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*Journal of Paleontology*, Vol. 58, No. 2, Trace Fossils and Paleoenvironments: Marine Carbonate, Marginal Marine Terrigenous and Continental Terrigenous Settings. (Mar., 1984), pp. 499-510.

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## EFFECT OF ZOOBENTHIC STANDING CROP ON LAMINAE PRESERVATION IN TROPICAL LAKE SEDIMENT, LAKE TURKANA, EAST AFRICA

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**ABSTRACT**—Fine-grained laminated lake beds are frequently interpreted as having developed under anoxic bottom-water conditions. The absence of pervasive bioturbation is considered to indicate O<sub>2</sub> levels too low to support burrowing metazoans. Evidence from Lake Turkana, Kenya, a large tropical Rift Valley lake, suggests that food-resource availability may be equally important in laminae preservation.

Oxygen and temperature measurements from localities throughout the lake show bottom waters to be saturated or supersaturated with respect to O<sub>2</sub>, even at great depths (>100 m). Strong regional winds keep bottom waters well mixed, even at the prevailing water temperatures (25–30°C) at which water is readily stratified.

Sediments cored in offshore settings of Lake Turkana consist of finely laminated clays with very little interstitial organic material. Primary productivity is extremely high on the margin of the lake, but phytoplankton populations in offshore regions are markedly less productive. In offshore settings relatively little of what is produced finds its way into the sediment as edible detritus. Benthos standing crops decline precipitously from nearshore to offshore environments. Those invertebrates present are principally epibenthic detritivores which have not significantly modified laminae in the underlying substrate. Oxygen in the undisturbed laminae drops off to undetectable values 4 cm below the sediment/water interface, further restricting the potential infauna.

This study is intended to inject a cautionary note into potential misinterpretations of lacustrine paleoenvironments, particularly for areas which experience tropical climates at the time of deposition.

### INTRODUCTION

THE paleolimnological community for many years, has been embroiled in a controversy concerning the significance and origin of various types of lamination in lacustrine sediments. The arguments are numerous (see Boyer, 1982, for a more complete review) but have primarily centered around the problems of interpreting the Green River Formation (Eocene) and its correlatives in Colorado, Wyoming and Utah.

Central to all of these arguments, regardless of the particular model espoused, is the *belief* that lacustrine laminae are in some way preserved due to the virtual absence of benthic infauna from the substrate resulting from low O<sub>2</sub> availability or high salinity. In a situation where benthic faunal populations are small, their disruptive effects on surficial laminae also would be limited.

Throughout the discussion of the mechanisms of laminae development, the actualistic basis from which we can compare and relate lithologic observations has been remarkably narrow. This is surprising in light of the long-standing tradition among sedi-

mentologists and paleoecologists of extensive monitoring of the physical and biological processes in the modern environment. Of the few studies of modern lakes that have been incorporated into our discussion of laminae formation, most have been conducted on northern temperate hardwater lakes of glacial origin, a particularly restricted class of models from which to draw deductive inferences. The vast majority of pre-Pleistocene lakes were *not* of this type. The problem is in part pedagogical in that lakes, if they are discussed at all in sedimentology classrooms, are considered as a single group of geologic entities, fostering the view that a single set of criteria and models has been developed to which all lakes and lake sediments may be compared. In reality lake-to-lake variation (as measured by any standard) is so great that generalizations and models have largely eluded our grasp (Leeder, 1982). The fact that only a few process-response models have been developed to describe the sedimentology of lakes reflects not the uniformity of lakes but rather our inability to develop general models as a result of their extreme diversity. Clearly, before

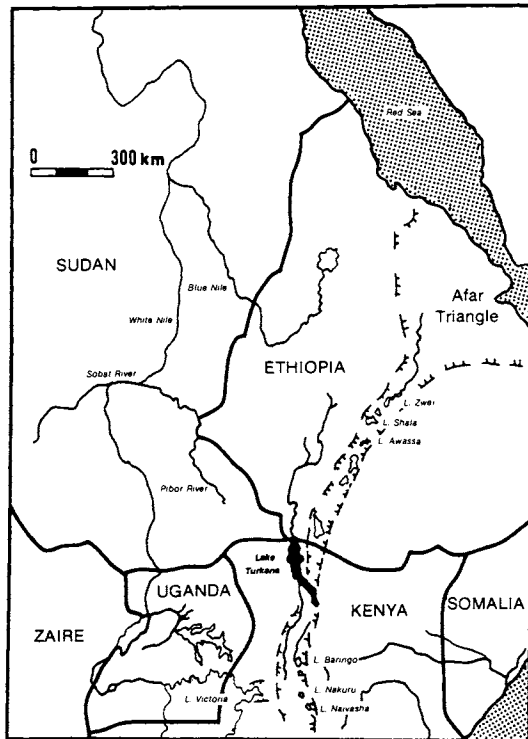


FIGURE 1—Location map of Lake Turkana, Kenya. Eastern Rift Valley shown by hachured lines.

much more sedimentological model building occurs in the realm of lacustrine laminae formation, we need to expand our actualistic data base. Modern lakes of nonglacial origin must be thoroughly studied so that patterns of sedimentation and bioturbation previously unnoticed might come to light. Because global climatic conditions have become more severe since the Tertiary, it is particularly important that we gather data from tropical and subtropical lakes in our quest to understand pre-Pleistocene lacustrine sedimentation.

In this paper I present environmental and biological data on a tropical lake where laminae are being formed and preserved in the absence of low oxygen or high salinity conditions. I do *not* suggest that this lake, Lake Turkana in East Africa, is an appropriate model for the Green River Formation, but rather that a more thorough evaluation of processes in modern tropical lakes is needed before the debate on the mechanisms of rhythmic formation is resolved.

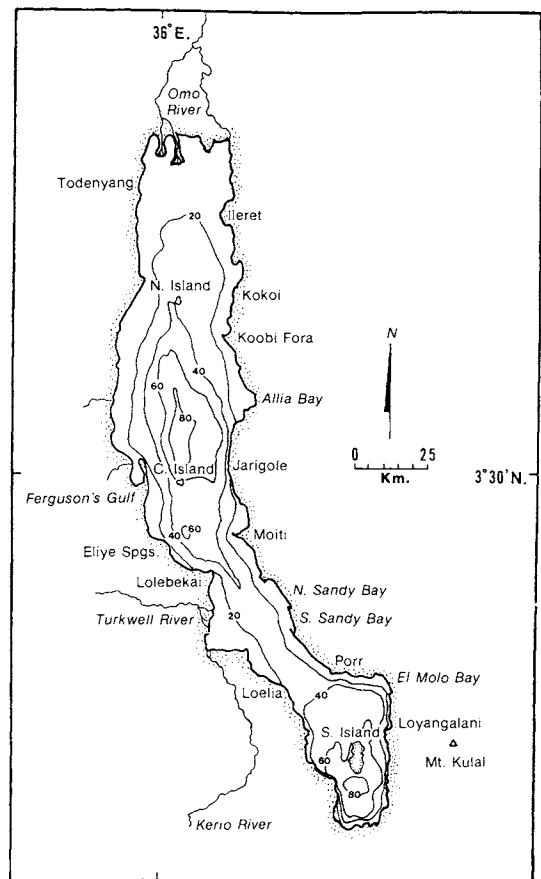


FIGURE 2—Bathymetric contour map for Lake Turkana. Contour interval is 20 m. Adapted from data from Hopson (1975).

#### LOCATION AND GENERAL SEDIMENTOLOGY

Lake Turkana is the largest lake in the Gregory (Eastern) Rift Valley of East Africa and the second largest internally drained lake on the African continent. Despite its geographic prominence, it remains perhaps the least studied of the African Great Lakes, due to its location in the remote northern region of Kenya. Figure 1 shows the lake's location. To the east of the lake, drainages are primarily in volcanic-rift related terrains, while the west side of the lake drains a mixed volcanic and Precambrian metamorphic terrain.

Figure 2 shows the bathymetry of Lake Turkana. It is intermediate in depth between the extremely deep lakes of the Western Rift Valley and the playas and shallow basins more typical of the Eastern Rift Valley.



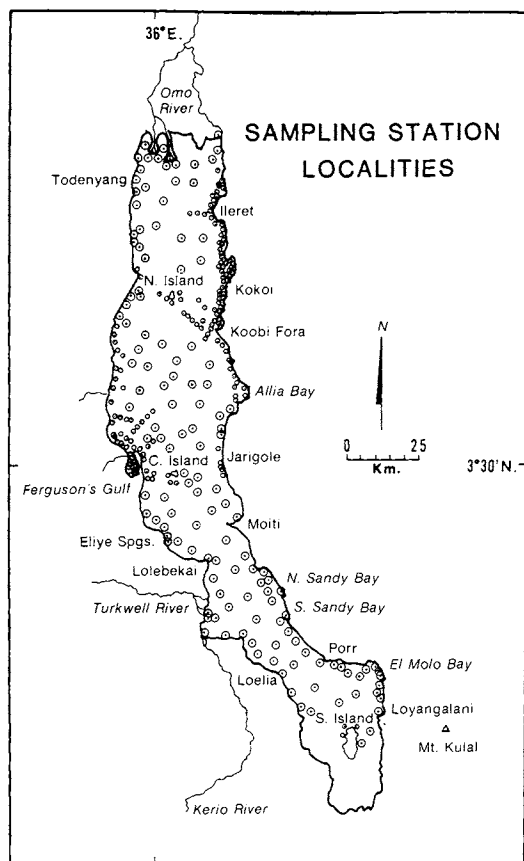


FIGURE 3—Benthos sampling station localities; 331 stations are recorded from 1978 and 1979 surveys.

Yuretich suggested that laminae develop in Lake Turkana as a response to periodic (and probably annual) fluctuations in sediment input from the Omo River, the Lake's principal influent stream.

Table 1 illustrates the characteristic water chemistry of Lake Turkana. The lake is moderately alkaline and saline and falls within the sodium chloride/sodium bicarbonate class, as do most other lakes in the Eastern Rift. Water chemistry is quite variable, both seasonally and over many years, a characteristic typical of closed basins in general.

#### METHODS

During two field seasons (July–September, 1978; July–November, 1979) 331 bottom samples were taken using a modified Ekman

dredge with 50-cm sidewalls and a surface collection area of 225 cm<sup>2</sup>. Sampling locations were determined by triangulation and are shown in Figure 3. The Ekman sampler penetrated far enough into most muddy and silty substrates to collect all infaunal macrofauna. Some shallow-water stations were collected by hand operation of the dredge over equivalent areas.

Sampling evenness was severely restricted by the logistical difficulties in operating small boats on Lake Turkana. Strong winds (derived from Mt. Kulal to the SE of the lake) and a fetch of up to 180 km combine to produce ferocious winds, even on relatively "calm" days. Typically, sampling was possible only after noon on the west side and central parts of the lake. Lower wind velocities on the east side frequently allowed morning sampling there. As a result, only occasional forays to midlake stations were attempted, as it was impossible to operate the dredge in deep water with swells in excess of 1 meter. Although the density of sampling for deep-water stations was significantly lower than in shallow water, the homogeneity of faunal samples from these widely separated deep-water stations suggests that low sample density probably is not an important problem. The distribution of faunas in the extreme south end of the lake has not yet been investigated. All faunal and sediment samples are stored at The Colorado College.

#### OXYGEN-TEMPERATURE PROFILES

Dissolved O<sub>2</sub> and temperature were monitored in 1978 and 1979 for selected stations using a YSI oxygen-temperature probe, accurate to 0.1 mg/l O<sub>2</sub> and 0.1°C. For a detailed discussion of water temperature and dissolved O<sub>2</sub> conditions in Lake Turkana see Hopson (1975). The primary reason for this study was to corroborate the general results obtained by Hopson with regard to the specific sampling areas studied in this report.

*Water temperature.*—Water temperatures vary within a relatively narrow range, as is typical for tropical lakes, and this variation is principally diurnal rather than seasonal (Figure 4). Minimum shallow-water surface temperatures of about 23°C are reached from one to two hours after sunrise (0700–0800 hours), and temperatures rise to a maximum

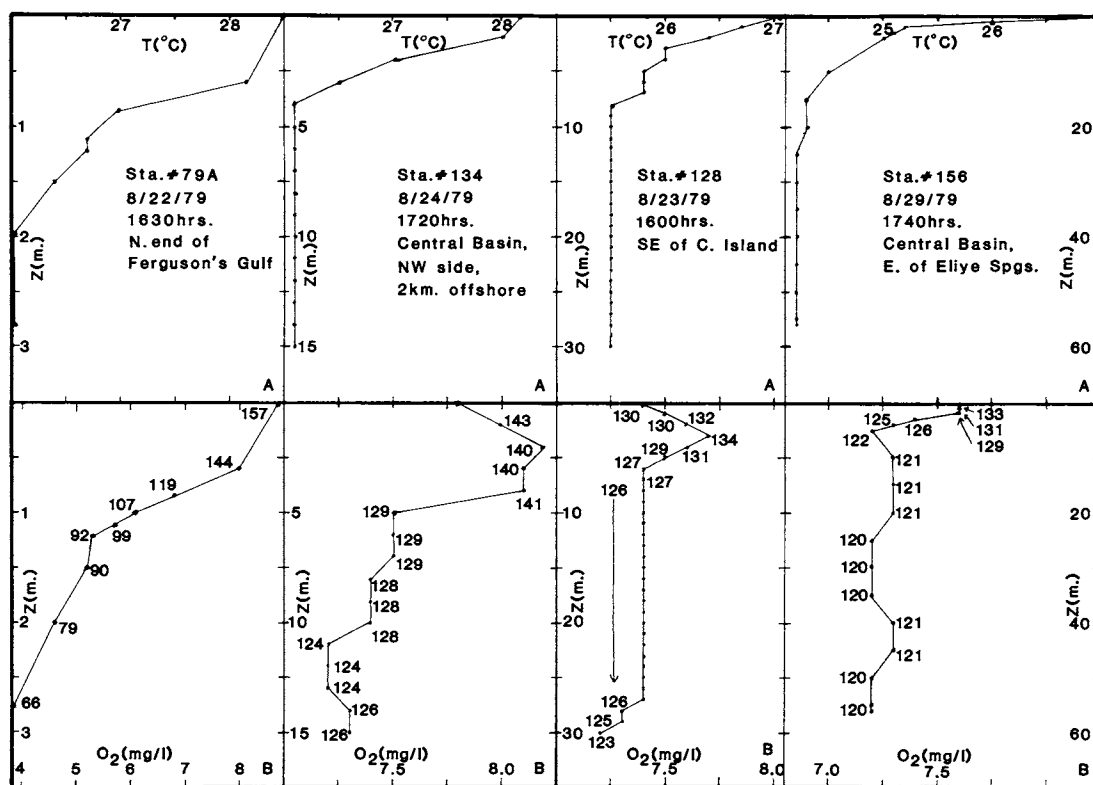


FIGURE 4—Typical water temperature and O<sub>2</sub> profiles at various depths. Profiles are all from late afternoon when thermal stratification reaches its maximum. Note that at stations 134, 128 and 156, the water column is well mixed, with O<sub>2</sub> supersaturated at all depths. Only in isolated or silled embayments such as Ferguson's Gulf (79A) is stratification evident. Numbers associated with O<sub>2</sub> profiles are %O<sub>2</sub> saturation.

of about 32°C in the late afternoon (around 1700 hours). In open and deep water, the daily fluctuation is more moderate with mean minimum and maximum temperatures between 25 and 30°C.

Bottom waters in the deep areas of the lake (greater than 40 m) vary between 24 and 25.5°C, which is slightly lower than the regional mean air temperature (Butzer, 1971). The difference is probably due to wind induced evaporative cooling (Baxter et al., 1965), through which surface waters cool and sink to the bottom in density flows. This magnitude of temperature fluctuation (1.5°C) at such depths is quite large compared with other African lakes (e.g., Talling, 1963; Coulter, 1963).

The water column of Lake Turkana proper is unstratified with respect to temperature,

due to strong regional winds. Weak surface stratification may develop during the late afternoon as the winds die down and surface-water temperature increases. Even these conditions are not strictly stratification in the traditional sense, since the thermocline usually extends to the surface with no true epilimnion. Water temperatures decline moderately (0.15–0.25°C/m) from the surface to 15–20 m depth, below which point further temperature decline is minimal. Surface water cooling commences around 1700 hours and mixing is enhanced by strong winds which commence about midnight. By early morning thermal stratification is effectively dissipated. The regular mixing of more thermally variable surface waters, discussed below, must introduce a larger degree of temperature heterogeneity to the Lake Turkana bottom waters

than is the case in occasionally stratified Lake Albert or "permanently" stratified Lake Tanganyika (both in Africa). In those lakes, temperature variations must be induced by the relatively slow process of conduction.

Occasionally, slightly higher (0.2–0.4°C) temperatures are recorded from bottom muds than in the immediately overlying water. Since only insignificant quantities of organic matter are present in most Lake Turkana deep-water substrates, it seems unlikely that this is due to local heat of oxidation. Thermal springs or elevated geothermal heat flow cannot be ruled out, but further investigation would be necessary to determine how widespread the phenomenon is.

Environmental conditions in marginal lacustrine settings were extensively monitored since these areas are commonly represented in ancient lake deposits, particularly as depocenters around ancient river inlets. One such area is the prominent shallow bay, Ferguson's Gulf, on the west side of the lake.

Stratification of the water column does seem to occur in Ferguson's Gulf (stations 79A and 79B). During the sampling period, a thin epilimnion (about 0.75 m) was underlain by a thermocline from 0.75–1.0 m, and a hypolimnion below 1 m. The thermocline had a very steep temperature gradient (4.5–5.0°C/m) despite its narrow vertical range.

Hopson (1974) stated that at station H1, located just north of Central Island, temperatures in the *early afternoon* "ranged only 1.9°C between extremes of 27.0° and 28.9° at the surface, 1.7°C between 26.0° and 27.7° at a depth of 5 m, and 0.6°C between 25.5° and 26.1° at 80 m." These figures are very close to those recorded at similar stations in the present study. The daily fluctuations recorded by the Lake Rudolf Fisheries Research Project (LRF RP) for single stations and depth, however, are smaller (about 1.0°C at all depths) than observed in this study. Hopson (1974) also notes that Ferguson's Gulf was stratified during 1973 and 1974.

*Oxygen profiles.*—(Figure 4) Lake Turkana proper is well oxygenated at all depths and at all times of the day. In this respect it is quite different from most large African equatorial lakes. The cause of this phenomenon can be found in its low depth/fetch ratio (Lake Turkana being both long and shallow), which

allows for regular mixing of the water mass. The average afternoon density gradient between the surface and 60 m water depth is  $1.8 \times 10^{-5}$  g/cm<sup>3</sup>/m, assuming average temperatures of 28 and 24.5°C, respectively. This gradient is adequate in temperate conditions to establish thermal and chemical stratification (Vallentyne, 1957; Cole, 1979). However, extremely long wind runs off the south end of the lake (Yuretich, 1976) prevent any density stratification from developing. Ratios of fetch to depths of surface-wave-induced mixing at various wind speeds are given by Smith and Sinclair (1972). Using the average wind speed for Lake Turkana of 13.7 km/hour given by Yuretich (1976) and assuming a 180 km fetch for the northern part of the lake, wave mixed depths of greater than 30 m are very likely, a value which would decline to about 10 m in the South Basin. Since most of the temperature and density variance is in the upper 10–20 m, thermal and chemical stratification will not occur. The water mass of Lake Turkana is supersaturated with respect to O<sub>2</sub>. Surface water in shallow areas (less than 3 m deep) averaged 153% O<sub>2</sub> saturation. This declines to a mean of 138% O<sub>2</sub> at the surface of medium depth waters (3–20 m) and 133% O<sub>2</sub> saturation at the surface of deep (greater than 20 m) water. Presumably this decline is related to more vigorous primary production in the lake shallows (documented by Hopson, 1975). Bottom waters also are well oxygenated. Nearly all stations in this study are slightly supersaturated with respect to O<sub>2</sub> at depth. The deepest sample station in this study had 7.2 mg O<sub>2</sub>/l (122% O<sub>2</sub> saturation at 25.0°C and 2 ppt salinity) at 83 m. Hopson (1975) stated that the minimum O<sub>2</sub> content found in the main lake during the LRF RP survey was 70% saturation at a depth of 80 m.

Ferguson's Gulf is O<sub>2</sub> stratified, with the chemocline occurring over the same depth interval as the thermocline. Below the chemocline, O<sub>2</sub> values of 60–90% saturation were found, suggesting that this stratification must be periodically disrupted. B. Harbott (oral commun., 1980) observed that at times during the survey, the O<sub>2</sub> content in the Gulf dropped to zero, but this never occurred during the 1979 field season. It is likely that periodic stratification also occurs in the many

small, restricted, temporary lagoons which form around the lake, as their bottom waters often exude a strong  $H_2S$  odor. Such areas are too shallow to show clearly defined epilimnia and hypolimnia; the entire water column instead gets continually less oxygenated at greater depths. J. Melack (oral commun., 1980) noted that Lake Nakuru, a very shallow, alkaline lake (less than 2 m maximum depth) is frequently stratified.

Outside of the Gulf,  $O_2$  profiles in shallow water are quite variable in shape. Periodic suspension of bottom mud or locally strong photosynthetic activity probably are responsible for this variability, as the profiles become more uniform in the more homogeneous water masses offshore.

Over 50% of all offshore (medium-deep water) stations showed  $O_2$  saturation maxima below the surface, at depths ranging from 1–4 meters. Metalimnetic oxygen maxima are discussed by Wetzel (1975), who believes that most  $O_2$  increases below the surface can be attributed to photosynthetic inhibition in the shallowest water layer. Given the intense equatorial sunshine (with high UV intensity) and the reduced algal colony counts at the surface relative to 1–5 m deep, found by Hopson (1975), an inhibitory mechanism quite likely lies behind the phenomenon at Lake Turkana as well.

#### OXYGEN DISTRIBUTION IN THE SUBSTRATE

In any evaluation of the distribution of the benthos of a lake, it is critical to know what conditions affect the infauna. Oxygen saturation of the substrate pore waters is perhaps the most critical parameter. Additionally, an understanding of  $O_2$  diffusion into the underlying substrate is important in the interpretation of oxygenated versus reduced sediments in core records of the lake.

Figure 5 illustrates  $O_2$  profiles of bottom muds in Lake Turkana. Some minor variations exist among the four profiles. Nevertheless, despite variations in time, water depth and location there is a general uniformity in  $O_2$  diffusion into bottom muddy substrates throughout the lake.

Just above the mud-water interface, oxygen content is always well above the minimum requirements for benthic invertebrates (see Hart and Fuller, 1974). B. Harbott (writ-

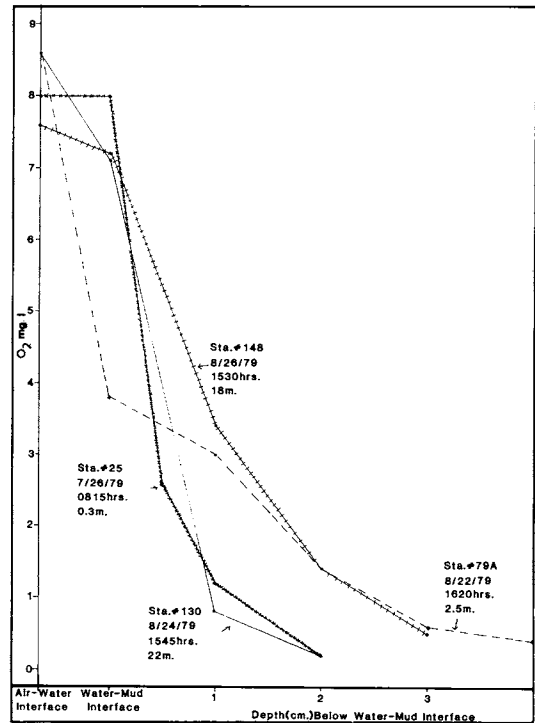


FIGURE 5—Oxygen profiles of bottom muds. Data from 4 water depths are illustrated.  $O_2$  content drops to negligible values within 3 or 4 cm of mud-water interface at all stations, despite high values just above this interface.

ten commun., 1980) stated that a diffuse layer of bottom water with suspended silts occurs in places above the substrate-water interface in Lake Turkana. Such substrate disturbance is probably a common phenomenon in African lakes and is known to deplete the  $O_2$  content of the epibenthic zone by increasing biological oxygen demand (BOD) (Beadle, 1974, p. 69–70). However, no suggestion of such disturbance was recorded in this study, either in terms of water turbidity in Van Doren water bottle samples from just above the bottom or in a decline in  $O_2$  levels immediately above the substrate. Note that the two samples (79A and unfigured 79B) with reduced epibenthic oxygen content are both from Ferguson's Gulf, where, as noted in the previous section, a state of semipermanent water stratification exists.

Below the interface,  $O_2$  content drops to unmeasurable values for the electronic probe



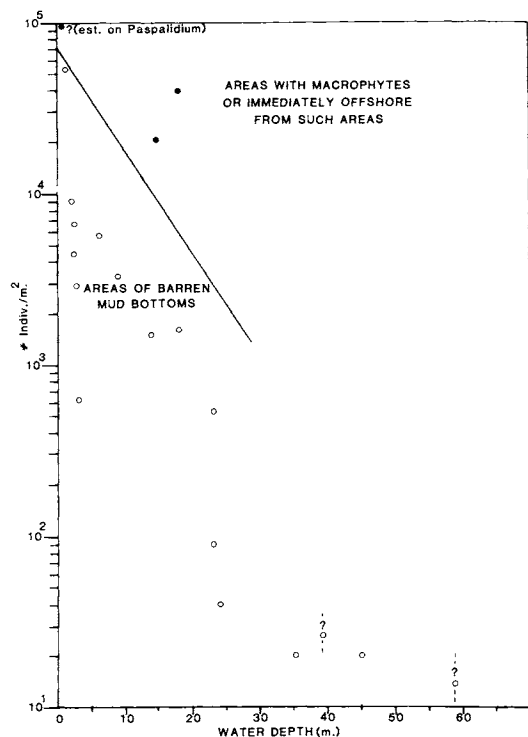


FIGURE 6—Ostracode population densities at varying water depths. Note the negative logarithmic relationship between population and water depth, with very few individuals found below 25 m. The line separates samples taken in areas of barren bottoms (open circles) from samples from areas with macrophytes (darkened circles) and does *not* denote a regression.

(less than 200  $\mu\text{g}/\text{l}$ ), within 4 cm in open lake samples. This is accompanied by a color change in the sediments, from an overlying (oxygenated) reddish-brown to an underlying olive-green. Only rarely do these sediments give off an  $\text{H}_2\text{S}$  or methane smell.

Low organic carbon content of the Lake Turkana sediments (Yuretich, 1976) suggests that the low  $\text{O}_2$  content in the underlying zone is *not* due to high BOD, but rather to a failure of the surface  $\text{O}_2$  to diffuse downward through these thixotropic muds. This lends further credence to the concept that the sediment-water interface in Lake Turkana is a distinct boundary, rather than a diffuse one, easily perturbed by bottom currents. No chemical oxygen demand measurements are available at this time.

#### BENTHONIC FAUNA OF LAKE TURKANA

Lake Turkana today has an impoverished benthos in terms of species richness in comparison with most permanent lakes of its size. What fauna exists is dominated by ostracodes.

Unlike insects (aside from chironomid larvae) the ostracodes occur frequently outside of vegetated littoral areas and are usually more abundant than molluscs or chironomids in terms of both population size and diversity in either littoral or profundal regions.

Three major, recurrent faunal associations occur in the Lake Turkana benthos: 1) a littoral, soft bottom association; 2) a littoral, rocky bottom and encrusting association; 3) a profundal (*sensu* Hutchinson, 1967), soft bottom association.

Considerable overlap of taxa exists among these associations. Even in optimal habitat areas, the associations are at best loose and irregular in terms of population dominance, with typical species often absent in what might seem ideal localities. (See Cohen, 1982, for details of Lake Turkana benthic invertebrate distribution. A checklist of Lake Turkana benthic invertebrates and their habitats is available from the author on request.)

#### POPULATION DENSITIES

Ostracode population sizes (Figure 6) show strongly negative, logarithmic correlation ( $r = 0.84$ ,  $P > 0.001$ ) with water depth on mud substrates, declining from thousands per meter<sup>2</sup> in the littoral zone to well under 100 per meter<sup>2</sup> at depths greater than 20 m.

In this analysis, total numbers of live adults and subadults (instars VIII–IX) of all species were counted. Replicate sampling was required at deep-water sites to bring totals up to countable values, and densities below 20 individuals/m<sup>2</sup> were considered unmeasurable.

Extremely high densities (approximately 10<sup>5</sup>/m<sup>2</sup>) are encountered in marshy areas where *Hemicypris klie* may be observed on plant (*Paspalidium*) stems. Muddy bottoms in the same area still support high population densities, but these are considerably reduced in relation to the vegetated areas. An important exception to this generalization occurs in sublittoral areas immediately adjacent to

TABLE 2—Zoobenthos standing crops and biomass estimates. Data are presented for 4 substrate categories. Masses in mg, population sizes in number/m<sup>2</sup>. Values are presented as order of magnitude ranges because individual measurements were found to be highly variable between similar stations.

Habitat	Taxonomic group	Combustible dry wt (mean)	Population size range	Dry wt. standing crop (mg/m <sup>2</sup> /kg/ha)
Littoral-vegetated mud bottom	Gastropods	1	10 <sup>1</sup> –10 <sup>2</sup>	(10–100/.1–1)
	Ostracodes	0.05	10 <sup>4</sup> –10 <sup>5</sup>	(500–5,000/5–50)
	Chironomids	0.03	10 <sup>2</sup> –10 <sup>4</sup>	(3–300/.03–3)
Total				(500–5,400/5–54)
Littoral-rocky bottom	Gastropods	1	10 <sup>1</sup> –10 <sup>3</sup>	(10–1,000/.1–10)
	Ostracodes	0.05	10 <sup>2</sup> –10 <sup>3</sup>	(5–50/.05–.5)
	Chironomids	—	—	—
	Ephemeroptera	2	10 <sup>2</sup> –10 <sup>3</sup>	(200–2,000/2–20)
Total				(220–3,100/2.2–31)
Shallow sub-littoral, mud bottom	Gastropods	1	10 <sup>2</sup> –10 <sup>3</sup>	(100–1,000/1–10)
	Ostracodes	0.05	10 <sup>2</sup> –10 <sup>4*</sup>	(5–500/.05–5)
	Chironomids	0.03	10 <sup>2</sup> –10 <sup>3</sup>	(3–30/.03–.3)
Total				(110–1,500/1.1–15)
Profundal (greater than 30 m)	Gastropods	1	10 <sup>1</sup> –10 <sup>2</sup>	(10–100/.1–10)
	Ostracodes	0.2	0–10 <sup>2</sup>	(0–20/0–.2)
	Chironomids	0.03	10 <sup>1</sup> –10 <sup>3</sup>	(.3–30/.003–.3)
Total				(10–150/.01–.15)

major inshore food supplies (i.e., marshlands or important drainages which bring in allochthonous plant debris). These areas, particularly near Alia Bay, locally may support extremely high population densities, even as deep as 18 m. Below 20 m population densities drop off very rapidly, and ostracodes are encountered only occasionally below 30 m.

#### ZOOBENTHOS BIOMASS

While numerically the ostracodes are the most abundant metazoan group present in the Lake Turkana benthos, their biomass is exceeded by those of both gastropods and chironomids in some areas. Estimates of dry weight biomass for four selected habitat types are presented in Table 2. Combustible dry weights were calculated using live/dry weight ratios for Lake Chad benthos (Lévêque, Dejoux and Lauzanne, 1979). A range of population sizes is presented, as these are always highly variable and often patchily distributed, making mean values of population size of questionable value.

Littoral mud bottoms support relatively large standing crops of zoobenthos. Values of 500–5,400 mg/m<sup>2</sup> (5–54 kg/ha) are low compared to Millbrink's (1977) results for Lake

Naivasha, Kenya (50,000 mg/m<sup>2</sup>) and Lake Nakuru, Kenya (60,000 mg/m<sup>2</sup>), but they are similar to those reported by Lévêque, Dejoux and Lauzanne (1979) for Lake Chad, West Africa (400–3,200 mg/m<sup>2</sup>) and by Burgis et al. (1973) for Lake George, Uganda (mean of 740 mg/m<sup>2</sup>). However, the overwhelming importance of ostracodes in this habitat in Lake Turkana is quite unusual because the Lake Chad shallow benthos is dominated by insects and gastropods and the Lake George benthos by oligochaetes. Extremely high rates of primary production have been reported by the LRFPR (over 1.5 mg O<sub>2</sub>/l/hour) in shallow water areas.

Rocky bottoms in the littoral zone, particularly in the South Basin, frequently support a large gastropod biomass with ostracodes subordinate and chironomids virtually absent. Baetid and taeniopterygid insect larvae are particularly important in rocky crevices but elsewhere are insignificant. No previous studies of rocky littoral biomass have been published for equatorial Africa; therefore comparisons are not possible. The results however, are well within the range of tropical littoral, zoobenthos biomass estimates discussed previously. Sampling problems have prevented any assessment of rocky bottom

biomass in the profundolittoral or profundal zones, and therefore the abundance of deeper water encrusting organisms remains to be determined.

Sandy bottoms, especially those in environments of high mechanical energy, support very low biomass. Almost no ostracodes or gastropods are found there, and usually there are less than 100 chironomids/m<sup>2</sup>.

Shallow sublittoral muddy bottoms display a marked decrease from the littoral in terms of biomass. The difference, a factor of 4 to 5 for minimum and maximum estimates, is very close to that noted by McLachlan (1969) in Lake Kariba (South Central Africa) during the period immediately after its damming. He found that the early appearance of aquatic macrophytes triggered an increase in zoobenthic biomass of 500% over muddy, unvegetated bottoms. As suggested earlier, sublittoral areas surrounding heavily vegetated shallows have anomalously high zoobenthic biomass. The areas just below continual wave activity are "sinks" for organic detritus washed offshore. Sediments as deep as 20 m (where slopes are high) may contain up to 10–15% macroscopic fibrous plant matter and leaf debris, and are not laminated. These same samples invariably yield high ostracode population densities.

The profundal zone of Lake Turkana presents an entirely different pattern of biomass than the shallow water regions. Recorded values are 0.01–0.15 mg/m<sup>2</sup>, which are exceptionally low for either tropical or temperate lakes (see Wetzel, 1975, p. 527). Ostracodes are particularly uncommon relative to their abundance in shallow water. This unusual paucity of biomass in the deeper parts of the lake was observed earlier by Hopson (1974), although no quantitative results were published at that time. Ferguson (1975) stated that "collections of tripton (settling organic debris) have given values of 20 g/m<sup>2</sup>/day-dry weight, but the nutritive value of this material has not yet been established." It is clear, however, from studies by Yuretich (1976) that very little organic carbon is available as ingestible detritus in the deep lake sediments. This is rather puzzling considering the relatively high productivity of Lake Turkana water (except in the South Basin). The LRFPRP (Hopson, 1975) recorded a rate of primary

productivity in the midsection of Lake Turkana of 1,094 mg O<sub>2</sub>/m<sup>2</sup>/hour.

#### ADDITIONAL CONTROLS ON LAMINAE PRESERVATION

The possibility remains that other environmental factors, aside from organic C availability in the substrate, may regulate profundal benthic biomass and thus, indirectly, laminae preservation. One possibility is that primary chemical factors other than O<sub>2</sub> availability, for example, alkalinity, pH or total dissolved solids, are responsible for a depauperate benthos. This possibility can be safely rejected, since repeated water analyses during the 1978–79 field seasons revealed no systematic variation in these parameters with varying water depths, and variation between substrate-interface waters and overlying water masses are well within the tolerance ranges of the principal benthic invertebrates found in Lake Turkana (Cohen, Dussinger and Richardson, 1983). Shallow-water gravity cores and dredge samples taken from mud bottoms with similar major-element water chemistry to Yuretich's core sample sites, show *both* high benthic biomass and uniformly mottled sediment structure.

The possibility that some trace element concentrations vary systematically from shallow to deep water, and are inhibiting deep-water benthos production cannot be addressed as easily. Yuretich's study of trace-element concentrations in the Lake Turkana sediments do not show any systematic variation with water depth, although the relationship between sediment, pore water and sediment-water-interface chemistry is hardly a simple one. At present a trace element influence on benthos distribution remains a possibility worthy of further investigation.

#### CONCLUSIONS

Four important observations arise from this study of Lake Turkana:

- 1) Deep water sediments are uniformly laminated but carbon poor.
- 2) The water column of Lake Turkana is sufficiently mixed such that bottom waters are well oxygenated. Anoxia, if it occurs at all, is restricted to shallow marginal basins.
- 3) Ecological studies of benthonic faunal

associations (Cohen, 1982) suggest that most of the organisms currently living on the bottom of Lake Turkana away from the shallows are epifaunal. Infaunal invertebrates are correspondingly rare.

4) Population densities of benthonic invertebrates decline precipitously away from the shoreline.

These observations suggest that organic carbon is prevented from entering an underlying sediment trap. Well oxygenated bottom waters prevent the buildup of organic detritus into what might otherwise be a rich food resource for benthonic organisms.

It is possible that reduced productivity offshore also limits the amount of food available as organic detritus in the mud. At present very little is known of the organic carbon flux in Lake Turkana. In particular, the fate of the extremely large biomass generated by very high inshore primary productivity is unknown.

What is clear, however, is that the small amount of organic detritus which reaches the bottom of the lake in deep water is almost entirely consumed by epifaunal organisms. The ability of such animals to mottle and disrupt sedimentary laminae apparently is insignificant. What effect they do have is limited by their small size to the uppermost few millimeters. If Yuretich (1976) is correct in his belief that sedimentation in Lake Turkana is mostly sporadic and associated with wet/dry season river inflow changes, then the possibility that small epifaunal invertebrate populations could disrupt laminae is even more remote.

The results of this study suggest that laminae preservation in lacustrine sediments may occur under a more variable set of environmental conditions than has been recognized previously. While limitations in benthonic invertebrate burrowing and sediment mottling still are recognized to be the principal factors allowing laminae preservation, the reasons for limited benthonic populations may be more complex. Trophic limitations (as in Lake Turkana), anoxia (recorded for other lakes), or as yet undescribed mechanisms may all be involved, depending upon the specific ecological conditions of a given lake. Therefore, it is vital that we exercise considerable caution in the application of

models of laminae formation with respect to ancient lake deposits.

#### ACKNOWLEDGMENTS

Support for much of the field work discussed here came from NSF grant EAR-77-2349 (University of California-Santa Cruz) to Leo Laporte and Kay Behrensmeier. I am grateful for their assistance and discussions with me on this subject. The manuscript was considerably improved by the comments and suggestions of three reviewers, Eric Leonard, Ken Stanley and Craig Feibel. The manuscript was typed by Carol Erickson. The author contributed to page costs for this article.

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\* Much of the unpublished literature derived from the Lake Rudolf Fisheries Research Project was published in 1983 by the University of Stirling as HOPSON, A. J. (ed.) *A Report of the Findings of the Lake Turkana Project*, 6 v., 1900 p.