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Trophic eggs and parental foraging for young by the catfish *Bagrus meridionalis* of Lake Malawi, Africa

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Summary. Parental bagrid catfish in Lake Malawi, Africa, appear to feed their young in a manner analogous to birds and social insects. The female produces eggs which are released and consumed by the catfish young. Indirect evidence suggests that the male leaves the nest to forage and returns with benthic invertebrates in its mouth that are fed to the brood. Such behavior is hypothesized to enhance the growth rate of the young and to reduce their susceptibility to predation.

Active parental feeding of young is well documented among endothermic vertebrates (Welty 1982) and social insects (Wilson 1971), but it has not been reported for fish. Bird and mammalian parents often forage and bring food back to their young, either regurgitating or directly feeding it to their young (Brown 1975). Social insects have gone one step further and produce eggs solely to feed young. Ovoviviparous sharks produce unfertilized eggs to feed the first young that hatch inside of the female (Moyle and Cech 1982). Also an analogous form of internal feeding has been suggested for the coelacanth, *Latimeria chalumnae* Smith (Wourms 1981; Balon 1984). However, the releasing of eggs and their subsequent external consumption by young has not been reported for vertebrates.

Parental bagrid catfish, *Bagrus meridionalis* appeared both to forage for the young, and to release unfertilized eggs to feed young. The male and female engaged in a division of labor (McKaye 1985). The male left the nest apparently to gather benthic invertebrates. Upon his return the young clustered under his head and fed on material passing through the gills (Fig. 1). The female was never observed engaging in this behavior. Instead, young were observed feeding near her vent. Subsequent stomach analysis of young catfish revealed that they were feeding upon her unfertilized ova.

Methods

From January through April 1984, a study of the breeding biology of the catfish, *B. meridionalis* was initiated to determine the survival rate of catfish young in relation to the adoption of cichlid young (McKaye and Oliver 1980; McKaye 1985). The catfish being studied occurred at depths primarily between 20–40 m at West Thumbi Island, Lake Malawi, Africa (see McKaye 1981 for map of region). Fourteen nests were marked with stakes and followed for periods ranging from two to nine weeks. Because of the depths at which these catfish bred, bottom time for diving observations was limited. Most of the time was spent moving from nest to nest censusing brood sizes and not in long detailed observations.

Individual broods were censused every three to ten days and the number of young and the mean size of the individuals were estimated. At the end of the study, seventeen young from four broods (minimum of four in a brood) were collected with a hand net. The standard lengths and weights were measured and the stomach contents analyzed. Three broods with young 20 mm in length (estimated age 15 days) were found that survived for at least another 45 days. These broods were used to estimate growth rates. Survival rates were determined from 14 broods by dividing the number of young of a given age class by the number of young remaining 15 days later.

At the end of the breeding season in April, two females were captured, and their ovaries dissected. A subportion of the eggs in the ovaries were counted and egg numbers were determined from volumetric extrapolations.

Results

Parental defense of the young was an important component of the parents' behavior and usually both parents engaged

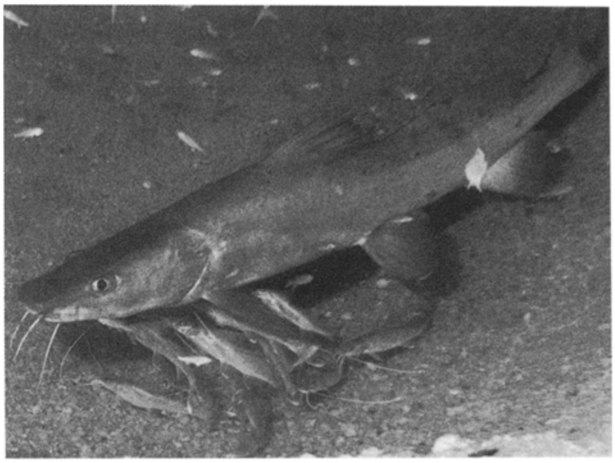

Fig. 1. Young catfish congregate underneath head of male. Larger ones aggressively secure position directly underneath and behind gills

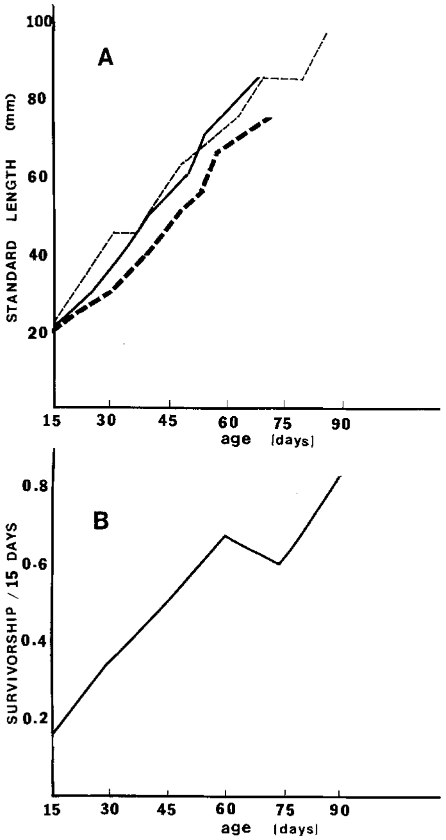

Fig. 2A. Increase in mean standard length of catfish in 3 broods through time. **B** Survivorship rate of young catfish per 15-day period

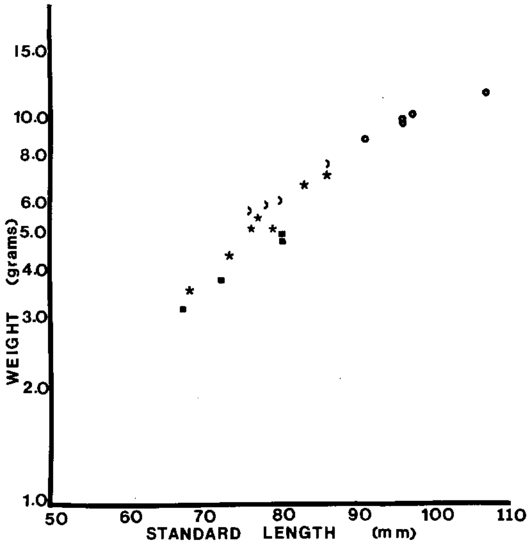

Fig. 3. Length-weight relationship of young catfish from four broods. Similar symbols represent individuals for the same brood. For example, the brood represented by * had one individual who weighed 7.2 gms and another one that weighed 3.6 gms

in this defense (McKaye 1985). When together, the female was usually on the outer perimeter of the nest and the male was in the interior with the young underneath. The young congregated underneath the head of the male and aggressively maneuvered for position underneath and behind the gills. Usually, the smaller ones were further away from this apparently preferred position (Fig. 1). The young foraged in the water column immediately below the male's head. The female usually remained on the periphery, attacking predatory cichlids. Twice I observed a female move to the center of the nest at which time young immediately oriented beneath her vent, began to feed presumably upon eggs and to fight for position. The young were never observed to leave the nest.

Ten of the eleven individuals captured from three broods with a tending female had consumed fish eggs which accounted for over 95% of the biomass in their stomachs. Some of these stomachs were completely full of eggs (>200 eggs). Six individuals captured in the late afternoon from a single brood with no permanently tending female but which were feeding under the male's head (Fig. 1) had no eggs in their stomachs. Chironomid larvae, zooplankton, and sand grains were the primary items in the stomachs of this latter brood. Besides eggs, chironomid larvae and zooplankton (95% *Diaphanosoma* and 5% diaptomids) were primarily found in the stomachs of three broods with a tending female. Also found in the stomachs were fish scales, a juvenile cichlid, amphipods, mayfly larvae and Diptera larvae.

The young catfish grew at a rate of approximately 1 cm per 10 days (Fig. 2A). The survivorship rate increased significantly as they aged (Kruskal-Wallis $P<0.01$). Only 18% survived the first 15 days freeswimming, but over 80% survived from 75–90 days free-swimming (Fig. 2B). There was a two-fold difference in weight between young captured at the same time in a single brood (Fig. 3).

There were approximately 16,000 eggs in the ovaries of one of the captured females (70 cm SL) and over 50,000 eggs in the other (110 cm SL). These eggs were identical in size (1.0–1.2 mm diameter) and color (white) to those found in the young catfish stomachs. Cichlid eggs, which are the only other likely egg source, are much larger (approximately 3 mm) and yellow (McKaye and Kocher 1983; McKaye 1984).

Discussion

The direct evidence from the feeding observations and stomach analysis clearly demonstrates that the fish eggs and benthic invertebrates are important components to the diet of young bagrid catfish. Fish eggs comprised 95% of the biomass in the stomachs of the young with a tending female. These eggs were identical in color and size to those found in the female's ovaries. The feeding by the young under the female's vent provides strong additional evidence that the young are getting the eggs from their mother.

The manner by which the young obtain benthic invertebrates is more uncertain. Two hypotheses can account for this. Either, the young collected the larvae themselves at times when I was unable to observe their feeding behavior, or one or both of the parents brought benthic invertebrates to them.

The stomachs from young collected at 1,500 h with no permanently tending female contained benthic invertebrates. These food items were not digested and had been consumed within at least two h of collection. Therefore, the hypothesis that the young foraged at night can be dismissed for the individuals examined in this study. Furthermore, catfish young have never been seen foraging away from the nest during over 100 nocturnal and 2,000 diurnal dives that I have made in Lake Malawi. Whether or not these young fish hunt for benthic invertebrates when a diver is absent will not be conclusively determined until deep water television monitoring is done in Lake Malawi.

The evidence is not unequivocal, but for the following reasons the most parsimonious explanation appears to be that one or both of the parents bring food: 1) the young, in the afternoon, have recently consumed benthic invertebrates in their stomachs; 2) they have not been observed feeding away from the nest; 3) they feed under the gills of the male when he returns (Fig. 1); 4) the male leaves the nest for extended periods which would be required for a parental foraging hypothesis.

Large females are capable of laying over 50,000 eggs yet the maximum number of eggs laid is approximately 3,000–4,000. The females appear to gain more by investing in eggs to feed the young which allows them to grow faster. This is dramatically demonstrated by the fact that the predation rate is four times greater for smaller size classes. A slight increase in growth rate which results in a lower rate of predation can have a major effect in increasing the final number of surviving young. If it is possible to "trade" an increase in brood size for an increase in growth, the latter strategy might be more successful. For example, using the empirically derived predation rates and assuming that they are strictly size related, a female starting with a brood of 50,000 young (over 10 times that ever observed) and a growth rate half of what was observed would only have four young surviving to 10 cm standard length. This number is only one fifth of the approximately 20 found in naturally occurring broods which began with 2,000–4,000 young. The parents, under this hypothetical scenario, would also have had to spend half a year guarding the young as compared with three months to achieve the same size. The assumption of a doubling of growth rate due to parental food supplementation is probably conservative, Tweddle (1975) based on fisheries statistics and known growth rates of fishes at the time reasonably concluded that *B. meridionalis* reached 10 cm standard length at 12 months of age. This estimated age for a 10 cm SL catfish is four times greater than observed in this study. However, studies of growth rates with and without parental feeding are still required to determine the actual increase in growth due to parental supplementation.

Clearly, enhancement of their young's growth rate by feeding could be advantageous for parents when predation is intense. Phylogenetic constraints will cause different strategies to be used by varying families of fishes. For example, in Lake Malawi the catfish feed their young, whereas females of the endemic cichlids produce larger eggs and keep them in their mouths. Again a reduction in total number of young produced might enhance the probability of survivorship. Larger eggs are produced which results in large offspring (Fryer and Iles 1972; Balon 1984; McKaye 1984). Catfish instead apparently feed the young and achieve a similar result. Active feeding by parents is probably not unique to *B. meridionalis*, just as mouthbrooding is not unique to cichlids (Oppenheimer 1970). I predict that similar behavior may be found among care giving fishes when observed in the field under the right ecological conditions.

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