

The schistosome intermediate host, *Bulinus nyassanus*, is a 'preferred' food for the cichlid fish, *Trematocranus placodon*, at Cape Maclear, Lake Malawi

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Over the last decade, transmission of the schistosome parasites of humans has increased in parts of Lake Malawi, possibly because over-fishing has led to a decline in the numbers of molluscivorous fish. The stomach contents of 51 wild-caught *Trematocranus placodon* from the Cape Maclear area of Lake Malawi have now been investigated and compared with the field abundance of snail species at two sites, close to where the fish were caught. The snails found in the fish stomachs were identified to genus or species on the basis of their shell fragments and/or opercula. The sizes of the prosobranchs consumed by the *T. placodon* were determined from their operculum sizes whereas the *Bulinus nyassanus* ingested by the fish were categorized as small (<4 mm) or large (≥4 mm) on the basis of their shell fragments. The proportion of the *Bu. nyassanus* ingested that were categorized as large increased with fish size. Furthermore, the relative abundance of *Bu. nyassanus* in the guts of the fish was considerably higher than in the field, indicating that the *T. placodon* had a 'preference' for *Bu. nyassanus* over the *Melanoides* species that dominated the snail fauna. Small specimens of *Bellamya* species were also consumed in a greater proportion than found in field.

The *Trematocranus placodon* (Regan 1922) in Lake Malawi are known to feed on gastropods, including *Melanoides* spp. and *Bulinus* spp. (Fryer and Iles, 1972; McKaye *et al.*, 1986; Chiota *et al.*, 1991; Msukwa and Ribbink, 1997). Stauffer *et al.* (1997) suggested that it was the decline in such snail-eating fish over the last decade that was at least partially responsible for the observed increase in the prevalence of human urinary schistosomiasis in Chembe village, which is located on the Nankumba Peninsula of Lake Malawi (Cetron *et al.*, 1996). The results of recent studies have shown that transmission of *Schistosoma*

haematobium (the parasite that causes urinary schistosomiasis) occurs not only in the streams, swamps and backwaters around the lake, via *Bu. globosus*, but also in the lake itself, via *Bu. nyassanus* — a snail species that is endemic to the lake (Madsen *et al.*, 2001, 2004). The protection of the molluscivorous fish, which can change the size and species composition of snail communities in natural ecosystems (Mittelbach, 1984; Brönmark and Weisner, 1996), is probably the only realistic measure that can currently be taken to reduce transmission in the open waters of the lake. The main aim of the present study was to compare the relative abundance of gastropod species eaten by *T. placodon* with that of the gastropod species found in the lake, to see if the fish

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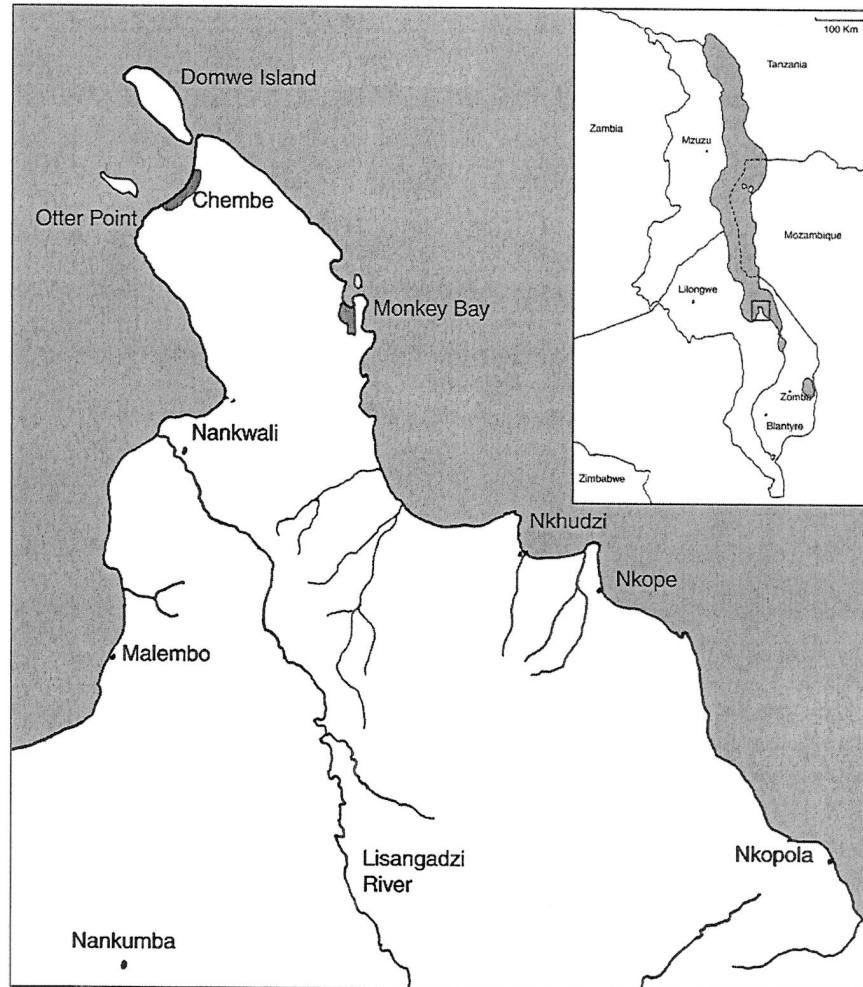


FIG. 1. The Cape Maclear area on Nankumba Peninsula in Lake Malawi.

'preferred' to eat (i.e. fed selectively on) any particular species or genus.

ANIMALS AND METHODS

Density of Gastropod Species

The snail collections were made, during July 2003, at Chembe village, which is located at Cape Maclear on the Nankumba Peninsula in Lake Malawi (Fig. 1). Since most schistosome-infected *Bu. nyassanus* are found in relatively shallow water, at a depth of <2 m (Phiri *et al.*, 1999), all snails investigated were collected within 50 m of the shoreline. The two collection sites used, which were

simply labelled A and B, were in the southern part of the village and were separated by about 600 m of shoreline.

Site A, at 14°01.980 S and 34°49.634 E, was about 50 m south-west of the Fisheries Research Station at Cape Maclear. Relatively few people used this site for domestic water-contact activities. Site B, at 14°01.817 S and 34°49.884 E, lay 581 m to the north-east of site A and had considerable human-water contact (bathing, swimming, washing etc).

At each site, nine transect lines perpendicular to the shore, and 5 m apart, were defined. Quantitative sampling was done using a Van-Veen grab (KC-Denmark,

Silkeborg, Denmark), which will sample a 250-cm² area of sediment to a depth of a few centimetres. Along each transect, two Van-Veen samples were taken 3, 6, 9, 11, 13, 15, 17, 19, 21, 24, 27, 30, 35, 40, 45, and 50 m from the shoreline. Each sample was sieved through a 1.5-mm mesh and the snails retained in the sieve were counted and identified to species, following the identification keys of Mandahl-Barth (1972) and the Danish Bilharziasis Laboratory (Anon., 1977). The *Melanooides* were grouped into three size categories, of snails that had shell heights of <10, 10–20 and >20 mm. The *Bu. nyassanus* were grouped into 1-mm shell-height classes. At each sample point, water depth was measured to the nearest 0.1 m, and the presence or absence of macrophytes (only *Vallisneria* sp. was ever found) was noted.

Stomach Contents

During June–July 2003, specimens of *T. placodon* swimming in Lake Malawi were caught in a hand net, by a scuba-diver (Stauffer *et al.*, 1997), at depths of 3–9 m in water just offshore from Chembe village. The standard length of each fish, from the tip of its snout to the hypural plate on its caudal peduncle, was measured to the nearest 0.1 cm. The fish were anaesthetized before they were dissected so that their stomachs and intestines could be isolated and preserved in 95% ethanol for later examination. The ovaries of the female fish were examined for eggs, and females with spent ovaries were excluded from the study as they were assumed to have been mouth brooding (and hence not feeding) when caught. The upper and lower pharyngeal bones were also dissected out and preserved in 95% ethanol. The lengths of the upper and lower pharyngeal jaws of each *T. placodon* were measured to the nearest 0.1 mm (Hoogerhoud, 1986), using a dissection microscope with an ocular scale.

The preserved stomachs and intestines from the fish were examined for snail

remnants. The snails that the fish had ingested were identified to genus, and in some cases to species, on the basis of the shapes, sculpture and colouration of the shell fragments (all snails) and the shape and spiralling of the opercula (prosobranchs). The number of specimens of each snail species was counted, and the approximate size of each specimen was estimated, using various approaches. For each specimen of a prosobranch species, the height of the operculum was measured to the nearest 0.1 mm, again using a dissection microscope with an ocular scale. The shell height of each specimen of *Bellamya* sp. or *Melanooides tuberculata* (the predominant *Melanooides* species at Cape Maclear) was then estimated from the operculum height. As the result of previous studies, the shell heights of *Bellamya* ($R^2=0.978$; $P<0.001$) and *M. tuberculata* ($R^2=0.933$; $P<0.001$) from the same general area as sites A and B were known to be linearly related to operculum height. The regression equations derived in these previous studies were therefore used, in the present study, to estimate the shell heights of the *Bellamya* and *M. tuberculata* consumed by the *T. placodon*, from the heights of the opercula recovered from the fish.

The number of *Bu. nyassanus*, which do not have an operculum, in the stomach contents of each fish could be estimated from their shells, which were found to be surprisingly intact. In most specimens the spire was intact and only the lower part of the shell was crushed. Even when the lower part of the shell was crushed, the columella was often almost complete. An estimate of the size of the entire shell, as either large (≥ 4 mm) or small (< 4 mm), was therefore made primarily from the spire.

When embryos were removed from 20 field-collected specimens of *Melanooides* spp. of various sizes, the largest embryonic *Melanooides* was found to have a shell height of 2.95 mm (data not shown). Any *Melanooides* below this size that were found in a fish's intestines or stomach were

therefore considered to be embryonic and ignored.

Statistical Analysis

The counts of *Bu. nyassanus* and *Melanooides* spp. were fitted to a negative binomial distribution, and the parameter k was estimated using the maximum-likelihood method (Elliot, 1975). The values for the proportion of all *Bu. nyassanus* found in a fish stomach that were categorized as large (≥ 4 mm) were arcsine-transformed, tested for normality, and then related to fish size using linear regression (Zar, 1984). Linear regression was also used to explore the relationships between the lengths of the upper or lower pharyngeal jaws and fish length. A P -value of <0.05 was considered indicative of a statistically significant difference or relationship. Ivlev's electivity index and its 95% confidence limits (Strauss, 1979) were used to determine whether the *T. placodon* investigated had shown any food selection.

RESULTS

Site Characteristics and Distribution of Snails

The gastropod fauna (see Table 1) was dominated by *Melanooides* species (primarily *M. tuberculata*). Almost all *M. tuberculata* at Chembe have a rather smooth shell, with only spiral lines. [This morph was referred

to as *M. virgulata* by Eldblom and Kristensen (2003) on the basis of morphology of the radula teeth. In a later study by Genner *et al.* (2004), however, this form, which is possibly invasive in Lake Malawi, was identified as *M. tuberculata*. Molecular characteristics also indicate that '*M. virgulata*' is a morph of *M. tuberculata* (Sørensen *et al.*, 2005) and the name *M. tuberculata* has therefore been retained for the present study.]

Along the transects, water depth ranged between 0.3 and 5.5 m at site A and between 0.2 and 4.9 m at site B. The change in mean depth with distance from the shore was similar at the two sites up to about 20 m from the shore, but at greater distances depth was greater at site A than at site B (Fig. 2).

At site A, *Vallisneria* sp. was found in a continuous zone between 19 and 30 m from the shore, from transect 5 to transect 9, at depths in the range 2.9–4.5 m. At site B, *Vallisneria* sp. was found in a continuous zone 40–50 m from the shore, from transect 3 to transect 8, at depths in the range 4.1–4.9 m.

Bulinus nyassanus was found at an overall density (arithmetic mean) of 4.9 individuals/m² at site A, with the highest densities found close to the shore (Fig. 3). The counts of *Bu. nyassanus* at site A (Fig. 4), when fitted to a negative binomial distribution using the maximum-likelihood estimation, gave a k -value of 0.196. At site B, *Bu. nyassanus* was found at an overall density of 18.1 snails/m²,

TABLE 1. The gastropod faunas observed at the two study sites on the shores of Lake Malawi, at Chembe village

Species	No. of snails and (% of collection at site)	
	Site A	Site B
<i>Bulinus nyassanus</i>	35 (1.9)	130 (4.6)
<i>Bulinus succinoides</i>	6 (0.3)	3 (0.1)
<i>Bellamyia</i> spp.	5 (0.3)	15 (0.5)
<i>Gabbiella stanleyi</i>	14 (0.8)	14 (0.5)
<i>Lanistes</i> spp.	5 (0.3)	15 (0.5)
<i>Melanooides</i> spp.	1801 (96.5)	2643 (93.7)
All	1866 (100.0)	2820 (100.0)

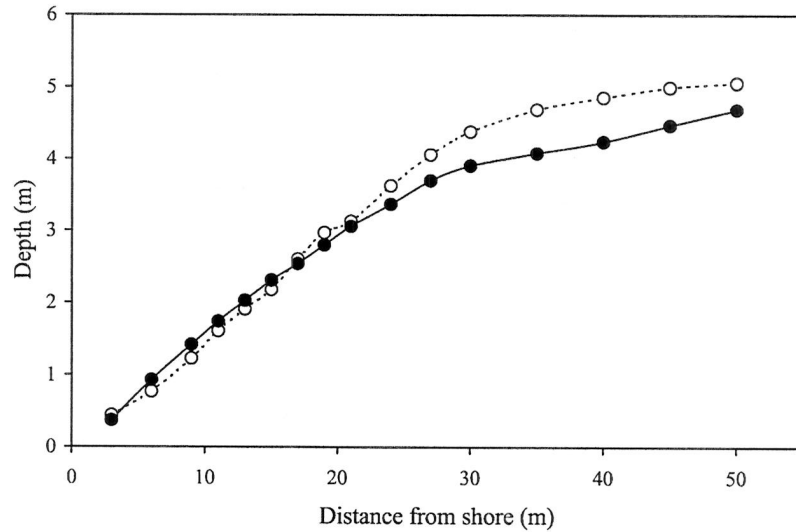


FIG. 2. The mean depths of water at different distances from the shore, as measured along nine transects at site A (○) and nine at site B (●), at Chembe village on Cape Maclear.

again with the highest densities close to the shore. The parameter k for the distribution of *Bu. nyassanus* at site B was found to be 1.217. More than 50% of the *Bu. nyassanus* found at the two collection sites were between 8 and 10 mm in shell height (Fig. 5).

Melanoides spp. were found at overall densities of 250.1/m² at site A, and 368.0/

m² at site B. The densities of *Melanoides* spp. at site A peaked 20–40 m from the shore whereas those at site B increased from about 35 m from the shore (Fig. 6).

Bulinus nyassanus did not occur in the *Vallisneria* bed at site A but was found in the *Vallisneria* bed at site B, at similar densities to those seen in *Vallisneria*-free areas at the same depths. In contrast, *Melanoides* spp.

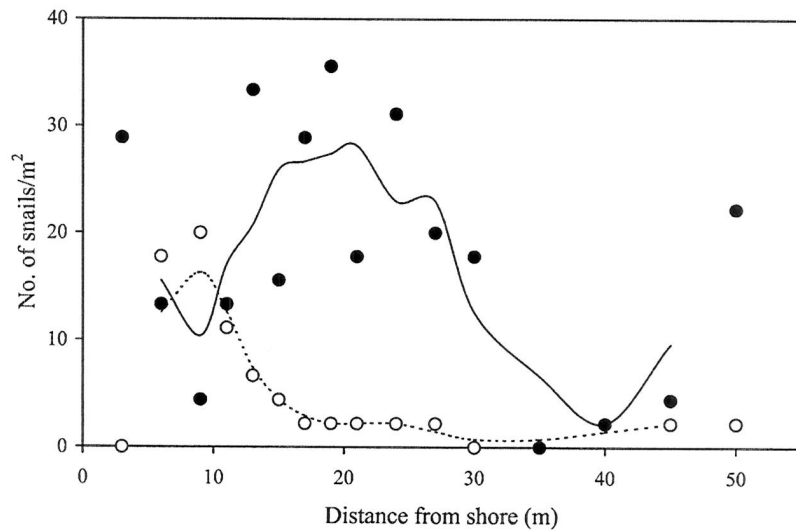


FIG. 3. The mean densities of *Bulinus nyassanus* at different distances from the shore, as measured along nine transects at site A (○) and nine at site B (●), at Chembe village on Cape Maclear. The trend lines depict moving means for three data-points.

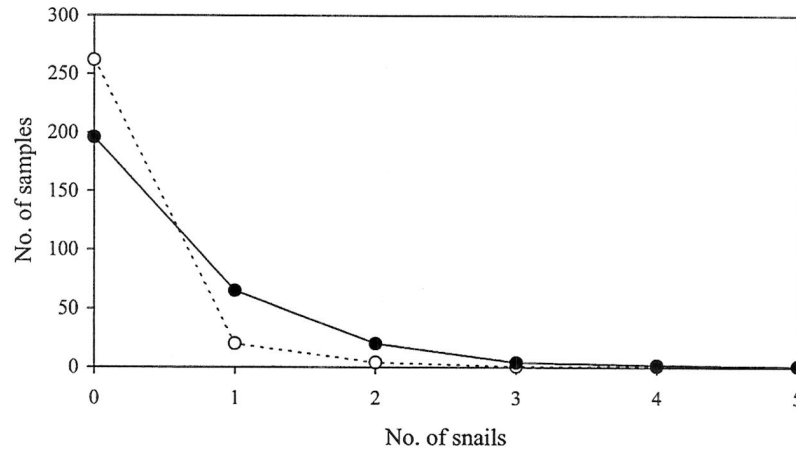


FIG. 4. The frequency distributions of the *Bulinus nyassanus* in transect samples from sites A (○) and B (●) at Chembe village, Cape Maclear, Lake Malawi.

occurred at higher density within the *Vallisneria* beds than on open sand at similar depths (Fig. 7). *Bulinus succinoides* was found only in association with *Vallisneria*, and almost all of the *Gabbiella stanleyi* collected were found in association with this macrophyte.

Stomach Contents

A few of the wild-caught *T. placodon* were excluded from the study because they were females with spent ovaries. The other 51 *T. placodon* that were caught, which ranged in standard length from 7.0 to 15.2 cm, were examined further. The lengths of these

fish's lower pharyngeal jaws varied between 5.3 and 15.6 mm. The lengths of the upper pharyngeal jaws varied between 3.0 and 9.4 mm. The lengths of the upper jaws ($R^2=0.85$; $P<0.001$) and lower jaws ($R^2=0.85$; $P<0.001$) were linearly related to fish length. Snail fragments were found in the stomachs and/or intestines of 44 of the fish, *Bu. nyassanus* representing almost one in every four (24.6%) of the snails found in the *T. placodon* (Table 2).

Large specimens of *Bu. nyassanus* (≥ 4.0 mm) were only found in *T. placodon* that measured >8.9 cm in standard length. There was a positive linear relationship

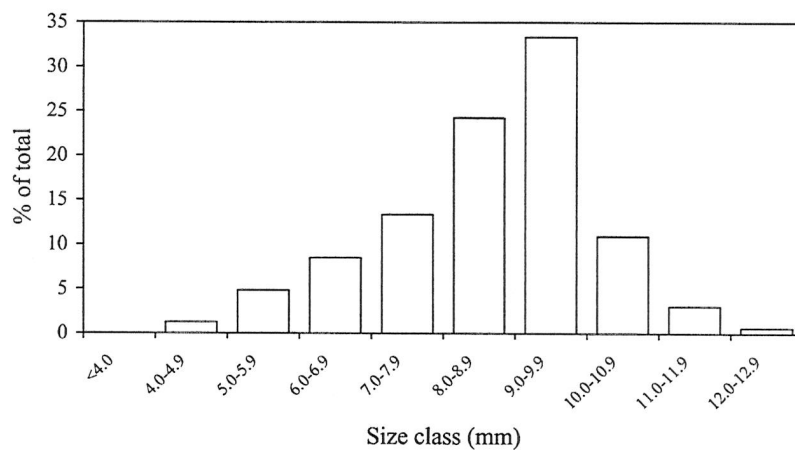


FIG. 5. The size distribution of the *Bulinus nyassanus* in the pooled samples from sites A and B at Chembe village, Cape Maclear.

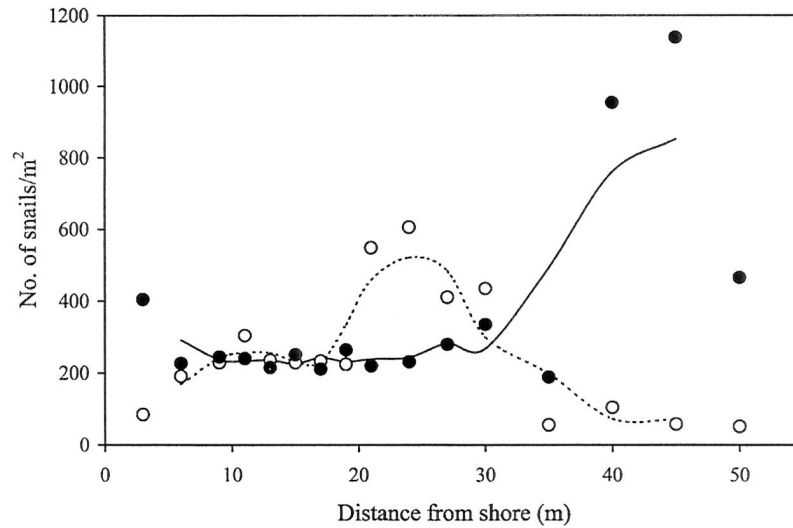


FIG. 6. The mean densities of *Melanoides* (all species) at different distances from the shore, as measured along nine transects at site A (○) and nine at site B (●), at Chembe village on Cape Maclear. The trend lines depict moving means for three data-points.

between the length of a fish and the proportion of all *Bu. nyassanus* found in that fish that were categorized as large ($R^2=0.398$; $F=23.177$; $P<0.001$).

Melanoides opercula were found in the stomachs/intestines of 26 fish, and the

largest, which measured 3.4 mm in height and was found in a 15.2-cm-long *T. placodon*, came from a snail with an estimated shell height of 15.4 mm. *Bellamyia* opercula were found in the stomachs/intestines of nine fish, and the largest, which measured 4.4 mm in height and was found in a 14.5-cm *T. placodon*, came from a snail with an estimated shell height of 9.2 mm. The largest *Melanoides* operculum found in a fish was positively correlated with the standard length of the fish ($R^2=0.737$; $F=70.131$; $P<0.001$).

The calculations of Ivlev's electivity indices indicated that *Bu. nyassanus* and *Bellamyia* spp. were each selected in a greater proportion than found in the field, whereas *Melanoides* and *Gabbiella* were each taken in a smaller proportion than found in the field (Fig. 8). The other species of snail identified in the stomachs/intestines of the fish were found in too low numbers for valid electivity indices to be calculated for them.

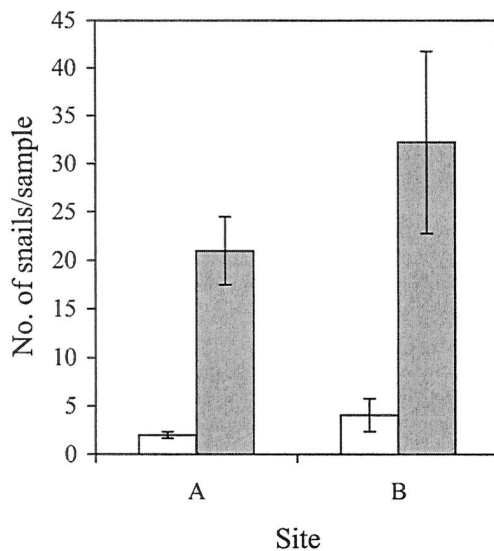


FIG. 7. The mean numbers of *Melanoides* (all species) caught per grab sample in areas of sites A and B where *Vallisneria* was present (□) or absent (■). The vertical lines indicate 95% confidence limits.

DISCUSSION

The results of the snail collection from sites A and B demonstrate that, at least close to

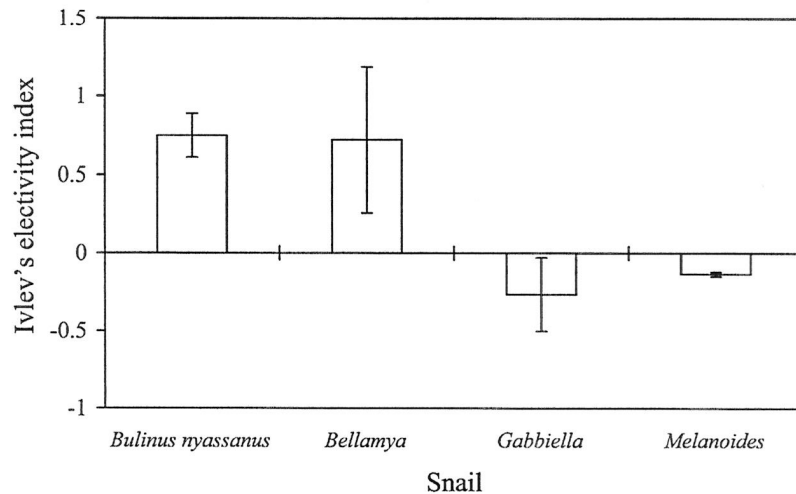


FIG. 8. Ivlev's electivity indices for the feeding of *Trematocranus placodon* on various snail genera or species at Chembe village, Cape Maclear, Lake Malawi. The vertical lines indicate 95% confidence limits.

Chembe village, the distribution of *Bu. nyassanus* is clustered and that *Bu. nyassanus* does not show a 'preference' for macrophytes. The densities of this species recorded in the present study, in July 2003 (4.9–18.1 individuals/m²), are all somewhat higher than that (1.6 individuals/m²) recorded in the same area, in February–March 1981, by Louda *et al.* (1983). Comparisons between studies and study sites have to be made with caution, however, as the depth profile of *Bu. nyassanus* density varies considerably between locations. It is possible, however, that all of the difference between the density recorded in 1981 (Louda *et al.*, 1983) and those recorded, in the same area, in 2003

(present study) can be attributed to seasonal variation in the numbers of *Bu. nyassanus*. Densities of this species are generally low in January–April, start to increase in April–June, and peak around September (Phiri *et al.*, 1999); in a September collection, for example, Genner and Michel (2003) found 90 *Bu. nyassanus*/m². It also seems quite possible, however, that the over-fishing of *T. placodon* and other molluscivorous fish at Cape Maclear (McKaye *et al.*, 1986; Stauffer *et al.*, 1997) has allowed the numbers of freshwater molluscs in the area to increase generally since 1981.

In the present study, *Melanoides* spp. were found at high densities at both site A and

TABLE 2. The distributions of the snail species in the diet of the *Trematocranus placodon* investigated, and in the field collections of living snails

Species	No. of fish found positive	No. and (%) of snails ingested by fish	No. and (%) of snails in field collections
<i>Melanoides</i> spp.	39	1042 (72.3)	4444 (94.8)
<i>Bulinus nyassanus</i>			
Large (≥ 4 mm)	22	92 (6.4)	165 (3.5)
Small (<4 mm)	36	262 (18.2)	0 (0)
All	37	354 (24.6)	165 (3.5)
<i>Bellamya</i> sp.	16	38 (2.6)	20 (0.3)
<i>Gabbiella stanleyi</i>	4	5 (0.3)	28 (0.5)
<i>Gyraulus</i> sp.	2	2 (0.1)	0 (0)
<i>Lanistes</i> sp.	0	0 (0)	20 (0.3)
<i>Bulinus succinoides</i>	0	0 (0)	9 (0.1)

site B (250 and 368 individuals/m², respectively), and were found in greater numbers when *Vallisneria* sp. was present than in areas of open sand. The maximum density of *Melanoides* recorded by Louda *et al.* (1983) was only 116.8 individuals/m², at a depth of 3 m. The densities of *Melanoides* spp. may vary greatly both spatially and seasonally, however, and this may explain the discrepancy between the present study and the 1981 results. It is also possible that the now dominating morph that seems to be invasive (Genner *et al.*, 2004) was absent when Louda *et al.* (1983) did their studies. Genner and Michel (2003) found 1350 *Melanoides*/m² in their September collection.

Bulinus succinoides was found exclusively in association with *Vallisneria* sp., consistent with earlier findings (Wright *et al.*, 1967; Mandahl-Barth, 1972; Phiri *et al.*, 1999). The thin shell of *Bu. succinoides* (Mandahl-Barth, 1972) probably makes it dependent on macrophytes as shelter from predation and wave action.

Comparisons between the gastropod distributions in the stomach contents of molluscivorous fish and the gastropod composition in the field should be made with caution because the feeding territory of the fish is usually much larger than the area over which the living snails are collected. In the present study, living snails were collected at depths of <5 m whereas the fish investigated were caught, usually a little further offshore, at depths of 3–9 m. In a separate study, in the same area and at the same time, however, the proportion of total snails represented by *Bu. nyassanus* varied very little (by <3%) between a depth of 4.6 m and a depth of 9.1 m (unpubl. obs.). As a feeding remnant in *T. placodon*, therefore, *Bu. nyassanus* appears to be over-represented when compared with its frequency in the snail fauna of the fish's feeding ground. *Trematocranus placodon* therefore appears to have a 'preference' for *Bu. nyassanus* (McKaye *et al.*, 1986) or, at least, is more likely to ingest a snail it encounters if that snail is *Bu. nyassanus* than

if that snail is of another species. Evers (2004) showed, on the basis of crushing resistance, that *Bu. nyassanus* has a higher prey value than *M. tuberculata* (the most common species at Chembe) unless the *M. tuberculata* measures >15 mm in shell height. It is possible that, if the density of *Melanoides* spp. (mainly the introduced morph of *M. tuberculata*) has increased in density in recent years, the increased availability of *Melanoides* could have resulted in reduced predation pressure on *Bu. nyassanus*.

In addition to *Bu. nyassanus*, *Melanoides* and *Gabbiella*, specimens of *Bellamya* and *Gyraulus* were found in the stomachs/intestines of the *T. placodon*. This is the first time that *Gyraulus* has been reported in the diet of *T. placodon*. Although Msukwa and Ribbink (1997) reported *Lanistes* as part of the diet of *T. placodon*, no specimens of this genus were identified in any of the stomachs/intestines investigated in the present study.

The present results revealed a size-dependent selection of both *Bu. nyassanus* and *Melanoides* by *T. placodon* in Lake Malawi. Other cichlid species have been found to perform such selection (Slootweg, 1987; Brodersen *et al.*, 2003). Slootweg (1987) found rates of encounter with snails of different size classes to vary considerably, and it could be that *T. placodon* are simply more likely to notice or encounter large snails than small snails of the same species, influencing the molluscivores' prey of 'choice' (Stephens and Krebs, 1984). *Bulinus nyassanus* is usually found in the upper 2–3 cm of the substratum (Phiri *et al.*, 1999) and a *T. placodon* attacks if it detects, via the enlarged pores on its chin, a movement in the sediment (Konings, 2001). The possibility that the fish pick snails at random and that their gut contents simply reflect the handling ability of the fish cannot be excluded.

Although not included in the present study, the smallest *T. placodon*, from the waters around Cape Maclear, that has been

found to have shell fragments in its gut had a standard length of 6.2 cm (unpubl. obs.). This is comparable with the minimum total length for a snail-feeding *T. placodon* as reported by Msukwa and Ribbink (1997) — 8 cm. Many of the *T. placodon* investigated in the present study were still juveniles and, as *T. placodon* changes its diet during its life (Msukwa and Ribbink, 1997), these young fish may have been demonstrating prey 'preferences' that were markedly different from those of their older counterparts. Osenberg and Mittelbach (1989) found that the diet of the North American pumpkin-seed sunfish (*Lepomis gibbosus*) varied, both in terms of the species and the sizes of the snails consumed, not only between sampling sites but also between sampling dates. A large seasonal variation in the number of *Bu. nyassanus* has been demonstrated (Phiri et al., 1999), and seasonal alterations in the *Bu. nyassanus* 'proportion' in the diet of *T. placodon* are inevitable. In the present study, also, the *T. placodon* were caught during their breeding season (Konings, 2001), which is reflected by the fact that a large proportion of the fish caught had egg-filled ovaries.

Although schistosome-associated morbidity in people can be kept low through repeated chemotherapy (WHO, 2002), the reduction is best maintained if some transmission control is conducted simultaneously. On Cape Maclear, the most realistic approach to transmission control would be control of the intermediate hosts. Sanitary improvements in the villages are not likely to affect the contamination of the lake with schistosome eggs, which seems mostly to derive from children swimming and playing in the lake. Chemical control of *Bu. nyassanus* is problematic, as this snail, unlike most other schistosome-transmitting snails, lives on exposed shorelines and is independent of macrophytes. The molluscicide of choice, niclosamide, is also highly toxic to fish, and a large fraction of the *Bu. nyassanus* population is found within the sediment and therefore out of reach of the

chemical. The only viable option for controlling *Bu. nyassanus* appears to be the protection, from over-fishing, of the cichlid fish species in the lake, so that their population densities can rise to a level where the fish can significantly reduce snail densities. Further experimentation along these lines is needed.

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