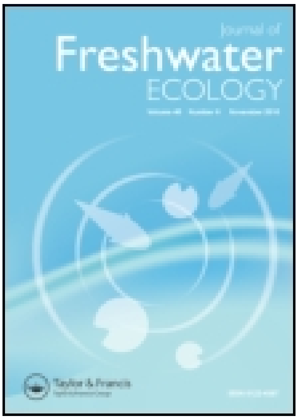

Journal of Freshwater Ecology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tjfe20

Prey selection under laboratory conditions by pond-bred Trematocranus placodon (Regan, 1922), a molluscivorous cichlid from Lake Malaŵi

Alexander S. Kefi [a] , Henry Madsen [b] , Jeremy S. Likongwe [a] , Wilson Jere [a] & Jay R. Stauffer Jr. [c]

[a] Aquaculture and Fisheries Science Department, Bunda College of Agriculture, University of Malaŵi, Lilongwe, Malaŵi

[b] DBL Centre for Health Research and Development, Faculty of Life Sciences, University of Copenhagen, Denmark

[c] School of Forest Resources, Penn State University, University Park, PA 16802, USA

Version of record first published: 22 May 2012.

Journal of Freshwater Ecology
Vol. 27, No. 4, December 2012, 517–526

Taylor & Francis
Taylor & Francis Group

Prey selection under laboratory conditions by pond-bred *Trematocranus placodon* (Regan, 1922), a molluscivorous cichlid from Lake Malaŵi

Alexander S. Kefi[a], Henry Madsen[b], Jeremy S. Likongwe[a], Wilson Jere[a] and Jay R. Stauffer Jr.[c]*

[a]*Aquaculture and Fisheries Science Department, Bunda College of Agriculture, University of Malaŵi, Lilongwe, Malaŵi;* [b]*DBL Centre for Health Research and Development, Faculty of Life Sciences, University of Copenhagen, Denmark;* [c]*School of Forest Resources, Penn State University, University Park, PA 16802, USA*

(*Received 30 January 2012; final version received 26 March 2012*)

Trematocranus placodon, a predator of freshwater snails in Lake Malaŵi, has been recommended for the control of schistosome intermediate hosts in aquaculture ponds. Fish from Lake Malaŵi were introduced into a pond close to Lilongwe and we attempted to elucidate whether pond-raised F_1 retain their ability to consume snails. In laboratory experiments, small fish (70–80 mm total length) preyed only on *Bulinus tropicus* while fish of the 100–110 mm and the 120–130 mm size classes also chose *B. globosus*. All three size classes of fish preferred *B. tropicus*, which was abundant in the pond where fish were raised. *Bulinus nyassanus* was consumed by the largest fish only. *Melanoides tuberculata* was not preyed upon, although this species dominates stomach contents of field collected *T. placodon*. *T. placodon* is a pharyngeal crusher and comparisons of the size and dentition of the pharyngeal bones revealed some differences between field collected and pond-bred fishes. Although pond-bred fishes are able to crush snails, the development of the pharyngeal teeth should be better controlled by fish diet. A hard diet early in life is a prerequisite for *T. placodon* to develop molariform teeth. Later once molariform teeth are developed, fish can be transferred to pond conditions for grow-up and snail control.

Keywords: cichlids; lake Malaŵi; prey choice; schistosomiasis; snail predators

Introduction

Trematocranus placodon, a molluscivorous cichlid species endemic to Lake Malaŵi, is an important predator of freshwater snails and overexploitation of this species and other molluscivorous cichlids has been linked to an increase in schistosome transmission in the southern part of Lake Malaŵi (Stauffer et al. 1997; Madsen et al. 2004). Schistosomiasis is a parasitic disease of major public health importance throughout the tropics that is caused by trematodes of the genus *Schistosoma* that require specific freshwater snail species to complete their life cycles. People are infected when they come in contact with water containing the larval stage (cercariae)

*Corresponding author. Email: vc5@psu.edu

ISSN 0270–5060 print/ISSN 2156–6941 online

http://dx.doi.org/10.1080/02705060.2012.686439
http://www.tandfonline.com

of the trematode. If infected persons defecate or urinate (depending upon the species of *Schistosoma*) in the water, eggs can be released that hatch and parasitize the intermediate host snail (Stauffer et al. 2006)

T. placodon has been recommended for control of intermediate host snails (e.g., *Bulinus globosus*) in aquaculture ponds (Chiotha et al. 1991). This fish species is a facultative molluscivore and will switch to other prey species if snails are not available. The pharyngeal mill of cichlids shows considerable phenotypic plasticity, with food type being important for morphological development (Meyer 1987; Huysseune et al. 1994; Mittelbach et al. 1999). When cultured under pond conditions, there may be a diet shift that could result in the pharyngeal jaws not being sufficiently developed (Slootweg et al. 1994). Culture conditions, especially feeding regimens, are important to ensure that the cultured fish retain their ability to feed on a hard diet such as snails (Stauffer et al. 1997). If the fish does not develop molariform teeth on the pharyngeal bones, it is unable to crush the mollusks (Stauffer et al. 1997). This study attempted to evaluate the potential of pond-bred *T. placodon* to feed on selected species of snails.

Methods

Pond-bred T. placodon

Twenty wild-caught *T. placodon* (mean body weight 54.8 g, mean total length (TL) 143.7 mm and mean standard length (SL) 116.4 mm) collected from Mangochi, Lake Malaŵi, were placed in an earthen pond at Bunda College of Agriculture, University of Malawi, Lilongwe at a sex ratio of 3:1 (female:male) in July 2005. The pond contained a dense population of *Bulinus tropicus*; therefore, no supplementary feeding was given. In March–April 2006, F_1 fishes of three size classes (TL of 70–80 mm (small), 100–110 mm (medium), and 120–130 mm (large)) were collected from the ponds by seining. A total of 70 specimens representing as much of the size variation as possible was killed and their pharyngeal jaws removed; large fish were rather few. The ventral pharyngeal bone was measured and molariform teeth counted along the midline (Figure 1). The jaw measurements and teeth counts were related to fish length and compared to those of field collected *T. placodon* (Kamanga, personal communication). The field sample consisted of 280 fish ranging from 40 to 141 mm, but only the size range covered by the sample of pond-bred fish was used for analysis.

Snails

Bulinus nyassanus and *Melanoides tuberculata* were collected from Lake Malaŵi at Chembe village, Cape Maclear. *B. globosus* were collected from a stream flowing into Lake Malaŵi at Monkey Bay, while *B. tropicus* were obtained from the fish farm located at Bunda College of Agriculture (University of Malaŵi). A Vernier caliper (KANON, KSM-20 200 mm × 0.05) was used to measure shell height of snails (from apex to the base of the aperture). The three *Bulinus* species (*B. globosus, B. nyassanus* and *B. tropicus*) and *M. tuberculata* were partitioned into three size classes (<7 mm, 7–10 mm, and >10 mm for *B. globosus* and *B. tropicus*; <7 mm, 7–9 mm and >9 mm for *B. nyassanus;* 5–10 mm, 10–15 mm and 15–20 mm shell height for *M. tuberculata*).

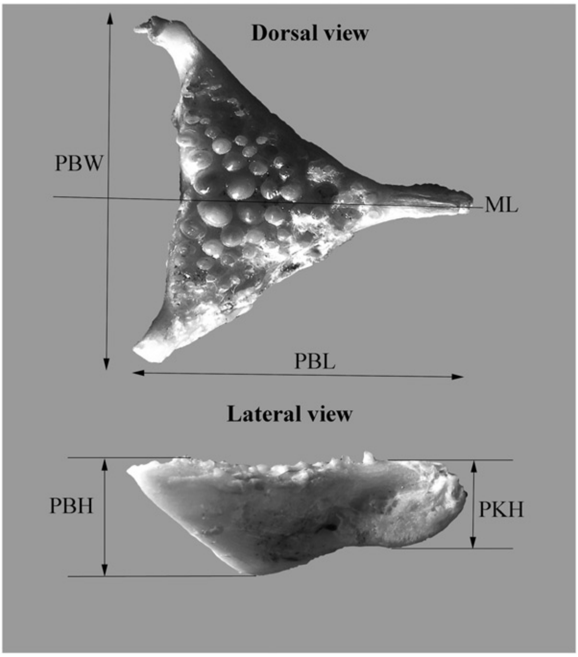

Figure 1. Photos of the lower pharyngeal bone of a pond-bred *T. placodon*. The molariform teeth adjacent to the midline were counted on both side of the midline, and bones were measured as indicated, that is, length (PBL), width (PBW), height (PBH), and keel height (PKH).

In the laboratory, experimental snail species were kept in different tanks containing dechlorinated tap water. Fed *ad libitum*, the snails and fish were maintained on 30% crude protein diet (fish meal 31.5%, soy beans 31.5%, maize bran 33.0%, wheat flour 1%, oil 1%, vitamins 1%, and minerals 1%) to condition them before the start of experiments. Feed for the snails were in meal form while pellets were used for the fish. Lettuce (after immersed for thirty seconds in boiling water) was also provided as food to *B. globosus* and *B. tropicus*; *B. nyassanus* does not feed on lettuce (Lundeba et al. 2006).

To avoid accumulation of waste at the bottom of the tanks and algal growth, cleaning was done twice a week. The aquaria were aerated before and during experiments. Each experimental animal was used only once.

Size selection experiment

Five specimens of each of the three size classes of one snail species were introduced in a circular tank filled with 20 L of water; two such tanks were used for each snail species. One specimen of *T. placodon*, deprived of food for 24 h prior to the trial, belonging to one of the three size classes, was introduced in each tank. The trial was repeated four times for each combination of snail species and fish size. The fish were allowed to feed for 72 h under a 12 h/12 h light/dark photo period. Containers were inspected regularly and the number of snails alive in each size category was counted at the end of the trial.

Species selection experiment

Five specimens (6–7 mm) of each of the four snail species were placed in each tank, as described earlier. One specimen of *T. placodon* belonging to one of three size categories was introduced in each tank. The trial was repeated eight times for each fish size.

Statistical analysis

Logistic regression (Hosmer and Lemeshow 1989) was used to examine significant differences in the fate of snails according to species and size. Measurements, standard length of fish, and measurements of the pharyngeal bone (Figure 1) were compared between pond-raised (this study) and field collected (Kamanga, personal communication) *T. placodon* using Sheared Principal Component Analysis (SPCA) (Rolf and Bookstein 1987), which factors the covariance matrix and restricts size variation to the first principal component (Humphries et al. 1981; Bookstein et al. 1985). All measurements were natural log transformed before analysis. Measurements (ln transformed) were compared individually between field collected and pond bred fish after adjusting for standard length of fish using multiple linear regression (analysis of covariance) and after checking that the slopes for the two fish origins did not differ significantly. Similarly, molariform teeth counts were compared between fish origins after adjusting for length of the pharyngeal bone using regression analysis. Significant differences were indicated by *p*-values less than 0.05.

Results

Pond-bred *T. placodon* consumed only *Bulinus* species (Figure 2). The largest snail size category was only consumed by the largest fish used in the experiment (Figure 2). Logistic regression showed significant ($p < 0.001$) differences among snail sizes and the interaction between snail species and snail size was significant ($p < 0.001$).

In the species selection trials pond-bred *T. placodon* preyed only on *B. globosus* and *B. tropicus*, but not on *B. nyassanus* nor *M. tuberculata* (Table 1). The smallest fish used in the experiment, however, preyed only on *B. tropicus* (Table 1). The number of *B. tropicus* consumed was significantly greater than that of *B. globosus* ($p < 0.05$).

The data used for comparison of jaw morphology are summarized in Table 2. There was no overlap in the minimum polygon clusters when SPCA2 was plotted against SPCA3 for the pharyngeal bones taken from pond-bred and the field collected *T. placodon* (Figure 3). Size accounted for 86.4% of the observed variance and the second principal component accounted for 7.1%. The main measurement responsible for this separation was the height of the ventral keel (factor loading −0.52). The relationship between height of the keel and pharyngeal bone length (both ln-transformed) is shown in Figure 4; height of the keel increased with length of the pharyngeal bone ($p < 0.001$) and keel height in pond bred fish was 42% of that of a pharyngeal bone of similar size from wild caught fish (i.e., $b = -0.8731$; $p < 0.001$). Keel height, however, was more variable in field collected fish than in pond bred fish (Figure 4). The number of molariform teeth increased with length of the pharyngeal bone ($p < 0.001$) and was greater in pond-bred ($b = 2.28$; $p < 0.001$) than in field collected fish (Figure 5).

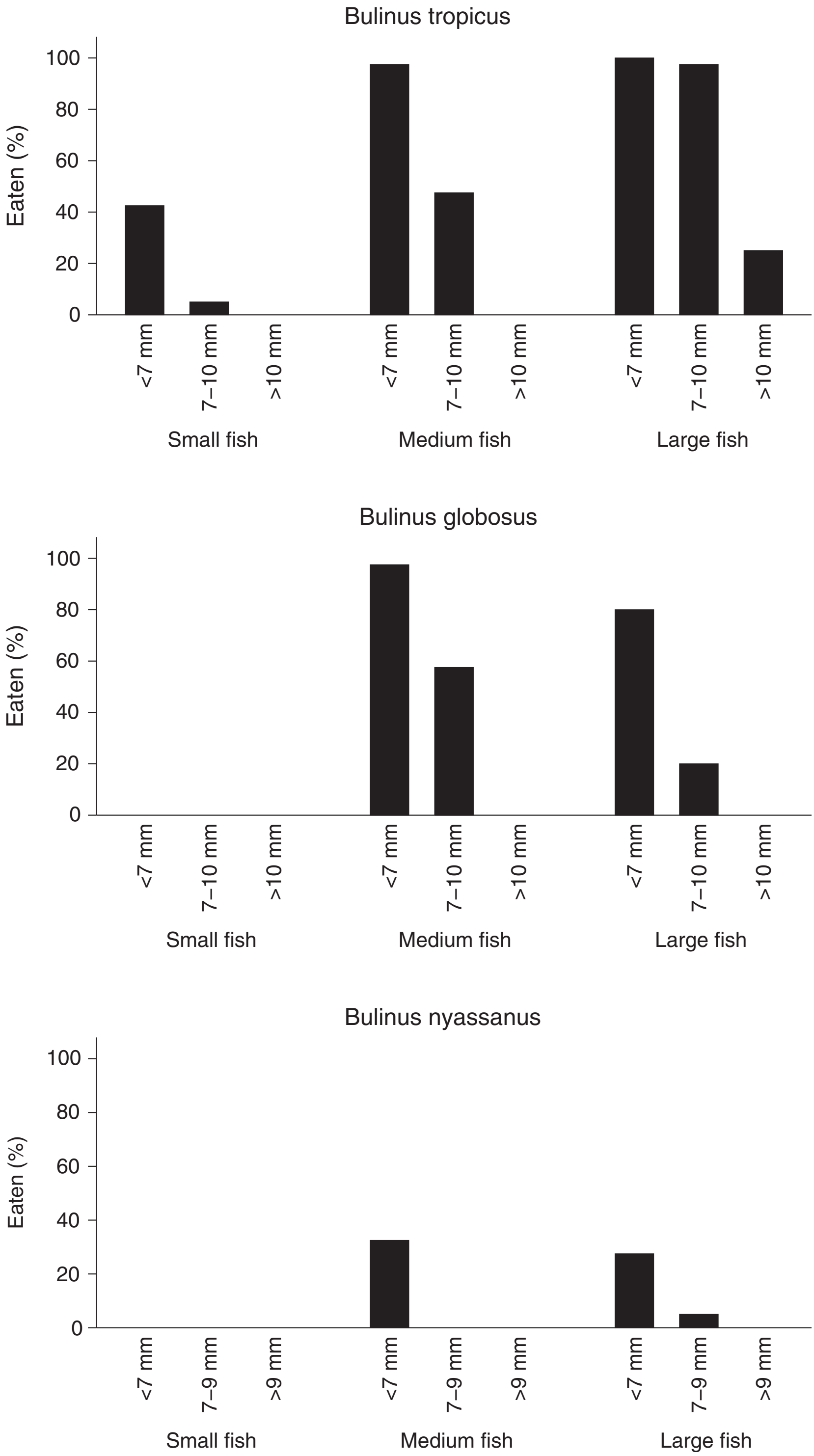

Figure 2. Percentage of snails of various species and sizes consumed by 1 specimen of *T. placodon* of different size (small: 70–80 mm; medium: 100–110 mm, or large: 120–130 mm) during 72 h. The total number of snails used for each combination of snail species, snail size and fish size was 40.

Table 1. Number of snails of various species consumed by 1 specimen of *T. placodon* of three different sizes during 72 h. The total number of snails used for each combination of snail species and fish size was 40.

	Small fish	Medium fish	Large fish
Bulinus tropicus	14	37	37
Bulinus globosus	0	30	34
Bulinus nyassanus	0	0	0
Melanoides tuberculata	0	0	0

Table 2. Summary of variables on pharyngeal bone of *Trematocranus placodon* from the field or from Bunda pond. *p*-values are for difference between the two groups after adjusting for standard length of fish.

	Field	Pond	*p*-value
No. of fish	177	70	
Standard length (mm)	79.8 (56.0–103.6)	79.9 (54.0–104.0)	–
PB length (mm)	8.6 (4.4–15.8)	9.0 (6.2–11.5)	<0.05
Width (mm)	8.8 (4.9–16.6)	8.3 (5.9–10.7)	n.s.
Height (mm)	3.7 (1.7–10.2)	2.9 (1.9–3.9)	<0.001
Keel height (mm)	3.1 (1.0–7.6)	1.2 (0.6–1.7)	<0.001
No. of molariform teeth	7.2 (2–12)	9.8 (6–13)	<0.001

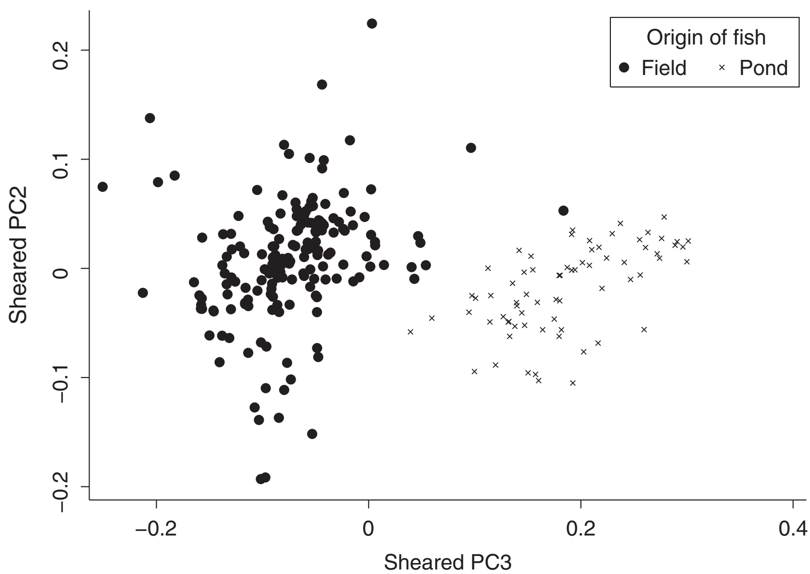

Figure 3. Sheared principal component analysis (SPCA) on pharyngeal bone measurements showing differences along sheared pc2 and pc3 scores between field collected and pond-bred specimens (F_1) of *T. placodon*.

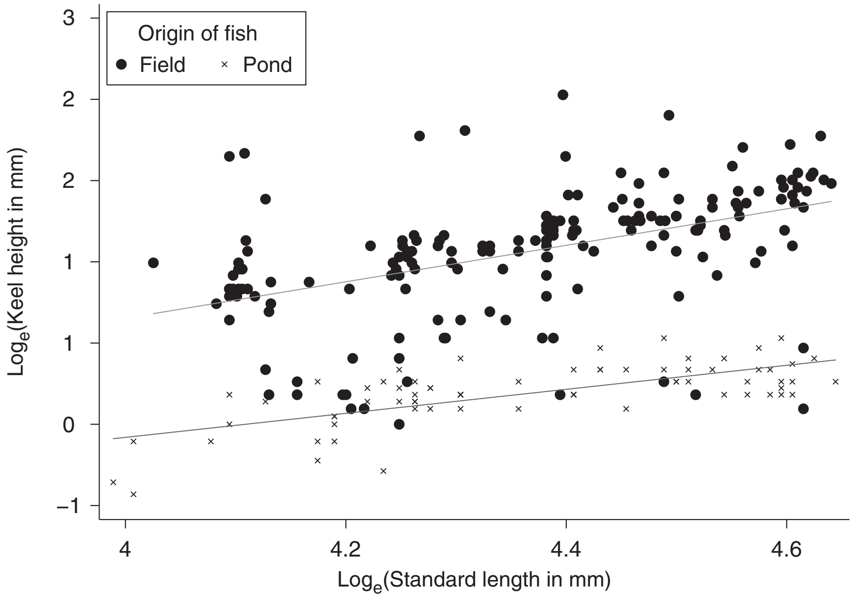

Figure 4. Keel height as a function of standard length of *T. placodon* collected from the field or pond-bred (F_1).

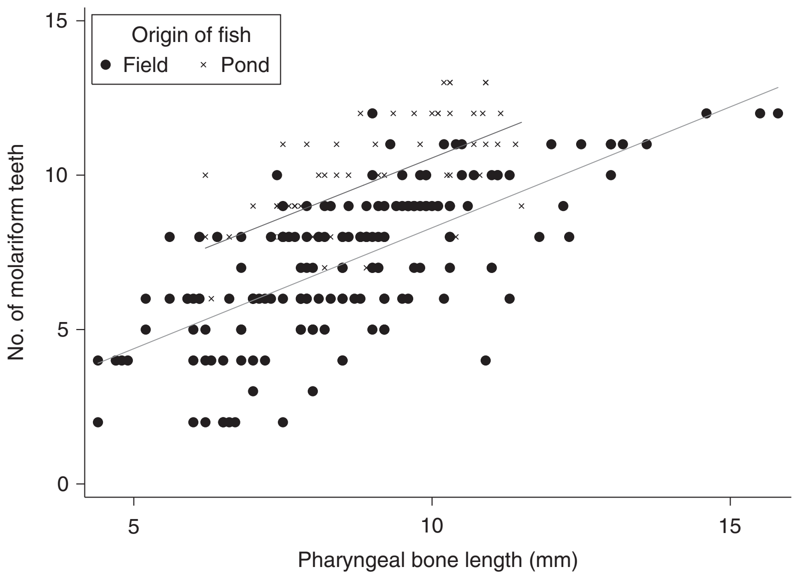

Figure 5. Number of molariform teeth as a function of pharyngeal bone length of *T. placodon* collected from the field or pond-bred (F_1).

Discussion

Pond-bred *T. placodon* preyed more on the smallest snails followed by the medium-sized snails, which was congruent with the results reported by Chiotha (1990). Slootweg (1987) found that *Haplochromis ishmaeli* ate a wide size-range of snails but the largest were usually not eaten. Brodersen et al. (2003) found that *Sargochromis codringtonii* preying on *Bellamya capillata* had a size-dependence on the snail size selection. The preference for small-sized snails may be a disadvantage to biological control of schistosome intermediate host snails in the short term because many studies have shown that prevalence of schistosome infection in host snails increases with the snail size (Coulibaly and Madsen 1990; Phiri 2002). Predation on small-sized specimens, however, would still influence the population dynamics by reducing recruitment into the larger and reproductively active group (Chiotha 1990). It may also prevent snails from living long enough to be infected and shed the cercariae (Chiotha 1990).

We showed that fish selected both *B. tropicus* and *B. globosus* although the former was preferred. Earlier studies by Chiotha (1990) using wild caught *T. placodon* on *B. tropicus*, *B. globosus* and *Biomphalaria pfeifferi* showed no preference for any of the three snail species. *S. codringtonii* preferred smaller *B. tropicus* (which is not the intermediate host for *S. haematobium*) to the larger *B. globosus*, the intermediate host for *S. haematobium* (Chimbari et al. 1996; Brodersen et al. 2003). Chiotha (1990) demonstrated that *B. globosus, B. tropicus*, and *B. pfeifferi* differed significantly in terms of crushing resistance. Evers et al. (2011) showed that *B. nyassanus* had a higher crush resistance than *B. globosus*. The selection by pond-bred *T. placodon* for *B. tropicus* and *B. globosus* is consistent with what would be predicted by optimal foraging efficiency. The preference by pond-bred *T. placodon* of *B. tropicus* only, which has a softer shell and lower calories than *B. globosus*, could be attributed to previous foraging experience or palatability.

It has been hypothesized that the hypertrophy of the pharyngeal bone of artificially bred *T. placodon* is due to the type of food encountered during development and, if fed on soft diets, molariform teeth on pharyngeal bones do not develop. Without these molariform teeth, the fish is not capable of crushing snails (Stauffer et al. 1997). Laboratory experiments show that trophic morphology of facultative molluscivores can be altered by rearing fish on different diets (Greenwood 1965; Hoogerhoud 1986; Meyer 1987; Wainwright et al. 1991) and it appears that these effects can sometimes be reversed during ontogeny by a second experimental manipulation of diet (Meyer 1987; Wainwright et al. 1991).

In this experiment, pond-bred *T. placodon* developed pharyngeal teeth necessary for mollusc crushing but they seemed to be less developed than those from field collected fish. This may be attributed, however, to the availability of *B. tropicus* in the earthen pond that held fish for the present experiment and because it is easier to crush than *Melanoides* spp. and *B. nyassanus*, which constitute the diet of wild fish. The failure by the fish to consume the prosobranch *M. tuberculata* may be attributed to high crushing resistance of the shell. Therefore, to maximize the potential of pond-raised fish in controlling snails, the development of molariform teeth and the robustness of the pharyngeal jaw should be facilitated by controlling the diet during the early life of fish.

Acknowledgements

We would like to thank the joint program of the United States of America National Science Foundation (NSF) and United States of America National Institutes of Health (NIH) program in Ecology of Infectious Diseases (DEB 0224958) for the financial support rendered towards the study. We are grateful to the Department of Aquaculture and Fisheries Science at

Bunda College of Agriculture, University of Malaŵi, for allowing us use of facilities in conducting this research.

References

Bookstein FL, Chernoff B, Elder R, Humphries J, Smith G, Strauss R. 1985. Morphometrics in evolutionary biology. Academy of Natural Sciences of Philadelphia, Special publication. 15:1–277.

Brodersen J, Chimbari MJ, Madsen H. 2003. Prosobranch mollusc species-and size preferences of *Sargochromis codringtonii* (Cichlidae) in Lake Kariba, Zimbabwe. African Journal of Aquatic Sciences. 22:179–182.

Chimbari MJ, Ndamba J, Madsen H. 1996. Food selection behaviour of potential biological agents to control intermediate host snails of schistosomiasis: *Sargochromis codringtoni* and *Tilapia rendalli*. Acta Tropica. 61:191–196.

Chiotha SS 1990. Biological control of human schistosomiasis using snail-eating fish [PhD. Thesis] [Maryaland]: University of Maryland, 161 p.

Chiotha SS, McKaye KR, Stauffer JR. 1991. Prey handling in *Trematocranus placodon*, a snail-eating cichlid fish from Lake Malaŵi. Ichthyological Explorations of Freshwaters. 2:203–208.

Coulibaly G, Madsen H. 1990. Seasonal density fluctuations of intermediate hosts of schistosomes in two streams in Bamako, Mali. African Zoology. 104:201–212.

Evers BN, Madsen H, Stauffer Jr. JR. 2011. Crush-resistance of soft-sediment gastropods of Lake Malaŵi: Implications for prey selection by molluscivorous fishes. Journal of Freshwater Ecology. 26:85–90.

Greenwood PH. 1965. Environmental effects on the pharyngeal mill of a cichlid fish. *Astatoreochromis alluadi* and their taxonomic implications. Proceedings of the Linnaean Society of London. 176:1–10.

Hoogerhoud RJC. 1986. Plasticity and allometry of pharyngeal jaws in the morphocline of insectivourous/molluscivorous *Haplochromis* (Pisces, Ciclidae). Proceedings of the 3rd European Workshop on Cichlid Biology, The Netherlands, Capron de Capron, M.D. and Fritzch, B. (Eds) The Netherlands.

Hosmer DW, Lemeshow S. 1989. Applied logistic regression. New York: John Wiley and Sons, 307 pp.

Humphries JM, Bookstein FL, Chernoff B, Smith GR, Elder RL, Poss SG. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology. 30: 291–308.

Huysseune A, Sire J-Y, Meunier FJ. 1994. Comparative study of lower pharyngeal jaw structure in two phenotypes of *Astatoreochromis alluaudi* (Teleostei: Cichlidae). Journal of Morphology. 221:25–43.

Lundeba M, Likongwe JS, Madsen H, Stauffer, Jr. JR. 2006. Preliminary study on the culture and breeding of *Bulinus nyassanus* (Mollusca: Pulmonata) under laboratory conditions. African Zoology 41:143–144.

Madsen H, Stauffer Jr. JR, Bloch P, Konings A, McKaye KR, Lilongwe JS. 2004. Schistosomiasis transmission in Lake Malaŵi. African Journal of Aquatic Sciences. 29:117–119.

Meyer A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. Evolution. 41:1357–1369.

Mittelbach GG, Osemberg CW, Wainwright PC. 1999. Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? Evolutionary Ecology Research. 1:111–128.

Phiri HTB. 2002. Distribution, density and infection rates of the intermediate hosts of Schistosoma species in selected lakeshore communities on Nankumba Peninsula [MSc. Thesis] [Denmark]: University of Malaŵi/Danish Bilharziasis Laboratory. 70p.

Rolf FJ, Bookstein FL. 1987. A comment on shearing as a method for "size correction". Systematic Zoology. 36:356–367.

Slootweg R. 1987. Prey selection by molluscivorous cichlids foraging on a schistosomiasis vector snail, *Biomphalaria glabrata*. Oecologia. 74:193–202.

Slootweg R, Malek EA, McCullough FS. 1994. The biological control of snail intermediate hosts of schistosomiasis by fish. Reviews in Fish Biology and Fisheries. 4:67–90.

Stauffer Jr. JR, Arnegard ME, Cetron M, Sullivan JJ, Chitsulo LA, Turner GF, Chiotha S, McKaye KR. 1997. Controlling Vectors and hosts of parasitic diseases using fishes. A case history of schistosomiasis in Lake Malaŵi. BioScience. 47:41–49.

Stauffer Jr. JR, Madsen H, McKaye KI, Konings A, Bloch P, Fererri C, Likongwe J, Makaula P. 2006. Schistosomiasis in Lake Malawi: Relationship of fish and intermediate host density to prevalence of human infection. EcoHealth. 3:22–27.

Wainwright PC, Osenberg GW, Mittelbach GG. 1991. Trophic polymorphism in Pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. Functional Ecology. 5:40–55.