Paleoecological approaches to the conservation biology of benthos in ancient lakes: a case study from Lake Tanganyika

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Abstract. A small number of ancient lakes (mostly >10⁶ y old) scattered around the globe contain an extraordinary percentage of the world's documented freshwater biodiversity. Endemic benthic invertebrates and fish in most of these lakes today face a variety of anthropogenic threats, including damaging fishing activities, water pollution, species introductions and translocations, climate change, and watershed disturbances.

Lake Tanganyika, one of the oldest and most diverse of the ancient lakes, provides a model for studying the effects on endemic faunal diversity from watershed disturbances caused by deforestation. Increased erosion rates around the northern portion of the lake are associated with substantially lower diversity levels for both benthic invertebrates and fish. Disturbance processes in the biologically complex littoral region of this lake that are related to this excess siltation include reductions in light penetration (affecting algal habitat and herbivory), reductions in habitat heterogeneity, and reduced connectivity between benthic habitat patches.

Paleoecological data for readily fossilized taxa may be used in Lake Tanganyika to determine background levels and variability in diversity and the historical relationship between human activities in the watershed and changes in benthic community structure. Biogeographic and paleoecologic studies of endemic ostracodes demonstrate that many taxa have extremely patchy distributions which are consistent with metapopulation models of organization. The extremely high diversities encountered in Lake Tanganyika and other ancient lakes may be dependent on nonequilibrium interactions between patchily distributed species, which undergo periodic but uncorrelated extinctions and recolonizations of appropriate habitat patches. Conversely, excess sedimentation along rocky coastlines may reduce habitat patch interconnections and lead to local extinctions, even in areas that are not directly affected by damaging siltation. Paleoecological data may be used by aquatic conservation biologists to determine the history of this and similar problems and, more generally, to obtain a dynamic view of diversity change in lakes through time.

Key words: extinction, conservation biology, ancient lakes, metapopulations, paleoecology, ostracodes, Lake Tanganyika.

For over a century a small number of lakes that contain large concentrations of endemic taxa have captivated the interest of evolutionary biologists (e.g., Smith 1881, Moore 1903, Doro- gostaisky 1923). These bodies of water are mostly large (>100 km²), tectonically formed lakes of great antiquity. They occur scattered around the globe, at both low and high latitudes. Many, such as the African Lake Tanganyika and Lake Malawi or the Russian Lake Baikal, owe their origin to rifting processes, whereas others, such as Lake Titicaca in the South American altiplano, have more complex tectonic origins (Nikolayev 1987, Tiercelin and Mondeguer 1991, Dejoux and Iltis 1992). Geological investigations using data from faulted outcrops, cores, and reflection seismic stratigraphy, show that many of these lakes are more than one million years old, and several, notably Lake Tanganyika and Lake Baikal, may be 10 million years old or more (Nikolayev 1987, Rosendahl 1987, Cohen et al. 1993a). Similar species-rich, long-lived lakes are known to have existed in the past, as inferred from rock outcrops and their contained fossils (Williamson 1981, Smith 1987). In contrast, the Laurentian Great Lakes of North American, as well as most of the lakes of North America and Eurasia, are much younger, having formed as a result of glacial excavation or moraine damming during the late Pleistocene (Carrow and Calkin 1985).

The extraordinary age of these lakes is in part responsible for the equally unusual levels of endemism observed in many of them (Fig. 1). The great variety of morphologies displayed within the numerous monophyletic species flocks in these lakes has generated extensive phylogenetic research into the historical origins of these organisms, as well as ecological research into understanding how this diversity is sustained.
(e.g., Brooks 1950, Stankovic 1960, Kozhov 1963, Fryer and Iles 1972, Greenwood 1974, Ribbink et al. 1983, Hori 1987, Michel et al. 1992, Stummbauer and Meyer 1992, Reinhthal 1993). For example, a great deal of importance has been attached to the role of key adaptations and subsequent niche partitioning at a finely divided level among epibenthic cichlid fish (Fryer and Iles 1972, Liem 1979, Hori et al. 1993). An implicit assumption behind this approach is that such niche partitioning must be a major part of the explanation for the maintenance of the very high levels of diversity observed in lakes like Malawi, Tanganyika, and Victoria.

However, not all ancient lakes display this pattern of high diversity and endemism. Some, like the many large lakes of the U.S. Great Basin, are in fact species poor, a result of repeated episodes of habitat area reduction, complete desiccation and/or salinity crises (Smith 1978, 1981, Smith and Street-Perrott 1983, Bradbury et al. 1989, Thompson et al. 1990). The ancient lakes that do contain large numbers of species all lie in areas that are either humid or receive substantial river inputs which offset evaporative losses. Most of them are also deep, including the two deepest lakes in the world, Baikal and Tanganyika, which may also serve to buffer them from short term effects of aridity and limnologic change.

**Anthropogenic threats to the benthos of ancient lakes**

Many of the species-rich ancient lakes lie in watersheds that either have large human populations or are heavily exploited for various natural resources (Cohen et al., in press). With a few notable exceptions, our present knowledge of how human disturbance is affecting the endemic biotas is still limited. Disturbances that have been either documented or suggested to be important may be grouped into five major categories: chemical pollutant discharges, fish-
ing activities, regional climate change, species introductions and translocations, and watershed disturbances. Because many of the lakes are in developing countries, the relative importance of the threats facing them often differs substantially from those in industrialized area.

Large lakes are critical water resources and, not surprisingly, pollution of ancient lakes causes concern because of effects on human health and well-documented threats to the lakes' biotas. Although most of the species-rich ancient lakes do not lie in heavily industrialized areas, their limnological characteristics often make them particularly vulnerable to water pollution and pollutant retention (Coulter and Jackson 1981). The tropical deep lakes are particularly sensitive to pollution because of a combination of long residence time of the water mass, and both lower oxygen concentrations and higher biological oxygen consumption at high temperature (Hecky and Bugenyi 1992).

Most of the ancient lakes support substantial fisheries, which have grown in recent years in response to human population pressures. Large catches, combined with a general lack of enforcement of existing regulations have led to serious overfishing problems and major ecosystem reorganizations with significant secondary ramifications for benthos, particularly in lakes Baikal, Lanao, Victoria, and Tanganyika (Galazy 1980, Kornfield and Carpenter 1984, Ndaro 1990, Coulter 1991, Lowe-McConnell 1993).

Global changes in temperature and precipitation as a result of increasing atmospheric concentrations of greenhouse gases are likely to have major consequences for the species-rich lakes of the world (Melack 1991, Cohen et al., in press). At present, the limited spatial resolution of Global Circulation Models constrains their applicability in even the largest lakes (Gates et al. 1992). Nevertheless, all of the major models (CCC, UKHI, and GFDL) suggest increases of 2–4°C for the African and South American lake basins based on 2× modern CO₂ (raised incrementally), and somewhat greater increases for the temperate and boreal lake basins.

Consequences of higher temperature in all lakes would include greater thermal stability of the water column and lowered dissolved oxygen levels in bottom waters. For lakes that weakly overturn or that already have low oxygen activities—like Biwa, Ohrid, Titicaca, and Victoria—serious reductions in the duration of the mixing interval or even permanent stratification and de-oxygenation of bottom waters might result in massive dieoffs of benthos. Also, many of the tropical ancient lakes are already in a precarious state of precipitation-to-evaporation balance and could easily become closed saline basins with slight increases in temperature or decreases in precipitation.

Every one of the species-rich ancient lakes is now known to house exotic species, and some of these introductions have been accompanied by disastrous consequences for the native fauna (Kornfield and Carpenter 1984, Barel et al. 1985, Ogutu-Ohwayo 1992). In some, like Lake Malawi, there is an additional problem of the translocation of highly localized endemics from one part of the lake to another (Ribbink et al. 1983). The most disastrous and best documented of these introductions is the Nile Perch introduction into Lake Victoria. The Nile Perch (Lates niloticus) is a large predatory centropomid fish which occurs naturally throughout much of northeastern and central Africa and was introduced into Lake Victoria during the 1950s and 1960s (Ogutu-Ohwayo 1992, Lowe-McConnell 1993). Perch populations increased dramatically during the 1980s, resulting in the extinction of an estimated 200 species of haplochromine cichlid fish (Goldschmidt et al. 1993, Witte et al. 1992, Kaufman and Ochumba 1993).

Nutrient loading in several of the ancient lakes has resulted in serious eutrophication problems, particularly at lakes Biwa and Victoria, and has threatened several species of endemic molluscs (Negoro 1981, Anonymous 1984, Maeda et al. 1992). Progressive eutrophication at Lake Victoria apparently began in the 1920s, as evidence by paleolimnological data on changes in fossil diatom floras and nutrient flux to the sediment (Hecky 1993). By the 1980s, excess nutrient loading had led to lakewide ecosystem restructuring (Ochumba and Kibaraa 1989, Hecky 1993). Oxygenation of bottom waters of the lake had ceased by the mid 1980s, and anoxia now occurs regularly at depths as shallow as 10 m, resulting in widespread dieoffs of fish and invertebrates (Kaufman 1992). Because this process was occurring simultaneously with the Nile Perch expansion, it is extremely difficult to retrospectively disentangle these two events, and in any case their effects are probably synergistic.

Deleterious effects of siltation (both in sus-
pension and after settling) have been demonstrated in numerous aquatic habitats (Aldridge et al. 1987, Kirk 1991, Somer and Hassler 1992), notably in North American rivers and streams, where the problem has contributed to the endangerment and extinction of numerous endemic mollusc species (Cooper 1984, Schmidt et al. 1989, Taylor 1989). At Lake Tanganyika, this problem is now serious in the northern region of the lake (Cohen et al. 1993b, Cohen et al., in press) where a rapid reduction of forest and woodland cover has resulted from local demands for fuel wood for making charcoal. The subsequent conversion of these areas to pasture and agricultural lands, particularly on steep slopes, has resulted in the release of massive quantities of silt into the lake in areas that would not normally receive such sediment pollution.

**Ostracodes in Lake Tanganyika**

Starting in 1991, my research group began to systematically collect data on comparative diversity levels in Lake Tanganyika offshore from heavily disturbed, moderately disturbed, and lightly disturbed or undisturbed areas to determine if a relationship exists between levels of watershed disturbance and the structure of the lake's biota, particularly in benthic and epibenthic environments. Our data base consists of information on four groups of organisms: ostracodes, molluscs, fish, and diatoms. Of these, our most extensive data set comes from the ostracodes, which we have now collected and counted both from dredge hauls and using SCUBA from over 100 sites around the lake. In Lake Tanganyika, ostracodes are represented by an extraordinarily diverse and morphologically derived fauna, representing at least seven monophyletic species flocks, and perhaps 200 endemic species.

In our initial analysis of ostracode species richness data, we broke the data sets down into four categories, hard vs. soft substrate and shallow water vs. deep water sites (Cohen et al., 1993b). Total species richness is significantly lower ($p < 0.05$) at higher disturbance sites than at less silted sites in both shallow water categories (for deep water sites the trends are similar, but the sample sizes are too small to be statistically significant). The strong differences between shallow (but not deep) water sites are consistent with the idea that siltation disturbance is more severe closer to the outfall of the sediment into the lake. This might be the result of such factors as nearshore hard-substrate inundation, loss of nearshore habitat heterogeneity, or reductions in ostracode food resources (algae and macrophytes).

Ostracode species richness patterns around the lake reveal a striking relationship with patterns of deforestation (inferred from aerial photo and satellite image data) for areas where we have both types of data (Cohen et al. 1993b). Other areas of low diversity occur around major river outlets, notably the Malagarasi River, which again are certainly areas of high sediment input, although we have no image data on deforestation here.

In 1991 and 1992, we collected diversity data on molluscs, ostracodes, and epibenthic fish using SCUBA divers (for all groups) and a Remotely Operated Vehicle (ROV, for fish only) tethered to the surface and operated by a pilot at the surface using the ROV's video camera. Our data sets on molluscs and fish from representative high, moderate, and low disturbance sites showed similar trends to the ostracodes, with lower species richness at highly disturbed sites. In deeper water, however, this pattern breaks down, with fewer species recorded at our moderately disturbed site than at the highly disturbed site, although at all depths the undisturbed site is substantially more diverse. Among fish taxa, herbivores represent a somewhat larger proportion of taxa at the low and moderate disturbance sites than at the highly disturbed site. This pattern might result from any number of scenarios, such as a linkage between sediment inundation and the elimination of appropriate substrates for benthic algae, or alternatively a reduction in light intensity at the high disturbance sites.

**The need for long-term and paleoecological data on anthropogenic impacts**

Many studies of how human activity affects the biota of the ancient lakes are hampered by a lack of baseline information on ecosystem variability and species diversity before the advent of large-scale alteration of these lakes and their watersheds. We do not know, for example, whether the diversity differences we are observing in Lake Tanganyika are actually the result
of changes in sediment input in deforested areas, or merely reflections of species richness patterns which existed before deforestation. To address this problem we need some kind of long-term historical data on both timing of deforestation and the history of diversity fluctuations to see if, in fact, there has been some historical linkage between the two. Unfortunately, historical, limnological, and biological records, either anecdotal or from systematic studies, are of insufficient duration to resolve either this question or many proposed impact/response issues in other lakes.

One approach to this problem is through the collection of paleoecological and sedimentological data from short cores. This approach has proven invaluable in reconstructing the history of human impacts and limnologic response in a variety of settings, primarily in European and North American lakes (e.g., Whitehead et al. 1990, Schelske 1991, Anderson 1993), but also in some of the species-rich lakes of Africa (e.g., Hecky 1993). At Lake Tanganyika, my research group and colleagues have begun to look at ostracode fossils, pollen, and sediments from cores collected offshore from deforested areas of the watershed as well as in relatively undisturbed areas in Tanzania in the southern part of the lake.

A preliminary analysis of two cores indicates significant differences between the patterns of ostracode and sediment accumulation between a disturbed and an undisturbed site (Figs. 2–4). The cores have not yet been directly dated or analyzed for pollen. However, assuming sediment accumulation rates typical for these environments elsewhere in the lake (3–5 mm/y, Tiercelin and Mondeguez 1991), they probably represent a record of the past 200–300 y. At the disturbed site, 86–DG–14, in central Burundi, there is a record of sedimentation dominated by coarse plant debris in the lower part of the core, replaced by increasing quantities of fine clays (Fig. 3A). This change would be consistent with a pattern of decreasing forest cover and increasing soil denudation over time, and is not evident in the undisturbed site core (86–DG–32, located near the Kipili Islands in southern Tanzania, Fig. 4A). The disturbed site, 86–DG–14, also shows an abrupt decrease in species richness and increase in ostracode abundance per gram of sediment at the top of the core (Fig. 3A). This change is not apparent in the undisturbed core 86–DG–32, where no apparent trend exists in sedimentology, species richness, or ostracode abundance (Fig. 4A). The species that disappear in the uppermost sample of 86–DG–14 are uniformly rare taxa, that is species that occur in proportions averaging less than one percent per sample. No such change is evident in the uppermost sample from the undisturbed site.

An analysis of variance of normally distributed diversity-level data between core sites below the uppermost two samples, where core data indicate a possible anthropogenic signal, reveals that there is a significant and strong difference in species richness between sites at the \( p < 0.001 \) level. Thus, our preliminary data suggest that species diversity was higher at the southern site than at the northern site before the past 100 y or so, but that this difference was exaggerated in recent times. It also suggests that productivity may have increased at the northern site, given the increased density of life assemblage ostracode fossils/g sediment up-core,
Fig. 3. A.—Stratigraphy for a short core—86-DG-14—taken from Lake Tanganyika at a site along the central Burundi coast (see Fig. 2) adjacent to a recently deforested watershed. Dominantly coarse-grained plant debris, which is present in the lower portion of this core, gives way up-core to progressively finer-grained sediments, which are mostly terrigenous clays and other clastic sediments. This change may reflect a transition from the erosion of forest litter to deeper soil erosion. It is accompanied by a change in the fossil ostracode abundance and (at the core top) a drop in diversity. The increase in ostracode density indicates either a major increase in secondary ostracode productivity, or a major decrease in sediment accumulation rates. The diversity decline comprises almost entirely species that were previously rare at the core site (and which are also rare in the lake today). B.—Fossil ostracode profile for the same core.
Fig. 4. A.—Stratigraphy for core 86–DG–32, which was taken near Kipili, Tanzania, in the southern part of Lake Tanganyika, offshore from an undisturbed watershed. Grain size varies erratically through this core, although compositionally the core comprises a mixture of clastic and lime muds and sands throughout. Note the absence of a core-top change in ostracode abundance or systematic change in diversity at this site in contrast to 86–DG–14 (Fig. 3A). B.—Fossil ostracode profile for the same core. Note the erratic and uncorrelated nature.
coupled with probable increasing sediment accumulation rates.

We are currently $^{210}$Pb dating several cores to determine precise sediment flux rates, and are also analyzing them for pollen content, to detect the actual timing of appearance of plant species that are agricultural and disturbance indicators. These analyses should clarify the historical sequence of correlated limnologic and watershed changes in disturbed areas of the lake.

Another interesting pattern which emerges from our core data is the extremely erratic pattern of proportional representation and absolute abundances exhibited through time for both common and rare endemic taxa (Figs. 3B, 4B). Many species, common and rare; repeatedly appear and disappear from the fossil record at the site. A paleoecologist looking at such data is tempted to speculate that major changes in environmental conditions must be responsible for these fluctuations through time, and to look for correlated process–response patterns between the ostracode abundances and some independent paleoenvironmental variable.

Four lines of evidence argue against any lake-wide explanation for these patterns. First, independent evidence from Late Holocene stromatolites demonstrates that lake level changes during the past 1000 y have been limited to $\pm$20 m from modern (a modest range in a lake $\sim$1500 m deep). Second, water residence times appear to have remained relatively constant during this same interval, as inferred from $^{18}$O data from the same stromatolites. The consistency between isotopic data from widely separated stromatolites of the same age, as well as the fact that no springs or seepages were observed near the collection sites, demonstrates that our isotope data are recording lake water rather than localized groundwater discharge. Third, the appearances and disappearances of specific taxa in the fossil records at both sites seem to be uncorrelated or random within cores. Finally, and perhaps most surprisingly, although the population sizes of individual species seem to rise and crash repeatedly at both core sites, the total number of taxa present remains remarkably constant.

Population structure of endemic benthic animals in Lake Tanganyika

The erratic distribution pattern of both common and rare endemics through time is also reflected in space in modern distribution patterns (Fig. 5). For both common and rare taxa there is a general absence of the well-defined depth zonation common to many benthic crustaceans in lakes. The same taxa may occur commonly in the littoral zone or at profundal depths, and then might be absent at the same depths at adjacent sites. Only a few of the over 100 ostracode taxa for which we have depth and habitat distribution data show any kind of apparent environmental specificity. The only predictable environmental contrasts that we observe between the many species of Lake Tanganyika ostracodes are the extremely broad distinctions between herbivorous species being largely restricted to the littoral zone, soft mud dwelling species limited to deep water, and rock dwelling species, which are limited to hard substrates.

When we look at the same four common taxa along a latitudinal transect on the same substrate type and all at sublittoral depths, this erratic distribution pattern becomes even clearer (Fig. 6). Apparently the distribution of these endemic species is extremely patchy in both space and time; populations appear and disappear from appropriate habitats in a temporally uncorrelated fashion, and are distributed spatially at present in an unpredictable fashion.

Another interesting feature about the distribution of these endemic ostracode taxa is that a very large number of species have been recovered at only one or a very small number of localities. Over twenty taxa, or about 15%, have only been recovered along a stretch of coastline 100 km long or less.

The patchy distribution data in time and space are consistent with the concept that the Lake Tanganyika ostracode species are orga-

of species occurrences, increases, and local extinctions here and at the site in Fig. 3B over the core history for several common taxa. The lack of similar patterns between taxa or sites argues that the fluctuations in abundance and local extinctions are probably not driven by lakewide events.
Fig. 5. Depth distribution patterns for several common (A) and rare (B) endemic ostracode taxa in Lake Tanganyika. These benthic species show little sensitivity to water depth or substrate, a pattern which is typical for most of the Tanganyikan ostracode endemics documented to date. Most Tanganyikan ostracode species occupy broad ranges of shallow littoral–profundal habitats, and display very patchy distributions, being absent in locations immediately adjacent to similar sites where they are abundant. The maximum depth range for all species (~100 m in the north basin) is determined by the depth of the oxicline.

nized as metapopulations (sensu Levins 1969), clusters of populations that are linked by limited genetic interchange through sporadic dispersal events. In metapopulations, the individual (local) populations normally undergo large fluctuations in population size and frequent patch extinctions. However, the entire metapopulation is buffered against local population fluctuations because of its makeup as a series of small patches, capable of providing founders for
recolonizing empty patches or invigorating declining ones.

In Lake Tanganyika, benthic animal species populations are limited largely to a one-dimensional intercommunication with adjacent populations along the shoreline (similar to the "stepping-stone" metapopulation model of Ray et al. 1991), because of the combined effects of steep underwater slope and the maximum depth of oxygenation, which is at about 100 m in the north basin and 200–250 m in the south basin (Fig. 2). Also, the tectonic (fault-bounded) origin of many of the species-rich ancient lakes, including Tanganyika, generates alternating soft and hard substrate within the littoral zone and provides a favorable setting for the formation of metapopulations. Strong dispersal capabilities may be selected against in ancient lake environments, because the probability of a propagule arriving at an appropriate new habitat patch is low (Olivieri et al. 1990). In this case, a metapopulation structure would stabilize the overall abundance of a species whose individual populations fluctuate wildly as a result of local environmental changes.

Correlated extinctions over board areas, such as might result from regional sediment inundation of a long stretch of rocky coastline could have disastrous effects for a species with the type of bathtub-ring distribution pattern that I am describing here. The fact that habitat patches around this lake margin can be recolonized principally by their two lateral neighbors makes the entire structure more vulnerable to extinction, because habitat destruction in one patch results in a break in the interconnectedness of the entire metapopulation. Under such conditions, it may be extremely difficult for species to recolonize appropriate but isolated habitat patches (Brown and Kodric-Brown 1977). A similar situation has been documented in the isolation of localized populations of the endemic lotic mollusc Tulotoma magnifica in the Coosa–Alabama River system (Herschler et al. 1990). Here, both siltation and river impoundment have resulted in habitat fragmentation, severely reducing or eliminating the potential for patch recolonization. Modelling patch interaction in lotic and lentic environments is also complicated by the great variability in size and physical structure.
of patches in most natural environments (Fahrig and Merriam 1994).

The possible existence of metapopulations among many benthic organisms in Lake Tanganyika has important implications for species coexistence and diversity maintenance. There is a general pattern in several of the ancient lakes, among not only ostracodes but also fish and molluscs, of broad sympatry of species that have very similar requirements for food and spatial resources (McKay and Marsh 1983, Hori et al. 1993, Michel 1994). A continuous state of flux in population sizes (a key component of a metapopulation structure), with some species just showing up at a patch, some others peaking, and yet others on the wane, might be the norm, and could be a key element in maintaining the extraordinary within-patch alpha diversity that we observe in the species-rich ancient lakes (Hanski 1983, Cohen 1994). Ancient lake endemics have become textbook examples of adaptive story-telling revolving around niche partitioning, in the cause of explaining the phenomenon of extraordinarily high within-habitat species diversity in some environments (e.g., Futuyma 1986). Although ecological differentiation almost certainly has played a role in these radiations, its primacy is open to question (e.g., McElroy et al., 1991). Endemic littoral species in Lake Tanganyika do show broad adaptations for existence in a wave-swept large-lake environment, and rarity of cosmopolitan African invertebrates and fish in the lake is probably a result of their inability to survive under these near-oceanic conditions. However, among the Lake Tanganyikan endemics that are sympatric within a given area, discrete adaptations for food or habitat types are much more difficult to discern.

A metapopulation model of wildly fluctuating but interconnected local population densities might help to explain how diversity is maintained in these lakes. Conversely, the elimination of intervening patches caused by broad habitat deterioration may lead to a cascading sequence of extinctions, both directly, through the loss of recolonization, and indirectly, by eliminating the very population structure that originally allowed the high alpha diversity among competitors to exist (Cohen 1994).

A metapopulation model for many ancient lake endemic taxa with highly localized distributions also forces us to reevaluate our notions about their conservation biology. Figure 7 illustrates the occurrence pattern of ostracode taxa with ranges smaller than 100 km of shoreline, broken into 100-km segments for the area where we have good data. Many of these taxa in fact are known from only a single locality. Some areas, particularly the northern part of the lake, seem to have disproportionate number of such local endemics. This northern concentration of local endemics is particularly noteworthy considering the fact that this same region faces the most serious environmental threats and, along

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**Fig. 7.** Regional endemism in ostracodes of Lake Tanganyika. Local endemics (defined as having a coastline range of <100 km) appear to be more numerous in the north, which is the region of the lake most affected by human activities. This pattern contrasts with fish and molluscs, both of which have relatively few local endemics restricted to the far northern end of the lake. Furthermore, fish are represented by numerous local endemics at the south end of the lake. Some of the endemic ostracode taxa are known as fossils form locations that are far from their current distribution. Therefore, it is uncertain to what extent the pattern of endemism observed today results from the evolution of the taxa in situ and their subsequent long-term range restriction to these areas, or whether their present ranges are merely a short-term biogeographic pattern which has varied dynamically through time.
at least the northeastern coast, displays lower local diversity than elsewhere. Total diversity and diversity of endemics are not marching in step here.

Conventional wisdom in conservation biology would be to consider these northern areas as hotspots of endemic diversity, worthy of special consideration in conservation planning. However, suppose that these patterns of endemism are actually much more dynamically changing over time than a simple present-day map would indicate, with outlier patches periodically recolonized or the current range abandoned? Can we be certain that patches that are adjacent to or within the current range of the taxon have not played an important role in the distributional history of this organism? Clearly not, but designing reserves requires that we come to grips with this problem. How we ultimately set up reserves for the ancient lake endemics and how much currently unoccupied area we incorporate into that reserve should depend on how lastingly or ephemeral the occupation of the local habitat patches really is.

We might get at this question through the initiation of long-term ecological monitoring studies, lasting many years. However, conservation biology is usually and unfortunately a crisis science, and the ancient lakes are no exception. At the present time, a Global Environmental Facility project for Lake Tanganyika is in its early phases and, as a part of this project, a series of reserves are going to be established in the lake over the next 5–10 y, along with a more general program of lake basin management. Conservation biologists at Lake Tanganyika will need to generate dynamic biodiversity assessments that incorporate the elements of time and change in evaluating habitat patches, but we will need this information quickly, much faster than a long-term monitoring study might allow. In fact, this concern extends beyond the ancient lakes, since there is good evidence that extreme patchiness and metapopulations can become established in other types of threatened lake systems, including small lakes (Fryer 1995).

One approach to this problem might be through the use of paleoecological data from radiometrically dated short cores, taken in and around proposed reserve areas. For organisms that leave an identifiable fossil record (including many benthic invertebrates), we may be able to determine the continuity or ephemerality of current local endemics in a given habitat patch. Conversely, we might be able to determine whether appropriate habitat patches that are currently unoccupied by these endemics have played a role in their distributional history in the past.

This integrated neontological–paleontological approach to the conservation biology of ancient lakes is clearly not applicable in all situations, as it is dependent on the vagaries of fossil preservability and sediment accumulation. Conversely, there are many young lakes throughout the world where paleobiological data could be used to solve problems in conservation biology. Numerous studies have demonstrated siltation impacts on both benthos and fish in North American and European lakes (Bass 1992, Smith et al. 1993). In some circumstances, paleobiological data also may be useful in lotic settings, associated with floodplain or shell midden deposits (e.g., Parmalee and Hughes 1993). This approach might provide significant new insights into the distributional history of the numerous endangered and endemic North American molluscs. Regardless of whether or not fossils are available, it is important that conservation biologists working on aquatic ecosystems take a much more dynamic view of how populations are organized in time as well as space when making management recommendations. This evidently requires substantial input from genetics and population biology, but paleobiology and sedimentology have important roles to play here too, because they can provide a deeper historical perspective to environmental change and biological response than is available from experimental or monitoring approaches alone.

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Literature Cited

ALDRIDGE, D. W., B. S. PAYNE, AND A. C. MILLER. 1987. The effect of intermittent exposure to sus-


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James H. Brown; Astrid Kodric-Brown
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