

Effects of Landscape Disturbance on Animal Communities in Lake Tanganyika, East Africa

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Abstract: Watershed deforestation, road building, and other anthropogenic activities result in sediment inundation of lacustrine habitats. In Lake Tanganyika, this threatens the survival of many rock-dwelling species by altering the structure and quality of rocky habitats. We investigated the relationship between habitat quality, as related to watershed disturbance intensity, and the biodiversity of faunal communities at three rocky littoral sites of low, moderate, and high disturbance. Turbidity measurements and other environmental observations confirmed that our lake sites represented a gradient of disturbance conditions. We documented differences in species density (number of species per constant area or time), species richness, abundance, and trophic ecology for fishes, molluscs, and ostracods. Fish censuses were performed by scuba divers at 1–20 m and by remotely operated vehicle (ROV) at 40–80 m. In the fish surveys, abundance, species density and richness, and herbivory reached their maxima at intermediate water depths. The depth range of herbivores, however, was restricted at higher-disturbance sites. The ROV fish surveys at the high-disturbance site showed high species richness despite low species density and abundance, and piscivores were proportionally more prevalent than in all other surveys. Molluscs censused by diver quadrats and sieve samples showed decreasing species richness and species density (sieve samples only) with increasing disturbance and no significant abundance trend. Ostracod species richness was similar between low- and moderate-disturbance sites but was markedly lower at the high-disturbance site (species density and abundance data were not available). Our faunal analyses suggest that all three taxonomic groups are negatively affected by sediment inundation but may have varying response thresholds to disturbance. Further, this study emphasized the utility of using complementary survey techniques to monitor and ultimately manage biodiversity in complex freshwater ecosystems.

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Efectos de la Perturbación del Ambiente sobre las Comunidades animales en el Lago Tanganyica, Africa Oriental

Resumen: *La deforestación de las cuencas, construcción de caminos y otras actividades antropogénicas resultan en la inundación de sedimento en los habitats lacustres. La sobrevivencia de muchas especies está en peligro en el Lago de Tanganyica debido al cambio de la estructura y calidad de habitats rocosos. En este estudio investigamos la relación entre la calidad del habitat, en función de la intensidad de la perturbación de la cuenca, y la biodiversidad de las comunidades faunísticas en tres áreas litorales rocosas caracterizadas por perturbación baja, moderada, y alta. Inicialmente, seleccionamos estos sitios basados en la extensión de la deforestación de las cuencas. Mediciones de turbidez y otras observaciones del medio ambiente confirmaron que estos sitios del lago representan un gradiente de las condiciones de perturbación. Documentamos las diferencias de densidad de especies (número de especies en una área o tiempo constante), riqueza de especies, abundancia y ecología trófica de peces, moluscos y ostracodos. El censo de peces fué hecho por buzos en los primeros 20 m de profundidad y por un vehículo operado remotamente (ROV) entre los 40 y 80 m. En el muestreo de peces, la abundancia, densidad y riqueza de especies y hábitos herbívoros alcanzaron sus máximos en profundidades intermedias. Sin embargo, el rango de profundidad de herbívoros, fue restringido en sitios de alta degradación. Las muestras de ROV en los sitios de alta degradación mostraron altas riquezas de especies a pesar de la baja densidad y abundancia, y los piscívoros fueron proporcionalmente más comunes que en las demás muestras. Los censos de moluscos obtenidos en cuadrantes mediante buceo y muestras tamizadas mostraron un decremento de riqueza y densidad de especies (muestras de cribado únicamente) con un incremento de la perturbación, sin ninguna tendencia de abundancia significativa. La riqueza de especies de ostrácodos fue similar entre los sitios de perturbación baja y moderada pero notablemente menor en los sitios de alta degradación (no hubo datos de densidad y abundancia específicas). Los análisis de fauna sugieren que los tres grupos taxonómicos están afectados negativamente por la inundación de sedimentos pero puede haber variantes en la respuesta a la perturbación. Además, este estudio da énfasis en la utilidad de usar técnicas complementarias de muestreo para observar y eventualmente manejar la biodiversidad de ecosistemas complejos de agua dulce.*

Introduction

Lake Tanganyika lies in the western branch of the African Rift. It is one of the world's largest, deepest, and oldest lakes, and harbors over 1400 species of animals, plants, and protists, many endemic to the lake (Coulter 1994). The ecosystem is characterized by species-poor pelagic communities but diverse littoral-sublittoral communities. The latter include largely endemic species flocks of cichlid and noncichlid fishes, molluscs, and crustaceans that are renowned for their morphological, ecological, and behavioral diversity (Coulter 1991). Extant biodiversity in Lake Tanganyika is threatened by a variety of human activities.

Sediment inundation resulting from watershed deforestation and other activities (e.g., municipal and industrial discharges, road building) is among the most immediate and important for littoral-sublittoral communities (Cohen et al. 1993; A. Vandellannoote, personal communication). Cohen et al. (1993) found low species richness among fishes and ostracods associated with adjacent watershed deforestation. Unfortunately, the responses of different taxonomic groups were not directly comparable because of differences in sampling methodologies.

Increases in the suspended sediment loads that are carried by influent water masses can alter rocky benthic habitats in several ways (Cohen et al. 1993). Increased turbidity may reduce light penetration and result in de-

creasing levels and maximum depths of benthic primary productivity in the littoral zone. In undisturbed areas of Lake Tanganyika, the rocky littoral zone normally experiences exceptional water clarity; the mean euphotic zone extends to 28 m (Hecky 1991), although benthic algae often grow well below this depth. Incoming sediments may also bind or release nutrients or toxins, altering energy flows through communities. Cracks and crevices fill with sediments, reducing habitat heterogeneity. This reduces the range of potential habitat types and predation refuges for many highly specialized, stenotopic, or juvenile fish and invertebrate species. Burial of rocky substrates also decreases the surface area available for epilithic algal growth and invertebrate colonization.

Concern about the potential effects of these anthropogenic disturbances is high in the riparian region because of the economic importance of the lake's biotic resources. Given this concern, how should the conservation biologist or manager monitor the health of such a complex freshwater ecosystem? Lake Tanganyika presents a formidable challenge because its littoral communities rival some marine environments in ecological complexity, and natural variability is poorly understood. We attempted to ascertain the consequences of landscape disturbance for lake biota by integrating environmental and faunal surveys to determine whether species density, species richness, and abundance change systematically along a disturbance gradient. In particular, we were in-

terested in determining whether different taxonomic groups responded in concert to environmental stress and whether we could detect changes in trophic structure among fish communities.

Our primary aim was to assess the effects of watershed disturbance on the unique fauna of Lake Tanganyika's nearshore rocky habitats. In addition, we were interested in developing protocols for monitoring biodiversity in this lake. Extensive knowledge of the diversity and distribution of Tanganyikan organisms (e.g., Brichard 1989; Coulter 1991) and the immediacy of human population pressures threatening the lake's ecological dynamics (Caljon 1992; Bootsma & Hecky 1993; Cohen et al. 1993; Coulter & Mubamba 1993; Lowe-McConnell 1993) made Tanganyika an appropriate subject for this study.

Methods

Study Sites and Data Collection

We collected census data for fishes, molluscs, and ostracods from rocky habitats at three sites in order to compare community diversity and sediment inundation. Our sites (Fig. 1) were located in the northern basin of the lake, where human population densities are most variable and a range of disturbance conditions exists. Sites were initially selected based on visually obvious differences in the extent of watershed deforestation. The extent of deforestation was confirmed qualitatively by ground surveys because recent LANDSAT images without cloud cover were not available for all three drainages.

Our low-disturbance site was at Cape Banza on the Ubwari Peninsula in the Democratic Republic of Congo (lat 4°3.07'S, long 29°14.64'E). Human population density is lower here than at our other sites (<5 people/km²; République du Zaïre 1988), and there are no roads. Watersheds are small, limiting sediment discharge. The area of the wa-

tershed adjacent to our study site is 0.23 km². Some deforestation has occurred along the eastern side of the peninsula since the late 1980s, including areas adjacent to our study site, but the watershed remains largely untilled.

Our moderate-disturbance study site was at Luhanga, approximately 11 km south of Uvira in the Democratic Republic of Congo (lat 3°30.35'S, long 29°9.43'E), where human population density is 20–50 people/km² (République du Zaïre 1988). The watersheds draining this area are considerably larger than those at Cape Banza: the area of the watershed adjoining this study site is 6.96 km². Deforestation has accelerated in this area during the past decade, and much of the watershed has been converted to cassava and banana cultivation. Nearby road work resulted in rubble accumulation in the shallower portions of the study location in 1992.

Our high-disturbance site was located approximately 3 km south of Gitaza in northern Burundi, offshore of the 28.9-km highway marker (lat 3°37.45'S, long 29°20.93'E), where human population density is 200–399 people/km² (République du Burundi Bureau Central de Recensement 1990). Watersheds in this region are also larger than on the Ubwari Peninsula, with the watershed onshore from this study site having an area of 2.33 km². Deforestation and conversion to cassava and banana cultivation is nearly complete. Other disturbances include road resurfacing with rubble input to shallow waters in 1992, fish collection for the international aquarium trade, and artisanal fishing activity (gill netting and purse seining).

At all sites, rocky habitats were interspersed with sandy or muddy habitats, which serve as sources of non-rocky habitat species. Bedrock at the three study sites is similar in chemical composition, so qualitative differences in incoming sediment stem from area, gradient, and land-use differences among the watersheds.

All turbidity measurements and faunal census data were collected during October–December 1992, coinciding with the rainy season at Lake Tanganyika, when

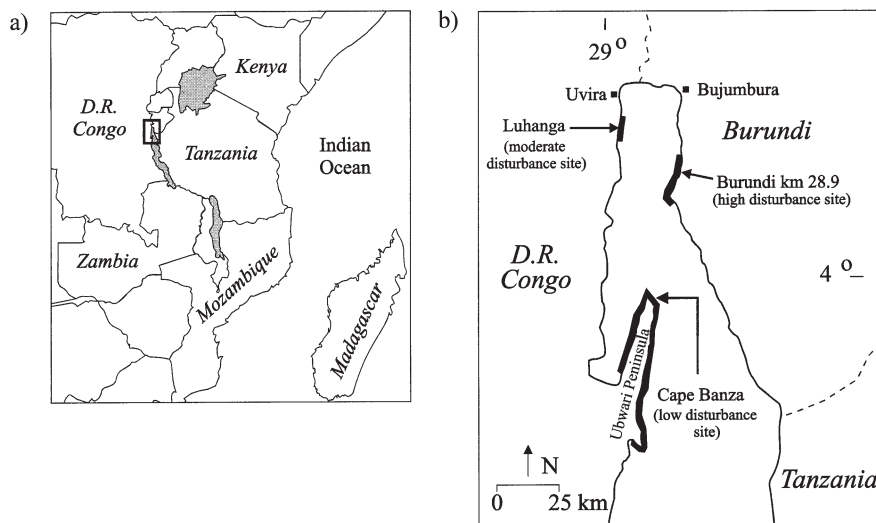


Figure 1. Map of east Africa, with the largest of the African Great Lakes depicted, from north to south: Lake Victoria, Lake Tanganyika, and Lake Malawi (D.R. Congo, Democratic Republic of Congo) (a) and location of biodiversity study sites (b). The area of continuous rocky littoral habitat near each study site is indicated by black shading (adapted from Brichard 1989).

lake and river turbidity and sediment discharge were all at their annual maxima. Given our limited window of opportunity to use the remotely operated vehicle (ROV), we chose to sample during the wet season in order to incorporate direct measurements of environmental differences among our sites.

Evaluation of Water Quality

Turbidity measurements were collected from lake waters and influent rivers near each site with a Hach (Model 2100P) turbidimeter. These values serve as a short-term proxy for measures of sedimentation rate over longer intervals. Turbidity measurements are on a logarithmic scale and were thus log-transformed before statistical analysis. Lake and river measurements were treated separately. Measurements taken within the lake reflected background turbidity levels in the water column but were strongly affected by time of day and wind speed, which influence standing primary productivity levels. Productivity levels also depend on nutrient concentrations, which may be affected by incoming sediment loads. River measurements were more important for assessing influent river sediment inputs; these values fluctuated with discharge pulses following rainfall and reflect actual sediment loads in influent rivers.

The maximum depth of benthic algal growth was recorded by scuba divers and a Phantom II ROV. The sampling arm of the ROV was used to excavate small trenches to determine whether sediments at each site were laminated or bioturbated. Laminated, or undisturbed, layers of sediment indicate depositional conditions (e.g., high sedimentation rate or anoxia) unsuitable for faunal inhabitation. Denser influent river waters follow lake bottom topography and deposit more sediment on rocky slopes than would be evident solely from observation of lake surface water turbidity (Craig 1974; Wombwell 1986). Although surface turbidity measurements reflect individual pulses of sediment influx, observations of sediment quality and algal growth were useful for inferring relative sediment deposition and light penetration conditions over the longer term among sites.

Faunal Censuses

Quantitative fish census data were collected at each site by scuba divers at depths of 1, 5, 10, and 20 m and by analyzing ROV videotapes taken at depths of 40, 60, and 80 m. Bottom time available to divers at 40 m was too short to collect quantitative data, but qualitative data were collected at 40 m at all sites for comparison of the two census methods.

The scuba transects involved laying out two parallel 25-m transect lines 2 m apart at each depth, allowing sufficient time for fishes to resettle, and then counting and identifying all fishes between the transect lines (cf.

Ribbink et al. 1983; taxonomy following Poll 1956, 1986; Liem & Stewart 1976; Travers 1988; Daget et al. 1991). At least two replicate samples were collected at each depth, each taking 20–30 minutes.

For deep-water fish surveys, we employed a Phantom II ROV operated from the mother ship via a 300-m tether. The ROV was equipped with a PISCES remote conductivity-temperature-depth (CTD) probe with pH and dissolved oxygen sensors and a video camera with laser telemetry for size determinations and telephoto capability for close-up identification work. Constant area transects proved impractical for the ROV fish surveys. Therefore, ROV census samples were time transects, with all fishes observed in 10-minute intervals of video footage at each study depth being counted and identified using only segments of videotape in which the ROV was moving along the transect (field of view approximately 2 m wide at 1 m in front of the camera). Three to five replicate samples were tallied at each depth. Because the pilot maintained a fairly constant ROV speed of approximately 0.1 knot (185 m/h), each 10-minute interval corresponds to approximately 30 m of travel. The ROV typically cruises approximately 1 m off the bottom.

The scuba and ROV transect data are not directly comparable because of differences in transect area and time (Bortone et al. 1986), acuity of the human eye compared to ROV lenses (Greene & Alevizon 1989), variable responses of fish species to divers versus the ROV, and the effects of decreasing light levels with depth on identification accuracy and fish reactions to diver or ROV presence. The scuba and ROV survey methods are both prone to certain biases. Diurnal transects underestimate nocturnal as well as cryptic species counts and abundances. Because our transect areas were large, small species were also underestimated. Although we tried to select sites with comparable habitat complexity, our sites differed in this respect because of sediment inundation at the more disturbed sites. With fewer refuges at these sites, we might expect to detect a higher percentage of all species and individuals living within the transect area. This tends to inflate diversity estimates at the more disturbed sites, giving a conservative estimate of diversity differences among sites. Many researchers exclude wandering species—those that do not permanently reside in the target habitat—because they can bias species counts toward an overestimation of within-habitat species diversity. For this reason we have followed other workers (e.g., Luckhurst & Luckhurst 1977) and excluded wandering species from all analyses (they are indicated in Appendix 1), although their observed abundances are reported in the fish species list.

Other potential censusing biases, which we believe were not major concerns in this study, are as follows. Visibility at all sites was 2–3 m, so we do not consider this a likely source of error. Consistency of species identifications among divers was not a problem either, be-

cause divers discussed survey observations after each dive and agreed upon consistent names for species in question. One individual was responsible for the identification of all fishes on the ROV transects, so those data were also internally consistent.

Fish species were assigned to six trophic groups based on available gut content and behavioral data: benthic algivores, phytoplanktivores, benthic invertivores, zooplanktivores, piscivores, and omnivores/unknown species (Poll 1953, 1956; Gashagaza & Nagoshi 1985; Mbomba 1983; Nshombo 1983; Yamaoka 1983; Brichard 1989; M. Hori, personal communication) (Appendix 1). These groups were intended to represent the dominant food type consumed by each species but do not necessarily reflect the dietary breadth of most species.

Mollusc diversity data were collected by scuba divers in the form of visual surveys (for larger taxa) and sieved sediment samples (taxonomy following von Martens 1897; Leloup 1953; Brown 1994; West 1997). Visual surveys consisted of tallies by species of all molluscs within 1-m² sampling quadrats. Quadrats were placed haphazardly on rocky substrate at each study depth, and smaller rocks were turned over to count all live molluscs. There were one to three replicates at each depth. Sediment samples were collected from 1-m² areas so that census coverage could include smaller and infaunal species. Sediments were coarsely sieved with a 2.0-mm screen. Both live and recently deceased individuals were counted (Appendix 2), and the latter were identified with the aid of Rose Bengal stain.

Ostracods were extracted from sediment samples taken from rocky crevices, ledges, or sandy patches adjacent to rocky habitats. We collected 250-cm³ sediment samples from the upper 1 cm of sediment. Samples were fine-sieved (100 µm sieve) to remove fine debris, and 350 individuals in each sample were identified to species with a stereomicroscope (following Rome 1962; Martens 1985; Wouters & Martens 1992, 1994) (Appendix 3). One sample was collected and tallied for each depth at all three sites. Of the estimated 200 ostracod species in Lake Tanganyika, the majority remain undescribed, but extensive collections of reference material at the University of Arizona (with A.S.C.) and the Royal Belgian Institute of Natural Sciences (with K.M.) made consistent identifications possible.

Data Analysis

Sample sizes for fish and mollusc surveys varied. Raw species counts in each transect or quadrat give an estimate of species density (number of species per constant area or time). It is also useful to be able to compare species richness in samples of constant size to account for variation in sampling intensity. To estimate the number of species expected with constant sample size, we used Hurlburt's rarefaction method (Magurran 1988). The smallest sample

size among compared samples served as the standard, and extremely small samples were discarded. We report both species density from raw species counts and species richness estimates based on rarefaction. We use the term *diversity* to encompass measures of both species density and species richness.

Faunal similarity among sites and across depths was calculated according to both Jaccard and Simpson similarity indices (Simpson 1960; Magurran 1988). Comparisons of faunal similarity were made between pairs of sites, with species lists pooled across depths for each site, and between adjacent depths within each site. Both indices are biased when species counts are highly dissimilar; the Jaccard index is biased toward greater differences, whereas the Simpson index is biased toward greater similarity.

We computed means for species density, rarefied species richness, and abundance for each site at each depth and for each site with depths pooled. Generally, replicate sampling was inadequate for comparisons among sites involving individual depths, but analysis of variance with replicates combined among depths provided conservative tests for between-site differences because pooling multiple depths increased within-site variability. Analysis of variance was performed, and the null hypothesis was that species density or richness, abundance, or turbidity varied more within sites (i.e., across depths) than among localities. When the null hypothesis could be rejected, pairwise *t* tests were used to compare individual sites. To correct for errors associated with multiple comparisons, the Bonferroni method was employed (Sokal & Rohlf 1995), giving an alpha criterion of 1.67% (=5%/3 possible comparisons).

Results

Water Quality

Cape Banza, the low-disturbance site, had significantly lower lake turbidity levels than the moderate (Luhanga) and high (Burundi) disturbance sites, which did not differ significantly from each other (Tables 1 & 2). River turbidity measurements reflected consistently increasing turbidity with disturbance, although the low- and moderate-disturbance sites were not significantly different from each other.

Maximum depths (z_{\max}) of benthic algal growth and bioturbation indicated that the observed turbidity gradient among our sites probably accurately reflected longer term average conditions. At the low-, moderate-, and high-disturbance sites, the z_{\max} values for benthic algal growth were 63, 50, and 35 m, and the z_{\max} values for bioturbation were 95, 92, and 75 m, respectively.

Divers noted that the rocky slope at Cape Banza was not inundated with sediments; the thin veneer of sedi-

Table 1. Results of analysis of variance for differences in turbidity, species density, rarefied species richness, and abundance among study sites in Lake Tanganyika.

Variable	Site ^a			F, df, p
	Cape Banza (low dist.)	Lubanga (moderate dist.)	Burundi (high dist.)	
Turbidity ^b				
lake	-0.38 (0.17)	-0.066 (0.17)	-0.084 (0.12)	5.48; 2,27; 0.005
river	0.63 (0.36)	0.88 (0.62)	1.87 (0.72)	36.12; 2,136; 0.005
Species density				
fishes (scuba)	23.1 (3.45)	19.6 (6.52)	17.8 (3.49)	3.05; 2,27; 0.05
fishes (ROV)	8.2 (3.51)	5.4 (1.79)	5.1 (3.18)	4.56; 2,35; 0.025
molluscs (quadrat)	3.3 (1.52)	2.7 (1.35)	2.5 (0.76)	1.21; 2,41; ns
molluscs (sieve)	14.8 (3.83)	10.6 (4.72)	6.4 (3.51)	13.97; 2,44; 0.025
ostracods	28.8 (5.40)	31.0 (4.74)	20.2 (4.02)	6.96; 2,12; 0.025
Rarefied species richness				
fishes (scuba)	17.7 (3.42)	18.8 (4.00)	12.3 (3.34)	7.76; 2,24; 0.005
fishes (ROV)	5.0 (0.82)	4.0 (0.86)	6.6 (1.81)	11.00; 2,25; 0.001
molluscs (quadrat)	5.0 (1.28)	3.1 (1.04)	1.8 (0.51)	8.12; 2,10; 0.025
molluscs (sieve)	8.3 (1.36)	5.9 (0.80)	3.8 (1.35)	19.91; 2,17; 0.005
Abundance				
fishes (scuba)	524.9 (476.0)	223.4 (159.6)	1015.0 (753.7)	5.98; 2,27; 0.01
fishes (ROV)	164.3 (122.9)	83.3 (45.0)	22.0 (17.9)	10.50; 2,35; 0.001
molluscs (quadrat)	12.8 (23.9)	20.7 (18.8)	27.8 (22.2)	1.48; 2,41; ns
molluscs (sieve)	79.4 (44.8)	160.3 (162)	86.4 (98.1)	2.77; 2,44; ns

^aMeans (and standard deviations) are reported for each data set in the site columns.

^bTurbidity measurements are given in log(NTU) where NTU is normalized turbidity units.

ment present at this locality was composed of locally derived shell fragments and other autochthonous organic detritus. In contrast, rocky slopes at Luhanga and Burundi were inundated by terrigenous sediments and covered with extensive bacterial mats starting at around 100 m at Luhanga and at 80 m at Burundi. No bacterial mats

were observed at Cape Banza in the deepest ROV observations at 96 m. Finally, shallow trenches dug by the ROV arm showed that the sediments blanketing the rocky slopes at Luhanga and Burundi were laminated, black, and rich in organic material, indicating rapid burial and accumulation of anoxic sediments.

Table 2. Results of Bonferroni-corrected pairwise *t* test comparisons of turbidity, species density, rarefied species richness, and abundance between study sites in Lake Tanganyika.

Variable	Site		
	Cape Banza-Lubanga (low-moderate dist.) t, df, p	Lubanga-Burundi (moderate-high dist.) t, df, p	Burundi-Cape Banza (high-low dist.) t, df, p
Turbidity			
lake	-4.34, 21, 0.001	0.23, 17, ns	3.99, 16, 0.01
river	-0.79, 53, ns	-8.11, 133, 0.001	3.41, 86, 0.01
Species density			
fishes (scuba)	1.55, 20, ns	0.74, 17, ns	-3.31, 17, 0.01
fishes (ROV)	2.56, 24, ns	0.35, 24, ns	-2.26, 22, ns
molluscs (sieve)	3.03, 36, 0.01	2.34, 24, ns	-5.64, 28, 0.001
ostracods	0.68, 8, ns	3.89, 8, 0.01	2.86, 8, ns
Rarefied species richness			
fishes (scuba)	-0.66, 17, ns	3.53, 14, 0.01	-3.41, 17, 0.01
fishes (ROV)	2.59, 21, ns	-4.21, 16, 0.001	2.53, 13, ns
molluscs (quadrat)	2.24, 7, ns	2.38, 9, ns	-4.85, 4, 0.01
molluscs (sieve)	4.44, 15, 0.001	3.43, 10, 0.01	-4.91, 9, 0.001
Abundance			
fishes (scuba)	1.99, 20, ns	-3.41, 17, 0.01	1.74, 17, ns
fishes (ROV)	2.30, 24, ns	4.42, 24, 0.001	-3.97, 22, 0.001

Faunal Censuses and Rarefaction

Across taxonomic groups, mean species density, species richness, and abundance varied with depth (Fig. 2). Fish and mollusc species richness peaked at shallow to intermediate depths and declined at greater depths, whereas ostracod species richness increased discontinuously up to 40 m.

In shallow (scuba) transects, mean rarefied fish species richness was significantly greater at Cape Banza (low disturbance) and Luhanga (moderate disturbance) than at the Burundi (high disturbance) site (Table 2), and mean

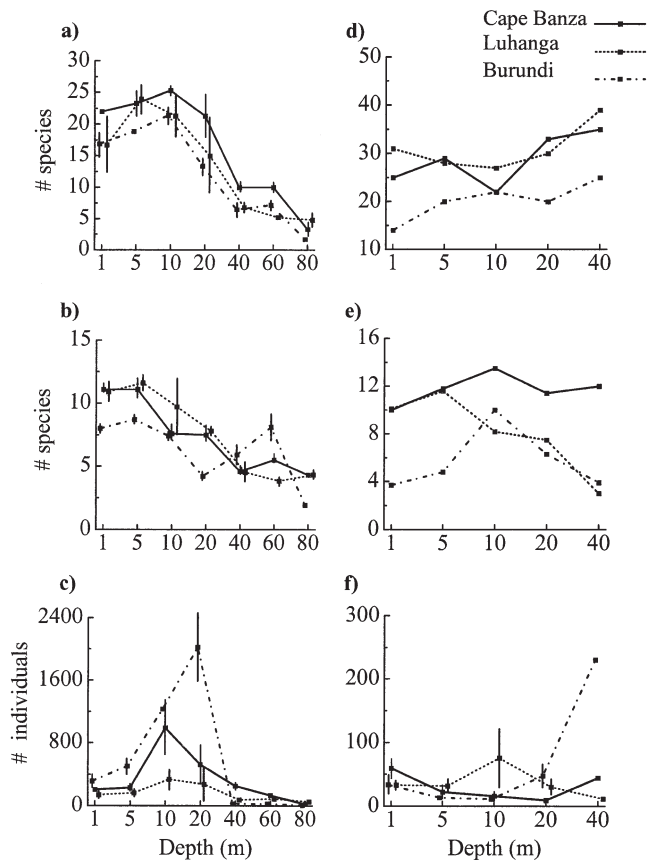


Figure 2. Profiles of species density (number of species per time or area transect), species richness (number of species in a constant sample size), and abundance (number of individuals per sample) against depth: fishes, species density (a); fishes, mean rarefied species richness at each depth (sample sizes used for rarefaction were 29 individuals for 0–20 m and 20 individuals for 40–80 m) (b); fishes, mean abundance per sample for scuba and ROV surveys (c); ostracods, species counts for each sample (d); molluscs, single rarefied estimate for each site with all samples (sieve + quadrat) at each depth pooled (e); molluscs, mean abundance per sample for sieve and quadrat data together (f). Error bars indicate the standard error for points representing multiple data points.

species density was significantly higher at Cape Banza than at Burundi. Average abundance data showed no obvious trend relating to sediment effects, with significantly fewer individuals at the moderate- than at the high-disturbance site. The ROV transects revealed different diversity trends in deeper waters (Table 1). Average rarefied species richness was significantly higher at Burundi than at Luhanga. Species density was lower at both Burundi and Luhanga than at Cape Banza in the analysis of variance, and the Bonferroni-corrected, pairwise *t* tests lacked adequate power to pinpoint the source of this difference. Abundance of fish in the ROV transects declined with increasing disturbance across sites; both Cape Banza and Luhanga had significantly more fishes than Burundi.

Mean rarefied mollusc species richness decreased with increasing disturbance regardless of whether quadrat or sieve data were considered, although not all pairwise comparisons were significant (Tables 1 & 2). Species density decreased with increasing disturbance only in the sieve data, with Cape Banza and Luhanga having significantly higher species density than Burundi. Mollusc abundance appeared to increase with disturbance in the quadrat data and showed no pattern in the sieve data. The variance, however, was too large to establish statistical differences.

Observed ostracod species richness was significantly higher at Luhanga than at Burundi. Because a constant number of individuals were counted for each sample, comparative abundance and density data were not available.

Fish Trophic Analyses

The proportional importance of herbivores (benthic algae and phytoplanktivores) declined at shallower depths with increasing disturbance (Fig. 3). The percentage of individuals feeding on benthic invertebrates and zooplankton increased with increasing depth at all sites, but did so more steeply at the moderate- and high-disturbance sites, compensating for the relative decline in herbivory. Piscivory was a relatively minor feeding mode at all sites and depths, except in the ROV survey of high-disturbance sites, where the highest percentage of piscivores was seen despite the low absolute numbers of individuals.

Numerical abundance of herbivores was also highest at Cape Banza and persisted to greater depths than at the more disturbed sites. Microcarnivores (benthic invertebrates and zooplanktivores) showed their largest peaks at Luhanga and Burundi, with zooplanktivores being especially abundant at the Burundi site. Piscivores made up only a small number of the individuals surveyed at all sites and depths.

Similarity Indices and Community Structure

Jaccard and Simpson indices show that fish faunal similarity was high across depths in the shallower portion of

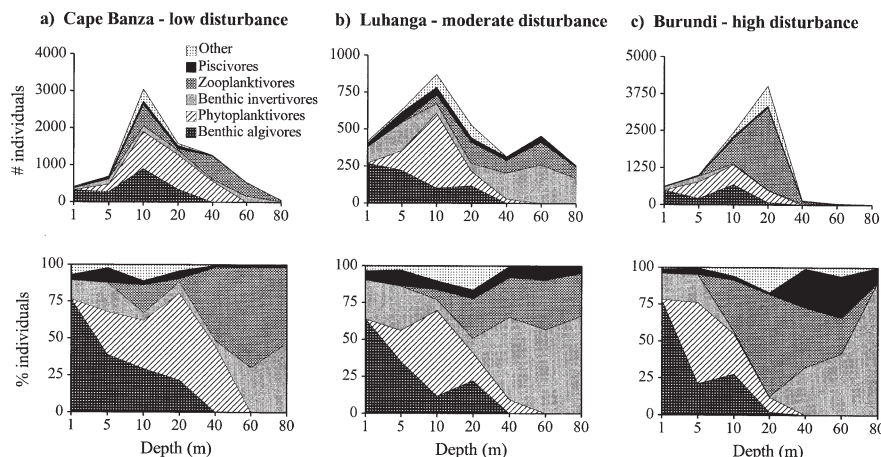


Figure 3. Depth profiles of total numbers of individuals and percentages of individuals belonging to each trophic group at each site: Cape Banza, low-disturbance site (a), Luhanga, moderate-disturbance site (b), and Burundi, high-disturbance site (c).

each survey and declined along with species density and richness starting between 20 and 40 m, and that faunal similarity among sites was higher in scuba transects and lower in ROV transects (Table 3). Faunal similarity for molluscs and ostracods was generally high as well, both among depths within a site and across sites.

Fish species abundances observed by scuba at Cape Banza and Luhanga were more equitably distributed and included more uncommon species than the Burundi fish fauna (Fig. 4). Similar trends were apparent for molluscs and, to a lesser extent, ostracods, but no clear differences were apparent in ROV fish surveys.

Discussion

Regional concern about the potential for serious human effects on the Lake Tanganyika ecosystem was spurred by observations of Lake Victoria’s dramatic ecological

turnover and instability over the last two decades (cf. Goldschmidt et al. 1993). Lakes Victoria and Tanganyika appear to be experiencing somewhat different forms of environmental degradation, however, and may manifest faunal responses quite differently as well. Cichlid species in Lake Victoria may find refuge from fishing and predation pressures in rocky habitats and marginal ponds and swamps (Ogutu-Ohwayo 1993), but reproductive barriers among cichlid species there are easily breached under the present eutrophic conditions, thereby reversing speciation-in-progress for many nascent species (Seehausen et al. 1997). In contrast, rocky habitat communities in Lake Tanganyika are most threatened by sediment inundation along heavily deforested shorelines, eliminating habitat and refuge alike for rock-dwelling fish, mollusc, and ostracod species. Turbidity measurements and other environmental observations clearly differentiated our low- and high-disturbance sites from each other, with the moderate-disturbance site being more similar to one

Table 3. Jaccard and Simpson indices of similarity for all taxonomic groups.*

	<i>Site</i>		
	<i>Cape Banza (low dist.)</i>	<i>Lubanga (moderate dist.)</i>	<i>Burundi (high dist.)</i>
<i>Averages across depths</i>			
Across depths			
fishes (scuba)	0.50–0.72	0.56–0.79	0.54–0.81
fishes (ROV)	0.33–0.66	0.29–0.50	0.22–0.36
molluscs (all)	0.62–0.84	0.52–0.74	0.43–0.71
ostracods	0.45–0.70	0.52–0.73	0.48–0.72
	<i>Site</i>		
	<i>Cape Banza-Lubanga (low-moderate dist.)</i>	<i>Lubanga-Burundi (moderate-high dist.)</i>	<i>Burundi-Cape Banza (high-low dist.)</i>
Across sites			
fishes (scuba)	0.63–0.87	0.53–0.82	0.44–0.82
fishes (ROV)	0.31–0.52	0.41–0.59	0.28–0.50
molluscs (all)	0.62–0.90	0.40–0.67	0.45–0.87
ostracods	0.50–0.68	0.39–0.68	0.52–0.85

*Similarity values between all pairs of adjacent depths within each site were averaged for each data set (across depths). Similarity values between pairs of sites are based on species lists pooled across depths for each site (across sites). Values are in the form of Jaccard-Simpson.

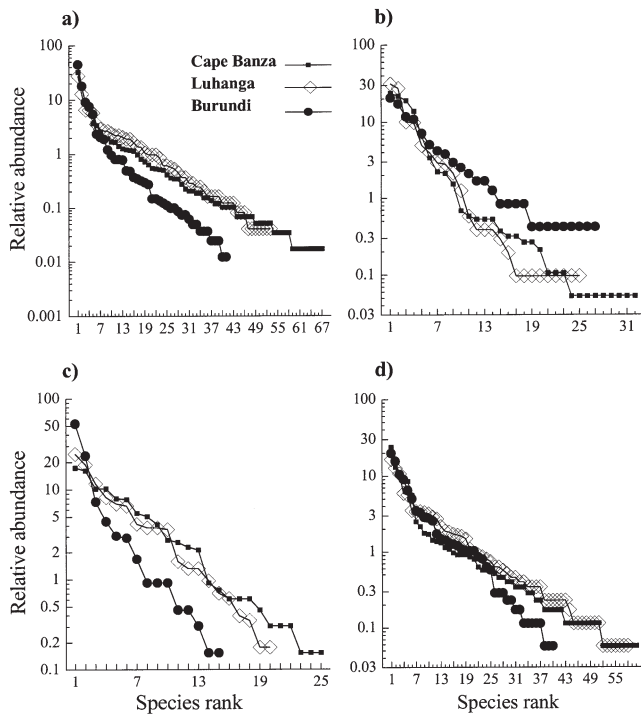


Figure 4. Rank abundance curves for surveyed communities fish (scuba) (a), fish (ROV) (b), mollusc (c), and ostracod (d).

or the other, depending on the variable. Our faunal data show that species richness and density correlated negatively with sediment disturbance level for fishes, molluscs, and ostracods in rocky Tanganyikan habitats, although the statistical comparisons, particularly between the moderate-disturbance site and either disturbance gradient end member, were not always robust. An exception to this pattern of declining species richness with increasing disturbance was that rarefied species richness in the ROV fish surveys was highest overall at the high-disturbance site. The only significant abundance trends were seen in the fish survey data. In shallow transects, the moderate-disturbance site had significantly fewer fishes than the high-disturbance site. In deep-water transects, fish abundance declined with increasing disturbance level.

Similarity Indices and Community Structure

To infer environmental quality from species assemblage data, it is important that species distributions be broad enough that a common species pool is shared across sites and that environmental tolerances of the constituent species are known. Further, it is important not to confound geographically circumscribed species distributions with interpretations of environmental tolerances or quality. Many of the numerically dominant species in all taxa were common to all three sites, as were a large number of the less dominant species (Appendices 1–3).

Declining similarity values for fishes at depths >20 m (both among and within sites) possibly reflected the disappearance of numerically dominant and widespread herbivorous species with increasing depth. The effect of decreasing light levels on visual fish identifications may also have contributed to lower similarity values at greater depths.

Ecological Tolerances

Depth profiles for fishes show that herbivores such as benthic algal feeders and phytoplanktivores were typically prevalent at shallower depths and were gradually replaced by microcarnivores (benthic invertivores and zooplanktivores) with increasing depth as algae became less abundant (Brichard 1989). The depth range of herbivore domination was restricted to shallower depths at more disturbed sites, with microcarnivory increasing at shallower depths compared to the low-impact site. A likely cause of this restriction is decreased water clarity or substrate inundation associated with increasing sediment influx (Table 1). The huge peak seen in zooplanktivore abundance at Burundi supports the hypothesis of McKaye and Gray (1984) that zooplanktivores, given their mobility, resettle disturbed areas more rapidly than benthic feeders.

Increased sediment loading may contribute to increased bacterial production by providing surplus nutrient influx and biological oxygen demand, leading to anoxic conditions near the substrate-water interface at depths much shallower than the oxycline. Laminated sediments, indicating little bioturbation and anoxic conditions, as shallow as 40 m at Burundi, and the presence of bacterial mats at Luhanga and Burundi both suggested a decline in oxygen levels near the sediment-water interface at our more disturbed sites.

Such conditions may help explain patterns of diversity and abundance observed at greater depths in our surveys. Fish abundance was high in all scuba transects but declined sharply with depth, particularly in the Burundi ROV census. In the mollusc surveys, abundance appeared to increase dramatically at the 40-m collection point of the high-impact site, although this peak was not statistically significant. Differences in oxygen metabolism between fishes and invertebrates could lead to differential tolerance to low-oxygen conditions. Michel (1994) noted that some gastropod species are more tolerant of hypoxic conditions than others, and Coulter (1967) and Verheyen et al. (1994) made similar observations among species of Tanganyikan fish. Alternately, the concurrent increase in mollusc abundance and decrease in fish abundance may reflect changes in trophic competition pressure between fishes and molluscs.

Differences in life history may also partially explain the community-level responses of fishes, molluscs, and ostracods to the same environmental stress. Long life

spans and low reproductive replacement rates may render fishes and molluscs more susceptible to localized extinction following individual disturbance events or with increasing levels of disturbance. Tanganyikan ostracods are not ecologically well known but probably have significantly shorter life spans than fishes and molluscs and may reproduce several times per year (Martens 1994). Ostracods, being primarily detritivores, may respond positively in terms of both diversity and abundance with increased sediment input up to some threshold of inundation (Table 1). Because of their different life-history traits, molluscan and ichthyofaunas may continue to reflect disturbance longer after environmental perturbation abates than do ostracod communities.

Finally, changes in sediment influx resulting from land-use changes may result in qualitative structural differences in lake habitats, selectively eliminating some habitats and increasing the area of others. Many cichlids distinguish appropriate habitat based on the particle size, aspect, and water depth of rocky habitats (Brichard 1989). Sediment loading may lead to greater habitat homogeneity in the littoral-sublittoral zones of Lake Tanganyika by burying relatively rare rocky outcrop patches. Several interrelated effects of changing habitat complexity may affect standing diversity or abundance levels. Simplification of habitat structure by infilling of cracks and crevices results in fewer refugia from predation for many species or their juveniles and less overall habitat area for cryptic and nocturnal species. Many Tanganyikan cichlids are substrate spawners, unlike their rocky-habitat counterparts in Lakes Victoria and Malawi, which rely on female mouth-brooding for reproduction (Poll 1986; Seehausen et al. 1998). Inundation of habitat substrate therefore may have selective and dire consequences for reproductive success for these fishes. Because benthic productivity on rocks greatly exceeds that on sandy substrates (C. O'Reilly, personal communication), a reduction in rocky substrate area may have magnified effects on diversity and abundance at higher trophic levels. This may be reflected in a higher susceptibility of stenotopic rock-dwelling fish species than of sand-dwellers to extinction, which relates both to the degree of specialization in rock-dwelling cichlids and to the relative rarity of and distance between rocky habitat patches (cf. Bruton & Merron 1990; Ribbink 1990; Lowe-McConnell 1993). Increasing disturbance regimes may select for less stenotopic species that are able to cross barriers and recolonize disturbed habitats.

Lake Basin Parameters and Conservation

Lake basin morphology has important implications for conservation planning because the habitable portion of the bottom of Lake Tanganyika is delimited by the intersection of the steep lake bottom morphology with the oxycline (approximately 100 m depth in the northern

part of the lake and 250 m in the southern basin), resulting in a narrow ring of benthic habitat that encircles the lake's perimeter (Cohen 1995). The patchy distribution of substrates on the lake bottom (rocky, sandy, muddy) may have stimulated speciation through evolutionary time by making demographic and genetic exchange between adjacent populations of stenotopic species improbable or impossible (Michel et al. 1992; Sturmbauer & Meyer 1993). Local endemism in fishes and ostracods is high, with species ranges often limited to small stretches of shoreline (Brichard 1989; Cohen 1994). The same patchy habitat distribution and the degree of habitat specificity and stenotopy that may have fostered the origination of species may also render them more vulnerable to extinction, because habitat destruction and fragmentation lead to greater distances between neighboring populations and diminish their ability to recover from both natural and anthropogenic environmental perturbations by recolonization (Bruton & Merron 1990). Although we might expect Lake Tanganyika to be initially more resilient than Lake Victoria to environmental pressures because of Tanganyika's greater volume and lower human population density, large-scale changes in habitat or water quality may be even more difficult to remediate in Lake Tanganyika because of the geographic distribution of habitat types and long flushing time, respectively (cf. Bootsma & Hecky 1993).

Caveats

One inherent difficulty in monitoring biodiversity is that surveys represent isolated time points. Thus, our data lack temporal perspective on faunal stability. Although we lack long-term data sets for our sites, previous research by Hori et al. (1983) and Sato et al. (1988) provides fish species lists for two of our sites for comparison. Although sampling protocols, areas surveyed, and total species richness differed between surveys in both cases, their lists allow rudimentary comparisons. Of the 37 species observed by Hori et al. (1983) at Luhanga, 86% were resampled in our scuba transects. At Cape Banza, 80% of the 35 species tallied by Sato et al. (1988) were observed by our scuba divers. Data from Nakai and Yuma (1988) also allowed comparison of molluscan faunal stability through time at Cape Banza. Of 11 species observed by them, 73% were also observed by our divers. These comparisons suggest that spatial and temporal variability in littoral habitat communities are comparable among sites, and that this variability is unlikely to affect the qualitative trends in our results.

Conclusions

Our preliminary results using scuba and ROV transects and sieve sampling to survey environmental conditions

and biodiversity in Lake Tanganyika appear promising. Fish, mollusc, and ostracod diversity generally correlated negatively with disturbance level, although each taxonomic group may have a different response threshold. Our analyses suggest that censuses of both fishes and invertebrates, particularly those groups whose environmental tolerances are known, could provide useful information about the specific impetus of environmental pressures (e.g., oxygen levels). Fishes and molluscs may be more sensitive than ostracods in the early phases of sedimentation impact. Fish data collected by scuba and ROV were not directly comparable because of methodological differences, but both data sets were necessary for generating meaningful trophic depth profiles. The ROV was critical for recording data on environmental thresholds, such as maximum depths of algal growth and oxygenation, beyond depths accessible by scuba. Although its deployment came at considerable financial and logistical cost, it revealed patterns that would otherwise have been missed in our surveys, such as the precipitous drop in fish abundance at depth at the high-disturbance site.

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Appendix 1

Distribution and relative abundance of fish species across study sites in Lake Tanganyika.^a

	Scuba (1–20 m)			ROV ^b (40–80 m)		
	Cape Banza (low dist.)	Lubanga (moderate dist.)	Burundi (high dist.)	Cape Banza (low dist.)	Lubanga (moderate dist.)	Burundi (high dist.)
Benthic algivores						
<i>Asprotilapia leptura</i>	+	+	–	–	–	–
<i>Cunningtonia longiventralis</i>	–	+	–	–	–	–
<i>Cyathobarynx furcifer</i>	+	+	+	–	–	–
<i>Eretmodus cyanostictus</i>	+	++	+	–	–	–
<i>Limnotilapia dardennii</i>	+	+	–	–	–	–
<i>Opbthalmotilapia nasutus</i>	+	+	++	–	–	–
<i>Opbthalmotilapia ventralis</i>	+	+	–	–	–	–
<i>Petrochromis ephippium</i>	+	+	–	+	–	–
<i>Petrochromis famula</i>	+	+	–	–	–	–
<i>Petrochromis fasciolatus</i>	+	+	+	–	–	–
<i>Petrochromis orthognathus</i>	+	+	+	–	–	–
<i>Petrochromis polyodon</i>	+	+	+	–	–	–
<i>Pseudosimochromis curvifrons</i>	+	+	–	–	–	–
<i>Simochromis babaulti</i>	–	+	+	–	–	–
<i>Simochromis diagramma</i>	–	+	–	–	–	–
<i>Simochromis marginatus</i>	+	+	–	–	–	–
<i>Simochromis</i> sp.	–	+	–	–	–	–
<i>Spathodus marlieri</i>	+	–	–	–	–	–
<i>Tanganicodus irsacae</i>	–	+	–	–	–	–
<i>Telmatocbromis dbonti</i>	+	–	–	–	–	–
<i>Telmatocbromis temporalis</i>	+++	++	+++	–	–	–
<i>Tropheus moorii</i>	+	++	+	–	–	–
<i>Tropheus polli</i>	+	–	–	–	–	–
Benthic invertivores						
<i>Aethiomastacembelus</i> cf. <i>albomaculatus</i>	–	–	+	+	–	–
<i>Aethiomastacembelus platysoma</i>	–	+	–	–	–	–
<i>Altolamprologus compressiceps</i>	+	+	+	+	–	+
<i>Auchenoglanis occidentalis</i>	–	–	–	+	+	–
<i>Aulonocranus dewindti</i>	+	++	+	–	–	–
<i>Chalinochromis brichardi</i>	+	–	–	–	–	–
<i>Chrysichthys</i> sp.	+	–	–	+	–	–
<i>Gnathochromis permaxillaris</i>	–	–	–	–	–	+
<i>Gnathochromis pfefferi</i>	–	+	+	–	–	–
<i>Julidochromis marlieri</i>	+	+	+	–	–	+
<i>Julidochromis transcriptus</i>	+	+	–	–	–	–
<i>Lamprologus callipterus</i>	+	+	+	–	–	–
<i>Lamprologus</i> cf. <i>finalimus</i>	–	–	–	+++	++++	++
<i>Lobochilotes labiatus</i>	+	+	+	–	–	–
<i>Neolamprologus furcifer</i>	+	+	+	+	–	–
<i>Neolamprologus leleupi</i>	+	+	–	–	–	–
<i>Neolamprologus modestus</i>	–	–	–	+	–	–
<i>Neolamprologus mondabu</i>	+	+	+	–	–	–
<i>Neolamprologus toae</i>	++	+++	–	–	–	–
<i>Neolamprologus tredocephalus</i>	+	+	+	–	–	–
<i>Neolamprologus</i> n.sp. “bifrenatus”	+	–	–	–	–	–
<i>Neolamprologus</i> n.sp. “orange”	+	–	–	–	–	–
<i>Reganochromis calliurus</i>	–	–	–	–	–	+
<i>Synodontis dbonti</i>	+	–	–	–	–	–
<i>Synodontis multipunctatus</i>	+	–	+	+	–	–
<i>Synodontis petricola</i>	+	–	–	–	–	–
<i>Synodontis</i> sp.	+	–	–	+	–	+
<i>Trematocara</i> sp.	–	–	–	–	+++	+++
<i>Xenotilapia</i> cf. <i>caudafasciata</i>	–	–	–	–	+	+
<i>Xenotilapia flavipinnis</i>	+	+	+	–	–	–
<i>Xenotilapia fluorescens</i>	–	–	–	+	–	–
<i>Xenotilapia sima</i>	+	+	+	–	–	–
<i>Xenotilapia</i> n.sp. “large”	–	–	–	–	–	+
<i>Xenotilapia</i> n.sp. “white-lip”	–	–	–	+	+++	++++
<i>Xenotilapia</i> sp.	–	–	+	+	++++	++

continued

Appendix 1 (continued)

	Scuba (1–20 m)			ROV ^b (40–80 m)		
	Cape Banza (low dist.)	Lubanga (moderate dist.)	Burundi (high dist.)	Cape Banza (low dist.)	Lubanga (moderate dist.)	Burundi (high dist.)
Phytoplanktivores						
<i>Lamprichthys tanganicanus</i>	+	+	+	–	–	–
<i>Neolamprologus brichardi</i>	++++	++++	++++	++++	++	–
<i>Neolamprologus gracilis</i>	+	–	–	–	–	–
<i>Neolamprologus multifasciatus</i>	+	–	–	–	–	–
<i>Neolamprologus savoryi</i>	++	++	++	+++	–	–
<i>Telmatochromis bifrenatus</i>	++++	++++	+++	–	–	–
Zooplanktivores						
<i>Cyprichromis microlepidotus</i>	+++	++	++++	++++	+	++++
<i>Cyprichromis</i> sp.	–	–	–	–	–	+
<i>Microdontochromis tenuidentatus</i>	++	–	–	–	–	–
<i>Neolamprologus calliurus</i>	+	+++	–	++++	++	–
<i>Paracyprichromis brieni</i>	++	+++	+++	–	–	–
<i>Paracyprichromis nigripinnis</i>	+	+	–	++++	++++	++++
<i>Tangachromis dbanisi</i>	–	–	–	–	–	+
Piscivores (including scale eaters)						
<i>Aethiomastacembelus cunningtoni</i>	–	–	–	–	–	+
<i>Aethiomastacembelus ellipsifer</i>	+	+	–	–	–	–
<i>Aethiomastacembelus moorii</i>	+	+	+	+	–	–
<i>Aethiomastacembelus</i> sp.	+	–	–	–	+	–
<i>Bathybates</i> sp. ^c	–	–	+	–	–	+
<i>Boulengerochromis microlepis</i> ^f	+	–	–	+	+	+
<i>Ctenochromis benthicola</i>	–	–	–	–	+	++
<i>Cyphotilapia frontosa</i>	+	+	+	+	++	++++
<i>Greenwoodochromis christyi</i>	–	–	–	–	+	++
<i>Haplotaxodon microlepis</i> ^c	+	–	+	–	–	–
<i>Hemibates stenosoma</i> ^f	–	–	–	–	–	+
<i>Lamprologus lemairii</i>	+	+	+	+	+	+
<i>Lates angustifrons</i> ^c	–	–	+	–	–	–
<i>Lates mariae</i> ^c	–	+	–	–	–	–
<i>Lates microlepis</i> ^c	+	–	–	–	–	–
<i>Lates</i> sp. ^c	–	–	–	+	–	–
<i>Lepidiolamprologus attenuatus</i>	+	+	–	–	–	–
<i>Lepidiolamprologus cunningtoni</i>	+	–	–	–	+	–
<i>Lepidiolamprologus elongatus</i>	+	++	+	+	+	++
<i>Lepidiolamprologus profundicola</i>	+	+	+	–	+	–
<i>Lepidiolamprologus</i> sp.	–	–	–	–	+	–
<i>Malapterurus electricus</i>	–	–	–	–	+	–
<i>Neolamprologus fasciatus</i>	+	+	–	–	–	–
<i>Perissodus microlepis</i>	+	++	+	+	–	–
<i>Perissodus paradoxus</i>	–	–	+	–	–	–
<i>Perissodus straelini</i>	+	–	–	+	–	–
<i>Perissodus</i> sp.	–	–	–	+	+	+
Omnivores/unknown						
<i>Lamprologus</i> sp.	–	–	+	–	–	–
<i>Neolamprologus</i> cf. <i>buescheri</i>	+	–	–	–	–	–
<i>Neolamprologus</i> cf. <i>wauthioni</i>	–	–	+	–	–	–
<i>Neolamprologus</i> n.sp. “black”	–	–	–	–	+	–
<i>Neolamprologus</i> n.sp. “small orange”	+	–	–	–	–	–
<i>Neolamprologus</i> n.sp. 2	–	–	–	++	+	–
<i>Neolamprologus</i> n.sp. 3	–	–	–	+	–	–
<i>Neolamprologus</i> sp.	–	–	–	+	–	–
Total species censused	64	52	38	28	23	22
Total species including wanderers	67	53	41	30	26	25
Total individuals tallied	5774	2457	8120	1883	1035	231
Rarefaction results	56.1	52 ^d	34.2	16.0	14.0	22 ^d

^a Abundance key: – absence of species in the surveys at this site; + species represents <2% of population at site (all depths); ++, species represents 2–5% of population; +++, species represents 5–10% of population; +++++, species represents >10% of population.

^b ROV, remotely operated vehicle.

^c Species considered “wanderers” and excluded from all quantitative analyses.

^d Sample used as a standard for rarefaction.

Appendix 2

Distribution and relative abundance of mollusc species across study sites in Lake Tanganyika.^a

	Site		
	Cape Banza (low dist.)	Lubanga (moderate dist.)	Burundi (high dist.)
Bivalves			
Family Unionidae			
<i>Caelatura burtoni</i>	++	+	+
Family Mutelidae			
<i>Mutela spekei</i>	+	-	-
Gastropods			
Family Thiariidae			
<i>Anceya giraudi</i>	++++	++++	++++
<i>Bridouxia giraudi</i>	++	++	++
<i>Bridouxia ponsonbyi</i>	+	+	-
<i>Bridouxia</i> sp.	+++	++++	-
<i>Lavigeria</i> n. sp. "fine striped"	++++	++	-
<i>Lavigeria</i> n. sp. "wide band"	-	+	-
<i>Lavigeria grandis</i>	++	+++	-
<i>Lavigeria</i> cf. <i>nassa</i> "fine ribbed"	+++	++	++++
<i>Lavigeria</i> cf. <i>nassa</i> "small fine"	+	+++	-
<i>Lavigeria</i> cf. <i>paucicostata</i> "coarse ribbed"	+	+	-
<i>Lavigeria</i> cf. <i>paucicostata</i> "sand lav"	+++	+	-
<i>Lavigeria</i> cf. <i>paucicostata</i> "spiny"	+	-	-
<i>Mysorelloides multisulcata</i>	+	-	-
New genus n.sp. "guillemei"	+	-	-
New genus n.sp.	+++	+++	+++
<i>Paramelania damoni</i> forme: <i>crassigranulata</i>	+	-	+
<i>Paramelania damoni</i> forme: <i>imperialis</i>	+	-	+
<i>Reymondia borei</i>	++++	++++	+
<i>Reymondia</i> n.sp. 2	++	+	-
<i>Reymondia</i> n.sp. 3	++	++	+
<i>Spekia</i> n.sp. "coheni"	++	+	++
<i>Spekia zonata</i>	-	-	+
<i>Stanleya neritinoidea</i>	+	-	+
<i>Stormsia minima</i>	+	+	++
<i>Syrnolopsis minuta</i>	+	-	-
<i>Synolopsis</i> sp.	+	+	+
<i>Tanganyicia rufofilosa</i>	-	-	+
Total number of species (quadrat + sieve)	27	19	15
Total number of individuals	653	1132.5	654
Rarefied species richness (site-wide)	27 ^b	18.8	15.0

^aAbundance key is the same as in Appendix 1.

^bSample used as a standard for rarefaction.



Appendix 3

Distribution of ostracod species across study sites in Lake Tanganyika.*

	Site		
	<i>Cape Banza</i> (low dist.)	<i>Lubanga</i> (moderate dist.)	<i>Burundi</i> (high dist.)
Superfamily Cypridoidea			
Family Candonidae			
<i>Candonopsis depressa</i>	+	+	-
<i>Candonopsis</i> n.sp. 7	-	-	+
<i>Candonopsis</i> n.sp. 8	+	+	-
<i>Candonopsis</i> n.sp. 11	-	-	+
<i>Candonopsis</i> n.sp. 12	+	-	-
<i>Candonopsis</i> n.sp. 13	+	-	-
<i>Candonopsis</i> n.sp. 15	-	+	-
Family Cyclopyrididae			
<i>Allocypria aberrans</i>	+	-	+
<i>Allocypria claviformis</i> group	+	++	++
<i>Allocypria bumilis</i>	+	+	+
<i>Allocypria</i> cf. <i>inclinata</i>	-	+	-
<i>Allocypria</i> n.sp. 5	+	-	+
<i>Allocypria</i> n.sp. 8	+	-	-
<i>Allocypria</i> n.sp. 10	+	-	+
<i>Allocypria</i> n.sp. 11	-	+	-
<i>Allocypria</i> n.sp. 16	+	-	+
<i>Allocypria</i> n.sp. 17	+	+	-
<i>Allocypria</i> n.sp. 18	-	+	-
<i>Mecynocypria complanata</i>	-	+	-
<i>Mecynocypria</i> cf. <i>conoidea</i>	+	+	+
<i>Mecynocypria deflexa</i>	+	-	+
<i>Mecynocypria emaciata</i>	+	+	+
<i>Mecynocypria opaca</i>	+	+	+
<i>Mecynocypria subangulata</i>	+	+	-
<i>Mecynocypria</i> n.sp. 8	+	+	+
<i>Mecynocypria</i> n.sp. 9	+	+	-
<i>Mecynocypria</i> n.sp. 14	+	+	-
<i>Mecynocypria</i> n.sp. 17	+	-	+
<i>Mecynocypria</i> n.sp. 19	+	-	-
<i>Mecynocypria</i> n.sp. 20	+	+	-
<i>Mecynocypria</i> n.sp. 22	+	-	-
<i>Mecynocypria</i> n.sp. 29 (opaca group)	+	+	+
<i>Mecynocypria</i> n.sp. 30	+	-	-
<i>Mecynocypria</i> n.sp. 31	+	+	-
<i>Mecynocypria</i> n.sp. 32	+	-	-
<i>Mecynocypria</i> n.sp. 33	-	+	-
<i>Mecynocypria</i> n.sp. 36	-	+	-
<i>Mecynocypria</i> sp.	-	+	-
Family Cyprididae			
<i>Cypridopsis bidentata</i>	-	-	+
<i>Cypridopsis obliquata</i>	+	-	-
<i>Cypridopsis serrata</i>	+	++	-
<i>Cypridopsis</i> n.sp. 5	++	++	++
<i>Cypridopsis</i> n.sp. 6 (species group)	+	++++	+
<i>Cypridopsis</i> n.sp. 8	+	-	+
<i>Cypridopsis</i> n.sp. 13	+	++	-
<i>Cypridopsis</i> n.sp. 15	-	+	-
<i>Cypridopsis</i> n.sp. 16	+	-	-
<i>Cypridopsis</i> n.sp. 17	-	-	+
<i>Cypridopsis</i> n.sp. 18	+	+	+

continued

Appendix 3 (continued)

	Site		
	Cape Banza (low dist.)	Lubanga (moderate dist.)	Burundi (high dist.)
<i>Cypridopsis</i> n.sp. 22	—	+	—
<i>Cypridopsis</i> n.sp. 23	—	+	—
<i>Tanganyikacypridopsis acanthodes</i>	+	+	+
<i>Tanganyikacypridopsis calcarata</i>	+	+	++
<i>Tanganyikacypridopsis depressa</i>	+	++	+
<i>Tanganyikacypridopsis</i> n.sp. 3	+	+	++
<i>Tanganyikacypridopsis</i> n.sp. 4	+	—	+
<i>Tanganyikacypridopsis</i> n.sp. 5	+	+	+
<i>Tanganyikacypridopsis</i> n.sp. 8	+	++	+
Superfamily Cytheroidea			
Family Cytherideidae			
<i>Archaeocyprideis tuberculata</i>	+	+	+
<i>Cyprideis</i> sp. (bolletje group)	—	+	—
<i>Cyprideis</i> n.sp. 1	+	+	+
<i>Cyprideis</i> n.sp. 24	—	+	—
<i>Mesocyprideis irsacae</i>	++++	++	++++
<i>Mesocyprideis</i> n.sp. 2b	+	+	+
<i>Romecytheridea ampla</i>	+++	++	+++
<i>Romecytheridea tenuisculpta</i>	+++	++++	+++
<i>Romecytheridea</i> n.sp. 13	++++	++++	+++
<i>Romecytheridea</i> n.sp. 15	—	+	—
<i>Romecytheridea</i> n.sp. 18	+	—	—
<i>Tanganyikacythere burtonensis</i>	+	+	+
<i>Tanganyikacythere caljoni</i>	++	—	—
Family Limnocytheridae			
<i>Gomphocythere alata</i>	+++	+++	++++
<i>Gomphocythere cristata</i>	+	+	++
<i>Gomphocythere curta</i>	++++	+++	++++
<i>Gomphocythere</i> n.sp. “downingi”	—	—	+
<i>Gomphocythere</i> n.sp. “woutersi”	+	+	—
<i>Gomphocythere</i> n.sp. 11	—	+	—
<i>Gomphocythere</i> n.sp.	+	+	—
Cytheroidea indet. 1	+	—	—
Superfamily Darwinuloidea			
Family Darwinulidae			
<i>Darwinula stevensoni</i>	—	+	+
New genus, new species 1	+	+	—
Total number of species:	60	56	42

*Abundance key is the same as in Appendix 1.

