Japanese Journal of Ichthyology
Vol. 34, No. 4 1988

魚類学雑誌
34巻4号 1988年

Reproductive Behavior and Homing after Downstream Spawning Migration in the River Sculpin, *Cottus hangiongensis*

Akira Goto

(Received April 18, 1987)

Abstract Reproductive behavior, distribution of spawning grounds and possibility of reproductive homing were studied and examined in the river sculpin, *Cottus hangiongensis*. The courtship, spawning behavior and parental care of this species, observed under artificial stream conditions using a fiber-scope, were quite similar to those of several congenous species already reported. In a natural river, the spawning grounds were restricted to the lower reaches within the distribution range of the species. Slightly before the spawning period, mature individuals inhabiting more upper reaches than the spawning area migrated downstream to the spawning area. The upstream movement of many individuals, apparently downstream migrants only, was observed just after the spawning period. By tracing the location at recapture, it was detected that a total of 11 marked individuals (10 females and 1 male) migrated downstream before spawning, and after spawning they migrated upstream and returned to the original home sections. This suggests the ability for reproductive homing.

The river sculpin, *Cottus hangiongensis* Mori, is a bottom dwelling cottid fish commonly distributed in the rivers of southern Hokkaido, Japan. This species has an amphidromous life cycle (sensu Myers, 1949) and the adults abundantly inhabit the lower course of rivers (Goto, 1981). The newly hatched pelagic larvae are transported into the sea from their spawning grounds in the rivers, and after spending about one month in the sea the juveniles ascend the river to live in riffles with gravelly substrata.

With regard to the breeding habits, *C. hangiongensis* is a nest spawner that breeds under rocks in spring, and the parental male guards the eggs deposited (Sato and Kobayashi, 1953; Goto, 1981). However, little has hitherto been recorded on the courtship, spawning and parental care behavior of this species, because it is quite difficult to observe their behavior performed in the dark and narrow cavity under a rock.

Recently, Goto (1986, 1987a) studied on the population structure, individual movements and mating system of *C. hangiongensis* in some natural rivers, with the following findings: this species is polygynous and larger males receive more spawnings, because females prefer to mate with such males. The mature sculpins gather at the restricted spawning area from various habitats slightly before the breeding period. Among them, both the mature females and males which inhabit the upper reaches migrate downstream for spawning. After spawning, some spent fish move upstream from the spawning area.

If the upstream migrants are identical to the previous downstream spawning migrants and they return to the original habitats, it is possible to infer that they have homing ability. Homing habits are biologically important behaviors exhibited by many fish species (Gerking, 1959; Malinin, 1969; Leggett, 1977; McKeown, 1984). In *C. hangiongensis*, however, it has not been shown whether the migrants return to the original home site after spawning.

The objectives of this study are to observe the reproductive behavior of the river sculpin using a fiber-scope, to estimate the extent of available spawning grounds within the distribution range, and to determine the homing ability of the downstream spawning migrants.

Materials and methods

For observation on the reproductive behavior, mature individuals of *C. hangiongensis* were captured in the Daitobetsu River near Hakodate, Hokkaido (Fig. 1), on April 29 and 30, 1985. They were transported to the Nanae Fish Culture Experimental Station, Hokkaido University. Gravid females having fully ripe eggs and males oozing milt when squeezed at the abdomen were

selected from them and kept separately in the holding cages. Six males and 20 females were transferred into the experimental section, which was located in a streamlet flowing through the station and was covered before and behind with wire netting as already described in my previous work (Goto, 1987a). On the stream bed, six rectangular concrete tiles of same size (30×30 cm) had been placed beforehand at regular distances.

The fish were kept in the section for 18 days from May 5 to May 22. During this period, observations were made using a fiber-scope and the behavior of the fish was recorded by video tape recorder (Fig. 2), because of the difficulty in observing directly the behavior under the tiles. Their behavior was analyzed by seeing the video repeatedly.

Field studies on the distribution of spawning nests along a stream and homing after downstream spawning migration were conducted in the Daitobetsu River for 4 years from 1983 to 1986. Within the lower reaches, six sections (St. 1-St. 6), separated from each other by 300–500 m, were established (Fig. 1). The physical characteristics of the sections were previously described (Goto, 1986).

In both April and May of 1985 and May of 1986, the breeding season, the spawning nests were located in every 6 sections, in order to find the range and suitability of spawning grounds along the river. Movements of individuals during this season, especially the probability of homing after downstream movement, were studied by a mark-recapture method. The methods of individual identification by fin spine and ray removed and recapture for marked fish had already been described (Goto, 1985, 1986). As a general rule, recaptures of marked fish were made monthly

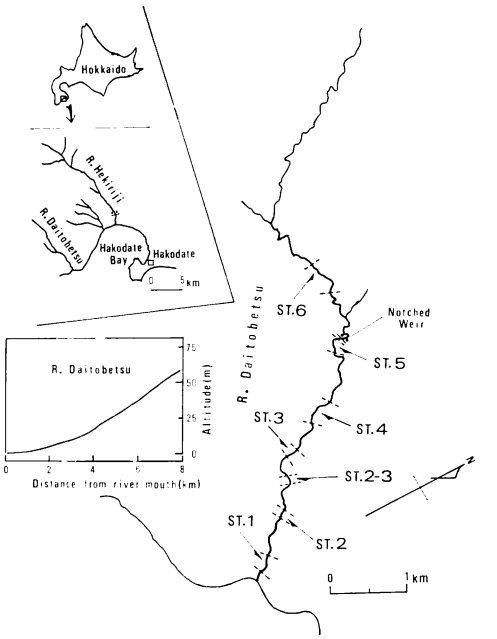

Fig. 1. Map of the Daitobetsu River and the study sites.

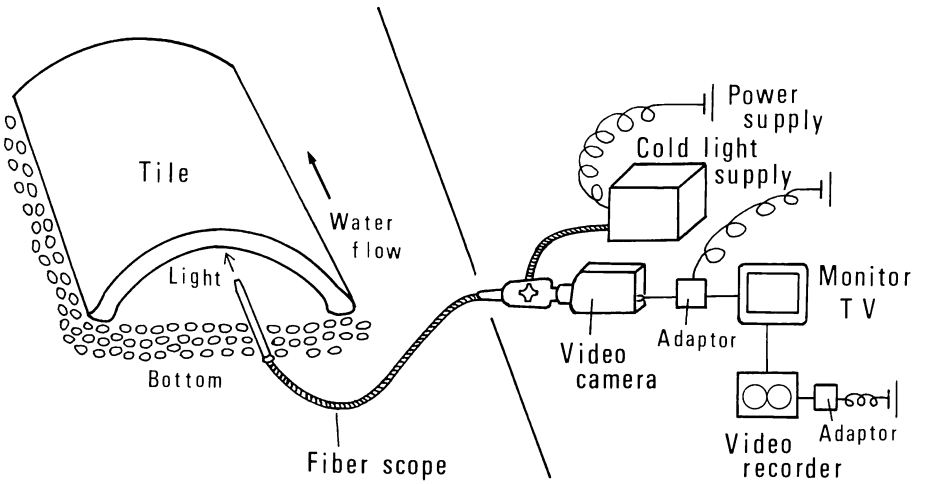

Fig. 2. Apparatus for observation on the reproductive behavior of *Cottus hangiongensis*. Reflections of fish behavior taken through a fiber-scope with lighting fixtures at the point were projected on a monitor television and recorded by a video tape recorder.

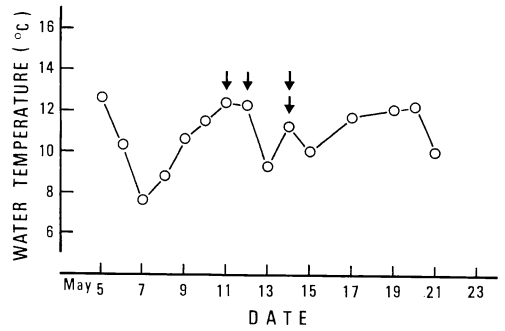

Fig. 3. Dates of spawning (arrows) and changes of water temperature (open circles) during the observation period of the behavior of *Cottus hangiongensis* in 1985.

with dip nets in each section. Movements of marked individuals were traced by the location of recaptures taken throughout the year. If marked fish which migrated downstream for spawning are subsequently recaptured within their original sections, it can be inferred that they have homed.

Results

Spawning behavior and parental care. By using a fiber-scope, it was possible to observe clearly the behavior of sculpins in a dark and narrow cavity under a tile, when direct observation was difficult.

Spawning behavior of *C. hangiongensis* was observed four times involving a dominant male and four different females: once on May 11 and 12 and twice on May 14 (Fig. 3). In every case, the spawning took place during the day from 11: 00 to 14: 00 and with quite similar behavioral patterns, as described below. The water temperature on the days of spawning ranged from 11° to 12°C at 12: 00 hrs.

The sequence of spawning behavior of *C. hangiongensis* was quite similar to that of *C. nozawae* (Goto, 1982). The dominant male, which was the largest among males, occupied a cavity under a tile as the nest and usually lay at the entrance with his darkish head facing outwards. The male sometimes turned upsidedown and undulated his body laterally in this position, apparently cleaning the roof of the nest with the anal fin, on which a female would shortly lay her eggs. When a female came into sight (Fig. 4A), the male dashed toward the female and returned swiftly to the original position in the nest cavity. At this time, the body coloration of the male turned pale black from cryptical greenish brown. The female followed him and entered the nest cavity.

In the nest, both the male and female lay side by side (Fig. 4B), and the male pressed up to the female, holding her in a corner. With this behavior, the male undulated his body vigorously and nodded his head frequently. After a few minutes, the male turned upsidedown and held his inverted body on the roof of the nest with the expanded dorsal, pectoral and caudal fins (Fig. 4C). Soon, the female followed him in the same manner and lay by the side of the male in the upside-down position. The male lay with his head underneath her and with his body twisted so that his tail kept alongside hers. In this position, the male opened his mouth to a great extent, with the gill-covers raised and all the fins spreaded, and slightly shivered his body for about ten seconds. This action appeared to indicate the male had released the milt, but no milky spot representing the milt was visible. Synchronized with the male's behavior, the female also opened her mouth widely and deposited eggs on the roof of the nest (Fig. 4D).

Soon after spawning, the male turned back to rightside-up position and lay on the floor of the nest. The spent female ramained on the deposited eggs in upside-down position for 20–30 minutes and then turned rightside-up. When the female did so, the male attacked her with antagonistic actions such as chasing and biting. Due to this behavior, the spent female was driven away from the nest and did not take any further part in the reproductive behavior.

After the first spawning, the male remaining in the nest mated with three different females in the same manner, and then he stayed in the nest to guard the eggs for about four weeks until they hatched. During this time, the male, lying at the nest entrance, leaped out to attack any intruder which approached his nest. Additionally, the male often fanned the eggs with his pectoral fins and in upside-down position undulated the body laterally, apparently cleaning the surface of the eggs with the anal fin which become longer as one of the secondary sexual characteristics (Goto, 1984).

Distribution of spawning nests along a natural

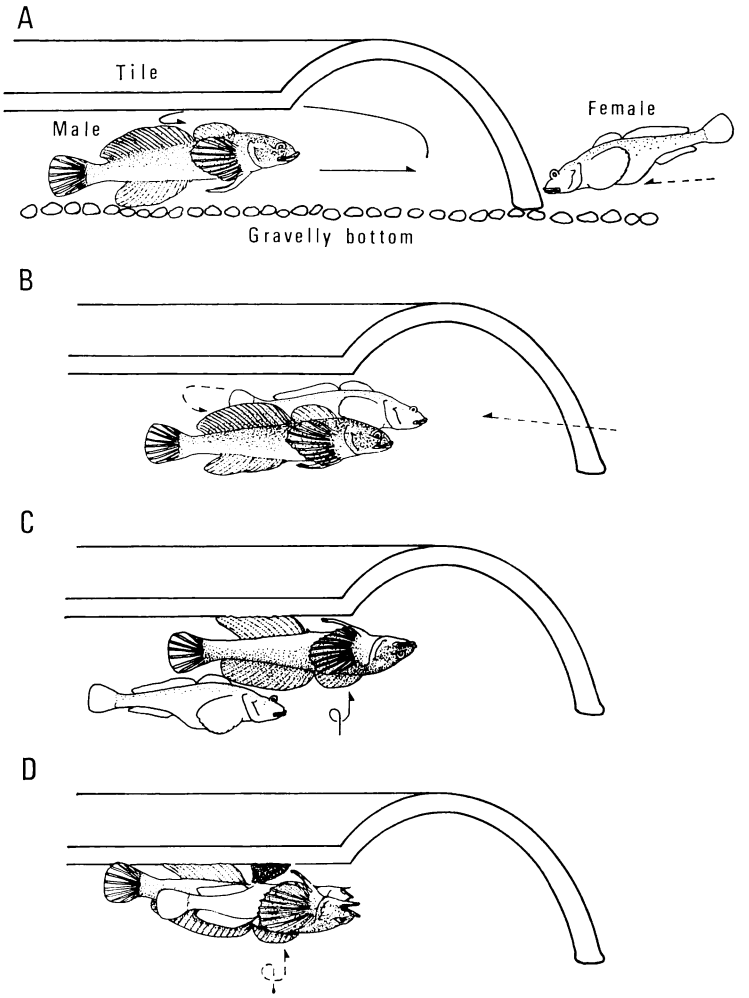

Fig. 4. Four stages in the spawning sequence of *Cottus hangiongensis*. A: When a male at the entrance of a tile encounters a female coming up to the nest, he dashes toward the female and returns to the original position. B: The female enters the nest cavity following the male and lies by his side. C: The male turns upsidedown before the female does so. D: After the female turned upsidedown, the male lies with his head underneath her and spawning occurs in this position.

river. In the Daitobetsu River, a total number of 41 egg-clusters were found in St. 1 through St. 6 in the 1985 spawning season; 14 egg-clusters in April and 27 egg-clusters in May (Table 1). Through 6 sections, the more abundant egg-clusters were observed in St. 1 and St. 2; 18 in St. 1 and 20 in St. 2. Only 3 egg-clusters were present in St. 3. In the remaining three sections farther upperstream, no egg-clusters were found. Similar distribution patterns of egg-clusters deposited along the river were also observed in May 1986.

These data demonstrate that the spawning area

Table 1. Number of deposited egg-clusters of *Cottus hangiongensis*, observed in the Daitobetsu River during the breeding periods of 1985 and 1986.

Section	1985			1986
	April	May	Total	May
1	5	13	18	11
2	8	12	20	9
3	1	2	3	1
4	—	0	0	0
5	0	0	0	0
6	0	0	0	0

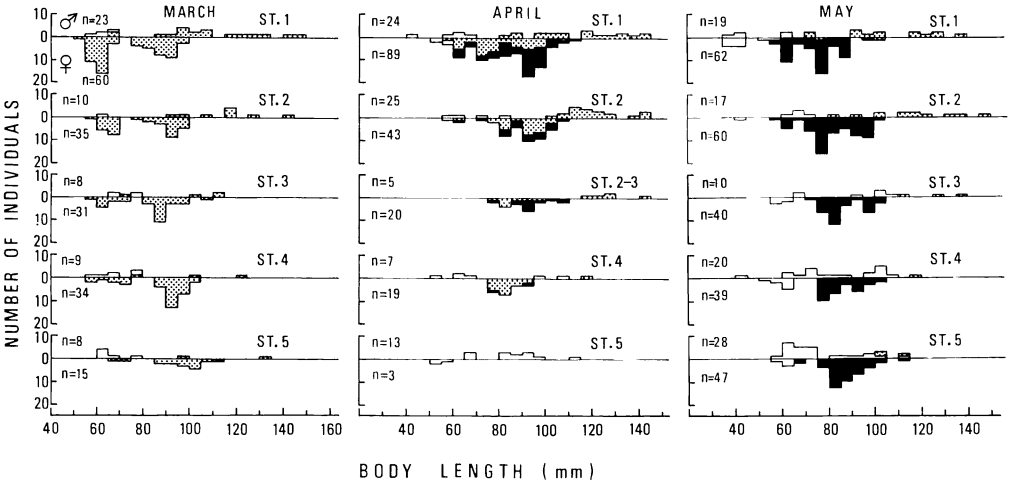

Fig. 5. Length-frequency distributions of *Cottus hangiongensis* captured monthly in each of 6 sections of the Daitobetsu River from March to May, 1985. □, immature fish; ⁘, mature fish; ■, spent fish.

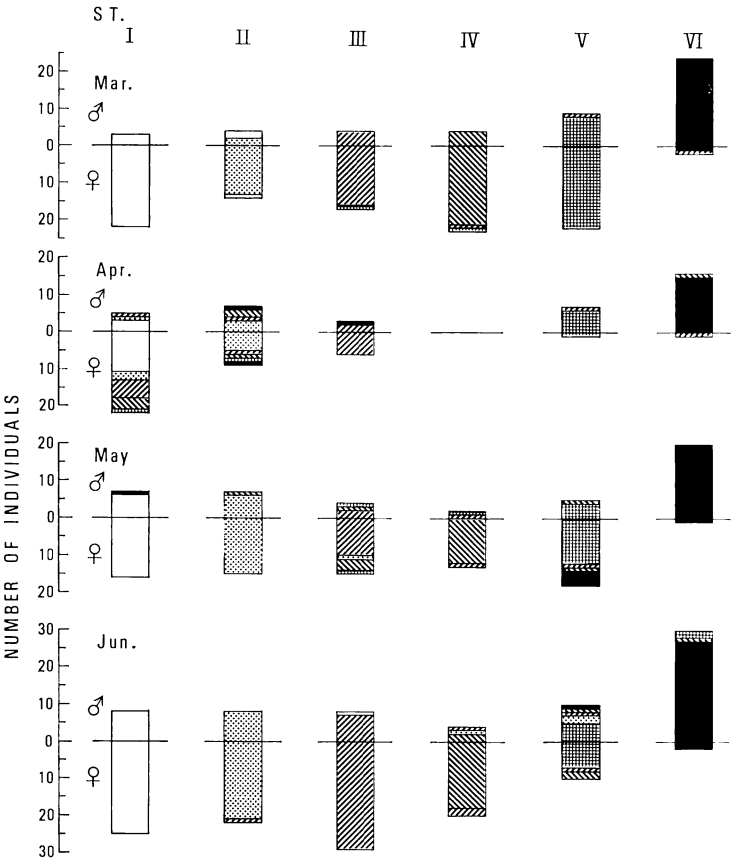

Fig. 6. Marked individuals recaptured in each of 6 sections of the Daitobetsu River from March to June, 1985. Shown are number of fish recaptured in the original sections above the total number of fish recaptured. □, fish marked in St. 1; ⁘, fish marked in St. 2; ▨, fish marked in St. 3; ▧, fish marked in St. 4; ▦, fish marked in St. 5; ■, fish marked in St. 6.

of *C. hangiongensis* is restricted to the lower reaches from St. 1 to St. 3 and the more suitable spawning grounds are located in the area from St. 1 to St. 2. This fact may be related to the observations that in the prespawning season the mature adults inhabiting further upstream locations than St. 3 migrate downstream mainly to the region from St. 1 to St. 2 for spawning (Goto, 1986).

Homing after downstream spawning migration. The length frequency distributions of *C. hangiongensis* captured monthly in each section from St. 1 to St. 5 of the Daitobetsu River from late March to late May 1985 are shown in Fig. 5. In late March, slightly prior to the breeding season, mature males and females were captured in all 5 sections, though there were considerable differences among the 5 sections in the relative abundance of mature males to the total catches and in the size composition of mature females. In late April, many spent females had already been found in each section lower than St. 4. In St. 5, on the other hand, no spent or mature females were captured, though 3 immature females were caught. This may indicate that mature females in St. 5 had already migrated downstream to the spawning grounds. In late May, only immature and spent females were captured in all 5 sections. Many spent females captured in St. 5 may have migrated upstream from the spawning grounds after spawning.

Movements of adult sculpins during the periods from March to June in 1985 were inferred from the mark-recapture data (Fig. 6). In late March, the prespawning period, all or almost all of the sculpins recaptured were in their original sections. In late April, the early spawning period, about half the sculpins recaptured in St. 1 and St. 2 were in the original section and the remaining recaptures were composed of individuals which were marked in the upstream sections; in St. 1, 2 of 5 males recaptured were individuals marked in St. 2 and St. 3 and 11 of 22 females recaptured were individuals marked in St. 2 (2 fish), St. 3 (5 fish), St. 4 (3 fish) and St. 5 (1 fish), and in St. 2, 4 of 7 males recaptured were individuals marked in St. 3 (1 fish), St. 4 (2 fish) and St. 6 (1 fish) and 4 of 9 females recaptured were individuals marked in St. 3 to St. 6 (each 1 fish). In each upstream section from St. 3, on the other hand, the recaptures were almost all in their original sections.

Table 2. Records on homing of marked individuals after downstream spawning migration in the Daitobetsu River.

Number of individuals	Marking				1st recapture			2nd recapture			3rd recapture		
	St.	Date	SL (mm)	Sex	St.	Date	SL (mm)	St.	Date	SL (mm)	St.	Date	SL (mm)
III-6	3	Oct. 15, '83	64.6	F	2–3	May 10, '84	67.6	3	Jun. 24, '85	81.2			
III-76	3	Nov. 14, '83	87.0	F	2–3	Jun. 2, '84	87.2	3	Nov. 20, '84	91.2			
III-99	3	Nov. 14, '83	67.8	F	2–3	May 20, '84	69.4	3	Mar. 22, '85	80.5	3	Jun. 6, '85	81.0
III-118	3	Nov. 14, '83	70.0	F	2–3	May 26, '84	70.1	3	Aug. 27, '84	75.2			
III-259	3	Aug. 27, '84	100.7	F	1	Apr. 28, '85	102.6	3	Jul. 21, '85	103.4			
IV-7	4	Oct. 26, '83	65.4	F	4	Mar. 23, '85	81.8	2	Apr. 27, '85	82.5	4	May 29, '86	89.0
IV-52	4	Nov. 23, '83	71.9	F	2–3	May 15, '84	72.3	4	Aug. 23, '85	83.9			
VI-7	6	Jul. 26, '84	84.1	F	5	May 31, '85	90.1	4	Sep. 16, '85	97.8	6	Jul. 17, '86	101.6
VI-15	6	Aug. 7, '84	76.9	F	5	May 31, '85	86.4	6	Jun. 21, '86	97.0			
VI-153	6	Oct. 4, '84	99.2	F	2	Apr. 29, '85	103.3	6	Jun. 21, '86	111.8	6	Jul. 17, '86	113.7
VI-239	6	Dec. 11, '84	123.0	M	2–3	Apr. 10, '85	123.3	6	Nov. 18, '85	129.8			

In late May, the late spawing period, all of the females recaptured in St. 1 and St. 2 were in their original sections. Among males recaptured in St. 1 and St. 2, a few individuals marked in the upstream sections were included; one of 7 fish in the both sections, and captured an individual marked in St. 6 and taken from St. 1 and another marked in St. 4 and captured in St. 2. In late June, the postspawning period, all of the sculpins recaptured in St. 1 and St. 2, except one female which was marked in St. 4 and recaptured in St. 2, were in the original section. These data show that the sculpins inhabited originally St. 1 or St. 2 and remained there even after spawning, whereas the downstream spawning migrants into St. 1 or St. 2 emigrated from the section after spawning. The male migrants, however, were inclined to stay in St. 1 or St. 2 longer than the female migrants probably due to the parental care habits. Therefore, it is suggested that the upstream movements observed after the spawning period are performed by the downstream migrants themselves, and there is a possibility that they may return to the original upstream section.

Direct evidence for homing to the original section is provided by the movements of marked individuals which were traced by the location at recapture (Table 2). The eleven sculpins, 10 females and 1 male, listed here are individuals which were marked in each section during the non-breeding period, were recaptured in the downstream section during the breeding period and then recaptured again in the original section during the non-breeding period. For instance, female III-259 marked in St. 3 on August 27, 1984, was recaptured in St. 1 on April 28, 1985, and recaptured again in St. 3 on July 21, 1985. Among 11 fish, the longest round-trip detected was approximately 10 km for female VI-153 which migrated downstream from St. 6 to St. 2 and returned to St. 6, the original section.

Discussion

The reproductive behavior of *C. hangiongensis*, observed in the present study, is basically similar to those of congenous species such as *C. gobio* (Morris, 1954), *C. poecilopus* (Starmach, 1962), *C. bairdi* (Savage, 1963) and *C. nozawae* (Goto, 1982), especially in view of the male's initiation of a sequence of courtship and spawning behavior, and the parental care of the deposited eggs by the male only.

The data on the distribution of deposited egg-clusters distinctly demonstrate that in the Daitobetsu River the spawning area is restricted to the lower reaches from St. 1 to St. 3. Although there was no direct observation of the spawning behavior in the reaches, the abundance of the egg-clusters deposited and the downstream spawning migration of mature fish into the reaches from the upperstream habitats suggest that the sculpins recognize the lower reaches as suitable spawning habitats. Mainly due to the polygynous mating style and the amphidromous life cycle, such a restricted spawning area within the lower reaches may be advantageous for this species. Because, if the spawning grounds are restricted and concentrated in the lower reaches, this may increase the chance of encountering a mate and may also contribute to decrease in the mortality rate of the flowing larvae (Goto, 1986).

In the Daitobetsu River, adult *C. hangiongensis* inhabiting the upper reaches apart from the spawning area migrate downstream to the spawning area slightly before the spawning period and after reaching sexual maturity (Goto, 1986, 1987b). Evidence on the movement of individuals suggests that at least some of such downstream migrants migrate upstream and return to the original home sites after participating in reproduction. According to Gerking's definition of homing as the return of an animal to a place formerly occupied rather than to equally probable places (Gerking, 1959), it is possible to infer that *C. hangiongensis* has the ability of reproductive homing. In cottid fishes, such homing behavior has not hitherto been reported for any freshwater species, though it is known that some intertidal species such as *Oligocottus maculosus* (Green, 1971; Khoo, 1974; Craik, 1980), *Clinocottus analis* (Williams, 1957) and *Clinocottus globiceps* (Green, 1973) have a distinct homing performance to the home pool.

What meaning does such reproductive homing have for individuals of *C. hangiongensis*, and why is there such difference between sexes in returning to the home sites, as females home more frequently than males? In the Daitobetsu River population, there exists the following life history variation in males along the course of the river: males inhabiting the lower reaches attain sexual maturity at smaller body size, younger age and continue to

spawn for many years, and the opposite holds true for males inhabiting the upper reaches (Goto, 1987b; Usui and Goto, 1987). For instance, males inhabiting St. 1 within the spawning area attain sexual maturity at about 70 mm SL and 2 or 3 years old, whereas males inhabiting St. 6, far from the spawning area, do so at about 120 mm and 4 or 5 years old. These large-sized altricial males inhabiting the upper reaches migrate downstream to the spawning area after sexual maturity and take part in reproduction. Thereafter, a majority of them appear to die a natural death and the remaining males survive probably for one more year after returning to the original home sites. In females, on the other hand, there is not such life history variation as found in males, though it has been found that at the same age females inhabiting more upper reaches become larger in size because of a higher growth rate (Goto, unpublished data). Females inhabiting the upper reaches attain first sexual maturity at 2 years old, as do females inhabiting the lower reaches, so that a majority of them survive for a few more years after downstream migration and subsequent spawning. The difference in mortality rate between sexes of the downstream migrants after spawning may explain the difference observed between sexes in the number of individuals returning to the home sites. If the survivals of downstream migrants return to the upperstream original habitats and live there, they would be able to maintain the higher growth rate so that they would attain larger body size. As a result, the migrants having the homing ability may increase their reproductive success in the next year, because larger males are more successful in mating with females (Goto, 1987a) and larger females have larger litter size (Goto, 1981).

This study on homing has raised the following question; what is the mechanism by which the migrants of *C. hangiongensis* find their home sites? Unfortunately, there has been no distinct evidence to answer the question. However, some observations on the restricted movements and the narrow home range of less than 50 m during the non-breeding season (Goto, 1986), indicating their home site fidelity, suggest that local topographical cues may be important for homing success. Olfactory cues may also play an important role in recognizing and orientating to the home site, as pointed out in fish species making restricted movement (Gunning, 1959; McKeown, 1984). Such sensory basis for homing has been experimentally examined with other non-migratory fish (Gunning, 1959; Khoo, 1974; Goff and Green, 1978). Further study is necessary to make clear if the migrants of *C. hangiongensis* have homing ability even during the non-breeding season, and to find what kind of cues are actually used for homing by this species.

Acknowledgments

I wish to express my heartful thanks to Drs. Keikichi Hamada and Fumio Yamazaki, Faculty of Fisheries, Hokkaido University, for their advice and encouragement. Mr. John Goodier corrected the manuscript, and I express sincere thanks. Thanks are also offered to Dr. Hiroshi Onozato and Mr. Shizuo Kimura, Nanae Fish Culture Experimental Station, Hokkaido University, for their kind advice and permission to use the facilities of the Station. This work was partly supported by a Grant-in-Aid for Special Project Reseach (Nos. 59115004, 60107002) from the Japan Ministry of Education, Science and Culture.

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

カンキョウカジカの繁殖行動とホーミング

後藤　晃

小川を仕切って設けた環境条件下において，カンキョウカジカの繁殖行動をファイバースコープを用いて観察した．また，北海道南部の大当別川において，流程に沿ったカンキョウカジカの産卵場の分布，および産卵期前後における成魚の移動と移動個体のホーミングの有無をmark-recapture 法によって調査した．本種の求愛行動，産卵行動および雄による卵保護行動は，同属の他種のそれらと極めて類似し，求愛行動・産卵行動は雄主導型であった．大当別川における本種の産卵場は河口近くからその約 2 km 上流地点までの下流部に限られた．産卵域より上流部に生息する成魚個体は，産卵期直前に産卵域へ降下移動した．一方，産卵域内に生息していた成魚個体は産卵期を通じて定住的であった．上流部から産卵降下移動した個体のうち，11 個体は産卵期に 産卵域内で再捕獲され，産卵後もとの上流部のそれぞれの生息域で再び再捕されたことから，産卵降下移動する個体はホーミング習性をもつことが示唆された．この産卵回遊とホーミングは，非繁殖期には産卵域を離れ，その上流部に生息する個体に高成長を保障し，雌にとっては一腹卵数の増加を，また雄にとっては大型化による繁殖成功度の増大をもたらすと考えられる．

(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)