Characterizing Molluscan Shell Accumulations: Ecological, Depositional and Taphonomic Variations on the Northern Luiche River Platform

Students: Oceana S. Castañeda (Dartmouth College)
                Christine S. O'Connell (Stanford University)

Mentors: Ellinor Michel and Mike Soreghan

Introduction

Shell gravel deposits represent geologic facies that persist into deep time as well as unique modern ecological habitats (Kidwell, 1986). Lake Tanganyika, East Africa, is home to numerous distinct facies and habitat types and provides a potential model system for understanding shell beds on a wider scale. In this ancient rift lake shell gravel occurs along axial, hinged and accommodation zone margins and seems to be particularly extensive near the mouths of relatively large rivers (Soreghan and Cohen, 1996). In the Kigoma region shell beds exist both on high-energy headlands and also blanketing the low-energy Luiche River delta platform (McGlue, et. al, 2005). However, little is understood about the mechanism by which these deposits may have formed. Examination of the northern Luiche River delta's shell gravel has the potential to suggest a formation mechanism for these shell lags. Lake Tanganyika houses a robust sedimentary record that can be used to understand past changes in paleoenvironmental dynamics, land use and lake chemistry. However, accurate interpretation of the sedimentation record depends directly on an accurate understanding and interpretation of modern sedimentation patterns and mechanisms.

The first step in understanding the depositional mechanism for the Luiche delta shell beds is to determine the source of the shell material. Lake Tanganyika's shell beds consist primarily of the bivalve genus *Caelatura* and the endemic gastropod species *Neothauma tanganyicense*, both of which are poorly understood ecologically. The distribution and abundance of *N. tanganyicense*, in particular, is sporadically recorded. Live specimens have been found at the southern and northern ends of the lake (Nakai, 1997; Leloup, 1953; H. Buescher, pers. comm.; A. Cohen, pers. comm.), and had not been recorded in the Kigoma region since an extensive biologic survey in 1946 (Leloup, 1953). We sampled extensively across the Luiche River delta at various depths prior to this study's beginnings, but observed no live *N. tanganyicense*. Live specimens in moderate densities (approximately 15 individuals per 15 meter line transect) were found recently north of Kigoma near Gombe Stream National Park at 3 meters depth (unpublished data). Similarly, live *Caelatura* have only been found occasionally within the Luiche delta hardpart deposits. The absence of live gastropods adjacent to or within the shell bed deposits complicates a complete understanding of the shells' origins.

Regardless, abundant *N. tanganyicense* and *Caelatura* shells are found in the shell gravel deposits on the northern Luiche River delta. We examined these shell gravel deposits in terms of sedimentation, taphonomic variation, and biologic differences. In order to determine the present extent of the shell gravel deposits on the northern Luiche River delta, we generated a high-resolution facies map. Variations in shell condition across the deposits was considered with a taphonomic analysis, as taphonomy can be used to interpret the origin of the shell deposits and possible transport mechanisms can be assessed based on comparative shell histories (Kidwell, 1986). Lastly, shell beds are manipulated by biologic activity; we analyzed the various habitat types present among the shell beds to further describe the system. We aimed to discern, then, whether shelly deposits of the Luiche River delta varied biologically, sedimentologically or taphonomically either by depth or with increasing distance from the river mouth. A qualitative description of the faces in tandem with a quantitative exploration of both pertinent geologic and biologic factors initially allowed us to characterize the substrate and provided a beginning for future work on the northern Luiche River delta platform.

Materials and Methods

Sample Sites

Shell-rich accumulations were studied on the N. Luiche Platform, an area of approximately 582 km^2 (Hartwell and Daudi, 2005). We surveyed eight sites on the northern portion of the river delta platform, defining four macro-transects located at approximately even intervals at 10° bearing from shore (T1-T4, Fig. 1). We sampled by SCUBA two sites along each macro-transect, one at 22 meters depth and a second at 8 meters depth. Exploratory dives at several depths throughout the platform were accompanied by qualitative searches for live *N. tanganyicense*. A second set of macro-transects within the same extent of the delta platform was used to define grab sampling locations. Grab samples were taken at depths of 5, 15, 25, 30, 35 and 45 meters. ArcView GIS 3.2a was used in tandem with GPS readings in the field to construct a sampling map.

SCUBA Sampling {tc "Sampling " \l 2}
We assessed each site for biologic, taphonomic and geologic variables. We used SCUBA to collect all biological samples and supplemented taphonomic and sedimentologic SCUBA sampling with grab samples. Sponge concentrations were assessed using a 15-meter line transect; sponges occurring within 0.75 meters of the line on either side were counted to estimate abundance along the transect. Sponge distribution and variation within site was qualitatively assessed throughout quantitative sampling. The same transect was then used to quantify biologic reworking of the substrate, counting incidences of fish nests and crab excavations within the same 1.5-meter swath of the transect line. During initial exploration dives on the Luiche River delta platform, we noticed fish reworking the substrate through several distinct means of nest building. In general, observed homes (which can, species dependent, act as either stages for courtship or as quarters for the rearing of young) consisted of a loose collection of shells, predominantly the large gastropod *N. tanganyicense*. These collections were seen on the level plain of the lakebed ('flat' nests), within depressions likely dug by the fish themselves ('depression' nests) or on raised plateaus of sediment ('raised' nests). Smaller mounds of sediment itself were observed on several occasions, often arranged in a symmetrical grouping. The four defined means of biogenic feedback – depression nests, flat nests, raised nests and fish mounds – were combined to create an index of total fish reworking. Due to constraints on SCUBA time, two transects were completed at 22 meters depth while three were completed at sites of 8 meters depth. Fish populations were assessed by an experienced icthylogical field technician, George Kazumbe, who recorded species presence and estimated abundance along the transect lines. Fisher's α was used as a diversity index for all fish species counts due to its ability to adjust for relatively small sample sizes. Further, both species diversity and species abundance data are taken into account within a single diversity index and yield an overarching measure of a site's fish population.

Taphonomic sampling included bulk substrate samples that we took within a quadrat of known area (size site dependent). The top ten centimeters within the given area was packaged in well-log bags and transported to the lab for analysis. If the bulk sample was thought to have less than approximately one hundred *Neothauma* shells, *Neothauma* shells were collected haphazardly in the area immediately surrounding the quadrat for subsequent taphonomic analysis. Sediment samples were taken by driving a glass jar directly into the substrate. Divers subsequently capped the jar by digging a parallel hole into the substrate and slipping the cap underneath the jar opening.

Divers photographed each site extensively underwater to provide a qualitative overview of the substrate composition, biologic activity, habitat complexity and general site arrangement. We used standardized photographs with a scale bar to estimate percent cover, sponge size, shell bed depth and nest dimensions. Photographs were edited for clarity by adjusting light and color levels and labeled with pertinent date and site information in Adobe Photoshop 6.0.

Physical Variables {tc "Physical Variables " \l 2}
Secchi disk measurements were taken at each site to assess extent of light penetration into the water column. Readings were recorded prior to SCUBA diver descent to avoid confounding visibility change due to disturbance of sediment by divers. Just above the lakebed, SCUBA divers collected three one-liter water samples for quantitative study. Within six hours each sample was tested in the lab for concentration of dissolved oxygen, pH and turbidity. Dissolved oxygen was assessed in units of parts per million (ppm) with a YSI Environmental Dissolved Oxygen meter. pH readings were subsequently taken using a Thermo Orion pH meter. Lastly, turbidity, expressed in Nephelometric Turbid Units (NTU), was measured with a Hach 2100P Turbidimeter. The collected water samples were then strained and filters were steeped for 24 hours in ethanol. Fluorescence of the ethanol was measured using Turner Designs'

Aquafluor fluorimeter and, after acidification of the sample, measured a second time. Calculations converted the difference in fluorescence into a concentration of chlorophyll a (in μg/L).

Bathymetric Sampling

A bathymetric survey of the northern Luiche platform was conducted using *Raytheon* echosounder, recording depths along the five macro-transects where grab sample data was collected. Depth readings and GPS points were recorded every 30 seconds while on each of the five transects, and at an interval of every minute when traveling between transects. Bathymetric contour lines were constructed from the data points using ArcView GIS.

Sedimentological Sampling

Sediment samples collected using a standard Ponar grab sampler were analyzed to determine the relative percentage of sandy and shelly material present at each site. Samples were homogenized and sieved at 1mm; based on prior qualitative observations all material larger than 1mm was considered shells and all material smaller than 1mm was considered sand. The sand and shell fractions from each site were then dried at 110 degrees C for 24 hours and weighed to calculate percent sand vs. shells. Bulk substrate samples collected using SCUBA were also sieved at 1 mm to separate sandy material from shelly material, and the percent sand present was calculated at each dive site. Fine-grained sediment samples collected using SCUBA were analyzed to determine the distribution of the fine-grained material. Samples were first sieved at 63 μm to separate the coarse material from the fine. The sand fraction (>63 μm) at each site was dried at 110 degrees C for 24 hours and weighed, and the material finer than 63 μm was transferred into a flask and diluted to a 200ml solution. This portion was dried and weighed to determine the mass of mud for comparison to the mass of coarse material. A 10ml subsample of the 200ml mud solution was removed for further analysis using the laser particle analyzer. Each 10ml sample was centrifuged, then treated with 0.5 M hydrogen peroxide and placed in a boiling bath for one hour, and then rinsed and centrifuged for 10 minutes. 1ml of the subsample was analyzed using the Spetrex laser particle counter to determine the distribution of grain size among material smaller than 63 μm.

The percentage of sand and shell material at each site determined from grab samples, in tandem with bulk sample substrate analysis and qualitative sedimentological analyses from underwater photographs, were used to construct a facies map on the Northern Luiche Platform.

Taphonomic Analysis

N. tanganyicense shells collected from 4 transects at depths of 8 meters and 22 meters, as well as several exploratory dives, were compared taphonomically. 100 shells from each site were ranked based on the presence of fragmentation, abrasion, encrustation, dissolution, and reduction and oxidation staining (after McGlue, et. al, 2005). The scoring system used to rank each shell is summarized in Table 1. However, ranking individual shells for fragmentation collected using SCUBA was determined to be misrepresentative of the overall fragmentation values, as large, whole shells tended to be more visible and easier to collect. In order to more accurately estimate fragmentation at each sample site, bulk substrate samples taken from each dive were sieved at 1 mm to separate sandy material from shelly material, and the shelly material was separated into whole and fragmented portions. Each portion was dried and weighed, and the percent fragmented material out of the total shelly material weight was used to characterize the percent of fragmentation at each site.

Statistical Analyses

The effect of site depth and distance from the Luiche River (macro transect location) on several distinct independent variables was quantified using a two-way analysis of variance (ANOVA). Depth and macro transect were both treated as fixed factors. Physical water variables – pH, concentration of dissolved oxygen, turbidity and concentration of chlorophyll a – were treated as independent variables, as were sponge abundances, fish diversity indices and instances of biogenic feedback. In all cases a probability of 5% or less constituted statistical significance. Tukey's test was used to further analyze statistically significant effects (α of .05 used). Independently, a Student's t-test was used to determine the effect of depth within each macro transect for the aforementioned variables. JMP IN 4.0.4 was used for all statistical analyses.

Ecological Variation: Habitat Characterization and Biogenic Feedback

With the exception of T4 (p = 0.43), each macro transect had a significantly higher abundance of sponges at its deep site than its shallow site (T1 p < 0.0001, T2 p = 0.0003, T3 p = 0.0003) by Student's t-test (Fig. 2). A two-way ANOVA examining the effect of depth and distance from the river on sponge abundance found a highly significant relationship (p < 0.0001, F ratio=13.9) between both of the model effects and abundance data. Tukey's test illustrated that deep sites are significantly different than shallow sites; it also determined that, depth aside, T4's mean abundance is significantly different than both the mean abundance for T1 and T3. T1, T2 and T3 have turbidities that fall within a single swath, but feature a bimodal series of sponge abundances by depth. T4, however, has relatively high mean turbidity levels and no sponge abundance bimodality – instead, both deep and shallow sites have low sponge abundances.

Deep sites, aside from that in T4, generally had a high density of sponges across the bottom. Moreover, the vast majority of the large branching sponges seen were located at deep sites. The same holds true for the majority of dark green sponges observed. A haphazardly collected sample taken from the deep site on T1 contained an estimated five distinct sponge morphotypes. Shallow sites, in contrast, had low sponge density on the flats between collections of fish nests and notably higher densities within the confines of depression-style fish nests. Qualitatively, a higher proportion of the sponges at shallow sites were tan or yellow, and a higher proportion of the morphotypes seen were globular or rounded.

Fish species' presence by depth are shown in Table 2. General foraging patterns are also listed, as are shell-related behaviors. Mean site Fisher's α values were determined by averaging fish species and abundance data along each repeated line transect (Fig. 3). Fish diversity as indicated by Fisher's α showed a decrease in the sites nearest the river, supported by an ANOVA (p = 0.0017, F ratio = 7.717). Tukey's test verified that T4 is significantly different from T1, T2 and T3 (which are not significantly different). Additionally, T2 showed a significant difference between the mean α of the deep and shallow sites. Fish abundance differed across the delta as well (Fig. 4). Within transects, mean fish abundance did not differ significantly by depth. ANOVA determined, however, that within the shallow sites there is significant variation (p = 0.0041, F ratio = 11.72) in total abundance across macro transects: Tukey's test demonstrates a significant difference between T4 and both T1 and T3.

Further, sites varied in the extent of observed biogenic feedback (Fig. 5). The large standard error margins for T1 and T3's shallow sites reflect the patchy nature of the local substrate. Both bottoms consisted of relatively inactive sand flats alternating with densely structured depression fish nest communities. Each of these seemingly autonomous communities could contain as many as seventy nests, and could encompass as much as a 10 m^2 area. When analyzed with a Student's t-test, macro transects T2 and T3 had significant differences (p = 0.0013 and p = 0.0068 respectively) between the deep and shallow sites, with shallow sites in both cases having more instances of reworking. ANOVA revealed that depth and distance from the river both significantly affect the abundance of fish nestbuilding (p = 0.0020, F ratio = 7.15). Shallow sites are significantly different than deep sites; furthermore, T3 was shown to have significantly more homes than T2 and T4.

Crab holes, either dug coarsely through exceedingly shelly substrate or as smooth holes into finer-grained sediment, also contribute to bioturbation of the Luiche River's shell beds. Though movement of shells themselves was minimal, crab excavations often radically altered local geometry and substrate topography. Furthermore, they serve to increase local shell fragmentation and change the taphonomic signature. Due to the patchy nature of crab nestbuilding within site, quantitative data do not reflect the importance of crab reworking in the larger scheme of the beds' biogenic feedback.

Finally, we examined trends in physical limnologic variables across the transects. Concentration of dissolved oxygen and pH were insignificantly affected by both depth and distance from the river according to ANOVA (p values of 0.336 and 0.236 respectively). Though mean pH differed significantly across depth for transect T1 and T2 according to Student's t-tests (p values of 0.018 and 0.005 respectively), the effect of depth does not seem to establish a robust pattern – T1 was more alkaline at its deep site, while T2 showed the opposite pattern and featured a higher pH at shallow depth (Fig. 6). Dissolved oxygen concentration did not differ significantly for any of the macro transects (Fig. 7) and percent saturation at each site was calculated based on water temperature and parts dissolved oxygen per million. All sites had over 90% saturation (Table 3).

Turbidity was significantly affected by distance from the river (ANOVA p < 0.0001, F ratio of 25.9); macro transects T1-T3 were not significantly different, whereas T4 differed significantly from all

three (Tukey's test). Depth did not correlate significantly with turbidity within any of the four macro transects (Fig. 8). However, it is notable that three of the four macro transects are more turbid at their deep sites – T3 is the single exception.

Concentration of chlorophyll *a* differed significantly with depth for the T3 (0.008 p) and T4 (0.008 p) macro transects by Student's t analyses (Fig. 9). Furthermore, distance from the Luiche affected chlorophyll a concentrations significantly (ANOVA p 0.002, F ratio 6.25). Tukey's test subsequently demonstrated that T1 concentrations are significantly different than T2, T3 and T4 concentrations (all of which are not significantly different). Chlorophyll *a* concentration decreases with proximity to the river mouth. When plotted against each other, concentration of dissolved oxygen does not correlate significantly with either concentration of chlorophyll *a* or turbidity (R^2 values of 0.0054 and 0.0317 respectively). Moreover, turbidity and chlorophyll *a* do not show a robust correlation ($R^2 = 0.0309$). Chlorophyll *a* concentrations also do not correlate with mean fish abundance ($R^2 = 0.346$).

Discussion

Several dominant ecological trends are observed on the Luiche River's northern platform. Throughout the delta, sponge abundance is nearly an order of magnitude higher at deep sites than at shallow sites (Fig. 2), and the only observed sites with a noticeable dominance of sponges by ground cover occurred at the deeper ends of studied macro transects, from approximately 18-23 m depth. Conversely, vibrant fish communities exist more prevalently at shallow depths – the only locations observed with densely structured fish nest beds occurred at depths of 7-13 m (Fig. 5). These communities (T1 and T3 shallow sites, quantitatively; other regions on the delta by observation) are accompanied by an increase in total fish abundance (Fig. 4), which is noticeably concentrated in the water column surrounding the remodeled nest habitats. Lastly, turbidity on the delta has a critical lower bound after which it acts as an obstacle to biodiversity and high species' abundances. T4 features a large spike in turbidity at both depths sampled (Fig. 8) and is accompanied by a decrease in sponge (Fig. 2) and fish (Fig. 4) abundance. Inspection of the habitat revealed a relatively uninhabited substrate where silt was being deposited and with few living creatures observed. T1, T2 and T3, on the contrary, seem to be affected equally by the influence of the river: turbidity does not change significantly across the gradient (Fig. 8) and biologic patterns do not follow robust correlations with distance from the river mouth (Figs. 2, 3, 4, 5).

Despite the presence of general trends, however, shell bed habitats on the Luiche delta remain enormously varied. High abundances of fish, for example (Fig. 4), are not necessarily accompanied by high instances of substrate reworking by fish (Fig. 5) – the shallow site on macro transect T2 is a prime example, with homebuilding decreasing proportionally more than fish abundance. In addition, algal mats of varying morphologies and densities were seen throughout the study area and at several depths, implying that perhaps photosynthetic activity and nutrient availability change slightly over small distances. These mats were found to cover both the extent of a sampled location and, alternatively, smaller patches within the confines of a single study site. Sponges, too, change drastically from locale to locale, representing various morphologies and morphological abundances throughout the Luiche River delta region. Indeed, the ecology of the lake's sponges continues to be poorly understood; turbidity seems to act as an influence in sponge distribution and species' presence at the extremes, but fails to explain distributional subtleties.

Sponges notwithstanding, the ecological factors driving the delta's complex habitat diversity remain unclear. Data concerning pH and concentration of dissolved oxygen show no robust trends and the epilimnion, as expected (Wetzel, 2001), seems to be well mixed locally. Concentrations of chlorophyll *a* do not correlate significantly with fish abundance, suggesting that primary productivity in the water column does not in this case act as a proxy for ecosystem productivity. Turbidity has perhaps the largest amount of control over the biological characteristics of the delta's shell beds habitats – at its highest levels it acts as a clear negative control over local ecology, despite its relatively weak larger trend.

Regardless of applicable ecological controls, ultimately the biological characteristics of the platform's shell beds affect the nature of the substrate itself. Fish nests act to physically change shell densities across the larger expanse of a shell bed site by consolidating shells within small areas. This differential substrate density, furthermore, leads to an increase in local sponge abundance; the sheltered environment created by single fish nests and, in particular, extensive fish nest communities creates an environment that promotes sponge growth due to the presence of hard parts, the removal by fish of dominant algal mat and the protection of depressions walls. Though no quantitative data is yet available, fish nests may also be acting as a source of increased sponge biodiversity in comparison to the relatively

bare sand flat surroundings found in many shallow environments. Finally, the time scale over which these fish homes manipulate their surroundings remains unclear. While extant, fish nests provide myriad ecological niches and affect local ecology. Once abandoned, however, the nests may or may not continue to shape substrate composition. Deserted nests were observed throughout the platform, but never in the densities found at vibrant shallow sites; notably, however, whether the dichotomy of living and dead fish nest structures is related to rapid shell bed turnover rate is unknown. Ultimately, the biology within modern shell bed habitats influences shell bed composition over deep time.

Depositional and Taphonomic Characteristics

<u>Results</u>

Morphology and Sedimentology
       The bathymetric data shows a gently sloping platform; further south near the Luiche River delta depth increases more slowly close to the shore shore, but drops off more steeply at around 40 m. (Fig. 10) Sandy material (75-100% sand) was most abundant close to the shore and again at around 40-50m depth, where there is a slight increase in slope across the platform. The highest concentration of shelly material was found at depths of around 15-25m. Mollusc shell accumulations are generally found on gently sloping platforms such as the Luiche, as steep slopes are likely to be much more unstable and prevent the accumulation of time averaged shell assemblages (Cohen, 1989). This correlates with the occurrence of shells on the Luiche Platform, as the most shell rich material (50-100% shells) is found on the relatively gently sloping regions near the center of the study area (Fig. 11)
       Both biological reworking and wave energy control the sedimentological structure and extent of the shells beds on the Northern Luiche platform. Shell bed thickness and shell concentrations vary with distance from the river as well as distance from shore. The concentration of shells as well as the thickness of the deposit increase with distance from shore along the shallow portions (0-10ft) of both the center exploratory transect and the exploratory transect south of the river. Also, among the shallow sites of the research transects, the shell deposit thickened from about 5 cm at T1 to greater than 15 cm at T3, suggesting at the very least a variable thickness to the deposit and perhaps a tapering of the shell-rich layer as shells are pushed northward by longshore currents. The presence of shells from the exclusively river-dwelling mollusks *Melanoides* and *Pila* washing up in numerous places along Ujiji beach as well as the concentration of shells along more southward-facing shorelines may suggest longshore transport of shelly material northward. No shelly material was observed at T4 shallow due to the influx of sediment from the river.
       The deeper suite of shell beds are relatively free of sediment with a slight dusting of sediment that increases with proximity to the river. In general the deep shell deposits are composed of a 10-15 cm thick layer of shelly material in variable amounts of a sand/mud matrix followed by a finer-grained shell-poor and water-rich faces.   At both T1 and T3 deep the shells were moderately packed into a sand/mud matrix. At T2 the top 7 cm of shelly material was loose with no substantial matrix followed by a 5cm layer of shells within a sand/mud matrix. There was no appreciable amount of shelly material at T4 due to the influx of sediment from the river.

Taphonomic Analysis
       Fragmentation is slightly higher overall on the shallow transects, and is also high at both deep and shallow sites near the river (65 and 59% fragmented material), and is highest in the middle of the platform (T3 shallow, 73%). (Fig. 12) Abrasion is higher at the shallow sites, and a large percentage of shells have a medium-high ranking (2), compared to the deep sites where there are more low (0) and low-medium (1) rankings. Abrasion values did not differ greatly across the platform laterally; however there was a slight increase in the frequency of mid-high abrasion rankings on the transect closest to the river transect closest to the river (ET S). (Fig. 13)
       Encrustation was higher at deep sites (Fig. 14); with a large amount of shells with high rankings (3-4). At shallow sites, high encrustation rankings occurred much less frequently. Values do not appear to change with distance from the river.
       There is little difference between the reduction values for shallow and deep sites; however, along the transects farthest from the Luiche river, reduction values are slightly higher. At the mid-depth transect

close to the river, reduction values are higher than at the deep and shallow sites for the same transect. The presence of strong oxidation staining is relatively low, although there were a large number of shells that had a small amount of oxidation staining. At the two transects farthest from the river, there is a higher frequency of mid-high range oxidation rankings at the deep sites; however in the middle of the Luiche River platform (T3), the opposite is true. At the transect closest to the river, both the shallow and the deep sites have a higher percentage of shells with oxidation staining than without, whereas at the mid-depth site on the same transect there are more shells without oxidation staining. Dissolution only occurred in high proportions at the shallow sites on the transects farthest from the river.

Discussion

Taphonomic differences can be used to interpret environmental and depositional conditions for shell accumulations at different locations, such as variations in hydrodynamics and biologic factors, and the amount of time shells have been exposed on the lake bottom (Kidwell, 1986). There are general trends that characterize each location; however, taphonomic differences within sites exist to some degree. In some instances, small relatively undamaged shells were found alongside large, highly abraded and encrusted shells. In general, variations between deep and shallow sites are more noticeable than variations with distance from the river.

The most noticeable difference between sites is found when comparing encrustation between the shallow and deep sites. Shells at deep sites have spent a longer amount of time exposed at the lake bottom, enabling the growth of encrusters. At several sites, (T1 and ET deep) shells are frequently bound by stromatolites, and encrustation by sponges is also common at deep sites, which correlates to the high amount of live sponges found at the deep sampling sites.

Higher abrasion values at the shallow sites may indicate a higher energy depostional environment where material is actively transported. Wave energy may aid in the transport of material across the platform, and future work should be done to investigate the effect of wave energy on shell transport. Abrasion and fragmentation proximal to the Luiche may be a result of transport and physical breakage by water and sediment inputs from the river. Significant fragmentation may also be caused by bioturbaters such as fish and crabs (Fursich and Flessa, 1987). Qualitatively, the deep sites have mainly old abandoned fish nests, as opposed to the shallow sites, which have a high concentration of live fish and transport of shells to construct brood nests. At deep sites, encrusted shells may be too heavy for fish to transport; conversely, shells may be deeply encrusted because they have been exposed in place on the lake floor without movement by bioturbaters.

Reduction staining does not seem to differ greatly between deep and shallow sites, or with distance from the river. There is a slightly greater percentage of shells with mid-high (2 or 3) oxidation rankings at shallow sites; this may be a result of more mixing and oxygenation of water at shallow depths; however data from the dive sites shows no significant difference between dissolved oxygen levels at deep and shallow sites. Oxidation values are noticeably higher near the river (ET S), and river water inputs enriched in iron could be locally altering these shells. Dissolution at found at shallow sites farthest from the river may be caused by chemical or biological factors; pH was found to be constant across the platform so chemical dissolution would have to be caused by outside hydrologic inputs. Localized stream runoff may contribute more acidic freshwater near the headland, and dissolved shells found at Ujiji Beach may be a result of overland runoff interacting with beach deposits, especially during the wet season. Both dissolution and oxidation show that river inputs are potentially affecting the shell deposits, and fragmentation and abrasion values show a slight increase near the river. However, variations between deep and shallow sites are more noticeable.

Conclusion

Both on a biologic and a taphonomic scale, variations in the characteristics of shell-rich deposits can be seen throughout the N. Luiche Platform. Macroinvertebrates and vertebrate populations vary in distribution and abundance both with depth and with distance from the Luiche River. Fish and crab ecology, in particular, affects local geometry. Differences in the bathymetry, as well as the substrate, affect the accumulation and preservation of shelly material. Indeed, the variations in taphonomic signature on the Luiche Platform, in tandem with substrate composition and patterns of biogenic reworking, can allow for interpretations of depositional mechanisms.

Biogenic, sedimentologic, and transport concentration mechanisms are all modes of shell bed formation (Kidwell, 1986). Storm activity and high wave energy, as well as turbidity currents, are possible modes of transporting exotic shells into different locations (Cohen, 1989); by that logic, underwater transport of *Neothauma tanganyicense* may be evidenced by abrasion found at the shallow sites. Alternatively, low sedimentation rates relative to hardpart accumulation are one possible mode of creating a high concentration of shelly material. However, despite extensive exploration, we observed no live specimens of *N. tanganyicense* on the Luiche Platform – thus, it is unlikely that shelly material is accumulating at present. Additionally, large-scale lake level fluctuation at relatively rapid rates is another possible mechanism for shell bed formation. Following this explanation, during periods of high lake level mud is deposited, and dead shells are able to accumulate on gently sloping platforms. As lake level drops, mud ceases to be deposited, and the sediments and shells are exposed sub-aerially; selective winnowing of fine sediments occurs, allowing for a concentration of shelly material (Cohen, 1989). Biogenic concentration can also contribute to the formation of shell lag deposits, and re-working by cichlid fish and crabs building brood nests on the lake floor is one mechanism by which shells are transported and re-deposited (Cohen, 1989).

We speculate that hydrological transport has not played a major role in concentrating shelly material on the Luiche Platform, based on the extremely localized effect of the river on ecology. Suspended sediments transported by the river did not influence sponge and fish abundance beyond T4, and although fragmentation and abrasion values are slightly higher close to the river, little lateral variation in the taphonomic signature does not suggest large-scale transport. Instead, we suggest that abundant live *N. tanganyicense* lived at one time on the Luiche, and that their hardparts were gradually concentrated over time. Lake level change and selective winnowing may have amplified large-scale deposition of these shelly accumulations. After initial deposition, myriad factors seem to have affected the nature of the substrate, including localized biogenic reworking and wave energy.

The extent and subtleties of these effects are poorly understood, and future work should be done to develop our knowledge of formation mechanisms and current influences on the morphology of shell-rich deposits. Moreover, the unique habitats forged within shell-bed communities have yet to be adequately described; an understanding of local sponge morphologies and distributional patterns, in particular, could shed light on current and paleoenvironmental physical variables. Ultimately, a thorough understanding of the interplay between biology and geology depends on further investigation of current community dynamics and long-term hardpart accumulation within shell-rich facies.

Works Cited

Cohen, Andrew, 1989. "The Taphonomy of Gastropod Shell Accumulations in Large Lakes: An Example from Lake Tanganyika, Africa." Paleobiology 15(1): 26-46.

Fursich and Flessa, 1987. "Taphonomy of Tidal Flat Molluscs in the Northern Gulf of California:

Paleoenvironmental Analysis Despite the Perils of Preservation." Palaios V2: 543-559.

Nakai, Katsuki, 1997. "Distribution and Abundance of Large-sized mollusks and empty shells of *Neothauma tanganyicense* on the sandy bottom of southern Lake Tanganyika." Ecological and Limnological Study on Lake Tanganyika and its Adjacent Regions, Vol. X.

Hartwell , R.J and Daudi, Florence, 2005. "Sediment Distribution and Analysis of TAFIRI Bay and Luiche River Platform, Lake Tanganyika, East Africa: A Prediction of hydrodynamic transport and wave-influenced deposition on clastic sedimentation." Nyanza Project Report: 31-36.

Kidwell, Susan et al., 1986. "Conceptual Framework for the Analysis and Classification of Fossil Concentrations." Palaios 1986 V1: 228-238.

Leloup, E. 1953. Gasteropodes. Exploration Hydrobiologique du Lac Tanganyika. Institut Royal des Sciences Naturelles de Belgique 3: 1-273.

McGlue, Mike et al., 2005. "Fossil Shell Accumulations in Lake Tanganyika." Nyanza Project Report: 43-53.

Soreghan, Michael and Cohen, Andrew, 1996. "Textural and Compositional Variability Across Littoral Segments of Lake Tanganyika: the effect of Asymmetric Basin Structure on Sedimentation in Large Rift Lakes." AAPG Bulletin V 80 (3): 382-409.

Wetzel, Robert. Limnology. Academic Press: San Diego, 2001.
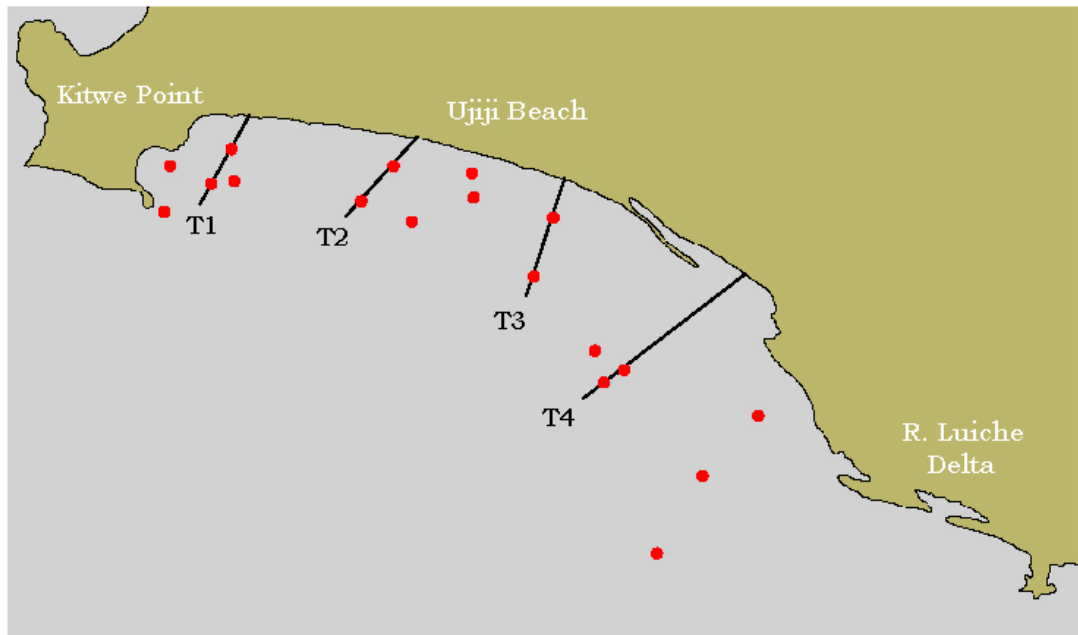
Fig. 1: Study site and research transects

Taphonomic Variable	0 = No Damage	1 = Low Damage	2 = Moderate Damage	3 = High Damage	4 = Very High Damage	Comments
Fragmentation	Whole shell; little to no chipping present on the lip	Whole shell; some chipping, with angular edge on the lip	Chipped angular edges, but still > 75% whole	Large shell fragment > 50% whole		Environmental energy proxy
Dissolution	No dissolution	Surface appears chalky with round craters forming on surface	Some small round holes on shell surface; holes are not angular or jagged along edges	Large roughly circular to oval holes; holes cover 50% or more of surface		My be a result of chemical or biologic processes
Abrasion	Shiny original luster; no wear	Surface appears dull; some bumpiness and irregular wear on lip	Dull; surface appears bumpy and "flaky", especially near the lip	Most of surface flaky and abraded; deeper pitted appearance present		External wear; hydrodynamics
Encrustation	None	Patchy coverage	Complete thin layer of coverage	Complete coverage; thick and bumpy	Thick raised bumpy surface; may be multiple shells bound together	Total coverage by all taxa – algae, calcareous micro-organisms
Oxidation Staining	Original color	Limited pink/orange patches	Dark pink to light red/orange	Deep reddish orange		Oxygenated bottom waters
Reduction Staining	Original color	Limited light gray patches	Medium gray to dark gray (mostly to fully covered)	Black (fully covered)		Anoxic environment, burial

Table 1: Taphonomic Variables
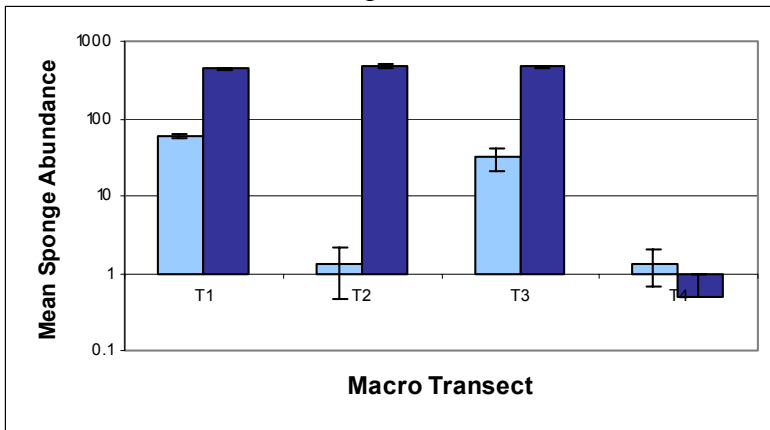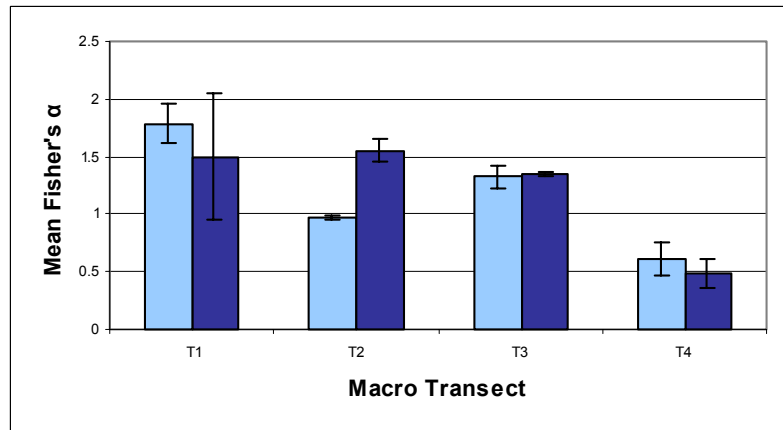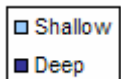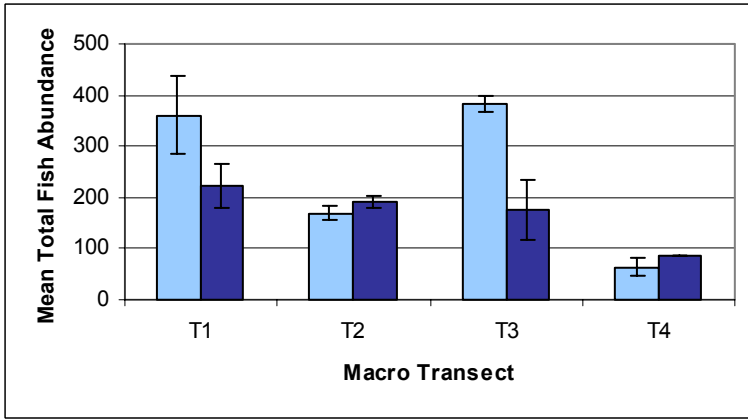

Fig. 2: Mean sponge abundance

Fig. 3: Mean Fisher's Alpha

Shallow
Deep

fig. 4: Mean fish abundance
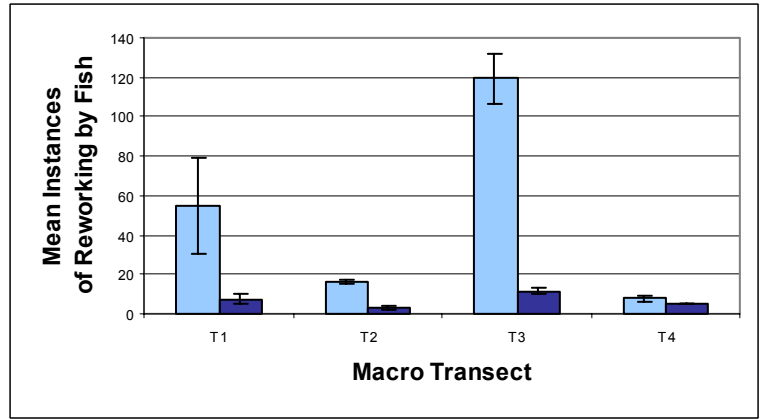

fig. 5: Mean reworking by fish
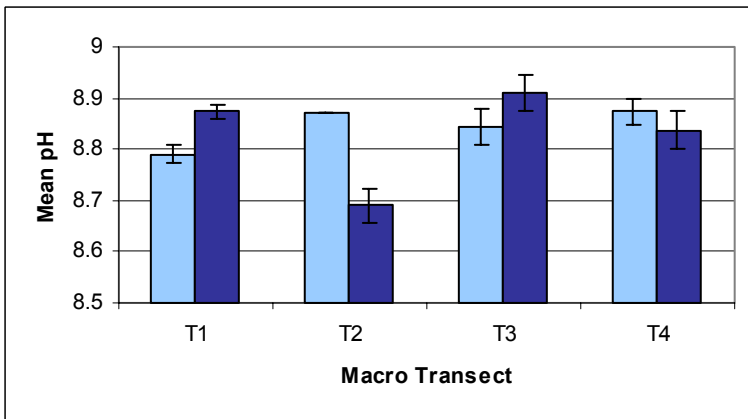
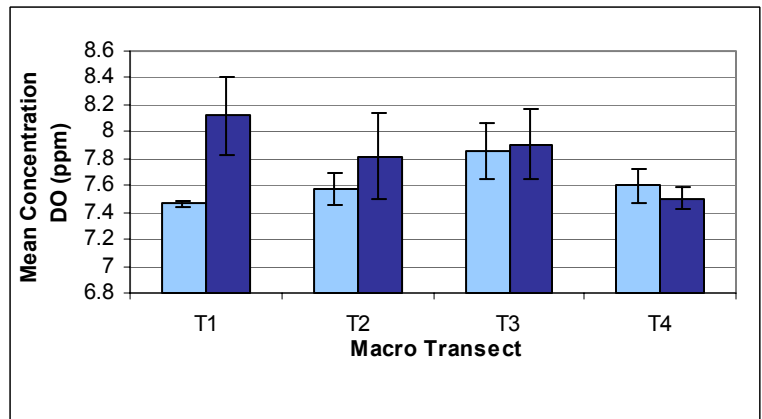

fig. 6: Mean pH

fig. 7: Mean concentration DO

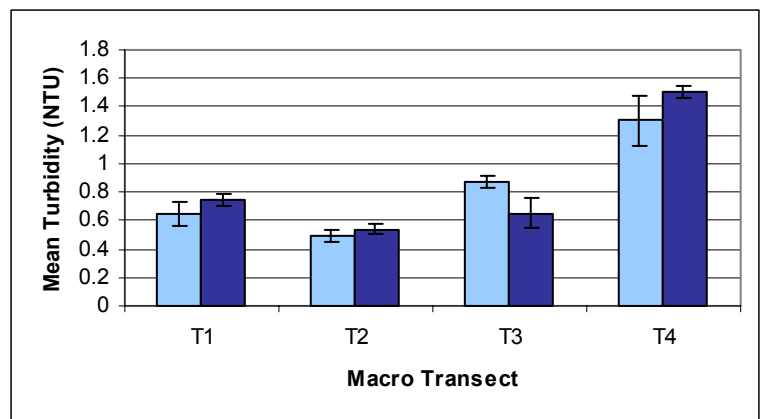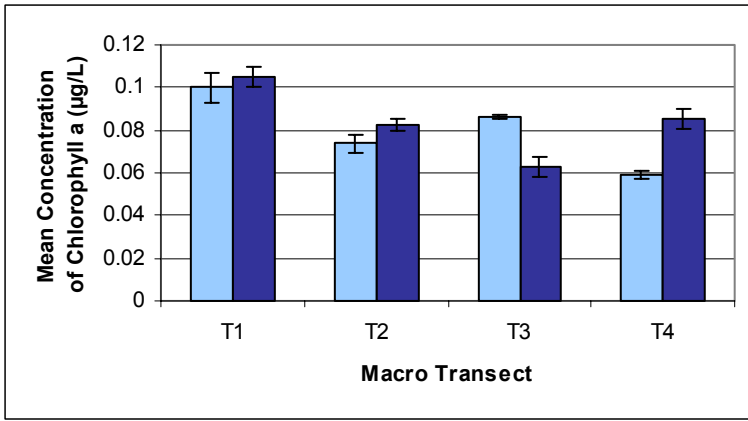| Macro Transect	Depth	Percent Saturation
T1	Deep	103
T1	Shallow	94
T2	Deep	97
T2	Shallow	95
T3	Deep	99
T3	Shallow	98
T4	Deep	94
T4	Shallow	95

Table 3: Mean percent saturation

fig 8: Mean turbidity
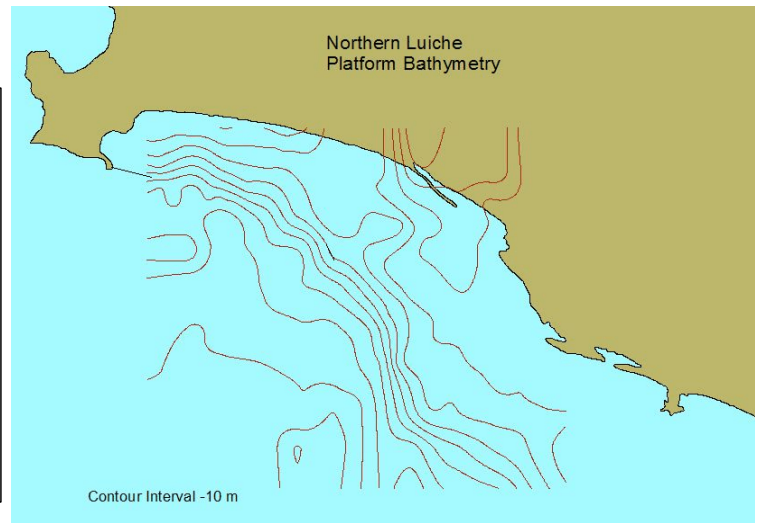
fig. 9: Mean conc. chlorophyll

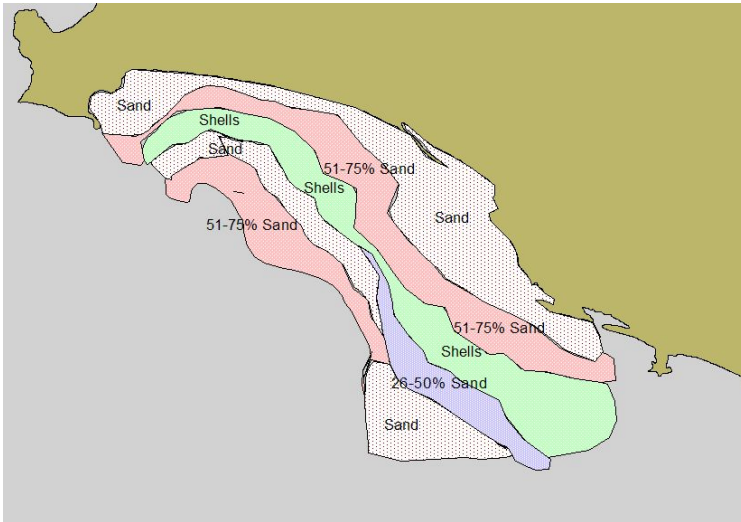fig 10: N. Luiche Bathymetry

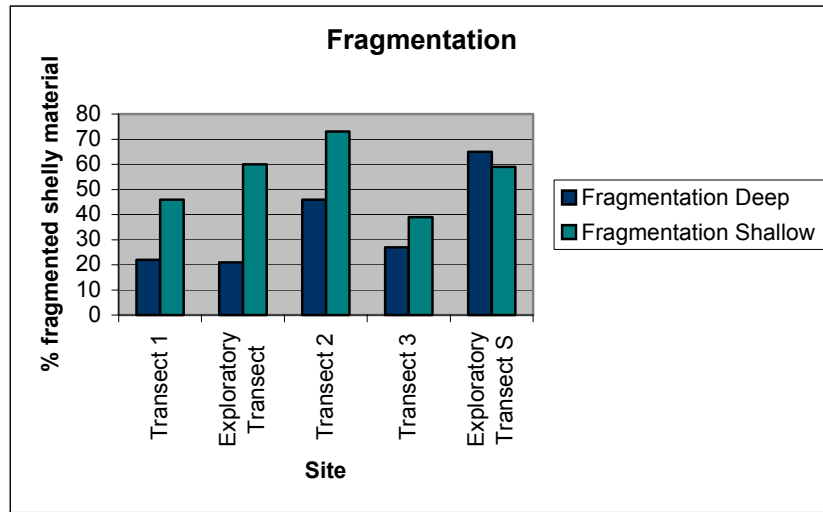fig. 11: Generalized facies map

fig. 12: Percent fragmentation

fig. 13: Deep and shallow abrasion

fig. 14: Deep and shallow encrustation