

SCALES OF ENDEMISM: CHALLENGES FOR CONSERVATION AND INCENTIVES FOR EVOLUTIONARY STUDIES IN A GASTROPOD SPECIES FLOCK FROM LAKE TANGANYIKA.

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Abstract The Lake Tanganyika benthos presents a highly biodiverse system on many spatial scales. We present here an analysis of regional (γ) diversity and local (α) diversity of the *Lavigeria* species flock, the most common and speciose of the endemic gastropods, across the currently accessible sections of lakeshore. We found significant differences in *Lavigeria* gastropod diversity among regions within the lake, and that regional species richness was strongly associated with the presence of local, short-range endemics. Species richness at individual sites was not correlated with total species richness of the surrounding region. Although sites frequently encompassed high sympatry of congeneric species, highly disjunct species distributions lead to non-predictable community assemblages.

Keywords distributions, 'thiarid', regional sampling, endemism, *Lavigeria*, alpha and gamma diversity

INTRODUCTION

Lake Tanganyika is renowned for spectacular radiations of endemic molluscs, crustaceans and fish. Within the malacofauna of this ancient rift lake, the 'thiarid' gastropods are by far the most species-rich and show exceptional morphological diversity and convergence with marine forms. At depth the lake is permanently anoxic (Coulter 1991), and due to the steep rifting margins benthic macro-organisms are restricted to a narrow rim commonly less than one kilometre wide. Despite this narrow distribution, the biogeography of Tanganyika's endemic species remains poorly known, making it difficult to inform conservation decisions.

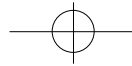
Several properties of the lake's diversity render it under threat from increasing anthropogenic disturbance. 1) Biodiversity is concentrated in the littoral zone (Coulter 1991); 2) many taxa are poor-dispersers whose distributions are restricted to suitable substrates (Cohen & Johnston 1987); and 3) the fauna forms ecologically complex communities specialised for clear water habitats (e.g. Hori, Gashagaza, Nshombo & Kawanabe 1993; West & Cohen 1994, 1996). Rocky littoral habitats are increasingly affected by increased levels of sedimentation resulting from watershed deforestation, road building, and other activities associated with increasing human population density (Cohen 1994). Evidence suggests that this has led to reduced species richness and abundance of fish, molluscs and ostracods on a regional scale (Cohen, Bills, Cocquyt & Caljon 1993; Alin *et al.* 1999). Pollution, though geographically limited, is also increasing as human population density grows (Cohen 1994).

Recently, there has been a call to break so-called conservation "planning paralysis" by establishing aquatic reserves in the lake (Coulter 1999). However, ecologically optimal reserves can only be established on the basis of reliable distribution and systematic data (Cohen 1992) that are only just now being collected for molluscs and cichlid fishes (Allison *et al.* 2000; McIntyre *et al.* unpublished data; Verheyen & Rüber 2000). If we are interested in ecosystem conservation rather than solely the preservation of economically important or pretty fish, then such a call pre-supposes sufficient knowledge of organis-

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mal diversity and distribution to generate judicious criteria. Here we will examine these issues with respect to one 'thiarid' snail species flock: the genus *Lavigeria*.

LAVIGERIA: DOMINANT ROCK-GRAZERS

Lavigeria species are the largest and most common benthic invertebrate grazers in the rocky littoral zone. They are present on virtually all rocky substrates to depths of 30 metres or more (Michel 1994). Some species appear to be confined to sand, gravel, or aquatic macrophytes (West, Michel, Todd, Brown & Clabaugh, in press). *Lavigeria* are gonochoristic, ovoviviparous, and brood their young, in some cases until very large sizes (Kingma & Michel 2000; Michel & Todd pers. obs.). As herbivores *Lavigeria* species are ideal indicators of ecosystem health in areas threatened by anthropogenic sedimentation (McIntyre *et al.* unpublished data). *Lavigeria* species also exhibit unusually high levels of sympatry, with up to six species coexisting at a single collecting site (McIntyre *et al.*, unpublished data; Michel 1995; Powers 2002). They are thus an important and conspicuous element of Tanganyikan biodiversity.

TAXONOMIC STATUS

The Tanganyikan 'thiarid' snails consist of 21 genera (18 endemic) and 77+ recognised species (72+ endemic) – the endemic genera comprising a 'superflock' (West & Michel 2000). *Lavigeria* is the most species-rich genus among these, and recent research has revealed it to consist of more than 35 species (Michel 2000). This contrasts with only one or two species recognised in modern published literature (Brown 1984, 1994; Brown & Mandahl-Barth 1987; Leloup 1953), and 56 species in the first monograph of the group (Bourguignat 1885, 1888, 1890).

Sound ecological assessment, and thus the foundation of conservation decisions, requires accurate identification of taxonomic units, whether these be formally described species or informally recognised Evolutionary Significant Units (ESUs) (Ryder 1986; Verheyen & Rüber 2000). Species flocks, the hyperdiverse endemic radiations that characterise island systems such as ancient lakes, pose particularly difficult problems for interpretation in this regard as they require detailed, comparative systematisation to assess the variation within and between taxa. Historically, only one major study has

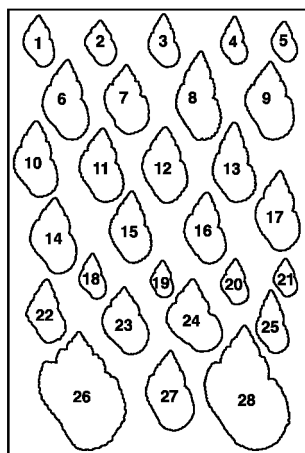
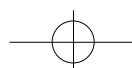
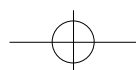
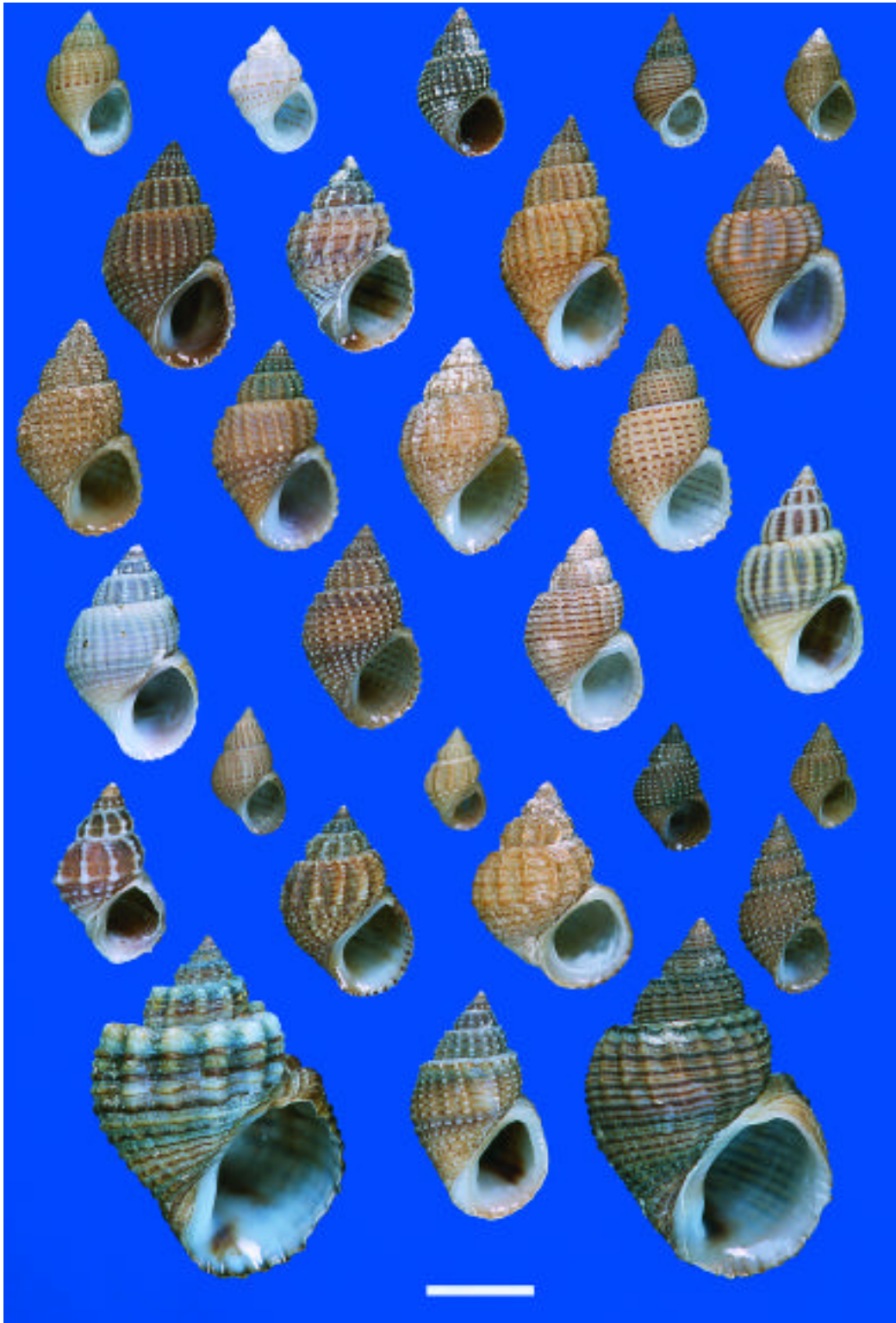
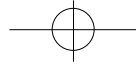
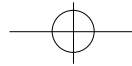


Fig. 1 The 28 species of *Lavigeria* included in this study: 1) sp. Y; 2) sp. AD; 3) sp. D; 4) sp. F; 5) sp. U; 6) sp. C; 7) *paucicostata* (Smith); 8) sp. T; 9) sp. N; 10) sp. H; 11) sp. E; 12) sp. Z; 13) sp. S; 14) sp. P; 15) sp. B; 16) sp. AC; 17) sp. Q; 18) sp. AA; 19) sp. X; 20) sp. M; 21) sp. K; 22) sp. J; 23) sp. A; 24) sp. W; 25) sp. L; 26) *coronata* Bourguignat; 27) *nassa* (Woodward); 28) *grandis* (Smith). The eleven species at the bottom of the figure, numbers 18-28, are found in the Kigoma region, Fig. 3. Scale bar = 10m.





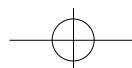


undertaken this kind of study for Tanganyikan molluscs (Leloup 1953). However, for some critical taxa the species concepts utilised were far too broad for ready re-interpretation of the biogeographic data in a modern systematic context. Specifically, Leloup was stymied by the variation in *Lavigeria* (which he referred to by another available name: *Edgaria*). Leloup identified six rather loosely defined morphological groups as infrasubspecific "formes" of a single recognised species, *Lavigeria nassa* (Woodward). For these "formes" he used the available species epithets: *globosa* Ancey, *grandis* Smith, *paucicostata* Smith, *giraudi* Bourguignat and *spinulosa* Bourguignat, together with his own "forme typica". Forme *globosa* was accurately delimited by Leloup and has subsequently been returned to the genus *Hirthis* Ancey as one of its two species (Brown & Mandahl-Barth 1987). Unfortunately, his recognition of the other five "formes" was inconsistent across his own large collections (Michel & Todd pers. obs.). These not only included *Lavigeria* species, but also members of two other genera: *Paramelania* Smith and an undescribed genus recognized subsequently (Michel 2000; submitted). We believe two major factors contributed to this confusion. Firstly, Leloup lacked the technology available to aquatic biologists today, such as SCUBA that has allowed observation and collection of living animals from their precise habitats. This has revealed substrate specificity for many species but also surprisingly high levels of microsympatric diversity of morphologically and genetically distinct taxa. Secondly, there was a problem of philosophical perspective. It was the dawn of Mayrian optimism for the practicality of a single 'biological' species concept and Leloup was reacting strongly against the typological, and vastly over-split, entirely shell-based, species proposed by Bourguignat for the Tanganyikan molluscs (Bourguignat 1885, 1888, 1890). Leloup's paucity of specific names remained largely unchanged in later taxonomic treatments, although it has been long recognised that the *Lavigeria* group was profoundly under-systematised (Brown 1984, 1996; Brown & Mandel-Barth 1987; Johnston & Cohen 1987).

SEM and light microscopy has allowed us to re-evaluate *Lavigeria* diversity by revealing systematically useful characters in protoconch and early teleoconch morphology, ontogeny and details of shell micro- and macrosculpture, opercular morphology, and periostracal and shell colour patterns (Michel 2000; Todd & Michel 2001). We have delimited working species-concepts and tested putative species identified in this way with those so far delimited by our continuing anatomical, life history and genetic studies (Kingma & Michel 2000; Michel 1995, 2000; Papadopoulos, Michel & Todd 2001; Papadopoulos & Todd 2001). Conchology is consistent with these data; thus shell morphology, in the absence of other characters, may be used to unequivocally identify *Lavigeria* species or ESUs. Twenty-eight species have been collected from rocky habitats within the regions sampled in this paper (Fig. 1).

Our species concepts also have a demonstrable practical utility. Among the *Lavigeria* in the Kigoma region (east central Lake Tanganyika shoreline), species identity is generally unambiguous. Students working with us with little or no prior experience are able to reliably identify species from their shells alone with a very limited amount of study.

Past biological research in Lake Tanganyika has been limited in general, and focused on pelagic organisms for fisheries or a few focal groups of cichlid fish in the benthos. Recent work has included a stronger ecological and genetic focus on components of the invertebrate benthic fauna due to improved technologies such as SCUBA for precise field collections and DNA molecular genetics for taxon and lineage identification. This is leading to greater resolution of species in other taxa besides *Lavigeria* (e.g., *Reymondia*, *Paramelania*, *Spekia*, *Tanganyicia*, West et al., in press, West et al., in revision). Furthermore, several large-scale projects have included aspects of benthic ecology in their missions. The Nyanza Project, a scientific research-training course that has run for five years of its ten-year duration, has focused on benthic ecology within its biology sector (www.geo.arizona.edu/nyanza/past.html), while the Lake Tanganyika



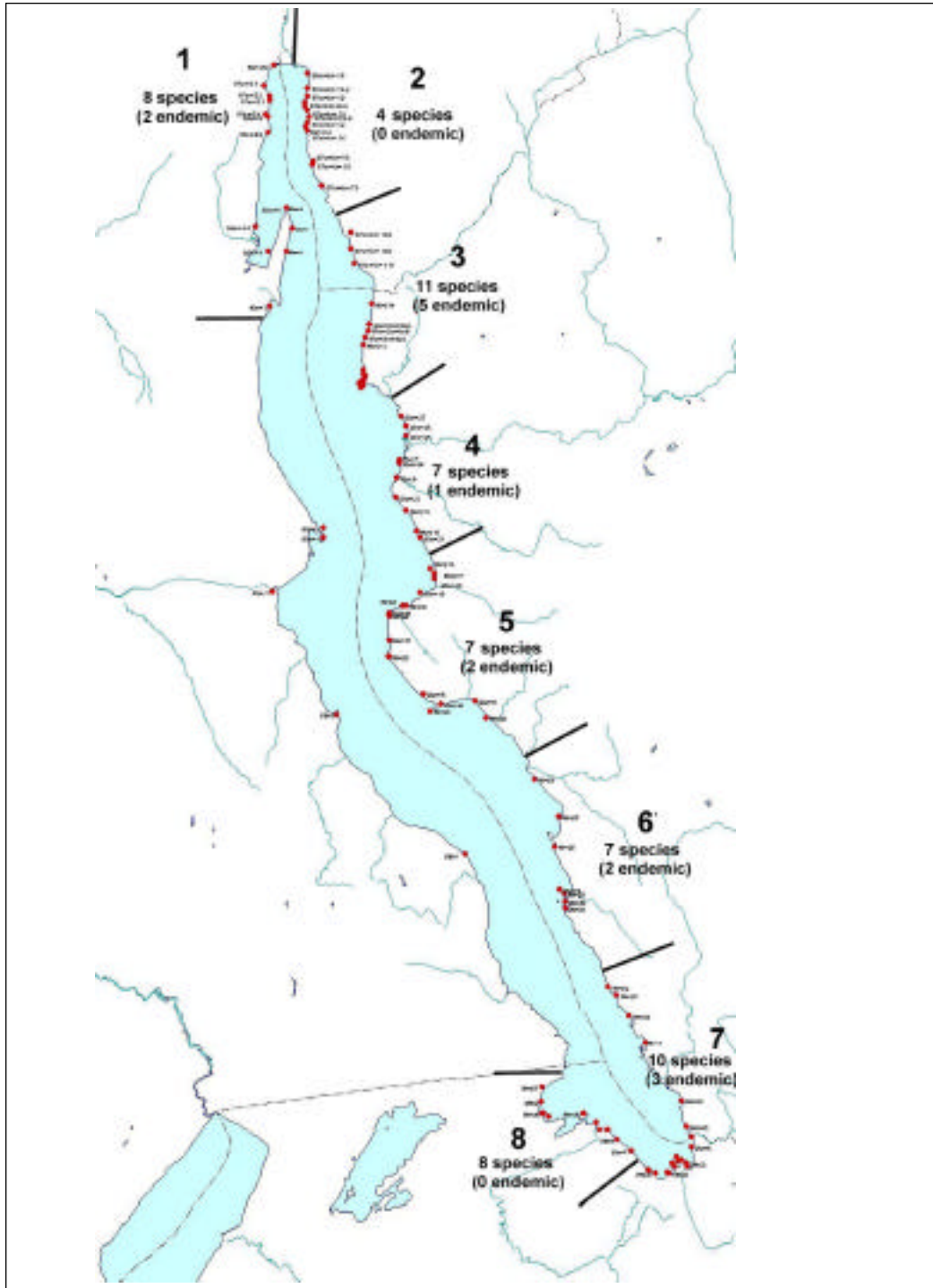
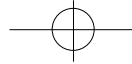


Fig. 2 Map of Lake Tanganyika, sampling sites indicated with dots, numbered regions 1-8 for this study shown with bars between regions. Number of total species per region and regional endemics indicated.



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Biodiversity Project (LTBP, a UN-GEF project, www.ltbp.org/) has included benthic surveys in its basic data collection phase. Both projects included a considerable emphasis on the malacofauna, thus provide comparative data of relevance for this study.

AIMS OF THE PAPER

The Lake Tanganyika benthos presents a highly biodiverse system on many spatial scales. We present here an analysis of regional () diversity and local () diversity of *Lavigeria* across the currently accessible sections of lakeshore. Our aim is not to make precise descriptions of specific species distributions, nor to suggest locations for potential aquatic parks, rather to underscore the character of endemic gastropod species distributions and the ramifications for informing conservation policy as well as ecological and evolutionary studies in the lake.

METHODS

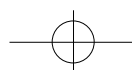
SAMPLING REGIONAL DIVERSITY

Over the past 15 years we have sampled over 150 rocky sites around the lake by SCUBA and snorkelling (Fig. 2) to catalogue molluscan diversity, determine community composition, and test for habitat disruption. Rocky substrate sites were defined as those where cobbles, boulders or bedrock dominate the substrate, although specimens found on gravel-sized clasts at these sites were included when found. Each site typically extended along several tens of metres of shoreline and from 1 to 5-20m in depth. Sampling was typically made by on one occasion by one or more divers, although collections from Burundi, northern Democratic Republic of Congo (ex-Zaire) and around Kigoma (Tanzania) were obtained from multiple visits. Our collections now comprise over 700 lots including 15,000 specimens of *Lavigeria*. We have identified all of our collections to species and entered substrate, depth, locality and abundance information into a Lake Tanganyika GIS database system (TangGIS) developed by the LTBP (www.ltbp.org/TANGIS.HTM). Apart from a few widely used names, species are referred to using a consistent system of open nomenclature until completion of a formal revision of the genus (Michel & Todd, in prep.). Twenty species of *Lavigeria* are keyed-out by shell characters and briefly described in West *et al.* (in press).

We tested for differences in species diversity at the regional scale by categorising sites into eight regional 'blocks' (Fig. 3). These consist of similar coastline lengths with a N-S running trend that are tectonically dominated by fault zones and thus by rocky substrates. Regions are separated from each other by soft substrate such as river deltas and sandy coastline (Cohen 1992) and were delimited so as to maximise their comparability of shoreline distance, substrate types and numbers of sites among regions. In total the eight regions contained 133 sites with the number of sites per region ranging from 9 to 25. After excluding twelve sites with insufficient individuals, our data included information on a total of 28 *Lavigeria* species from 121 sites in 483 lots (species/site occurrences).

ANALYSIS

We used these data to examine 1) cumulative species curves of regional richness; 2) the



relationship between local and regional diversity; 3) the relationship between endemism and overall species richness within regions, and 4) percentage site occurrence of each species. All measures, unless otherwise specified, are based on rarefied values to control for variation in sample size. Rarefied species richness was estimated at local and regional scales using PRIMER 5 (Primer E Ltd: Plymouth UK). At the local scale, minimum sample size of 20 individuals was used for each site. This ensured that poorly sampled sites did not provide artificially low diversity estimates. At the regional scale,

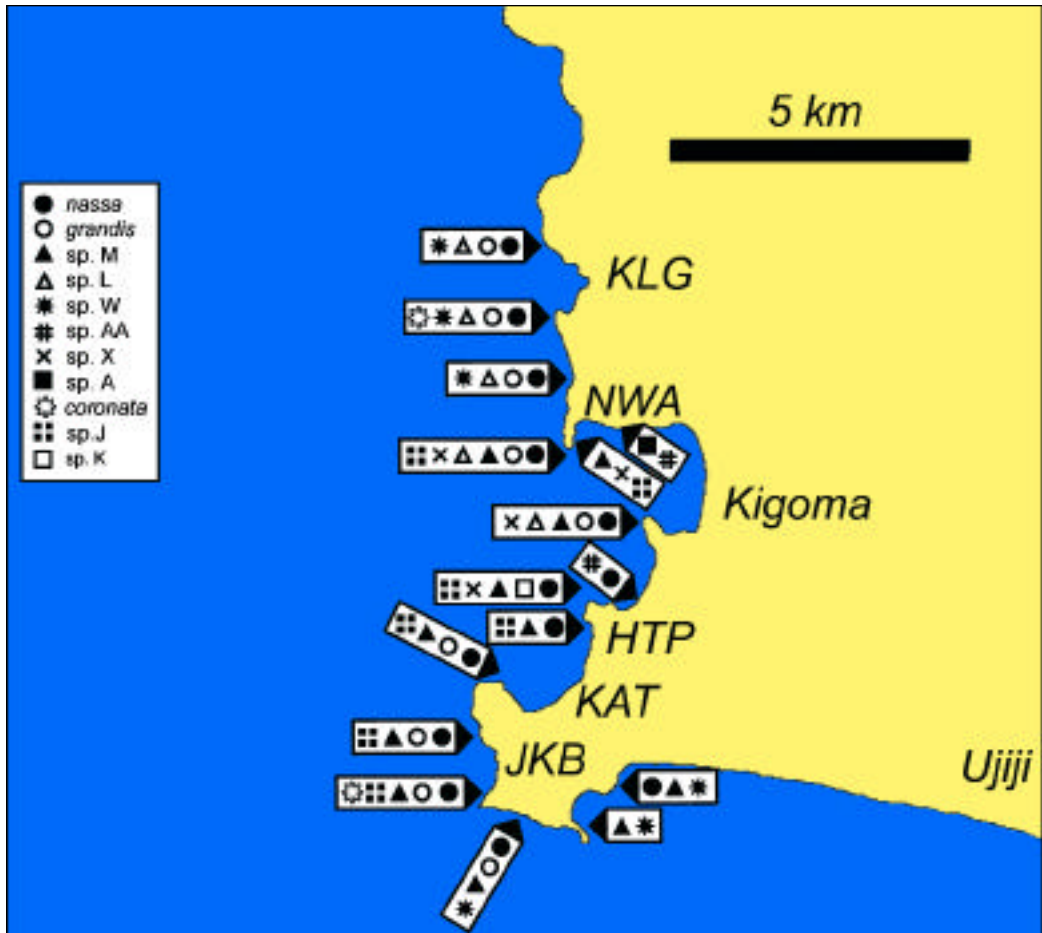
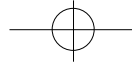


Fig. 3 Map of Region 3, Kigoma area, with site occurrences of 11 species shown. Map oriented along North-South vertical. Generalised site name abbreviations indicated: KLG = Kalalangabo; NWA = Nondwa; Kigoma town; HTP = 'Hilltop Point'; KAT = Katabe Bay; JKB = 'Jakobsen's Beach' (left of label). 'Mzungu Beach' (mentioned in text) is south facing coastline just south of JKB, Luanza Point is in the middle of Kigoma Bay (opposite Kigoma label). Note differences in species distributions. *Lavigeria nassa* and *grandis* are widely distributed along much of the shoreline. Species Land M are limited to stretches of sites north and south of Nondwa Point, with one area of sympatry in the middle of Kigoma Bay (Luanza Point, not labelled). Species J is widely found in the Kigoma region, sometimes in very high numbers, but is unique to this area, to the best of our knowledge. Species W, *coronata* and species AA each have unusual 2-point occurrences, but are not concordant with each other. Species K is rare and found only in the Kigoma region. Species X and sp. A are more common on soft substrates, but are occasionally found on the hard substrates sampled here.



all samples were pooled and regional species richness was estimated at a rarefied sample size of 290 individuals, a number determined by the size of the smallest regional collection. Subsequently linear regression was used to assess the relationship between regional and local species richness with Statistica 5 (StatSoft Inc., Tulsa, USA). Finally we used the same technique to examine the relationship between regional species richness and number of regional endemics.

EXAMINING WITHIN-REGION DIVERSITY

We discuss local distribution patterns along the well-sampled coastline in the area around Kigoma, Tanzania (Region 3) to provide the framework for interpreting within-region *Lavigeria* occurrence and diversity (Fig. 3). Over recent years this has been the lakeshore base for the Lake Tanganyika Biodiversity Project (<http://www.ltbp.org>) and for the Nyanza Project, a research-training course (<http://www.geo.arizona.edu/nyanza/past.html>).

RESULTS

REGIONAL SPECIES RICHNESS

All species accumulation curves (Fig. 4) follow similar trajectories with a steep rise in species diversity for the first 100 individuals and asymptote reached by 200 individuals. This indicates that our sampling was sufficient to identify real differences in species

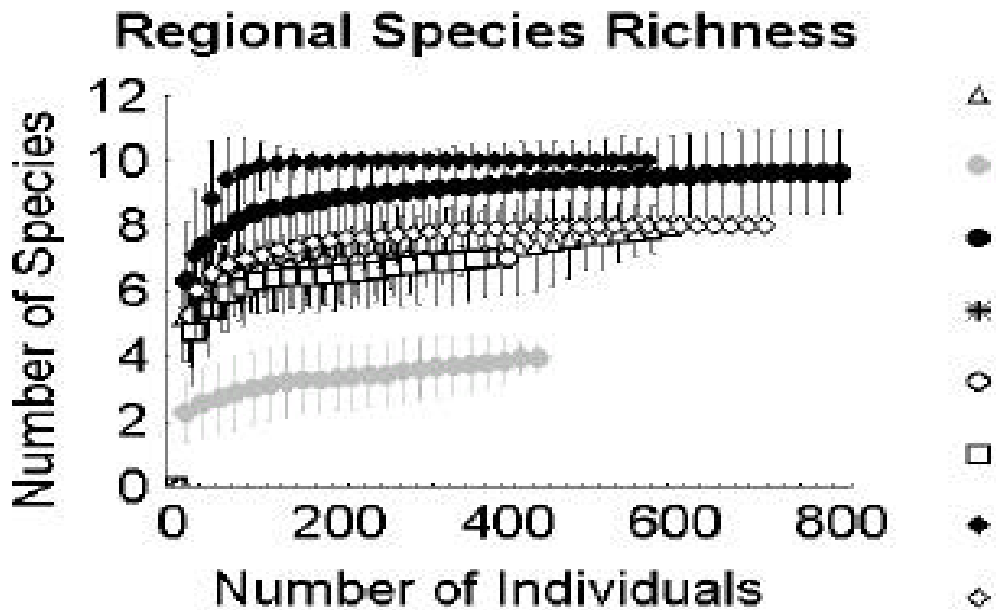
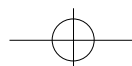
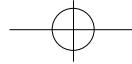


Fig. 4 Cumulative species richness curves for all eight regions. These generally level off quickly, with the strongest increase at sample sizes below 200 individuals and in some cases approaching an asymptote, indicating surprisingly saturated sampling. Confidence intervals based on simulation. We distinguish three levels of diversity among regions: high diversity (filled symbols, Regions 3 and 7), moderate diversity (open symbols, Regions 1, 4, 5, 6, 8) and low diversity (grey symbols, Region 2).





diversity between the regions. Considerable variation was discovered among regions with absolute ranges between 4 and 11 (mean = 7.8) and rarefied ranges between 3.6 and 10 (mean = 7.3). Regions fell into three distinct clusters identifiable using both species accumulation curves (Fig. 4) and a plot of local against regional richness (Fig. 5a). The three groupings are as follows: a) Low Diversity (Region 2). Despite containing 12 survey sites and repeated sampling over several years over most available rocky shoreline (Michel 1995, Johnston & Cohen 1987), it has by far the lowest richness with a total of just four species. No regional endemic *Lavigeria* species have been identified in this area; b) Moderate Diversity (Regions 1, 4, 5, 6 & 8). These sites have total richness ranging from 7 to 8 species with little or no regional endemism (0 to 2 endemics per region); c) High Diversity (Regions 3 and 7). These regions possessed the highest species richness with 11 and 10 species respectively. Both also contained high levels of regional endemism, with 5 and 3 species respectively.

There was no significant relationship between regional and local species richness ($r^2 = 0.07$, $p = 0.26$, Fig. 5a). The minimum species richness of 1 to 2 species per site, and the highest species richness of 4 to 5 species per site were found in all sampling regions, with the exception of Region 2. The relationship between regional endemism and regional species richness was marginally significant ($r^2 = 0.46$, $p < 0.06$, Fig. 5b), thus indicating that regional endemics contribute to differences among regions. Comparisons of rarefied local richness (Fig. 5c) show that the most diverse regions are not necessarily comprised of the most diverse sites. Regions 3 and 7, although clearly the most species rich with most endemics, have only moderate within-site diversity. This is indicative of a high between-site () diversity.

LOCAL DIVERSITY – THE PREVALENCE OF PATCHINESS

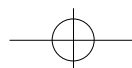
Our sampling in Region 3 (around Kigoma, Tanzania) is of great enough resolution to uncover some details of the patchiness of local endemic species distributions that may help explain the unusual large-scale patterns. We are confident in identifying these species as local endemics as we have sampled extensively along the Kigoma shoreline (Fig. 2, region 3, detail shown in Fig. 3) and widely but less intensively in the immediate surrounding areas.

The 28 sampled species of rock-dwelling *Lavigeria* show a wide range of variation in the scale of their distributions (Fig. 5d). Some species are widely distributed including *L. nassa*, present at 47% of sites and *L. grandis*, present at 45% of sites. Where present, these taxa generally occur in abundance and are recorded from all eight regions. We thus do not find it surprising that these were among the first species described from early European explorer's collections (Smith 1881, Woodward 1859).

In contrast to these widely occurring species, some species have very limited ranges. One example is *L. coronata*, a species restricted to two sites ten kilometres apart flanking Kigoma Bay (Fig. 3). This taxon is intriguingly absent from intervening sites even though apparently suitable rocky substrates are present (Gathogo 2001). *Lavigeria* sp. W has a similarly disjunct distribution. These species cannot legitimately be called (single) point endemics (Fig. 3), but do have very short ranges.

SPECIES-HABITAT PREDICABILITY

Lavigeria species differ considerably in their habitat fidelity. *L. grandis* and *L. coronata* for example are found in clear, shallow waters of less than 10 metres depth and are almost exclusively present on large rocks, boulders and bedrock. *L. nassa* is commonly found in the same habitats, but has wider substrate tolerance including small rocks, sediment-rich areas and deeper waters. Another taxon *L. sp. J* also has a wide habitat tolerance ranging from bedrock through to cobbles and occasionally coarse sand. Interestingly, the degree of habitat specialisation of these taxa appears to no predictor of biogeographic



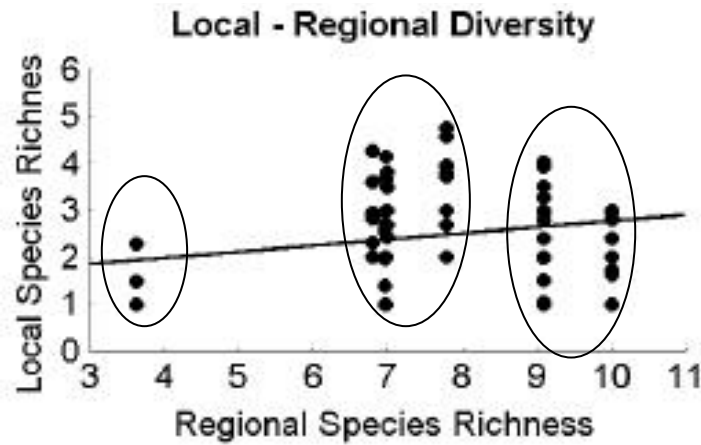
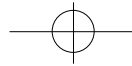


Fig. 5a Plot of local (site) and regional richness estimated using Chao 2 showing no correlation – sites within regions may range from having one to five species. This is concordant with a highly patchy distribution and limited dispersal among regions. The three groups of low, moderate and high diversity regions are evident here, and would cluster even more strongly with rarefactions based on larger sample sizes, as is evident from Fig. 4. The moderate cluster consists of five regions as some points are plotted on top of each other.

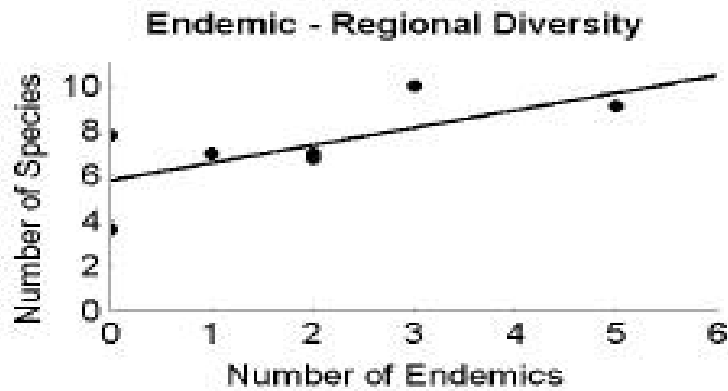
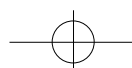


Fig. 5b There is a clear association of high regional diversity with high degrees of endemism. This suggests that as sampling intensity increases so increasingly more endemics are recovered, indicating them to be either rare or very patchily distributed (including point endemics). The points for three regions, 1, 5, 6, are plotted on top of each other.

range. For example, although *L. grandis* and *L. coronata* are both habitat specialists, only *L. grandis* is widely distributed. Similarly of *L. nassa* and *L. sp. J*, both apparent habitat generalists, only *L. nassa* is widely distributed around the lake.

Within our samples many apparently rare species present on rocky substrates turned out to be more abundant in other habitats. For example, *L. sp. AA* was known in our rocky substrate collections from just two individuals, one from each of Regions 1 and 3. However recently it was found in abundance at two sites, first between cobbles in Kigoma Bay and secondly just 5km to the north among macrophytes. No geographically intermediate populations of this are known although again, suitable habitats appear to be present. This indicates that substrate specificity may differ between geographically subdivided populations of the same species.



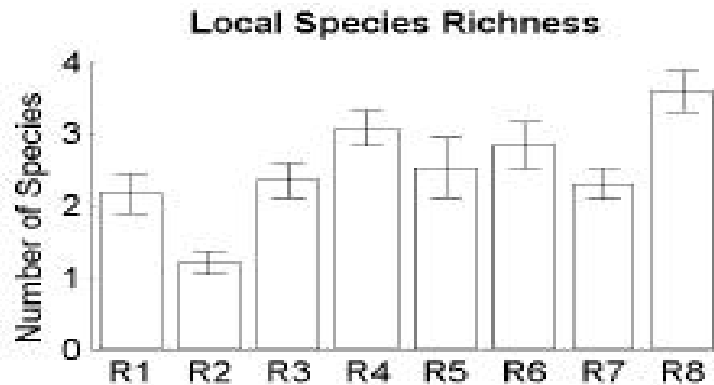
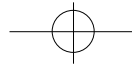


Fig. 5c Average local (site) species richness by region based on rarefaction to 20 individuals/ site. Rarefaction compensates for differences in sampling intensity. Region 2 has the lowest diversity per site as well as lowest regional diversity. The most diverse regions, however, Regions 3 and 7, have low within-site diversity, indicating that their high diversity is a result of patchy distribu-

FEW PREDICTABLE ASSEMBLAGES

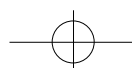
The unpredictability of species-habitat preference is unlikely to have a simple environmental explanation, primarily because even though sets of these species are found in sympatry at some sites, the same species sets do not recur at other sites. For example, *L. coronata* and *L. sp. W* have highly disjunct distributions to the north and south of Kigoma Bay. They are sympatric on boulders at one site to the north (Kalalangabo), whereas they are disjunct to the south. *Lavigeria coronata* is only present at 'Jakobsen's Beach', while in contrast *L. new sp. W* is found to the south and around the point at 'Mzungu Beach'.

SPATIAL AND TEMPORAL ABUNDANCE SHIFTS

Local endemics are not always rare species within communities, instead they tend to be patchily distributed. The common discovery pattern for a new species has been to find only a few specimens in initial collections. However later more focused work revealed each of these to be abundant and sometimes to dominate communities as the shoreline is explored in more detail. For example, *L. sp. J* was rare in early collections made on wave-exposed bedrock of 'Hilltop'. However later more intensive sampling in a more sheltered adjacent bay revealed temporally fluctuating densities of as much as 600 individuals per square metre (McIntyre *et al.* unpublished data; Michel pers. obs.). Other nearby shorelines showed lower, but more constant abundance (Powers 2002; Zorich 1999).

COMPARISON WITH PREVIOUS WORK AND CONSERVATION IMPLICATIONS

Our assessments of regional diversity for *Lavigeria* can be directly compared with a recent study by the LTBP, where molluscs were used as total biodiversity indicators in the first wide-ranging, quantitative sampling programme directed at conservation assessment (Allison *et al.* 2000). Rapid lake-wide surveys by the LTBP discovered only six species of *Lavigeria*. This was possibly due to the use of broader species concepts than those hitherto developed. Regionally LTBP surveyed transects of rocky substrates between 0 and 15m in four aquatic reserves. It is possible to directly compare our results with those obtained from two of these reserves: Gombe and Mahale National Parks in Tanzania. For these comparisons we restricted our data to those from localities within boundaries of the National Parks. This totalled five sites for Gombe and twelve for Mahale. At Gombe the LTBP surveys found four species compared to our three, but the



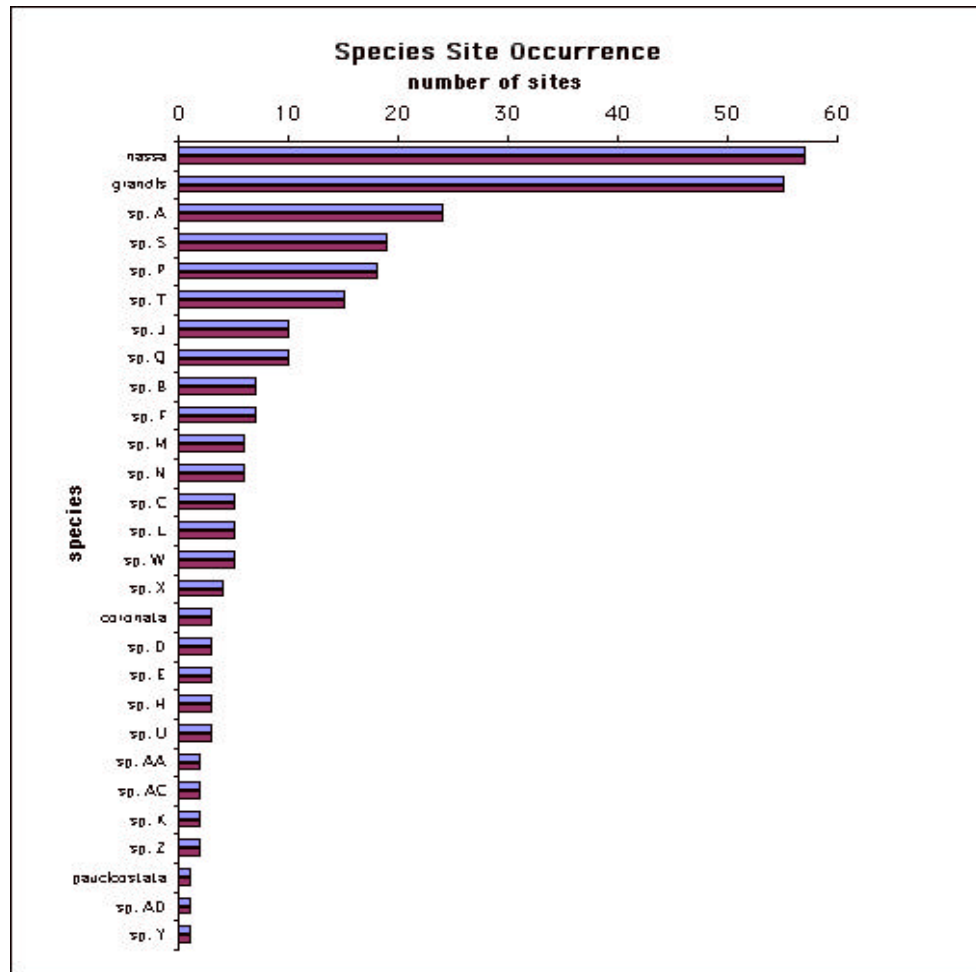
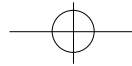


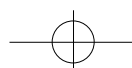
Fig. 5d Number of sites at which each species occurs, based on the analysed data set of 121 sites. *L. nassa* and *L. grandis* are the most widely distributed, whereas many species are practically point endemics.

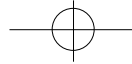
extensive Mahale surveys found only four compared to our seven species, two of which, *L. sp. D* and *L. sp. E*, are endemic to Region 5. It is possible that the Mahale species went unrecognised, as many of the LTBP identifications were made underwater and algal-coated sympatric species can be difficult to distinguish.

DISCUSSION

REGIONAL SPECIES RICHNESS

Our results demonstrate that there are considerable differences in *Lavigeria* gastropod diversity among regions within the lake, and that regional species richness is strongly associated with the presence of local endemics. Species richness at individual sites was not correlated with total species richness of the surrounding region, a result contrasting with diversity patterns found in other diverse aquatic systems (e.g. Karlson & Cornell





2002). Such a pattern is likely to be a consequence of small spatial distributions and high levels of endemism among the *Lavigeria*, which are in turn likely to be linked to poor dispersal ability. Similar patterns are being revealed in other gastropod groups with elevated diversity, such as the 'short-range' endemics in Australian hydrobiids (Clark & Richardson 2002; Harvey 2002; Ponder & Colgan 2002).

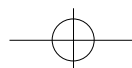
Lake-wide clines of diversity, for example from north to south, were not apparent in the data. These suggest that ecological variables associated with latitude, such as depth of the anoxic layer (100m in the north, 250m in the south (Bootsma & Hecky 1993; Coulter 1991; Plisnier *et al.* 1999) and rainfall (Savijarvi & Jarvenoja 2000) are not associated with levels of diversity. Moreover, there was no apparent concentration of diversity within the northern, central or southern palaeo-basins as might be predicted from a single centre of origin or invasion. Instead, the regions with the highest and lowest levels of species richness are both in the northern basin (Regions 2 and 3). Sampling of the Congo coast facing our study areas will provide replicate tests of these lake-wide patterns in the future. The Congo coast is, at least for the extant fauna, an almost independent linear coastline (Michel *et al.* 1992). Dispersal across the open pelagic is highly improbable for these gastropods and the benthos encounters an anoxic barrier to direct contact below depths of 100-200m.

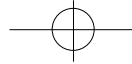
The Burundi coastline has the least diverse *Lavigeria* fauna, and also possesses a comparatively low level of diversity for other taxa (Alin *et al.* 1999; Cohen *et al.* 1993). One possible explanation is that a high human population density in this region, and associated deforestation and agricultural activity, has resulted in high levels of sediment impact on the littoral zone (Alin *et al.* 1999; Cohen *et al.* 1993). This may have affected habitat structure resulting in an overall loss of diversity (McIntyre *et al.*, unpublished data; Rivers 2001), but it is also possible that diversity is low in this region for reasons independent of recent anthropogenic impacts (Cohen 2000).

While we are confident that these results are consistent with real patterns in species richness, we must be cautious in our interpretation of the results on local scales. For example, high local richness of Region 8 (Fig. 5c) suggests that this section of the Zambian coastline may be under-sampled. One possible explanation for the elevated local richness is that many of the sites relatively few specimens have been collected and only a few sites had large numbers of particular species. Similar consideration should be given to the surprisingly low local richness of sites within Region 3. It is likely that very large numbers of individuals belonging to *L. sp. J* at a small proportion of the sites could have resulted in a depression of the rarefied local richness values. We expect that even the most diverse regions (Regions 3 & 7) have the potential to reveal higher diversity with increased sampling. Our sampling has been intensive near Kigoma, but less intensive sampling in more distant sections of Region 3. Over the five years that the Nyanza Project has run to date, we have effectively found a new species each year by exploring new stretches of coastline.

DIVERSITY, ABUNDANCE AND ORIGINS OF LAVIGERA REGIONAL ENDEMICS

Lavigeria species exhibit distributions that range from extremely wide- to very short-range endemics. Certainly the highest diversity of *Lavigeria* is on rocky substrates, although additional soft-substrate *Lavigeria* are present that were not included in this analysis. One explanation for the patchy distributions of rock-dwelling *Lavigeria* identified is that there may be fine-scale habitat requirements that have not yet been identified, perhaps for particular rock types or current regimes. An alternative explanation is that there are temporally shifting populations distributions as would fit a stochastic metapopulation model. The metapopulation perspective has been suggested for the similarly patchily distributed ostracods found in soft substrates of Lake Tanganyika with support from temporal information provided by sediment cores (Cohen 2000).





Stochastic and selective processes can, of course, operate simultaneously on different taxa or time slices. It is the relative importance of each process that concerns us for conservation of endemic diversity. If extant distributions fluctuate with time due to recruitment from neighbouring metapopulations, conservation efforts must include wider areas and potential source populations should also be protected. Temporally static populations are easier to conserve and reserve design can generally be smaller (Cohen 2000). We are only beginning to accumulate extensive quantitative data on *Lavigeria* distributions (McIntyre *et al.* unpublished data). Rare taxa do occur in our analysis, however our data suggest that this is not the norm for this species flock. Instead our intensive sampling of the Kigoma region indicates that when *Lavigeria* taxa are rare in collections, it is because sites of peak abundance have not yet been located or adequately sampled. *Lavigeria* endemics are of interest not only for speciation studies, but also for implementing effective long-term conservation plans. We expect some regional endemics, such as *L. sp. J*, *L. sp. M* and *L. sp. W* will prove to be primary endemics that evolved locally. The presence of more widely occurring long-dead shells in *L. coronata*, suggests that today's live occurrences represent relict populations of a formerly much more widely distributed species.

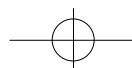
We can use the existing data to estimate total richness in this clade, even though the whole Tanganyikan shoreline has not yet been sampled. Each of our sampled regions (block) has a mean 1.9 endemic species (range = 0 to 5, rarefied 2.5) and so the poorly sampled Congo littoral must be expected to house a number of unrecorded endemics. In fact, we have recorded these in the few sites we have collected for *Lavigeria* to date. If its diversity parallels that of the eastern shore, and we estimate another four regions on the Congo shoreline, then there may be more than 43 rock-dwelling *Lavigeria* species in total.

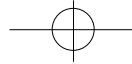
LOCAL DIVERSITY - THE KIGOMA EXAMPLE

We feel that Region 3 is probably not exceptional in its patchiness of *Lavigeria* distributions. We expect that our recorded diversity is high from this region partly because we have had the opportunity to repeatedly sample the shoreline and partly as a result of its tectonic and structural geological heterogeneity. Other regions of the lake are likely to reveal similar patterns on more detailed sampling, as is indicated by our analyses. It has been suggested that the Kigoma Bay area represents a microcosm of the lake's entire gastropod fauna (Bandel 1998). In contrast, our comparisons both within the area and among regions demonstrate how heterogeneous the gastropod fauna can potentially be over a range of spatial scales (also Sekandende 2000; Solomon 2001). If *Lavigeria* species exhibit patchy distributions and short-range endemism around Kigoma, their sister taxa are likely to do so elsewhere as well.

CONCLUSIONS: CONSERVATION IMPLICATIONS OF LARGE AND LOCAL SCALE PATCHINESS
These data on *Lavigeria* distributions underscore how systematics and sampling work hand in hand. Both can dramatically alter conclusions on structure of biodiversity that inform conservation policy. With lower species resolution and more limited site sampling, the LTBP (Allison *et al.* 2000) concluded that habitat conservation alone was sufficient for conserving the endemic mollusc diversity of Lake Tanganyika. Our results suggest that this will potentially protect the major endemic genera, but narrowly distributed endemics such as many of the *Lavigeria* species may require broader geographic protection, as well as habitat protection.

Our study suggests the encouraging perspective that assessment of regional diversity can be accomplished by sampling relatively few individuals. It is true that this sampling must occur over a number of sites within a region, as our data shows single site diversity does not predict regional diversity and individual species distributions may be





extremely patchy. Furthermore, a quick and efficient sampling programme that reveals differences in regional diversity will give a reliable indication of the importance of that region for conserving *Lavigeria* diversity. Specifically, only the initial slopes of the rarefied diversity curves, as seen in Fig. 4, need be compared and it is not critical to know the conspecificity of populations across regions. This is likely to prove crucial for future biodiversity assessments because many *Lavigeria* species, though often relatively easily distinguished within a site or region, can be difficult to correlate from one region to another or to identify in a lake-wide context. Notably, within some *Lavigeria* clades, the systematic status of some distinguishable allopatric populations, whether allospecies or geographic forms, is still uncertain.

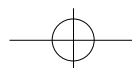
Lavigeria is by far the most speciose gastropod genus in Lake Tanganyika, thus this approach brings us much closer to understanding the real patterns of molluscan diversity in the lake. Further analyses of these data, such as environmental correlates of species occurrences, need to be undertaken. Such information is necessary to predict relative species diversity of sites and to develop effective regional sampling strategies. For other Tanganyikan gastropods systematic reassessment of species diversity is required before distributional analyses can be fruitfully conducted. This is particularly desirable for potentially speciose soft-substrate taxa such as *Paramelania* and *Syrnolopsis*. Comparative distributional patterns of soft and rocky substrate dwellers would provide us with essential information for both evolutionary studies and conservation needs.

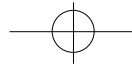
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REFERENCES

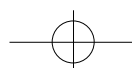
- ALIN S.R., COHEN A.S., BILLS R., GASHAGAZA M.M., MICHEL E., TIERCELIN J.J., MARTENS K., COEVELIERS P., MBOKO S.K., WEST K., SOREGHAN M., KIMBADI S. & NTAKIMAZI G. 1999 Effects of landscape disturbance on animal communities in Lake Tanganyika, East Africa. *Conservation Biology* 13: 1017-1033.
- ALLISON E.H., PALEY R.G.T., NTAKIMAZI G., COWAN V.J. & WEST K. 2000 *Biodiversity Assessment and Conservation in Lake Tanganyika* BLOSS Final Technical Report Lake Tanganyika Biodiversity Project RAF/92/G32 189pp.
- BANDEL K. 1998 Evolutionary history of East African fresh water gastropods interpreted from the fauna of Lake Tanganyika and Lake Malawi *Zentralblatt für Geologie und Paläontologie* 1 1: 233-292.
- BOOTSMA H.A. & HECKY R.E. 1993 Conservation of the African Great Lakes – a limnological

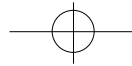




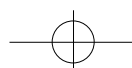
16 E. MICHEL, J.A. TODD, D.F.R. CLEARY, I. KINGMA, A.S. COHEN & M.J. GENNER

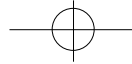
- perspective *Conservation Biology* **7**(3): 644-656.
- BOURGUIGNAT J.R. 1885 *Notice prodromique sur les mollusques terrestres et fluviatiles recueillies par M. Victor Giraud dans la région méridionale du Lac Tanganika*. V. Tremblay, Paris, 110pp.
- BOURGUIGNAT J.R. 1888 *Iconographie malacologique des animaux mollusques fluviales du Lac Tanganyika* Corbeil, Paris.
- BOURGUIGNAT J.R. 1890 *Histoire Malacologique du Lac Tanganika (Afrique Equatoriale)* Annales des Sciences Naturelles de Paris, Zoologie Serie 7 **10**: 1-267.
- BROWN D.S. 1980 *Freshwater Snails of Africa and their Medical Importance* Taylor & Francis, London.
- BROWN D.S. 1994 *Freshwater Snails of Africa and their Medical Importance* Revised 2nd edition. Taylor & Francis, London.
- BROWN D.S. & MANDAHL-BARTH G. 1987 Living molluscs of Lake Tanganyika: a revised and annotated list *Journal of Conchology* **32**: 305-327.
- CLARK S.A. & RICHARDSON B.A. 2002 Spatial analysis of genetic variation as a rapid assessment tool in the conservation management of narrow-range endemics *Invertebrate Systematics* **16**: 583-587.
- COHEN A.S. 1992 Criteria for developing viable underwater natural reserves in Lake Tanganyika *Mitteilungen. Internationale Vereinigung für Theoretische und Angewandte Limnologie* **23**: 109-116.
- COHEN A.S. 1994 Extinction in ancient lakes: biodiversity crises and conservation 40 years after J. L. Brooks In K. Martens, B. Gooderis, & G. Coulter (eds) *Speciation in Ancient Lakes*. *Archiv für Hydrobiologie – Beihefte. Ergebnisse der Limnologie* **44**: 451-479.
- COHEN A.S. 2000 Linking spatial and temporal change in the diversity structure of ancient lakes: Examples from the ecology and palaeoecology of the Tanganyikan ostracods In A. Rossister, & H. Kawanabe, (eds) *Ancient Lakes: Biodiversity, Ecology and Evolution* *Advances in Ecological Research* **31**: 521-537
- COHEN A.S, BILLS R., COCQUYT C.Z. & CALJON A.G. 1993 The impact of sediment pollution on biodiversity in Lake Tanganyika *Conservation Biology* **7**: 667-677.
- COHEN A.S. & JOHNSTON M.R. 1987 Speciation in brooding and poorly dispersing lacustrine organisms. *Palaios* **2**: 426-435.
- COULTER G.W. 1991 *Lake Tanganyika and Its Life*. Oxford University Press, London.
- COULTER G.W. 1999 Sustaining both biodiversity and fisheries in ancient lakes; the cases of Lake Tanganyika, Malawi/Nyasa, and Victoria. Pp. 177-187 In H. Kawanabe, G.W. Coulter, & A.C. Roosevelt, (eds). *Ancient Lakes: Their Cultural and Biological Diversity*. Kenobi, Belgium.
- GATHOGO P.N. 2001 Characterisation of near-shore substrate along the eastern shore of Lake Tanganyika at Kigoma area, western Tanzania *Nyanza Project Reports* (www.geo.arizona.edu/nyanza/past.html), 6pp.
- HARVEY M.S. 2002 Short-range endemism among the Australian fauna: some examples from non-marine environments *Invertebrate Systematics* **16**(4): 555-570.
- HORI M., GASHAGAZA M.M., NSHOMBO M., KAWANABE H. 1993 Littoral fish communities in Lake Tanganyika – irreplaceable diversity supported by intricate interactions among species *Conservation Biology* **7**(3): 657-666.
- JOHNSTON M.R. & COHEN A.S. 1987 Morphological divergence in endemic gastropods from Lake Tanganyika: Implications for models of species flock formation *Palaios* **2**: 413-425.
- KARLSON R.H. & CORNELL H.V. 2002 Species richness of coral assemblages: Detecting regional influences at local spatial scales *Ecology* **83**(2): 452-463.
- KINGMA I. & MICHEL E. 2000 Variation in reproductive strategies in the ovoviviparous genus *Lavigeria* (Gastropoda: Thiaridae) from Lake Tanganyika, East Africa (in Dutch) *Correspondentie Blad van de Nederlandse Malacologische Vereniging* **312**: 15-24.
- LELOUP E. 1953 *Gastéropodes. Resultats scientifiques de l'exploration hydrobiologique du Lac Tanganyika (1946-1947)* *Institute Royale des Sciences Naturelle Belgique* **3**(4): 1-272.
- MCINTYRE P., MICHEL E., FRANCE K., MULONGAUBALU M., RIVERS A., HAKIZIMANA P. & COHEN A. (submitted) Direct and indirect effects of anthropogenic sedimentation on benthic herbivores in Lake Tanganyika, East Africa. 40 MS pgs, 8 figs.
- MENONE C. 2000 Snail diversity and abundance at sediment disturbed and undisturbed sites





- around Kigoma, Tanzania *Nyanza Project Reports* (www.geo.arizona.edu/nyanza/past.html), 3pp.
- MICHEL E. 1994 Why Snails Radiate: A Review of Gastropod Evolution in Long-lived Lakes, Both Recent and Fossil. In K. Martens, B. Gooderis, & G. Coulter (eds) *Speciation in Ancient Lakes*. *Archiv für Hydrobiologie – Beihefte. Ergebnisse der Limnologie* **44**: 285-317.
- MICHEL E. 1995 *Evolutionary Diversification of Rift Lake Gastropods: Morphology, Anatomy, Genetics, and Biogeography of Lavigeria (Mollusca: Thiaridae) in Lake Tanganyika* PhD thesis, Department of Ecology & Evolutionary Biology, University of Arizona, Tucson.
- MICHEL E. 2000 Phylogeny of a gastropod species flock: exploring speciation in Lake Tanganyika in a molecular framework In A. Rossister, & H. Kawanabe, (eds) *Ancient Lakes: Biodiversity, Ecology and Evolution* *Advances in Ecological Research* **31**: 275-302.
- MICHEL E. in revision *Vinundu*, a new genus of gastropod (Cerithioidea: 'Thiaridae') with two species from Lake Tanganyika, East Africa *Journal of Molluscan Studies*.
- MICHEL A.E., COHEN A.S., WEST K.A., JOHNSTON M.R. & KAT P.W. 1992 Large African Lakes as natural laboratories for evolution: Examples from the endemic gastropod fauna of Lake Tanganyika *Mitteilungen. Internationale Vereinigung für Theoretische und Angewandte Limnologie* **23**: 85-99.
- PAPADOPOULOS L.N., MICHEL E. & TODD J.A. 2001 Homology in sculptured shell morphology: An example from a clade of the *Lavigeria* (Thiaridae) species flock of Lake Tanganyika *Abstracts, World Congress of Malacology 2001, Vienna, Austria*, (L. Salvini-Plawen, J. Voltzow, H. Sattmann & G. Steiner (eds), *Unitas Malacologica* p. 263.
- PAPADOPOULOS L.N. & TODD J.A. 2001 How to recognize adulthood and homology: Defining cladistic characters in a clade of the *Lavigeria* (Thiaridae) species flock of Lake Tanganyika *Abstracts, World Congress of Malacology 2001, Vienna, Austria*, (L. Salvini-Plawen, J. Voltzow, H. Sattmann & G. Steiner (eds), *Unitas Malacologica* p. 264.
- PLISNIER P.D., CHITAMWEBWA D., MWAPE L., TSHIBANGU K., LANGENBERG V. & COENEN E. 1999 Limnological annual cycle inferred from physical-chemical fluctuations at three stations of Lake Tanganyika *Hydrobiologia* **407**: 45-58.
- PONDER W.F. & COLGAN D.J. 2002. What makes a narrow-range taxon? Insights from Australian freshwater snails *Invertebrate Systematics* **16**: 571-582.
- PONDER L.P. 2002 Substrate preference and microhabitat use among gastropods of Lake Tanganyika *Nyanza Project Reports* (www.geo.arizona.edu/nyanza/past.html) 5pp.
- RIVERS A.R. 2001 The effect of sediment deposition on gastropod fecal content *Nyanza Project Reports* (www.geo.arizona.edu/nyanza/past.html), 6pp.
- RYDER O.A. 1986 Species conservation and systematics, the dilemma of subspecies *Trends in Ecology and Evolution* **1**: 9-10.
- SAVIJARVI H. & JARVENOJA S. 2000 Aspects of the fine-scale climatology over Lake Tanganyika as resolved by a mesoscale model *Meteorology and Atmospheric Physics* **73** (1-2): 77-88
- SEKANDENDE B. 2000 Patchiness in Gastropod Abundance and Diversity at Jakobsen's Beach: A Depth Survey using SCUBA *Nyanza Project Reports* (www.geo.arizona.edu/nyanza/past.html) 5pp.
- SMITH E. A. 1881 On a collection of shells from Lakes Tanganyika and Nyassa and other localities in East Africa *Proceedings of the Zoological Society of London* **1881**: 276-300.
- SOLOMON C.T. 2001 A preliminary investigation into trophic niche partitioning among closely related thiarid snails in Lake Tanganyika *Nyanza Project Reports* (www.geo.arizona.edu/nyanza/past.html) 5pp.
- TODD J.A. & MICHEL E. 2001 Species diversity of the *Lavigeria* species flock (Gastropoda: Thiaridae) of Lake Tanganyika – a re-evaluation using multiple datasets *Abstracts, World Congress of Malacology 2001, Vienna, Austria*, (L. Salvini-Plawen, J. Voltzow, H. Sattmann & G. Steiner (eds) *Unitas Malacologica* p. 355.
- VERHEYEN E., & RUBER L. 2000 Conservation of the endemic cichlid fishes of Lake Tanganyika: Implications from population-level studies based on mitochondrial DNA In A. Rossister, & H. Kawanabe, (eds) *Ancient Lakes: Biodiversity, Ecology and Evolution*, *Advances in Ecological*





18 E. MICHEL, J.A. TODD, D.F.R. CLEARY, I. KINGMA, A.S. COHEN & M.J. GENNER

Research **31**: 539-551.

WEST K. & COHEN A. 1994 Predator-prey coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika In K. Martens, B. Gooderis, & G. Coulter (eds) *Speciation in Ancient Lakes. Archiv für Hydrobiologie – Beihefte. Ergebnisse der Limnologie* **44**: 267-283.

WEST K. & COHEN A. 1996 Shell microstructure of gastropods from Lake Tanganyika: adaptation, convergent evolution and escalation *Evolution* **50**: 672-681.

WEST K. & MICHEL E. 2000 The dynamics of endemic diversification: molecular phylogeny suggests an explosive origin of the thiarid gastropods of Lake Tanganyika In A. Rossister & H. Kawanabe (eds) *Ancient Lakes: Biodiversity, Ecology and Evolution, Advances in Ecological Research* **31**: 331-354.

WEST K., MICHEL E., TODD J.A., BROWN D. & CLABAUGH J. in press *The gastropods of Lake Tanganyika: diagnostic key and taxonomic classification with notes on the fauna (International Association of Theoretical and Applied Limnology, Occasional publication, 2)* 132 pp., 102 figs.

WEST K., NAKAI K., & MARTENS K. in revision Two new members of Lake Tanganyika's gastropod species flock with some taxonomic comments on the group (Prosobranchia: Cerithioidea: Thiaridae). *Journal of Molluscan Studies*.

WOODWARD S. P. 1859 On some new freshwater shells from Central Africa *Proceedings of the Zoological Society of London* **1859**: 348-351.

ZORICH N. 1999 Snail Distribution and Diversity South of Kigoma Bay, Lake Tanganyika, East Africa *Nyanza Project Reports* (www.geo.arizona.edu/nyanza/past.html) 5pp.

