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Fish predation as a factor in the distribution of Lake Malawi gastropods

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Summary. Gastropod densities in Lake Malawi, Africa drop dramatically below 4.5 m water depth. Weed beds disappear and the number of molluscivorous cichlids increases below this depth. When molluscivores were excluded from open sand habitat by cages, due to migration and reduced predation, the density of snails increased by 40–60% within a week. Alternatively, when adult *Cyrtocara placodon* were placed into the cages, snail density equaled the controls. The molluscivores disproportionately consumed snails of the genus *Bulinus* relative to those of the more heavily armoured genus, *Melanoides*. Cichlid molluscivores are hypothesized to be responsible for preventing the thin shelled bilharzia vector snail, *Bulinus globosus*, from successfully invading the open shore areas of Lake Malawi. Lake Malawi may be relatively free of this human disease because of snail predation by cichlids.

Key words: Cichlids – Foraging – Bilharzia – *Melanoides* – *Bulinus*

Research upon the processes which determine species densities and richness in soft sediment communities have concentrated primarily upon marine systems (Peterson 1979). When predators are experimentally removed from these communities the total density of the infauna usually increases (Peterson 1979). However, when large epibenthic predators are excluded from grassbeds the effect on the invertebrate community is minimal (Young et al. 1976; Young and Young 1977; Peterson 1979). Similar patterns also emerge within temperate freshwater systems. Here, predators appear to reduce the density of invertebrates which occur over the open bot-

tom versus more structured habitats (Crowder and Cooper 1982; Coull and Wells 1983; Gilinsky 1984). Although one study using "cage experiments" concluded that vertebrate predation was not important in structuring a freshwater benthic macroinvertebrate community (Thorpe and Bergey 1981), the results of this study have been questioned by subsequent workers (Crowder and Cooper 1982; Gilinsky 1984).

No experimental studies appear to have been conducted in tropical freshwater lakes to determine the importance of predation on invertebrate distribution. However, Vermeij and Covich (1978) have theorized that molluscivorous fishes have played a major role in the evolution of shell form in freshwater gastropods. They also suggest that cichlid fishes may be responsible in part for determining the distribution and densities of gastropods in the African Rift Valley Lakes. Vermeij and Covich (1978) hypothesized that these gastropods have evolved behavioral means of avoiding molluscivores and that predation pressure is reduced by the use of spatial refuges. However, as they state, "the effectiveness of behavioral refugia for freshwater snails has not been extensively evaluated". Data concerning snail behavior (Louda and McKaye 1982), distribution (Louda et al. 1983), and density (Louda et al. 1984) in Lake Malawi, indicate that cichlid predation might influence the patterns observed.

The Great Lakes of Africa with their extensive snail faunas and molluscivorous cichlids provide an excellent opportunity to examine Vermeij and Covich's (1978) hypothesis that gastropod morphology, behavior and distribution have been strongly influenced by the presence of these fishes. Furthermore, such an examination allows us to determine, within tropical freshwater lakes, the generality of the view that vertebrate predators are important in reducing invertebrate prey densities in areas of low structural heterogeneity.

Lake Malawi has 19 species of shallow-water gastropods which have a marked vertical distribution pattern (Louda et al. 1983). The gastropods reach peak densities between 3 and 4.5 m and then their numbers drop dramatically with greater depths. The overall density of these species appeared uniform between 6–24 m (Louda et al. 1983). In the case of the most common genus, *Melanoides* the numbers were highest at 3.0 m but the size of *Melanoides* was greatest at 6.0 m in the open sand (Louda et al. 1983). The increased density of *Melanoides* was correlated with the presence of the dense weed beds of *Vallisneria* and *Potamogeton*. Louda et al. (1983) hypothesized that either differential availability of food or increased predation by mollusc feeding cichlids may determine the patterns observed.

Lake Malawi contains a group of mollusc feeding cichlids, which occur in shallow water above 25 m. The primary molluscivorous species are *Cyrtocara placodon*, *Cyrtocara anaphrymis*, *Cyrtocara sphaerodon*, and *Trematocranus microstoma*. This paper reports upon the distribution of these molluscivores, their stomach contents, and in situ cage experiments to test the hypothesis that differential predation by fishes is responsible for the lower number of snails at depths below 4 m and away from the refuge provided by weeds.

Methods and materials

Distribution of molluscivorous cichlids

Within the Cape Maclear region of Lake Malawi (See McKaye 1981 for map of region) there are over a dozen species which will consume snails (see also Fryer and Iles 1972). However, in the shallow waters above 15 m four species of molluscivores dominate: two oblique striped species, *C. anaphyrmis* and *C. sphaerodon*; and two spotted species, *C. placodon* and *T. microstoma*. These four species account for over 90% of the fishes which feed on gastropods in depths above 15 m (McKaye, unpublished data). All of these species can be easily distinguished when captured or while occupying a nest for breeding (McKaye 1984). However, a diver swimming visual transects cannot always distinguish between *C. anaphyrmis* and *C. sphaerodon*. Though the two spotted species, *C. placodon* and *T. microstoma* are presently placed in different genera, they are closely related (McKaye and Stauffer in preparation) and also cannot be consistently differentiated by visual transects. Therefore, the visual data are presented as the oblique striped molluscivores, and the spotted molluscivores.

The number of the oblique striped molluscivores (*C. anaphyrmis/sphaerodon*) was estimated by two divers counting the fish within 5 m of the bottom and within 2 m on either side of a 50 m transect line laid along a depth contour (100 m² of bottom surface for each). From November 1977 until July 1978 and in June and July 1979 at least two of these 100 m² transects were made each month at 3 m depth intervals (1.5 to 30.0 m).

The distribution of the spotted molluscivores (*C. placodon/T. microstoma*) was determined between January 1984 and April 1984 on enlarged transects, at closer intervals. Each diver counted all individuals within 4 m on each side of the line. Transects in this case were run bi-weekly at six sites at 1.5 m depth intervals.

Stomach analysis

The cichlids were collected at depths between 3 and 30 m, either with trammel nets or by a diver chasing individual fish into a block net. The stomachs of the fishes were removed immediately after the trammel net was recovered or the diver returned to the surface. The number and size of the snails in each stomach were recorded and measured following Louda et al. (1983).

Fish exclusion and inclusion experiments

Twelve 1 × 1 × 1 m cages constructed of 1.3 cm pipe and 0.64 cm mesh were used (Fig. 1). The cage legs were pushed approximately 20 cm into the sand. Six of the cages were completely enclosed (experimental treatment); three had a top and two corner sides, and three had a top and two opposite sides with netting (cage controls). Sand plots, 1 × 1 m, served as unmanipulated controls. Six cages, three experimental and three control, were put in place and left for one week, at the end of which all snails in the one meter area were collected and counted, following methods of Louda et al. (1983). Nine replicates for each treatment were made at a 6 m depth in March of 1984.

A second set of experiments was run in April 1984. In this set we used the six completely netted cages; three contained 4 adult *C. placodon* and three were left empty. Marked 1 × 1 m sand quadrats nearby served as controls (in the previous experiment the cage controls and open sand controls were equivalent - see Results). At the end of the experiment, rotenone was used to kill the experimental fish, and their stomachs were analyzed. All snails were collected as above.

Laboratory feeding experiments

A 120 l aquarium was filled with sand 3 cm deep. Five snails each of three different genera *Melanoides* spp. (3–9 mm), *Gabiella stanylei* (3–4 mm); we were unable to find any other sizes at the time of these experiments) and the bilharzia vector *Bulinus globosus* (3–9 mm) were measured and placed into the aquaria. They were allowed to acclimate 24 h. A single *C. placodon* adult (135–105 mm SL) which had been held without food for 48 h was introduced into the aquaria. After 24 h the fish was removed and its stomach contents analyzed. The remain-

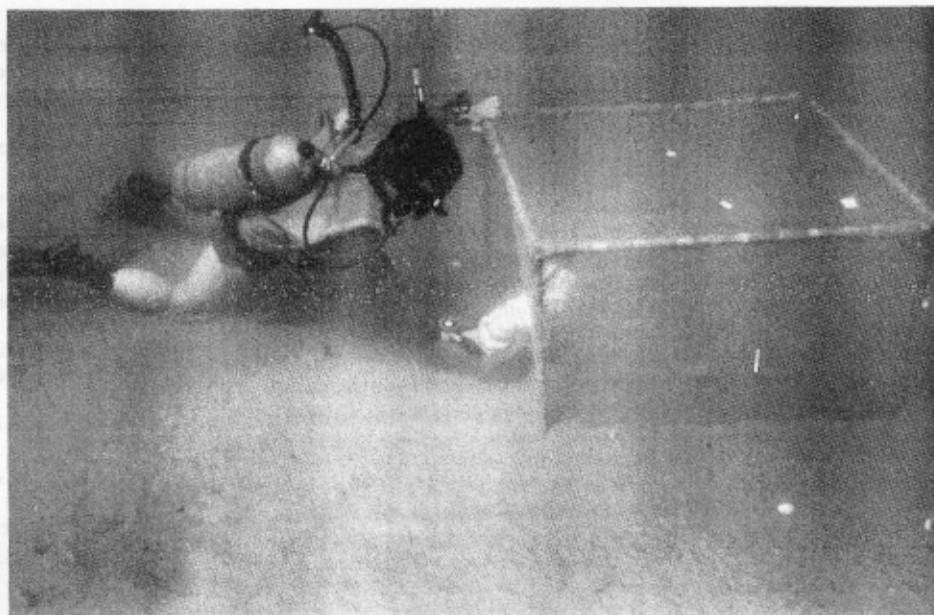


Fig. 1. $1 \times 1 \times 1$ m cage used in experimental treatments. Scuba diver is applying rotenone to collect *Cyrtocara placodon* which were enclosed in the cage for one week

ing snails in the aquarium were counted and measured. This protocol was repeated five times with different fish and snails. The percentage of each size class eaten in the 24-h period was determined for each snail genera.

Results

Distribution of molluscivorous cichlids

The peak distribution of the striped *C. anaphymis/C. sphaerodon* was at 7.5 m with approximately one individual per every 10 m^2 (Fig. 2 b). Below 10 m and above 6 m the average number of these species was approximately one per 100 m^2 (Fig. 2 b). The peak distribution of the spotted *C. placodon/T. microstoma* was at 6.0 m with approximately one and a half individuals every 10 m^2 (Fig. 2 b). Below 10 m the average number of individuals was approximately one third that of the peak. In water shallower than 10 m the density was approximately one individual per every 20 m^2 (Fig. 2 b).

Stomach analysis of cichlids caught over open sand

Three snail genera, *Melanoides*, *Bulinus*, and *Gabiella* were found in the stomachs of all four cichlid species. *Melanoides* snails comprised over three-quarters of all the snails found in the stomachs (Table 1). The median length of *Melanoides* found in the stomachs of all the species ranged between 2–4 mm length (Fig. 3), as contrasted to a median length of 8 mm found over open sand (Fig. 4). The median length for *Bulinus* in the cichlid

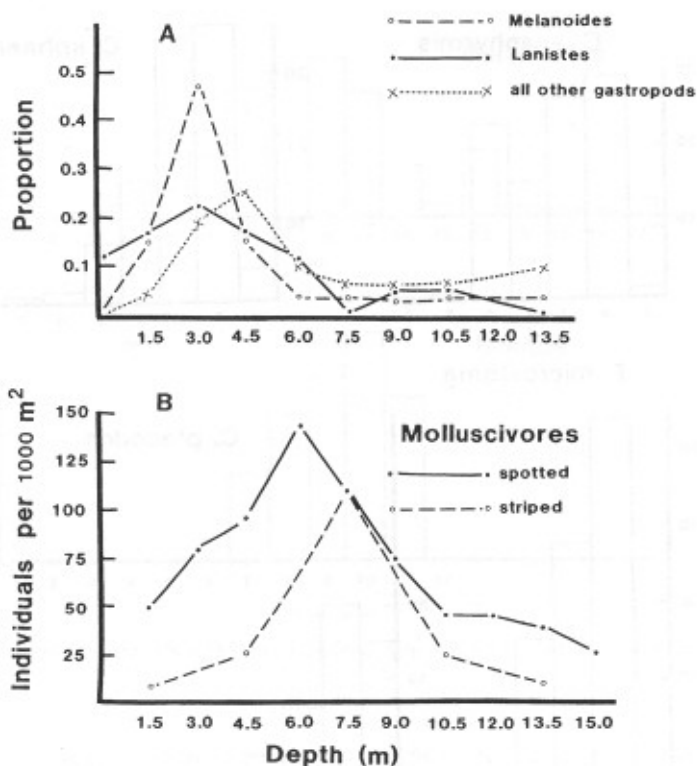


Fig. 2 a. Relative distribution of *Melanoides* and other gastropods over the water depth gradient at Cape Maclear (From Louda et al. 1983). b Distribution of the primary molluscivores over the water depth gradient at Cape Maclear. Spotted molluscivores – *C. placodon* and *T. microstoma*; striped molluscivores – *C. anaphymis* and *C. sphaerodon*.

Table 1. Percentage of snails of each genus in the stomachs of cichlid molluscivores

Fish species	N	<i>Melanoides</i>	<i>Bulinus</i>	<i>Gabiella</i>
<i>Cyrtocara placodon</i>	219	77.2%	21.0%	1.8%
<i>Trematocranus microstoma</i>	59	94.9%	1.7%	3.4%
<i>Cyrtocara anaphymis</i>	143	78.3%	16.1%	5.6%
<i>Cyrtocara sphaerodon</i>	549	84.2%	8.6%	7.2%

N total number of snails in stomachs

stomachs ranged between 3–4 mm (Fig. 5); whereas over open sand the median was 9 mm (Fig. 4).

Fish exclusion experiment

In the cages that excluded fish the mean number of snails present was 55.1 per m², in the cage control the number of snails was 39.0 m², and over the

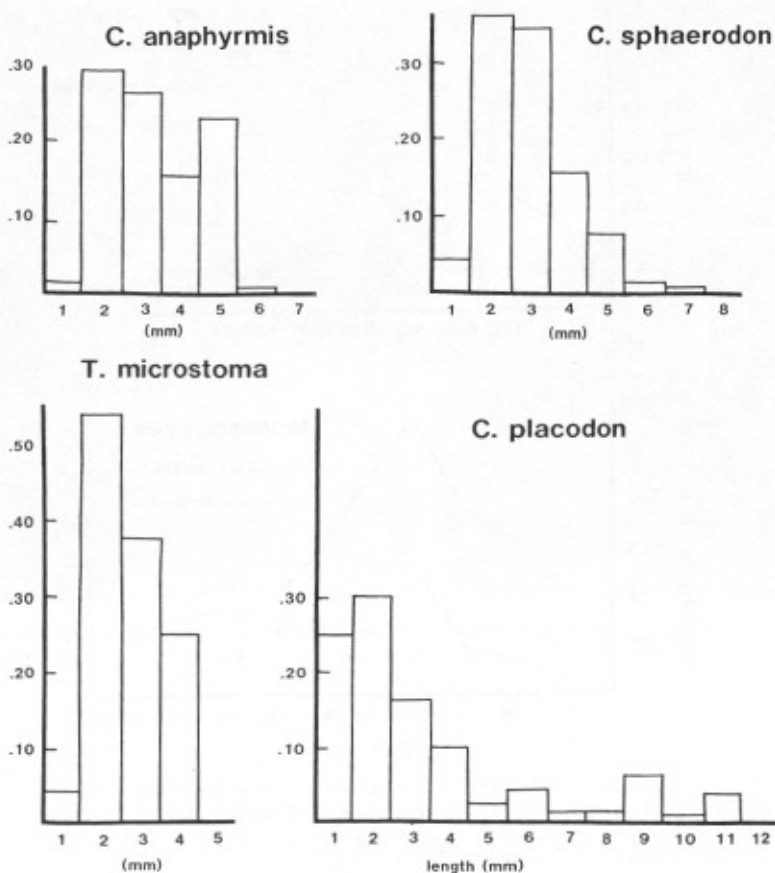


Fig. 3. Proportion of *Melanoides* spp. size classes in the stomachs of cichlid molluscivores. (*C. anaphyrmis* N=112; *C. sphaerodon* N=462; *T. microstoma* N=56; *C. placodon* N=169)

open sand the mean was 33.6 snails/m². These results were significantly different (Kruskal-Wallis, d. f. = 2, H = 9.0, $P < 0.05$). The mean length of *Melanoides* both in the enclosures (N=939) and the open controls (N=582) was 8.7 mm (S. D. 2.2 and 2.3 respectively).

Fish inclusion experiment

The cages with no fish in them had a mean of 100.9 snails per m², the cages with fish had a mean of 67.9 snails per m² and the open sand control had a mean of 70.5 snails per m² (Kruskal-Wallis, $P < 0.05$). There was no significant difference among the mean size of the snails in the fish enclosures (8.7 mm), over open sand (8.7 mm) and in fish enclosures (8.4 mm S. D. 2.6, ANOVA, $P > 0.05$). All of the *C. placodon* held for one week in the cages had freshly eaten snails in their stomachs. Although the mean length of snails eaten by *C. placodon* in the enclosures was greater than for *C. plac-*

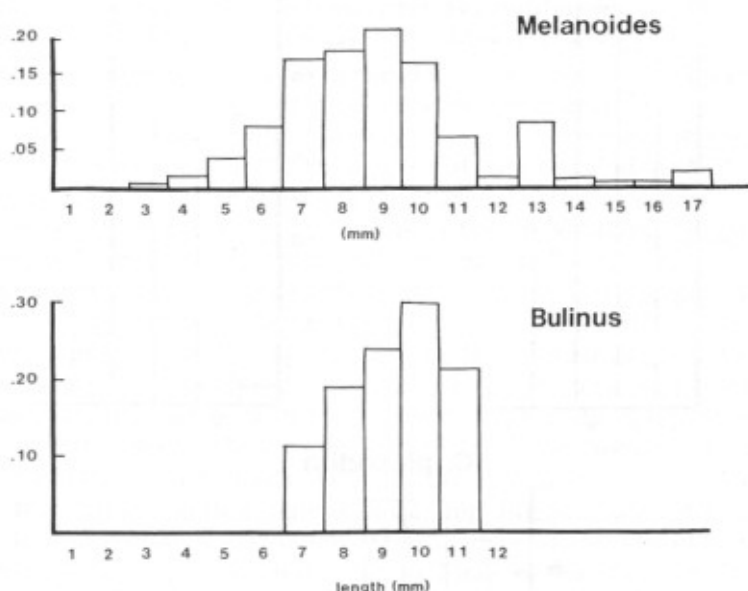


Fig. 4. Proportion of *Melanoides* spp. (N=582) and *Bulinus* spp. (N=17) size classes over open sand

odon taken over open sand, (N = 46, 3.89 mm S. D. 2.4 vs N = 169, 3.22 mm S. D. 2.6) this difference was not significant (t -test, $P > 0.05$).

Laboratory feeding experiments

The fish selectively fed on the smaller size classes of all three genera (Fig. 6). All of the 3 mm snails were consumed. In the 4–5 mm size range all of the *Bulinus* were eaten; half of the *Gabiella* and 40% of the *Melanoides*; in the 6–7 mm size range half of the *Bulinus* were consumed and 20% of the *Melanoides*; in the 8–9 mm size range none of the *Melanoides* were consumed and half of the *Bulinus* were taken. The differences in the proportion of each species taken above the 3 mm size class were significant (Kruskal-Wallis $P < 0.05$).

Discussion

Louda et al. (1983) suggested that one hypothesis to explain the drop in the density of Lake Malawi gastropods below 4 m was due to increased predation there by cichlid fishes. Vascular macrophyte (weed) beds in shallower water were hypothesized to provide a refuge for snails and to reduce predator efficiency in capturing them. This study supports the predation hypothesis and migration of snails into a refuge. When fish were removed from 1 m plots the standing crop of snails increased between 40–60% within one week. In cages where fish had access and/or where they were confined, the number of snails did not differ from densities in open sand areas. The dis-

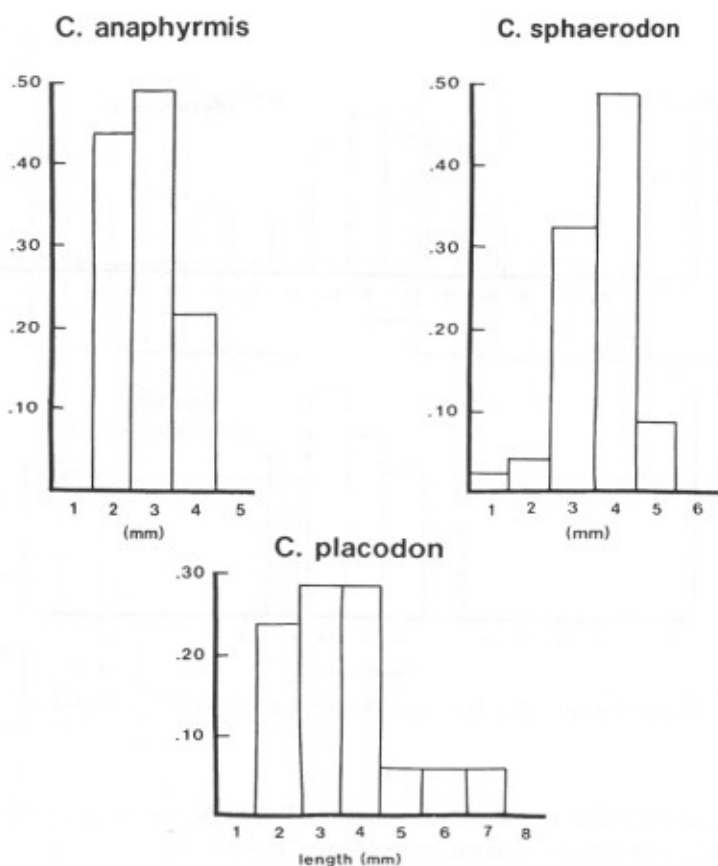


Fig. 5. Proportion of *Bulinus* spp. size classes in the stomach of cichlid molluscivores. *T. microstoma* ate only one *Bulinus* spp. (Table 1) and is not included in this figure. (*C. anaphymis* N=23; *C. sphaerodon* N=47; *C. placodon* N=46)

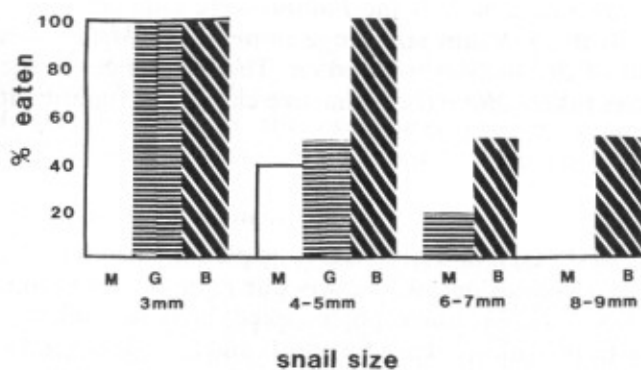


Fig. 6. Proportion, by total length, of *Melanoides* (M), *Gabiella* (G) and *Bulinus* (B) eaten during 24 h period by *Cyrtocara placodon*

tribution of snail feeding fishes reinforces the hypothesis that predation influences snail densities over open sand since the highest number of predators occur at depths just below the weed beds (Fig. 2). Although the predators are concentrated at depths deeper than the area inhabited by the bulk of their prey, the efficiency of capturing prey not hidden among plants, is probably higher in this region (McKaye 1977; McKaye et al. 1979).

An interesting anomaly occurred in the data. The stomach analysis and aquarium experiment indicate that predators feed primarily upon smaller snails. Yet, contrary to expectation, there was no proportional increase in the number of smaller snails in cages where fish were excluded. Nor was there any increase in the size of snails in cages where the fish were enclosed. There are three probable explanations for these sampling results. First, our stomach analyses are based on counting small intact snails. This may bias against including larger snails in stomach analysis. Larger snails may have been fragmented by the crushing action of the cichlid's pharyngeal jaw and hence are under-represented in the stomachs (Liem 1973). Secondly, although we controlled for cage effect with both partial cages and enclosures we did not control for a simple "fish disturbance effect." The lack of fish stirring up the bottom as they feed may increase detritus and food resources for the snails. Thirdly, the snails are nocturnal and large snails move up to 2 m in a night (Louda, unpublished data). All snails are subject to some risk of predation. Hence, they all move into areas where the probability of predation is reduced. Since so few small snails occur over open sand (Fig. 4) a differential effect would not be evident within the short time span of these experiments. The most parsimonious and consistent explanation, in our opinion, is the third one and that cichlid molluscivores are important in the reduction in snail numbers of all size classes in open sand areas.

Regardless of which hypothesis ultimately proves to be correct, these experiments have demonstrated the following. 1) The presence of fish, especially snail feeding cichlids, was responsible for the reduction of snails in open sand. When fish were removed the snail densities increased, and when fish were enclosed snail densities decreased. 2) Snails are behaviorally capable of moving into refuges from fishes in a relatively short period of time (at least within a week). This latter result is consistent with behavioral data reported by Louda and McKaye (1982) for another snail *Lanistes nyassanus*.

Comparison of snail size distributions and densities among studies shows three things. First, snail densities in this study are as high or higher than those previously reported for this area (Louda et al. 1983). These data reinforce the earlier observations of a high degree of variation, both among sections of the shore (2-fold differences in this study) and among patches within a site (Louda et al. 1983; Louda and McKaye in prep.). The reasons for this patchiness are still unknown. Second, the higher density estimates in this study approach the levels of *Melanoides* and *Bellamya* reported for Lake Chad (Daget and Leveque 1969). Third, there has been an increase in recovery of small snails with sampling experience.

The field and aquarium data indicate that the molluscivorous cichlids disproportionately feed upon the thinner shelled *Bulinus* spp. *Bulinus* was found four times more commonly in the stomachs of these fishes relative to *Melanoides* than we found them over open sand in this study, or our earlier study (Louda et al. 1983). Vermeij and Covich (1978) have hypothesized that increased shell thickness in *Melanoides* is a co-evolved adaptation to reduce predation by cichlids in the lakes of Africa. Our data support that view, as *C. placodon* consumes a lower proportion of the larger sizes of the thick shelled species (Fig. 6).

Interestingly, the most common and fragile *Bulinus* species lives in marshy areas within Lake Malawi. Here snail feeding fishes cannot consume them because the thick marshes cannot easily be penetrated by these large molluscivores. This thin shelled species, *Bulinus globosus* a vector for the human disease bilharziasis (schistosomiasis), was preferentially consumed in our laboratory experiments. Lake Malawi is one of the few lakes in Africa which is relatively free of this disease. We suggest that the snail feeding cichlids within the lake may be responsible for preventing the fragile bilharzia vector *B. globosus* from successfully invading the lake. This hypothesis agrees with Vermeij and Covich's (1978) theory on the role of shell thickness in freshwater snails; if this hypothesis is correct, the management of the snail feeding fishes in the lake could be of importance to human health. Reduction of molluscivores in the lake could lead to increased populations of snail vectors in the open lake. Also, if these fishes prove to be effective in eliminating bilharzia vectors within a natural ecosystem, they could be successfully utilized within aquaculture ponds to eliminate the vector snails that often infect these ponds. Such a possibility deserves further examination.

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