Effects of Parental Care on Egg Survival Estimated from an Experimental Removal of Nest-Guarding Males in the River Sculpin Cottus amblystomopsis

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Parental care characterizes reproductive habits in three freshwater sculpin genera, *Cottus*, *Trachidermus* and *Cottocomephorus* (Tsukahara, 1952; Scott and Crossman, 1973; Chernyaev, 1985). Their reproductive style is speleophils, characterized by nest spawning, adhesive eggs and moderately developed embryonic respiratory structures, according to Balon's (1975, 1985) definition of reproductive guilds in fishes.

In some Cottus species, spawning behavior and male parental care behavior have been observed under both natural and artificial conditions (Simon and Brown, 1943; Morris, 1954; Starmach, 1962; Savage, 1963; Goto, 1982, 1988a). The reproductive behavior of Cottus is initiated by the male. It involves the formation of the male's reproductive territory under a flat-bottomed stone, courtship, spawning behavior and paternal egg care. Morris (1954) observed in the bullhead C. gobio that nesting males aerate the eggs by fanning their pectoral fins, and guard the eggs against predators of both their own species and other species. Similar paternal care behavior is found in C. nozawae (Goto, 1982) and C. hangiongensis (Goto, 1988a). The significance of paternal care for offspring survival in freshwater sculpins has been little studied (Downhower and Yost, 1977), though there have been many studies on the male's role in the three-spined stickleback Gasterosteus aculeatus which demonstrate the importance of paternal care (Black, 1971; Sargent and Gebler, 1980; Pressley, 1981; Giles, 1984). In fishes, few field studies have experimentally tested the assumed benefit of paternal tending (Downhower and Yost, 1977; Dominey, 1981, cited in Bain and Helfrich, 1983; Blumer, 1985; DeMartini, 1987).

The amphidromous sculpin *Cottus amblystomopsis* Schmidt is widely distributed in Hokkaido Island of Japan and in Sakhalin of USSR (Goto,

1975a, b, 1981, 1983). In this species, spawning occurs in the lower reaches of rivers in early spring. Nesting males generally mate with several females, and then guard the deposited egg-cluster which is attached strongly to the roof of the nest until hatching (Goto, 1975a and unpublished data).

In the present study, I experimentally removed guarding males in order to determine whether or not male attendance actually benefits offspring, and to examine the function of parental egg care in the river sculpin *C. amblystomopsis*.

Materials and methods

This study was conducted on natural populations of the Hekiriji and Ryukei Rivers of southern Hokkaido, Japan. Observation were made on individually marked nests of *C. amblystomopsis* during May and June in 1984.

Just after the spawning period, the nests were located in the lower reaches of the rivers. Each of the nest sites was marked by small metal pickets with flags (Fig. 1A), and was isolated with a "capture trap cage" modified from the "capture box" of Downhower and Brown (1977), to examine whether developing eggs were guarded by a male and to photograph the egg-clusters adhering to the underside of rocks (Fig. 1B). Guarding males were randomly removed from about half of the nests. In nests both with and without a guarding male, the egg-cluster was observed at 2-day intervals to estimate the progressive loss of developing eggs, by comparing it with the initial volume of the egg-cluster on the photograph.

Results and discussion

The survival rates of eggs in nests with and without the guarding males are presented in Table 1. In all the 6 nests with a male, the eggs survived at a high rate and all nests produced hatched eggs. The body size of the males had no effect on the hatching rate. In contrast, the loss of eggs in 5 nests without the males was remarkably greater, and no nest produced hatched eggs. Death of eggs was mainly due to fungal infection, predation, or suffocation.

For example, the eggs in nests R3 and H5 were infected with fungi and died within 6 days after removal of the males. In nest H2, the eggs were

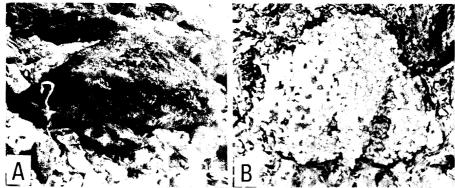


Fig. 1. Photographs showing an individually marked nest site (A) and the initial shape of an egg-cluster at finding (B) of *Cottus amblystomopsis*.

eaten by young fishes of the floating goby *Chaenogobius annularis* and the congeneric sculpin *C. hangiongensis* 6 days and 8 days after removing the males, respectively. Egg predation by conspecific or heterospecific sculpins has been noted in other *Cottus* species (Simon and Brown, 1943; Bailey, 1952; Zarbock, 1952; Downhower and Yost, 1977). These results suggest that in *C. amblystomopsis* the guarding males effectively protect the eggs from fungal infection and predation. In nests R1 and H3, although the eggs appeared to suffer almost no fungal infection and predation, the loss of eggs increased gradually and no eggs hatched. Paternal care in this species consists

mainly of cleaning, defending and fanning the eggs, as in the closely related species *C. nozawae* (Goto, 1982). Therefore, this egg loss may be attributed to an oxygen deficiency induced by the lack of male's fanning in the nests, as shown in the brown bullhead *Ictalurus nebulosus* (Blumer, 1986).

In any case, the male-removal experiments suggest that male attendance increases offspring survival in this species. Similar advantages resulting from male parental care have been found in the mottled sculpin *C. bairdi* (Downhower and Yost, 1977). Presumably the significance of parental care for offspring survival will be held to be common to the *Cottus* species, whose members

Table 1. Survival rate of developing embryos effected by removal of the parental male from nests of *Cottus amblystomopsis*. H indicates hatching. * The stage of embryos was determined according to Goto (1977): FNC, formation of nasal cavity; PPW, pigmentation of peritoneal wall; PRE, pigmentation of retina; TB, tail bud. ** A young (52 mm SL) of the floating goby *Chaenogobius annularis* was found in the nest. *** A young male (64 mm SL) of the river-sculpin *Cottus hangiongensis* whose stomach was full of eggs was found in the nest.

Nest	Initial date	River	Initial stage of embryo*	Removal of parental male (SL, mm)	Survival (%)						
					2	4	6	8	10	12	14 (days)
R 1	May 25	Ryukei	PRE	Yes (145.7)	95	80	50	40	20	0	
R 2	May 27	Ryukei	FNC	No (120.7)	99	95	90	H			
R 3	May 28	Ryukei	PRE	Yes (118.5)	95	0					
R4	May 28	Ryukei	PRE	No (167.1)	99	95	80	70	30	Н	
H1	May 29	Hekiriji	PPW	No (131.3)	95	90	80	Н			
H2	May 29	Hekiriji	PRE	Yes (122.2)	95	90	70**	5***	0		
H3	May 29	Hekiriji	TB	Yes (89.3)	95	90	80	70	5	0	
H4	May 30	Hekiriji	FNC	No (101.6)	95	90	80	70	Н		
H5	May 30	Hekiriji	PRE	Yes (119.2)	95	90	0				
H6	May 31	Hekiriji	TB	No (109.9)	99	99	99	99	90	50	Н
H7	June 4	Hekiriji	FNC	No (108.0)	99	90	90	90	Н		

all exhibit the male parental care. The occurrence of male parental care in fishes has been attributed to the absence of sufficient breeding sites in species that attach their eggs to the stems or rocks (Blumer, 1977; Perrone and Zaret, 1979; Baylis, 1981). Recently, many theoretical studies have shown that the evolution of parental care is favored by natural selection if the net advantage of care (cost-benefit trade-off) is positive (Williams, 1975; Maynard Smith, 1977, 1982; Werren et al., 1980; Gross and Sargent, 1985).

Marine and catadromous sculpins such as Leptocottus armatus (Jones, 1962) and Trachidermus fasciatus (Tsukahara, 1952) which have been considered to be ancestral to Cottus (Yabe, 1985), exhibit paternal care. Probably, paternal egg care preadapted Cottus species to invade freshwater habitats (Gebhardt, 1987; Goto, 1988b), and may have been maintained to maximize the reproductive success in fluvial and/or lacustrine habitats where brood survival would be decreased remarkably under the conditions of no parental attendance (Baylis, 1981; Goto and Maekawa, 1985). Moreover, their polygynous mating system should be taken into account to explain the evolution of parental care performed by male alone in Cottus, as pointed by Kuwamura (1987).

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エゾハナカジカにおける卵の生存に対する雄保護の効果 後藤 晃

1984 年 5-6 月に、北海道南部の流渓川と戸切地川において雄による卵保護が認められたエゾハナカジカの産卵巣を 11 箇見いだし、そのうちの5巣から保護雄を除去した。その後2日毎に産卵巣の観察を行ない、保護雄の有無による卵の生存率の違いを調べた。雄のいる巣ではいずれの場合にも卵は高い生存率を保ち、孵化に至った。これに対して、雄を除去した巣では卵の生存率が急に減少し、5 巣とも孵化前に全滅した。卵の減砂素の原因は、主に水生菌の感染による死亡、排食お果からの原因は、主に水生菌の感染による死亡、以上の結果から、不種の雄の卵保護行動は上述した死亡要因によってもたきまれる卵の生存率の低下を防ぐうえで極めて有効な役割を果していると考えられる。

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