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Movement and Population Size of the River Sculpin *Cottus hangiongensis* in the Daitobetsu River of Southern Hokkaido

Akira Goto

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Abstract Individual movements and population size of the amphidromous sculpin *Cottus hangiongensis*, excluding young-of-the-year smaller than 50 mm in body length, were studied from October 1983 to December 1984 in 5 separate sections of the Daitobetsu River of southern Hokkaido, by using mark-recapture methods. During the non-breeding season, distinct inclinations in density, body length distribution and sex ratio of *C. hangiongensis* populations were found along the course of the river. The population density was the highest, 3.45 per m^2, in the lowest section and decreased in the upper sections. Larger males were found in larger numbers toward the lower reaches, whereas the sex ratio, which was biased in favor of females, was generally more striking upstream. These characteristics of the population structure may result from the amphidromous life history and the polygynous mating system of this species. Many marked fish were recaptured within the original sections, where they had been marked and released, throughout the year. During the non-breeding season, especially, the mean movement was 40.6 m, with the greatest movement being 92 m. During the breeding season, on the other hand, some sculpins appeared to move downstream before spawning and upstream after spawning. Such downstream spawning migration may increase the chance of encountering a mate, and for females it may enhance the chance of encountering larger males. Moreover, it may also contribute to a decrease in the mortality rate of their flowing larvae.

River sculpins of the genus *Cottus* found in Japan have various life history patterns: catadromous for *C. kazika* (Kuroda, 1947), amphidromous for *C. hangiongensis* (Goto, 1977a, 1981) and *C. amblystomopsis* (Goto, 1975, 1980), and fluvial for *C. nozawae* (Goto, 1975, 1977b, 1980) and the "large-egg type" of *C. pollux* (Mizuno and Niwa, 1961). The larvae of *C. hangiongensis* Mori, an amphidromous species, are carried by currents into the sea soon after hatching and then after pelagic life in the sea for about one month, the juveniles ascend uprivers. They are commonly distributed in the rivers of southern Hokkaido (Sato and Kobayashi, 1951; Goto, 1977a, 1981, 1984a). The adult fish of this species inhabit benthically the lower reaches of rivers and feed on larvae of aquatic insects and occasionally on small fish throughout the year (Goto, 1981).

Although river sculpins are generally thought to be relatively sedentary during the non-breeding season (McCleave, 1964; Brown and Downhower, 1982), the spatial stability and movements of adult *C. hangiongensis* populations are hitherto unknown. In the mottled sculpin *C. bairdi*, Bailey (1952) noted limited movement with typical yearly movements of approximately 50 m in a Montana stream, and Brown and Downhower (1982) reported that the mean movement of this species was 1.2 m from June through July in two tributaries of the Gallatin River, Montana. McCleave (1964) estimated that the home range of mottled sculpins was somewhat less than 50 m. On the other hand, Shetter and Hazzard (1939) found considerable instability in a population of mottled sculpins and slimy sculpins (*C. cognatus*) in a Michigan stream.

In the present study, the amphidromous sculpin *C. hangiongensis*, excluding young-of-the-year which were smaller than 50 mm in body length, was studied in the Daitobetsu River of southern Hokkaido throughout the year, in order to determine the spatial stability and movement of the population and to estimate the population size by using mark-recapture methods.

Study area and methods

Study area. The Daitobetsu River studied originates on Oshima Mountain of Hokkaido and

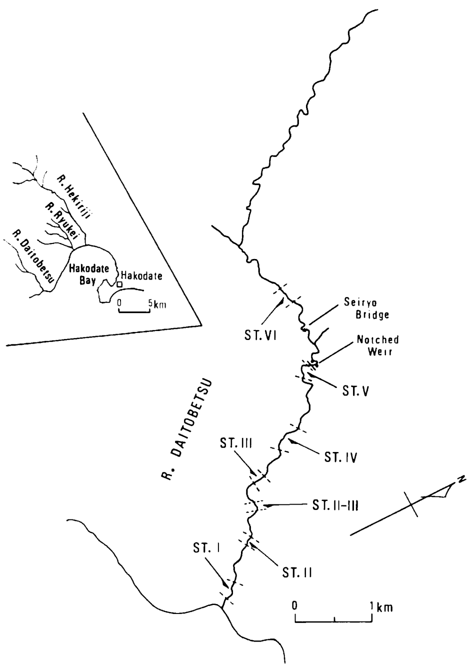

Fig. 1. Map of the Daitobetsu River showing the sections studied.

drains into Hakodate Bay (Fig. 1). It is characterized by relatively high gradients and is about 17 km long. In this river, there is a notched weir approximately 4 km upstream from the river mouth, which partially blocks upstream migration of amphidromous sculpins (Goto, 1984a) so that only a small number of adult *C. hangiongensis* are distributed in waters further upstream from the weir (Goto, 1974).

The study sites were set up within the lower reaches from the river mouth to the notched weir because the spawning grounds of this species and the distribution of the main population were restricted to the lower reaches. Within the lower reaches, five sections, (I-V), 300–500m off each other in length, were established (Fig. 1). The physical characteristics of each section are shown in Table 1. Section I, being 215 m long and 5.2 m wide on the average, consists of Bb type (Kani, 1944; Mizuno and Kawanabe, 1981) with an abundance of various sized rocks. Both Sections II and III, 130 m long and 7.8 m wide and 150 m long and 7.9 m wide respectively, consist of Aa-Bb transition type. Section II has a relative abundance of rocks of various sizes and Section III, of which the bottom mainly consists of gravels, has relatively few rocks. Section IV, the longest section, with a length of 430 m and 5.8 m in width, consists of Aa type and has a rocky bottom in most parts. Section V, being 210 m long and 6.2 m wide, consists of Aa type and is relatively abundant in various sized rocks. Additionally, Section VI, being located upstream beyond the notched weir and consisting of Aa type, was prepared to study the upstream migration of sculpins from below the weir (Fig. 1).

Methods for mark-recapture study. Studies on population estimates and movement of individuals of *C. hangiongensis* were conducted in the Daitobetsu River from October, 1983 to December, 1984. Sculpins larger than 50 mm in body length, which were captured with dip nets and selected from total catches, were anesthetized for a few minutes with approximately 0.0001% ethylaminobenzoate solution before marking. Fish were examined to determine sex by external sexual characters (Goto, 1984b), standard length was measured to the nearest 0.1 mm, and then the fish were marked by removing combinations of 1st dorsal-fin spines and 2nd dorsal-fin rays. Detailed procedures for individual marking has been described elsewhere (Goto, 1985). After mark-

Table 1. Physical characteristics of each section of the Daitobetsu River studied.

Section	Length (m)	Width (m)	Area (m^2)			
		Range Mean	Hayase	Hirase	Pool	Total
I	215	2.6– 8.2 (5.2)	850	250	50	1150
II	130	4.0–12.2 (7.8)	520	260	210	990
III	150	4.8–11.4 (7.9)	640	410	60	1110
IV	430	3.3– 7.7 (5.8)	1430*	510**	490	2430
V	210	4.6– 9.3 (6.2)	470	440	330	910

* This figure includes 470 m^2 of Hayase Rapids with rock bottom.
** This figure includes 170 m^2 of Hirase Rapids with rock bottom.

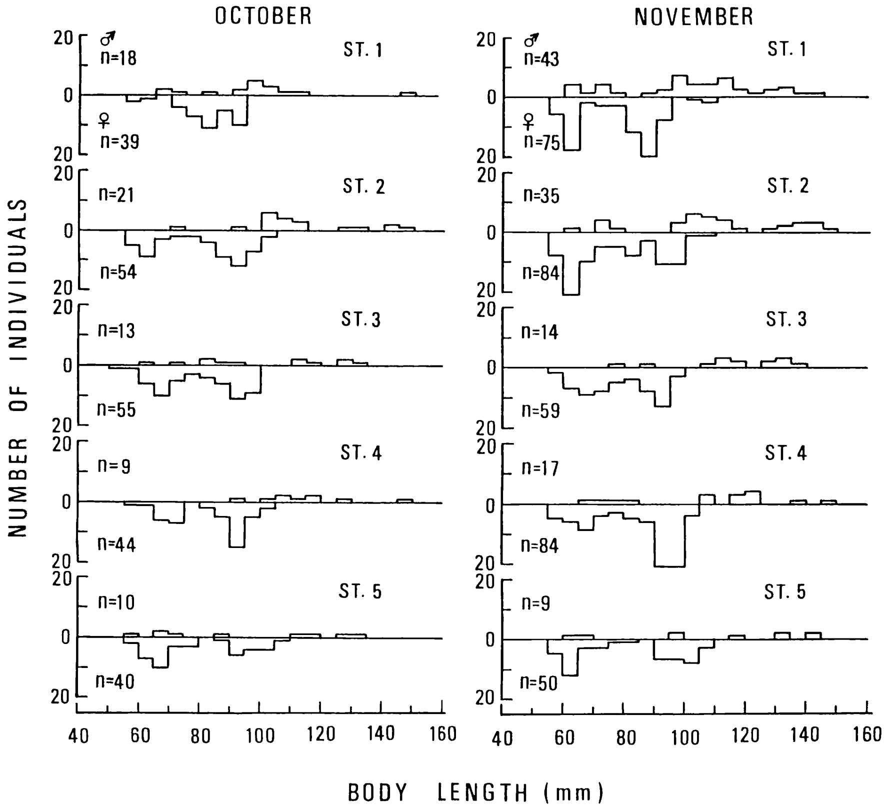

Fig. 2. Length frequency distributions for *Cottus hangiongensis* captured in 5 sections of the Daitobetsu River in October (left side) and in November (right side), 1983.

ing, the fish were placed in a holding crof until completely recovered from the anesthetic, at which time they were released near the middle of each section. During this study, an approximate total of 2,500 sculpins were marked individually in all five sections (I-V).

As a general rule, recapture of marked fish was attempted in each section in every month, from one month after the first marking in October 1983, except in January and February of 1984 when the river was covered with snow. Dip nets were used in recapture attempts, with nearly equal catching efforts, every time. Especially during the period from mid April to early June, 1984, fishing by using dip nets for recapture was done generally every five days in the region between Section II and Section III (Section II-III).

Results

Body length distribution and sex ratio for each section. The body length frequency distributions of male and female sculpins larger than 50 mm are shown for the samples captured in Sections I through V in October and November 1983 (Fig. 2). As pointed out by Goto (1984b), sexual dimorphism in body size where males were larger than females, was found in all sections, particularly in Sections I and II which were located in the lower reaches of the river. Females ranging from 50 mm to 110 mm in body length, mainly appeared to be 1^+ and 2^+ aged fish with the modes of 60–70 mm and about 85–95 mm respectively. In males, the body length ranged from 55 mm to 150 mm, though the age composition could not be inferred from the size distributions.

The sex ratio of sculpins was biased in favor of females at every section in the both months. Moreover, such bias in the sex ratio was generally more striking in the upstream direction where the male/female ratio varied from approximately 1:2 in Section I to about 1:5 in Section V (Fig. 2).

Spatial stability and movement. Movement of sculpins was estimated from the data on location when the marked fish were recaptured (Table 2). Fish recaptured were divided into two groups: one group consisting of recaptures found in their original sections and the other group consisting of recaptures found in sections other than the original sections at which they were released after marking. The latter group was further divided according to whether fish were recaptured in sections in lower reaches or in the upper reaches.

The majority of sculpins recaptured were present in their original sections throughout the year (Table 2). Especially from October 1983 through mid April 1984, all fish were recaptured in the original sections, except two fish, one of which was captured in a downstream section in November and the other which was captured in an upstream section in December. From mid April to May, however, only a few individuals of the total catches were recaptured downstream; in Section II-III, 5 of 63 (7.9%) recaptured fish in April and

Table 2. Movement of *Cottus hangiongensis* throughout the year in the Daitobetsu River.

Recapture month	Number recaptured	Number recaptured in original section	Number recaptured in other sections	
			Upstream	Downstream
Nov., 1983	42	41	0	1
Dec., 1983	95	94	1	0
Mar., 1984	51	51	0	0
Apr., 1984	63	58	0	5*
May, 1984	150	129	0	21
Jun., 1984	120	92	24	4**
Aug., 1984	96	69	20	7
Sep., 1984	98	83	14	1
Oct., 1984	103	87	15	1

* These fish were captured on Apr. 18, 25 and 30.
** These fish were captured on Jun. 2 and 9.

Table 3. Thirty sculpins which moved downstream during the period from late April to early June in the Daitobetsu River, 1984.

Recapture date	Original section	Recapture section	Number of fish	Sex		Body length (mm)
				Male	Female	
Apr. 18	IV	II–III	1	1		138.4
	III	II–III	1		1	90.4
Apr. 25	III	II–III	2	1		120.9
					1	94.9
Apr. 30	III	II–III	1		1	82.2
May 5	IV	II–III	1		1	90.3
May 10	III	II–III	3	1		127.3
					2	67.6, 73.9
	V	II–III	1		1	89.8
May 15	III	II–III	3		3	69.2–73.6
	IV	II–III	2		2	71.8, 72.3
May 20	III	II–III	2		2	69.4, 85.1
	V	II–III	3		3	65.5–105.5
May 26	III	II–III	5		5	66.6–91.1
	IV	II–III	1		1	101.0
Jun. 2	III	II–III	2		2	87.0, 87.2
	IV	II–III	1		1	68.0
Jun. 9	V	II–III	1		1	103.4
Total			30	3	27	

21 of 150 (14.0%) recaptured fish in May. The remaining 58 and 129 marked fish were recaptured in their original section, Section II-III in April and May respectively. Since then, the number of fish recaptured in the downstream sections decreased until October, 1984. On the other hand, the number of marked fish recaptured in the upstream sections increased abruptly in June and then continued to be relatively high in number until October; 24 of 120 (20.0%) recaptured fish in June, 20 of 96 (20.8%) in August, 14 of 98 (14.3%) in September and 15 of 103 (14.6%) in October.

Recaptures in the downstream sections demonstrate that sculpins moved downstream before the time of recapture, whereas those found in the upstream sections indicate the inverse situation. Although techniques for recapture used in this

Table 4. Fourty-four sculpins which moved upstream during the period from June to August in the Daitobetsu River, 1984.

Recapture date	Original section	Recapture section	Number of fish	Sex		Body length (mm)
				Male	Female	
Jun. 2	II	II–III	1		1	76.4
Jun. 9	II	II–III	3		3	65.6–93.5
Jun. 23	I	II	4	1		88.1
					3	68.6–85.5
Jun. 26	II–III	III	9	2		84.8, 102.9
					7	67.8–93.2
Jun. 30	II–III	IV	1		1	75.1
	III	IV	2		2	65.6, 65.7
July 3	II–III	V	3	1		120.2
					2	99.6, 102.7
Aug. 7	I	VI	1		1	80.8
	IV	VI	1	1		87.5
	V	VI	1	1		87.6
Aug. 27	I	III	1		1	75.2
	II	III	1		1	71.7
	II–III	III	6	2		90.0, 107.8
					4	74.8–93.5
Aug. 29	I	II	1	1		97.1
Aug. 30	I	IV	2	1		118.9
					1	79.8
	II–III	IV	2		2	70.2, 74.0
	III	IV	2	1		84.8
					1	73.2
Aug. 31	II–III	V	1		1	77.2
	III	V	1		1	84.8
Total			44	11	33	

Table 5. Home range of *Cottus hangiongensis* during the non-breeding season in the Daitobetsu River.

Section	Distance moved (m)										Total number of fish
	0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	
I	1 (0)*	1 (0)	1 (0)		2 (0)		3 (0)	3 (0)			11 (0)
II		2 (1)	1 (0)	3 (1)	2 (0)	2 (0)	5 (0)				15 (2)
III	4 (3)	2 (1)	3 (1)							1 (1)	10 (6)
Total	5 (3)	5 (2)	5 (1)	3 (1)	4 (0)	2 (0)	8 (0)	3 (0)		1 (1)	36 (8)

* Figures in parentheses indicate the number of fish which moved downstream from the point of release.

Table 6. Summary of a mark-recapture study of *Cottus hangiongensis* during the non-breeding season in sections I through V of the Daitobetsu River.

	Section I					
	X/8	XI/5	XII/3	III/9	Sum	x̄
No. of fish caught	57	128	149	83	417	104.3
No. of unmarked fish	57	123	130	68	378	94.5
No. of recaptures	—	5	19	15	29	13.0
No. of first time recaptures	—	5	19	14	28	12.7
No. of fish marked	57	111	129	—	297	99.0
Proportion of recaptures in catch	—	0.039	0.128	0.181		0.116
Proportion of marked population caught	—	0.088	0.113	0.051		0.084
Cumulative proportion of marked population caught	—	0.088	0.143	0.094		

	Section II					
	X/11	XI/12	XII/7	III/10	Sum	x̄
No. of fish caught	75	119	111	45	350	87.5
No. of unmarked fish	75	100	79	33	287	71.8
No. of recaptures	—	19	32	12	63	21.0
No. of first time recaptures	—	19	27	11	57	19.0
No. of fish marked	75	95	75	—	245	81.7
Proportion of recaptures in catch	—	0.160	0.288	0.267		0.238
Proportion of marked population caught	—	0.253	0.188	0.049		0.163
Cumulative proportion of marked population caught	—	0.253	0.271	0.233		

	Section III					
	X/15	XI/14	XII/12	III/16	Sum	x̄
No. of fish caught	68	73	76	39	256	64.0
No. of unmarked fish	68	69	52	25	214	53.5
No. of recaptures	—	4	24	14	42	14.0
No. of first time recaptures	—	4	24	12	40	13.3
No. of fish marked	68	69	52	—	189	63.0
Proportion of recaptures in catch	—	0.055	0.316	0.359		0.243
Proportion of marked population caught	—	0.059	0.175	0.074		0.103
Cumulative proportion of marked population caught	—	0.059	0.204	0.212		

	Section IV					
	X/26	XI/23	XII/19	III/19	Sum	x̄
No. of fish caught	53	101	68	43	265	66.3
No. of unmarked fish	53	94	59	35	241	60.3
No. of recaptures	—	7	9	8	24	8.0
No. of first time recaptures	—	7	7	8	22	7.3
No. of fish marked	53	88	58	—	199	66.3
Proportion of recaptures in catch	—	0.069	0.132	0.186		0.129
Proportion of marked population caught	—	0.132	0.064	0.040		0.079
Cumulative proportion of marked population caught	—	0.132	0.099	0.111		

Table 6. (continued)

	Section V					
	X/22	XI/21	XII/17	III/22	Sum	x̄
No. of fish caught	50	59	47	23	179	44.8
No. of unmarked fish	50	52	36	21	159	39.8
No. of recaptures	—	7	11	2	20	6.7
No. of first time recaptures	—	7	10	2	19	6.3
No. of fish marked	49	49	36	—	134	44.7
Proportion of recaptures in catch	—	0.119	0.234	0.087		0.147
Proportion of marked population caught	—	0.143	0.112	0.015		0.090
Cumulative proportion of marked population caught	—	0.143	0.173	0.142		

study did not allow for determination of an accurate time when the marked fish moved before their recapture, the fact that there was only one fish recaptured in a downstream section from October 1983 to mid April 1984 (Table 2), strongly suggest that sculpins rarely moved downstream during that period. Therefore, almost all of the 30 marked sculpins which were recaptured in the downstream sections from late April to early June appeared to move downstream during this periods (Table 3). The downstream movement of male sculpins seemed to be restricted in occurrence to the beginning of the periods from mid April to early May, whereas females appeared to move downstream throughout the period. The longest downstream movement that was detected was approximately 2.2 km from Section V to Section II-III, for 5 females which had been marked in Section V and were recaptured in Section II-III. The three males which were recorded to have moved downstream were larger than 120 mm in body length, while the body length of 27 females varied from 65.5 mm to 105.5 mm.

In comparison, the upstream movement of sculpins was observed from June to August. Forty-four marked fish were recaptured in the upstream sections during this period (Table 4). Both male and female sculpins appeared to move upstream throughout this period. The longest upstream movement that was detected was approximately 4.1 km from Section I to Section VI, for one female which had been marked in Section I and was recaptured in Section VI. The body length of 11 males which were recorded to have moved upstream ranged from 84.8 mm to 120.2 mm, while that of 33 females varied from 65.6 mm to 102.7 mm.

Home range. Since it was inferred that the movement of sculpins was restricted to a range almost within the original sections during the non-breeding season, the distances moved during one month, from October to November 1984, were estimated by measuring the length between the point of release and the point of recapture in Sections I to III (Table 5). All sculpins recaptured were within 80 m from the original point of release except for one fish which was observed in Section III and was recaptured at a point 92 m away. The mean movement was 40.6 m for 36 recaptures. The direction of movement was dependent on the direction of stream flow. Of 36 movements in an upstream or a downstream direction, 28 were in the upstream direction ($\chi^2=11.11$, 1 df, $P<.001$). These observations sug-

Table 7. Jolly-Seber estimates of population numbers and population densities of adult *Cottus hangiongensis* in each of 5 sections of the Daitobetsu River in December, 1983.

	Section				
	I	II	III	IV	V
Population numbers	3,970	502	176	853	128
Population densities (/m²):					
in the whole area	3.45	0.507	0.159	0.351	0.103
in the rapids area	3.61	0.644	0.168	0.440	0.141

gest that the river sculpins have home ranges of less than 100 m and that they are inclined to move upstream within the home range during the non-breeding season.

Population size. A summary of a mark-recapture study, carried out in Sections I through V during the non-breeding period from October to November 1984, is indicated in Table 6. In Section I, for example, a total of 297 individuals were marked during this period. Of the total 417 captures, 29 (7.0%) were recaptures of marked fish. Twenty-eight fish (6.7%) were recaptured at least once and one fish (0.2%) was recaptured twice. With regard to the other sections, there were a total of 245 marked fish and 63 recaptures in Section II, 189 marked fish and 42 recaptures in Section III, 199 marked fish and 24 recaptures in Section IV, and 134 marked fish and 20 recaptures in Section V. The highest recapture rate to the total number of marked fish was 25.7% in Section II and the lowest was 9.8% in Section I. The proportion of recaptures in the monthly catches varied from 35.9% in Section III on March 16 to 3.9% in Section I on November 5.

By using the mark-recapture data shown in Table 6 and the Jolly-Seber method (Seber, 1973), the sculpin population, excluding young-of-the-year smaller than 50 mm in body length, was estimated for each section (Table 7). The population size in Section I was 3,970, the largest value among the 5 sections. From the area of 1,150 m^2, the population density in Section I was estimated to be 3.45 per m^2. The estimates of population size and density per m^2 were 502 and 0.507 in Section II, 176 and 0.159 in Section III, 853 and 0.351, and 128 and 0.103 in Section V respectively. When densities were compared in both the whole area and the rapids area for the 5 sections, they were remarkably high in Section I and were inclined to decrease toward the upstream sections from II to V, though an inverse relationship was found between Section III and Section IV.

Discussion

In the Daitobetsu River, the amphidromous sculpin *C. hangiongensis* generally spawns from late April to late May, and has a polygynous mating system, i.e., one male mates with about 5 females on the average (Goto, 1977a, 1981, in press). During the non-breeding season, the distinct inclinations in population density, size composition and sex ratio for the *C. hangiongensis* population were found to vary according to the course of the river. Population density was highest in lowest reaches and was inclined to decrease in the upstream direction. Larger males were more abundant toward the lower reaches, whereas the sex ratio, which was biased towards a greater number of female, was generally more striking upstream. Such characteristics of population structure may result from the life history and mating habits of this species. In *C. hangiongensis,* being an amphidromous fish, the juveniles which ascend upriver from the sea densely populate the benthic, shallow stream margins of the river mouth for a few weeks (Goto, 1981, 1984a). Subsequently, the juveniles disperse and move upstream. These ecological characteristics in the early life cycle are some of the most important influences resulting in inclination of population densities to decrease in the upstream direction along the course of the river. Relating mainly to such gradients of densities, spawning grounds of *C. hangiongensis* are found more abundantly in the lower parts of the distribution range (Goto, 1981). In addition, this species is polygynous. Goto (in press) reported that one male mated with an average of about 5 females in the Daitobetsu River and larger males were inclined to mate with a larger number of females. Therefore, these reproductive characteristics may cause the inclinations of the sex ratio and length distribution according to the course of the river as stated above.

Recapture of many marked sculpins within each original section throughout the year would demonstrate that the adult fish of *C. hangiongensis* moved within an extremely restricted area. Such a restricted area may be called the "home range" of the sculpins, according to the definition which was defined by Gerking (1953) as "the area over which the animal normally travels." Especially during the non-breeding season, the mean distance in which the sculpins moved was within 40.6 m, with the greatest movement being 92 m. These observations suggest that *C. hangiongensis* has a home range of generally less than 50 m, and the size of the home range may be consistent with that estimated in the mottled sculpin *C. bairdi* by McCleave (1964). For the mottled sculpin, McCleave (1964) reported that the home range was somewhat less than 50 m. Recently, Brown and

Downhower (1982) estimated that the mean movement of the mottled sculpin was 1.2 m, with 14.3 m being the greatest recorded movement in June and July. However, these are rough estimates in all cases and thus are not suitable for accurate comparison because the home-range size is influenced by many factors, including stream width, riffle-pool development and food abundance, as pointed out by McCleave (1964).

During the breeding season, on the other hand, only a few marked sculpins were recaptured in the downstream sections from late April to early June, and in the upstream sections from June to August (Table 2). These observations do not necessarily show that a downstream or upstream movement had occurred throughout those periods because the sculpins recaptured in each late period might have moved downstream or upstream before the time of recapture. Therefore, it is reasonable to presume that some sculpins move downstream before spawning and upstream after spawning. Since the longest downstream movement recorded was about 2.2 km and the longest upstream one was about 4.1 km, and such long movements occurred only during the breeding season, the movements may be called a kind of spawning migration in the downstream direction. For freshwater sculpins, a downstream spawning migration has been reported only in catadromous fish such as *Trachidermus fasciatus* (Tsukahara, 1952), *C. kazika* (Kuroda, 1947) and the coastal populations of *C. asper* (Krejsa, 1967). On the other hand, upstream spawning migration has been observed in *C. semiscaber* (Simon and Brown, 1943) and *C. rhotheus* (Thomas, 1973) which may have a fluvial life history. It appears that the downstream spawning migration observed in *C. hangiongensis* is the first reported for amphidromous sculpins.

In spite of many *C. hangiongensis* adults being sedentary in Section II-III, why do adults in further upstream sections move downstream before spawning? As already stated, *C. hangiongensis* is a polygynous species of which one male mates with several females, and of which spawning grounds are distributed more abundantly in the lower course of the river (Goto, 1981, in press). With regard to reproductive behavior, a male of this species occupies space under a rock as a spawning nest and then mates there successively with various females. The females may choose a larger male for a mate prior to mating (Goto, in prees). In the Daitobetsu River, the population density was highest in the lower reaches and was inclined to decrease upstream. The large-sized males were more abundant in the lower parts of the distribution range. Therefore, if the adult fish inhabiting the upper stream move downstream before spawning, they may have a better chance of encountering a mate and chances that females encounter larger males also increase. In addition, if the females deposit their eggs in the lower reaches, the larvae hatched from the eggs can flow downstream a shorter distance to the sea and thus will be able to reach it in a shorter time. If the time in which the larvae spend reaching the sea is shorter, the mortality rate of them may be lower because the flowing larvae, taking nutrition only from the yolk, can scarcely survive in fresh water for more than 5 days due to starvation and/or unsuitable osmoregulation (Goto, unpublished data). These may be important factors contributing to the development of downstream spawning migration in *C. hangiongensis,* though it is not clear whether all adult sculpins inhabiting the upper stream or only a part of them do migrate downstream for spawning.

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(Laboratory of Embryology and Genetics, Faculty of Fisheries, Hokkaido University, Hakodate 041, Japan)

大当別川におけるカンキョウカジカの河川内移動と個体数

後藤　晃

北海道南部の大当別川において，河口から上流約 4 km 地点までの流域にほぼ等間隔に 5 つの調査区域 (I～V) を設けた．各区域で採集されたカンキョウカジカの成魚 (体長 50 mm 以上) に個体識別マークを施し，mark-recapture 法によって，河川内移動，home range，流程に沿った個体群密度の変化について調査した．非繁殖期において，生息密度，体長組成及び性比に流程に沿った傾斜が認められた．つまり，生息密度は，最下流域の区域 I で最も高く (3.45 尾/m^2)，上流に向うにつれて低くなる．大型の雄は下流域に多く，上流に向うにつれて減少する．また，性比 (♂ : ♀) は区域 I では約 1 : 3 であり，上流に向うにつれて雌の比率がより高くなる．この時期には，各個体の生息場所は安定しており，その home range は流程で平均 40.6 m であった．一方，繁殖期には，数 km に及ぶ河川内での移動が認められた．つまり，繁殖期前期には，上流域に生息していた個体が下流方向に，また，繁殖終了期には，下流から上流方向に移動が起こる．この繁殖期にみられる移動は産卵回遊の一形態とみなされ，本種の両側回遊性の生活環，個体群構造の特徴及び一夫多妻的婚姻システムからみて，適応的な行動習性であると考えられる．

(041 函館市港町 3-1-1 北海道大学水産学部発生学・遺伝学講座)