

Night Spawning and Paternal Mouthbrooding of the Cardinalfish *Cheilodipterus* *quinquelineatus*

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Mouthbrooding of eggs has been reported for many cardinalfishes (Apogonidae), but only in 10 species or so have courtship and spawning been described (see review in Thresher, 1984; Kuwamura, 1983a, 1985). The general pattern of their reproductive behavior is as follows. Pair spawning occurs in the daytime, though most apogonids are nocturnal in feeding; eggs are extruded in a large mass of 2–3 cm in diameter and the male snatches it up into its mouth from the female's abdomen; the male incubates only one clutch at a time. However, the spawning pattern of *Cheilodipterus lineatus* appears to be very different from above, according to a field observation by Fishelson (1970). Spawning of this species occurred shortly after sunset; a small egg ball (2.0–2.5 mm in diameter) was expelled and attached to the substrate; after the male picked it up, he resumed courting another (or the same ?) female, but no further mating was confirmed due to the darkness. Fishelson suggested that the male might carry several spawns and that the spawning behavior of *C. lineatus* resembled that of substrate-brooding cichlids. If so, the similarity may suggest that mouthbrooding in apogonids is derived from a substrate-brooding ancestor (see Baylis, 1981).

To confirm whether this is a common pattern of spawning in genus *Cheilodipterus*, I investigated the reproductive behavior of *Cheilodipterus* spp. at coral reef area in Okinawa, southern Japan. These species began courtship at dusk, and night spawning was observed in *C. quinquelineatus* Cuvier. Its spawning behavior resembled those of most apogonids, however, not that described by Fishelson (1970) for *C. lineatus*.

Materials and methods

From 1982 to 1985 field observations were made

using SCUBA at the fringing reef on the southeast coast of Sesoko Island (26°38'N, 127°54'E), Okinawa. *C. quinquelineatus* was widely distributed from the reef flat to the reef slope and also at patch reefs scattered on the offshore sand flat. Most observations were conducted at one of the coral patches where adults (8–13 cm in total length) were abundant. It was situated about 50 m offshore from the reef edge (St. 2 in fig. 1 of Kuwamura, 1983b). The coral patch was mainly composed of a massive *Porites*, about 4 m in diameter and 2 m in height, with various crevices and holes. Bottom depth was 6 m at high tide. Mouthbrooding males were found from the end of April to the end of September, but not at the beginning of March and at the end of October (no observations in other months).

More than 30 dives were made at dusk and at night at this coral patch to observe courtship and spawning behavior. Thirty to 40 min after sunset, the fish could no longer be seen by the natural light and an underwater flash-light with a red filter was used. Ten specimens were tagged by the subcutaneous injection of colored dyes (for method, see Thresher and Gronell, 1978), and their daytime resting sites were recorded daily in August 1982.

Results

Adults of *C. quinquelineatus* were relatively quiescent during the daytime, distributed either as individuals in small holes and crevices or forming loose aggregations in larger holes. After sunset the cardinalfish became mobile, gradually leaving their resting sites. About 30 min after sunset, they dispersed toward the surrounding sand bottom to forage. Seven out of 10 tagged specimens used the same daytime resting site for more than 2 weeks; the remaining 3 changed their daily resting sites, but always within 2 m of the original site.

Pair formation and courtship began about 1 h before sunset. The female visited the male's daytime resting site to court. Spawning was observed three times: at 2021 (1 h after sunset; 20 July 1984), 2125 (2 h 13 min after; 7 August 1985) and 2130 (2 h 21 min after; 12 August 1985). Some pairs were engaged in courtship for two or three consecutive dusks before spawning, but the

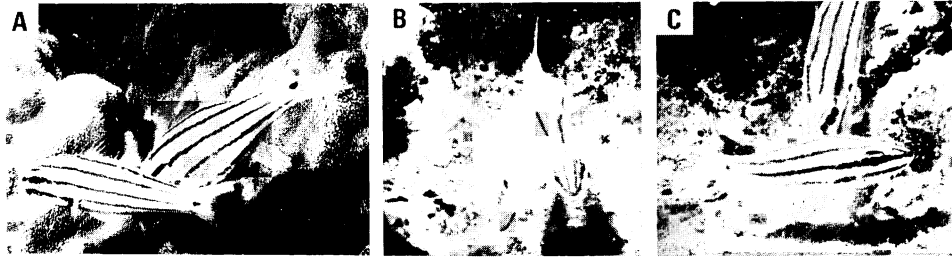


Fig. 1. Courtship and spawning of *Cheilodipterus quinquelineatus*. A, head down approach by the female; B, spawning position with vents together (right: female); C, the male's trial to inhale the egg ball hanging from the female's belly, after failure in the first trial from behind (see text for detail).

pairs parted within 30 min after sunset and dispersed toward the sand flat.

Pairs were composed of individuals having similar sizes; the size difference was usually within 1 cm. Out of 24 courting pairs, the female was larger than the male in 9 pairs, the male was larger in 2 pairs, and in the remaining 13 pairs the sexes looked almost equal in size. The color pattern of courting fish did not conspicuously differ from the daytime coloration with five longitudinal dark lines on a whitish background and with a dark spot, surrounded by a yellow circle, on the caudal peduncle (see fig. in Thresher, 1984, p. 91 for color photo). The longitudinal lines sometimes paled in the posterior-ventral part of the body, especially in the female, during courtship. Females could be distinguished by their swollen abdomens on the day of spawning.

Pair formation began with tail quivering (TQ), with the body flexed slightly in a sigmoid shape. The male and female alternately exhibited TQ in front of each other. TQ occurred predominantly early in courtship, declining afterwards. The most frequently seen courtship display was a head down approach (HD) of the female towards the male. Starting from 10–20 cm behind the male, the female drew close to the male's postero-lateral side, trembling her body while maintaining a head down posture (Fig. 1A). During repeated HDs, the male often exhibited slight mouth openings (MO) intermittently. When other conspecifics approached the pair, the female, as well as the male, always attacked them. If the male left the courtship site, the female always followed him. They returned to the original site if and when courtship continued.

HD and MO were repeated for more than 2 h until spawning. From about 1 h before spawning, the male and female often took side by side posi-

tion with vents together (VT). Spawning took place in this position (Fig. 1B). Eggs were extruded in a large ball of 2–3 cm diameter. A few seconds after spawning, the male drew back 10–20 cm, hesitated for several seconds and then took the egg ball from the female's vent and into his mouth.

In one case, the male was unable to inhale the egg mass, probably due to the presence of an underwater flash for photography. After about 1 min, he tried once more to take the eggs from a perpendicular direction to the female's body (Fig. 1C), but again failed. A few minutes later, the egg ball fell onto the rocky substratum, after which neither the female nor male tried to pick it up. The egg ball was observed for another 5 min, during which no other fishes were observed to prey upon the eggs.

In the other two observed spawnings, courtship displays ceased and both individuals became quiescent after the male had inhaled the egg ball. In one case the female left the egg-incubating male 2 min after spawning; in the other she remained with the male for more than 20 min. On the days after spawning, mouthbrooding males resided solitarily or in loose aggregations at or near the courtship sites. After sunset, most of them dispersed towards the sand flat along with non-brooding fish. Some, however, remained on the reef even 1–2 h after sunset. It was not confirmed whether or not they stayed there throughout the night.

Discussion

Spawning by cardinalfishes is generally assumed to occur at night, though only diurnal or dusk spawning has thus far been reported (Thresher, 1984; Kuwamura, 1985). The present study con-

firmed that *Cheilodipterus quinquelineatus* spawned early in the night, more than 1–2 h after sunset. By that time, most apogonids, as well as other nocturnal and diurnal fishes that are potential egg predators, had disappeared from around the coral patch (Kuwamura, unpublished). Therefore, it seems advantageous for *C. quinquelineatus* to prolong spawning until that time. This may also be the case with *C. macrodon* and *C. subulatus*, which also began courtship at dusk (although spawning by these species has not yet been observed; Kuwamura, unpublished). However, another smaller species of cardinalfish, *Apogon cyanosoma*, spawned at noon at the same coral patch (Kuwamura, unpublished). In this case, several wrasses, mainly *Thalassoma lunare*, vigorously chased the mouthbrooding male just after mating whereupon he lost the eggs 4 min later. Probably the male was robbed of his egg mass by the wrasses. The spawning time of *A. cyanosoma* and other diurnal spawning apogonids seem to be more determined by predation risk on courting parents (see Kuwamura, 1981) rather than egg predation.

It has been suggested that mouthbrooding has evolved from a substrate-brooding ancestor (Oppenheimer, 1970; Baylis, 1981). In the Apogonidae, mouthbrooding is clearly the rule for the family, because no substrate-brooders have been reported (Kuwamura, 1983a; Thresher, 1984). Although the spawning behavior of *C. lineatus* is similar in some respects to that of substrate-brooders (Fishelson, 1970), *C. quinquelineatus* spawning behavior in the present study differed from the former, and resembled those of other apogonids. At present, it seems difficult to conclude that mouthbrooding in apogonids is derived from substrate-brooding. Although further studies on the reproductive behavior of *Cheilodipterus* spp. are indeed necessary, an alternative course of evolution may also be suggested. Mouthbrooding of apogonids may have evolved not through substrate-brooding but directly from “transfer brooding” (Balon, 1975), in which the female carries a cluster of eggs hanging from her genital pore during a prolonged search for a suitable place to attach them. When the predation pressure on the egg mass during hanging from the female’s body is high, selection should favor immediate mouthbrooding by the male (Kuwamura, 1983a). Antecedent conditions of mouthbrooding should be different among fish groups.

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ヤライイシモチの夜間産卵と雄による口内保育

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沖縄県瀬底島のサンゴ礁においてヤライイシモチの繁殖行動を潜水観察した。日没の約1時間前から雌雄1対のペアを形成して求愛を始め、日没の1-2時間後に産卵した。直径2-3cmの卵塊が一気に産み出され、数

秒後、まだ雌の腹部からぶら下っているうちに、雄が口にくわえた。他のテンジクダイ科魚類の産卵行動と比較して、夜に産卵することの意味およびこの科における口内保育行動の起源について若干考察した。

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