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SPECIATION IN ANCIENT LAKES

Ecological correlates of species differences in the Lake Tanganyika crab radiation

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<?InsertOnReleaseOF OFYear?><?InsertOnReleaseOF OFMonth?><?InsertOnReleaseOF OFDay?>
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Abstract

The endemic crabs of Lake Tanganyika include a phenotypically diverse clade that exhibits recent divergence and low phylogenetic species resolution. There are indications that ecological niche segregation has played a prominent role in the divergence of this clade. We used habitat surveys, gut content analyses and stable isotope analyses to test the extent to which morphological species are ecologically different. Our data show some interspecific segregation in depth, substrate type and mean stable isotope signatures. At the same time, a considerable level of ecological niche overlap is evident among species of *Platythelphusa* that coexist in rocky littoral habitats. We consider these results in the framework of adaptive radiation theory, and we discuss general ramifications for the maintenance of species diversity in Lake Tanganyika.

Introduction

Lake Tanganyika is unique among the African Great Lakes in harbouring an endemic radiation of freshwater crabs (genus *Platythelphusa*) (Cumberlidge et al., 1999; Marijnissen et al., 2004; Reed & Cumberlidge, 2006). In spite of marked levels

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of phenotypic diversity within the Lake Tanganyika endemic crab clade, phylogenetic resolution based on mitochondrial markers is low (Marijnissen et al., 2006; Marijnissen, 2007). There is evidence that initial divergence of the platythelphusid clade took place less than c. 3 Myr ago (Marijnissen et al., 2006). The relatively young ages of the platythelphusid species could explain the apparent incongruence between their phenotypic diversity and genetic similarity (e.g. Moran & Kornfield, 1993; Albertson et al., 1999). The approximate period of platythelphusid divergence corresponds to inferred periods of major cladogenesis in several Lake Tanganyika ~~cichlid~~ cichlid and *Synodontis* catfish lineages ~~(Duftner et al., 2005; Koblmüller~~ (Koblmüller et al., 2004, 2005, 2006, 2007; Duftner et al., 2005; Day & Wilkinson, 2006). It is likely that the contemporaneous divergence of these clades was induced by substantial environmental ~~changes,~~changes when the lake level dropped considerably during a period of aridification in eastern Africa (Cane & Molnar, 2001). Lake level changes offer ecological opportunities by providing novel resource-rich environments in which ecological diversification and adaptive radiation can take place.

The theory of adaptive speciation predicts that reproductive isolation evolves as a consequence of adaptation to different ecological niches (Schluter, 2000). Adaptive radiations are characterised by elevated levels of divergence among taxa as a response to natural selection acting directionally on ecologically relevant traits. Indeed, there is increasing evidence that the outstanding phenotypic diversity and rapid speciation of the cichlid species flocks in the African Great Lakes has to a large extent been facilitated by ecological niche diversification (Albertson & Kocher, 2006). The majority of studies on adaptive radiations in aquatic ecosystems have ~~focused~~focussed on fish (reviewed in Schluter, 2000), although intriguing results are also emerging from studies on Lake Baikal amphipods (Takhteev, 2000), Lake Ohrid limpets (Albrecht et al., 2006~~),~~,) and gastropods from the Malili Lakes on Sulawesi (Von Rintelen et al., 2004). Because Lake Tanganyika harbours a wide range of groups with elevated levels of species richness and endemicity, including not only fish but also ostracods, copepods, gastropods, shrimp, ~~leeches,~~leeches and sponges, it provides an outstanding system to test how ecological opportunities may facilitate adaptive radiation in a diverse array of aquatic taxa. Although there are morphological indications that ecological processes have been important in the evolution of several of these species flocks (Michel, 2000; West ~~et al,~~et al., 2003; Fryer, 2006), for most Lake Tanganyika ~~endemics~~endemics, sufficient data to explore adaptive radiation across their entire clade remains lacking.

The platythelphusid crabs are an ideal test case to investigate common effects of shared environmental history and ecological opportunities that have shown to be significant in cichlid speciation. There are some indications that ecological niche partitioning played an important role in facilitating platythelphusid divergence. The majority of the nine platythelphusid species occur sympatrically, and up to five species have been found to coexist in rocky littoral areas. Evert (1970) suggested that some of the unusual phenotypes exhibited by Lake Tanganyika crabs have ecological significance. For instance, the elongated slender legs of the presumed predominantly deep lake dwelling species *Platythelphusa tuberculata* Capart, 1952 , and *P. praelongata* Marijnissen et al., 2004 , might facilitate movement and tactile predation on mud (Fig. 1; Evert, 1970; Marijnissen et al., 2004). Marked differences also exist in the shape and maximum size of the carapace (Marijnissen et al., 2004: ~~Table 2).~~ Table 2). The small, rounded body of *P. maculata* Cunnington, 1899 , and *P. polita* Capart, 1952 , appears to provide advantages for living inside empty gastropod shells. *Platythelphusa conculcata* Cunnington, 1907, *P. immaculata* Marijnissen et al., 2004, and *P. echinata* Capart, 1952 , have markedly flattened carapaces (Cumberlidge et al., 1999; Marijnissen et al., 2004), which matches

well with the narrow crevices in rocky substrates where they are most commonly found (S. A. E. Marijnissen, personal observations). The largest-bodied platythelphusid species, *P. armata* A. Milne-Edwards, 1887 , has greatly enlarged claws that were suggested to have coevolved with Lake Tanganyika's heavily armoured gastropods (West et al., 1991; West & Cohen, 1994). Furthermore, comparative analyses have revealed marked differences in claw functional morphologies between all platythelphusid species, indicating a considerable level of trophic partitioning (Marijnissen, 2007). Although there are thus several phenotypic clues to differentiation in resource use, it remains to be shown to which extent platythelphusid species occupy distinct ecological niches.

Fig. 1 Hypothesis for the evolution of the endemic Lake Tanganyika crabs [+], (With exception of *P. polita*. for which no genetic sequences are presently available), based on mitochondrial genes (16S rRNA and COII mtDNA, tree adapted from Marijnissen, 2007). arm = *Platythelphusa armata*; con = *P. conculcata*; den = *P. denticulata*; ech = *P. echinata*; imm = *P. immaculata*; mac = *P. maculata*; tub = *P. tuberculata*; pre = *P. praelongata*; ply = *Potamonautes platynotus* (all males, except *P. praelongata*). Scale ~~bar = 50 mm.~~ [+] ~~With exception of *P. polita*. for which no genetic sequences are presently available~~ bar = 50 mm

Determining ecological correlates of species differences in Lake Tanganyika endemic crabs is relevant not only relevant from an evolutionary point of view, but it is also essential for conservation purposes. There is growing concern about the conservation of biodiversity in Lake Tanganyika ~~(Cohen~~ (McIntyre et al., 2004; Cohen et al., 2005; McIntyre et al., 2005; Darwall et al., ~~2005).~~ 2005). Effective decisions on conservation of biodiversity rely on an understanding of ecological divergence among key taxa. Crabs are common in the lake and they are expected to have a major influence on lacustrine foodweb interactions through their role as prey for fish (Hori, 1983; Coulter, 1991; Hori et al., 1993) and consumers of benthic organisms (e.g. West et al., 1991). If patterns of species divergence and coexistence of Lake Tanganyika's endemic crab species are controlled by ecological differentiation, this could have important implications for conservation decisions as it entails high sensitivity to habitat disturbances. Alternatively, species might be functionally equivalent and diversity could be maintained through versatility (Bellwood et al., 2006).

The aim of this paper is to assess if the platythelphusid species differ in ecological niche realisation. We include *P. denticulata*, although its taxonomic status is uncertain, and it is possibly a hybrid taxon (Marijnissen et al., unpublished data). We also include another endemic Lake Tanganyika species, *Potamonautes platynotus* (Cunnington, 1907), to determine if its ecological niche is distinct from that of the platythelphusid species with which it coexists. Because this is the first study to empirically examine the ecology of the endemic Lake Tanganyika crabs, our approach is exploratory rather than diagnostic. In order to examine the ecological correlates of species differences in these crabs, we use a combination of data from habitat surveys, gut contents and stable isotope analyses. We consider our results in the framework of adaptive radiation theory and we discuss other factors that are likely to play a role in the divergence of the platythelphusid clade.

Methods

Study system and sites

Lake Tanganyika is the oldest (~9–12(~9–12 my) and deepest (max. 1,470 m) of the East African Rift lakes (Coulter, 1991). The shoreline is steeply sloped in most areas. Different substrate types are interspersed along the shoreline on scales of 10–1,000 m,10 to 1,000 m, but even on smaller scales substrates can be patchy (Michel et al., 2004). We surveyed an area of approximately 50 km along the Tanzanian shoreline of the lake between 2001 and 2004. Within this area, 16 study sites were selected based on accessibility and substrate composition (Fig. 2). The substrate at 12 sites (MWG to ZGU) was composed of boulders, cobbles, pebbles,pebbles and/or aggregations of empty *Pleiodon spekii* (Woodward, 1859) freshwater mussel shells,shells interspersed with sand. Four sites were situated west of a river delta (Luichi River, see Fig. 2), where the substrate consisted of mud with extensive beds of empty shells from the endemic gastropod *Neothauma tanganyicense* Smith, 1880 , and *Coelatura burtoni* (Woodward, 1859) shell hash.

Fig. 2 Lake Tanganyika. (A) Map of Lake Tanganyika, (B) Study sites that were surveyed for crab habitat specificity. Acronyms (local names in brackets): MWG = Mwamgongo village; GMB = Gombe Stream National Park; KLG = Kalalangabo (Lemba village); EUP = Euphorbia (Kasazi Hill); NDW = Nondwa Point; LUA = Luansa Point (Kigoma Bay); HTP = Hilltop Hotel; KZG = Kazanga/Bangwe Point; JKB = Jakobsen's Beach (Mwamahunga); ZNG = Mzungu; KTW = Kitwe Point; MNO = Meno Hill; UJJ = Ujiji; KMJ = Kangamoja; LUI = Luichi river northernmost outlet; MGU = Mgumile

Habitat specificity

To provideIn order to obtain presence/absence data on each crab species, we surveyed 16 study sites at depths ranging between 0 and 30 m. A minimum of five surveys waswere conducted per site. Each site was systematically searched for crabs using SCUBA or snorkelling. Notes were made on crab species, size (carapace width), life stage (juvenile or adult see Cumberlidge, 1999:, p. 324; Marijnissen et al., 2004: Table 2)Table 2) and sex, as well as on the habitat in which each individual crab was found. Substrate types were categorised according to a modified Udden-Wentworth scale (Wentworth, 1922): fine sediment (0.00025–0.062 mm), sand (0.062–2.00 mm), pebbles (2.00–64.00 mm), cobbles (64.00–256.00 mm), boulders (> 256 mm),(>256 mm) and aggregations of *P. spekii* or *N. tanganyicense*. Information about the habitat of *P. tuberculata*, which can occur to depths of 190 m (Coulter, 1991), was obtained by combining information on catch localities obtained from fishermen with substrate information from Lewis (2002) and William (2002).

Additional information on habitat specificity for each species was obtained using a stratified random sampling strategy at 10 out of 16 sites (MWG to ZNG, see Fig. 2) in rocky littoral areas. At each site, divers established 20 replicate 50*50 cm50 × 50 cm quadrats at 5 m5-m depth. The slope of the substrate was recorded for each quadrat. We also collected and counted all snails that were visible on rock surfaces within five random quadrats at each site. For each of these quadrats, we quantified chlorophyll *a* concentration,concentration as well as the relative amount of organic and inorganic matter, following the method used by McIntyre et al. (2005).(2004). By firmly placing a sealed cover over the upward face of a flat lying cobble, a fixed surface area of the underlying sediment and periphyton could be brought ashore for analyses. All material surrounding the cover was scrubbed away and carefully discarded. This provides a sample of attached and unattached material from the rock's surface of a constant and known area. The aufwuchs and loose organic and inorganic material protected underneath the cover was removed, suspended in

~~water,~~water and ~~homogenized.~~homogenised. Subsamples were collected on precombusted ~~glass-fibre~~glass–fibre filters (Whatman GF/C, Maidstone, UK). One subsample was extracted in 90% ethanol for ~~24 hours,~~24 h and analysed for chlorophyll *a* after acidification (Moed & Hallegraeff, 1978). Another subsample was dried to a constant mass at 60°C, weighed, combusted at 500°C for ~~3 hours,~~3 h and reweighed to determine the organic content (Sutherland, 1998).

We tested for differences in the habitat specificity among species with a PERMANOVA test on each data set (i.e. surveys of substrate types across depths, and stratified random sampling using quadrats at ~~5 m~~5-m depth). After log ~~(x + 1)~~$(x + 1)$ transformation of the data using PRIMER 6 (Primer-E Ltd, Plymouth UK), a matrix was constructed of pairwise differences in habitat similarity between pairs of individuals based on the Ochiai similarity index (Ochiai, 1957). Similarity indices are often used to assess niche differentiation and overlap between pairs of morphologically or otherwise distinct entities in ecological communities (e.g. Grant et al., 1985; Safran & Omori, 1990; Lehman, 2000). We included the variable 'species' as a fixed factor in a PERMANOVA model, using a type III sum of squares and 9999 permutations under the reduced model using the Ochiai similarity matrix. We also performed a ~~Principal Coordinates Analysis~~principal coordinates analysis (PCO) on the same matrix to visually examine variation in similarity of habitat specificity among individuals and species. This procedure has the advantage that the ordination can be based on a distance or similarity matrix that is derived from a wide selection of metrics or semi-metrics, including ~~presence-absence~~presence–absence data (Jackson et al., 1989; Litvak & Hansell, 1990). Because our data includes many overlaying PCO scores that cannot be distinguished using standard biplots, we applied two-dimensional binning to effectively visualise different scores. The scores are displayed by symbols, the size of which is proportional to the number of points in that bin. For all ~~biplots~~biplots, 50 bins were used on both axes (2,500 squares in the two-dimensional space). The symbol for each score was randomly shifted slightly from the bin centre to prevent superposition of scores for different species.

We also examined whether habitat specificity within the rocky littoral zone is related to crab body size (measured as carapace width). Data were displayed using Box plots as developed by Tukey (Frigge et al., 1989). ~~Kolmogorov-Smirnov~~Kolmogorov–Smirnov tests of normality indicated that the data deviated significantly from normality and would not follow a normal distribution following appropriate transformations ~~(P < 0.001).~~(P < 0.001). Because of our large sample size ~~(N = 1401)~~(N = 1401), parametric methods are expected to have more statistical power than nonparametric methods, and we therefore tested the significance of differences in mean crab carapace width and life stage among substrate types using a general linear model multivariate analysis of variance (GLM MANOVA), followed by Tukey's HSD pairwise comparisons with α = 0.05 in SPSS 11.0.4. (SPSS Inc. 2005).

Diet composition

Specimens for dietary analyses were collected between 2002 and 2004 at three sites (HTP, JKB and KMJ, see Fig. 2) along the Tanzanian shoreline of Lake Tanganyika. Crabs were collected by hand at depths between 5 and 10 m using SCUBA, and killed in 98% ethanol within ~~20 minutes~~20 min after collection. Only adult, intermolt specimens were included in the analyses. Foreguts as well as mid- and hindguts were carefully dissected, after which the contents were washed into a Petri dish and viewed

under a dissecting microscope. We only used specimens ~~with ≥ 50%~~with ≥50% full foreguts. Food items were identified to the lowest possible taxonomic level and also categorized as detritus, vascular plant matter, algae, gastropods, aquatic insects and ostracods. The proportional representation of each category was determined using the percentage occurrence method (Williams, 1981). Percentage frequency of occurrence (PO) was estimated as ~~(N~~(N_1~~/N~~$/N_2$~~)*100,~~$) \times 100$, where N_1 is the number of individual crabs that consumed food item ~~x,~~x, and N_2 represents the total number of individuals.

Stable isotope analyses

The stable isotopic composition of an organism represents an average ratio related to the utilized portion of its diet that is integrated in its tissue over a specific period of time. Stable isotopes of carbon and nitrogen (δ^{13}C and δ^{15}~~N)~~N) accumulate in a predictable way between consumers and their diet, and they can be useful in providing quantitative information on trophic niche segregation between organisms (Newsome et al., 2007, and references therein). We collected samples for stable isotope analyses between August and November 2002 from the same three sites where specimens for gut content analyses were collected, with the exception of *P. tuberculata*. Samples of this species were obtained from specimens collected by fishermen. In total, 83 adult intermolt specimens were collected for stable isotope analyses, including a minimum of six individuals (three males and three females) per species. Each individual specimen was measured and sexed, after which a piece of leg muscle tissue was dissected. All samples were transferred onto ethanol-cleaned aluminium foil, and dried until constant weight at 60°C ~~for ≥ 48 hours.~~for ≥48 h. Subsamples of dried material were analysed for stable carbon and nitrogen isotopes using a Europa Scientific 20/20 Isotope Ratio Mass Spectrometer (Iso-Analytical Ltd., Cheshire, UK). Isotope ratios are expressed in delta notation (δ) to indicate deviations from standard reference material (Vienna PDB carbon standard and atmospheric nitrogen). Average reproducibility based on replicate measurements was within approximately 0.1‰ for both δ^{13}C and δ^{15}~~N. To~~N. In order to examine patterns of trophic segregation between species, a dual-isotope plot δ^{13}C and δ^{15}~~N~~N values was constructed. We tested for differences in stable isotope composition between sexes and among species with a PERMANOVA test using the programme ~~PERMANOVA + within~~PERMANOVA+ within PRIMER 6 (Primer-E Ltd, Plymouth UK). After normalizing the data within PRIMER 6, a matrix was constructed based on the Euclidean difference in isotope composition between pairs of species. Sex and species were included as fixed factors in the PERMANOVA model, using a type III sum of squares and 9999 permutations under the reduced model.

Results

Habitat specificity

A total of 1,401 crabs were sampled during random searches at 16 sites along the Tanzanian coastline of Lake Tanganyika, and 404 crabs were sampled during quadrat surveys at a subset of 10 sites. *Platythelphusa polita* and *P. praelongata* were not found during any of our surveys. *Platythelphusa maculata* appears to be restricted to beds of empty *N. tanganyicense* shells near

the outlet of the Luichi River (Fig. 2), where the substrate comprises silt and mud. Out of a total of 1,805 crabs that were collected during our surveys, the numbers of individuals per species decreased in the following order: *P. conculcata* (588), *P. echinata* (491), *P. armata* (347), *Po. platynotus* (239), *P. maculata* (67), *P. immaculata* (61), P. *denticulata* (12). *Potamonautes platynotus* is the only species that was also occasionally observed outside of the lake on pebble and cobble beaches. *Platythelphusa tuberculata* was not found during our surveys in the shallow benthic zone between 0 and 30 m; however, this species was regularly caught in the nets of fishermen that reportedly fished on the platform that extends approximately 14 km west from the Luichi River delta (Fig. 2), at depths ranging from approximately 50 to ≥100 m. Most of the sediments on this platform are composed of fine silt and mud derived from the Luichi River and/or from pelagic rainout of suspended fine sediments (Lewis, 2002; William, 2002).

The results of PCO based on the surveys of substrate type across depths (0–30 m) are shown in Fig. 3. The first two PCO axes explain 39.9% and 35.1% of the variation in the dataset (Table 1). Substrate types with the highest vector loadings were boulders, cobbles, pebbles and sand. With the exception of *P. tuberculata* and *P. maculata*, all species are associated with these four vectors. Although species distributions along the axes thus show considerable overlap, the frequency of the observations within each substrate type differs for each species. Significant differences were found in the similarity of substrate specificity among species (Pseudo-$F_{5,321}$ = 10.029, $P < 0.001$). Significant pairwise differences between species that coexist within the rocky littoral included *P. armata* and *P. conculcata* ($P = 0.002$), *P. armata* and *P. echinata* ($P < 0.001$), *P. armata* and *P. immaculata* ($P = 0.044$), *P. conculcata* and *P. echinata* ($P = 0.010$), *P. conculcata* and *Po. platynotus* ($P < 0.001$) as well as *P. echinata* and *Po. platynotus* ($P < 0.001$). Other pairwise comparisons were not significant ($P > 0.05$).

Fig. 3 Principal coordinate (PCO) ordination plot of the two first axes of crab species habitat specificity based on random surveys of different substrate types across depths (0–30 m) at 16 sampling sites along the Tanzanian coastline of Lake Tanganyika. Species abbreviations as in Fig. 1. The relative size of the symbols is proportional for the number of individual observations per species for each habitat type (see text). FS = fine sediment (0.00025–0.062 mm); SAN = sand (0.062–2.00 mm); PEB = pebbles (2.00–64.00 mm); COB = cobbles (64.00–256.00 mm); BLD = boulders (>256 mm); MUS = aggregations of *Pleiodon spekii* freshwater mussel shells; NTS = *Neothauma tanganyicense* shells

Table 1 Percentage of variation explained by individual axes of principal coordinates analysis of the parameters relating to Fig. 2

Axis	Individual (%)	Cumulative (%)
1	39.88	39.88
2	35.07	74.95
3	20.58	95.53
4	15.65	111.18

Additional information on species habitat specificity was obtained from the quadrat surveys at 5-m depth within the rocky littoral zone. The first two axes of the PCO explained 64.2% and 24.6% of the total variance in the species dataset (Fig. 4, Table 2). Influential habitat variables are slope, total organic matter and chlorophyll *a*, as well as relative snail abundance and inorganic matter. *Platythelphusa armata*, *P. conculcata*, *P. echinata* and *Po. platynotus* were associated with all vectors. *Platythelphusa denticulata* was only associated with snail abundance and inorganic matter, while *P. immaculata* was only associated with slope, total organic matter and chlorophyll *a*. Significant differences were found among species (Pseudo-$F_{7,1463}$ = 108.680, $P < 0.001$). Pairwise tests between species showed that all comparisons between species were significant ($P < 0.006$) with the exception of the comparisons between *P. denticulata* and *P. conculcata* ($P = 0.18$), *P. denticulata* and *P. immaculata* ($P = 0.490$) as well as *P. denticulata* and *Po. platynotus* ($P = 0.554$).

Fig. 4 Principal coordinate (PCO) ordination plot of the two first axes of crab species habitat specificity within the rocky littoral zone at 5-m depth in Lake Tanganyika. Species abbreviations as in Fig. 1. The relative size of the symbols is proportional for the number of individual observations per species for each habitat type (see text). SLP = slope of the substrate, CHLA = chlorophyll *a*; TOM = total organic matter; IOM = total inorganic matter; SAB = relative snail abundance

Table 2 Percentage of variation explained by individual axes of principal coordinates analysis of the parameters relating to Fig. 3

Axis	Individual (%)	Cumulative (%)
1	64.24	64.24
2	24.61	88.84
3	14.79	103.63
4	7.07	110.7

Both the mean body size (carapace width) as well as the life stages of crabs had a significant effect on the use of substrate type within the rocky littoral zone (GLM MANOVA size $F = 330.480$, df = 3, $P < 0.001$; life stage $F = 195.716$, df = 3, $P < 0.001$). While relatively broad ranges of size classes are found in all rocky littoral substrate types, cobbles and boulders harbour larger crabs than sand and pebbles (Fig. 5).

Fig. 5 Distribution of crab carapace widths (CW) among different substrate types in the rocky littoral zone. Box plots represent CW median and interquartile range with whisker ends corresponding to the first and the last decile. Individual observations beyond these limits are plotted as circles. Abbreviations as in Fig. 3. Different letters above box plots indicate significant differences in mean crab CW among substrate types at α = 0.05 (Tukey's test: $P < 0.001$)

Diet composition

We collected a total of 574 adult crabs for dietary analyses, of which 386 had ≥50% full foreguts. The diet composition of the six species that were included in the gut content analyses is shown in Fig. 6. The majority of individuals

in each species had ingested some amount of detritus (including sand and silt as well as indeterminate organic matter). Vascular plant matter, algae, ostracods, parts of aquatic insects, fragments of gastropod shells and opercula were also found in the guts of individuals from all six species. Vascular plant matter consisted predominantly of bark and plant debris with a terrestrial origin. Algal taxa included typical benthic diatoms (*Encyonema* sp., *Rhopalodia* sp., *Nitzschia* sp. and *Surirella* sp.), and green algae (*Oocystis* sp. and *Ulothrix* sp.) as well as cyanobacteria (*Anabaena* sp., *Chroococcus* sp. and *Oscillatoria* sp.). Ostracods included species of Cyprididae, Cyclocypridae (*Mecynocypria* sp.) and Limnocytheridae (*Gomphocythere* sp.). Parts of aquatic insect larvae that could be determined from gut contents were most frequently assigned to caddisflies (including Ecnomidae and Hydropsychidae), and mayflies (including Baetidae and Ephemeridae) as well as chironomids (Chironominae, including *Dicrotendipes* sp.). Gastropod shell fragments were assigned to the endemic Tanganyikan genera *Lavigeria*, *Stormsia/Reymondia* and *Vinundu*. Gut contents revealed no apparent differences in the types of dietary constituents that were ingested among the six species. However, comparison of percentage-occurrence values in each dietary category revealed several differences. Gut contents of *P. maculata* and *P. echinata* included detritus more frequently than those of other species. Furthermore, *P. armata* appears to consume gastropods more frequently than any of the other species.

Fig. 6 Percentage occurrence of the various food categories in the six species analysed. Numbers of specimens analysed per species: *Potamonautes platynotus* (n = 28); *Platythelphusa armata* (n = 74); *P. maculata* (n = 32); *P. echinata* (n = 98); *P. conculcata* (n = 128); *P. immaculata* (n = 20). Det = detritus; pam = vascular plant matter; alg = algae; gst = gastropods; ins = aquatic insects; osc = ostracods

Stable isotope analyses

Crab isotopic signatures ranged from −12.4 to −21.2‰ $\delta^{13}C$ and from 3.6 to 6.4‰ $\delta^{15}N$. We found a significant difference in isotope composition among species (Pseudo-$F_{6,94}$ = 23.622, P < 0.001). There was no difference between sexes (Pseudo-$F_{1,94}$ = 0.008, P = 0.920), nor was there a significant interaction (Pseudo-$F_{6,94}$ = 1.453, P = 0.165). Pairwise tests between species showed that all comparisons between species were significant (P < 0.012) with the exception of the comparison between *P. armata* and *P. maculata*. The distribution of individuals of each species along axes defined by $\delta^{13}C$ and $\delta^{15}N$ is presented in Fig. 7. The deep, muddy-substrate dwelling *P. tuberculata* is segregated from other platythelphusid species by its high mean $\delta^{15}N$ signature. Within the rocky substrate species complex, *P. conculcata* exhibits the lowest $\delta^{15}N$ values. Pairwise tests showed significant differences between mean $\delta^{13}C$ and/or $\delta^{15}N$ between species, with the exception of the comparison between *P. armata* and *P. maculata,* which overlap in both mean $\delta^{13}C$ and $\delta^{15}N$ values (Table 3).

Fig. 7 Stable carbon and nitrogen isotope signatures of Lake Tanganyika endemic crab species. Each data point represents an individual organism

Table 3 Pairwise distances (Tukey's test) of mean δ^{13}C and δ^{14} ~~N~~N isotope composition among adult individuals of Lake Tanganyika endemic crab species

	Species	P. tuberculata	P. conculcata	P. immaculata	P. maculata	P. echinata	P. armata
δ^{13}C	P. conculcata	5.05*			ns		
	P. echinata	2.12*	2.92*	2.16*	ns	ns	
	P. immaculata	ns	5.08*				
	P. maculata	3.73*	ns	3.76*			
	P. armata	2.79*	2.25*	2.83*	ns	ns	
	Po. platynotus	5.48*	ns	5.51*	ns	3.35*	2.68*
δ^{14} ~~N~~N	P. conculcata	3.25*					
	P. echinata	ns	2.41*	1.20*	1.16*		
	P. immaculata	2.04*	1.21*				
	P. maculata	1.99*	1.25*	ns			
	P. armata	1.72*	1.52*	ns	ns	0.89*	
	Po. platynotus	2.27*	0.98*	ns	ns	1.43*	ns

~~*Significant~~* Significant difference of means at $\alpha = 0.05$; ns is non-significant difference at $\alpha = 0.05$

Discussion

The platythelphusid clade meets at least three out of four of Schluter's (2000) criteria for adaptive radiations: (i) common ancestry, (ii) rapid ~~divergence,~~divergence and (iii) differentiation in functional traits (Marijnissen et al., 2006; Marijnissen, 2007). Although the level of genetic resolution between platythelphusid species is low (Marijnissen et al., 2006; Marijnissen 2007~~)~~), the addition of ecological data provides more definition and insight into the processes that may have contributed to the divergence of these crabs (Fig. 1). A possible scenario is that Lake Tanganyika was initially invaded by a generalist ancestor, which diverged through adaptation to distinct muddy and rocky habitats. Subsequent divergence occurred predominantly in rocky habitats, where species adapted to fill specific spatial and/or dietary niches.

Our growing understanding of platythelphusid relationships and ecology accommodates this scenario in several major points. The most basal species of the platythelphusid clade is *P. echinata*, is a habitat generalist, of which adult specimens occur at a range of depths in rocky habitats, on muddy substrates, as well as in empty *N. tanganyicense* shells. Our results corroborate previous indications that *P. tuberculata,* which is phylogenetically relatively basal and an unambiguously distinct lineage, is found in ~~deep, muddy,~~deep muddy parts of the lake (Coulter, 1991; Marijnissen et al., 2004), and is trophically highly distinct. The phylogenetic relationships of the species found in rocky habitats are less resolved, indicating either a more recent divergence or

introgression. This is paralleled in ecology, where habitat and trophic preferences overlap to a greater degree than among the species basal in the phylogeny. Three species occur sympatrically in rocky habitats, including *P. conculcata* and *P. immaculata,* as well as *P. armata*. In addition, *P. denticulata* appears to prefer rocky habitats, but the results for this taxon might be biased due to its low sample number. Our surveys furthermore show that the small, round-bodied *P. maculata* is distinct in exhibiting a marked preference for empty *N. tanganyicense* shells. *Potamonautes platynotus* is derived from a lineage that invaded Lake Tanganyika separately. Although the ecological niche of this species exhibits marked overlap with the platythelphusid species that ~~inhabit~~inhabits rocky substrates, *Po. platynotus* is unique in that it is occasionally observed on the lake's margin outside of the water. This contrasts with the platythelphusid crabs, which appear to be fully aquatic.

It is likely that partitioning of ecological niche variables supports species diversity of the Lake Tanganyika crabs. The results of ~~the Principal Coordinates Analyses (PCO)~~PCO indicate that although individual crabs can be associated with a range of ~~variables~~variables, such as depth, chlorophyll *a* ~~concentration,~~concentration and relative amount of organic and inorganic matter, the majority of individuals exhibit species-specific patterns in habitat preferences. Differentiation in habitat specificity within the rocky littoral appears to be mainly a function of substrate size (Fig. 5). Adults of small-bodied ~~species~~species, such as *P. conculcata*, *P. immaculata*, and *P. echinata* , are partially relieved from competition by having access to substrates that are too small for adult *P. armata* and *Po. platynotus*. We also found a significant influence of life stage on preferred substrate. This makes it likely that ontogenetic shifts in habitat use play an additional role in facilitating species coexistence within rocky littoral areas. Size-related habitat use is common among crustaceans and is most often attributed to protection from predation (Hudon & Lamarche, 1989; Navarette & Castilla, 1990; Richards, 1992; Platvoet et al., ~~2007).~~2007). Predation-mediated habitat use may lead to increased competition within the refuge. Ecological niche partitioning between similar-sized adult individuals of different species that coexist within the same refuge might subsequently take place through specific adaptations allowing exploitation of different food items.

Comparative analyses of claw functional morphologies ~~has~~have revealed marked differences among the endemic Lake Tanganyika crab species, indicating a considerable level of trophic divergence (Marijnissen, 2007). In contrast, our gut content analyses showed no clear evidence of specialization (Fig. 6). In spite of marked divergence in claw functional morphologies, different species show broad overlap in the type of food items that they can handle and ingest. Comparison of percentage occurrence of each dietary category nonetheless revealed several differences. *Platythelphusa armata* consumes gastropods more frequently than any of the other crab species. This is in agreement with expectations based on claw traits and predation ~~experiments~~experiments, indicating that *P. armata* is a highly derived molluscivore (West et al., 1991; West & Cohen, 1994; Rosales et al., 2002; Marijnissen, 2007; Michel et al., unpublished data). Detritus comprised an important component in the guts of all species that were examined. This can either be the result of non-selective foraging behaviour, or it might reflect partially digested food that could not be identified. Determination of crustacean diets based on gut contents is associated with several well-recognized limitations, due to the effects of mastication and under-representation of readily homogenised food items (e.g. Hill, 1976). Examination of gut content alone might therefore not accurately reflect dietary intake. Furthermore, our gut content analyses

are limited because of the fact that the crabs were only collected during daytime. It is likely that foraging patterns are dictated by the risk of being predated upon, and nocturnal activity might thus be different from diurnal activity.

Stable isotopic signatures offer the advantage of spatio-temporal integration of the assimilated food, and are thus useful in providing additional insight ~~in~~into questions of dietary partitioning. Comparison of mean δ^{13}C and/or δ^{15}~~N~~N values between our focal taxa revealed that signatures of individual specimens show considerable overlap. However, there were significant differences in mean δ^{13}C and/or δ^{15}~~N~~N values among species, with the exception of the comparison between *P. armata* and *P. maculata*. These results imply that although there are overall trophic differences among species, individuals within species can exhibit a range of foraging strategies. Work on other phenotypically diverse lacustrine species flocks has shown that closely related endemics often exploit a broader range of resources than what would be expected based on their specialized feeding morphologies (Liem & Osse, 1975; Liem, 1980; Genner et al., 1999). This apparent discrepancy can be explained if specialization is based on non-preferred resources while also allowing exploitation of more preferred common resources (Robinson & Wilson, 1998).

Perhaps the most significant criterion of an adaptive radiation is a correlation between divergent phenotypes and differentiation in ecological niches. Although we have observed segregation in depth, substrate type and mean stable isotope signatures, it is also evident that a considerable level of ecological versatility exists among platythelphusid species that coexist in rocky littoral areas. This may act to relax interspecific competition by allowing opportunistic resource use and could result in some resilience to habitat disturbance. It is also possible that niche partitioning occurs along variables that we ~~haven~~have not yet measured. However, since we have addressed the most common ecological niche segregation variables in this study, our data should provide a robust first indication of the level of interspecific differentiation. The possibility that environmental factors are not the sole force driving platythelphusid divergence should also be investigated. Recent ~~field~~ field and experimental studies have demonstrated that rapid ecological radiation is often entangled with forces of sexual selection (Van Doorn & Weissing, 2001; Arnegaard & Kondrashov, 2004; Barluenga & Meyer, 2004; Kidd et al., 2006). The presence of marked intraspecific differences in relative claw size and shape between males and females is an indication that sexual selection might have contributed to platythelphusid speciation (Marijnissen, 2007). Furthermore, interspecific hybridization has been pointed out as a process that is likely to be important in adaptive radiations, because it has the potential to elevate rates of response to disruptive or divergent selection (Seehausen, 2004). There is increasing evidence that hybridization has affected speciation in African cichlid radiations (Salzburger et al., 2002; Smith et al., 2003; Schliewen & Klee, 2004; Schelly et al., 2006; Koblmüller et al., 2007). It is readily conceivable that Lake Tanganyika endemic crabs are similarly prone to hybridization, and further investigation of the level of gene flow within the clade is a topic of importance.

It is becoming clear that the platythelphusid radiation exhibits many parallels with species flocks of cichlid fish in the African Great Lakes. Further work on these dynamic invertebrate residents of Lake Tanganyika's benthos promises critical tests of diversification hypotheses that are based so far largely on cichlid systems, and will provide more insight into the ecological functioning of this unusually diverse ancient lake system.

Acknowledgements

References

Albertson, R. C. & T. D. Kocher, 2006. Genetic and developmental basis of cichlid trophic diversity. Heredity 97: 211–221..

Albertson, R. C., J. A. Markert, P. D. Danley & T. D. Kocher, 1999. Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malawi, East Africa. Proceedings of the National Academy of Sciences of the USA 96: 5107–5110..

Albrecht, C., S. Trajanovski, K. Kuhn, B. Streit & T. Wilke, 2006. Rapid evolution of an ancient lake species flock: ~~Freshwater~~freshwater limpets (Gastropoda: Ancylidae) in the Balkan Lake Ohrid. ~~Organisms~~Organisms, Diversity & Evolution 6: 294–307..

Arnegaard, M. E. & A. S. Kondrashov, 2004. Sympatric speciation by sexual selection alone is unlikely. Evolution 58: 222–237..

Barluenga, M. & A. Meyer, 2004. The Midas cichlid species complex: incipient sympatric speciation of Nicaraguan cichlid fishes? Molecular Ecology 12: 2061–2076..

Bellwood, D. R., P. C. Wainwright, C. J. Fulton & A. S. Hoey, 2006. Functional versatility supports coral reef biodiversity. Proceedings of the Royal Society Biological, Series 273: 101–107..

Cane, M. A. & P. Molnar, 2001. Closing of the Indonesian seaway as a precursor to east African aridification around 3–4 million years ago. Nature 411: 157–162..

Capart, A., 1952. Exploration hydrobiologique du Lac Tanganyika (1946–1947), resultats scientifiques - Crustacés, Décapods, Brachyures. Institut Royal des Sciences Naturelles de Belgique 3: 41–67..

Cohen, A. S., M. R. Palacios-Fest, E. S. Msaky, S. A. Alin, B. McKee, C. M. O'Reilly, D. L. Dettman, H. Nkotagu & K. E. Lezzar, 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IX. Summary of paleorecords of environmental change and catchment deforestation at Lake Tanganyika and impacts on the Lake Tanganyika ecosystem. Journal of Paleolimnology 43: 125–145..

Coulter, G. W., 1991. Lake Tanganyika and ~~its life.~~Its Life. Oxford University Press, London, UK..

Cumberlidge, N., 1999. The ~~freshwater crabs~~Freshwater Crabs of West Africa, family Potamonautidae. Faune et Flore Tropicales ~~No~~No. 35. IRD, Paris..

Cumberlidge, N., R. von Sternberg, I. R. Bills & H. Martin, 1999. A revision of the genus Platythelphusa A. Milne-Edwards, 1887 from Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae). Journal of Natural History 33: 1487–1512..

Cunnington, W. A., 1899. On a new brachyurous crustacean from Lake Tanganyika. Proceedings of the Royal Society of London 1899: 697–704..

Cunnington, W. A., 1907. Zoological results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunnington, 1904–1905. Report on the Brachyurous Crustacea. Proceedings of the Royal Society of London 2: 258–276..

Darwall, W., K. Smith, T. Lowe & J.-C. Vié, 2005. The status and distribution of freshwater biodiversity in Eastern Africa. Occasional Paper of the IUCN Species Survival Commission 31. IUCN, Gland, Switzerland: 1–36..

Day, J. J. & M. Wilkinson, 2006. On the origin of the *Synodontis* catfish species flock from Lake Tanganyika. Biology Letters 2: 548–552..

Duftner, N., S. Koblmüller & C. Sturmbauer, 2005. Evolutionary relationships of the Limnochromini, a tribe of benthic deepwater cichlid fish endemic to Lake Tanganyika, East Africa. Journal of Molecular Evolution 60: 277–289..

Evert, M. J., 1970. Le Lac Tanganyika et sa faune. Mémoire de licence. Université de Louvain, Belgium..

Frigge, M., D. C. Hoaglin & B. Iglewicz, 1989. Some implementations of boxplot. American Statistical 43: 50–54..

Fryer, G., 2006. Evolution in ancient lakes: ~~Radiation~~radiation of Tanganyikan atyid prawns and speciation of pelagic cichlid fishes in Lake Malawi. Hydrobiologia 568: 131–142..

Genner, M. J., G. F. Turner, S. Barker & S. J. Hawkins, 1999. Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. Ecology Letters 2: 185–190..

Grant, S. A., D. E. Suckling, H. K. Smith, L. Torvell, T. D. A. Forbes & J. Hodgson, 1985. Comparative studies of diet selection by sheep and cattle: ~~The~~the Hill grasslands. Journal of Ecology 73: 987–1004..

Hill, B. J., 1976. Natural food, foregut clearance rate and activity of the crab *Scylla serrata*. Marine Biology 24: 109–116..

Hori, M., 1983. Feeding ecology of thirteen species of *Lamprologus* (Teleostei: Cichlidae) coexisting at a rocky-shore of Lake Tanganyika. Physiology and Ecology Japan 20: 129–149..

Hori, M., M. M. Gashagaza, M. Nshombo & H. Kawanabe, 1993. Littoral fish communities in Lake Tanganyika: irreplaceable diversity supported by intricate interactions among species. Conservation Biology 7: 657–666..

Hudon, C. & G. Lamarche, 1989. Niche segregation between American lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*). Marine Ecology Progress Series 52: 155–168..

Jackson, D. A., K. M. Somers & H. H. Harvey, 1989. Similarity coefficients: measures of co-occurrence and association or simply measures of occurrence? The American Naturalist 133: 436–453..

Kidd, M. R., C. E. Kidd & T. D. Kocher, 2006. Axes of differentiation in the bower-building cichlids of Lake Malawi. Molecular Ecology 15: 459–478..

Koblmüller, S., N. Duftner, C. Katongo, H. Phiri & C. Sturmbauer, 2005. Ancient divergence in bathypelagic deepwater cichlids: mitochondrial phylogeny of the tribe Bathybatini. Journal of Molecular Evolution 60: 297–314..

Koblmüller, S., N. Duftner, K. M. Sefc, M. Aibara, M. Stipacek, M. Balnc, B. Egger & C. Sturmbauer, 2007. Reticulate phylogeny of gastropod-shell-breeding cichlids from Lake Tanganyika - the result of repeated introgressive hybridization. BMC Evolutionary Biology 7: 7..

Koblmüller, S., W. Salzburger & C. Sturmbauer, 2004. Evolutionary relationships in the sand dwelling cichlid lineage of Lake Tanganyika suggest multiple colonization of rocky habitats and convergent origin of biparental mouthbrooding. Journal of Molecular Evolution 58: 79–96..

Koblmüller, S., C. Sturmbauer, E. Verheyen, A. Meyer & W. Salzburger, 2006. Mitochondrial phylogeny and phylogeography of East African squeaker catfishes (Siluriformes: Synodontis). BMC Evolutionary Biology 6: 49..

Lehman, S. M., 2000. Primate community structure in Guyana: a biogeographic analysis. International Journal of Primatology 21: 333–351..

Lewis, C., 2002. Elucidating the interplay between tectonic and climatic controls on modern depositional processes in the Luiche delta. Nyanza Project Reports 2002 University of Arizona, Tuscon: 1–7..

Liem, K. F. & J. W. M. Osse, 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. American Zoologist 15: 427–454..

Liem, K. F., 1980. Adaptive significance of intra- and interspecific differences in the feeidng repertoires of cichlid fishes. American Zoologist 20: 295–314..

Litvak, M. K. & R. I. C. Hansell, 1990. A community perspective on the multidimensional niche. Journal of Animal Ecology 59: 931–940..

Marijnissen, S. A. E., 2007. Lake Tanganyika crabs: ~~Evolution,~~evolution, ecology, and implications for conservation. PhD thesis, University of Amsterdam, the Netherlands..

Marijnissen, S. A. E., F. R. Schram, N. Cumberlidge & E. Michel, 2004. Two new species of Platythelphusa A. Milne-Edwards, 1887 (Decapoda, Potamoidea, Platythelphusidae), comments on the taxonomic position of P. denticulata Capart, 1952 from Lake Tanganyika, East Africa. Crustaceana 77: 513–532..

Marijnissen, S. A. E., E. Michel, S. R. Daniels, D. Erpenbeck, S. B. J. Menken & F. R. Schram, 2006. Molecular evidence for recent divergence of Lake Tanganyika endemic crabs (Decapoda: Platythelphusidae). Molecular Phylogenetics and Evolution 40: 628–634..

McIntyre, P. B., E. Michel, K. France, A. Rivers, P. Hakizimana & A. S. Cohen, 2004. Individual- and assemblage-level effects of anthropogenic sedimentation on snails in Lake Tanganyika. Conservation Biology 19: 171–181..

Michel, E., 2000. Phylogeny of a gastropod species flock: exploring speciation in Lake Tanganyika in a molecular framework. In Rossiter, A. & H. Kawanabe (eds.), Advances in Ecological Research. Ancient Lakes: ~~Biodiversity~~ Biodiversity, Ecology and Evolution. Academic Press, San Diego: 275–302..

Michel, E., J. A. Todd, D. F. R. Cleary, I. Kingma, A. S. Cohen & M. J. Genner, 2004. Scales of endemism: challenges for conservation and incentives for evolutionary studies in a gastropod species flock from Lake Tanganyika. Journal of Conchology 3: 155–172..

Milne-Edwards, A., 1887. Observations sur les crabes des eaux douces de l'Afrique. Annales des Sciences ~~Naturelles.~~Naturelles, Paris 7: 161–191..

Moed, J. R. & G. M. Hallegraeff, 1978. Some problems in the estimation of chlorophyll *a* and phaeopigments from pre- and post-acidification spectrophotometric measurements. Internationale Revue der Gesammten Hydrobiologie 63: 787–800..

Moran, P. & I. Kornfield, 1993. Retention of ancestral polymorphism in the mbuna species flock (Pisces: Cichlidae) of Lake Malawi. Molecular Biology and Evolution 10: 1015–1029..

Navarette, S. A. & J. C. Castilla, 1990. Resource partitioning between intertidal predatory crabs: interference and refuge utilization. Journal of Experimental Marine Biology and Ecology 143: 101–129..

Newsome, S. D., C. Martinez del Rio, S. Bearhop & D. L. Phillips, 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5: 429–436..

Ochiai, A., 1957. Zoogeographic studies on the soleoid fishes found in Japan and its neighbouring regions. Bulletin of the Japanese Society of Scientific Fisheries 22: 526–530..

Platvoet, D., J. T. A. Dick, C. Macneil, M. C. van Riel & G. van der Velde, 2007. Interactions between two invasive species, *Dikerogammarus villosus* Sowinsky and *Gammarus tigrinus* Sexton (Crustacea, Amphipoda). Biological Invasions (in press)..

Reed, S. R. & N. Cumberlidge, 2006. Taxonomy and biogeography of the freshwater crabs of Tanzania, East Africa (Brachyura: Potamoidea: Potamonautidae, Platythelphusidae, Deckeniidae). Zootaxa 1262: 1–139..

Richards, R. A., 1992. Habitat selection and predator avoidance: ontogenetic shifts in habitat use by the Jonah crab *Cancer borealis* (Stimpson). Journal of Experimental Marine Biology and Ecology 156: 187–197..

von Rintelen, T., A. B. Wilson, M. Meyer & M. Glaubrecht, 2004. Escalation and trophic specialization drive adaptive radiation of freshwater gastropods in ancient lakes on Sulawesi, Indonesia. Proceedings of the Royal Society London, Series B 271: 2842–2850..

Robinson, B. W. & D. S. Wilson, 1998. Optimal foraging, specialization, and a solution to Liem's paradox. American Naturalist 151: 223–235..

Rosales, A. B., S. A. E. Marijnissen, E. Michel & P. B. McIntyre, 2002. Snail susceptibility to crab predation: a case study of co-evolution from Lake Tanganyika, East Africa. Integrative Comparative Biology 42: 1303..

Safran, P. & M. Omori, 1990. Some ecological observations on fishes associated with drifting seaweed off Tohoku coast, Japan. Marine Biology 105: 395–402..

Salzburger, W., S. Baric & C. Sturmbauer, 2002. Speciation via introgressiove hybridization in East African cichlids? Molecular Ecology 11: 619–625..

Schelly, R., W. Saltzburger, S. Koblmüller, N. Duftner & S. Sturmbauer, 2006. Phylogenetic relationships of the lamprologine cichlid genus Lepidiolamprologus (Teleastei: Perciformes) based on mitochondrial and nuclear sequences, suggesting introgressive hybridization. Molecular Phylogenetics and Evolution 38: 426–438..

Schliewen, U. K. & B. Klee, 2004. Reticulate sympatric speciation in Cameroonian crater lake cichlids. Frontiers in Zoology 1: 5..

Schluter, D., 2000. The ~~ecology~~Ecology of ~~adaptive radiation.~~Adaptive Radiation. Oxford University Press, Oxford..

Seehausen, O., 2004. Hybridization and adaptive radiation. Trends in Ecology and Evolution 19: 198–207..

Smith, E. A., 1880. On the shells of Lake Tanganyika and of the neighbourhood of Ujiji, Central Africa. Proceedings of the Zoological Society of London 1880: ~~344–325.~~344–352..

Smith, P. F., A. Konings & I. Kornfield, 2003. Hybrid origin of a cichlid population in Lake Malawi: implications for genetic variation and species diversity. Molecular Ecology 12: 2497–2504..

Sutherland, R. A., 1998. Loss on ignition estimate of organic matter and relationships to organic carbon in fluvial bed sediments. Hydrobiologia 389: 153–167..

Takhteev, V. V., 2000. Trends in the evolution of Baikal amphipods and evolutionary parallels with some marine malacostracan faunas. In Rossiter, A. & H. Kawanabe (eds.), Advances in Ecological Research. Ancient Lakes: Biodiversity, Ecology and Evolution. Academic Press, San Diego: 197–220..

Van Doorn, G. S. & F. J. Weissing, 2001. Ecological versus sexual selection models of sympatric speciation: a synthesis. Selection 2: 17–40..

Wentworth, C. K., 1922. A scale of grade and class terms for clastic sediments. Journal of Geology 30: 377–392..

West, K. & A. S. Cohen, 1994. ~~Predator-prey~~Predator–prey coevolution as a model for the unusual morphologies of the crabs and gastropods of Lake Tanganyika. Archiv für Hydrobiologie/Ergebniss der Limnologie 4: 267–283..

West, K., A. S. Cohen & M. Baron, 1991. Morphology and behaviour of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine ~~predator-prey~~predator–prey coevolution. Evolution 45: 589–607..

West, K., E. Michel, J. Todd, D. Brown & J. Clabaugh, 2003. The gastropods of Lake Tanganyika: diagnostic key, classification and notes on the fauna. International Association of Theoretical Applied Limnology SIL. Occasional Publication 2: 1–123..

William, E., 2002. Spatial relationship of grain size and coarse sediment mineralogy on the shallow Luiche delta platform and its river streams. Nyanza Project Reports 2002. University of Arizona, Tuscon: 1–7..

Williams, M. J., 1981. Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). Journal of Experimental Marine Biology and Ecology 52: 103–113..

Woodward, S. P., 1859. On some new freshwater shells from Central Africa. Proceedings of the Zoological Society of London 1895: 348–351..