Lunar cyclic spawning of a mouthbrooding cichlid, *Cyprichromis leptosoma*, in Lake Tanganyika

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Lunar reproductive cycles have rarely been documented in freshwater fishes (Schwanck, 1987; Nakai et al., 1990), although common among marine reef fishes (Robertson et al., 1990). Several hypotheses for lunar synchronous spawning have been proposed, based on the effects of the tidal regime on planktonic egg dispersal or hatching from adult habitats (Robertson et al., 1990). However, these hypotheses cannot be applied to fishes inhabiting freshwater bodies, where the lunar cycle never causes tidal fluctuations. However, some authors have proposed several explanations for the adaptive significance of lunar cyclic reproductive activity in freshwater fishes, based on the effects of moonlight. (1) Moonlight provides a cue for pairs to spawn at the same time (Schwanck, 1987). (2) Spawning prior to a full moon enhances the effectiveness of nocturnal parental care of the brood (Schwanck, 1987; Nakai et al., 1990; Rossiter, 1991). (3) Dispersal of young during the fourth quarter of the lunar cycle and the new moon improves the survival of young dispersing under the cover of darkness (Nakai et al., 1990).

Cichlid fishes that dominate the coastal fish communities in Lake Tanganyika have two well-developed patterns of parental care, substrate brooding and mouthbrooding (Coulter, 1991; Keenleyside, 1991). In this lake, about one third of the cichlid species are substrate brooders and the remainder mouthbrooders (Poll, 1986). Lunar cyclic spawning has been reported in some substrate brooders, but never in mouthbrooders. However, the spawning activity of a mouthbrooding cichlid, *Cyprichromis leptosoma*, in fact follows the lunar cycle at the southern end of the lake. I examined whether or not any of the three explanations for lunar spawning synchroneity are applicable to this species, and herein propose an alternative explanation that considers interspecific relationships between juvenile *C. leptosoma* and substrate brooding species cohabiting the area.

Materials and Methods

Field studies were conducted off a rocky shoreline at Kasenga, 8 km northeast of Mpulungu, Zambia, from the beginning of September to mid-December 1996, with the aid of SCUBA.

Cyprichromis leptosoma is a mouthbrooding cichlid, the females incubating eggs and young in the buccal cavity (Kuwamura, 1986). Adults are found mainly in deeper water (at depths of 4–20 m), where they form large schools and feed on zooplankton (Konings, 1988). At Kasenga, *C. leptosoma* tended to form large schools assorted by size. Non-breeding *C. leptosoma* frequently swam in a larger area along the shore feeding on zooplankton in open water, while small juveniles tended to form static schools close to the rocky substrate. Breeding males defended mating territories clustered in three dimensions in the water column, each individual remaining at a certain distance from conspecific males. Within or near the cluster of male mating territories, hundreds of mouthbrooding females formed a large sedentary school.

I established a study area (2 m×2 m grid) at a depth of 6–17 m for 140 m (ca. 4500 m^2) along the shore, which included the school of mouthbrooding females near its center (for further details of study area, see Watanabe, 2000). The study area had a rocky substrate and sloped gently. During the study period, the water temperature was 25–26°C. Eight searches conducted 150 m along the shore from each side of the study area failed to locate any schools of mouthbrooding females.

In order to examine whether or not *C. leptosoma* was characterized by lunar spawning synchroneity, seven to nine mouthbrooding females in the sedentary school were sampled on the days of the new moon, first quarter moon, full moon and third quarter moon, over four lunar cycles (sixteen days in total). These females were collected individually with a small-meshed gill net and immediately put into a plastic bag in order to collect their entire brood. The broods were categorized into five developmental stages: (1) eggs, (2) yolk-sac larvae less than 10 mm in total length (TL) and without distinct pigmentation, (3) yolk-sac larvae less than 14 mm TL with dark pigmentation and 4 or 5 horizontal white bands on the body, (4) yolk-sac larvae less than 17 mm TL, and (5) juveniles (yolk completely absorbed). The larvae within each brood were usually at the same developmental stage.

Independent juveniles of this species usually occurred within the breeding territories of substrate brooding cichlids. To examine the frequency of occurrence of juveniles in such territories, I made routine censuses of the distribution of independent young *C. leptosoma* in the study area at 2–7 day intervals (23 times in total).

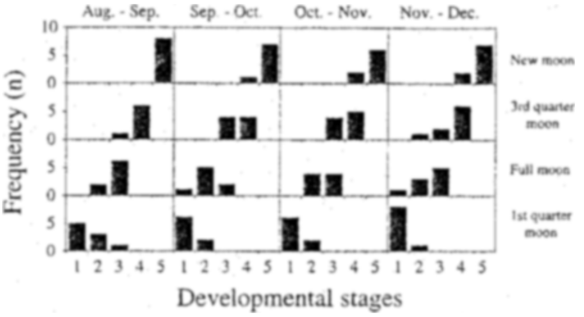

Fig. 1. The frequency distribution of developmental stages of offspring mouthbrooded by female *Cyprichromis leptosoma* in relation to the lunar cycle. See text for the developmental stages.

Results and Discussion

Lunar cyclic spawning. Females collected during the same lunar phase had broods at almost the same developmental stage (Fig. 1), such appearing sequentially as the lunar phase progressed. This trend was consistent in each lunar cycle. Twenty-six of 28 females incubating eggs were caught on the day of the first quarter moon. The proportion of females with eggs was significantly greater than a quarter (25%) of all females with eggs (Fisher's exact test [extended], df=3, $p<0.001$). Since a 3–8 day interval occurs between fertilization and hatching in other mouthbrooding cichlids (Welcomme, 1967; Yanagisawa, pers. com.), spawning should peak during the first quarter of the lunar cycle (including the day of the first quarter moon). The results indicated that the reproductive activity of *C. leptosoma* in the study area followed a lunar cycle, such being the first demonstration of lunar synchronous spawning in mouthbrooding cichlid fishes in Lake Tanganyika.

Juveniles after independence. The total number of juvenile *C. leptosoma* 15–24 mm TL observed in each census ranged from 204 to 1622 (860.8±92.2 SE, $n=23$). During the study period, juveniles were observed associated with host juveniles in the breeding territories of 5 substrate brooding species, *Lepidiolamprologus profundicola* (20–25 cm TL), *L. attenuatus* (10–17), *Perissodus microlepis* (12–17), *Neolamprologus pulcher* (6–8) and *N. savory* (5–7). A large number of juvenile *C. leptosoma* had been recorded as intermingled with a school of juvenile *L. elongatus* in the census area in 1995, but such was not seen during this study. *C. leptosoma* juveniles associated with juveniles of other species, were at the smallest size recorded for independent juveniles of that species, comprising 65.9% (±5.0 SE; range 35–98.4%, $n=23$) of all *C. leptosoma* juveniles found in the census area. In every case, the territory owners were very aggressive towards approaching brood-predators. Therefore, it is likely that young *C. leptosoma* benefit from the territorial behavior of the "host" species (Ochi & Yanagisawa, 1996). The breeding territories of other cichlids therefore seem to be important nurseries for juvenile *C. leptosoma* just after release from the female's mouth.

Of the small juvenile *C. leptosoma* associated with heterospecific juveniles, many were commonly found in the breeding territories of *L. profundicola*. In the censuses, 48.5% (±5.2 SE; range 0–93.3%) of the juveniles were found in territories of *L. profundicola*, 24.6% (±4.3 SE; range 1.4–67.4%) in *N. pulcher* territories, 21.2% (±5.2 SE; range 0–93.7%) in *P. microlepis* territories, 3.7% (±2.2 SE; range 0–47.2%) in *L. attenuatus* territories and 1.9% (±0.6 SE; range 0–12%) in *N. savory* territories.

The breeding territories including juvenile *C. leptosoma* numbered were 11 for *L. profundicola*, 2 for *L. attenuatus*, 3 for *P. microlepis* and in the dozens for *N. pulcher* and *N. savory*. However, juvenile *C. leptosoma* occurred in all of the breeding territories of the former 3 species (the broods of which survived over two weeks), whereas at least 200 *N. pulcher* and 70 *N. savory* breeding territories were scattered over the study area. Thus, the territories of the latter two species were less often used as nurseries compared with the other host species.

Lepidiolamprologus profundicola was the largest host species, effectively driving piscivorous fishes away from the former's breeding sites (Watanabe, 2000). Of the total number of guarded broods, the number that survived for at least two weeks was 1 of 8 *L. elongatus* (12.5%), 2 of 25 *L. attenuatus* (8.0%), 3 of 18 *P. microlepis* (16.7%) and 11 of 12 *L. profundicola* (91.7%). A major explanation for the disappearance of these broods was most likely predation. Therefore, juvenile *C. leptosoma* appeared to have the best chances of survival in the territories of *L.*

profundicola. *N. pulcher* and *N. savory*, the smallest host fishes, may not be able to defend against brood predators as well as other, larger host species.

Significance of lunar cyclic spawning in *C. leptosoma*. The lunar phase may act as a cue to synchronize reproductive readiness within a population. Such synchronized activity may be favored in colonial brooders because it provides enhanced defense against egg predators (Dominey, 1981). In *C. leptosoma*, brooding females stay within or near the cluster of male mating territories, although it is unlikely that the latter increase the efficiency of guarding the broods, which are incubated in the female's mouth.

Tanganyikan substrate brooders spawn synchronously during the second quarter of the lunar cycle (Nakai et al., 1990; Rossiter, 1991; Gashagaza, 1991), thus enabling parent fishes to protect their eggs and young from predation more effectively on bright nights. However, this explanation cannot be applied to *C. leptosoma*, broods remaining in the mother's buccal cavity for about 1 month.

Another explanation for lunar synchronous spawning, proposed by Nakai et al. (1990), is related to the dispersal of independent young of 'hole-brooders'. Young hole-brooders leave their nest sites during the fourth quarter of the lunar cycle, soon after completion of yolk absorption. It is possible that the darkness at night during this moon phase improves the survival of dispersing young while they seek a new habitat. In *C. leptosoma*, however, newly-released young do not all disperse and have been observed forming schools of various sizes in the study area (Watanabe, 2000). A moonless night would not affect the survival of dispersing young in this case.

In the study area, *L. profundicola* lays eggs on the side of a rock on day 10.4 (±1.9 SD, $n=11$) of the lunar cycle and protect their brood for two weeks (Watanabe, 2000; Nakai et al., 1990; Gashagaza, 1991). Juvenile *C. leptosoma* use the breeding territory of *L. profundicola* as a safety zone from their potential predators (Watanabe, 2000). I hypothesize that the enhanced survival of *C. leptosoma* juveniles under the protection of *L. profundicola* has led to the evolution of lunar cyclic spawning of *C. leptosoma* at Kasenga. Juvenile *C. leptosoma* can remain under the protection of *L. profundicola* parents for the longest time if they are released when the hosts start to defend their breeding territories. Figure 1 shows that *C. leptosoma* juveniles which had grown from eggs spawned in the first quarter of the lunar cycle were released from the mouths of females during the first quarter of the next lunar cycle. Parents of *L. profundicola* started to defend their breeding territories around the second quarter. Because these results indicated that *C. leptosoma* females release their juveniles a little before the protective hosts become available, the question arises as to why the time lag? Since *L. profundicola* is a large piscivore, it is very dangerous for other species to approach defended breeding sites. Female *L. profundicola* begin to frequent breeding sites 2–4 days before spawning (around the first quarter moon), although they leave and return to the sites frequently (Watanabe, personal observation). Female *C. leptosoma* may therefore be able to detect breeding sites of *L. profundicola* and safely release their juveniles in the vicinity of the latter just before the hosts establish their breeding territories.

This hypothesis also predicts that a lunar synchronous spawning cycle should not occur in areas where most juvenile *C. leptosoma* do not benefit from the protection of a host species that has lunar cyclic reproduction. Geographic comparative studies should provide an opportunity to test this.

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