



## The impact of taphonomic processes on interpreting paleoecologic changes in large lake ecosystems: ostracodes in Lakes Tanganyika and Malawi

Lisa E. Park<sup>1\*</sup>, Andrew S. Cohen<sup>2</sup>, Koen Martens<sup>3</sup> and Rebecca Bralek<sup>1</sup>

<sup>1</sup>*Department of Geology, University of Akron, Akron, Ohio 44325-4101, USA;* <sup>2</sup>*Department of Geosciences, University of Arizona, Tucson, Arizona 85721, USA;* <sup>3</sup>*Royal Belgian Institute of Natural Sciences, Brussels B-1000, Belgium;* \**Author for correspondence (e-mail: lepark@uakron.edu)*

Received 17 December 2001; accepted 11 December 2002

*Key words:* Taphonomy, Ostracoda, Lake Tanganyika, Lake Malawi, Time averaging

### Abstract

Nonmarine ostracodes are often used as proxy indicators for the biotic response to climate as well as anthropogenic changes in large lakes. Their large numbers, small size and sensitivities to environmental conditions make them ideal for assessing how organisms respond to environmental perturbations. However, little is known about the various taphonomic processes related to preserving these organisms in the lacustrine fossil record. Without understanding the amount of time averaging associated with these assemblages, any interpretation of their biodiversity and paleoecology may be problematic.

To address these issues, we conducted actualistic experiments to determine transport, time-averaging, and the amount of taphonomic bias in ostracode sub-fossil assemblages. Sand transport experiments revealed significant mixing at all sites at shallower depths and significant mixing on rocky substrates but not sandy ones. Comparisons with ostracode material collected along the experimental transects support this model and demonstrate time averaging in both the sandy and rocky substrates. Preservation models were derived from the experimental data and applied to interpreting the paleobiologic record of ostracodes from piston cores in both Lake Tanganyika and Malawi. The core record reveals assemblages that have undergone significant time-averaging, and in the case of Lake Malawi, preservational degradation. In the core examined from Tanganyika, most assemblages resemble the time-averaged experimental model with respect to species richness, percentage of articulated shells and heavy bias towards adult dead individuals. In the Malawi cores, most of the valves were preserved only as internal molds. The taphonomic signature of these samples resemble the time-averaged assemblages of Tanganyika cores, even though carapaces are not often present.

Both the experimental and live/dead valve data suggest significant time-averaging and transport, smearing seasonal-yearly data in some environments involved in using ostracodes to assess biotic changes as a result of climate and or anthropogenically-induced environmental change. Ostracode species richness estimates were impacted by time averaging because transport of dead valve material occurs at high percentages in the shallow depths and on the rocky substrates, suggesting that the ostracode death assemblages in these areas will not reflect living populations. In addition, ecologic models based only upon death assemblages will be less resolved than those based upon live assemblages. A time averaging index was derived using the % dead juveniles ratio, as well as sedimentation rate and information on the population dynamics, if known.

---

\*This is the second in a series of four papers published in this issue collected from the 2000 GSA Technical Session 'Lake basins as archives of continental tectonics and paleoclimate' in Reno, Nevada. This collection is dedicated to Dr. Kerry R. Kelts; Drs. Elizabeth Gierlowski-Kordesich and H. Paul Buchheim were the guest editors of this collection.



## The impact of taphonomic processes on interpreting paleoecologic changes in large lake ecosystems: ostracodes in Lakes Tanganyika and Malawi

Lisa E. Park<sup>1\*</sup>, Andrew S. Cohen<sup>2</sup>, Koen Martens<sup>3</sup> and Rebecca Bralek<sup>1</sup>

<sup>1</sup>*Department of Geology, University of Akron, Akron, Ohio 44325-4101, USA;* <sup>2</sup>*Department of Geosciences, University of Arizona, Tucson, Arizona 85721, USA;* <sup>3</sup>*Royal Belgian Institute of Natural Sciences, Brussels B-1000, Belgium;* \**Author for correspondence (e-mail: lepark@uakron.edu)*

Received 17 December 2001; accepted 11 December 2002

*Key words:* Taphonomy, Ostracoda, Lake Tanganyika, Lake Malawi, Time averaging

### Abstract

Nonmarine ostracodes are often used as proxy indicators for the biotic response to climate as well as anthropogenic changes in large lakes. Their large numbers, small size and sensitivities to environmental conditions make them ideal for assessing how organisms respond to environmental perturbations. However, little is known about the various taphonomic processes related to preserving these organisms in the lacustrine fossil record. Without understanding the amount of time averaging associated with these assemblages, any interpretation of their biodiversity and paleoecology may be problematic.

To address these issues, we conducted actualistic experiments to determine transport, time-averaging, and the amount of taphonomic bias in ostracode sub-fossil assemblages. Sand transport experiments revealed significant mixing at all sites at shallower depths and significant mixing on rocky substrates but not sandy ones. Comparisons with ostracode material collected along the experimental transects support this model and demonstrate time averaging in both the sandy and rocky substrates. Preservation models were derived from the experimental data and applied to interpreting the paleobiologic record of ostracodes from piston cores in both Lake Tanganyika and Malawi. The core record reveals assemblages that have undergone significant time-averaging, and in the case of Lake Malawi, preservational degradation. In the core examined from Tanganyika, most assemblages resemble the time-averaged experimental model with respect to species richness, percentage of articulated shells and heavy bias towards adult dead individuals. In the Malawi cores, most of the valves were preserved only as internal molds. The taphonomic signature of these samples resemble the time-averaged assemblages of Tanganyika cores, even though carapaces are not often present.

Both the experimental and live/dead valve data suggest significant time-averaging and transport, smearing seasonal-yearly data in some environments involved in using ostracodes to assess biotic changes as a result of climate and or anthropogenically-induced environmental change. Ostracode species richness estimates were impacted by time averaging because transport of dead valve material occurs at high percentages in the shallow depths and on the rocky substrates, suggesting that the ostracode death assemblages in these areas will not reflect living populations. In addition, ecologic models based only upon death assemblages will be less resolved than those based upon live assemblages. A time averaging index was derived using the % dead juveniles ratio, as well as sedimentation rate and information on the population dynamics, if known.

---

\*This is the second in a series of four papers published in this issue collected from the 2000 GSA Technical Session 'Lake basins as archives of continental tectonics and paleoclimate' in Reno, Nevada. This collection is dedicated to Dr. Kerry R. Kelts; Drs. Elizabeth Gierlowski-Kordesich and H. Paul Buchheim were the guest editors of this collection.

## Introduction

Time averaging and transport has long been recognized as a significant problem in the paleobiologic record, particularly when trying to reconstruct paleoecologic associations from densely fossiliferous horizons (Kidwell et al., 1986). Since fossil concentrations are primarily composed of hard parts affected by post-mortem processes, almost all fossil deposits experience some type of time averaging, even those considered to be within the sub-fossil range. In the paleolimnologic record, where temporal resolution from high sedimentation rates can be yearly and even seasonal, time averaging, even in the most recent of deposits, can still be problematic, particularly when addressing questions related to paleoclimatic signals, biodiversity changes, and paleoecologic changes through time (Anderson, 1990; Larsen and MacDonald, 1993; Verschuren, 1999) (Figure 1). Even with highly resolved lake beds, there is still the problem of stratigraphic incompleteness, due to both low spatial resolution and lateral transport of species and age-classes, making what might appear in a core as a seasonal or yearly deposit much coarser. There is no previous study that addresses either transport or mixing in the limnologic record for ostracodes.

Common problems expected from time-averaging include the over-estimation of species richness, exclusion of rare species, and/or mixing of temporally ecologically-incompatible assemblages (Fursich, 1990). For example, if species richness was estimated within a core sequence that has undergone a dramatic change in sedimentation due to climate or land use change, it is often assumed that the species richness before and after this change have the same amount of time averaging. However, if the amount of time averaging shifts in response to the sedimentation regime, then this assumption is not valid. Thus, the completeness of fossil and sub-fossil assemblages and their utility for paleoecologic analysis in lake systems may depend upon the degree of time averaging as it relates to frequency and type of environmental regime.

### Sedimentation patterns and the paleobiologic record of large lakes

Large lakes, particularly in the East African Rift System (EAR) are deep, geologically long-lived (millions of years old), and tectonic in origin. Most have incredibly diverse faunas and act as important archives for paleoclimatic information within the last 250 ka. The

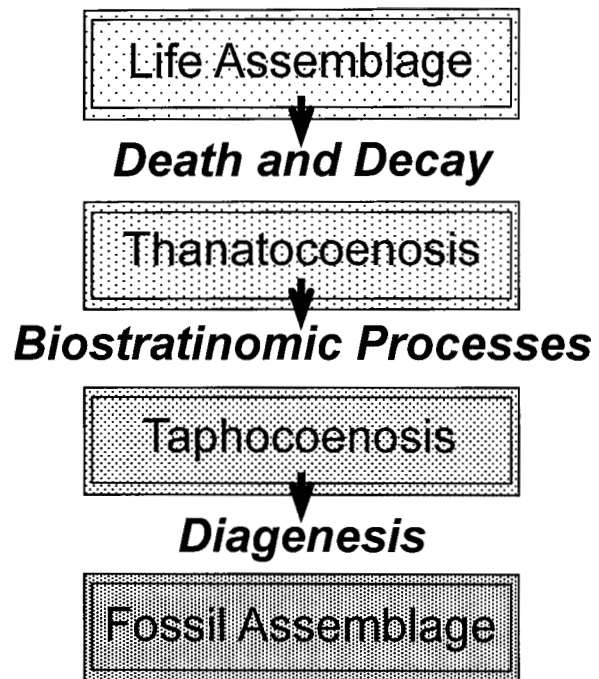


Figure 1. Flow chart describing the fossilization process from life to death assemblage. Terms from Fursich (1990).

short- and long-term paleobiologic records in these lakes are characterized by abundant diatom and pollen records, as well as ostracode, mollusk, and fish elements. These latter elements are more commonly found in shorter cores or those recovered from above 200 m water depth (Wells et al., 1999). Sampling of both long and short cores is often in 1 cm thick intervals collected every 5–10 cm, and is estimated to capture a signal with decadal to thousand year resolution for Tanganyikan cores. This high resolution record makes these lakes excellent choices for doing long-term paleoclimatic and paleoecologic studies.

### Lakes Tanganyika and Malawi

Lake Tanganyika is the oldest (9–12 Ma) and deepest lake (maximum depth 1470 m) in Africa and is well-known for its endemic species-rich faunas, especially the economically important cichlid fish. Over 185 cichlid fish species (180 of which are endemic), 68 gastropod species (45 of which are endemic) and 80 ostracode species (almost all of which are endemic) have been described from Tanganyika, with perhaps 80 or more new species yet to be described. Because of their large numbers and sensitivities to environmental

conditions, ostracodes have been used to assess the impacts of anthropogenic activities such as pollution, pesticides, and sediment influx on the overall biodiversity of the lake (Cohen, 1994, 1995). Previous studies have found a significant decrease in species richness in areas highly impacted by increased sedimentation from deforestation in the surrounding watershed (Cohen et al., 1993). Designated areas of underwater conservation will soon be proposed based on ecologic surveys of ostracode species distribution and changes in species richness through time. These

surveys are primarily based upon dead valve data collected using SCUBA, ponar, and grab samplers.

Tanganyika is long (~650 km) and narrow (~80 km max. width) and divided into eight tectonically-formed sub-basins (three bathymetric basins) (Haberyan and Hecky, 1987; Scholz and Rosendahl, 1988; Tiercelin and Mondeguer, 1991) (Figure 2A). The tectonic activity that produced these basins is also responsible for the patchy distributions of rock and sand substrates that alternate along the shore, providing a wide variety of habitats and potential for niche subdivision. The sub-

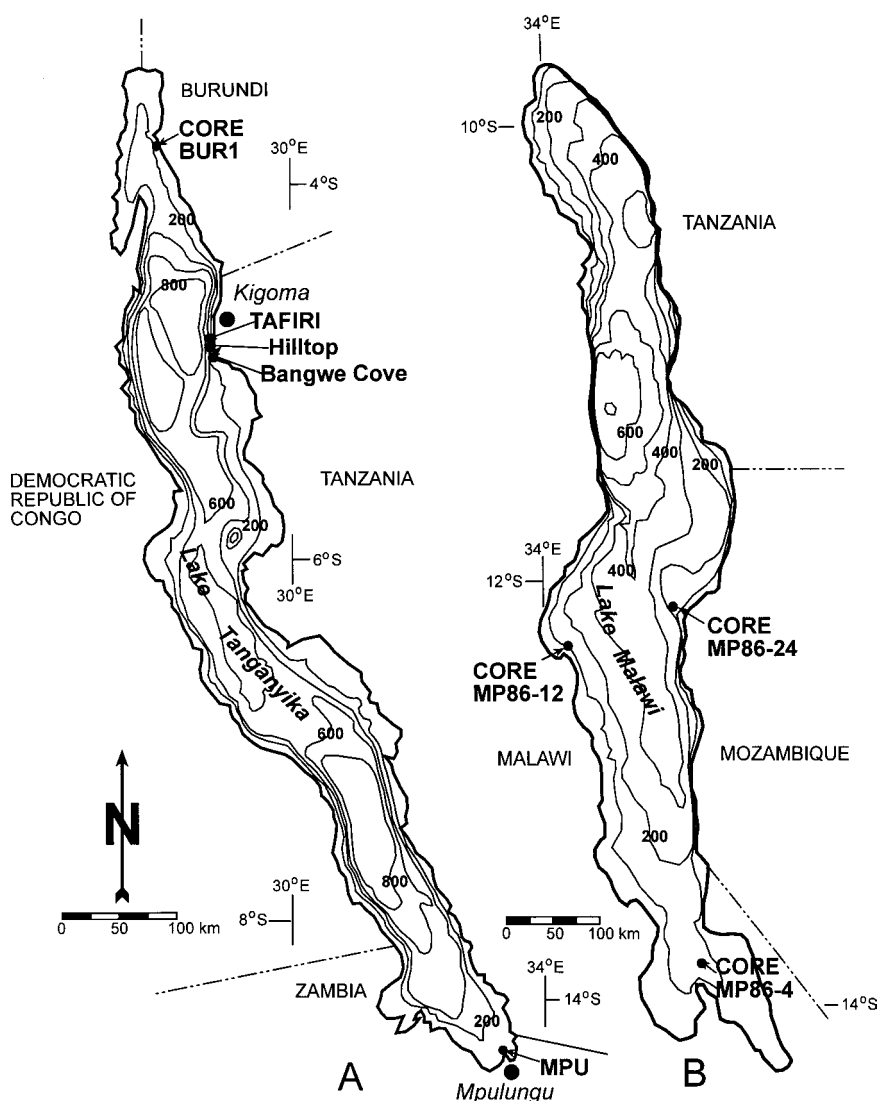


Figure 2. (A) Location map of Lakes Tanganyika and (B) Malawi within the East African Rift System. Note core locations (BUR1, MP86-4, MP86-12 and MP86-24) and experimental site locations (TAFIRI, Hilltop, Bangwe Cove and MPU) are indicated on each bathymetric map. The towns of Kigoma, Tanzania and Mpulungu, Zambia are also noted. Contour interval is 200 m for Lake Tanganyika and 100 m for Lake Malawi.

strates vary in character from mud, silt, sand, shell lags, stromatolites, and rocks. The geologic history and resultant sedimentation patterns may be important to ostracode speciation because distribution patterns of species vary according to substrate and depth and often have corresponding morphologic innovations.

Lake Malawi is also an ancient lake that is over 700 m deep and over 6 Ma years old (Scholz and Rosendahl, 1988). It is separated into several basins (Figure 2B). The sediments in the north basin are almost continuously varved with alternating bands of diatom ooze and silty clays. Sediments in the south basin are generally laminated but homogeneous in grain size and composition due to the long transport distance from the major river inputs to the north. Lithologic changes occur and are recorded in response to lake level fluctuations by changing base level, sediment supply, catchment area conditions, and biotic boundary conditions (Scholz and Rosendahl, 1988; Scholz et al., 1990).

Despite its long history and similarity in morphology and formation to Tanganyika, Lake Malawi has a dramatically different biodiversity pattern. Approximately 1000 fish species are estimated to have evolved in Malawi, in spite of having a rather modest degree of molecular genetic and morphologic change (Kornfield, 1978; Moran et al., 1994; Parker and Kornfield, 1997). Given this tremendous diversity, it is even more remarkable that the living prosobranch gastropod and endemic ostracode faunas have undergone only a limited amount of speciation (Martens, 1994; Michel, 1994). Understanding the biotic history of this lake, particularly from cores recovered from deep drilling, will provide critical insights into this enigmatic pattern.

### Ostracodes

Ostracodes are small, bivalved crustaceans, and like pollen, diatoms and chironomids, are often used as proxy indicators for biodiversity and conservation assessments in large lakes. Because of their small size, primarily benthic lifestyle, and niche specificity, they make excellent indicators for the littoral biotic response to changes in the physical and chemical conditions to a lake due to sedimentation regime, and/or lake level fluctuations. Ostracode faunas are found throughout the oxygenated littoral zone of these lakes. In Tanganyika, it varies from 100–250 m and in Malawi it averages at

230 m depth. However, most species occur between 0–20 water depth. Detailed analyses of the Tanganyika fauna have indicated that most species are patchily distributed in metapopulations along the lake margin. Therefore, most species can be found throughout the lake, and in all sub-basins (Park et al., 2000).

### Purpose of study

The purpose of our study was to create a model for time-averaging of ostracode assemblages in large, long-lived lakes and apply it to cores from Lakes Tanganyika and Malawi. This is of particular significance because ostracodes are often used as proxy indicators for biodiversity assessments as well as paleoecologic indicators of community dynamics. In order to determine the amount and significance of time averaging due to transport, we first determined if there was significant transport at specific depths and in specific substrates using recovery experiments as well as surface collections of live and dead ostracodes. We used this data to determine if ostracodes are transported out of their life habitats and if their death assemblages accurately reflect life assemblages. By using the absolute estimates derived from this data, we developed a model for estimating the amount of time averaging in an assemblage and how it will impact the biodiversity and paleoecologic estimates in large lakes.

Specifically, we wished to address the following questions: (1) are ostracodes transported along a bathymetric gradient and if so, what is the time span and depth in which significant transport occurs? (2) is there a difference in the amount of out of habitat transport between sandy substrates (shallow shoaling margins) and rocky substrates (steep escarpment margins)? (3) do ostracode assemblages bear distinctive taphonomic features that can be used to recognize the amount of temporal resolution in each deposit? (4) where do the deposits from Lake Tanganyika and Malawi cores fall in such a scheme? (5) what sorts of paleoecologic signals can be resolved from long term (down core) records? (6) does the average surface sample of dead valves collected in the lake have significant time averaging? and (7) how does this affect the temporal resolution of the ostracode assemblage? or (8) do the high sedimentation rates in these settings ameliorate the impact on the resolution of the core record?

## Materials and methods

### *Experimental data*

Rate of loss and transport experiments were conducted in Lake Tanganyika (summer, 1998), using brightly colored sand, approximately the same size (600  $\mu\text{m}$ ) and weight (0.1 mg) as adult ostracodes. We deposited equal quantities of sand (~500 g) along bathymetric transects at 2.5, 6, and 10 m, for a total of four transects; two along sandy substrates and two along rocky substrates near Kigoma, Tanzania and Mpulungu, Zambia (Figure 2A). For the rocky substrates, the colored sand was left at each site for 4 days and then recollected using a vacuum pump. Since the experimental sand was so brightly colored, it could easily be identified and recaptured.

On the sandy substrates, measured quantities were put in small, flat, open-mouthed containers, 1.5 cm high and with their tops level with the natural sand substrate. They were recovered and placed in plastic bags before bringing to the lake surface to ensure no loss of sample in the collection process. In all cases, the sand was dried and weighed after recollection. Both the rocky and sandy substrates were replicated near Kigoma, Tanzania (e.g., TAFIRI-Tanganyika Research Station, near Kigoma, Hilltop and Bangwe Cove) and Mpulungu, Zambia.

### *Live/dead*

In addition to the colored sand experiments, sixty-three surface samples were collected from rocky and sandy substrates at the same depth along the same bathymetric transects at 4 sites, including TAFIRI, Hilltop, Bangwe Cove, and Mpulungu, Zambia. The samples were processed using the freeze-thaw method (*sensu* Forester, 1986), wet sieved using 63 and 125  $\mu\text{m}$  mesh, and picked for all ostracodes (live and dead). Special care was taken to include all juveniles (ostracodes have eight instar molts), which are typically found on the 63  $\mu\text{m}$  mesh in the 63–125  $\mu\text{m}$  sieved fraction, yielding an average of at least 300 ostracodes/sample.

### *Collection of live and dead Gomphocythere samples*

Tanganyika dead specimens used in our analyses were pooled from a subset of over 350 samples collected on many separate expeditions on the lake, including the Belgian Hydrobiological expedition of 1946–47, and

the expeditions of Cohen in 1986 and 1989, Martens in 1990, Cohen et al. in 1992, and Martens in 1992. Live specimens from the 1990, 1991, and the two 1992 expeditions were sorted from the dead and stored in buffered alcohol. Most collections were made using SCUBA at various depths, but some samples were collected using ponar and grab samplers. Samples were sorted into live, dead, and then counted. Dead data reflect a random count of 350 valves per sample site. Because of the smaller number of live individuals, all species per sample were identified and counted and their relative abundance calculated.

### *Tanganyika and Malawi core material*

Piston cores from Lake Tanganyika were recovered from 50 m of water just offshore from Bujumbura in Burundi, and about 10 km from the Ruzizi River delta (BUR1). They are archived at the Université de Occidental du Bretagne, France and were sampled in 1 cm slices for ostracodes at 10 cm intervals in 1992 by Park (Figure 2A). Samples were processed using the freeze-thaw method (*sensu* Forester, 1986) and picked for ostracodes. The Malawi piston cores (M86-4P, 12P and 24P) were recovered in 1986 and are stored at the Large Lakes Observatory, in Duluth, Minnesota. They were sampled at 10 cm intervals using the same procedure as in Lake Tanganyika by Park in 1999 (Figure 2B).

## Results

### *Sand-transport experiment*

In the shallow rocky substrate depths of 2.5 m, only 7.4% (dry weight) of the colored sand was recovered after 4 days, whereas 63.4% of the sand was recovered from the sandy substrate at that same depth. At 6 m, 6.1% was recovered from the rocky substrate and 65% of the sand was recovered from the sandy substrate. None of the colored sand was recovered from the >10 m depths in either rocky or sandy substrates (Figure 3). Thus, in sandy substrates, there is less transport down gradient than in rocky substrates; however, at greater depths (>10 m), there is significantly more transport in both rocky and sandy substrates. This suggests that there is a greater amount of out of habitat transport in all rocky habitats and at depth in both sandy and rocky habitats.

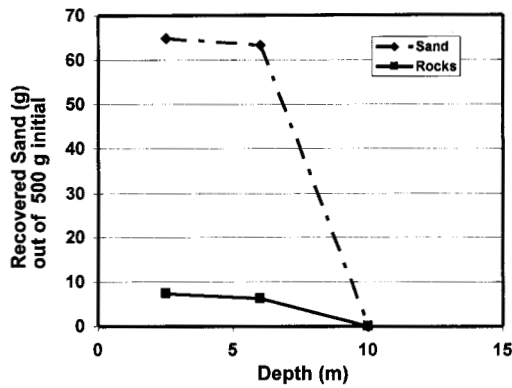


Figure 3. Experimental transport and recovery data from colored sand studies in Lake Tanganyika, showing the % of the sand recovered in each environment and site.

Live/dead experiment

Comparisons of the species richness (total number of species, both live and dead) along a bathymetric transect at all sites indicate that the percentage of total species (both live and dead) recovered increases with depth (Figure 4A). This is similar to the pattern observed in the marine macro-benthic shelly record (Zuschin et al., 2000) and is comparable to the pattern produced in our sand transport and recovery experiments.

Plotting the percentages of dead juveniles as well as adult live individuals recovered from each transect in both substrate types reveals a marked decrease in the percentages of both categories along a bathymetric gradient at all sites and in both the sandy and rocky substrates (Figure 4B and 4C). Although this is an op-

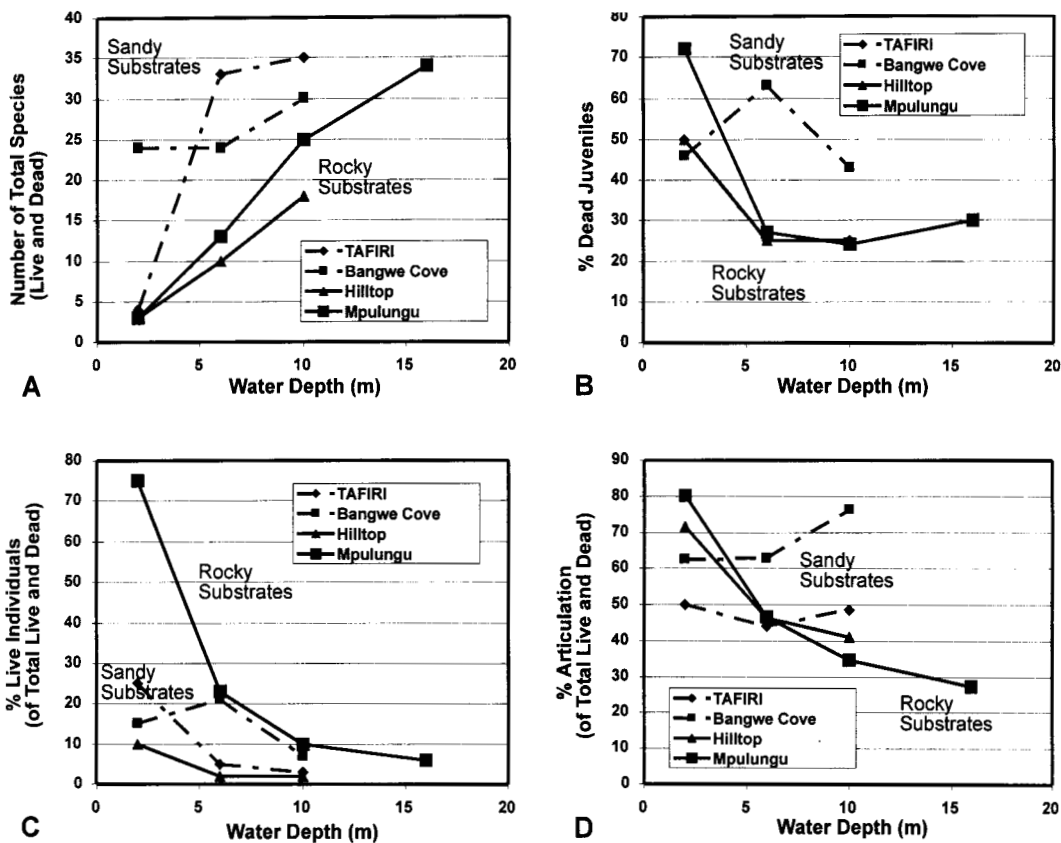


Figure 4. (A) Species richness (total species, both live and dead) along a bathymetric transect at all sites indicating that the number of species recovered increases with depth, (B) the percentage of dead juvenile individuals from each sample collected along a bathymetric transect at each site (TAFIRI, Hilltop, Bangwe Cove, and Mpulungu), (C) the percentage of live individuals of total individuals in both rocky and sandy substrates, and (D) the percentage of articulated individuals from each live/dead sample collected along a bathymetric transect at each site (TAFIRI, Hilltop, Bangwe Cove, and Mpulungu).

posite trend from the species richness, it is consistent with the experimental transport and recovery data as well as trends documented in marine studies (Kidwell and Bosence, 1991; Meldahl et al., 1997; Kidwell, 1998; Kowalewski et al., 1998; Olszewski, 1999). If significant transport occurs, the expected pattern will be one with fewer juveniles down gradient because of size sorting and winnowing of smaller and less robust shells. Likewise, the percentage of live individuals decreases dramatically with depth, suggesting a shift from life-dominated assemblages in the shallower depths to death assemblages down gradient (Figure 4C). This trend is also confirmed with the relative percentage of dead individuals of two *Gomphocythere* species, *G. alata* and *G. cristata*, in both rocky and sandy substrates (Figure 5).

The percentage of articulated individuals (both live and dead) shows a slightly different pattern depending on the substrate. In rocky substrates the percentage of articulated individuals (both live and dead) dramatically decreases with depth at both sites in the experimental transects (Figure 4D). At these sites, the percentage of articulated individuals dropped from an average of 75–35%, strongly suggesting that disarticulation increases with depth in rocky substrates. However, in the sandy substrates, the percentage of articulated individuals (both live and dead) either stayed the same or increased with depth. This difference in down gradient pattern between substrates is similar to the results from the colored sand transport and recovery experiments.

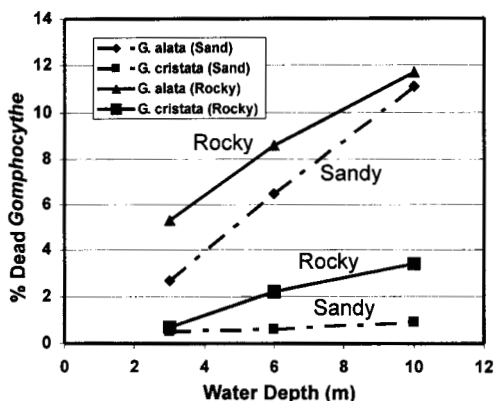


Figure 5. The relative percentage of dead individuals of two *Gomphocythere* species, *G. alata* and *G. cristata* in both rocky and sandy substrates in Lake Tanganyika.

#### *Ostracodes from Tanganyika and Malawi cores*

Given the experimental data, is it possible to evaluate the ostracode assemblages recovered from piston cores in order to assess how much time averaging has taken place in those deposits and therefore determine the scale at which paleoecologic and paleobiologic questions can be asked. To answer this question, we evaluated the species richness as well as the percentage of juveniles (vs. adults) and articulated dead individuals in cores from Lakes Tanganyika and Malawi.

In the Tanganyika core (BUR1), taken at 50 m of water depth, relative species richness is low, given the high number of species found in this lake (>160 species) (Figure 6). While the number of individual valves in each sampled core interval was high, the relative number of species was low, similar to the shallower depths of the experimental transport and surface live/dead data. The relative number of dead juveniles, however, was high, similar to the experimental surface collection data and decreased down-core (Figure 6), while the relative percent of articulated individuals was comparatively low for the entire core length (Figure 6). In addition to the articulation being extremely low, which suggests transport, the valves often had a frosted appearance and were sometimes pitted with algal borings and discolored (either very dark grey or orange), suggesting long residence time in the near surface sediments. In addition to the long residence time, the

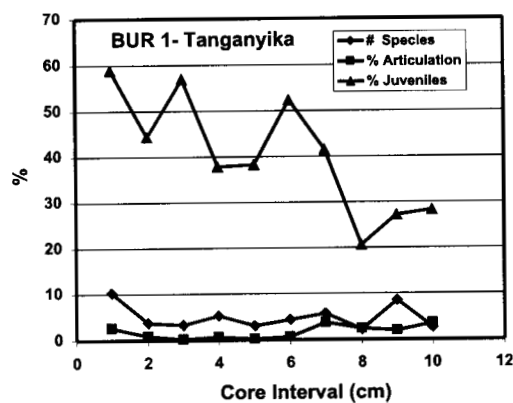


Figure 6. The number of species from core samples taken from BUR1 in 50 m of water depth in the northern basin of Lake Tanganyika, near Bujumbura, Burundi; the percentage of juveniles from core samples taken from BUR1 in 50 m of water depth in the northern basin of Lake Tanganyika, near Bujumbura, Burundi, and the percentage of articulated (dead) individuals from core samples taken from BUR1 in 50 m of water depth in the northern basin of Lake Tanganyika, near Bujumbura, Burundi.



dark color of some of the valves may also suggest post-mortem dysaerobic conditions (Boomer et al., 1996).

The Malawi cores were quite different, particularly with respect to ostracode assemblages. While abundant mollusks (primarily *Melanooides tuberculata*) were recovered, only two complete ostracode valves were recovered from the three cores sampled (M86-24P, 12P and 4P); the remaining material consisted of internal molds, which were very abundant, particularly in M86-24P. The Malawi cores also differed from the Tanganyika cores in that the species richness (based on recognizably different morphs of each mold) was relatively high and comparable to the live/dead surface sample experimental data from greater water depths (10 and 16 m) (Figure 7). In addition, the percentage of juveniles increased down core, but the articulation was relatively low, similar to the Tanganyika core (Figure 7). The dissolution of valves in this context also suggests destructive diagenesis that can also contribute to resolution problems in the record.

*Taphofacies*

If one were to estimate grain size, sedimentation rate, and environmental energy for various environments, sample and core sites could be plotted onto such a schematic representation, reflecting the taphonomic fidelity of each deposit. These plots can be considered taphonomically-controlled facies and can serve as pre-

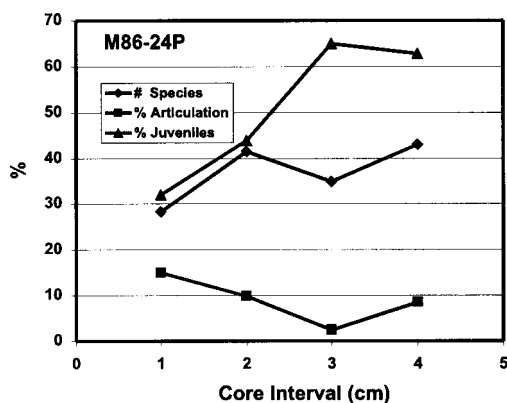


Figure 7. The number of species from core samples taken from M86-24P in approximately 200 m of water depth; the percentage of juveniles from core samples taken from M86-24P in approximately 200 m of water depth; and the percentage of articulated individuals from core samples taken from M86-24P in approximately 200 m of water depth.

dictive tools for estimating how much time averaging is likely to affect a deposit (Figure 8). This is quantitatively corroborated by Principle Component Analyses (Figure 9) and a Bray-Curtis cluster analysis (Figure 10), which indicates that the samples can be grouped upon the amount of articulation, number of juveniles present, and species richness, which is reflective of the depositional environment (i.e., substrate type, relative energy and depth). These factors all are influenced by the amount of species possibly present.

Based upon these parameters and correlations, time-averaging estimates can be produced to determine the resolution of the record with respect to the scale of paleoecologic interest. Experimental data have also indicated that the time averaging represented in the fossil assemblage is not necessarily dependent on sedimentation rate.

*Time averaging index (TI)*

Experimental data and the recovery of ostracodes from cores suggest that the juvenile-adult ratio, represented by the % juveniles and % articulated valves, are the most useful variables to predict the fidelity of an ostracode sample. This can be summarized in the following equation:

$$TI = X_i - 1/Y_i \quad (1)$$

A simple calculation of this index can be used if little is known about the deposit other than the number of

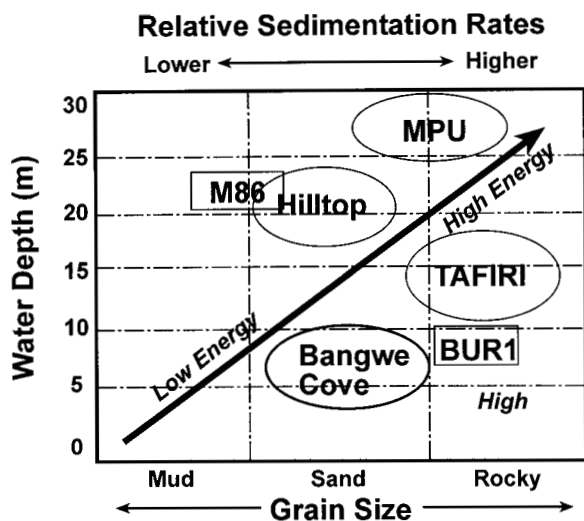


Figure 8. Sedimentation rate, depth and grain size as a function of depositional energy. The experimental sites, TAFIRI, Bangwe Cove, Hilltop and Mpulungu are plotted as well as the cores, BUR1 (Lake Tanganyika) and M86-24P (Lake Malawi).

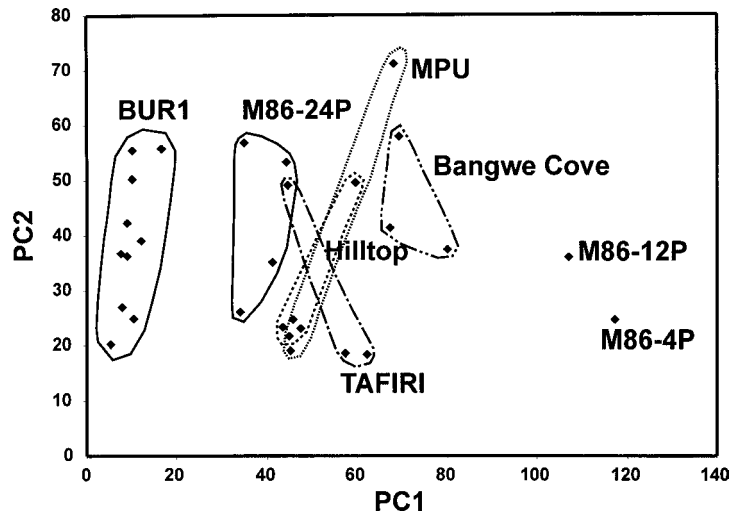


Figure 9. Principle component analysis of the three taphonomic variables (number of species, percent articulation, percent juveniles) of the ostracodes in Lakes Tanganyika and Malawi. Plot is PC1 vs. PC2 and accounts for 47% of the variation within the dataset.

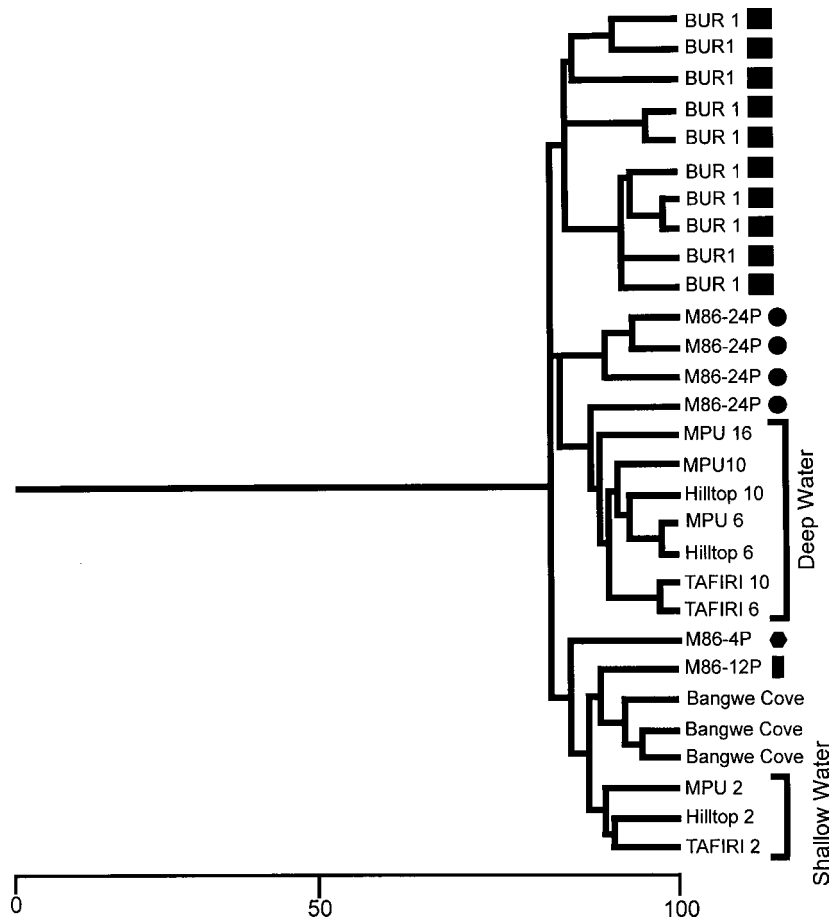


Figure 10. Bray-Curtis cluster analysis of the taphonomic variables (species richness, % dead juveniles and % dead:live articulation) and each site sampled.

individuals and no information about population dynamics or sedimentation rate can be ascertained. If collected as a live assemblage, the juvenile ratio should be close to 0.88, where  $X_i$  is the number of instars and  $Y_i$  is the number of individuals in a sample. If the assemblage is heavily time averaged, the ratio will be closest to 0.11.

However, if more is known about the parameters of the deposit, the amount of time averaging can be further estimated if population size and sedimentation rate are calculated. The organism loss rate can be estimated by how many valves are lost per year; this number will be close to 10% or a valve per individual per year. This equation, summarized below, can be used with greater accuracy to determine the type of question that can be addressed using a specific dataset

$$T = ((dN/dt) - z)/x, \quad (2)$$

where  $T$  is the amount of time represented by a sample within a piston core,  $N$  is the total momentary population size,  $t$  is time,  $z$  is the organism loss rate (how many valves are lost) ( $\text{yr}^{-1}$ ) and  $x$  is the average sedimentation rate (sediment thickness) ( $\text{yr}^{-1}$  for homogeneous sediments). These two equations can be used either in conjunction with or exclusive of one another.

## Discussion

The transport and recovery experiments suggest that (a) there is significant out of habitat transport at shallower depths and (b) that there is more out of habitat transport in rocky substrates than in sandy ones. This latter conclusion may be due to the fact that the sandy substrates usually occur on shoaling margins while the rocky substrates typically occur on the steep escarpment margins of the lake. Although the primary agent for this transport is bottom currents, there is also a biologic component on the rocky substrates, as male cichlid fish graze on the rocks and line their mating craters with the sand from the rocks.

In addition, comparison of live and dead populations from similar depths and substrates indicate that there are distinct distribution affinities delineated in the live material but that pattern is obscured with dead valves, even with increased statistical robustness. In most cases, there are distinctive depth and substrate associations shown with the ostracodes collected live, and little, if any, clear associations demonstrated in datasets generated with counts of 500 dead valves for each depth and substrate.

Both the experimental colored sand data as well as the live/dead valve data did not reject the hypothesis that transport is the primary problem rather than *in situ* time averaging. Both are deemed to be significant in the loss of resolution of the record and suggest that there can be significant loss of fidelity in using ostracodes to assess biodiversity and conservation measures. Ostracode species richness estimates are impacted by time averaging because transport of dead valve material occurs at higher percentages in the shallow depths and on the rocky substrates, suggesting that the ostracode death assemblages in these sensitive areas will not necessarily be reflective of the life assemblages. In addition to this, ecologic models based only upon death assemblages will be less resolved than those models based upon live assemblages. Thus, transport becomes important when utilizing ostracodes as proxy indicators for biodiversity and conservation practices in deep, steep gradient lakes such as Tanganyika and Malawi, and should be considered in any model developed.

## Implications for paleobiology, paleoecology, and conservation

The amount of transport experienced by biologic proxy indicators is important in evaluating questions related to paleobiology, paleoecology, and conservation, where the record needs to be resolved to seasonal and yearly variability in some cases. In evolutionary studies, determining the timing of diversification of the endemic radiations in Lakes Malawi and Tanganyika is dependent upon having a record that is well resolved, extending back at least several thousands of years. These rates can vary, but previous work done on the ostracode clade *Gomphocythere* (Park and Downing, 2000) suggests that it can be far less than the average 2 million years suggested by conventional studies (Raup, 1991). In fact, the rates in cichlid fish have been estimated to be as little as tens of thousands of years.

Other questions that are constrained by the temporal resolution of the deposit would include those related to evolutionary escalation and predator/prey arms races. Again, the amount of time represented in these deposits requires a resolution at least on the order of thousands of years. However, when considering questions concerning paleoecology and community response to environmental change requires varying time scales on the order of tens to thousands of years. Questions regarding interspecific relationships would require a yearly to decadal resolution. While these constraints

can limit the scope of investigation, by evaluating the amount of time averaging in core deposits using the simple metrics provided, a better understanding of the temporal window can be obtained.

## Acknowledgments

We wish to acknowledge and thank the following individuals for their assistance in this project: Simone Alin, Catherine O'Reilly and Melissa Hays for help with the field data acquisition of the experimental transects, Jean Jacques Tiercelin for access to BUR1 core from GEORIFT resources, Thomas Johnson for access to Malawi cores in Duluth, Doug Ricketts and Yvonne Chan for logistical support at the Large Lakes Observatory (Duluth, MN). We would also like to thank Susan Kidwell and Thomas Cronin for their helpful comments on this manuscript. A special thanks to Elizabeth Gierlowski-Kordesch and the editors of the *Journal of Paleolimnology* for compiling this issue. We would also like to thank the Governments of Tanzania, Burundi, Zambia and Malawi for their support of the different portions of data acquisition for this project. This work was supported by ATM 9619458 and EAR 9510033, as well as University of Akron Faculty Research Grant #1728 and the Stoller Research Fund, the University of Arizona Sulzer Research Fund, Sigma Xi, The Paleontological Society, The Geological Society of America, and Chevron. This paper is IDEAL publication no. 135 and is dedicated to the memory of Kerry Kelts, who inspired us all.

## References

- Anderson N.J. 1990. Spatial pattern of recent sediment and diatom accumulation in a small, monomictic, eutrophic lake. *J. Paleolim.* 3: 143–160.
- Boomer I., Whatley R.C. and Keyser D. 1996. Metallic and organic deposits on carapaces of living *Cyprideis torosa* (Ostracoda) in dysaerobic environments. Proceedings of 2nd European Ostracodologists Meeting, Glasgow 1993, British Micropaleon. Soc., London, pp. 163–170.
- Cohen A.S. 1994. Extinction in ancient lakes: Biodiversity crises and conservation 40 years after J.L. Brooks. In: Martens K., Goddeeris B. and Coulter G. (eds), Speciation in Ancient Lakes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 44: 451–479.
- Cohen A.S. 1995. Paleocological approaches to the conservation biology of benthos in ancient lakes: a case study from Lake Tanganyika. *J.N. Am. Benthic Soc.* 14: 654–668.
- Cohen A.S., Bills R., Cocquyt C.Z. and Caljon A.G. 1993. The impact of sediment pollution on biodiversity in Lake Tanganyika. *Cons. Biol.* 7: 667–677.
- Forester R.M. 1986. Determination of the dissolved anion composition of ancient lakes from fossil ostracodes. *Geology* 14: 796–798.
- Fursich F.T. 1990. Fossil concentrations and life and death assemblages. In: Briggs D.E.G. and Crowther P.R. (eds), *Palaeobiology: A Synthesis*. Blackwell Scientific, London, pp. 235–239.
- Haberyan K.A. and Hecky R.E. 1987. The Late Pleistocene and Holocene stratigraphy and paleolimnology of Lakes Kivu and Tanganyika. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 61: 169–197.
- Kidwell S.M., Fursich F.T. and Aigner T. 1986. Conceptual framework for the analysis of fossil concentrations. *Palaios* 1: 228–238.
- Kidwell S.M. and Bosence D.W.J. 1991. Taphonomy and time-averaging of marine shelly faunas. In: Allison P.A. and Briggs D.E.G. (eds), *Taphonomy: Releasing the Data Locked in the Fossil Record*. Plenum Press, New York, pp. 115–209.
- Kidwell S.M. 1998. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30: 977–995.
- Kornfield I. 1978. Evidence for rapid speciation in African cichlid fishes. *Experientia* 34: 335–336.
- Kowalewski M., Goodfriend G.A. and Flessa K.W. 1998. High resolution estimates of temporal mixing within shell beds: the evils and virtues of time-averaging. *Paleobiology* 24: 287–304.
- Larsen C.P.S. and MacDonald G.M. 1993. Lake morphometry, sediment mixing and the selection of sites for fine resolution palaeoecological studies. *Quat. Sci. Rev.* 12: 781–792.
- Martens K. 1994. Ostracod speciation in ancient lakes: a review. In: Martens K., Goddeeris B. and Coulter G. (eds), *Speciation in Ancient Lakes*. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 44: 203–222.
- Meldahl K.H., Flessa K.W. and Cutler A.H. 1997. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* 23: 207–229.
- Michel E. 1994. Why snails radiate: a review of gastropod evolution of long-lived lakes, both recent and fossil. In: Martens K., Goddeeris B. and Coulter G. (eds), *Speciation in Ancient Lakes*. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 44: 285–317.
- Moran P., Kornfield I. and Reinthal P. 1994. Molecular systematics and radiation of the haplochromine cichlids of Lake Malawi. *Copeia*: 274–288.
- Olszewski T. 1999. Taking advantage of time-averaging. *Paleobiology* 25: 226–238.
- Park L.E., Cohen A.S. and Martens K. 2000. Ecology and speciation of the ostracod clade, *Gomphocythere* in Lake Tanganyika, East Africa. *Verh. Internat. Verein. Limnol.* 27: 1–5.
- Park L.E. and Downing K.F. 2000. Implications of phylogeny reconstruction for ostracod speciation modes in Lake Tanganyika. *Adv. Ecol. Res.* 31: 303–330.
- Parker A. and Kornfield I. 1997. Evolution of the mitochondrial DNA control region of the mbuna (Cichlidae) species flock of L. Malawi, E. Africa. *J. Mol. Evol.* 45: 70–83.
- Raup D.M. 1991. A kill curve for Phanerozoic marine species. *Paleobiology* 17: 37–48.
- Scholz C.A. and Rosendahl B.R. 1988. Low lake stands in Lake Malawi and Tanganyika, East Africa, delineated with multifold seismic data. *Science* 240: 1645–1648.
- Scholz C.A., Rosendahl B.R. and Scott D.L. 1990. Development of coarse-grained facies in lacustrine rift systems: examples from East Africa. *Geology* 18: 140–144.

- Tiercelin J.J. and Mondeguer A. 1991. The geology of the Tanganyika Trough. In: Coulter G.W. (ed.), *Lake Tanganyika and Its Life*. Oxford University Press, London, pp. 7–48.
- Verschuren D. 1999. Sedimentation controls on the preservation and time resolution of climate-proxy records from shallow fluctuating lakes. *Quat. Sci. Rev.* 18: 821–837.
- Wells T.M., Cohen A.S., Park L.E., Dettman D.L. and McKee B.A. 1999. Ostracode stratigraphy and paleoecology from surficial sediments of Lake Tanganyika, Africa. *J. Paleolim.* 22: 259–276.
- Zuschin M., Hohenegger J. and Steininger F.F. 2000. A comparison of living and dead molluscs on coral reef associated hard substrata in the northern Red Sea – implications for the fossil record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 159: 167–190.