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Behavioral and trophic plasticity of juvenile *Tilapia mossambica* in utilization of the unstable littoral habitat

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Synopsis

Juvenile *Tilapia mossambica* Peters (2.5–10.0 cm standard length) in Lake Sibaya, South Africa, move daily from deep offshore waters to shallow (<0.5 m) littoral areas where they feed for several hours and then return to deep water. The timing of these movements varies in response to changing physical and biological features of the littoral environment. During this study (December 1973 – February 1976), lake level rose more than 1 m. At the start of the study, littoral areas visited by juvenile *T. mossambica* were free of vegetation and debris, but at higher lake levels trees and brush from the eroding shoreline were common in nearshore littoral waters. When the littoral zone was free of debris, juvenile *T. mossambica* visited nearshore waters only during daylight hours. After a 0.65 m rise in lake level and considerable accumulation of debris, these fish were abundant in the littoral zone only at night. This reversal can be attributed to efforts by juvenile *T. mossambica* to avoid their principal predator, the catfish *Clarias gariepinus*. At low lake level *C. gariepinus* ventured into the littoral only at night but at higher lake levels this predator was found within flooded vegetation during the day. When further increases in lake level flooded marginal grasslands, juvenile *T. mossambica* abandoned the littoral zone in favor of this newly created eulittoral habitat where potential fish predators did not occur. With the change in habitat, the diet changed from benthic detrital aggregate to periphyton. These observations suggest the importance of behavioral and throphic plasticity in the ability of tilapia to utilize unstable habitats.

Introduction

Tilapia are well known for their ability to colonize and effectively exploit unstable shallow-water habitats in the tropics and subtropics (Lowe-McConnel 1975). Their success in these habitats has been attributed to their ability to rapidly alter both life-history characteristics and trophic level in response to changes in their environment (Fryer & Iles 1969). Fundamental life-history alterations have been shown in growth pattern, in age at maturity, and in fecundity (Bruton & Allanson 1974, Noakes & Balon 1982). Alterations in trophic level involve switching from herbivory to carnivory and vice versa as the availability of animal prey changes (Bowen 1982).

During a study of the feeding of juvenile *Tilapia mossambica* in Lake Sibaya we observed a complete reversal of diel movement pattern and feeding

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periodicity which suggested these fish are capable of more subtile, finely tuned responses to the environment than previously reported. In the present report, we document this reversal and describe concomitant changes in the feeding habitat to consider how this alteration in behavior may benefit *T. mossambica* under the new environmental conditions.

Study site

Lake Sibaya (32°40′E, 27°25′S) has a surface area of about 65 km^2, a maximum depth of about 40 m and a mean depth of about 13 m. Secchi disk values for the open water vary only slightly from 3.4 m. The basin is endorheic and lake level fluctuates in response to both short term and annual variations in rainfall. Pitman & Hutchison (1975) estimate that lake level fluctuated over a 3.5 m range between 1914 and 1969. In the interval between the start of this study in December 1973 and March 1975, an increase of 0.65 m resulted in considerable shoreline erosion and accumulation of terrestrial vegetation in nearshore waters. Further increases in lake level between March 1975 and February 1976 flooded extensive portions of marginal grasslands.

Juvenile *Tilapia mossambica* (2.5–10.0 cm standard length) move daily from deep water to shallow littoral areas where they feed on benthic detrital aggregate (Bowen 1978, 1979). They show a marked preference for unvegetated littoral sand terraces where they comprise 98% of seine catches and are uncommon elsewhere in the littoral zone. Unvegetated sand terraces are found along about 40% of the lake margin. Further details of the Lake Sibaya ecosystem are given in Allanson (1979).

Methods

Diel movements and feeding activities of juvenile *T. mossambica*, 2.5–10.0 cm standard length, were studied during four 24 h periods; two in December 1973, and two in March 1975. Fish were collected from a terrace (1–2 m maximum depth) along the southeast shore at two-hour intervals using a 15 m bag seine. The number of specimens caught, and weather and wave conditions were recorded for each collection. Diving observations were made during daylight hours to confirm the presence or absence of *T. mossambica* and other fishes in terrace waters.

Arbitrarily selected specimens (N = 15) were used to estimate the mean weight of gut contents for each catch. The abdominal cavity of each specimen was opened to minimize postmortem digestion and the specimen was fixed immediately in 10% formalin. In the laboratory, the gut content of each fish was removed, dried for 24 h at 70°C, cooled in a desiccator, and weighed. The fish, including digestive tract, was dried at 80°C in a vacuum oven to constant weight.

A regression of fish dry weight against dry weight of gut contents per fish dry weight was not significant ($r^2 = 0.179$, $p >> 0.05$, N = 35). Thus no significant allometry was present over the range of fish sizes used in this study (0.6–11.2 g dry weight), and mg food per g fish was directly comparable for all sizes of fish.

The December 1973 studies were prior to, and the March 1975 studies were well after the start of shoreline erosion that brought small trees, brush and riparian grass into littoral waters. Conditions at these times are referred to as low lake level and high lake level, respectively.

Results and discussion

Diel movements

The maximum number of fish taken in a single catch varied considerably from day to day with no apparent relationship to environmental conditions. For example, under uniformly calm weather conditions during the week of March 2, 1975, maximum daily catches per seine haul ranged from 34 on March 4 to 318 on March 8. As a result, we compare diurnal movements to and from the terrace habitat in terms of relative rather than absolute numbers for each 24 h period.

At low lake levels we found these fish were common in the littoral zone only during daylight hours (Figs. 1, 2) (see also Minshall 1970, Bruton & Boltt 1975). In contrast, at high lake level in March 1975 we found *T. mossambica* were common in the

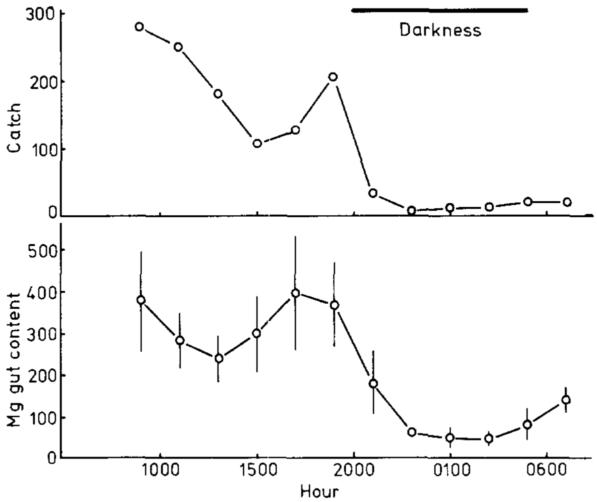

Fig. 1. Diurnal abundance and feeding activity of juvenile *T. mossambica* on the terrace starting 0900 h, December 15, 1973. A strong onshore wind caused increasingly heavy wave action that reached peak intensity at 1500 h, and the lake was calm by 1900 h. Confidence limits to mean mg gut content in all figures calculated as $\pm$ $t_{[0.5, N-1]}$ times the standard error.

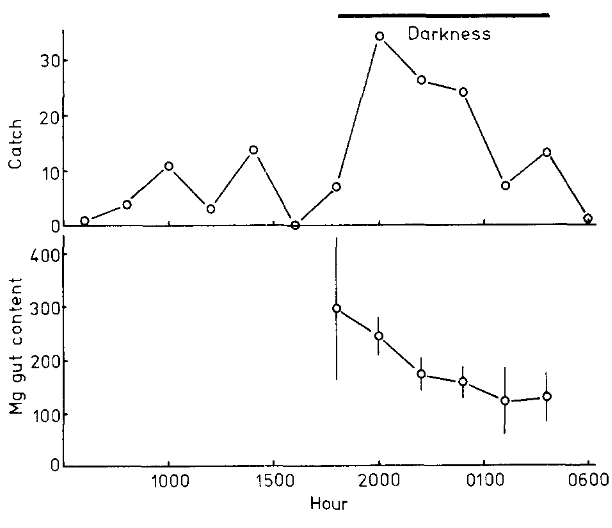

Fig. 3. Diurnal abundance and feeding activity of juvenile *T. mossambica* on the terrace starting 0800 h on March 4, 1975. The lake was calm throughout the sampling period. Specimens caught during daylight hours were located in flooded riparian grass within two meters offshore. Their diet was considerably different from the diet consumed by other juvenile tilapia and thus data for gut fullness is not plotted for comparison here.

littoral zone for only a few hours after dark (Figs. 3, 4). This latter finding was confirmed by numerous additional collections in March and July, 1975 and by diving observations.

Daily movements similar to the ones observed in Lake Sibaya at low lake level have been reported for juveniles of other cichlid species in Lake Vic-

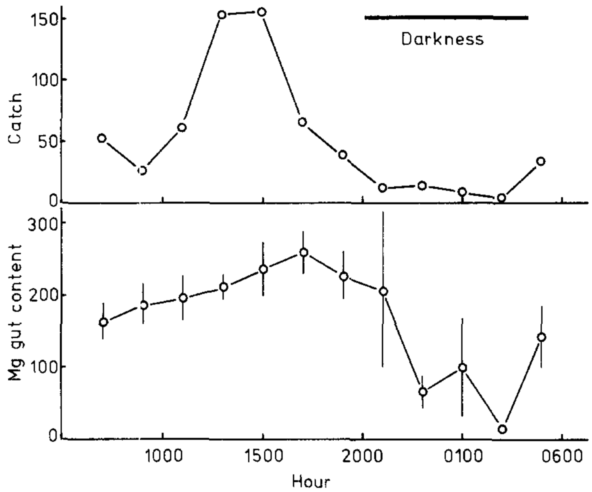

Fig. 2. Diurnal abundance and feeding activity of juvenile *T. mossambica* on the terrace starting 0700 h on December 27, 1973. Moderate wave action continued throughout the day until about 2000 h when the lake become calm.

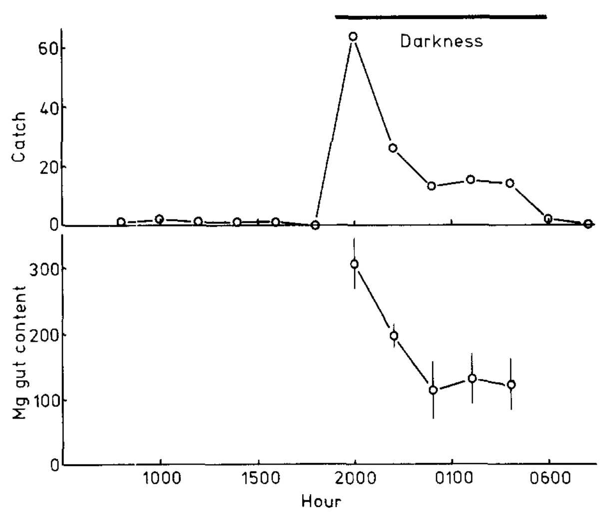

Fig. 4. Diurnal abundance and feeding activity of juvenile *T. mossambica* on the terrace starting 0600 h on March 7, 1975. The lake was clam throughout the sampling period.

toria (Welcomme 1964) and Lake McIlwaine (Caulton 1975). These movements can be explained by the fact that fish commonly seek the warmest water available. Caulton concluded that the fish migrate shoreward as shallow nearshore waters warm during the day and return to deeper waters as nearshore waters cool during the evening to temperatures below those of the open water. Maximum nearshore temperatures on Lake Sibaya terraces do not exceed thermal preferenda established for juvenile *T. mossambica* (Badenhuizen 1967, Donnaly 1969), so Caulton's explanation appears to account for daily movements at low lake level in Lake Sibaya.

The reversal of daily migrations under conditions found in March 1975 can be attributed to an effort by juvenile *T. mossambica* to avoid their principal predator, the catfish *Clarias gariepinus*. In Lake Sibaya, this catfish feeds largely on juvenile *T. mossambica* (Bruton 1979a, b). The distribution of *C. gariepinus* is made obvious to both tilapia and divers by its requirement for air to be taken at the surface every few minutes (Bruton 1978). As the dark colored predator rises from concealment on the bottom to the surface, it is seen in strong contrast to the silver air-water interface. When the lake is calm, this surfacing behavior is readily observed from shore. At low lake level, *C. gariepinus* (itself the major prey of the fish eagle, *Haliäetus vocifer*) ventured into the shallow littoral only at night. At high lake level, numerous *C. gariepinus* were found in patches of drowned vegetation nearshore during the day. Results of our study suggest that the presence of this predator provides sufficient stimulus to overcome the tendency for juvenile *T. mossambica* to seek warm nearshore waters during the day and defers movement onto the terrace until dark.

Diel feeding activity

A previous study of diet selection by *T. mossambica* in Lake Sibaya showed juveniles feed only in shallow water (Bowen 1979) and thus feeding behavior of fish collected from terrace waters reflect feeding during the full diel cycle. With the assumption that feeding rate is proportional to gut fullness (Elliott & Persson 1978), the diel pattern of feeding activity may be compared for high and low lake levels. Under both conditions, fish fed when they were most numerous in terrace waters (Figs. 1, 2, 3, 4). Little feeding was apparent at times when few fish were present. This observation suggests that 1) conditions which are unfavorable for the presence of large numbers of juveniles on the terrace are also unfavorable for feeding, and 2) that juveniles enter terrace waters only to feed. Further examination of these data suggests that feeding at high lake level in March 1975 may have been less productive than feeding at low lake level. The intensity of feeding indicated by gut fullness data appears to have been similar for all four periods studied but the duration of the feeding period at high lake level was less than one half that found for low lake level. Most feeding at high lake level ended before midnight when nearshore waters have usually cooled to temperatures below that of the open water and are as much as 10°C below the midday maximum (Bruton 1979). Since feeding rate has been shown to be directly proportional to temperature for several fish species, including the closely related *Tilapia rendalli* (Davis & Warren 1967, Smit 1968, Caulton 1978), we would expect feeding at high lake level to result in a smaller daily meal than feeding at low lake level.

Soon after the March 1976 samples were taken, juvenile *T. mossambica* began to abandon the terrace in favour of a new eulittoral habitat created as rising water flooded marginal grasslands. By February 1976, juvenile *T. mossambica* were common in this new habitat during daylight hours, and it was extremely difficult to collect them from terrace waters at any time (A. Bruton, personal communication). The only *C. gariepinus* to colonize the eulittoral were very small (modal total length 16 cm) (Bruton 1978), and did not feed on *T. mossambica* juveniles in the size range considered in the present study (Bruton 1979b).

The switch from the terrace to the eulittoral habitat was accompanied by a switch in diet from benthic detrital aggregate to epiphytic algae. The few specimens collected from the terrace during daylight hours at high lake level had been feeding on epiphytic algae attached to *Acacia* branches and other debris from the eroding shoreline. Direct observation of juveniles that later moved into the eulittoral indicated that periphytic algae was the principal food utilized.

Within a feeding period, heavy wave action appears to have interfered with feeding. Gut fullness values declined as fish left the terrace during the period of heavy wave action on December 15. As the lake calmed and fish returned, gut fullness values increased rapidly. In addition, within sample variation for gut fullness values was much greater on December 15 than on other dates. Either some fish were more successful than others in feeding under heavy wave conditions or the fish as a group fed sporadically when subjected to strong waves.

Conclusions

Juvenile *T. mossambica* in Lake Sibaya move daily between two habitats which offer specific advantages and disadvantages for their two principal activities: feeding to support growth and sheltering to avoid predation (Cushing 1975). Although the shallow littoral habitat contains nutritionally adequate food (Bowen 1979), its disadvantages are that the shallow waters confine fish to a small volume so they are effectively concentrated for predators, and that periods of heavy wave action interfere with feeding. Although the deep water habitat lacks nutritionally adequate food, it allows fish to disperse to very low densities so that the probability of predator encounter is low.

Other studies of predator avoidance by littoral fishes have concluded that the littoral zone actually offers protection to potential prey. Studies reviewed by Stein (1979) indicate that rocks, macrophytes and organic debris offer camouflage, hiding spots and complex escape routes, and that 'predatory success declines as habitat complexity increases.' The difference between these habitats and the littoral zone utilized by juvenile *T. mossambica* in Lake Sibaya lies in the degree of habitat complexity. Littoral areas preferred by *T. mossambica* are nearly homogenous with no cover of any sort. The accumulation of piles of debris increased habitat complexity enough to provide refuges for *C. gariepinus* but did not provide shelter for even a fraction of the great numbers of juvenile *T. mossambica* that utilize the shallow littoral zone.

The results reported here indicate that juvenile *T. mossambica* can quickly alter their schedule of daily movements, feeding behavior and diet in response to changing conditions in the unstable littoral zone. It appears that these fish select a schedule likely to maximize feeding success while minimizing exposure to predation. This behavioral plasticity offers further support for the thesis that although African cichlids of the tilapia group remain flexible generalists, they possess special abilities for utilization of unstable habitats (Fryer & Iles 1969, Bruton & Allanson 1974, Bruton & Boltt 1975).

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