Journal of Freshwater Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t925992003

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Online publication date: 06 January 2011

Biology of the Molluscivorous Fish *Trematocranus placodon* (Pisces: Cichlidae) from Lake Malaŵi

H. Madsen[a], K.C.J. Kamanga[b], J.R. Stauffer, Jr.[c,d], and J. Likongwe[b]

ABSTRACT

Tramatocranus placodon is a facultative molluscivore endemic to the Lake Malaŵi catchment basin, Malaŵi, Africa. *T. placodon* feeds on both *Bulinus nyassanus*, which is a host of human urinary schistosomes, and *Melanoides* spp. in the open waters of Lake Malaŵi. We found that there was a dietary shift from insects and small snails to larger snails as the fish grew, and this correlated with the development of the lower pharyngeal bone, which is instrumental in crushing snails. There was also an increase of the proportion *B. nyassanus* in the diet just before the onset of spawning.

INTRODUCTION

Urinary schistosomiasis (*Schistosoma haematobium*) is common among both indigenous people and ex-patriots in the village of Chembe, which is located on the shores of Lake Malaŵi (Madsen 2001, Stauffer et al. 2006). Transmission in the open waters of Lake Malaŵi is a relatively new development (Stauffer et al. 1997) and is attributed to the intermediate host *Bulinus nyassanus* (Madsen et al. 2001). The emergence of the importance of *B. nyassanus* as an intermediate host may be related to over-fishing of the snail-eating fishes in the lake (Stauffer et al. 2007). One of the most abundant molluscivores in Lake Malaŵi is *Trematocranus placodon*, and its abundance has been linked to the density of intermediate host snails in the lake (Stauffer et al. 2006).

Trematocranus placodon grows to a maximum total length of 23 cm (Konings 1990). Konings (1990) reported that from July to September, males defended large crater bowers (70 cm in diameter) but suggested that they might use pits abandoned by other species. *T. placodon* has a wide distribution in the lake, and it is abundant in depths shallower than 20 m, with an average preference of 5 m and 1.5 individuals per every 10 m^2 (Konings 1990). It also occurs in Lake Malombe and upper and middle Shire River (Turner 1996). *T. placodon* mainly forages on gastropods on sandy bottoms of shallower waters. It also possibly feeds in groups, relying on group members to locate food (Chiotha et al. 1991). The fish is a facultative molluscivore and can have well developed pharyngeal jaws with a strong dentition of primarily molariform teeth, depending upon diet. Ingested snails are moved to the pharynx where they are crushed (Fryer and Iles 1972). Although it is regarded as a facultative snail-feeder, little is known about dietary preference and its reproductive capacity. Therefore, it is difficult to assess the potential of this fish to act as a biological control of intermediate host snails of *S. haematobium* or to develop management strategies to increase population densities *in situ*. The purposes of this study were to provide information on food selection and reproductive potential of *T. placodon* in the open waters of Lake Malaŵi.

MATERIALS AND METHODS

Fish sampling and preservation

Samples of *T. placodon* were collected from the southern end of Lake Malaŵi on Nankumba Peninsula in front of Chembe Village at Cape Maclear (34°50'E; 14°5'S).

[a] DBL – Centre for Health Research and Development, Faculty of Life Sciences, University of Copenhagen, Thorvaldsensvej 57, 1871 Frederiksberg C, Denmark.
[b] Bunda College of Agriculture, University of Malaŵi, Lilongwe, Malaŵi.
[c] School of Forest Resources, Penn State University, University Park, Pennsylvania 16802 USA.
[d] Corresponding author; E-mail: vc5@psu.edu

Fish were captured by SCUBA divers, who encircled fish with a 6.35 mm mesh monofilament net. We collected approximately 30 fish every month from November 2003 to August 2004 to cover four seasons -- November to December (end of dry season), February to March (rainy season), May to June (start of dry season), and August (dry season). We anesthetized fish with clove oil and recorded standard length and weight. Subsequently, we euthanized them with 1% formalin and preserved them with 10% formalin. After two weeks in formalin, fish were permanently stored in 70% ethanol.

We grouped fish into the following standard length (SL) size groups: <50 mm, 50-99.99 mm, and >100mm. We removed and preserved stomachs of all the fish and the gonads of the female fish in 70% ethanol for later examination. We measured dimensions of the lower pharyngeal bone (length, width, height, and keel height) and counted the number of molariform and villiform teeth along the entire periphery and along parallel lines on either side of the midline.

Stomach contents

We identified snails in the stomachs based on shells and/or opercula (depending on species). We counted the number of each species based on the number of whole snails, snail fragments (spire part only), and opercula. We measured the height of each operculum to the nearest 0.01 mm with an ocular scale mounted in a dissecting scope. We enumerated other food types (e.g., scales, insects, and fish).

Snail sampling

We collected snails at the same time and locality of the fish collections. To estimate prey preference we compared relative abundance of snails in the environment to that in the fish stomach. We removed opercula and embryos from 50 field-collected specimens of *Melanoides* spp. of various sizes and recorded shell heights of the field-collected specimens using vernier calipers. We measured the shell height of all snails (minimum 2.95 mm) to determine the minimum prey size of the species available in the field using a dissecting microscope with an ocular scale. We assumed that *Melanoides* spp. below this minimum size entered the stomachs via the brood pouch of adults. We measured heights of opercula using a microscope with an ocular scale. The relationship between the shell height and operculum height was used to estimate shell height of the *Melanoides* spp. found in the stomach.

Reproduction

We recorded gonad maturity stages, fecundity, gonadosomatic index (GSI) and reproductive seasonality of female *T. placodon*. We based our assignment of developmental stages as per Msukwa and Ribbink (1997). In the final analysis, we classified all individual fish with active/spent gonads as mature.

We investigated reproductive seasonality using different stages of maturity of the gonads and counted the number of mature eggs in weighed samples of the ovaries to estimate egg production. We calculated the GSI as follows: GSI (%) = {weight of gonads (g) /weight of fish (g)}*100. Finally, we used the highest proportion of ripe gonads and abundance of mouth-brooding females among the specimens examined to determine peak breeding season.

Statistical analysis

We used a simple linear regression model to determine the relationship between the lower pharyngeal bone measurements and fish size, and between the operculum height and shell height for *Melanoides* spp. The equation derived from the linear regression model predicted the shell height of the snails, which the fish ate. All test p values <0.05

were considered significant. The relationship between GSI and oocyte weight was determined with a simple linear regression. The number of *B. nyassanus* found in stomachs of *T. placodon* was analyzed using negative binomial regression (Hilbe 2008) with month and size-class as predictors and the total number of snails counted as an offset. The ancillary parameter was estimated using a full maximum likehood estimation, which was then entered in a generalized linear model (Hilbe 2008). Only significant factors were retained in the final model.

RESULTS AND DISCUSSION

Ventral pharyngeal bone measurements

Standard length of the fish ranged from 30 mm to 141 mm. Length, width, height, and keel height of the lower pharyngeal bone increased linearly with standard length of the fish and correlated linearly with one another (Table 1). The number of molariform teeth increased with fish size; mt = 0.1555*SL+1.1209, where mt is the number of molariform teeth and SL is standard length of the fish ($r^2 = 0.305$). Addition of the number of villiform teeth, the square term of this number, and area of the bone as predictors of molariform teeth resulted in $r^2=0.7062$. Standard length of fish was still a significant predictor ($p<0.05$). Number of villiform teeth was a negative predictor ($p<0.001$), but the relationship was not linear; also the squared term was significant and area was positively related to the number of molarifom teeth ($p<0.001$) when adjusting for the other factors. The relationship was further analyzed by calculating the proportion of molariform teeth of the total count (molariform plus villiform); this proportion ranged from 0.02 to 0.76 and increased significantly ($p<0.001$) with fish size (regression analysis on arcsine transformed proportions). The development of the pharyngeal bone, which increases in size as the fish matures was correlated with a shift in diet. Previous studies have shown that factors such as handling time and ability to crush snails vary with fish size (Slootweg 1987, Msukwa and Ribbink 1997).

Stomach contents

Snails dominated the stomach contents of *T. placodon*. Even for the smallest size class of *T. placodon*, we found remnants of *Melanoides* spp. in more than 80% of the stomachs (Fig 1). Shell height of *Melanoides* spp. was related to operculum height and calculated by ht = 5.3397*op - 4.0486, where ht is shell height and op is the operculum height. The prevalence of *B. nyassanus* increased with size of the fish, 40%, 60%, and 80% in the <70 mm, 70-99 mm, and ≥100 mm size classes, respectively. Fish consumed a considerable amount of other sources of food such as insects, fish larvae, and detritus material. Although, the tendency of fish to consume snails of any species increased with

Table 1. Correlation coefficients between jaw measurements, tooth counts, and fish size.

	Jaw length	Jaw width	Jaw height	Keel height	Molariform teeth	Villiform teeth
Jaw width	0.978					
Jaw height	0.894	0.905				
Keel height	0.897	0.917	0.944			
Molariform teeth	0.715	0.732	0.732	0.737		
Villiform teeth	-0.493	-0.542	-0.600	-0.591	-0.731	
Standard length	0.735	0.706	0.723	0.690	0.552	-0.337

fish size, they consumed considerable amounts of other food items. The largest specimen of *Melanoides* spp. as estimated from operculum size was 15.2 mm in shell height.

T. placodon did not prefer *B. nyassanus* during the months of November to March (rainy season) but ate a higher proportion from May to August (dry season) (Fig. 2). In the field, density of *Bulinus* spp. was generally lower than that of *Melanoides* spp. Negative binomial regression showed that fish in the <50 mm and 50-100 mm size classes consumed 59% ($p<0.05$) and 62% ($p<0.01$) when adjusting for the effect of month and interaction between size class and month. During August, consumption of *B. nyassanus* by the >100 mm size class was 2.59 times greater ($p<0.001$) than during the other months combined. For the 50-100 mm size class, the consumption of *B. nyassanus* in August was 5.03 times that during the other months combined. The smallest size class was not represented in August. The ancillary parameter was estimated at 0.88 and this model did not show signs of over-dispersion (Pearson/df=0.942).

Even the smallest size class of *T. placodon* (<50 mm) fed on snails, but *B. nyassanus*

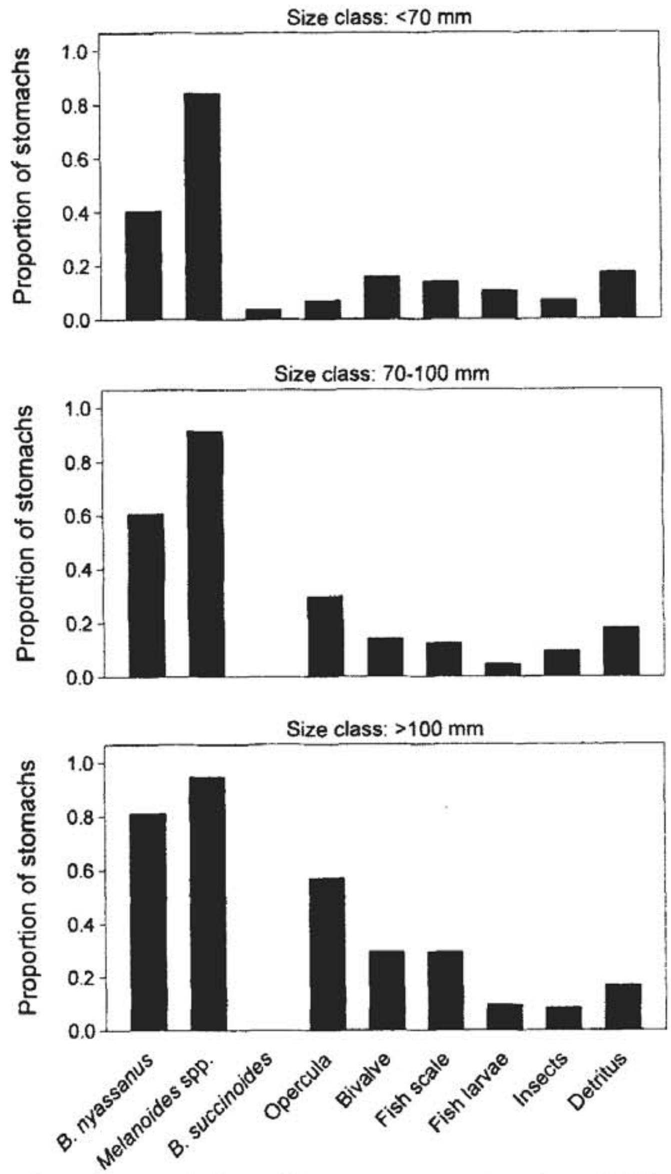

Figure 1. Proportion of stomachs from *Trematocranus placodon* of different sizes with various items (N=57, 127, and 95 for the three size classes, respectively).

constituted a smaller fraction of the snails consumed than was the case for the larger fish. *Melanoides* spp. predominated in the stomach content, and this is probably because of their appreciable abundance in the field. *Melanoides* spp. were very dense in the shallow water at Cape Maclear, and although *Melanoides tuberculata* has been shown to compete with schistosome intermediate host snails in other areas, its presence seems to favor *B. nyassanus* by alleviating predation pressure (Evers 2004).

The proportion of *Melanoides* spp. eaten declined as the fish grew, while that of *B. nyassanus* increased. This observation is congruent with the findings of Evers (2004), who demonstrated that *B. nyassanus* had a higher prey value at bigger size (<15 cm) as compared to *Melanoides* spp.

Relatively, the proportion of snails, insects, and other food types was lower in the stomach contents of the fish during the rainy season (November to March) than during the dry season (May to August). This observation corresponded to the relative abundances of food types in the environment. It may, however, be driven by the onset of the breeding season when many fishes switch to foods with higher percentages of lipid and energy content.

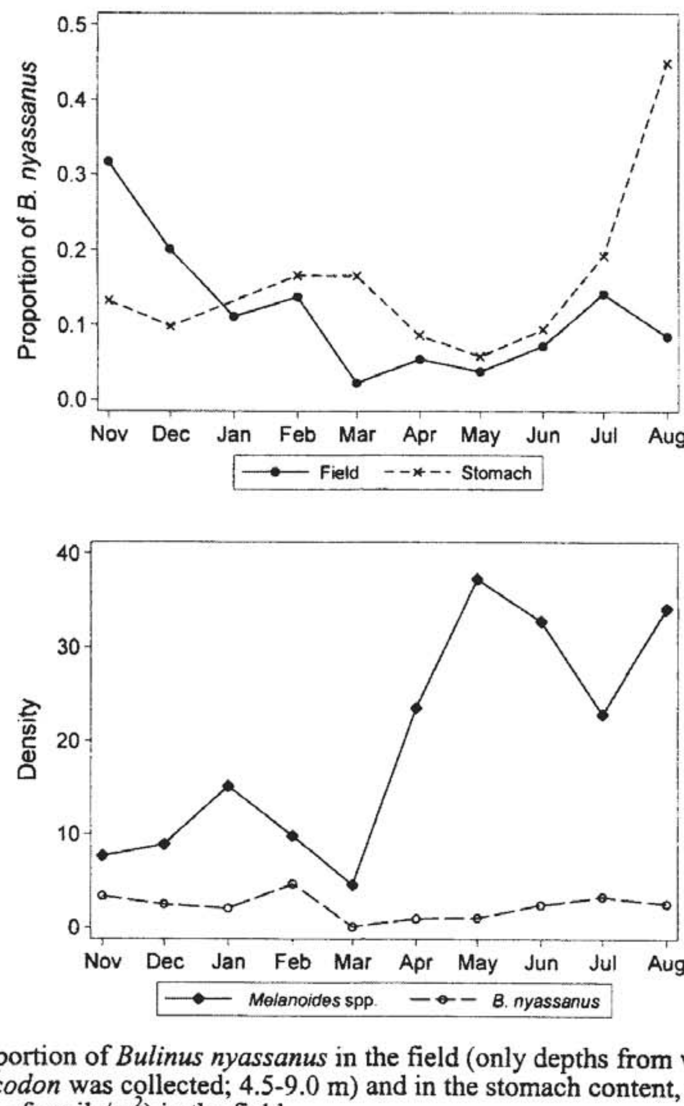

Figure 2. Proportion of *Bulinus nyassanus* in the field (only depths from where *T. placodon* was collected; 4.5-9.0 m) and in the stomach content, and density (no. of snails/m^2) in the field.

Fish life history

Juvenile females were found in all samples but showed variation over time. During the November-December, 52% of the fish were juvenile, and this figure dropped during the subsequent months to a minimum of 18% in August. Fish in the immature and spent stages represented on average 20% of the fish. Mature gonads (ripe and spent) were present throughout the year, but the highest proportion was found in August (42%). The lowest proportion was in February–March.

The fecundity of *T. placodon* ranged from 44 to 263 eggs/female and correlated positively with body weight (r^2= 0.6893). The GSI ranged from 2.13 to 4.71 and was not linearly related to gonad weight. It was relatively stable from December to May where it started to increase steadily (Fig. 3).

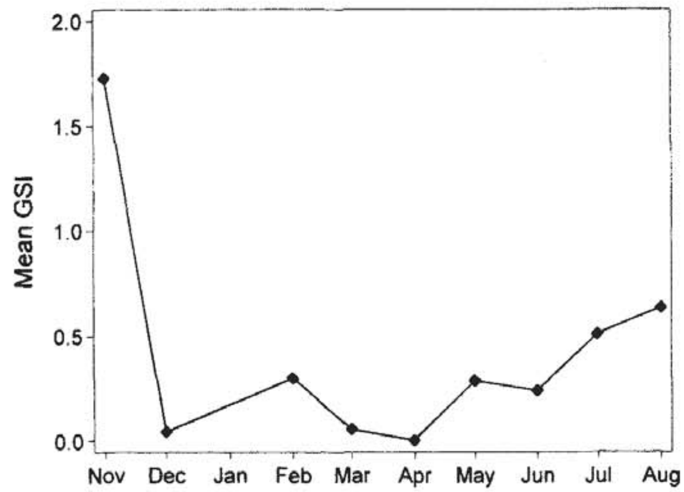

Figure 3. Mean gonadosomatic index of females of *T. placodon* larger than 70 mm.

ACKNOWLEDGMENTS

Funding was provided by the NSF/NIH joint program in Ecology of Infectious Diseases (DEB-0224958). The work was conducted in collaboration with Malaŵi Fisheries Department, Malaŵi Parks and Wildlife Department, and Bunda College of Agriculture, University of Malaŵi.

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Received: 8 March 2010 Accepted: 25 April 2010