

## Distribution of Gastropod Genera over a Vertical Depth Gradient at Cape Maclear, Lake Malawi

BY

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(2 Text figures)

### INTRODUCTION

LAKE MALAWI in the eastern rift valley of Africa holds a unique resource in its abundant and highly diverse fauna. For example, over 250 species of fishes have been described from this lake, most of them belonging to the family Cichlidae (e.g., MARSH *et al.*, 1981). The gastropods, most of which are endemic to Lake Malawi, also present an ecologically and evolutionarily interesting array. The molluscs are abundant, relatively unknown, and the primary food source of an important subset of cichlids (JACKSON *et al.*, 1963; FRYER & ILES, 1972) including: *Cyrtocara* ('*Haplochromis*') *anaphymis*, *C. mola*, *C. placodon*, *C. sphaerodon*, and *Trematocranus microstoma* (McKaye and Louda, unpublished data). Information on snail composition, abundance, distribution, feeding, and life history cycles is, consequently, important both to an understanding of gastropod community dynamics in the African lakes and to the management of the sand bottom fish community in Lake Malawi.

This paper reports upon the distribution and relative abundance of the sand-dwelling gastropod genera along a vertical depth gradient in southern Lake Malawi. The data were collected at the west end of a 4km section of the sand beach at Cape Maclear (34°50' E; 14°5' S), 12km west of Monkey Bay. The two main questions underlying this study were: (1) what is the structure of the snail assemblage, a critical resource for the mollusc-feeding fishes, and (2) how does that structure vary along the water depth gradient? We quantified: vertical distribution, density, and population size structure of the gastropod genera present between 0-26m depths. These data are among the first direct observations of gastropod population parameters and community structure in the deep lakes of Africa.

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### THE GASTROPODS

Four genera of streptoneuran (prosobranch) gastropods and one genus of basommatophoran gastropod are part of the sand community. The basommatophoran genus is *Bulinus* Müller (Planorbidae); *Bulinus* is represented by one species in the open sand areas, *B. nyassanus* (Smith), and by another one, *B. succinoides* (Smith), on more heterogeneous substrates such as among aquatic macrophytes (WRIGHT, KLEIN & ECCLES, 1967; LOUDA & GRAY, personal observation). The prosobranch genera include, in order of decreasing adult size: *Lanistes* Montfort (Ampullariidae), *Bellamya* Jousseau (Viviparidae), *Melanoides* Olivier (Thiaridae), and *Gabbiella* Mandahl-Barth (Bithyniidae).

The "apple snails" of the Family Ampullariidae (Pilidae) are represented in our samples by three nominal species of the genus *Lanistes*. The largest snail at Cape Maclear is *L. nyassanus* Dohrn, which reaches 55mm total length and 42mm aperture length. *Lanistes solidus* Smith, another heavy-shelled species endemic to Lake Malawi, is smaller and with a higher spire (BROWN, 1980). Both of these species are reported dredged down to 30m (MANDAHL-BARTH, 1972). We have observed living specimens of *L. nyassanus* to 39m and of *L. solidus* down to 20m (LOUDA, MCKAYE, KOCHER & STACKHOUSE, 1983). The third species, *L. ellipticus* Martens, is rare. *Lanistes ellipticus* is similar to *L. solidus*; however, *L. ellipticus* has an open umbilicus and straight columella, the axis around which the shell spirals, and a much lighter-weight shell. It is reported to be abundant in swamps along the shore of Lake Malawi but not to be found in the main lake (BROWN, 1980: 54). The two latter species may not, in fact, be distinct since *L. solidus* may be a heavier, lacustrine (lake) form of *L. ellipticus* (D. S. Brown, personal communication).

The genus *Bellamya* belongs to the family Viviparidae. Female snails of this family carry the developing young in the lower part of the oviduct. In *Bellamya* the young are released at the stage of about three whorls (BROWN, 1980). Three forms of *Bellamya* occur at Cape Maclear; *B. jeffreysi* (Frauenfeld) Mandahl-Barth, a medium-sized

(40 × 30 mm) species whose shell is heavier than that of any other member of the genus (BROWN, 1980), is the predominant form on our transect. *Bellamyia robertsoni* (Frauenfeld) Mandahl-Barth and *B. capillata* (Frauenfeld) Germain also occur but are much less common. The second most common species, *B. robertsoni*, is a less heavy form that consistently has a higher spire but which may or may not be distinct from *B. jeffreysi* (BROWN, 1980; Gray, unpublished data). Finally, *B. capillata* were found infrequently in our samples; this species occurs more typically in marshy habitats along the lake shore rather than over open sand in the lake. *Bellamyia capillata*, which occurs in a variety of local forms, is hardly distinguishable from *B. unicolor*, a widespread northern species (BROWN, 1980), except in having fewer and larger embryos (MANDAHL-BARTH, 1973). CROWLEY *et al.* (1964) consider all of the forms synonymous with *B. unicolor*.

The majority of the species in our samples belong to the genus *Melanoides* in the family Thiariidae (Melaniidae). Ten nominal species occur and nine of these are endemic (SMITH, 1877; CROWLEY *et al.*, 1964; MANDAHL-BARTH, 1968a, 1972; BROWN, 1980, and personal communication). These species are: *Melanoides tuberculata* (Müller), the cosmopolitan species; *M. pergracilis* (Smith), *M. nodicincta* (Dohrn), *M. nyassana* (Smith), *M. magnifica* (Bourguignat), *M. truncatelliformis* (Bourguignat), *M. polymorpha* (Smith); *M. pupiformis* (Smith); *M. turrítispira* (Smith); and *M. simonsi* Smith. This interesting group is composed of small to medium-sized snails (10-47 mm total length for adults). They also represent the predominant portion of the molluscs in the stomach contents of the snail-feeding fishes examined at Cape Maclear (McKaye & Louda, unpublished data). Little, in particular, is known about the occurrence and biology of the majority of these Malawian species (Brown, 1980, and personal communication).

The last family, Bithyniidae, is represented by one species in Lake Malawi, *Gabbiella stanleyi* (Smith). This endemic species is small (5.3 × 3.3 mm) and distinctive. It is commonest in the littoral zone down to about 12 m (BROWN, 1980) and is active at night on the surface of *Vallisneria* blades (Louda, personal observation). It also has been dredged from 95 m (MANDAHL-BARTH, 1968b). This small species also appears to be a major component of the fish diets (McKaye & Louda, unpublished data); this is contrary to the suggestion of WRIGHT, KLEIN & ECCLES (1967) who thought the heavier shell of *G. stanleyi*, compared to that of *Bulinus succinoides*, was a successful predator defense that allowed open grazing on the blades of *Vallisneria*.

## MATERIALS AND METHODS

Samples were collected by aid of SCUBA during February-March 1981 to determine the density, distribution, and population size structure for the gastropod genera over the depth gradient at Cape Maclear. We recorded the number and size of all live gastropods found in 50 × 50 cm × 5 cm deep samples of substrate (N = 93), collected into individual sealable plastic bags by SCUBA divers. Pairs of samples were collected 25 m apart at 12 depths, from 0.25 to 25.5 m at 3 m increments (N = 8 per depth for 0.25-10.5 m and N = 4 per depth for 13.5-25.5 m). A major discontinuity in microhabitat occurs in 3.0-4.5 m depths where patches of aquatic vascular macrophytes occur (*Potamogeton* sp. and *Vallisneria* sp.). Consequently, separate samples were collected for comparison of density and snail size from two beds of the macrophytes at 3.0-3.75 m and 4.5 m in April 1981. Samples within the weed beds were placed in patches of high stem density and were compared to samples collected along the transect over open sand substrate at the same depths.

## RESULTS

**Depth Distribution:** The center of distribution for all of the genera occurring at Cape Maclear was in the shallow portion of the depth gradient (Figure 1). The median depth for all gastropods collected (N = 514) was 3.0 m. These data particularly reflect the distribution of *Melanoides*, the most common gastropod genus in our collection (N = 458); 51.1% of all *Melanoides* found were in samples from the 3.0 m depth. The three other common genera appear to be displaced along the depth contour, one shallower and two deeper. The medians of these distributions from our samples are as follows: *Lanistes* 1.5-3.0 m, *Bulinus* 3.0-4.5 m, and *Bellamyia* 4.5-6.0 m.

**Density:** Densities of all gastropods varied from 0.5 to 30.8 individuals per ¼ m<sup>2</sup> (2-123 snails/m<sup>2</sup>) over the entire depth gradient sampled at Cape Maclear (Table 1). The highest concentration (123/m<sup>2</sup>) was found in samples from 3.0 m depth. *Melanoides* species represent the predominant snails in our samples (89%) and the exceptionally high density at this depth reflected the density of *Melanoides* there (117/m<sup>2</sup>). However, when this factor is partitioned out, the density of the other gastropod genera in our area was still highest from 3.0-4.5 m (Table 1). Among the other more common genera, *Lanistes* densities were highest at 3.0 m

**Table 1**  
Density of gastropod genera over the depth contour at Cape Maclear, Lake Malawi (#/50 × 50 cm).

Depth (m)	N	All gastropods		<i>Melanooides</i>		Non- <i>Melanooides</i>		<i>Lanistes</i>		<i>Bulinus</i>		<i>Bellamyia</i>	
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
0.25	8	0.6	0.71	0.0	—	0.6	0.74	0.6	0.74	0.0	—	0.0	—
1.5	8	13.2	10.85	12.3	11.73	0.9	0.64	0.8	0.71	0.1	0.34	0.0	—
3.0	8	30.8	6.93	29.2	7.75	1.5	0.93	1.0	0.76	0.2	0.46	0.2	0.71
4.5	8	9.2	5.18	8.0	5.23	1.5	1.31	0.9	0.99	0.4	0.52	0.3	0.71
6.0	8	2.3	1.64	1.5	1.70	0.9	0.64	0.6	0.74	0.0	—	0.2	0.45
7.5	8	2.0	1.27	1.9	1.24	0.1	0.34	0.0	—	0.1	0.34	0.0	—
9.0	8	1.5	1.10	1.2	1.05	0.4	0.52	0.2	0.45	0.0	—	0.1	0.34
10.5	8	2.4	0.99	2.1	0.99	0.4	0.52	0.2	0.45	0.1	0.34	0.0	—
13.5	4	2.2	1.30	1.8	1.50	0.5	0.58	0.0	—	0.2	0.50	0.2	0.50
16.5	5	2.0	0.63	1.6	0.54	0.4	0.55	0.0	—	0.2	0.45	0.2	0.40
19.5	4	2.7	1.30	2.5	1.30	0.2	0.50	0.2	0.50	0.0	—	0.0	—
22.5	4	1.4	1.50	1.2	1.50	0.2	0.50	0.2	0.50	0.0	—	0.0	—
25.5	4	0.5	0.50	0.5	0.58	0.0	—	0.0	—	0.0	—	0.0	—

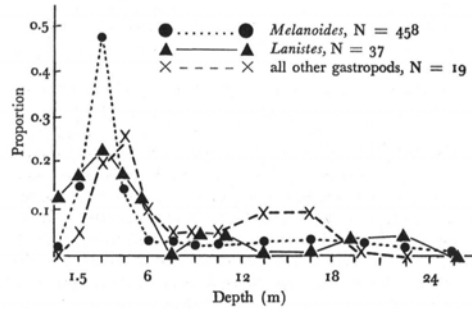


Figure 1

Relative distribution of each of the two main genera and of all other gastropods over the water depth gradient, Research Station site, Cape Maclear, February-March 1981

(4.0 snails/m<sup>2</sup>) while those of *Bulinus* (1.6 snails/m<sup>2</sup>) and *Bellamyia* (0.9 snails/m<sup>2</sup>) appeared highest at 4.5 m or relatively evenly spaced along the depth gradient.

**Size with Depth:** The large number of *Melanooides* collected (N = 458) allows us to examine if individual size varies with depth. Interestingly, there was a significant increase in mean snail size (total length) at the 6.0 m depth along our transect (Figure 2). *Melanooides* size also increased in the protected, vascular macrophyte microhabitats. Average

size for *Melanooides* was significantly greater in both of the weed beds than it was on the adjacent open sand at each of the two depths where weed beds occurred (Mann-Whitney U, p < 0.05; Table 2). Furthermore, the *Melanooides* in among stems of *Vallisneria* at 4.5 m appeared to be larger than those among the stems of *Potamogeton* at 3.0-3.75 m (Table 2).

DISCUSSION

At Cape Maclear the gastropod genera were concentrated in the shallow portions of the 0.25-25.5 m depth gradient

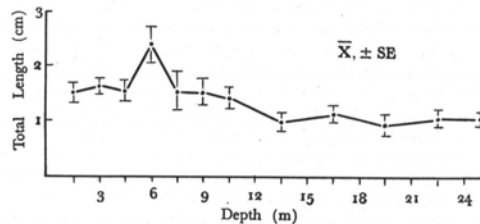


Figure 2

Size distribution of *Melanooides* individuals (Total Length, cm; N = 458) over the water depth gradient, in the sand microhabitat at the Research Station site, Cape Maclear, February-March 1981

Table 2.  
Density and size of *Melanooides* in different microhabitats at 3.0-4.5 m on the depth contour.

Location	Density (#/50 × 50cm)			Size (Total length, mm)		
	N	$\bar{X}$	SD	N	$\bar{X}$	SD
Open Sand						
3.0m	8	29.2	7.76	8	16.3	1.90
4.5m	8	8.0	5.23	7	15.7	2.46
Together	16	18.6	12.70	15	16.0	2.12
Weed beds						
<i>Potamogeton</i> , 3.4 m	4	11.5	11.73	4	21.0	4.48
<i>Vallisneria</i> , 4.5 m	4	13.5	5.07	4	29.6	4.96
Together	8	12.5	8.43	8	25.3	5.03
Mann-Whitney U test of Comparisons: p <sup>1</sup>						
For each microhabitat, by depth						
Open sand: 3.0 vs. 4.5 M		< 0.001			n.s.	
<i>Potamogeton</i> vs. <i>Vallisneria</i>		n.s.			0.058	
Comparison of microhabitats						
3.2m: Sand vs. <i>Potamogeton</i>		0.072			0.042	
4.5m: Sand vs. <i>Vallisneria</i>		0.048			< 0.006	

<sup>1</sup>Two-tailed, n.s. = p > 0.10

(Figure 1). This general result is consistent with information available on prosobranchs in benthic communities of other African lakes, such as Lake Chad (LÉVÊQUE, 1967, 1972, 1973; DUPONT & LÉVÊQUE, 1969; BROWN, 1974, 1980), Lake George (see BROWN, 1980) and Lake Léré, about 350 km south of Lake Chad (DEJOUX, LAUZANNE & LÉVÊQUE, 1971). However, our study appears to be the first aimed specifically toward examining vertical distribution patterns of benthic snails in the deep African lakes; consequently, direct data for comparison are not available at present. Similar patterns have been found, though, for distribution of marine gastropods (VERMEIJ, 1972; BERTNESS, 1977; LOUDA, 1979). Furthermore, and quite interestingly, the data suggest there may be a replacement pattern occurring among genera along the depth contour in the shallow regions. The medians of distribution for the genera were ordered: *Lanistes*, *Melanooides*, *Bulinus*, and *Bellamya* between 1.5 and 6.0 m depth, suggesting some resource partitioning may occur among overlapping gastropod genera.

Two striking results were apparent in relation to gastropod density. As expected, density and dispersion varied along the gradient. Densities were highest at 3.0 m for gastropods overall. However, the extent of variation exhibited among samples within any one depth was striking. This was especially true in shallow portions of the gradient. Standard deviations were equal to the means (Table 1), suggesting that snail densities vary greatly between localities at the same depth (0.5-30.8 per 0.25/m<sup>2</sup>).

Significant local variation in gastropod density is consistent with the results of Lévêque and his colleagues in Lake Chad (references above). However, estimates of maximum density and relative abundance for the two genera (*Melanooides*, *Bellamya*) which also occur in both Lake Chad and Lake Malawi, are approximately an order of magnitude higher in Lake Chad (DAGET & LÉVÊQUE, 1969). Interestingly, each of these genera in Lake Chad is represented by only one species (*M. tuberculata* and *B. unicolor*) while in Lake Malawi at Cape Maclear each of these genera is represented by multiple forms. Interspecific competition may decrease the carrying capacity of sand bottom for *Melanooides*; alternately, however, other factors which differ between the benthic systems of the two lakes, such as fish species and density, may determine the lower densities of *Melanooides* in Lake Malawi.

The second striking result in relation to snail density was the variation observed at 3.0 and 4.5 m depths between snails occurring in weedy versus in open sand areas. The density of *Melanooides* was significantly greater at 3.0 m than at 4.5 m over open sand (Table 2). However, overall in open sand versus in a vascular macrophyte (weed) bed at 3.0-4.5 m no significant difference in density occurred. This result leads to two hypotheses. First, we suggest that the presence of sparse *Potamogeton* stands at 3.4 m led to decreased density of *Melanooides* at that depth compared to open sand by concentrating fish predators of snails in that area (Table 2). Second, increased *Melanooides* density

was associated with the presence of the denser *Vallisneria* bed at 4.5 m, leading us to suggest that high density stands of this species provide a refuge for *Melanoides* from molluscivorous fishes (Table 2). The contributions of macrophyte species and density and of water depth to these patterns, however, cannot be separated definitively in our observations. Consequently, these hypotheses are being examined further.

The strongest pattern associated with the contrast between samples from the macrophyte beds and those from the adjacent open sand areas, however, was in average size of snails found. Mean total length for *Melanoides* observed was significantly greater in amongst the weeds, both among *Potamogeton* stems and among *Vallisneria* rosettes, than at similar depths over the open sand (Table 2). Since all samples were collected over the same period of time during the day (1000-1500 hrs), these apparent patterns are not explained by activity patterns related to diurnal cycles as some of other species (*Lanistes*) may be (GRAY, 1980, LOUDA & MCKAYE, 1982). The two main mechanisms to explain these patterns are: (1) differential food availability leading to higher growth among the weeds, and (2) differential predation pressure leading to higher survivorship amongst the weeds. Our observations to date suggest that these are not mutually exclusive hypotheses and that they merit further research.

#### SUMMARY

Five genera of gastropod molluscs occur over the sand bottom at Cape Maclear, Lake Malawi (*Lanistes*, *Bellamyia*, *Melanoides*, *Gabbiella*, *Bulinus*). These snails are the primary food for at least six species of the sand-dwelling cichlids. Knowledge of the population dynamics of these gastropods should contribute to the understanding and management of fisheries in southern Lake Malawi. The distribution, densities, and relative abundances of the predominant gastropod genera were determined. Additionally, the size distributions in relation to depth and cover of vascular macrophytes were quantified for the most common genus, *Melanoides*. The results show that: (1) gastropods occurred at all depths sampled; (2) gastropod densities (to 123/m<sup>2</sup>) were highest in shallow (1.5-4.5 m) water depths; (3) gastropod distributions were patchy; and (4) density of *Melanoides* was highest at 3.0 m but size of *Melanoides* was highest: at 6.0 m in open sand and at 3.0-4.5 m in vascular macrophyte microhabitats. Either differential availability of food or differential predation by fishes among alternative microhabitats, or both, could account for these patterns.

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