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

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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., MASON et al., 1981). The gastropods, most of which are endemic to Lake Malawi, also present an ecologically and evolutionarily interesting array. The moluscs are abundant, relatively unknown, and the primary food source of an important subset of cichlids (JACKSON et al., 1983, FAYE & ILES, 1972) including: Cyrtocara (Haplochromis) asaphymas, C. mtola, C. placodon, C. spheroodon, and Threatacreanus microstomus (McKAY and LOUDA, unpublished data).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 1km section of the sand beach at Cape Maclear (34°56' E; 14°55' 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 molluscs-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 0-30m depths. These data are among the first direct observations of gastropod population parameters and community structure in the deep lakes of Africa.

THE GASTROPODS

Four genera of streptoneuran (prosobranch) gastropods and one genus of basommatophoran gastropod are part of the sand community. The basommatophoran genus is Bullina MÜLLER (Planorbididae); Bullina is represented by one species in the open sand areas, B. nyasanae (SMITH), and by another one, B. saccioides (SMITH), on more heterogeneous substrates such as among aquatic macrophytes (WEIGHT, KLEIN & ECCLES, 1967; LOUDA & GRAY, personal observation). The prosobranch genera include, in order of decreasing adult size: Lainesia Montfort (Ampullariidae), Bellamya Joussemae (Viviparidae), Melanoides Olivier (Thiaridae), and Gabiella Mandahl-Barth (Bithyniidae).

The “apple snails” of the Family Ampullariidae (Pilaiae) are represented in our samples by three nominal species of the genus Lainesia. The largest snail at Cape Maclear is L. nyasanae Dohrn, which reaches 55 mm total length and 42 mm aperture length. Lainesia solidae 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. nyasanae to 98m and of L. solidae down to 30m (LOUDA, MCKAY, KOCHE & STACKHOUSE, 1983). The third species, L. elliptica Martens, is rare. Lainesia elliptica is similar to L. solidae, however, L. elliptica 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. solidae may be a heavier, lacustrine (lake) form of L. elliptica (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, 1983). Three forms of Bellamya occur at Cape Maclear: B. jeffreys (Fraenkefeld) 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. Bellamya robertsoni (Frauenfeld) Mandali-Barch and B. capillata (Frauenfeld) German also occur but are much less common. The second most common species, B. robertsoni, is a less heavy form that consistently has a higher spine but which may or may not be distinct from B. jeffreysii (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. Bellamya 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 (Mandali-Barch, 1973). Crompton et al. (1964) consider all of the forms synonymous with B. unicolor.

The majority of the species in our samples belong to the genus Melanosoma in the family Thiaridae (Melanosomatidae). Ten nominal species occur and nine of these are endemic (Smith, 1977; Crompton et al., 1964; Mandali-Barch, 1968a, 1972; Brown, 1980, and personal communication). These species are: Melanosoma tuberculatum (Müller), the cosmopolitan species; M. pergracilis (Smith), M. nozakii (Dobhna), M. squamosa (Smith), M. magnifica (Bourguignat), M. truncatuliformis (Bourguignat), M. polynora (Smith); M. papuana (Smith); and M. simoni 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 mollusces in the stomach contents of the small-feeding fishes examined at Cape Maclear (McKay & Lousa, 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, Rhytididae, 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 (Lousa, personal observation). It also has been dredged from 95 m (Mandali-Barch, 1968a). This small species also appears to be a major component of the fish diets (McKay & Lousa, unpublished data); this is contrary to the suggestion of Wragg, Klein & Eccles (1967) who thought the heavier shell of G. stanleyi, compared to that of Bulinus nassutus, 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 collected 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 0.25-3.5 m and N = 4 per depth for 3.5-25.5 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 mean 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 medium depth for all gastropods collected (N = 514) was 3.0 m. These data particularly reflect the distribution of Melanosoma, the most common gastropod genus in our collection (N = 458); 51.1% of all Melanosoma found were in samples from the 3.0 m depth. The three 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: Lunatia 1.5-3.0 m, Bulinus 3.0-4.5 m, and Bellamya 4.5-6.0 m.

Density: The densities of all gastropods varied from 0.5 to 30.8 individuals per m² (2-215 snails/m²) over the entire depth gradient sampled at Cape Maclear (Table 1). The highest concentration (123/m²) was found in samples from 3.0 m depth. Melanosoma species represent the predominant snails in our samples (89%) and the exceptionally high density at this depth reflected the density of Melanosoma there (117/m²). 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, Lunatia densities were highest at 3.0 m.


**Table 1**

Density of gastropod genera over the depth contour at Cape Maclear, Lake Malawi (7/50 × 50 cm).

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>N</th>
<th>All gastropods</th>
<th>Melanoidea</th>
<th>Non-Melanoidea</th>
<th>Laminids</th>
<th>Bulimids</th>
<th>Bollinids</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>X</td>
<td>SD</td>
<td>X</td>
<td>SD</td>
<td>X</td>
<td>SD</td>
</tr>
<tr>
<td>0.25</td>
<td>8</td>
<td>0.6</td>
<td>0.71</td>
<td>0.6</td>
<td>0.74</td>
<td>0.6</td>
<td>0.74</td>
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<td>1.5</td>
<td>8</td>
<td>13.2</td>
<td>10.85</td>
<td>12.3</td>
<td>11.73</td>
<td>0.9</td>
<td>0.64</td>
</tr>
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<td>3.0</td>
<td>8</td>
<td>30.8</td>
<td>6.99</td>
<td>29.2</td>
<td>7.75</td>
<td>1.5</td>
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</tr>
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<td>8</td>
<td>9.2</td>
<td>5.18</td>
<td>8.0</td>
<td>5.25</td>
<td>1.5</td>
<td>1.51</td>
</tr>
<tr>
<td>6.0</td>
<td>8</td>
<td>23.1</td>
<td>1.64</td>
<td>15.5</td>
<td>1.76</td>
<td>0.9</td>
<td>0.64</td>
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<td>1.24</td>
<td>0.1</td>
<td>0.54</td>
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<td>1.05</td>
<td>0.4</td>
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</tr>
<tr>
<td>10.5</td>
<td>8</td>
<td>2.4</td>
<td>0.99</td>
<td>2.1</td>
<td>0.99</td>
<td>0.4</td>
<td>0.52</td>
</tr>
<tr>
<td>13.5</td>
<td>4</td>
<td>2.2</td>
<td>1.30</td>
<td>1.8</td>
<td>1.50</td>
<td>0.5</td>
<td>0.58</td>
</tr>
<tr>
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<td>0.34</td>
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<td>1.30</td>
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<td>22.5</td>
<td>4</td>
<td>1.4</td>
<td>1.50</td>
<td>1.2</td>
<td>1.50</td>
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<tr>
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<td>0.5</td>
<td>0.58</td>
<td>0.0</td>
<td>—</td>
</tr>
</tbody>
</table>

**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

(40 snails/m³) while those of *Bulimis* (1.6 snails/m³) and *Bollinids* (0.9 snails/m³) appeared highest at 4.5m or relatively evenly spaced along the depth gradient.

**Figure 2**

Size distribution of *Melanoidea* individuals (Total Length, cm); N = (28) over the water depth gradient, in the sand microhabitat at the Research Station site, Cape Maclear, February-March 1981

**DISCUSSION**

At Cape Maclear the gastropod genera were concentrated in the shallow portions of the 0.25-25.5m depth gradient.
Table 2.

<table>
<thead>
<tr>
<th>Location</th>
<th>Density (40/50 X 50cm)</th>
<th>Size (Total length, mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>X</td>
</tr>
<tr>
<td>Open Sand</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.0m</td>
<td>8</td>
<td>29.2</td>
</tr>
<tr>
<td>4.5m</td>
<td>8</td>
<td>8.0</td>
</tr>
<tr>
<td>Together</td>
<td>16</td>
<td>18.6</td>
</tr>
</tbody>
</table>

Wedge beds

- *Potamageton, 3.4m*
  - 4 | 11.5 | 11.73| 4 | 21.0 | 4.48|
  - 4 | 15.5 | 5.67| 4 | 29.6 | 4.96|
  - 8 | 12.5 | 8.43| 8 | 25.3 | 5.05|

Mann-Whitney U test of Comparisons: p

- For each microhabitat by depth
  - Open sand: 3.0 vs. 4.5 M
    - *Potamageton vs. Vallonia*
    - < 0.001
  - 3.2m: Sand vs. Potamageton
    - n.s.
  - 4.5m: Sand vs. Vallonia
    - n.s.

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 (*Melanoideas, Bellamya*) which also occur in both Lake Chad and Lake Malawi, are approximately an order of magnitude higher in Lake Chad (Dubret & 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 *Melanoideas*; alternatively, 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 *Melanoideas* 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 open sand areas. The density of *Melanoideas* 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 *Potamageton stands* stands at 3.4 m led to decreased density of *Melanoideas* at that depth compared to open sand by concentrating fish predators of snails in that area (Table 2). Second, increased *Melanoideas* density...
ACKNOWLEDGMENTS

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Literature Cited

SUMMARY

Five genera of gastropod molluscs occur over the sand bottom at Cape Maclear, Lake Malawi (Lamellina, Bulimina, Melanosididae, Echinulina, Bidentina). 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, Melanosididae. The results show that: (1) gastropods occurred at all depths sampled; (2) gastropod densities (to 125/m²) were highest in shallow (1.5–4.5 m) water depths; (3) gastropod distributions were patchy; and (4) density of Melanosididae was highest at 3.0 m but size of Melanosididae 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.

was associated with the presence of the denver Vellinaeria bed at 4.5 m, leading us to suggest that high density stands of this species provide a refuge for Melanosididae 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 Melanosididae observed was significantly greater in amongst the weeds, both among Potamogeton stems and among Vellinaeria 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 (9000-1500 hrs), these apparent patterns are not explained by activity patterns related to diurnal cycles as some of other species (Lamellina) may be (Gray, 1980, Lozda & McKay, 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.

