream areas. Body size and age at the first sexual maturity of females slightly increased towards the upstream, from 52 mm SL and 2 years in the most downstream area to 72 mm SL and 2–3 years in the uppermost site. Longevity was estimated to be 7 years in the downstream areas and 8–9 years in the upstream sites. These results suggest that female life history varies along the course of the river and thus allow us to consider the following alternative reproductive tactics: when females stay in the lower reaches, they attain sexual maturity at a smaller body size and younger age, and have a small clutch size, but when females migrate into the upper reaches, their maturity is delayed until they reach a larger body size and older age, and have a greater clutch size.

Life-history variations have been studied in many fishes and considered to be adaptive responses to environmental changes (Alm, 1959; Nikolsky, 1963; Murphy, 1968; Stearns, 1983; Stearns and Crandall, 1984; Stearns and Koella, 1986). Even within species variations in life histories are evident in a large number of freshwater fishes such as pigmy whitefish, *Prosopium coulteri* (McCart, 1970), lake whitefish, *Coregonus clupeaformis* (Fenderson, 1964), arctic charr, *Salvelinus alpinus* (Nordeng, 1983), American shad, *Alosa sapidissima* (Carscadden and Leggett, 1975), sunfishes, *Lepomis macrochirus* and *L. gibbosus* (Gross, 1982, 1984), slimy sculpin, *Cottus cognatus* (Foltz, 1976; McDonald et al., 1982) and bullhead, *C. gobio* (Fox, 1978; Mann et al., 1984). Some of these intraspecific variations occur in the form of polymorphism within one population in a geographic area.

The river-sculpin *Cottus hangiongensis* Mori is a bottom-dwelling fish abundantly distributed in the rivers of southern Hokkaido and in the Sea of Japan along the coast of Hokkaido Island, Japan (Sato and Kobayashi, 1951; Goto, 1981). This species has an amphidromous life cycle, of which details have been previously described (Goto, 1981). Immediately after hatching from

eggs deposited in the lower course of rivers, the larvae are swept to the sea by the flows. After spending a pelagic life in the sea for about one month, the juveniles ascend rivers to grow and mature as benthic individuals in the lower river course (Goto, 1974, 1981, 1984a).

Recently, Goto (1987a) found that *C. hangiongensis*, a nest-spawner like its congeneric species, has a polygynous mating system and that females prefer to mate with larger nesting males for increasing their reproductive success. He also demonstrated that there is a life-history variation in male *C. hangiongensis* along a river course: sexual maturity in males occurs at smaller body size and younger age in lower reaches and at larger body size and older age in upstream areas (Goto, 1987b). As for the females of this species, however, it has not been reported how life-history variation exists.

In the present study, the growth patterns in fishes from one particular year-class and its individual members, age and size at maturity, and longevity were examined in female *C. hangiongensis* along the course of a river in order to elucidate their life-history variation. Possible explanations of female life-history variation and the role which the variation may play in the reproduc-

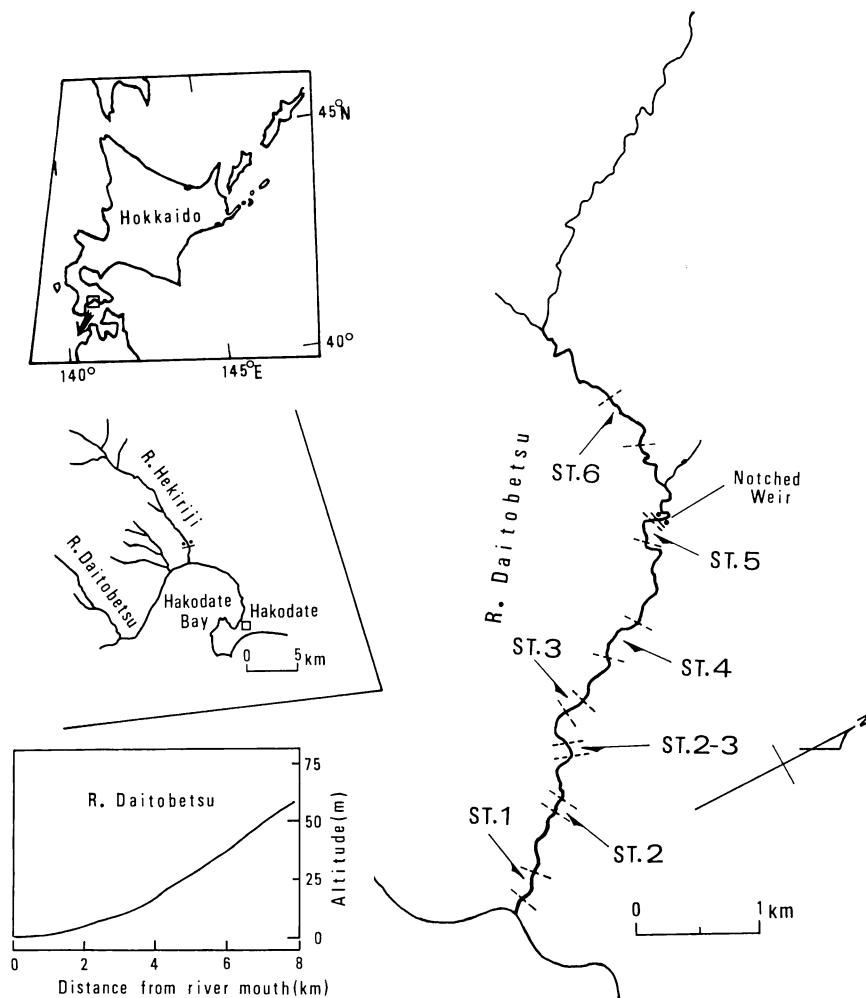


Fig. 1. Location and map of the Daitobetsu River and study sections.

tive system are presented.

Study area and methods

Fieldwork was conducted from October 1983 to December 1987 in the Daitobetsu River of southern Hokkaido, Japan. The Daitobetsu River is about 17 km long and has a steep gradient (Fig. 1). Seven study sections were established along the lower 6 km of the river (Fig. 1). Study section 2-3 (between St. 2 and St. 3) was monitored only during the spawning period of 1984. The detailed environmental characteristics of the river and of each of the seven sections have previously been described by Goto (1986, 1987a, b).

Throughout the study period, dipnet collections

(3 mm stretched mesh) of *C. hangiongensis* were made at monthly intervals in each section, except the period from January to March when the river was ice-covered. Female sculpins larger than 50 mm in standard length (measured to the nearest 0.1 mm with a divider) were selected from the total catches, anesthetized and then individually marked by removing fin spines and rays (Goto, 1985). At each sampling time, the sex, maturity and standard length of fish captured were examined. The sex was determined by the external sexual characters: females have a short anal fin and no genital papilla (Goto, 1984b). The maturity of females was determined by whether or not the fish have fully ripe yellow-colored eggs. From October 1983 to November

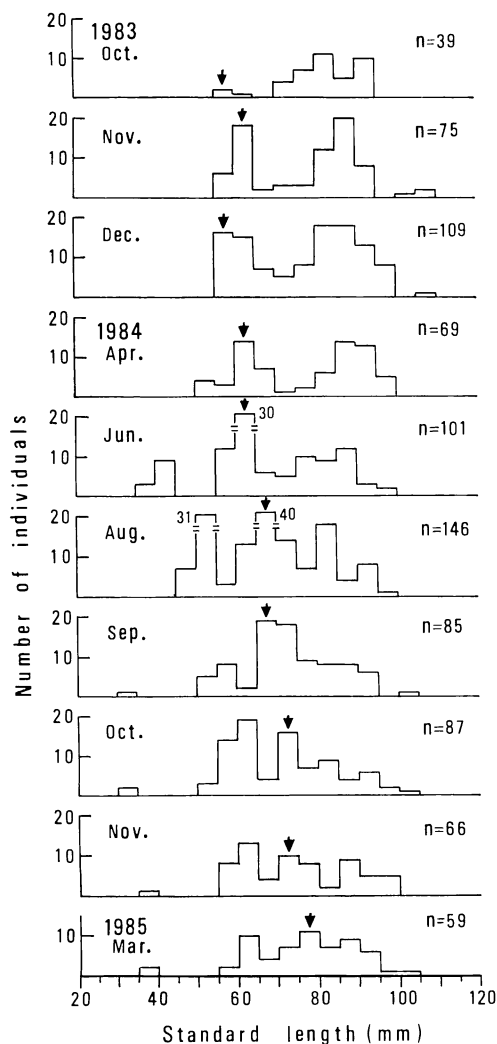


Fig. 2. Length-frequency distribution of female *Cottus hangiongensis* captured in St. 1 of the Daitobetsu River from October 1983 to March 1985. Arrows indicate the mode of 1982 year-class.

1986, a total of approximately 2,800 female individuals were marked: 651 fish in St. 1, 590 in St. 2, 374 in St. 2-3, 421 in St. 3, 448 in St. 4, 297 in St. 5, and 61 in St. 6.

Results

Growth within the 1982 year-class and its variation. On the monthly length-frequency histograms of the females captured in St. 1 from October 1983 to March 1985, it was impossible

to distinguish clearly the 1982 year-class from the 1981 or 1983 year-class except the samples captured in October 1983 (Fig. 2). However, the mode of the histograms of the 1982 year-class was distinctly different from that of the other year-classes throughout this period. Therefore, estimates of the monthly mean standard length of the 1982 year-class could only be derived from the recaptured females, which had fallen within each modal range on the histograms and had been marked during this period. The same constraints also applied to the remaining study sections. By plotting their mean lengths against time (Fig. 3), the growth of the recaptured females from St. 1 can be seen to have occurred during the intervals represented by a series of sequential sigmoid curves. Representing the age of a fish by adding one year after each April, the mean length of the females in St. 1 was 62 mm at age 2, 74 mm at age 3, 80 mm at age 4 and 85 mm at age 5. The mean length of the females at age 1 in St. 1 was 37 mm when estimated from the samples of the 1983 year-class. These corresponded well with the body sizes at each age as estimated by the otoliths (Goto, 1984b). By the same method, similar growth curves were also drawn for the females of the 1982 year-class in Sts. 3 and 5 (Fig. 3). For the females in St. 3, the mean length was 68 mm, 81 mm, 87 mm and 93 mm at age 2 to 5, respectively. In St. 5 it was 82 mm, 90 mm and 98 mm at ages 3, 4 and 5, respectively. A comparison of the age-specific average sizes derived from the three growth curves demonstrated that the growth of females varies along the river course: the females caught in the lower reaches exhibit slow growth and those caught in upstream areas have grown more rapidly (Table 1).

Table 1. Mean annual growth increment in standard length (mm) of females of the 1982 year-class in the three sections of the Daitobetsu River. * Figures in parentheses indicate the mean annual growth increment estimated from the 1983 year-class.

Age (year)	St. 1	St. 3	St. 5
0	(36.7)*	(39.9)	—
1	(24.8)	(27.6)	(28.5)
2	12.5	13.9	13.9
3	5.7	5.3	7.9
4	5.4	5.8	8.1

Goto: Growth and Maturity in Female Sculpin

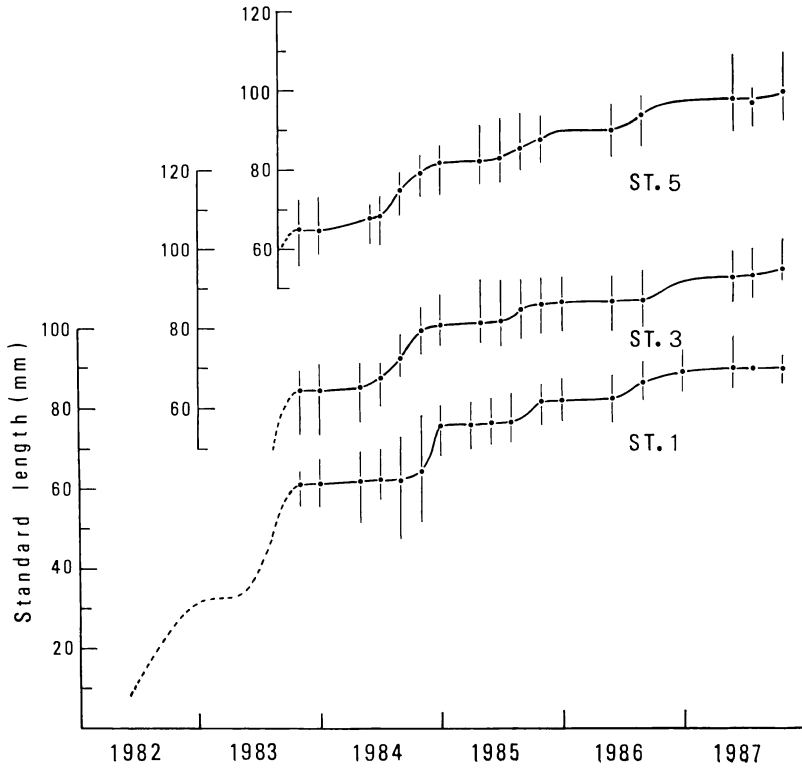


Fig. 3. Growth curves of the 1982 year-class in female *Cottus hangiongensis* in three different sections of the Daitobetsu River. Black dots and vertical bars indicate mean of standard length and the range of variation, respectively. Growth represented by the broken lines was estimated from the 1983 year-class.

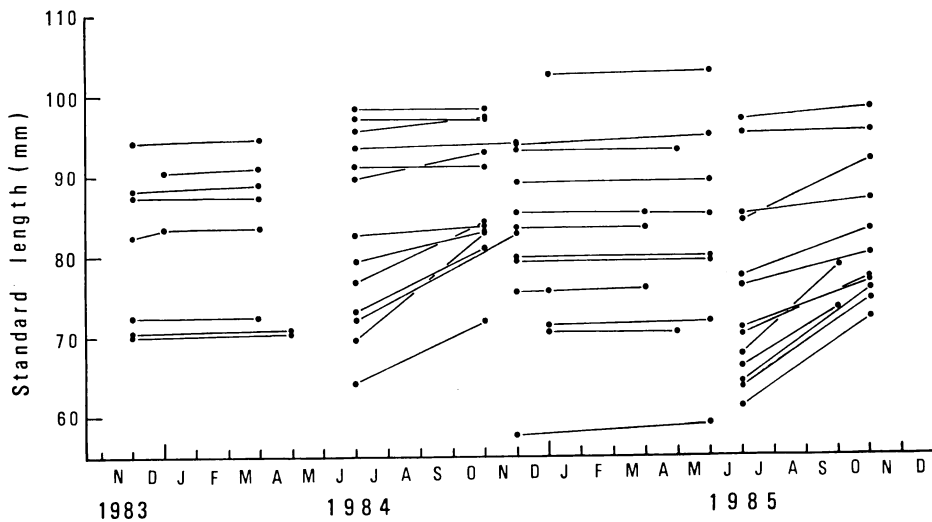


Fig. 4. Growth increments of individual female *Cottus hangiongensis* in the growing season (June to October) and in the non-growing season (November to May).

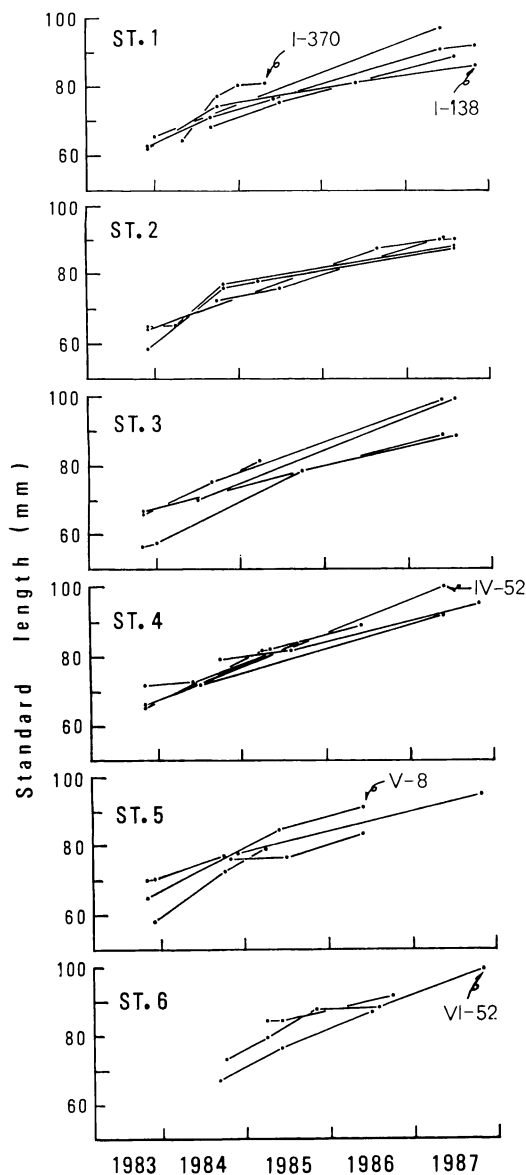


Fig. 5. Growth patterns of individual 1982 year-class female *Cottus hangiongensis* in each of the 6 sections of the Daitobetsu River.

Calculated annual growth increments show that this is true, especially among fish older than age 3 (Table 1). Thus, older females of the same age are considerably larger upstream.

Seasonal growth. The growth patterns depicted in Fig. 3 suggest that female sculpins grew rapidly from spring to autumn, almost ceasing to grow during winter. To examine this growth pattern

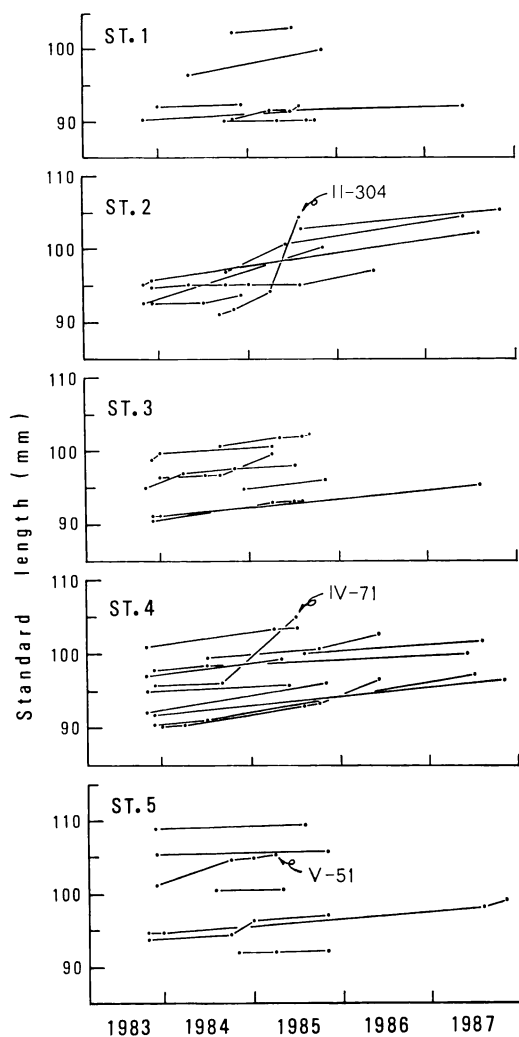


Fig. 6. Growth patterns of individual female *Cottus hangiongensis* over 90 mm SL in 5 sections of the Daitobetsu River.

more fully, individual growth was delineated by separating the year for convenience sake into the two distinct periods from June to October and from November to May (Fig. 4). Undoubtedly, growth in length was more pronounced from June to October, when the water temperature was generally higher than 10°C. On the other hand, females grew little or none from November to May during which period two phases were included: the period at low water temperature (0° to 10°C) from November to March, and their breeding period through April to May (Goto, 1981, 1987a). This female seasonal growth

pattern is slightly different from that of the males probably because of their greater energy loss during spawning (Goto, in press). For individuals larger than 80 mm SL, however, this differential growth pattern with season was somewhat obscured in females from the lower reaches because of their less annual growth increment, although it was still held true of females from the upstream areas (Fig. 3, Table 1).

Individual growth and its variation. The growth of marked females of the 1982 year-class from each of the 6 sections was estimated from their increases in body length at successive recaptures in their section of the first capture (Fig. 5). In general, these plots become more steeply inclined among fish from upstream areas, again an evidence of improved growth. Among females inhabiting the same section, however, considerable growth variations occurred in spite of the narrow range compared with that of the males (Goto, in press). Such individual growth variation demonstrates evidence of a unique growth pattern for each individual female. Among the females ($n=5$) in St. 1, for example, female I-370 grew most rapidly in early life, so that the body length reached 77 mm in the autumn at age 2 (the third autumn) and 81 mm at just age 3. Unfortunately, it was impossible to estimate the following growth of this female because of no recaptures afterwards. On the other hand, female I-138 exhibited slow growth, and was only 74 mm and 81 mm in the third autumn and at just age 4, respectively. Among the females from St. 1, individuals growing rapidly at young ages tended to grow slowly afterwards. This was not always the case with females from other sections. In St. 5, female V-8 grew rapidly in the first autumn (65 mm SL), and continued to grow fast afterwards. Consequently, this female reached 85 mm at just age 3 and 91 mm at age 4. Similar individual growth

patterns were also observed for females IV-52 and VI-52 from St. 4 and St. 6, respectively.

Variation in individual growth was also substantial among large females over 90 mm SL, which had once attained to their first maturity and then continued to mature annually (Fig. 6). Almost all of these females from 5 sections generally had little growth or ceased to grow, in spite of the differences in their initial body size represented. As shown in females II-304, IV-71 and V-51, however, a few females grew rapidly.

Size and age at maturity, longevity and maximum size. The minimum body size at first sexual maturity was 51.8, 56.8, 57.1, 57.8, 65.0 and 72.0 mm SL in females from St. 1 to St. 6, respectively. The proportion of females which were sexually mature in each of the 3 sections is indicated in Table 2 for the 1982 year-class. In all 3 sections no females were mature at age 1. At St. 1, all females older than age 2 were mature. At Sts. 3 and 5, 88% of females ($n=34$) and 38% of females ($n=8$) at age 2 were mature, respectively; and all older females were mature. Thus, age at first maturity in females varied along the river course, being slightly greater upstream.

The estimated longevity of females in each of the 6 sections was 7 years in both Sts. 1 and 2, and 8 years in the remaining sections except St. 5 where it was 9 years (Table 3). These data suggest that females tend to survive slightly longer upstream. On the other hand, the maximum body size of females differed considerably among sections, being generally greater upstream. Throughout all sections, the maximum body size recorded was 114.0 mm SL in St. 5.

Discussion

In the present study, it was evident that growth in female *C. hangiongensis* varied considerably

Table 2. Maturity of female *Cottus hangiongensis* of the 1982 year-class in three sections of the Daitobetsu River.

Section	Maturity at each age (year)									
	II		III		IV		V		VI	
	n	% mature	n	% mature	n	% mature	n	% mature	n	% mature
St. 1	30	100	40	100	14	100	6	100	4	100
St. 2	34	88	25	100	11	100	8	100	5	100
St. 5	8	38	23	100	10	100	12	100	6	100

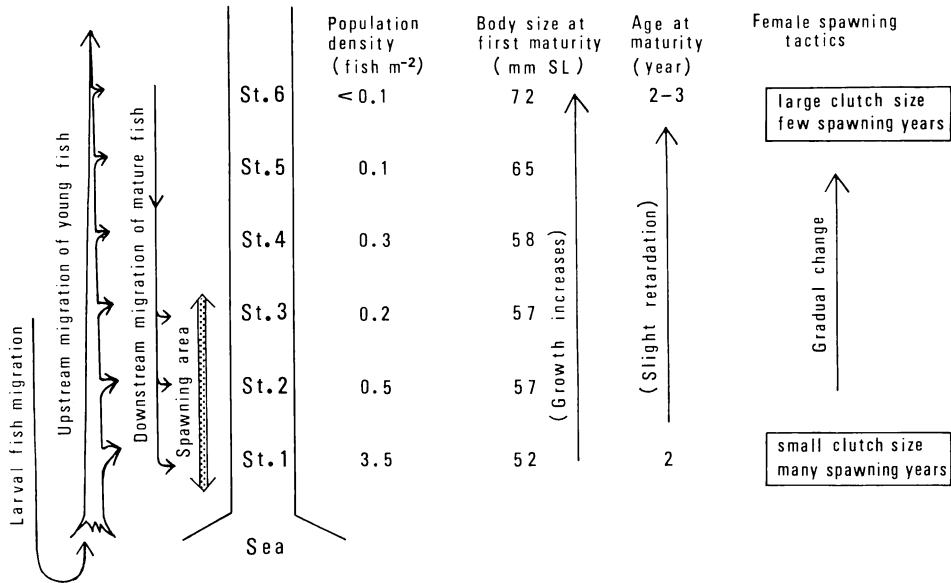


Fig. 7. Schematic diagram of the female reproductive tactics of *Cottus hangiongensis* in the Daitobetsu River.

along the river course and among individual fish. As for the growth variation along the river course, female sculpins had the same tendency as that shown in males, though the range of variations was markedly narrow in the former compared with the latter (Goto, in press). For males, he suggested that such growth variation stemmed from the differences of age at maturity and additionally from the differences of growth rate during the immature period. In this study, age at first sexual maturity in females varied slightly along the river course, from 2 years in St. 1 to 2-3 years in St. 5. Therefore, it is reasonable to consider that the growth variation in females resulted mainly from the differences of growth rate having no relation with maturity. Compared within the same age groups, in fact, the

annual growth in females was greater upstream (Table 1). This may be a reliable reason why female growth variations along the river course are markedly less than those in males. Furthermore, this variation in female growth rate might arise from differences in food conditions, since individual sculpins experienced the following different environmental conditions along the river course: the sculpin densities markedly decrease upstream, whereas the biomass of aquatic insects (the main food for river-sculpins) increases upstream (Goto, 1981, 1986; Yamamoto et al., 1988).

In addition to the growth variation along the river course, the minimum body size and age at first sexual maturity tended to increase upstream from 52 mm SL to 72 mm SL and from 2 years to 2-3 years, respectively. Therefore, it may be concluded that female *C. hangiongensis* exhibit clinal variation in life history along the course of the river, though the variation was somewhat inconspicuous compared with that in the male (Goto, 1987b): sexual maturity at smaller body size and lesser age occurs in the lower reaches and at larger size and slightly older age in upstream areas.

How is such life-history variation in female *C. hangiongensis* caused during the ontogenetic process, and what relationships does the varia-

Table 3. Longevity and maximum body size of females recorded from each of the 6 sections of the Daitobetsu River.

Section	Longevity (year)	Maximum body length (mm)
1	7	97.8
2	7	99.0
3	8	104.5
4	8	103.9
5	9	114.0
6	8	113.7

tion have to their reproductive system? As already reported in the male life-history variation (Goto, 1987b; Usui and Goto, 1987), this species has an amphidromous life cycle and the upstream movement of young individuals appears to occur gradually throughout the period from the summer at age 0 to the next summer. As a result, the migration of the youngest individuals into St. 6 appears to take place during the summer at age 1. In this period, the body size of young sculpins was small in the downstream site and larger upstream. This suggests that either larger individuals among the young females inhabiting downstream areas may migrate further upstream or individuals migrating further upstream grow more rapidly in their new habitat.

As stated before, *C. hangiongensis* is a nest-spawner and has a polygynous mating system wherein male mating success is positively correlated with the body size of males (Goto, 1987a). Thus, in males, upstream and downstream individuals differ in the manner in which they achieve reproductive success. Early maturing males in downstream areas accumulate a few spawnings per season several times in a lifetime. In contrast, upstream males obtain more spawnings per season, but are reproductively active for only a few seasons during their lifetime (Goto, 1987b). For female sculpins, however, the relationship between life-history variation and reproductive tactics seems to require another explanation, because the female reproductive success may be determined in ways different from that of the male.

Like many congeneric species (Mann, 1971; Patten, 1971; Foltz, 1976; Daniels, 1987), clutch size is positively correlated with body size in female *C. hangiongensis*, almost all of which spawn only once a season in spite of the existence of a few twice spawners (Goto, 1987a, 1988). Thus, the female lifetime reproductive success can be estimated nearly from the annual clutch size backcalculated from their body sizes and the number of reproductive years. In female *C. hangiongensis* from the Daitobetsu River, therefore, the following alternative reproductive tactics may exist: when females stay in the lower reaches, they attain sexual maturity at smaller body size and lesser age, and have a small annual clutch size; in contrast, when females migrate to the

upper reaches, their maturity is delayed until they reach a larger body size and slightly greater age, and have a greater annual clutch size (Fig. 7).

Similar life-history or reproductive tactics have been observed minutely in the females of the bullhead, *C. gobio* (Fox, 1978; Mann et al., 1984) and American shad, *Alosa sapidissima* (Carscadden and Leggett, 1975). In the bullhead, however, this occurred between the populations from different geographic areas: the low productive stream population from northern England vs. the high productive one from southern England. In the American shad, on the other hand, the life-history variation occurred among populations from four locations, more than 40 km apart from each other, in the St. John River. Therefore, the alternative life-history or reproductive tactics in female *C. hangiongensis* may be unique due to being formed along only the lower 6 km of a river. Further study is necessary to elucidate if the evolutionary stability of clinal alternative life-history tactics has been established in female *C. hangiongensis*.

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カンキョウカジカ雌の生長と成熟年齢、および生活史変異

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北海道南部の大当別川において、河口から上流約6 km
地点までの流域にほぼ等間隔に7つの調査区域 (St.) を
設けた。各 St. で採集されたカンキョウカジカの雌成魚
(体長50 mm 以上) に個体識別を施し、mark-recapture
法によって、各 St. 毎に同一年級群の生長、個体生長、

成熟サイズと年齢、及び寿命について調査した。同一年
級群の生長は、流程に沿った生息場所によって変異が認
められ、下流ではゆっくりとした生長で、上流に向うに
つれて高生長となる。個体生長に関しても同様の変異の
傾向が認められたが、各個体の生長は同一の生息場所集
団の中でも変異に富むことが観察された。初成熟体長は
最下流域における52 mm から最上流域での72 mm へ
と著しく異なった。一方、初成熟年齢は2 または3 年
であるが、上流では3 年で成熟する個体の割合が高くな
る。また寿命は7~9 年と推定されたが、これにも上流
に向って高齢化する傾向が認められた。以上の結果から、
本種の雌の生活史は流程に沿って変異し、低生長の
下流では若齢・小型で成熟するのに対して、上流では生
長がよく、高齢・大型で成熟すると結論された。また、
このような雌の生活史変異が繁殖システムとの関係で如
何なる意味を有するののかについて考察した。

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